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# Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology

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## ABSTRACT

This paper contains formal definitions of the Early to Middle Aragonian (Late Early–Middle Miocene) small-mammal biozones from the Aragonian type area in North Central Spain. The stratigraphical schemes of two 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, have been compared. This comparison allows the analysis of the order of shared mammal events in the two countries, and the quantification of the resulting asynchronies based on their temporal correlations. The order of the events is very similar in Spain and Switzerland. In order to estimate the diachrony, two age-model options are used for the Swiss record. Our preferred option yields no discrepancies with SW European paleomagnetic and radiometric calibrations of the Ramblian and Early Aragonian bioevents. All Swiss first taxa occurrences precede those in the Aragonian type area by 0.74Myr on average. The asynchronies (1-2Myr) of the species arriving in the Late Middle to Early Late Aragonian may be higher than in the Early Aragonian (0-1Myr). The implications for the biochronological mammal Neogene system are discussed. Evidence is given confirming the unfeasibility of a formal European biozonation, since it is realised, that 1) most indicator species and many genera of rodents yielding the most detailed zonations have limited geographical ranges hampering recognition of the mammal Neogene zones; and 2) first and last taxon occurrences are diachronical. Therefore, the mammal Neogene system based on a sequence of time-ordered reference localities is preferred to the one based on selected bioevents "developed in widespread geographic areas".

***KEYWORDS*** **Rodents. Lagomorphs. Insectivores. Miocene. Faunal events.**

## INTRODUCTION

The main features of the history of the European mammal fauna are well known, and serve as a relative-age tool for the continental sediments in which they are found. Since the non-recurrent compositional and evolutionary changes are more numerous than, for instance, those of floral and invertebrate records, small mammals provide the most detailed subdivisions, and hence optimal precision for correlation. The Miocene-Pliocene record has been divided into 17 successive mammal Neogene units (*e.g.*, Mein, 1975a, b; De Bruijn *et al.*, 1992), which have become the main biochronological scheme on continental scale.

On the other hand, the eventful mammal history is an object of study in its own right when we wish, for example, to understand its relations to the profound changes of climate and paleogeography that affected the European landscape during the Neogene. In this case, the mammal history obviously has to be independently calibrated to the time scale. Such calibrations (usually paleomagnetic or radiometric) 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 the localities and the mammal taxa is patchy in space as well as in time. This is due to 1) the nature of the fluvial, lacustrine or karst facies yielding mammal faunas; 2) the very limited geographical ranges of most species and many genera; 3) presence of several local anagenetic lineages; and 4) first and last taxon occurrences (FO's and LO's, respectively) are, more often than not, diachronical (*e.g.*, Daams and Freudenthal, 1981; De Bruijn *et al.*, 1992; Van Dam, 2003). Consequently, the locally obtained ages for FO' and LO's that are used as dates for continent-wide immigrations and extinctions, are to be mistrusted *a priori*, as long as synchrony and/or diachrony of the events have not been evidenced. Unfortunately, there exists a great lack of spatially distributed absolute dates (Van Dam, 2003), and in our opinion, a number of the existing numerical age determinations are not rigorous enough to be reliable. This is because of the use of 1) second or third order correlations, 2) radiometric ages with very large uncertainty intervals, 3) insufficient number of recorded paleomagnetic chrons making independent correlation to the Geomagnetic Polarity Time Scale (GPTS) impossible (Daams *et al.*, 1999b), and 4) the use of poor-quality polarity signals (Abdul Aziz *et al.*, 2008, 2010).

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 always been considered as singular (De Bruijn *et al.*, 1992; Martínez, 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 uniform, and there are certainly more Central European influences in coastal basins as the Vallès-Penedès and Levante than there are in the inland basins such as the Madrid and Calatayud-Montalbán basins (Agustí *et al.*, 1984; Agustí, 1990) and therefore the Spanish record can not be considered as homogeneous.

In order to obtain robust correlations between different European bioprovinces we compare two overlapping Early to Middle Miocene records in Europe, each of which (at least in large part) has reliably been tied to the time scale. Firstly, the mammal fauna sequence from the Upper Freshwater Molasse (OSM) of the Alpine Foreland Basin in Switzerland, recently updated by Kälin and Kempf (2009); and secondly, the record of the Aragonian type area in North-Central Spain (Daams *et al.*, 1999a; Van der Meulen *et al.*, 2005; Van Dam *et al.*, 2006). The two records represent different bioprovinces and provide the unique opportunity to compare different faunal histories on the basis of time, as shown by Kälin and Kempf (2009). The latter authors define 13 local biozones, which they correlate MN4 to MN7/8, and demonstrate age discrepancies of 0.5-1.0Myr with the Spanish correlations to MN4, MN5 and MN6. These authors particularly attribute the discrepancies to the diachronous, east-west immigration of cricetids and they come to the striking conclusion that, for instance, the faunas attributed to MN4 in Spain and Switzerland barely overlap in time. In this paper, we elaborate the comparisons of the two bioprovinces by Lindsay (2001) and Kälin and Kempf (2009, and references therein), and discuss the variable asynchronies (Lindsay, 2001) amongst small mammal taxa and the implications for the current use of the mammal Neogene-system.

The existing Aragonian biozonation (Daams *et al.*, 1999a) faithfully reflects the faunal changes, but lacks precise definition of the zone boundaries. The paleomagnetically calibrated sections offer the opportunity to date the zone boundaries, on the condition, however, that the zones are unambiguously defined. Therefore, first the Lower to Middle Aragonian biozonation will be formally described and their boundaries dated, in order to facilitate the comparison with the Swiss zonation. Then we discuss the existing time control for the two successions, the order of selected bioevents, and the estimates of their synchrony or asynchrony.

## THE SPANISH RECORD (CALATAYUD-MONTALBÁN BASIN)

### Geological Setting

A very short summary of the geology and sedimentology of the Calatayud-Montalbán Basin is presented here. For recent overviews, including biostratigraphy and the correlations to the geomagnetic polarity timescale, we refer to articles by Daams *et al.* (1999a, b) and Alcalá *et al.* (2000) and references therein. The Calatayud-Montalbán Basin is a long (100km) and narrow (10–26km) basin (Fig. 1) filled with coarse alluvial fan clastics (along the borders), mudstones, and carbonates. The latter two were deposited in shallow temporary lakes situated in low-relief areas distally of the alluvial fans (Daams *et al.*, 1999a). The deposition of the mudstone carbonate alternations of different Middle and Upper Miocene sections in the endoreic Calatayud-Montalbán and the nearby Teruel basins has been related to astronomically induced climate changes, dry-humid oscillations in particular (Krijgsman *et al.*, 1997; Abdul Aziz, 2001). In our sections from the Aragonian type area, there is no clear cyclicity; however, elsewhere, the mentioned authors have demonstrated the existence of four different scales of sedimentological cycles, which they interpret as the expression of climatic changes induced by eccentricity and precession (400,000, 100,000, and 23,000 years) and of obliquity (41,000 years). The small-scale mudstone-carbonate cycles have been related to the precession cycle; mudstones correspond to maxima, with relatively dry climate conditions, and carbonates to precession minima, with relatively wet conditions. In addition, based on the Spanish small mammal record, Van Dam *et al.* (2006) show the existence of turnover cycles with periods of 2.4-2.5 and 1Myr, and linked them to low-frequency modulations of Milankovitch oscillations.

### Biostratigraphy of the Aragonian

We refer to Daams and Freudenthal (1988) and Daams *et al.* (1999a) for extensive summaries and discussions of the 30-years history since the definition of the Aragonian (Daams *et al.*, 1977). It should be emphasized that the students of the Aragonian consider it to be a mammal-based chronostratigraphic unit, the geographical scope of which is limited to terrestrial sediments of Spain. This is contrary to its original definition as a "Superstage" in the "International Symposium on Mammalian Stratigraphy of the European Tertiary" in Munich in 1975 (Fahlbusch, 1976). The type section and additional reference sections of the Aragonian Stage are situated near Villafeliche (Province of Zaragoza, North-Central Spain), and extensively described and discussed in Daams *et al.* (1999a). We follow the subdivision of Lower (Zones B-C), Middle (D-E) and Upper Aragonian (F-G) of Daams *et al.* (1987). The substages are based on the two most important faunal changes that took place around the Zone C-D and the Zone E-F boundaries, respectively (Van der Meulen and Daams, 1992; Krijgsman *et al.*, 1994; Daams *et al.*, 1999a; Van der Meulen *et al.*, 2005; Van der Meulen and Peláez-Campomanes, 2007). The ages of the substages and their correlation to the Astronomical Tuned Neogene Time Scale (ATNTS2004; Lourens *et al.*, 2004) will be discussed after the descriptions of the biostratigraphical zones of the Early and Middle Aragonian.

Figures 2 to 5 show the distribution of the micromammal taxa recorded in the Aragonian type area. The data are based on the complete collections of micromammals. In order to have an estimation of the relative proportion of each order, the database contains approximately 43,000 first and second molars of rodents, almost 3,500 third

