Original article

Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe☆

Biostratigraphie ou biochronologie ? Leçons des événements à petits mammifères du Miocène inférieur et moyen en Europe

Albert J. van der Meulen[a], Israel García-Paredes[b,c], M.Ángeles Álvarez-Sierra[d], Lars W. van den Hoek Ostende[c], Kees Hordijk[a], Adriana Oliver[b], Paloma López-Guerrero[d], Verónica Hernández-Ballarín[b], Pablo Peláez-Campomanes[b,*]

[a] *Institute of Earth Sciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, The Netherlands*
[b] *Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/José Gutiérrez Abascal 2, 28006 Madrid, Spain*
[c] *Netherlands Centre for Biodiversity-Naturalis, Darwinweg 2, 2333 CR Leiden, The Netherlands*
[d] *Departamento/UEI de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense e Instituto de Geología Económica (CSIC-UCM), C/José Antonio Novais 2, 28040 Madrid, Spain*

Abstract

Since the proposition in 1975 of the European Neogene Mammal (MN) scale by Pierre Mein, the amount of taxonomical, stratigraphical and chronological information around Europe has increased exponentially. In this paper, the stratigraphical schemes of three of the best studied areas for the Lower and Middle Miocene, the Aragonian type area in Spain and the Upper Freshwater Molasse from the North Alpine Foreland Basin in Switzerland and Bavaria, are compared. The correlation of their local biostratigraphies are discussed. Sixteen rodent's events are studied and ranked in the three areas according to their local biostratigraphy. This study shows, and quantifies for the first time, the significant asynchronies of the different included rodent events. The MN-system is discussed in the light of those results. In accordance, we propose that it is still useful but only in a biochronological way, as a sequence of time-ordered reference localities allowing coarse long-distance correlations. In order to obtain better temporal resolution, this system has to be combined with local biostratigraphies that are well calibrated to the time scale, implementing the information about synchrony and diachrony of mammal events in different areas.

Keywords: Rodentia; Chronology; MN-system; Asynchrony; Central Europe; Spain

Résumé

Depuis la proposition par Pierre Mein, en 1975, de l'échelle des mammifères néogènes d'Europe (MN), la quantité d'information taxinomique, stratigraphique et chronologique en Europe a augmenté exponentiellement. Dans cet article, les séquences stratigraphiques de trois des régions les plus étudiées pour le Miocène inférieur et moyen, la région-type de l'Aragonien en Espagne et la Molasse supérieure du Bassin Nord-Alpin en Suisse et en Bavière, sont comparées, et la corrélation de leurs biostratigraphies locales discutée. Seize événements à rongeur sont étudiés et ordonnés dans les trois régions d'après leur biostratigraphie locale. Cette étude montre et quantifie pour la première fois, les importantes asynchronies de ces différents événements. Le système MN est discuté à la lumière de ces résultats. En conséquence, nous proposons que ce système reste utile seulement d'un point de vue biochronologique, comme séquence ordonnée dans le temps de localités-repères permettant des corrélations grossières à longue distance. Afin d'obtenir une meilleure résolution temporelle, ce système doit être combiné avec des biostratigraphies locales bien calibrées dans le temps, en intégrant les informations de synchronie et de diachronie des événements à mammifères dans différentes régions.

Mots clés : Rodentia ; Chronologie ; Système MN ; Asynchronie ; Europe centrale ; Espagne

---

1. Introduction

The non-recurrent compositional and evolutionary changes of the European mammal fauna history have been extensively used as a relative-age tool for the continental sediments in which they are found. Based on these characteristics, Mein (1975a, 1975b) proposed the subdivision of the Miocene-Pliocene record into 17 successive Mediterranean Neogene units based on mammals (MN). The strength of this scheme lies in its simplicity and it is one of the reasons why the MN-system has become the primary biochronological framework for faunal correlation of the European Neogene. After 35 years, the system still facilitates communication between scientists working in different regions, and doubtlessly it contributed a great deal to the success of European mammal palaeontology.

The MN-system has been extensively used for correlations from local to continental scale, although not always with the same philosophy (De Bruijn et al., 1992). Thus, various authors consider the MN-system as biostratigraphical (e.g., Steininger, 1999; Agustí et al., 2001), while according to others it should be used as a biochronological scheme (De Bruijn et al., 1992; Van Dam, 2003). Using the MN-system as a biostratigraphical scheme is in itself tempting, given the exponential increase of the stratigraphical information. However, biostratigraphy involves not only the fossil content but also the bodies of rock that include it. Therefore, in our opinion, the MN-system as defined by Mein (1975a, 1975b) and modified by the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS; De Bruijn et al., 1992) can never be considered as a biostratigraphical scale, because it is exclusively based on fossil associations and the biological evolution that they reflect (Fahlbusch, 1991; Van Dam et al., 2001).

Since the introduction of the MN-system, the number of localities has soared. Hundreds of publications have tightened our grip on the taxonomy and phylogeny of Neogene mammals. For some areas we have detailed stratigraphical information, allowing us to track faunal development to a degree unheard of in 1975. This increase in the local biostratigraphical knowledge and the recognition of the different MN units in various geographical regions, have resulted in the local recognition of 'MN boundaries' and the assignation of very different ages for each of them (Bolliger, 1997; Heissig, 1997; Kälin, 1997; Kempf et al., 1997; Daams et al., 1999a, 1999b; Agustí et al., 2001; Abdul Aziz et al., 2008, 2009; Kälin and Kempf, 2009). Most of those boundaries between successive MN units have been characterized by a single or a combination of bioevents that were not necessarily always coincident in the different regions.

In order to avoid circular reasoning on the isochrony or diachrony of any faunal event, the mammal history obviously has to be independently calibrated to the time scale. Such calibrations (usually palaeomagnetical or radiometrical) are local by definition because they are based on properties of the rocks from which the fossils derive, or from other rocks with which they are closely associated. The distribution of both localities and mammal taxa is patchy in space as well as in time; consequently, the locally-obtained ages for first and last occurrences of taxa (FO's and LO's, respectively), used as dates for continent-wide immigrations and extinctions, are a priori to be mistrusted as long as synchrony and/or diachrony of the various events have not been demonstrated.

In order to demonstrate the synchrony or diachrony of bioevents and its magnitude, we analyze and discuss the sequence and timing of several small mammal events recognizable in areas were an independent calibration to the time scale has been proposed, and compare them with what can be observed in other European records. Previous to this main goal we discuss the chronologies established for three different Early and Middle Miocene micromammal records: the Aragonian type area in north Central Spain (Daams et al., 1999a; Van der Meulen et al., 2005, in press; Van Dam et al., 2006); the Upper Freshwater Molasse (OSM) of the North Alpine Foreland Basin (NAFB) in Switzerland, recently updated by Kälin and Kempf (2009); and the OSM of the North NAFB in Bavaria, Germany (Abdul Aziz et al., 2008, 2009). Probable correlations between existing local biostratigraphies are suggested. Finally, we discuss the different approaches to the European mammal chronology, paying special attention to the original definition and current uses of the MN-system.

2. Chronology of local biostratigraphies

Irrespective of whether one is interested in long distance correlations or in the regional faunal history, each study tracking changes through time starts with establishing a local biostratigraphy, necessarily linked to the local lithostratigraphical record, and ultimately to chronostratigraphy and geochronology by other independent stratigraphical disciplines (magnetostratigraphy, cyclostratigraphy, etc.). Despite the recent increase of new independent correlations to the time scale, there still exists a strong need of spatially distributed absolute dates (Van Dam, 2003). Moreover, in our opinion, a number of the existing numerical age determinations are not rigorous enough to be reliable (Daams et al., 1999b). This is due to the use of:

- second or third order correlations;
- radiometric ages with very large uncertainty intervals;
- insufficient number of recorded palaeomagnetical chrons, making independent correlation to the Geomagnetic Polarity Time Scale (GPTS) impossible;
- the use of poor-quality polarity signals.

In Europe, there are three overlapping Lower to Middle Miocene records that have been tied to the time scale, at least in a large part:

- the record of the Aragonian type area in north Central Spain (Daams et al., 1999a; Van der Meulen et al., 2005, in press; Van Dam et al., 2006);
- the mammal fauna sequence from the Upper Freshwater Molasse (OSM) of the North Alpine Foreland Basin in Switzerland (Bolliger, 1997; Kälin, 1997; Kempf et al., 1997; Kälin and Kempf, 2009);

- the OSM in Bavaria, Germany (Abdul Aziz et al., 2008, 2009).

The three records represent two different bioprovinces and provide a unique opportunity to compare different faunal histories through time, as shown by Kälin and Kempf (2009). Local biostratigraphical schemes have been proposed for each of the three areas considered in this study (Heissig, 1997; Daams et al., 1998, 1999a; Böhme et al., 2002; Abdul Aziz et al., 2008; Kälin and Kempf, 2009; Van der Meulen et al., in press). Fig. 1 shows the proposed correlations of the compared European records to the Astronomical Tuned Neogene Time Scale (ATNTS2004; Lourens et al., 2004).