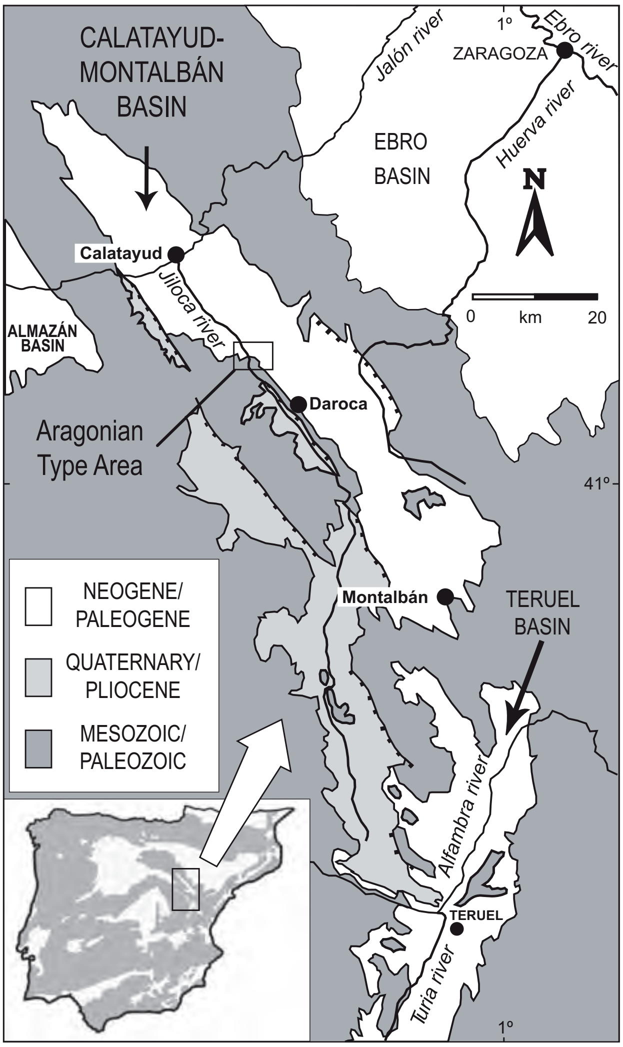

**FIGURE 1** | Location of the Calatayud-Montalbán Basin in Spain and synthetic geology of the region.

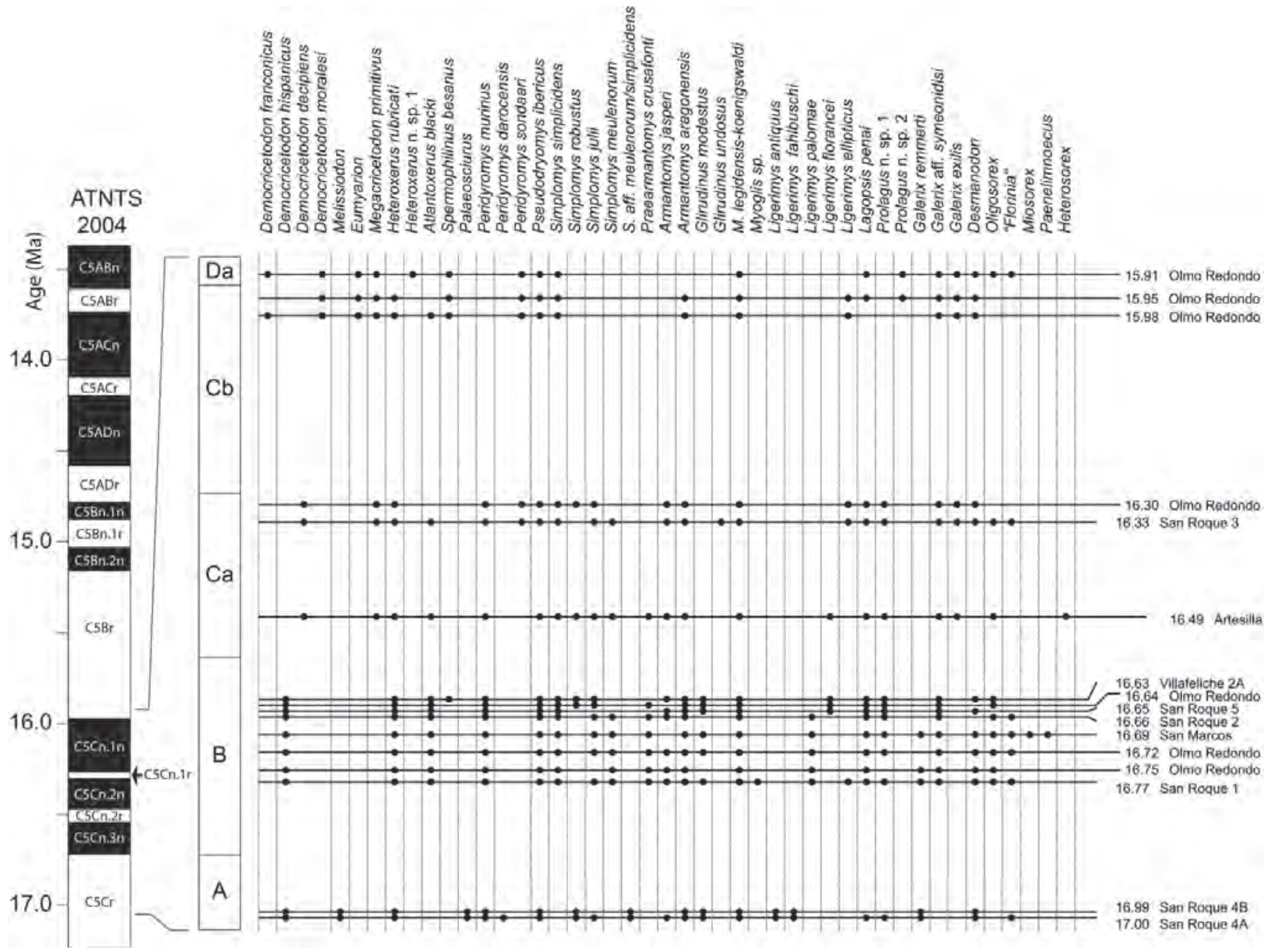

**FIGURE 2** | Distribution chart of rodents, lagomorphs and insectivores from the San Roque and Olmo Redondo sections, supplemented with the biostratigraphically interpolated Artesilla locality in the Aragonian type area.

premolars of lagomorphs and 1,050 first and second molars of insectivores. The combined distribution of rodents, lagomorphs and insectivores is presented for the first time. The localities are grouped by stratigraphical section in order to show the superpositions of the micromammal associations. The three main sections are: Valdemoros-Las Umbrias (Aragonian type section), Vargas-Fuente Sierra, and Olmo Redondo-San Roque. In addition, there are other four important, although shorter, sections that are: La Col, Villafeliche 4, Valdemoros 3, and Las Planas 4. Finally two more localities have been included: Artesilla and Valdemoros 8A. The proposed correlations between different sections are based on lithostratigraphy and biostratigraphy (Daams *et al.*, 1999a).

## Early and Middle Aragonian biozones in the type area

The field evidence of the sequence of the zones is given in Figures 2-5, which show the superposition, composition, and biostratigraphical designation of the assemblages from three (partly composite) sections that are sedimentologically described by Daams *et al.* (1999a). The ages of the localities from magnetostratigraphically measured sections are in bold. Those of the other localities were estimated by their biostratigraphical position and interpolation in the directly dated faunal sequence.

We will continue the use of the informal names of Zones B-G introduced and characterized by Daams and Freudenthal (1981), but defining the biozones B to E (Early to Middle Aragonian) formally, in accordance with the latest characterizations (Daams *et al.*, 1999a, b). It appeared that the lower part of Zone C is sufficiently different from the upper part to introduce its subdivison into Ca and Cb here. Formal definitions are needed to provide the boundaries with numerical ages of optimal precision. The revision of the zones is opportune, because new data have become available since the overview of Daams *et al.*

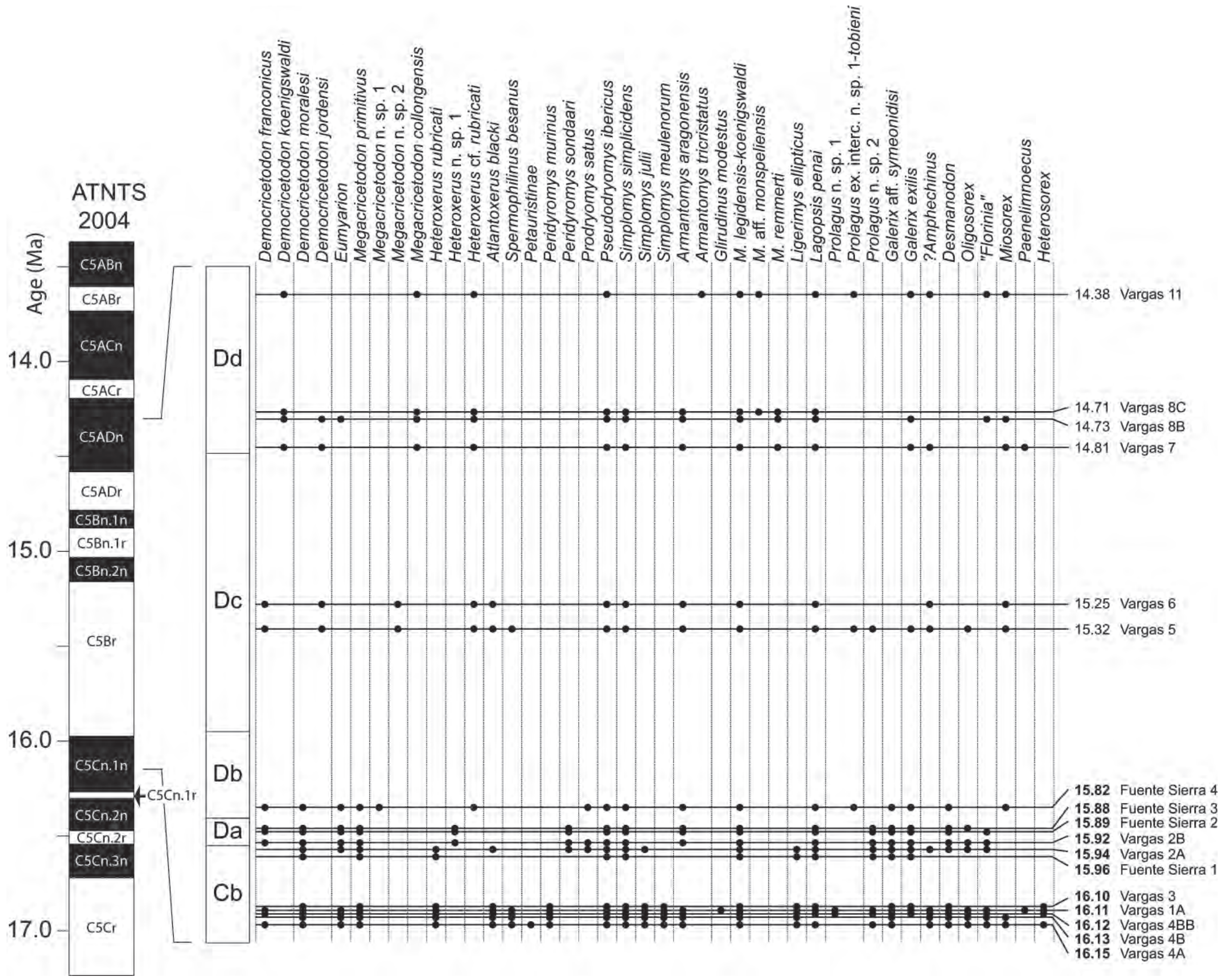

**FIGURE 3** | Distribution chart of rodents, lagomorphs and insectivores from the Fuente Sierra-Vargas section in the Aragonian type area. Ages from magnetostratigraphic sections are highlighted in bold.

(1999a): revision of the medium sized *Democricetodon* by Van der Meulen *et al.* (2003), revision of the Gliridae from the Early and Middle Aragonian (García-Paredes, 2006; García-Paredes *et al.*, 2009; García-Paredes *et al.*, 2010), the revision of the Insectivora (Van den Hoek Ostende and Furió, 2005; Van den Hoek Ostende *et al.*, 2009), the revision of *Megacricetodon* from Artesilla (Zone Ca) by Oliver Pérez *et al.* (2008) and from other localities (Oliver *et al.*, 2009a, b), and the current revision of the Eomyidae. The evolution of two anagenetic lineages of *Democricetodon* (Van der Meulen *et al.*, 2003) is used in the new zonal definitions. The lineages are *D. hispanicus-D. decipiens-D. moralesi-D. jordensi-D. lacombai* (Zones A-E) and *D. franconicus-D. koenigswaldi-D. larteti* (Zones Cb-G3). It should be mentioned that these lineages are not recognized by Freudenthal (2006) because of our allegedly erroneous stratigraphy (see below); we refute his claims in the Appendix (On-line Supplementary material). We use some new biostratigraphical data on the Ochotonidae from the revision of the Aragonian representatives by Hordijk (2010). Therefore, we now present the Early to Middle Aragonian biozonation based on a more complete knowledge of the small mammal fauna. The biostratigraphy of the large mammals is given in Daams *et al.* (1998).