2.1. Aragonian type area

The Aragonian type section and its directly adjacent areas have yielded a detailed micromammal faunal succession, which stands out as one of the best known terrestrial records from the European Early to Middle Miocene. Since the overview of Daams et al. (1999a) new data from the Aragonian type area (Calatayud-Montalbán basin) have become available: e.g., revision of the sciurid *Atlantoxerus* by Peláez-Campomanes (2001), medium-sized *Democricetodon* by Van der Meulen et al. (2003), Gliridae from the Early and Middle Aragonian (García-Paredes, 2006; García-Paredes et al., 2009, 2010), *Megacricetodon* from several localities (now in progress, and Oliver Pérez et al., 2008; Oliver et al., 2009), the revision of the Eomyidae by Álvarez-Sierra (now in progress), the revision of the Aragonian Ochotonidae by Hordijk (now in progress) and the revision of insectivores (now in progress, and Van den Hoek Ostende and Furió, 2005; Van den Hoek Ostende et al., 2009). The new taxonomical information and stratigraphical distribution of lower and middle Aragonian faunas are summarized in Van der Meulen et al. (in press). Younger faunas from the Calatayud-Montalbán basin are currently under study by López Guerrero; the results will lead to a revision of the upper Aragonian and lower Vallesian biostratigraphy.

Daams et al. (1999a) proposed the last Aragonian chronological framework included in Fig. 1 based on the reinterpretation of the biostratigraphical correlation between the Armantes and Vargas sections (Daams et al., 1999b), which are two of the four high-resolution sections in the Calatayud-Montalbán basin correlated magnetostratigraphically to the GPTS (Krijgsman et al., 1994, 1996). In this paper we use the recalibrated ages of the faunas proposed by Van Dam et al. (2006) in accordance to

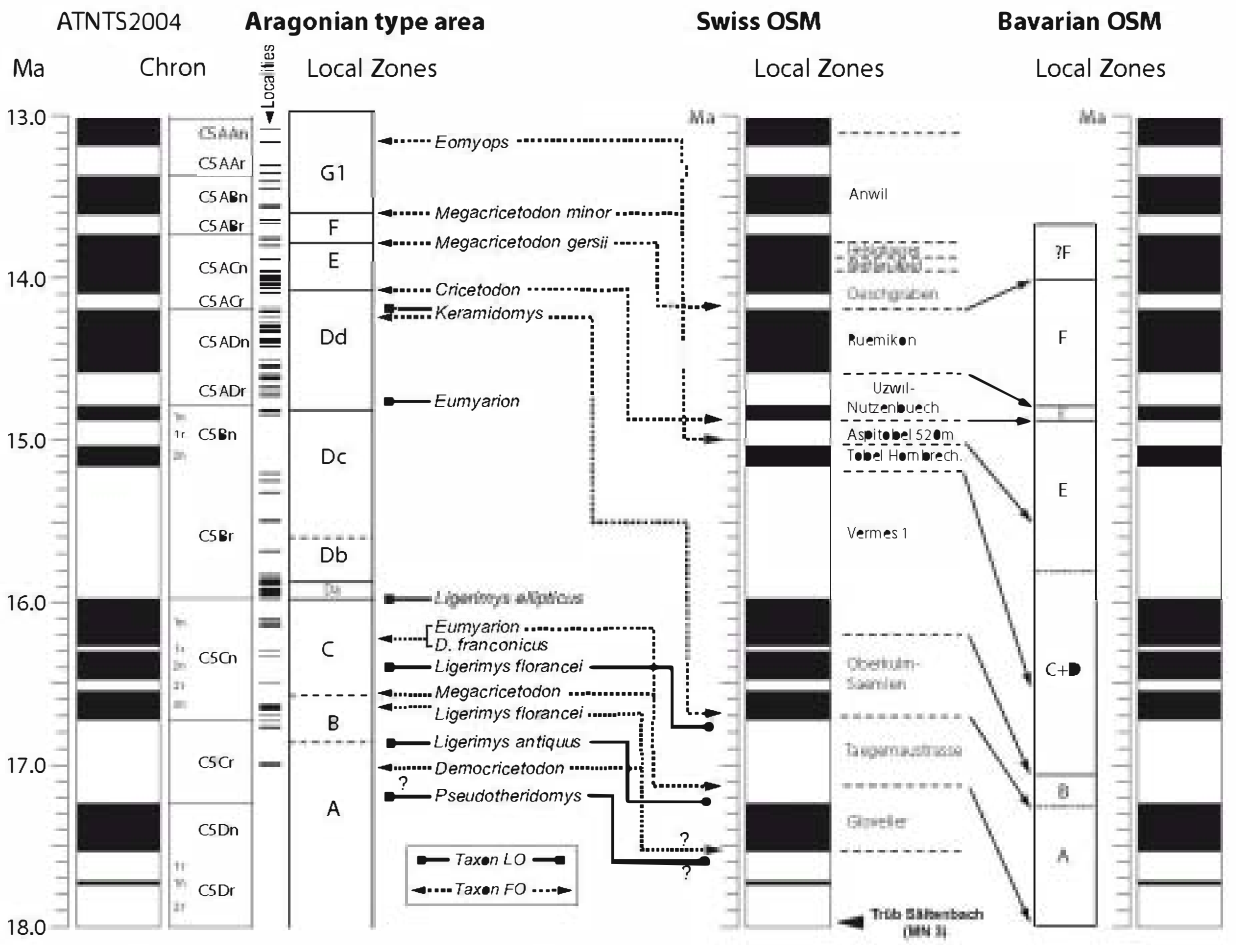

Fig. 1. Proposed correlations of the three compared European records to the ATNTS2004 (Lourens et al., 2004): Aragonian type area in North Central Spain (Daams et al., 1999a; Van Dam et al., 2006), the Upper Freshwater Molasse of the North Alpine Foreland Basin in Switzerland (Kälin and Kempf, 2009), and the Upper Freshwater Molasse in Bavaria (Abdul-Aziz et al., 2009).

the ATNTS2004 (Lourens et al., 2004). All chrons from the upper half of C5Cn.1n to C5AAn have been recognized in the Aragonian type area, providing reliable constraints for the ages of the faunas of upper Zone C to Zone F (from ∼16.3 to 13.7 Ma). The Olmo Redondo-San Roque section in the western part of the type area (Daams et al., 1999a), containing few meters of the uppermost Ramblian and the lowermost part of the Aragonian, has not yet been analyzed palaeomagnetically. This section includes the lower part of the Vargas-Valdemoros sedimentary unit, and represents uppermost Zone A, Zone B, and lower Zone C. The numerical ages of these faunas and the biozone boundaries are based on sedimentary rates obtained in the overlaying sediments that were analyzed palaeomagnetically.

The beginning of the Aragonian (Zone B) is recognized by the First Common Occurrence (FCO) of *Democricetodon hispanicus*, which is found in the locality San Roque 1 from the Olmo Redondo-San Roque section at an estimated age of 16.77 Ma. Together with the age of San Roque 4B (SR4B, uppermost Zone A, upper Ramblian) in the same section, the lower boundary of the Aragonian is constrained by the estimated ages of 16.99-16.77 Ma. *Democricetodon hispanicus* is present with very low numbers in San Roque 4B and San Roque 4A (∼17.0 Ma), and constitutes the oldest occurrence of the genus with an estimated age in Spain. The mentioned ages indicate that the entry and increase in relative abundance of the genus in the Aragonian area took place in the late Ramblian during chron C5Cr (17.235–16.721 Ma, ATNTS2004).

The beginning of the Middle Aragonian (Zone Da) is easily recognized by the rapid decrease and extinction of the eomyid *Ligerimys ellipticus*, which is a common to dominant taxon in Zone C. The extinction takes place between Vargas 2A and Vargas 2B (3 m above Vargas 2A) in the Vargas section, which constrains the Early-Middle Aragonian boundary to 15.94–15.92 Ma. The lowermost fauna (La Col A) of the La Col section (not analyzed palaeomagnetically) contains less than 1% of *L. ellipticus*; otherwise its composition is typical of Zone Da. Therefore, La Col A has been biostratigraphically situated between Vargas 2A, in which 22% of the rodent teeth belong to *L. ellipticus*, and Vargas 2B, in which the eomyids are absent. This leads to an estimated age of 15.93 Ma for La Col A, and the Early-Middle Aragonian boundary may be constrained further to 15.935 Ma. Magnetostratigraphical calibration shows that the boundary lies close to the lower boundary of chron C5Br (15.974–15.032 Ma, ATNTS2004; Daams et al., 1999a).

The Middle-Late Aragonian boundary, equivalent to the Zone E-Zone F boundary, is drawn in the magnetostratigraphically calibrated type section itself, between the localities Las Umbrías 20 and Las Umbrías 22 (Daams et al., 1999a), which have an age of 13.80 Ma and 13.76 Ma, respectively (Van Dam et al., 2006). According to Krijgsman et al. (1996) the boundary lies about 1/10 below the top of chron C5ACn (14.095–13.688 Ma, ATNTS2004; Abels et al., 2005). Since we use here the revised age of the top of chron C5ACn (Abels et al., 2005) the Middle-Late Aragonian boundary is slightly younger than in Krijgsman et al. (1996).

The magnetostratigraphical calibrations allow correlation of the Aragonian to the ATNTS2004. The Early Aragonian is equivalent to the latest Burdigalian. The base of the Middle Aragonian is only 30 ky younger than the base of the Langhian, provisionally established at 15.974 Ma (Lourens et al., 2004), and its top is 100 ky younger than the base of the Serravallian (13.82 Ma, Abels et al., 2005). Thus, the Middle Aragonian coincides very closely with the Langhian.

2.2. *The Upper Freshwater Molasse of Switzerland*

Recently, Kälin and Kempf (2009) presented a stratigraphical framework for the Upper Freshwater Molasse (OSM) of Switzerland based on large dataset of mammal biostratigraphy, magnetostratigraphy and radiometric ages derived from bentonite layers. In Fig. 1 we present the chronostratigraphy of the local biostratigraphical zones proposed by the latter authors for the OSM of Switzerland. According to their results, the Swiss faunas between 15.3 to 13.0 Ma are well constrained by the combination of magnetostratigraphical and radiometric ages of three bentonites yielding ages of 14.20 ± 0.08 Ma, 14.91 ± 0.09 Ma, and 15.27 ± 0.12 Ma (Kälin and Kempf, 2009 and literature therein). The magnetostratigraphy of the lower part of the composite sequence is, however, less conclusive because the different studied sections contain large gaps. Two different interpretations have been proposed: the first one is based on Schlunegger et al. (1996) and Agustí et al. (2001); the second one (represented in Fig. 1) is from Kälin and Kempf (2009: fig. 8), which in its turn is based on Kempf et al. (1997: fig. 10). The interpretation of the latter has been challenged by Agustí et al. (2001), Aguilar et al. (2003), and Larrasoaña et al. (2006) as far as the calibration of the Schwändigraben section to the GPTS is concerned.

In the original calibration of this section given by Schlunegger et al. (1996), the ‘basal marls’ containing the Eimättili fauna (Tägernaustrasse assemblage biozone, MN 4; after Kempf et al., 1997) is correlated to chron C5Cn2.r (16.54-16.47 Ma), and the locality Hasenbach 1 (Trub-Sältenbach biozone, MN3b) to chron C5En. Kälin (1997) reports a new fauna from Trub-Sältenbach (reference locality for the biozone of the same name) in between Hasenbach 1 and Eimättili. According to the calibration by Schlunegger et al. (1996), Trub-Sältenbach falls in the lower part of chron C5Cr, giving it an age of about 17.2 Ma (Agustí et al., 2001). Kempf et al. (1997) recalibrate the section, correlating Eimättili to C5Cr and Trub-Sältenbach to the lower part of C5Dr. However, according to Agustí et al. (2001: p. 254), insufficient arguments are provided to rule out the original calibration of the Schwändigraben section and “their alternate correlation results in a very poor fit with the GPTS”. Therefore, Agustí et al. (2001) place the lower boundary of Tägernaustrasse biozone between C5Cr and C5Cn.2r, i.e. between 17.2 and 16.5 Ma, the estimated age of the youngest locality of the Trub-Sältenbach biozone, which corresponds to the ‘cricetid vacuum’ in Switzerland. Kälin and Kempf (2009) assume the presence of a hiatus in the ‘basal marls’ to explain the strongly condensed appearance of the measured reversed chron in comparison to the duration of chron C5Cr, with which they correlate it. Such an assumption is not necessary in the case of the original calibration to chron C5Cn.2r.

The reference fauna of Glovelier (only locality included in the Glovelier assemblage biozone) is the oldest Swiss fauna with *Democricetodon* and *Ligerimys florancei*, but, as it comes from a karstic fissure filling, no numerical age estimate can be given (Kälin, 1997; Kälin and Kempf, 2009). It is biochronologically older than the Tägernaustrasse assemblages because Glovelier lacks *Megacricetodon* and *Eumyarion*, and still contains *Ligerimys antiquus*. Kälin and Kempf (2009) tentatively give it an age around 17.5 Ma using the above-mentioned recalibrated ages of biostratigraphically adjacent faunas, but according to the calibration of Schlunegger et al. (1996) and Agustí et al. (2001) it should be younger than ~17.2 Ma. The latter calibration of the Tägernaustrasse biozone fits the geochronological data from southwestern Europe much better than its recalibration. Larrasoaña et al. (2006) provide reliable magnetostratigraphical evidence to correlate Pico del Fraile 1, a 'cricetid vacuum' fauna (Zone A) in the Ebro basin (Spain) without *Democricetodon*, to chron C5Dn (17.533–17.235 Ma). Aguilar et al. (2003) derive a similar correlation for Beaulieu (17.5 Ma), a southwestern French fauna representing the 'cricetid vacuum'.

2.3. *The Upper Freshwater Molasse in Bavaria*

The local biostratigraphy of the Upper Freshwater Molasse in Bavaria was proposed by Heissig (1997) and updated by Böhme et al. (2002) and Abdul Aziz et al. (2009). The oldest biozone (OSM A) is characterized by the presence of *L. florancei* together with *Megacricetodon*. So, other than the Swiss and Aragonian type area record, the OSM series itself does not have faunas with *Democricetodon* and *Ligerimys* but without *Megacricetodon*. Such faunas are, however, known from fissure fillings in the nearby Frankonische Alp, such as Petersbuch 2 and Erkertshofen 1 and 2. The youngest biozone (OSM F) is characterized by the FO of *Cricetodon* aff. *aureus* and *Anomalomys gaudryi* (Abdul Aziz et al., 2008). According to Abdul Aziz et al. (2009) further subdivision of the latter biozone is possible (OSM F and OSM F?) based on the molar size increase in the *Cricetodon* lineage.

The faunal development of the German and Swiss parts of the NAFB is nearly identical (Kälin and Kempf, 2009). Yet, a recent stratigraphical synthesis of the Bavarian part of the Northern Alpine Foreland Basin shows major differences in the interpretation of the absolute ages with the Swiss record (Abdul Aziz et al., 2008, 2009; Prieto et al., 2009). Notably, these differences are found in the Early to early-Middle Miocene part of the age model, which depends heavily on the magnetostratigraphy of the Puttenhausen section. As Abdul Aziz et al. (2008, 2009) indicated, the palaeomagnetical results of this section are not reliable, pointing out the possibility of an incorrect calibration to the ATNTS2004.

According to faunal correlations proposed by Abdul Aziz et al. (2008) the younger part of OSM C + D, represented by the locality Sandelzhausen and the upper part of the Puttenhausen section (Puttenhausen E), is very similar to the Swiss faunas from Tobelholz and Vermes 2. The latter faunas were correlated by Kälin and Kempf (2009) to the Vermes 1 and Tobel Hombrechtikon biozones, respectively. Abdul Aziz et al. (2008) considered the correlation to Tobel Hombrechtikon (and thus to chron C5Bn.2) unwarranted because of the absence of *Megacricetodon* aff. *bavaricus* in this Swiss locality. However, their own faunal correlation with the Tobelholz locality in the Zürich section fits the correlation to chron C5Bn.2 perfectly. Tobelholz lies between the Urdorf und Küsnacht bentonites, dated at 15.27 ± 0.12 Ma and 14.91 ± 0.09, respectively (Kälin and Kempf, 2009: fig. 5B); as a result, the proposed correlation of the Puttenhausen section to the GPTS proposed by Abdul Aziz et al. (2008) is in direct conflict with the bentonite dates. Therefore, we accept the correlation to chron C5Bn.2 (15.0 to 15.2 Ma) of Sandelzhausen and Puttenhausen E based on the stratigraphical framework of Kälin and Kempf (2009).

3. Correlation of local biostratigraphies

Zone A, which belongs to the Ramblian, is the oldest recognized local biozone in the Aragonian type area (localities of San Roque 4A and 4B). In this area, it is characterized by the presence of *L. antiquus*, *Melissiodon* and, although rare, the first record of *Democricetodon*. Depending on the criterion used to define MN 4 (FO or FCO of *Democricetodon*), these faunas could be considered as MN3 or MN4 (Fig. 2). In Switzerland, there is only one locality with a similar faunal composition, Glovelier. This karstic locality differs from the Spanish locality San Roque 4B in the presence of *L. florancei*, which is not recorded in Spain until the end of Zone B. Therefore, based on the presence of *Democricetodon* and the absence of *Megacricetodon*, the Glovelier biozone could be correlated with the upper part of Spanish Zone A and Zone B (Fig. 2). Other European localities that may be correlated with these biozones based on the latter criterion are Petersbuch 2, Erkertshofen 1 and 2 in Germany (Ziegler and Fahlbusch, 1986), Dolnice 1 and 2 in the Czech Republic (Fejfar, 1990), Oberdorf 3 and 4 in Austria (Steininger et al., 1998), and Béon 2 and Artenay in France (Bulot et al., 2009).

The presence of *Megacricetodon* in combination with the presence of *Ligerimys* has been used to define local biozones all over Europe. In Spain it characterizes Zone C, in Switzerland the Tägernaustrasse biozone, and in Germany the OSM A. In previous works (e.g., Daams et al., 1999a), Zone C has been correlated with the upper part of MN 4 because *Ligerimys* is still present. If we use the species level instead of the genus level, Tägernaustrasse biozone and OSM A should be correlated with the lower part of Zone C of Spain, based on the presence of *L. florancei* and *Megacricetodon*. The latter taxa are present in La Romieu, reference locality of MN4. Nevertheless, the peculiar faunal composition of La Romieu, with two species of *Megacricetodon* and four species of *Democricetodon*, makes accurate correlation of both the Spanish and the Swiss faunas to the MN4 reference fauna impossible (Kälin and Kempf, 2009). The only locality in the Calatayud-Montalbán basin that contains *L. florancei* and *Megacricetodon* is Artesilla (Van Der Meulen and Daams, 1992), which represents the FO of the latter genus (Oliver Pérez et al., 2008). The high cricetid diversity of the La Romieu fauna