The following abbreviations are used: FO–first occurrence, FCO–first common occurrence, LO–last occurrence, LCO–last common occurrence, Ma–Millions of years ago, Myr–Millions of years, kyr–Thousands of years. These occurrence data refer to the Aragonian type area only. The frequent use of "common occurrence" expresses our intention to draw easily recognizable boundaries associated with faunal changes, because both FO's and LO's are often associated with rare and

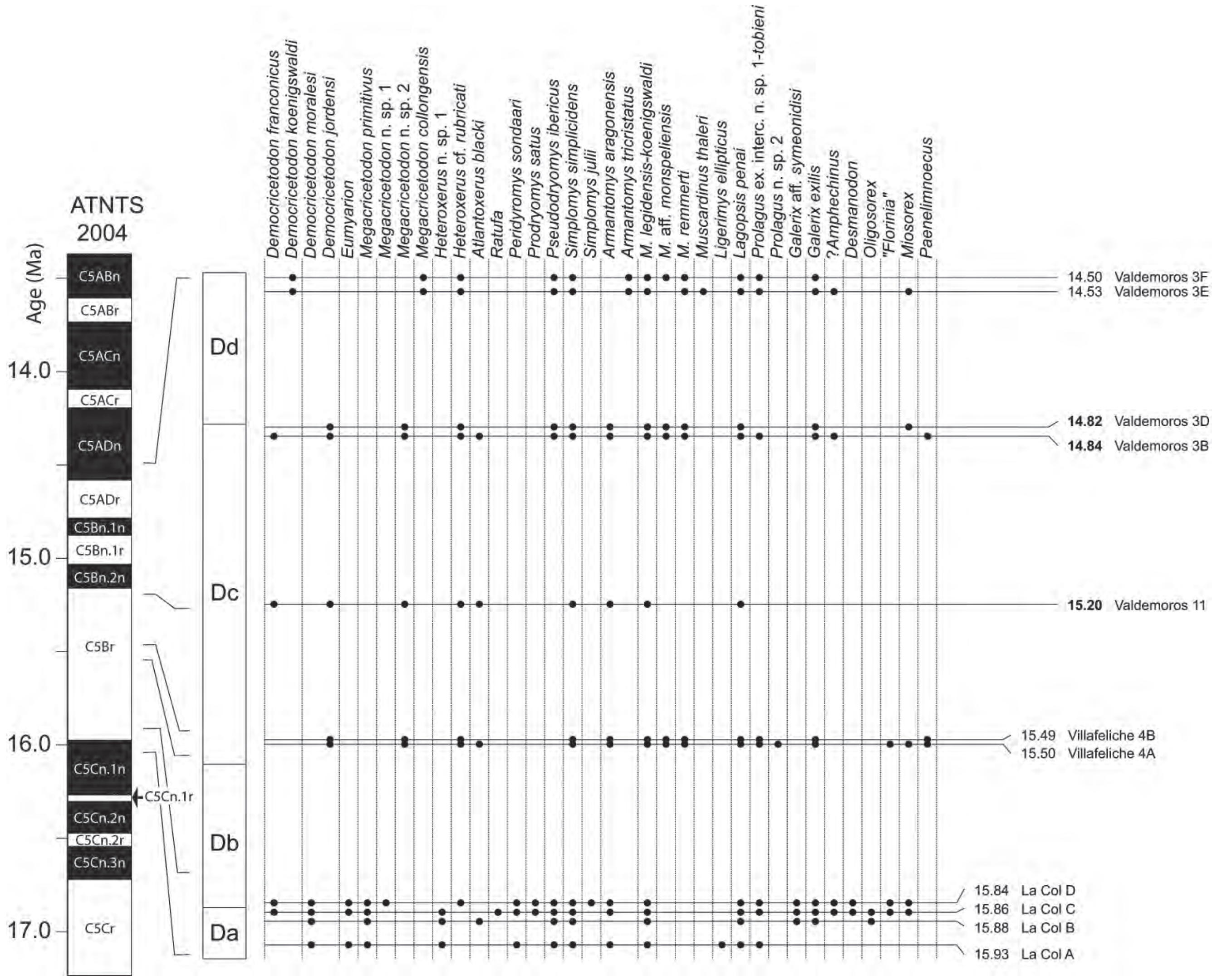

**FIGURE 4** | Distribution chart of rodents, lagomorphs and insectivores from the La Col, Villafeliche 4 and Valdemoros 3 sections in the Aragonian type area. Ages from magnetostratigraphic sections are highlighted in bold.

inconsistent occurrences. An age preceded by "~" indicates that it refers to the age of a locality not found in a paleomagnetically measured section.

## Definitions of Zones A to E

Zone A: LCO of *Eucricetodon*-FCO *Democricetodon* Interval Zone.

FO and LO: Zone A contains the FO of *Democricetodon hispanicus* and *Galerix symeonidisi* in the uppermost part, and the LO of *Palaeosciurius, Melissiodon*, *Ligerimys antiquus* and *L. fahlbuschi.*

Composition. The assemblages are characterized by the high abundance, and sometimes dominance, of eomyids; glirids are common and diverse; cricetids are mostly absent ("cricetid vacuum"). However, *Melissiodon* can be found throughout this zone and *Democricetodon* is present in the uppermost part, but is rare.

Youngest locality. SR4B (~16.99Ma).

Remarks. *Melissiodon* has been found in younger localities (Zone Ca) from the nearby Teruel area (unpublished data) and from the Valencia area (Robles *et al.*, 1991).

Zone B: FCO *Democricetodon hispanicus*-FO *Megacricetodon primitivus* Interval Zone.

FO and LO: Zone B contains the FO of *Atlantoxerus blacki, Ligerimys palomae* and *L. florancei*, and the FCO of *Galerix symeonidisi. Ligerimys palomae* is restricted to the lower part of this zone, and is then replaced by *L. florancei.*

Composition. The assemblages are dominated by *Lagopsis penai* and glirids. The faunas are equitable.

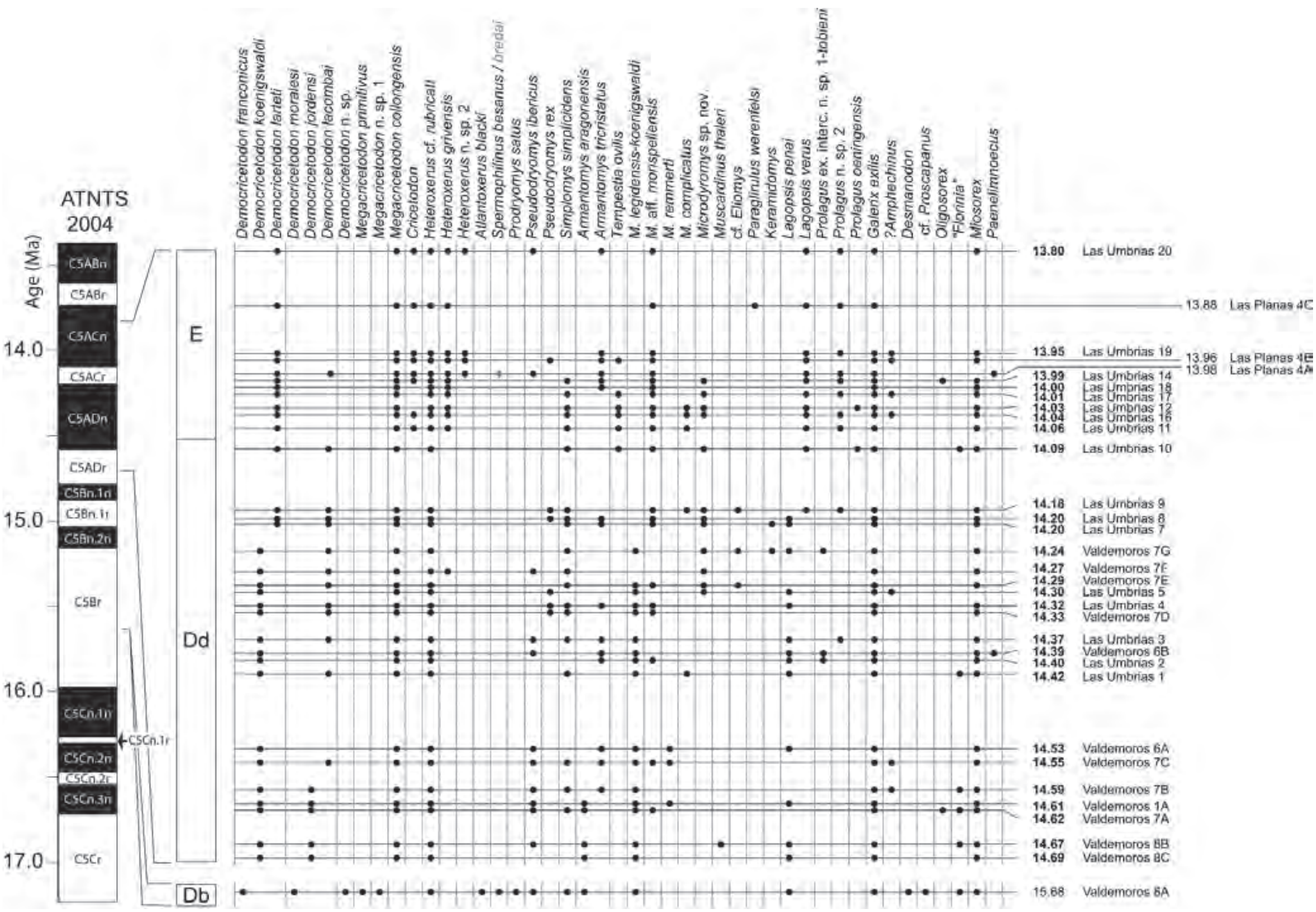

**FIGURE 5** | Distribution chart of rodents, lagomorphs and insectivores from the Valdemoros-Las Umbrias and Las Planas 4 sections in the Aragonian type area. Ages from magnetostratigraphic sections are highlighted in bold.

Eomyids are less frequent than in Zones A, Ca and Cb.

Oldest locality. SR1 (~16.77Ma).

Youngest locality. VL2A (~16.63Ma).

Zone Ca: *Megacricetodon primitivus-Democricetodon decipiens* Concurrent Range Zone.

FO and LO: Zone Ca contains the FO of *Megacricetodon* and the LO of *Praearmantomys crusafonti*, *Armantomys jasperi, Simplomys robustus* and *Ligerimys florancei*.

Composition. The assemblages are characterized by the reoccurrence of *Heterosorex* (absent since the lowermost part of Zone Z, Ramblian), the rareness of *Microdyromys legidensis-koenigswaldi* and the decrease of lagomorph abundances. Within this zone *Ligerimys florancei* is replaced by *L. ellipticus.*

Oldest locality. ART (~16.49Ma).

Youngest locality. OR4A (~16.30Ma).

Remarks. *Armantomys jasperi* has been described from the younger locality of Casetón 1A (Zone Dd, Prov. Teruel, Spain) by Daams in 1991 (see García-Paredes and Van den Hoek Ostende, 2007 for nomenclatorial comments and correct date of publication of species described in Daams, 1991). *Eumyarion* has been described from coeval localities in the Teruel area (unpublished data) and in the Valencia area (Daams and Freudenthal, 1974; Robles *et al.*, 1991).

Zone Cb: *Democricetodon moralesi-Ligerimys ellipticus* Concurrent Range Zone.

FO and LO: Zone Cb contains the FO of *Democricetodon franconicus, D. moralesi, Eumyarion*, *Prodryomys satus* (uppermost part), *Amphechinus, Prolagus* n. sp. 2, and the LO of *Heterosorex, Peridyromys murinus* and *Simplomys meulenorum*.

Composition. The assemblages are dominated by *L. ellipticus* and cricetids; *Microdyromys koenigswaldi* is common; ochotonids are represented by three species.

Oldest locality. VR4A (16.15Ma).

Youngest locality. VR2A (~15.94Ma).

Remarks. *Peridyromys murinus* is known from the younger locality of Casetón 1A (Zone Dd; Daams and Freudenthal, 1981).

Zone Da: LCO *Ligerimys ellipticus*-FO *Megacricetodon* n. sp. 1 Interval Zone.