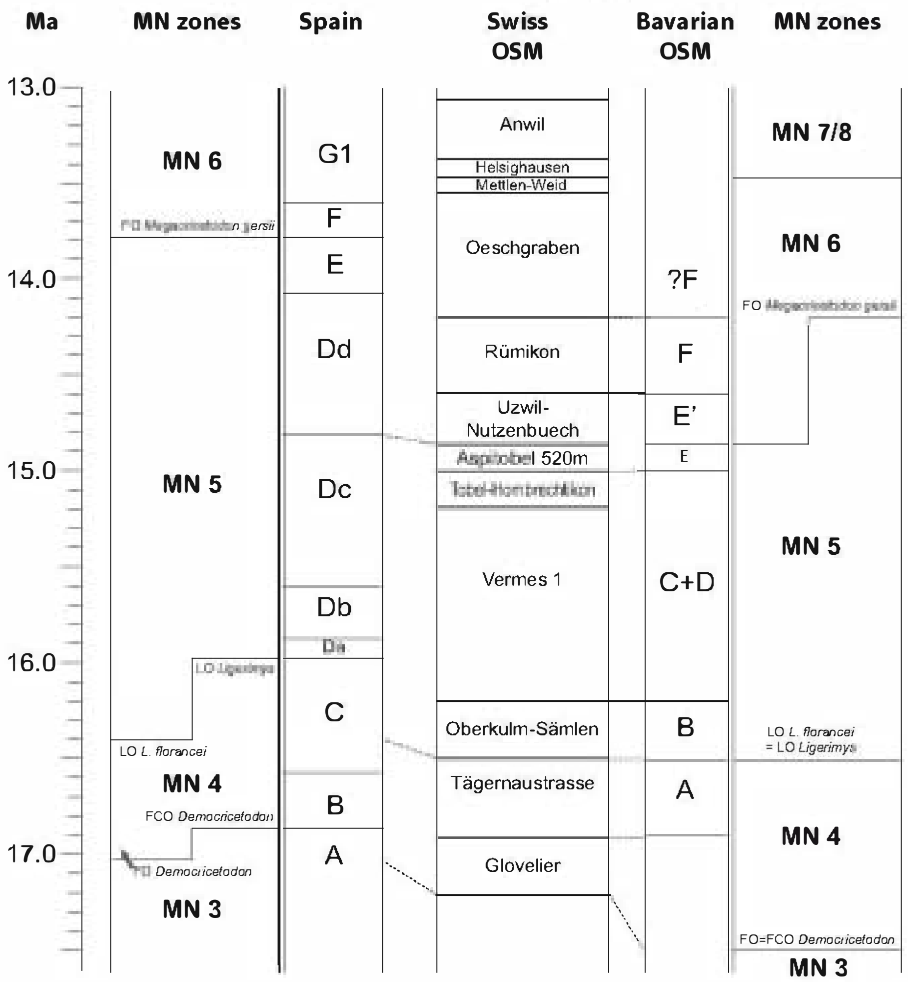

Fig. 2. Comparisons between Spanish, Swiss and German local biostratigraphies. The chronology used for the Swiss and German record is after Kälin and Kempf (2009) with the exception of the paleomagnetical correlations for the lower part of the scale which follow Schlunegger et al. (1996) (see text for discussion). Possible correlations between local biostratigraphies are indicated by dashed lines. For the distribution of the MN units, several possibilities are included, depending on the used criteria.

could indicate a younger age relative to Artesilla, which shows closer faunal similarities with the Pellecahus fauna (Ginsburg and Bulot, 2000).

The correlations between other Spanish early Middle Miocene biozones and the Central European ones are more difficult due to the low number of shared taxa. Therefore, the correlations can only be established based on the proposed chronologies (Fig. 2). The correlation between Swiss and Bavaria is nevertheless straightforward, because they have an almost identical distribution of taxa (Kälin and Kempf, 2009). Despite these similarities, there are discrepancies in the correlations between Swiss (Kälin and Kempf, 2009) and German biozones (Abdul Aziz et al., 2008, 2009), and especially in the proposed chronology, as has been discussed in previous Section 2.3. The main discrepancy is the correlation of OSM F. According to Abdul Aziz et al. (2008), OSM F correlates with the Swiss Biozone of Rümikon and OSM E′ with Uzwil-Nutzenbuech, while according to Kälin and Kempf (2009: fig. 10) OSM F correlates with biozones Uzwil-Nutzenbuech, Rümikon and with the lower part of Öschgraben. In Figs. 1 and 2 we use the biostratigraphical correlations proposed by Abdul Aziz et al. (2008, 2009). The chronology proposed by these authors is, however, very different to the one proposed by Kälin and Kempf (2009). In our opinion the correlation of Sandelzhausen and Puttenhausen E to chron C5Cn.2n and chron C5Cn.2r, respectively, proposed by Abdul Aziz et al. (2008) is not sufficiently supported by the magnetostratigraphical results, while the chronology based on the Swiss record is supported by the bentonite dating, which constrains the correlation of Tobelholz to chron C5Bn.2n.

The MN 5 reference fauna of Pont Levoy-Thenay is easily correlatable with the Swiss and German records by the presence of *Megacricetodon lappi* and corresponds to the short biozones of Aspitobel 520 m in Switzerland and OSM E in Germany. On the other hand, the only species in common between Pont Levoy-Thenay and the Spanish record is *Megacricetodon collongensis*, mainly known from Zone Dd. According to the magnetostratigraphical interpretation (Fig. 1), Pont-Levoy-Thenay should be correlated to early Zone Dd faunas.

The MN 6 reference fauna of Sansan was correlated by Daams et al. (1999a) to the Las Planas 5B fauna (chron C5ABn) from the Aragonian type section, and its numerical age estimated as approximately 13.6 Ma, based on the presence of *Megacricetodon gersii* and *M. minor*. The new results presented by Kälin and Kempf (2009) and our comparison with the Spanish fossil record indicate that *M. minor* is of little biostratigraphical value, as evidenced by its very diachronic dispersal, that is probably related to a preference for more specific enviromnental conditions. This interpretation is supported by the absence of this species in faunas from the Madrid basin, which have almost identical compositions in comparison to the Calatayud-Montalbán ones (Peláez-Campomanes et al., 2003). Therefore, the estimated age of Daams et al. (1999a) for the Sansan fauna is too young; correlation to the lower part of chron C5ACn (approximately 14 Ma) is more probable, and is also supported by its correlation to the Swiss record (Kälin and Kempf, 2009).

4. Small mammal events

The Early and Middle Miocene European small mammal record shows a strong provincialism, hampering even the correlation between areas that are geographically not far apart. The Spanish record has been always considered as singular (De Bruijn et al., 1992; Martinez, 1997; Steininger, 1999) and, despite being one of the most dense and extensively studied, its results have been ignored or treated superficially because of the difficulty of correlation with other European records (Daams, 1998). Singular, of course, does not necessarily imply uniformal, and there are certainly more Central European influences in coastal basins as the Vallès-Penedès and Levante than there are in the inland basins (Agustí et al., 1984; Agustí, 1990).

The European mammal community compositions during the Miocene are rather dissimilar, although there are several biological events that can be recognized at European scale and that have been used to calibrate and correlate the different local records. Nevertheless, the chronologies of most biological events have not been studied in detail using independent sources of local dating to determine their isochrony. Van der Meulen et al. (in press) pointed out 13 bioevents shared between the Aragonian record (based on the Calatayud-Montalbán basin) and the Upper Freshwater Molasse of Switzerland for the Early and Middle Miocene. Table 1 shows these events with the addition of another three: the last occurrence of *Pseudotheridomys*, the last occurrence of *L. antiquus* and the first occurrence of *Eomyops*. The order of the events presented in Table 1 follows that of the Swiss record as given by Kälin and Kempf (2009). The events have been ranked in the Swiss OSM, the Bavarian OSM and the Spanish Aragonian type area according to their local biostratigraphies. If events occur in the same locality (Spain) or biozone (Switzerland and Germany), their ranking numbers are the mean of their positions in their local biostratigraphy. In this procedure, the FO of *Democricetodon franconicus* and *Eumyarion* represent the relative positions 9 and 10 within the local Aragonian biostratigraphy and since both occur for the first time in the same locality (Vargas 4A, 16.15 Ma) we assign both to rank number 9.5.

Table 1
Ranking of the faunal events shared among the Upper Freshwater Molasse of the North Alpine Foreland Basin in Switzerland (SW), the Upper Freshwater Molasse in Bavaria, Germany (GER), and the Aragonian type area in North Central Spain (SP).

Bioevent	SW	GER	SP
FO *Megacricetodon gersii*	16	–	14
FO *Cricetodon*	15	15	13
FO *Eomyops*	14	14	16
FO *Megacricetodon minor*	13	13	15
FO *Keramidomys*	12	12	12
LO *Ligerimys*	10	10	11
LO *Ligerimys florancei*	10	10	8
LO *Melissiodon*	10	10	4.5
FO *Megacricetodon*	7	7.5	7
FO *Eumyarion*	7	7.5	9.5
LO *Ligerimys antiquus*	7	5	4.5
FO *Ligerimys florancei*	3.5	6	6
FO *Democricetodon franconicus*	3.5	3.5	9.5
FO *Democricetodon*	3.5	3.5	3
LO *Pseudotheridomys*	3.5	–	2
< Cricetid Vacuum >	1	–	1

In order to compare the sequence of events we have performed non-parametric correlations, using SPSS 17.0 software (SPSS, 2008), between the Swiss and Spanish records (Swiss and Bavarian records are almost identical and therefore the latter have not been included). The results reveal a highly significant correlation between the Swiss and Spanish bioevent sequences (Spearman's rho = 0.826, $p < 0.001$ and Kendall tau = 0.703, $p < 0.001$), indicating a close similarity between them.