Composition. The assemblages are dominated by cricetids and there is a lower diversity of squirrels and glirids than in the previous Zone. *Microdyromys koenigswaldi* is the commonest glirid. The lower most locality (La Col A) contains the last, very rare *Ligerimys ellipticus*.

Oldest locality. COLA (~15.93Ma).

Youngest locality. COLC (~15.86Ma).

Zone Db: *Megacricetodon* n. sp. 1 Range Zone.

FO and LO: Zone Db contains the FO of *Microdyromys remmerti*, and the LO of *Democricetodon moralesi*, *Peridyromys sondaari*, *Prodryomys satus, Simplomys julii, Desmanodon* and *Galerix symeonidisi. Democricetodon* sp. and *Megacricetodon* n. sp. 1 are restricted to this Zone. Composition. The zone is characterized by the presence of six cricetid species; glirids are less abundant than in the previous Zone. Zone Db is further characterised by the co-ocurrence of two *Megacricetodon* species, which are under revision because of nomenclatural problems.

Oldest locality. COLD (~15.84Ma).

Youngest locality. VA8A (~15.68Ma).

Zone Dc: FO *Democricetodon jordensi* - FO *D. koenigswaldi* Interval Zone.

FO and LO: Zone Dc contains the FO of *D. jordensi, Megacricetodon* n. sp. 2 and *Microdyromys* aff. *monspeliensis,* and the LO of *Atlantoxerus blacki* and *Spermophilinus besanus*.

Composition. The assemblages have low numbers of species; cricetids are the dominant taxa, *Megacricetodon* is generally the most common. *Microdyromys* is represented by three species in the area for the first time.

Oldest locality. VL4A (~15.50Ma).

Youngest locality. VA3D (14.82Ma).

Zone Dd: FO *Democricetodon koenigswaldi*-FRO *Heteroxerus grivensis* Interval Zone.

FO and LO: Zone Dd contains the FO of *Democricetodon lacombai, D. larteti, Armantomys tricristatus, Pseudodryomys rex, Microdyromys complicatus, Tempestia ovilis, Heteroxerus grivensis, Keramidomys thaleri, Muscardinus thaleri, Lagopsis verus* and *Prolagus oeningensis,* and the LO *Eumyarion and Microdyromys koenigswaldi.*

Composition. The assemblages are dominated by *Democricetodon koenigswaldi, D. larteti* and *Megacricetodon collongensis*. The *Democricetodon hispanicus-lacombai* lineage is rare in the record. The FO of *Democricetodon lacombai, D. larteti, Armantomys tricristatus* and *Lagopsis verus* represent new evolutionary stages within pre-existing anagenetic lineages. Most of the immigration events take place in the upper part of this zone.

Oldest locality. VR7 (~14.81Ma).

Youngest locality. LUM10 (14.09Ma).

Zone E: FCO *Heteroxerus grivensis*- FO *Megacricetodon rafaeli* Interval zone

FO and LO: Zone E shows the FO of *Cricetodon,* and an as yet undescribed new species of *Heteroxerus*; the range of the latter is restricted to the Zone. *Pseudodryomys ibericus, Simplomys simplicidens, Pseudodryomys rex, Megacricetodon collongensis* and *Democricetodon lacombai* have their last occurrences.

Composition. The assemblages are mostly dominated by *Megacricetodon*, less by *Democricetodon larteti*; four species of ground squirrel are present.

Oldest locality. LUM11 (14.06Ma).

Youngest locality. LUM20 (13.80Ma).

## Discussion of the biozones

The above formal definitions and the introduction of Zones Ca and Cb are the further elaboration of the lower part of the zonation of Daams and Freudenthal (1981) and later refinements (Daams and Freudenthal, 1988; Van der Meulen and Daams, 1992; Daams *et al.*, 1999a). Figures 2 to 5 illustrate that our biozones are solidly based on their superposition in the different sections of the type area. Figure 6 summarises the taxon ranges based on the available information from the different sections. Zones A, B, and E have remained essentially the same since their creation. The subdivision of Zone C is based on the small turnover indicated by extinctions in Ca and immigrants in Cb (see the definitions). Zone D has changed considerably: Daams and Freudenthal (1988) proposed a threefold division D1, D2 and D3 based on their interpretation of the evolution of cricetids, which was found to be erroneous (Daams *et al.*, 1999a, b; Van der Meulen *et al.*, 2003, and see below). Van der Meulen and Daams (1992) interpolated D0 between Zones C and D1; it is equivalent with Zone Db (Daams *et al.*, 1999a). The replacement of D0–D3 by Zones Da, Db, Dc and Dd has been extensively discussed in the latter publication.

In earlier studies, faunas from outside the type area have been used in the Aragonian sequence (*e.g.*, Daams and Freudenthal, 1988; Van der Meulen and Daams, 1992): Casetón 1A and 2B (subzone D1) and Regajo 2 and Valhondo 4 (D3), Moratilla 2 and Muela Alta (D0) are situated in the Calamocha area, some 30km to the SE. These correlations affected the zone characterizations with the inclusion of taxa, which at the time had not been encountered in the type area, such as *Democricetodon (=Pseudofahlbuschia) lacombai* for D3, and the co-occurrence of two *Megacricetodon* species for D0. This situation has been remedied by the later field campaigns. *Democricetodon lacombai* is present in the type section from locality Valdemoros 7C upwards (Zone Dd-E), and the presence of the two *Megacricetodon* species characterizing Zone Db has been demonstrated in the Middle Aragonian sections of La Col and Fuente Sierra, and in locality Valdemoros 8A laterally of the type section (Daams *et al.*, 1998, 1999a, Van der Meulen *et al.*, 2003). Furthermore, the faunas of San Roque 4 located in the type area are characteristic of Zone A, which was originally based on the faunas of Bañón (Daams and Freudenthal, 1981). Thus, the present Aragonian zonation is exclusively based on superposed faunas in the type and additional sections near Villafeliche (Daams *et al.*, 1999a; Figure I available at Electronic appendix, www.geologica-acta.com).

Freudenthal (2006) disagrees with the evolution of the Aragonian *Democricetodon* revised by Van der Meulen *et al.* (2003), because in his opinion the faunal sequence of Daams *et al.* (1999a), which is followed in this paper, is incorrect. Freudenthal's starting point, his disagreement with the relative stratigraphic position of only two localities (Valdemoros 3B and Valdemoros 1A), is based on demonstrably erroneous tectonical arguments. He provides an alternative sequence based on calcareous marker beds without, however, providing the lithological features, with which the northern and southern exposures of these beds can be followed unambiguously across the Rambla de Vargas. We refer to the Appendix (On-line Supplementary material) where we give arguments, that his alleged lithological sequence results in a biostratigraphically mixed and untenable succession.

## TIME CONTROL OF THE COMPARED SUCCESSIONS

### Aragonian type area

The chronology of the Aragonian area is based on high-resolution magnetostratigraphical correlations of four sections in the Calatayud-Daroca area to the GPTS (Krijgsman *et al.*, 1994, 1996). The correlations have been improved by the reinterpretation of the biostratigraphical correlation between the Armantes and Vargas sections (Daams *et al.*, 1999b), which resulted in the current chronological framework (Daams *et al.*, 1999a). The first

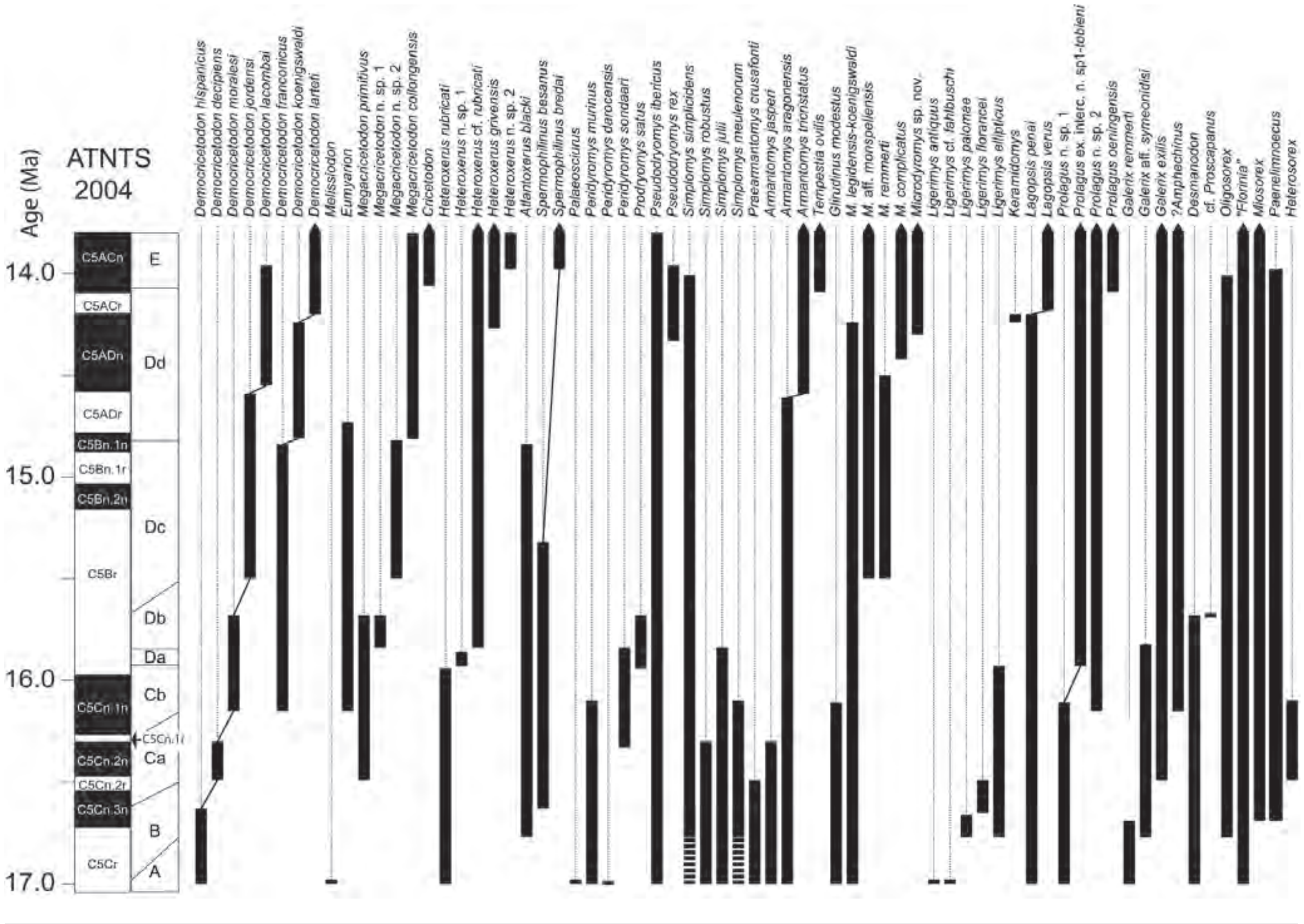

**FIGURE 6** | Distribution ranges of the most characteristic micromammal taxa from the Aragonian type area.

correlations were made by reference to Cande and Kent (1995), in this paper we use Van Dam's *et al.* (2006) recalibrated ages of the sections in accordance to the ATNTS2004 (Lourens *et al.*, 2004). All chrons from the upper half of C5Cn.1n to C5Aan have been recognised in the Aragonian type area, providing reliable constraints for the ages of the faunas of Zone Cb to Zone F (from ≈16.3Ma to 13.7Ma), their precision depending on the density of the faunal record. The Olmo Redondo-San Roque section in the western part of the type area (Daams *et al.*, 1999a), containing the lowermost part of the Aragonian and the few meters of the uppermost Ramblian, has not yet been measured paleomagnetically. This section in the lower parts of the Vargas-Valdemoros sedimentary unit represents uppermost Zone A (SR4A and SR4B), Zone B (OR1-3, SAM, SR1-3, VL2A), and Zone Ca (ART, SR3, OR4A). The numerical ages of these faunas and the zone boundaries present are based on sedimentary rates obtained in the higher, paleomagnetically measured, part of the sediments.