The availability of sections with palaeomagnetical and/or radiometrical time control in the studied areas allows to study the timing of each event independently (Fig. 1). One of the important results of the work of Van der Meulen et al. (in press) is the establishment that while the age of the various events can be highly diachronical, the sequence of events is quite similar. Secondly, deviations from the general order of events between regions may provide useful information on the history of specific taxa and regions, or, alternatively, can help to detect a highly improbable combination of taxa or ordination of faunas.

4.1. Eomyids

According to Kälin and Kempf (2009), the sequence of eomyids events in the Swiss record is: LO *Pseudotheridomys*, FO *L. florancei*, LO *L. antiquus*, LO *L. florancei*, FO *Keramidomys* and FO *Eomyops*. The Spanish record shows the same sequence, but there is no overlap between the ranges of *L. antiquus* (Zones Z and A) and *L. florancei* (Zones B and lower C). *L. florancei* is present in Switzerland around 17.0 Ma (Kempf et al., 1997), while it appears in the Aragonian type area at 16.66 Ma. In the Bavarian part of the North Alpine Foreland Basin (NAFB) and nearby areas, the FO of *L. florancei* is estimated by Abdul Aziz et al. (2009) close to 18.0 Ma based on lithostratigraphical correlations with the sediments containing the Czech locality of Orechov. In contrast to the Spanish and Swiss record, the LO of *Pseudotheridomys* is after the FO of *L. florancei* in the German and Czech NAFB, since the two taxa are recorded together in localities such as Erkertshofen 2 (*Ligerimys* aff. *florancei*), Dolnice 1, Dolnice 2 and Dolnice 3 (Álvarez Sierra, 1987; Fejfar, 1990; Escarguel and Aguilar, 1997).

Ligerimys florancei and *L. ellipticus* are coeval species in the localities Can Martí Vell 1 and 2 of the Vallès-Penedès basin (Agustí, 1983). In contrast, they never co-occur in the Calatayud-Montalbán record, where *L. florancei* is replaced by the endemic species *L. ellipticus* between 16.30 and 16.15 Ma. The LO of *L. ellipticus* is in La Col A with an estimated age of 15.97 Ma (Van Dam et al., 2006). The extinction of *L. florancei* and its replacement by *Keramidomys* is used as a common criterion to distinguish between MN 4 and MN 5 faunas in Central Europe. This occurs in Switzerland between 16.8 and 16.4 Ma (Kälin and Kempf, 2009), and around 17.2–17.3 Ma in Bavaria (Abdul Aziz et al., 2009). Following the widely used criterion of the presence of *Ligerimys*, the Aragonian Zone C has always been correlated with MN 4. We now have to conclude that the extinction of the genus *Ligerimys* as MN zone-recognition tool has to be abandoned, since the stratigraphical ranges of *L. ellipticus* in Spain and *Keramidomys* in Switzerland and Bavaria partially overlap. The extinction of the species *L. florancei* may be used instead, when the event can be shown to be synchronous. *Keramidomys* has been found in Spain as a transient species (sensu Van der Meulen et al., 2005 and Van der Meulen and Peláez-Campomanes, 2007), occurring in two Zone Dd localities only, Valdemoros 7G (14.23 Ma) and Las Umbrías 7 (14.19 Ma), much later than its FO in Switzerland. *Eomyops* first occurrence in Switzerland is at the base of Aspitobel 520 m (15.0 Ma), while in Spain it is not recorded until Zone G1 (13.5 Ma). The FO of *Eomyops* is the last considered eomyid event in both areas.

4.2. Melissiodon

The early LO of *Melissiodon* in upper Zone A in the Aragonian type area (before the FOs of *L. florancei* and *Megacricetodon*; Daams et al., 1999a) seems to be a local phenomenon. *Melissiodon* is known from other Spanish Zone C localities, in the nearby Teruel basin and from the locality of Buñol in the Valencia area (Robles et al., 1991), where it is recorded together with *Megacricetodon* and *L. ellipticus*. Therefore, the LO of *Melissiodon* postdates the LO of *L. florancei* in Spain. In the Swiss and Bavarian records, the LO of *Melissiodon* is within Tägernaustrasse and OSM A biozones, respectively, and coincides with the LO of *L. florancei* (Table 1).

4.3. Democricetodon, Megacricetodon, Eumyarion

The co-occurrence of *Democricetodon, Megacricetodon* and *Eumyarion* after the cricetid vacuum, combined with the presence of *Ligerimys,* is used to recognize MN 4. The cricetids are immigrants into Europe and become important elements in the European faunas of the Middle Miocene (the first two genera in particular).

In Central and Western Europe the entry of *Democricetodon* predates that of *Megacricetodon*. Throughout Europe, localities have been described which contain *Democricetodon*, but lack *Megacricetodon*, such as: San Roque 4A and 4B as well as all the localities from Zone B in Spain; Dolnice 1 and 2 in the Czech Republic; Oberdorf 3 and 4 in Austria; Glovelier in Switzerland; Petersbuch 2, Erkertshofen 1 and 2, Achen 17 in Germany; and Artenay and Béon 2 in France (Ziegler and Fahlbusch, 1986; Fejfar, 1990; Kälin, 1997; Steininger et al., 1998; Daams et al., 1999a; Pippèrr et al., 2007; Kälin and Kempf, 2009; Bulot et al., 2009). These faunas with *Democricetodon* as the only modern cricetid differ in their eomyid component. In San Roque 4A and 4B, the uppermost part of the Ramblian Zone A, *Democricetodon hispanicus* is accompanied by *L. antiquus* and *L. fahlbuschi*, while *D. franconicus* from Dolnice 1, Dolnice 2 and Achen 17 is accompanied by *Pseudotheridomys* and *L. florancei,* in Glovelier by *L. antiquus* and *L. florancei,* and in Erkertshofen 1 and 2 by *L. florancei* and *L.* aff. *florancei*, respectively. In the localities from the Aragonian Zone B, the eomyids present with *Democricetodon* are *L. palomae* at the lower part, and *L. florancei* at the upper part.

The oldest Spanish faunas with rare *Democricetodon* are San Roque 4A and San Roque 4B. They have been placed in Zone A, as Zone B is defined on the regular occurrence of this taxon (Daams et al., 1998, 1999a; Van der Meulen et al., in press). Both the San Roque 4 localities and those of the lowermost Zone B have been correlated to chron C5Cr (17.2–16.7 Ma, Lourens et al., 2004). Although these correlations are based on sedimentation rates, we accept them as best available evidence to be used until the palaeomagnetical analysis of the sediments themselves. The interpretation is supported by the magnetostratigraphically well-constrained findings of Larrasoaña et al. (2006). They correlate Pico del Fraile 1 (Zone A, Ebro basin), a locality without *Democricetodon*, to chron C5Dn (17.533–17.235 Ma), which also fits the age estimation of Beaulieu in Southern France as given by Aguilar et al. (2003).

Unfortunately, no magnetostratigraphy is available for the karstic fissure filling of Glovelier. Thus, its correlation to chron C5Dn is circumstantial and based on the calibration of the Tägernaustrasse faunas to C5Cr (Kempf et al., 1997). A correlation to chron C5Dn has also been proposed for the Oberdorf 3 and 4 faunas in Austria (Steininger et al., 1998). Another fauna, Achen 17 from southeastern Germany, similar to the Czech faunas of Dolnice 1 and 2 by the presence of *Democricetodon* cf. *franconicus* and *Pseudotheridomys* and the absence of *Megacricetodon,* has been dated as 17.8 ± 0.3 Ma based on the strontium content of otoliths (Pippèrr et al., 2007). Given these chronological results, the age of the Orechov fauna, supposedly representing the earliest occurrence of *Megacricetodon*, close to 18 Ma as proposed by Abdul Aziz et al. (2009), is untenable.

The order in which *Eumyarion* and *Megacricetodon* enter the record differs in the various regions. The FO of *Eumyarion* predates that of *Megacricetodon* in Czech and Austrian localities such as Dolnice 1, Dolnice 2, Oberdorf 3 and Oberdorf 4, which are indirectly correlated to chron C5Dn (Steininger et al., 1998). *Megacricetodon* and *Eumyarion* are not present before chron C5Cr in Switzerland. The entry of *Megacricetodon* in the Calatayud-Montalbán basin is estimated between 16.63 and 16.49 Ma (during the gap between Villafeliche 2A and Artesilla), and the entry of *Eumyarion* between 16.30 and 16.15 Ma. In other Spanish basins the latter entry is probably slightly older since *Eumyarion* is already present in the locality of Buñol (Levante basin; Daams, 1976) and in Can Martí Vell (Vallès-Penedès basin; Agustí, 1983) with an age that could be slightly younger than Artesilla (16.49 Ma) based on the eomyids and the evolutionary stage of *Democricetodon*. The asynchrony of these immigrations is therefore in the order of 0.5 to 1 million years according to the proposed chronologies in each area. The asynchrony in the FO of *Eumyarion* is considerably larger than that of *Democricetodon* and *Megacricetodon*.

The second group of *Megacricetodon* events involves the FO of *M. minor* and the FO of *M. gersii*. The FO of *M. minor* forms a major discrepancy between the three sequences of first entries. In Spain, as opposed to Switzerland and Germany, the FO of *M. minor* occurs after that of *Cricetodon* and *M. gersii*. *Megacricetodon minor* apparently disperses less easily than the others, which might indicate that it is a less opportunistic species. This is also illustrated by *M. minor* never reaching the Madrid basin in the centre of the Iberian Peninsula (Peláez-Campomanes et al., 2003). *M. gersii* has not been recorded in Germany (Heissig, 1997), presumably because of the absence of fossil record covering the temporal distribution of this species.

4.4. Cricetodon

The FO of *Cricetodon* (*C.* aff. *aureus*) in Switzerland is in Uzwil-Nutzenbuech. This first occurrence is correlated to chron C5Bn.1n, with an estimated age of 14.9 Ma (Kälin and Kempf, 2009), and slightly postdates the FO in Bavaria (Abdul Aziz et al., 2009). The FO of the genus in Spain is in Las Umbrias 11 (chron C5ACn, 14.06 Ma). The asynchrony of the immigration of *Cricetodon* into the three areas is, therefore, in the order of 0.9 million years. Daams et al. (1999a) correlated Zone E (with the first appearance of the genus at its base) to MN5 and Zone F to MN6 because it contains the first *Megacricetodon gersii*. De Bruijn et al. (1993) note that the Spanish material, referred to as *Cricetodon* n. sp. 3 from Las Umbrias 11 (= Las Planas 5A2), is unknown from elsewhere and consequently represents a separate immigration not comparable to the Swiss event. New studies on this material and new findings of Cricetodontini from the Calatayud-Montalbán basin (now in progress, and López-Guerrero et al., 2008, 2009), will help to understand the evolution and dispersal of this interesting tribe.

4.5. Discussion

According to the age models presented in Fig. 1 for the three studied areas, the considered events are, in general, strongly diachronical. The inferred asynchronies are surprisingly high between the Swiss and Bavarian record (Fig. 1). As noted above, much of this can be resolved by revising the interpretation of the Puttenhausen section, which had yielded less reliable palaeomagnetical result according to Abdul Aziz et al. (2008, 2009). Asynchronies between Spain and Central Europe are high, around 0.5 to 1 my, for most of the events when the age model of Kälin and Kempf (2009) is considered. The events in Switzerland and Bavaria predate their occurrences in Spain. Considering the age model of Schlunegger et al. (1996) the calculated asynchronies between Spain and Central Europe for the FOs of *M. gersii, M. minor* and *Cricetodon* have the same values than in the Kälin and Kempf (2009) age model, since they are based on well-constrained ages in both areas. For the other events, the use of the proposed correlations by Schlunegger et al. (1996) implies lower asynchronies. In this case, the FO of *Democricetodon* and the LO of *L. florancei* are considered synchronous, because clear diachrony cannot be shown given the available time resolution. The asynchrony of *D. franconicus* is not real, because it concerns a second immigration in Spain that does not occur in Switzerland. The asynchronies in the FO of *Eumyarion* and LO of *Melissiodon* only apply to the Calatayud-Montalbán basin, since the first may have arrived 0.2-0.3 my earlier in eastern basins of coastal Spain, and *Melissiodon* went extinct about 0.3-0.4 my later in the Teruel basin. The diachronous LO of *Ligerimys* and the FO of *Cricetodon* cannot be considered as reliable, because they refer to different species. The strong diachrony of *Keramidomys* and *Megacricetodon minor* are realistic, and could be explained by the non-invasibility of the Calatayud-Montalbán basin during a large part of the middle Aragonian, attributed to the special environmental conditions with a dry and highly disturbed environment (Van der Meulen et al., 2005).

In summary, the increase on the stratigraphical knowledge of three Early and Middle Miocene European records from three different geographical regions, allows us to study in depth, for the first time, the timing of several shared rodent events. The results indicate that, considering only rodents, it is very difficult to propose a continental biochronological scale of high temporal resolution, because there are a limited number of events recognizable at continental scale and in addition they generally show significant asynchronies between areas.

5. European mammal chronology

Before the development of stratigraphical disciplines like magnetostratigraphy, cyclostratigraphy and the refinement of radiometric methods of absolute dating, biostratigraphy and biochronology were the most used methodologies as relative-age tools for continental sediments. The difference between these two methods is their relation with the rocks that contain them. Biostratigraphy is defined in the International Stratigraphic Guide as: “The element of stratigraphy that deals with the distribution of fossils in the stratigraphic record and the organization of strata into units on the basis of their contained fossils” (Salvador, 1994). On the other hand, biochronology is not a stratigraphical discipline and therefore has no relationship with the stratigraphical record and could be defined as the elements and procedures of the palaeontology that deals with the temporal relationships between the fossils and the palaeobiological entities that produce them (López-Martínez and Truyols Santonja, 1994).

European mammal faunas were customarily grouped and ordered by assigning them to the MN-system, originally defined as the biozonation of the Mediterranean Neogene based on Mammals (Mein, 1975a, 1975b). MN-system consists of 17 numbered units, within each of which Mein (1975a, 1975b) included a set of characteristic localities from seven geographical regions across Europe. Despite the original name given by Mein (1975a, 1975b), the MN-system cannot be considered as a biostratigraphical scale, because it has no relationship with the stratigraphical record, and should be treated as a biochronological system dealing with the temporal ordination of the fossil record.

Each of the 17 MN units was characterized by the combination of three criteria (Mein, 1999, 2000):

- presence of characteristic representatives, generally short-lived, of evolutionary lineages;
- characteristic associations of temporally short co-occurrences of two or more genera;
- first appearances of genera.

It is important to realize that those criteria are not equivalents to biostratigraphical ones used to define biozones, because they are not necessarily all present in the same fauna. Therefore, they may not co-occur in the fossil record, and even be selected from different areas for some of the MN units, representing composite associations of faunal events. In addition, in later versions of the MN-system, and in order to avoid arbitrary changes on their taxonomical contents, a reference locality was assigned to every MN unit representing their stage-of-evolution (Fahlbusch, 1976, 1991; De Bruijn et al., 1992). Consequently, a local fauna is placed in a MN-unit according to the reference locality with which it shows the highest similarity on taxonomical or evolutionary stage of their respective mammal associations. This procedure, even if one restricts the comparisons to Western Europe, suffers from the usual problems of biostratigraphical correlations since the distribution of both the localities and the mammal taxa is patchy in space as well as in time. This is due to (Daams and Freudenthal, 1981; Fahlbusch, 1991; De Bruijn et al., 1992; Van Dam, 2003):

- the discontinuous nature of the fluvial, lacustrine or karstic facies yielding mammal faunas;
- the limited geographical ranges of most species and many genera;
- the presence of several local anagenetic lineages;
- FOs and LOs are, more often than not, diachronical.

This ambiguity on the nature of the MN scale introduced by several authors (see Van Dam, 2003, for an historical review) resulted in the system nowadays being frequently used as if it were a biostratigraphical scale instead of the biochronological scheme as which it was originally proposed (Mein, 1975a, 1975b) and later recommended by De Bruijn et al. (1992). This misuse of the MN-system has produced inconsistencies such as the definition of MN boundaries (Steininger, 1999) or the confusion between local and continental durations of the units (see Fahlbusch, 1991 for a more elaborate theoretical discussion). Thus, MN boundaries have been dated by extrapolating local-fauna ages in different areas to ages and durations of the units for broader European use (Steininger, 1999; Agustí et al., 2001). This confusion between local and continental duration of MN units produced that some authors used local MN chronology to establish erroneous interpretations and chronological inferences at continental scale. Costeur et al. (2007), for instance, discussed the need of a change in the chronology of several reference localities based on a supposed change in the community structure reflected in their cenograms. In addition to the inadequate use of repeatable features of past communities for biochronological interpretations, such as the community structure (cenograms), only a small part of the available chronostratigraphical and biostratigraphical information is used and superficially, when not incorrectly, treated. Costeur et al. (2007) did not realize that the MN units that they used to estimate faunal ages are strongly diachronical in the different areas considered, as discussed by previous authors and which they themselves represent in their fig. 1. Costeur et al. (2007) used Agustí et al. (2001) MN boundary ages for Western Europe to estimate numerical ages for faunas without chronological information. An example to illustrate the misuse of the available chronological information is among several such cases their estimate of the MN6 locality of Derching 1b in the Swiss OSM.

The numerical age assigned by Costeur et al. (2007) to Derching 1b, a locality below the Brock-Horizon, is 13.7–12.5 Ma, which is the duration of the MN6 unit proposed by Agustí et al. (2001) for Western Europe. In contrast, for other localities like Gallenbach 2b in Germany, which is above the Brock-Horizon and thus younger than Derching 1b, Costeur et al. (2007) used the age (14.5 Ma) estimated by Heissig (1997), which is in accordance with the duration of the MN6 (14.9–13.5 Ma) proposed by Steininger (1999) and Kälin and Kempf (2002) for the Central European record. As a consequence, the estimated ages used by Costeur et al. (2007) for these localities are incompatible with their relative stratigraphical position.

The MN-system proposed by Pierre Mein has been an important tool to correlate European Neogene localities that has allowed an incredible development on the European mammal palaeontology. Because of the strong provincialism in Europe during the Neogene, a biochronological system is still necessary because of the lack of complete regional high resolution stratigraphical frameworks due to the discontinuity of the continental fossil record. Nevertheless, as discussed by Fahlbusch (1991) the system should not be built on the criteria on which MN-system is based, since they are too inaccurate for clear-cut definitions of time units. As shown in previous sections of this work, most of the studied biotic events are significantly asynchronous, and even the ones that could be considered as synchronous between the studied areas cannot be considered as geologically instantaneous (Fahlbusch, 1991). The MN-system could be used instead as a biochronological succession of reference faunas to which the different mammal assemblages can be relatively placed, as recommended by De Bruijn et al. (1992). Even so, the MN-system remains a coarse, but necessary tool. It represents a system of convenience, which provides a hold for mammal palaeontologists in discussions comparing faunas from different parts of the European continent. On a regional scale, obviously, a detailed stratigraphical framework based on local biozonation, supported by superposition, radiometric ages and palaeomagnetostratigraphy, is far superior and in our opinion the best way to proceed.