The beginning of the Aragonian (Zone B) is recognized by the FCO of *Democricetodon hispanicus*, which is found in locality SR1 of the Olmo Redondo-San Roque section and has an estimated age of 16.77Ma. Together with the age of SR4B (uppermost Zone A, late Ramblian), in the same section, the lower boundary of the Aragonian is constrained by the estimated ages 16.99-16.77Ma. *Democricetodon hispanicus* is present with very low numbers in SR4B and SR4A (~17.0Ma) and constitutes the oldest occurrence of the genus in Spain having an estimated age. The mentioned ages indicate that the entry and increase in numbers of the genus in the Aragonian area took place in the late Ramblian during chron C5Cr (17.235-16.721Ma, 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 common to dominant in Zone Cb. The extinction takes place between VR2A and VR2B (3m above VR2A) in the Vargas section (Fig. 3), which constrains the Early-Middle Aragonian boundary to 15.94-15.92Ma. The lowermost fauna (locality COLA) of the La Col section (not analyzed paleomagnetically, Fig. 4) contains less than 1% of *L. ellipticus*, otherwise its composition is typical of Zone Da. Therefore, COLA has been biostratigraphically interpolated between VR2A, in which 22% of the rodent teeth belong to *L. ellipticus*, and VR2B, in which the eomyid is absent. This leads to an estimated age of 15.93Ma for COLA, and the Early-Middle boundary may be constrained further to 15.935Ma. Magnetostratigraphic calibration shows the boundary to fall close to the lower boundary of chron C5Br (15.974-15.032Ma, ATNTS2004) (Daams *et al.*, 1999a).

The Middle-Late Aragonian boundary, equivalent to the Zone E-F boundary, is drawn in the magnetostratigraphically calibrated type section itself, between the localities LUM20 (13.80Ma) and LUM22 (13.76Ma) (Krijgsman *et al.*, 1996; Van Dam *et al.*, 2006). The boundary lies about 1/10 below the top of chron C5ACn (14.095-13.688Ma, 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 that of Krijgsman *et al.* (1996).

The magnetostratigraphic calibrations allow correlation of the Aragonian and its substages to the ATNTS2004. The Early Aragonian is equivalent to the latest Burdigalian. The base of the Middle Aragonian is only 30kyr younger than the base of the Langhian (15.974Ma), and its top is 100kyr younger than the base of the Serravallian (13.82Ma, Abels *et al.*, 2005). Thus, the Middle Aragonian coincides very closely with the Langhian. The base of Zone H, the lower zone of the Vallesian (Daams and Freudenthal, 1981), has been dated at 11.1Ma by Garcés *et al.* (2003) in the Nombrevilla section near Daroca. The Late Aragonian is therefore equivalent to the complete Serravallian and the earliest part of the Tortonian, which begins at 11.625Ma (Hüsing *et al.*, 2007).

## The Upper Freshwater Molasse of Switzerland

The Swiss faunas between 15.3 and 13.0Ma are well constrained by the combination of magnetostratigraphy and radiometric ages of three bentonites yielding ages of 14.20±0.08Ma, 14.91±0.09Ma, and 15.27±0.12Ma (Kälin and Kempf, 2009; and literature therein). The magnetostratigraphy of the lower part of the sequence is, however, controversial, as the sections contain large gaps caused by thick conglomerates. Below, we apply two different age models: Option A is based on Schlunegger *et al.* (1996) and Agustí *et al.* (2001); Option B is from Kälin and Kempf (2009: Fig. 8), which in its turn is based on the one of Kempf *et al.* (1997). 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 Schlunegger's *et al.* (1996) original calibration of this section, the "basal marls" containing the Eimättili fauna (Tägernaustrasse assemblage zone, MN4; after Kempf *et al.*, 1997) is correlated to chron C5Cn2.r (16.47-16.54Ma), and the locality Hasenbach 1 (Trub-Sältenbach zone, MN3b) to C5En. Kälin (1997) reports a new fauna (Trub-Sältenbach, reference locality of the zone of the same name) in between Hasenbach 1 and Eimättili. According to Schlunegger's *et al.* (1996) calibration, Trub-Sältenbach falls in the lower part of chron C5Cr, giving at an age of about 17.2Ma (Agustí *et al.*, 2001). Kempf *et al.* (1997) recalibrate the section, correlating Eimättili to C5Cr (17.2-16.7Ma) and Trub-Sältenbach to the lower part of C5Dr. However, according to Agustí *et al.* (2001), 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 zone between C5Cn.2r and C5Cr, *i.e.* between 16.5Ma and 17.2Ma, the estimated age of the youngest locality of the Trub-Sältenbach zone that 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 fauna of Glovelier (reference and only locality of the Glovelier Assemblage Zone) is the oldest Swiss fauna with *Democricetodon* and *Ligerimys florancei*, but as it comes from a karst fissure 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 17.5Ma 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 ±17.2Ma.

The original calibration of the Tägernaustrasse zone fits the geochronological data from SW Europe much better than its recalibration (Aguilar *et al.*, 2003; Larrasoaña *et al.*, 2006). The latter provide reliable magnetostratigraphic evidence to correlate Pico del Fraile 1, a "cricetid vacuum" fauna (Zone A) in the Ebro Basin (Spain) without *Democricetodon*, to chron C5Dn (17.533-17.235Ma). Aguilar *et al.* (2003) derive a similar correlation for Beaulieu (17.5Ma), a south-western French fauna representing the "cricetid vacuum".

We present in Table 1 the age estimates of the Swiss biozone boundaries that are relevant to the bioevents shared in Switzerland and Spain. The ages derived from the age model of Schlunegger *et al.* (1996) and Agustí *et al.* (2001) are given as Option A, the ones of Kälin and Kempf (2009) based on Kempf *et al.* (1997) as Option B. The upper three boundaries are the same in both models as they are considered to be reliable (see above). The estimate of the base of the Oberkulm-Sämlen (=top of Tägernaustrasse) in Option A is the midpoint (16.35Ma) between the base of the Vermes zone (16.2Ma, Kälin and Kempf, 2009) and the top of chron C5Cn.2r (16.5Ma). The base of the Tägernaustrasse zone is the midpoint (16.85Ma) between the here estimated base of the Oberkulm-Sämlen zone (16.35Ma) and that of the Trub-Sältenbach locality (17.2Ma, Agustí *et al.*, 2001). The base of Glovelier zone is estimated by the here used estimates of the Tägernaustrasse zone (17.05Ma) and the mentioned age of Trub-Sältenbach locality by Agustí *et al.* (2001).

**TABLE 1** | Age difference in the Swiss biostratigraphy; Option A according to Schlunegger et al. (1996) and Option B according to Kälin and Kempf (2009)

| Biostratigraphy | Option A | Option B |
|---|---|---|
| base Oeschgraben | 14.20 | 14.20 |
| base Uzwil-Nutzenbuech | 14.80 | 14.80 |
| base Aspitobel 520 | 15.00 | 15.00 |
| base Oberkulm-Sämlen | 16.35 | 16.70 |
| base Tägernaustrasse | 16.85 | 17.20 |
| base Glovelier | 17.05 | 17.60 |
| Age Loc Trub-Sältenbach | 17.20 | 18.00 |

## SHARED BIOEVENTS IN SPAIN AND SWITZERLAND DURING THE EARLY TO MIDDLE MIOCENE

Kälin and Kempf (2009: Fig. 9) compare the Swiss and the Spanish biozonation of Daams *et al.* (1999b) through their correlations to the mammal Neogene-system. They note that the numerical ages yielded for the MN4 to MN6 units in Spain are ca. 0.5-1.0Myr younger than those based on their calibrations. This mismatch is attributed to diachrony caused by the westward migration of the modern cricetids *Democricetodon* and *Cricetodon*, and the diachronous extinction of *Ligerimys*. Moreover, they correctly point to the lack of mammal Neogene-relevant markers in Spain and, as they convincingly evidence, to the asymmetric position of mammal Neogene reference localities within the units they characterize hampering the mammal Neogene assignments of local successions. Kälin and Kempf (2009) restricted their comparison with Spain to the few diachronies mentioned above, because of the few taxa that the two basins have in common. There are, however, more relevant shared events, thirteen of which we have selected (Table 2): the "cricetid vacuum", eight FO and LO of cricetids immigrating into Europe after the "cricetid vacuum", and four of the eomyids *Ligerimys* and *Keramidomys* (Fig. 7). The FO *Democricetodon* and LO *Ligerimys* have been included in the list as these generic events are widely used as markers of the beginning and the end of MN4, respectively, in spite of the fact that they concern different species (see below).

## ORDER OF EVENTS

Table 2 shows some remarkable discrepancies between the two sequences: for example, *Megacricetodon minor*

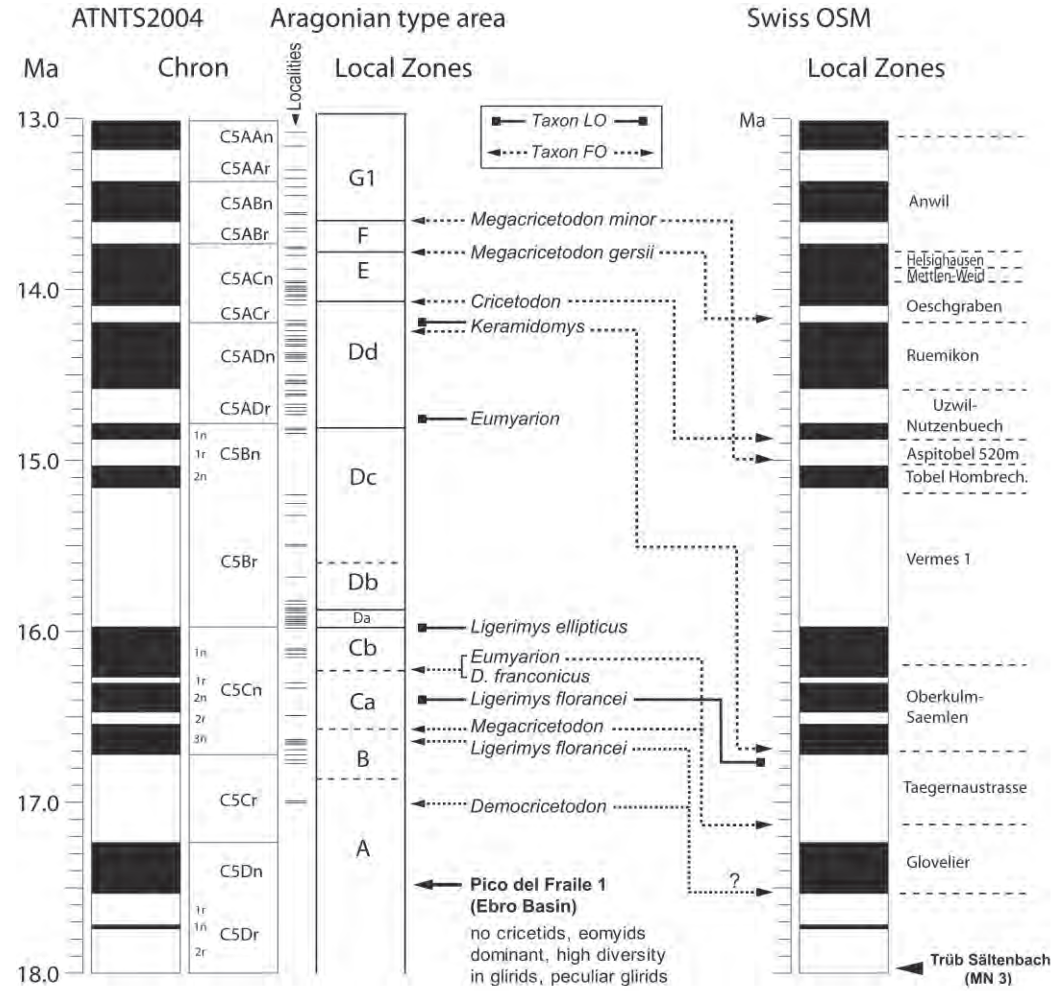

**FIGURE 7** | Comparison between Spanish and Swiss (Kälin and Kempf, 2009) local biostratigraphies indicating several biotic events discussed in the main text.

arrives before *Cricetodon* and *M. gersii* in Switzerland and after the latter two in Spain. We have ranked the events in the two countries according to their local biostratigraphies in the two columns at the right in Table 2. If events occur in the same locality (Spain) or biozone (Switzerland), 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 7 and 8 within the local Aragonian biostratigraphy and since both occur for the first time in the same locality (Vargas 4A, 16.15Ma) we assign both to rank number 7.5. In order to compare both sequences we have performed non parametric correlations using SPSS 17.0 software (SPSS, 2008). The results reveal a highly significant correlation between the Swiss and Spanish bioevent sequences (Spearman's rho = 0.826, $p<0.001$; Kendall tau = 0.703, $p<0.001$) indicating the high similarity between them.

The starting point of the comparison is the "cricetid vacuum" that has been recognized as a West and Central European interval devoid of cricetids except for *Melissiodon* (Daams and Freudenthal, 1988). It postdates the levels with *Eucricetodon* and precedes the immigration of the "modern" cricetids *Democricetodon, Megacricetodon* and

**TABLE 2** | Ranking of the faunal events shared between Switzerland and Spain. SW: Switzerland, SP: Spain

| Label | Bioevent | Ranking | |
|---|---|---|---|
| | | SW | SP |
| 13 | FO *Megacricetodon gersii* | 13 | 12 |
| 12 | FO *Cricetodon* | 12 | 11 |
| 11 | FO *Megacricetodon minor* | 11 | 13 |
| 10 | FO *Keramidomys* | 10 | 10 |
| 9 | LO *Ligerimys* | 8.5 | 9 |
| 8 | LO *Ligerimys florancei* | 8.5 | 6 |
| 7 | LO *Melissiodon* | 7 | 3 |
| 6 | FO *Megacricetodon* | 6 | 5 |
| 5 | FO *Eumyarion* | 5 | 7.5 |
| 4 | FO *Ligerimys florancei* | 3 | 4 |
| 3 | FO *D. franconicus* | 3 | 7.5 |
| 2 | FO *Democricetodon* | 3 | 2 |
| 1 | <Cricetid vacuum> | 1 | 1 |

*Eumyarion*. In the two discussed areas, *Democricetodon* is the first to appear: in Switzerland with *D. franconicus* and in Spain with *D. hispanicus*. These species closely resemble each other (Fahlbusch, 1966; Freudenthal, 1967; Van der Meulen *et al.*, 2003), and may represent local variants of the same species. The latter authors report the appearance of *D. franconicus*, morphologically indistinguishable of the Central European representatives, in Zone Cb, in which it co-occurs with *D. moralesi*, a Spanish descendant of *D. hispanicus*. Thus, in Spain *D. franconicus* appears to have immigrated twice: the first time in Zone A as the locally adapted variant *D. hispanicus*, and the second time in Cb as a "true" *D. franconicus*.

The FO of *Ligerimys florancei* coincides with that of *D. franconicus* in Glovelier in Switzerland, but its arrival is delayed in Aragón, where its first occurrence is during Zone B. Nevertheless, in both countries the arrivals of *Megacricetodon* and *Eumyarion* postdate those of *Democricetodon* and *L. florancei.* In the Swiss record, the former appear in the Tägernaustrasse zone, while in Calatayud-Montalbán Basin they enter successively: *Megacricetodon* in Zone Ca and *Eumyarion* in Cb. The latter's late entry is probably partly due to the local conditions of the Aragonian type area, which were unfavourable to *Eumyarion* during Zone Ca. In other Spanish basins the entry of *Eumyarion* is probably older since it is present in Buñol (Levante basin; Daams, 1976; Adrover *et al.*, 1987; Robles *et al.*, 1991; Ruiz-Sánchez *et al.*, 2003) and Can Martí Vell (Vallès-Penedès basin; Agustí, 1983) correlated to Zone Ca, based on the eomyids and the evolutionary stage of *Democricetodon.*

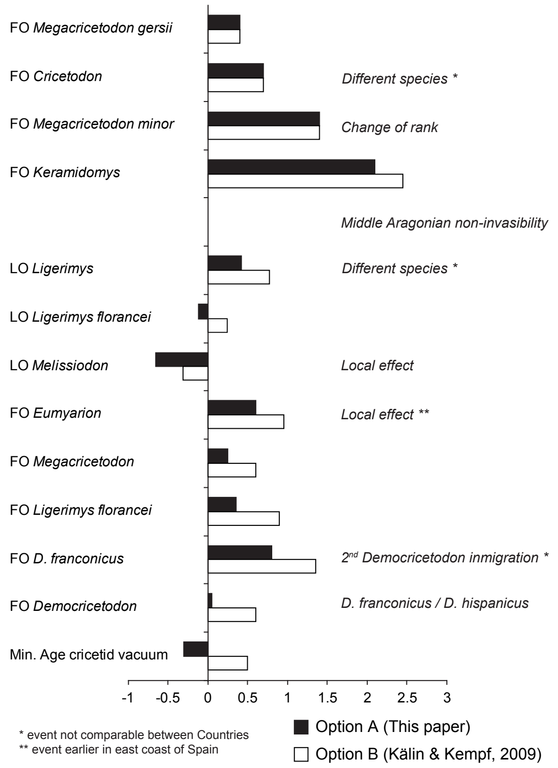

**FIGURE 8** | Bar chart showing the asynchronies of the 13 biotic events recognised in the Aragonian type area and the Upper Freshwater Molasse of Switzerland. The order of events follows the Swiss ranking.

The early LO of *Melissiodon* in upper Zone A in the Aragonian type area (before the FO's of *Ligerimys florancei* and *Megacricetodon*) seems also to be a local phenomenon, because even in the nearby Teruel Basin and in the Valencia Basin *Melissiodon* is known from Zone Ca. In the Swiss record, *Ligerimys florancei* is the last representative of the genus, and so the two events (LO of the genus and species) have the same rank. On the other

**TABLE 3** | Age estimation of different faunal events according to Option A and B in Switzerland and Spain, and the calculated asynchrony between both areas according to each chronological option. A positive/negative asynchrony means that the event occurred later/earlier in Spain than in Switzerland

| | | Age estimates in Ma | | | Asynchrony in Myr | |
|---|---|---|---|---|---|---|
| Label | Bioevents | Swiss (A) | Swiss (B) | Spain | option A | Option B |
| 13 | FO *Megacricetodon gersii* | 14.2 | 14.2 | 13.8 | 0.4 | 0.4 |
| 12 | FO *Cricetodon* | 14.8 | 14.8 | 14.1 | 0.7 | 0.7 |
| 11 | FO *Megacricetodon minor* | 15 | 15 | 13.6 | 1.4 | 1.4 |
| 10 | FO *Keramidomys* | 16.35 | 16.7 | 14.25 | 2.1 | 2.45 |
| 9 | LO *Ligerimys* | 16.35 | 16.7 | 15.93 | 0.42 | 0.77 |
| 8 | LO *Ligerimys florancei* | 16.35 | 16.7 | 16.4 | -0.05 | 0.3 |
| 7 | LO *Melissiodon* | 16.35 | 16.7 | 17.01 | -0.66 | -0.31 |
| 6 | FO *Eumyarion* | 16.85 | 17.2 | 16.25 | 0.6 | 0.95 |
| 5 | FO *Megacricetodon* | 16.85 | 17.2 | 16.6 | 0.25 | 0.6 |
| 4 | FO *Ligerimys florancei* | 17.05 | 17.6 | 16.7 | 0.35 | 0.9 |
| 3 | FO *D. franconicus* | 17.05 | 17.6 | 16.25 | 0.8 | 1.35 |
| 2 | FO *Democricetodon* | 17.05 | 17.6 | 17 | 0.05 | 0.6 |
| 1 | Min. Age 'cricetid vacuum' | 17.2 | 18 | 17.5 | -0.3 | 0.5 |

hand, in the Aragonian record *L. florancei* is replaced by the endemic *L. ellipticus* between the localities Artesilla and San Roque 3 of Zone Ca. In other Spanish basins the latter species can be coeval, as is the case of the localities Can Martí Vell 1 and 2 (Vallès-Penedès basin; Agustí, 1983). *Ligerimys ellipticus* continues, as a frequent taxon, to the end of Zone Cb and disappears at the beginning of Zone Da. This shows that the extinction of a genus may fail to function as a correlational tool for taxonomical reasons.

*Keramidomys* is a resident species in Switzerland from the Oberkulm-Sämlen to Uzwil-Nutzenbuech zones, while it is a rare, transient species in Spain, where it entered in late Zone Dd after a dry period with a high degree of disturbances during the Middle Aragonian (Van der Meulen *et al.*, 2005).

The FO of *Megacricetodon minor* forms the only one major discrepancy between the two sequences of first entries. In Spain, as opposed to Switzerland, the FO of *M. minor* occurs after the FO's of *Cricetodon* and *M. gersii*. *Megacricetodon minor* apparently disperses less easily than the others, assumedly because of it being a less opportunistic species. This is also illustrated by the fact that *M. minor* never reached the Madrid Basin in the centre of the Iberian Peninsula (Peláez-Campomanes *et al.*, 2003).

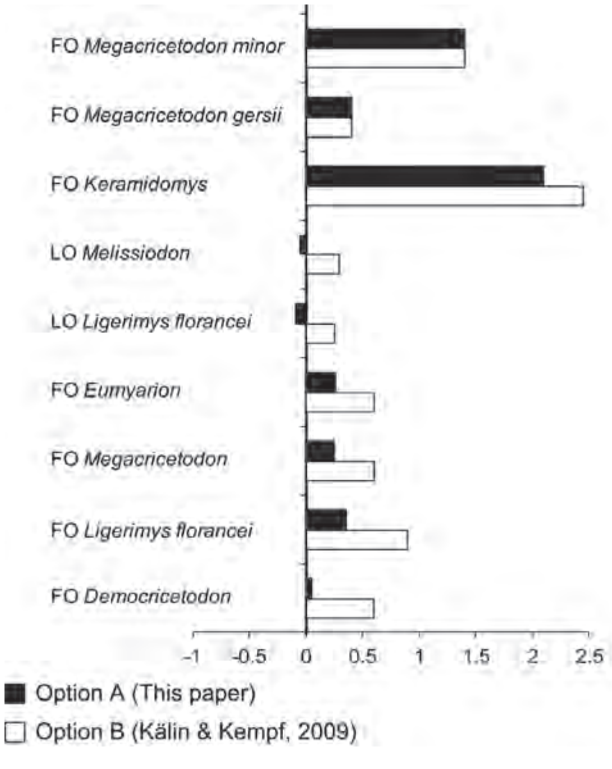

**FIGURE 9** | Bar chart showing the asynchronies of the biotic events comparable in Spain and the Upper Freshwater Molasse of Switzerland. The order of events follows the Spanish ranking.