6. Concluding remarks

This study on the dispersals of Early and Middle Miocene rodent species based on the most recent stratigraphical information from the three best known records (Spain, Switzerland and Germany) has shown considerable asynchronies between the different studied rodent events. Nevertheless, these asynchronies are less important than suggested in previous published works based on the local duration of the MN zones. First, because one of the sources of diachrony are the different definitions of MN units depending on the studied geographical region; and second, because the chronological interpretations of Central Europe have been estimated too old as discussed in previous sections.

Since the proposition in 1975 of the European Neogene Mammal scale by Pierre Mein, the amount on taxonomic, stratigraphical and chronological information around Europe has increased exponentially. The MN-system has been a very useful tool to correlate faunas at continental scale, allowing to have a common biochronological language more refined than the Stages or Land Mammal Ages. The system has evolved several times, and not always in the same direction (Van Dam, 2003), and therefore it is used with different philosophy by different authors. In this way, the MN units have been either used as biostratigraphical or as biochronological zones, and the question arises which use should be encouraged.

Prior to the establishment of a biostratigraphical or biochronological scale based on mammals, first and last occurrences in different areas need to be calibrated and compared in order to prove isochrony or diachrony of the events. Transforming the MN-scheme into a formal European biozonation is therefore rather difficult, because of the limited geographical ranges of most of the taxa on which the more detailed zonations are based, and because widespread taxa generally have first and last occurrences (FOs and LOs) that are diachronical (Daams and Freudenthal, 1981; De Bruijn et al., 1992), as has been proven for Miocene rodents in this paper.

Therefore, the MN-system based on a sequence of time-ordered reference localities (De Bruijn et al., 1992) is encouraged. We fully agree with the 'dual system' proposed by Van Dam (2003) to use the low-resolution MN-system on continental scale, and local/regional biostratigraphies side by side. The former allows coarse long-distance correlations, while the latter, with limited geographical scope, can be calibrated to the time scale and increase the highly needed information about synchrony and diachrony of mammal events in different areas.

Acknowledgements

First, we thank the organizers and editors of this volume in honor to our colleague Pierre Mein. We are grateful for the opportunity to contribute to this tribute for his vital contribution to mammal palaeontology. We thank all the colleagues and students that helped us with the field work during many years. We acknowledge Netherlands Centre for Biodiversity-Naturalis (The Netherlands), Institute of Earth Sciences of the Utrecht University (The Netherlands) and Museo Nacional de Ciencias Naturales-CSIC (Spain) for the facilities provided to study their collections. We thank Isaac Casanovas and Jordi Agustí for their constructive comments, which helped to improve our manuscript. We acknowledge financial support by the Spanish MICINN projects CGL2004-02094/BTE, CGL2007-65208, CGL2008-04200/BTE and Research Group UCM 910607. IG-P acknowledges the support, in the form of a postdoctoral contract of the FECYT/MICINN. AO and VHB have a FPU and FPI predoctoral grants (MICINN), respectively, and PL-G has a UCM predoctoral grant.

References

Abdul Aziz, H., Böhme, M., Rocholl, A., Zwing, A., Prieto, J., Wijbrans, J.R., Heissig, K., Bachtadse, V., 2008. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). International Journal of Earth Sciences 97, 115–134.

Abdul Aziz, H., Böhme, M., Rocholl, A., Prieto, J., Wijbrans, J.R., Bachtadse, V., Ulbig, A., 2009. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences 99, 1859–1886.

Abels, H.A., Hilgen, F.J., Krijgsman, W., Kruk, R.W., Raffi, I., Turco, E., Zachariasse, W.J., 2005. Long-period orbital control on Middle Miocene global cooling: Integrated stratigraphy and astronomical tuning of the Blue Clay Formation on Malta. Paleoceanography 20 (PA4012), 1–17.

Aguilar, J.P., Antoine, P.O., Crochet, J.Y., López-Martínez, N., Métais, G., Michaux, J., Welcomme, J.L., 2003. Les mammifères du Miocène inférieur de Beaulieu (Bouches-du-Rhône, France), comparaison avec Wintershof-West et le problème de la limite MN3/MN4. In: López-Martínez, N., Peláez-Campomanes, P., Hernández Fernández, M. (Eds.), En torno a Fósiles de Mamíferos: Datación. Evolución y Paleoambiente. Coloquios de Paleontología Volunen Extraordinario, 1. pp. 1–24.

Agustí, J., 1983. Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallès Penedès, Cataluña, España). Estudios Geológicos 39, 417-430.

Agustí, J., 1990. The Miocene Rodent Succession in Eastern Spain: A zoogeographical appraisal. In: a zoogeographical, appraisal., In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. NATO ASI Series. Series A: Life Sciences, 180. Plenum Press, New York, pp. 375–404.

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., Moyà-Solà, S., Pons Moyà, J., 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. Paléobiologie continentale 14, 33-46.

Álvarez Sierra, M.Á., 1987. Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior español. Scripta Geologica 86, 1–207.

Böhme, M., Gregor, H.J., Heissig, K., 2002. The Ries- and Steinheim meteorite impacts and their effect on environmental conditions in time and space. In: Buffetaut, E., Koerbel, C. (Eds.), Geological and biological effects of impact events. Springer, Berlin Heidelberg, pp. 215–235.

Bolliger, T., 1997. The current knowledge of the biozonation with small mammals in the Upper Freshwater Molasse in Switzerland, especially the Hörnli-Fan. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'École pratique des Hautes Études, 21. Institut Montpellier, Montpellier, pp. 501–513.

Bulot, C., Antoine, P.O., Duranthon, F., 2009. Rongeurs et lagomorphes du Miocène inférieur de Béon 2 (MN4, Montréal-du-Gers, SW France). Annales de Paléontologie 95, 197–215.

Costeur, L., Legendre, S., Aguilar, J.P., Lécuyer, C., 2007. Marine and continental synchronous climatic records: towards a revision of the European Mid-Miocene mammalian biochronological framework. Geobios 40, 775–784.

Daams, R., 1976. Miocene rodents (Mammalia) from Cetina de Aragón (province of Zaragoza) and Buñol (province of Valencia), Spain. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series B 79, 152–182.

Daams, R., 1998. Book Review: 'The evolution of Western Eurasian Neogene Mammal faunas', edited by Bernor, Fahlbusch and Mittmann. Palaeogeography, Palaeoclimatology, Palaeoecology 139, 101–106.

Daams, R., Alcalá, L., Álvarez Sierra, M.Á., 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 (2A), sciences de la terre et des planètes 327, 625–631.

Daams, R., Freudenthal, M., 1981. Aragonian: the stage concept versus Neogene Mammal Zones. Scripta Geologica 62, 1–17.

Daams, R., van der Meulen, A.J., Álvarez Sierra, M.Á., Peláez-Campomanes, P., Calvo, J.P., Alonso Zarza, M.A., Krijgsman, W., 1999a. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37, 103–139.

Daams, R., van der Meulen, A.J., Álvarez Sierra, M.Á., Peláez-Campomanes, P., Krijgsman, W., 1999b. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165, 287–294.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heizmann, E., Mayhew, D.F., van der Meulen, A.J., Schmidt-Kittler, N., Telles Antunes, M., 1992. Report of the RCMNS working group on fossil mammals. Reisenburg 1990. Newsletters on Stratigraphy 26, 65–118.

De Bruijn, H., Fahlbusch, V., Saraç, G., Ünay, E., 1993. Early Miocene rodent faunas from the eastern Mediterranean. Part 3: The genera *Deperetomys* and *Cricetodon* with a discussion of the evolutionary history of the Cricetodontini. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B 96, 151–216.

Escarguel, G., Aguilar, J.P., 1997. Les Eomyidés *Pseudotheridomys* et *Ligerimys* (Rodentia, Mammalia) du Miocène inférieur du sud de la France : évolution et biostratigraphie. Palaeontographica Abt. A 247, 25–58.

Fahlbusch, V., 1976. Report on the International Symposium on Mammalian Stratigraphy of the European Tertiary. Newsletters on Stratigraphy 5, 160–167.

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.

Fejfar, O., 1990. The Neogene VP sites of Czechoslovakia: a contribution to the neogene terrestric biostratigraphy of Europe based on rodents. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. NATO ASI Series, Series A: Life Sciences 180, Plenum Press, New York, pp. 211–236.

García-Paredes, I., 2006. Patrones evolutivos de los Gliridae (Rodentia, Mammalia) del Mioceno inferior y medio del área tipo de Aragoniense (Cuenca de Calatayud-Montalbán). Ph.D. thesis, Universidad Complutense de Madrid.(unpublished).

García-Paredes, I., Peláez-Campomanes, P., Álvarez-Sierra, M.Á., 2009. Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene. Zoological Journal of the Linnean Society 157, 622–652.

García-Paredes, I., Peláez-Campomanes, P., Álvarez-Sierra, M.Á., 2010. *Microdyromys remmerti* sp. nov., a new Gliridae (Rodentia, Mammalia) from the Aragonian type area (Miocene, Calatayud-Montalbán basin, Spain). Journal of Vertebrate Paleontology 30, 1594–1609.

Ginsburg, L., Bulot, C., 2000. Le cadre stratigraphique du site de Sansan. In: Ginsburg, L. (Ed.), La faune miocène de Sansan et son environnement. Mémoires du Muséum national d'Histoire naturelle, 183. pp. 39–67.

Heissig, K., 1997. Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the Upper Freshwater Molasse of Bavaria. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'École pratique des Hautes Études. Institut Montpellier 21, Montpellier, pp. 546–547.

Kälin, D., 1997. The mammal zonation of the Upper Marine Molasse of Switzerland reconsidered: a local biozonation of MN 2-MN 5. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'École pratique des Hautes Études. Institut Montpellier 21, Montpellier, pp. 515–535.

Kälin, D., Kempf, O., 2002. High-resolution mammal biostratigraphy in the Middle Miocene continental record of Switzerland (Upper Freshwater Molasse, MN 4-MN 9, 17-10 Ma). Environment and Ecosystems Dynamics of the Eurasian Neogene-Meeting: the Middle Miocene Crisis, Abstract book. November 2002, Frankfurt 67.

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.

Kempf, O., Bolliger, T., Kälin, D., Engesser, B., Matter, A., 1997. New magnetostratigraphic calibration of Early to Middle Miocene mammal biozones of the North Alpine Foreland Basin. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'École pratique des Hautes Études. Institut Montpellier 21, Montpellier, pp. 547–561.

Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., van Dam, J.A., 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.

Krijgsman, W., Langereis, C.G., Daams, R., van der Meulen, A.J., 1994. Magnetostratigraphic dating of the middle Miocene climate change in the continental deposits of the Aragonian type area in the Calatayud-Teruel basin (Central Spain). Earth and Planetary Science Letters 128, 513–526.

Larrasoaña, J.C., Murelaga, X., Garcés, M., 2006. Magnetobiochronology of Lower Miocene (Ramblian) continental sediments from the Tudela Formation (western Ebro basin, Spain). Earth and Planetary Science Letters 243, 409–423.

López-Guerrero, P., Álvarez-Sierra, M.Á., García-Paredes, I., López-Antoñanzas, R., Oliver, A., 2009. Cricetodontini (Rodentia, Mammalia) from the upper Aragonian and lower Vallesian of the Toril-Nombrevilla section (Middle and Upper Miocene, Calatayud-Daroca basin, Zaragoza, Spain). Journal of Vertebrate Paleontology 29 (supplement to 3), 161A.

López-Guerrero, P., Álvarez Sierra, M.Á., López Antoñanzas, R., Oliver Pérez, A., Peláez-Campomanes, P., 2008. Cricetodontini (Cricetidae, Rodentia) del Aragoniense superior (Mioceno Medio) de Nombrevilla 2 (Zaragoza, España). In: Esteve, J., Meléndez, G. (Eds.), Palaeontologica Nova. Publicaciones del Seminario de Paleontología de Zaragoza 8. pp. 259–271.

López-Martínez, N., Truyols Santonja, J., 1994. Paleontología. Editorial Síntesis, Madrid.

Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, D., 2004. The Neogene Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geologic Time Scale 2004. Cambridge University Press, Cambridge, pp. 409–440.

Martinez, J.N., 1997. La question de l'« endémisme » ibérique au cours du Miocène. Rapports avec la biochronologie mammalienne. Geobios 30 (supplément 2), 203–211.

Mein, P., 1975a. Résultats du groupe de travail des vertébrés: biozonation du Néogène Méditerranéen à partir des mammifères. In: Senes, J. (Ed.), Report on Activity of RCMNS Working Groups (1971-1975). VIth Congress of the Regional Committee of Mediterranean Neogene Stratigraphy, Bratislava, pp. 78–81.

Mein, P., 1975b. Proposition de Biozonation du Néogène Méditerranéen à partir des mammifères. Trabajos sobre Neógeno/Cuaternario 4, 112–113.

Mein, P., 1999. European Miocene Mammal Biochronology. In: Rössner, G., Heissig, K. (Eds.), The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 25–38.

Mein, P., 2000. La biochronologie des mammifères néogènes d'Europe. L'échelle MN, son application à la succession des faunes du Portugal. Ciências da Terra (UNL) 14, 335–342.

Oliver, A., López-Guerrero, P., García-Paredes, I., Álvarez-Sierra, M.A., Peláez-Campomanes, P., 2009. Evolution of *Megacricetodon* tooth pattern through geometric morphometric analysis. Journal of Vertebrate Paleontology 29 (supplementto 3), 158A.

Oliver Pérez, A., López Guerrero, P., Peláez-Campomanes, P., 2008. Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España). In: Esteve, J., Meléndez, G. (Eds.), Palaeontologica Nova. Publicaciones del Seminario de Paleontología de Zaragoza 8. pp. 317–329.

Peláez-Campomanes, P., 2001. Revision of the Aragonian (Miocene) *Atlantoxerus* (Sciuridae). Journal of Paleontology 75, 418–426.

Peláez-Campomanes, P., Morales, J., Álvarez Sierra, M.A., Azanza, B., Fraile, S., García Paredes, I., Hernández Fernández, M., Herráez, E., Nieto, M., Pérez, B., Quiralte, V., Salesa, M.J., Sánchez, I.M., Soria, D., 2003. Updated biochronology of the Miocene mammal faunas from the Madrid basin (Spain). In: Reumer, J.W.F., Wessels, W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia, 10. A volume in honour of Hans de Bruijn, Deinsea, pp. 431–441.

Pippèrr, M., Reichenbacher, B., Witt, W., Rocholl, A., 2007. The Middle and Upper Ottnangian of the Simssee area (SE Germany): Micropalaeontology, biostratigraphy and chronostratigraphy. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 245, 353–378.

Prieto, J., Böhme, M., Maurer, H., Heissig, K., Abdul Aziz, H., 2009. Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate. International Journal of Earth Sciences 98, 1767–1791.

Robles, F., Belinchón, M., García-Flor, J., Morales, J., 1991. El Neógeno continental de Buñol y del valle del rio Cabriel. In: De Renzi, M., Márquez-Aliaga, A., Usera, J. (Eds.), El estudio de la Forma Orgánica y sus consecuencias en Paleontología Sistemática, Paleoecología y Paleontología Evolutiva. Revista Española de Paleontología Volumen Extraordinario, pp. 205–215

Salvador, A., 1994. International Stratigraphic Guide: a guide to stratigraphic classification, terminology, and procedure. International Subcommission on Stratigraphic Classification of IUGS International Commission on Stratigraphy. International Union of Geological Sciences, Geological Society of America, Boulder.

Schlunegger, F., Burbank, D.W., Matter, A., Engesser, B., Mödden, C., 1996. Magnetostratigraphic calibration of the Oligocene to Middle Miocene (30–15 Ma) mammal biozones and depositional sequences of the Swiss Molasse Basin. Eclogae Geologicae Helvetiae 89, 753–788.

SPSS, 2008. Statistical package for the social sciences for windows, Rel. 17.0. SPSS Inc., Chicago.

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, G.E., Heissig, K. (Eds.), The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 9–24.

Steininger, F.F., Daxner-Hock, G., Haas, M., Kovar-Eder, J., Mauritsch, H., Meller, B., Scholger, R.M., 1998. Stratigraphy of the "Basin Fill" in the Early Miocene lignite opencast mine Oberdorf (N Voitsberg, Styria, Austria). Jahrbuch der Geologischen Bundesanstalt-Austria 140, 491–496.

Van Dam, J.A., 2003. European Neogene mammal chronology: past, present and future. In: Reumer, J.W.F., Wessels, W. (Eds.), Distribution and migration of Tertiary mammals in Eurasia: a volume in honour of Hans de Bruijn, Deinsea 10. pp. 85–95.

Van Dam, J.A., Abdul Aziz, H., Álvarez Sierra, M.Á., 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 Dam, J.A., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. Journal of Vertebrate Paleontology 21, 367–385.

Van den Hoek Ostende, L.W., Furió, M., 2005. Spain. In: Van den Hoek Ostende, L.W., Doukas, C.S., Reumer, J.W.F. (Eds.), The fossil record of the Eurasian Neogene insectivores (Erinaceomorpha, Soricomorpha, Mammalia). Part I. Scripta Geologica Special Issue 5. pp. 149–284.

Van den Hoek Ostende, L.W., Furió, M., García-Paredes, I., 2009. New data on *Paenelimnoecus* from the Middle Miocene of Spain in support of the subfamily Allosoricinae (Soricidae, Mammalia). Acta Palaeontologica Polonica 54, 159–164.

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., García-Paredes, I., Álvarez-Sierra, M.A., van den Hoek Ostende, L.W., Hordijk, K., Oliver, A., Peláez-Campomanes, P., in press. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta.

Van der Meulen, A.J., Peláez-Campomanes, P., 2007. Residents and transients in the fossil record. In: Levin, S.A. (Ed.), Encyclopedia of Biodiversity. Elsevier, New York, pp. 1–7.

Van der Meulen, A.J., Peláez-Campomanes, P., Daams, R., 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain). In: López-Martínez, N., Peláez-Campomanes, P., Hernández Fernández, M. (Eds.), En torno a Fósiles de Mamíferos: Datación. Evolución y Paleoambiente. Coloquios de Paleontología Volumen Extraordinario, 1. pp. 385–441.

Van der Meulen, A.J., Peláez-Campomanes, P., Levin, S.A., 2005. Age structure, residents, and transients of Miocene rodent communities. The American Naturalist 165, E108–E125.

Ziegler, R., Fahlbusch, V., 1986. Kleinsäuger-Faunen aus der basalen Oberen Süsswasser-Molasse Niederbayerns. Zitteliana 14, 3–58.