The FO of *Cricetodon* (*C.* aff. *aureus*) in Switzerland is in Uzwil-Nutzenbuech, which is correlated to chron C5ADr giving it an estimated age of 14.8Ma, and in Spain in LUM11 (chron C5ACn, 14.06Ma). De Bruijn *et al.* (1993) note that the latter, referred to as *Cricetodon* n. sp. 3 from 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 us to understand the evolution and dispersal of this interesting tribe.

## SYNCHRONY AND ASYNCHRONY

Lindsay (2001) defines asynchrony as the interval of time between diachronous events. Figure 8 shows the asynchronies of the first and last occurrences in Switzerland and Calatayud-Montalbán Basin according to the two age models A and B (Table 1). Their order is the same as that in Table 3. The few negative asynchrony values represent the events that occur earlier in Spain than in Switzerland. The great majority of the events in Switzerland predate their occurrences in Spain. In both Swiss age models the FO's of *M. gersii, Cricetodon* and *M. minor* have the same values since they are based on well constrained ages in both areas. In the other cases Option A shows the lower asynchronies. We consider an event synchronous if clear diachrony cannot be shown given the available time resolution.

It is allowed to speak of the FO of *Democricetodon* as an event, only if one follows our opinion that *D. hispanicus* is a "subspecies" of *D. franconicus* (see above). In that case, the FO of *Democricetodon* is synchronous according to age model A. The asynchrony of *D. franconicus* is not real, as it concerns a second immigration in Spain, which does not occur in Switzerland. The asynchronies of the FO of *Eumyarion* and LO of *Melissiodon* only apply to Calatayud-Montalbán Basin, as is argued above. The first may have arrived 0.2-0.3Myr earlier in eastern basins of coastal Spain, and *Melissiodon* got extinct about 0.3-0.4Myr later in the Teruel Basin. The LO of *Ligerimys florancei* represents the second synchronous event according to age model A. The diachronous LO of *Ligerimys* and the FO of *Cricetodon* are not real as they refer to different species (see above). The peaks of asynchrony of *Keramidomys* and *Megacricetodon minor* are realistic, but we note that the latter is partly due to its late arrival following that of *M. gersii* in Spain.

Taking the above remarks into account, Figure 9 presents in our opinion the best estimates of the asynchronies between Switzerland and Spain, based on age model A. The events have been put in the order of those in Spain, and the non-comparable ones are left out. Furthermore, the events labelled as local in Figure 8 (the FO of *Eumyarion* and the LO of *Melissiodon*) have been given estimated asynchronies based on their occurrence some 100km outside the Aragonian type area in the locality of Montalvos in the Teruel Basin. This preliminarily studied fauna is biostratigraphically interpolated between Artesilla (16.49Ma) and San Roque 3 (16.33Ma) in the Aragonian type area, and is given the estimated age of ≈16.4Ma.

Admittedly, the time differences between the early Aragonian events in Switzerland and Spain are quite rough estimations. However, it is fair to say that the low asynchronies found for the FO of *Democricetodon* and the LO of *L. florancei* and *Melissiodon* do not exclude the possibility of synchrony. The asynchrony of *L. florancei*, an estimated 0.35Myr, is comparable to the one of *Megacricetodon gersii* (0.4Myr), which is considered realistic because of the well-constrained ages in the two countries. There is no independent confirmation of the low asynchronies (0.25Myr) of the FO of *Megacricetodon* and *Eumyarion*. The high asynchronies (2.1 and 1.4Myr, respectively) of the FO of *Keramidomys* in Zone Dd and of *Megacricetodon minor* in Zone F are attributed to the non-invasibility of the Calatayud-Montalbán Basin during a large part of the Middle Aragonian due to the special environmental conditions with a dry and highly disturbed environment (Van der Meulen *et al.*, 2005). The high asynchrony of *M. minor* is, at least partly, due to its slower dispersal capacity than *M. gersii*, which arrived before the former in Switzerland but after it in Spain.

## COMPARISON OF THE SPANISH AND SWISS BIOZONES

Figure 10 shows the correlations of the Spanish and Swiss biozones according to age model A and including data from the Teruel and eastern coastal basins of Spain (Fig. 9). Faunal resemblances are poor due to the comparison of two different bioprovinces. The greatest similarity is found between the intervals of upper Zone A–lower part Zone Ca with Glovelier–Tägernaustrasse. This is the interval between the entry of *Democricetodon* and the extinction of *Melissiodon*. The first event is calibrated above to chron C5Cr, the second to the lower to middle part of C5Cn. The interval is characterised by several, partly temporary, immigrations of northern taxa into the Iberian Peninsula increasing the faunal similarity with Central Europe. During the earlier part (uppermost Zone A and Glovelier) the two areas share the first *Democricetodon franconicus/hispanicus* and the last *Ligerimys antiquus* co-occurring with *Melissiodon*, as well as the biostratigraphically less important presences of *Peridyromys, Microdyromys legidensis-koenigswaldi* and possibly *Simplomys simplicidens*. Zones B-Ca and Tägernaustrasse have the first *Megacricetodon* and *Eumyarion*, the last *Melissiodon* and the presence of *Ligerimys* (cf.) *florancei* in common. The presence of *Democricetodon franconicus* in Zone Cb in the Calatayud-Montalbán Basin after the extinction of *Melissiodon* is a peculiar and so far unexplained phenomenon.

The faunal resemblances during Zones Da-Dc and Vermes 1 to Aspitobel 520m are extremely poor. The important change that takes place around the boundary between Aspitobel 520m and Uzwil-Nutzenbuech approximately coincides with the evolutionary step of *Democricetodon franconicus* to *D. koenigswaldi* and the extinction of *Eumyarion* around Dc-Dd in the Calatayud-Montalbán Basin, if we take the ages of the two boundaries into account, 14.9 and 14.81Ma, respectively. Faunal resemblances start to moderately increase from the later part of Zone Dd onward. Most of the species appearing in Spain that potentially have correlational value (*Keramidomys, Megacricetodon gersii* and *M. minor*) are diachronous in comparison with Switzerland (see above).

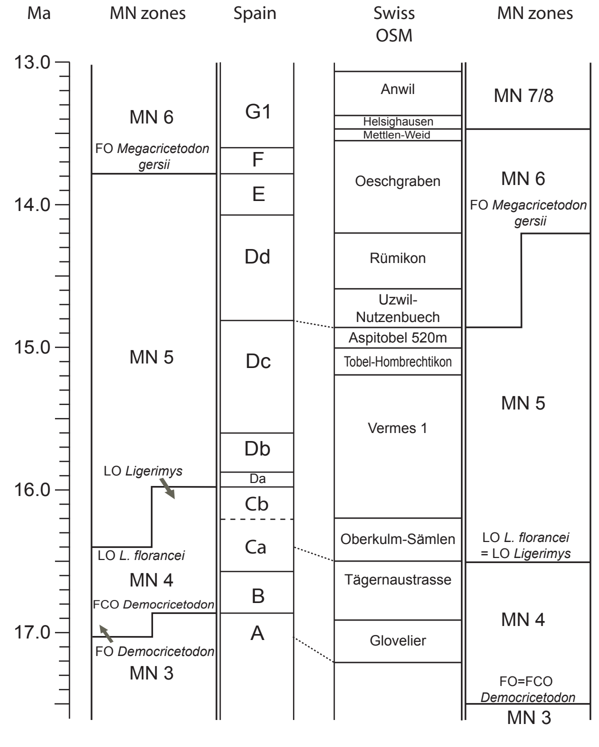

**FIGURE 10** | Comparisons between Spanish and Swiss local biostratiraphies. For the correlations to mammal Neogene units, several possibilities are included, depending on the used criteria. Dashed lines indicate possible correlations.

## IMPLICATIONS FOR EUROPEAN MAMMAL CHRONOLOGY

European mammal faunas are customarily grouped and ordered by assigning them to the Mammal Neogene biochronologic system (Mein, 1975a, b; Fejfar, 1989; Fahlbusch, 1991; De Bruijn *et al.*, 1992). It consists of 17 numbered units, each of which is characterised by a reference locality representing the stage-of-evolution of the unit. In addition, a mammal Neogene unit is recognised by one or a combination of three criteria: a) presence of short-lived species, often stages of anagenetic lineages; b) the temporally short co-occurrences of two or more genera; c) first appearances of genera (Mein, 1999, 2000). In practice, also extinction events are being used. A local fauna is placed in the mammal Neogene unit according to the reference locality with which it shows the highest similarity. This procedure suffers from the usual problems of biostratigraphical correlations due to variable spatial distributions of taxa, differences in migration rates, and local evolutionary trends, even if one restricts the comparisons to Western Europe. These inherent uncertainties of correlations are realised, but many specialists take them for granted, as the system seems to work well enough to be used for general studies at a sub-continental scale. Although not recommended by De Bruijn *et al.* (1992), mammal Neogene boundaries have been dated by extrapolating local-fauna ages in different areas to ages and durations of the units for European use (*e.g.*, Agustí *et al.*, 2001). We show below that this approach is unwarranted and we treat the mammal Neogene system as a time-ordered sequence of reference localities allowing rough long-distance correlations (*e.g.*, De Bruijn *et al.*, 1992). The assignments of the Spanish and Swiss biozones to the MN3-MN6 are shown in Figure 10, which we will now discuss.

### MN3

The reference locality Wintershof-West contains *Ligerimys antiquus, Eucricetodon* and *Melissiodon* (De Bruijn *et al.*, 1992), but faunas of the “cricetid vacuum”, containing only the latter genus, are included in MN3 as well. Zone A (Upper Ramblian) is characterized by *L. antiquus*, the last *Eucricetodon,* presence of *Melissiodon* and of the first rare *Democricetodon* in the upper part. In spite of the latter, Zone A has been correlated to the MN3 on the basis of the general faunal composition (Daams *et al.*, 1999a). *Democricetodon* is common in Zone B, the lowermost zone of the Aragonian, which is customarily placed in MN4. Kälin and Kempf (2009) place Glovelier in MN4 (see below).

### MN4

The faunal composition of the reference locality La Romieu is badly in need of revision, as it is unknown in the rest of Europe. In particular, the occurrence of four species of *Democricetodon* and two of *Megacricetodon* together with *Ligerimys antiquus* and *L. florancei* is peculiar, and may indicate faunal mixing and/or errors in species identification. Consequently all faunas from upper Zone A to Ca are correlatable to La Romieu. Kälin and Kempf (2009) assign the faunas of the Glovelier and Tägernaustrasse zones to MN4. Glovelier is the oldest Swiss fauna with the FO of *Democricetodon* co-occurring with *Ligerimys antiquus* and *L. florancei* and is included in MN4 (Kälin, 1997; Kälin and Kempf, 2009). Thus, different criteria are used to correlate to MN4: the first common occurrence of *Democricetodon* in Spain, and the first occurrence of *Democricetodon* in Switzerland (see Fig. 10). Since MN4 faunas contain the last *Ligerimys* species (*e.g.*, Mein, 2000), Zone Cb faunas (all with *L. ellipticus*) have been assigned to MN4 as well (Daams *et al.*, 1999a; and literature therein). Kälin and Kempf (2009) use the last occurrence of *L. florancei*, the extinction of which we assume on the basis of age model A to be isochronous with that in Spain and predates the extinction of *L. ellipticus* (see Fig. 10). Thus, the Spanish faunas of upper Zone Ca to Cb may be placed in MN4, while the approximately coeval Swiss faunas of Overkulm-Sämlen and lower Vermes 1 may be placed in MN5, applying the same, commonly used, criterion, *i.e.* the extinction of the genus *Ligerimys*, which appears to be diachronous.

### MN5

Pontlevoy-Thenay, the MN5 reference locality, contains the cricetids *Cricetodon aureus, Megacricetodon collongensis,* and *M. lappi*. The latter is a characteristically large *Megacricetodon*, also present in Central Europe, but never found in Spain. *Cricetodon aureus* is the first *Cricetodon* in Western Europe; however, as noted above, the first *Cricetodon* in Zone E in Spain belongs to a different lineage (De Bruijn *et al.*, 1993). In spite of that, Zone E faunas have always been assigned to MN5 based on the presence of the genus. Superzone D faunas (from the LO of *Ligerimys* to the FO of *Cricetodon*) have long been placed in MN4b, which was later accepted to be equivalent to MN5 (see extensive discussion in Daams *et al.*, 1999a, b).

The Oberkulm-Sämlen zone is characterized by the absence of *Ligerimys* and the entry of *Keramidomys*, the typical eomyid of MN5 faunas in Central Europe. It is very rare in Spain, where it is present in Zone Dd (see above). The Aspitobel 520m Zone is defined by the short range of *Megacricetodon lappi,* reliably estimated from approximately 15.0 to 14.9Ma (Kälin and Kempf, 2009). This places Pontlevoy-Thenay near the transition of Zones Dc to Dd, confirming their MN5 assignment.

## MN6

Daams *et al.* (1999b) correlate Sansan, the reference locality of MN6 to Las Planas 5B (Zone G1) as the faunas have *Megacricetodon gersii* and *M. minor* in common. They propose the estimate of ±13.6Ma for the age of Sansan, because Las Planas 5B is calibrated to chron C5ABn (Krijgsman *et al.*, 1994). As we have shown above, *M. minor* arrived in Spain after *M. gersii* in Zone F, while the FO of the latter precedes that of *M. gersii* in Switzerland. It can, therefore, not be ruled out that the co-occurrence of the two species in Sansan (southern France) predates that in Spain. Kälin and Kempf (2009) correlate Sansan to the Swiss locality Niderwis (Oeschgraben Zone), which corresponds to approximately 14.1Ma. It seems to us, that their estimate is more reliable than both the one of Sen (1997) and of Daams *et al.* (1999b). Consequently, the reference locality of MN6 corresponds to the late Middle Aragonian rather than to the Late Aragonian.

Zone F is the lowermost zone of the Upper Aragonian, and assigned to MN6 on the basis of the presence of two different species of *Megacricetodon*, *M. gersii* and *M. rafaeli* (Daams and Freudenthal, 1988). In Switzerland, Zone Uzwil-Nutzenbuech is considered the oldest zone assigned to MN6. This assignment is based on indirect arguments because of the scarceness of biostratigraphically useful micromammal taxa in Sansan (Kälin and Kempf, 2009). They accepted Neudorf (=Devínská Nová Ves, Slowak Republic) as the oldest locality of MN6 (after Mein, 1989: Table 1), which is correlatable to the Uzwil-Nutzenbuech Zone. Another option would be to take the FO of *Megacricetodon gersii* in Switzerland for recognising MN6 (Fig. 10).

## DISCUSSION

Kälin and Kempf (2009) compare the mammal Neogene units as they recognise them in the Swiss mammal succession with those recognised in Spain by Daams *et al.* (1999a). They note the numerical ages given to mammal Neogene boundaries in Spain are 0.5-1.0Myr younger than in Switzerland. The MN4 unit for instance, which in both countries is recognised in accordance with the generally accepted interval between the FO *Democricetodon* and the LO of *Ligerimys*, begins in Spain at about the same time it ends in Switzerland. The time difference between the two events in both areas is some 0.8Myr. They relate the extinction of *Ligerimys* to an environmental change towards more arid conditions that may have been caused by "a climatic change that appeared later in Spain than in Switzerland" (Kälin and Kempf, 2009). The entry of *L. florancei* in Spain is estimated to fall in the same chron, C5Cn.3n, *i.e.* coeval with its extinction in Switzerland. The entry of *D. franconicus* in Spain is some 0.4-0.5Myr after its extinction in Switzerland. Their interpretation suggests that the range expansions of the shared MN4 markers moved more or less in concert over the western part of Europe as if they followed a climatic envelope. Our preferred age model (Option A) results in a more individualistic response to climate change, which we consider more realistic (Davis *et al.*, 1998). We have argued that the immigration of *Democricetodon* may be isochronous within the time resolution, while the extinction of *Ligerimys* is diachronous, but the overlap of MN4 faunas is substantially larger than suggested by the Swiss authors. The asynchronies found for *Keramidomys* and *Megacricetodon minor* are considerably larger than the Late Ramblian to Early Aragonian ones. This can be explained by unsuitable environmental conditions of the Middle Aragonian (Zone Dc in particular) prevalent in Spain, which ended with the succession of immigrations starting during Zone Dd (Van der Meulen *et al.*, 2005).

## CONCLUDING REMARKS

This study of the dispersals of several Early and Middle Miocene rodent species on the basis of the magnetostratigraphy of the Early and Middle Aragonian and of age model A for Switzerland has shown considerable variation of the asynchrony of the events. It confirms what has already been suspected for a long time; that the fossil history of terrestrial Europe is biogeographically and ecologically too complex to presume isochrony of any bioevent. In Tables 8-12 from De Bruijn *et al.* (1992), for instance, stratigraphical taxon ranges for Central Europe and SW Europe are given separately to demonstrate the commonness of diachrony. The tables adequately illustrate their opinion that no boundaries should be defined, let alone dated. On the contrary, Agustí *et al.* (2001) propose to redefine the mammal Neogene units of Western Europe by choosing immigration events to mark the beginning of each of the units. The ages of the immigration are taken from paleomagnetically calibrated sections in Spain or Switzerland, and assigned as the age of the mammal Neogene boundary. We disagree with this approach, which, implicitly or explicitly, assumes isochrony of the immigrations over the whole subcontinental area. Instead, calibrated first occurrences in different areas should be compared and used to prove isochrony or diachrony of the events.

In our opinion, a formal European biozonation is impossible, since it is realised that 1) most species and many genera of rodents yielding the most detailed zonations have very limited geographical ranges leading to several local anagenetic lineages; and 2) first and last taxon occurrences (FO's and LO's) are diachronical (*e.g.*, Daams and Freudenthal, 1981; De Bruijn *et al.*, 1992). Therefore, the mammal Neogene system based on a sequence of time-ordered reference localities (*e.g.*, De Bruijn *et al.*, 1992) is preferred to the one of Agustí *et al.* (2001), which is based on selected bioevents "developed in widespread geographic areas". We fully agree with the "dual system" proposed by Van Dam (2003), following the suggestions of De Bruijn (2001), to use the low-resolution mammal Neogene system on a continental scale, and local/regional biostratigraphies side by side. The former allows rough 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. Diachronous migrations, provinciality and endemism, are considered handicaps for "establishing a reliable system of European mammal-based chronology" (Van Dam, 2003), but they are the very stuff of the dynamic mammal history paleobiologists wish to reconstruct.

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# Electronic appendix Rebuttal of Freudenthal's (2006) sequence of the Aragonian faunas

Freudenthal (2006) postulates that the faunal sequence proposed by Daams et al. (1999b) is incorrect and he rearranges the order of the localities according to their position relative to calcareous marker beds. Our Table A1 partly reproduces Table 2 of Freudenthal (2006), in which his resulting sequence is given. The marker-bed sequence and codes are after Freudenthal (2006): The calcareous Las Umbrías unit, which overlies the Valdemoros-Vargas unit, is indicated by "U", the marker beds in the Valdemoros-Vargas unit are numbered from older to younger (1-11), and the preceding "N" and "S" indicate their position North and South of the valley of Rambla de Vargas. We omitted the localities situated outside the type area (Córcoles, Buñol, Moratilla 2 and 3, Muela Alta, Casetón 1A and 2B), as being not relevant to the present discussion. Finally, we added our and Daams and Freudenthal (1988) zone assignments. Comparing our faunal sequence (see the numerical ages in Table A1) with the one of Freudenthal (2006) reveals that the two are completely incompatible. The first one is based on observed superposition in different sections that have been correlated lithostratigraphically (where possible), biostratigraphically, and magnetostratigraphically (Figs. 2-5). On the other hand, the one of Freudenthal starts from an, in our opinion, erroneous tectonical argument, and is based on lateral correlations of marker beds without regard of the faunal contents of the grouped faunas, a procedure we deem doubtful.

The starting point of Freudenthal's "re-evaluation" of the Aragonian zonation is the relative stratigraphical position of only two localities: Valdemoros 1A (VA1A) and Valdemoros 3B (VA3B). In his opinion, contrary to ours, the former is the older and the latter is the younger locality. Freudenthal (2006) justifies his opinion on the basis of tectonics: "The locality Valdemoros 1A is situated in the Valdemoros-Vargas sedimentary unit, which is strongly affected by a tectonic phase. Valdemoros 3B, on the other hand lies at the base of the subhorizontal Umbrías unit that was deposited after the end of that tectonic phase. VA1A is clearly older than VA3B". However, this tectonical argument is obviously untenable. The geological map clearly shows that the Las Umbrías unit is affected by folding both in the type section and in the Vargas section (Supplementary material, Figs. A1 and A2). The fact that locally no such folding is seen near VA3B, in contrast to VA1A, is due to its further distance from the southern basin margin. Therefore, the section of Freudenthal (2006; Fig. 2) gives an unrealistic blending of the different situations in the two separate valleys. Additionally, other faunas very near the base of the Las Umbrías Formation belong to Zone Dd (for instance, Vargas 11, Las Umbrías 1, 2, 3 and Valdemoros 6B, 7C, and 7D). In our opinion, the Valdemoros 3 section contains a hiatus between Valdemoros 3D (Zone Dc) and the overlying Valdemoros 3E (Zone Dd), which is situated very near the very base of the Las Umbrías unit. We conclude that the section is not representative of the study area and not suitable to postulate the tectonic phase of Freudenthal (2006).

Freudenthal (2006) does not provide lithological features of the marker beds, which allow him to follow them unambiguously in the field. We maintain that it is impossible to follow these beds throughout the area from the West, where the oldest localities are present, to the East where the type section is located. The lower lithological (Valdemoros-Vargas) unit shows clear lateral facies changes parallel to the NW-SE running edge of the basin. Furthermore, the thickness of the unit in the type section is some 100meters less than in the more western Vargas section (Daams *et al.*, 1999a). The overlying Las Umbrías unit is present in the whole area and shows that the underlying mammal-bearing part of Valdemoros-Vargas unit measures some hundred meters in the Vargas and only thirty meters in the type section. In the Vargas section 14 superposed faunas have been collected, representing Zones Cb, Da, Db, Dc and Dd. In the Valdemoros section there are 10 localities, all representing Zone Dd. Valdemoros 8A cannot be correlated lithologically to the section, in spite of its proximity. Its geological context is not understood and is oversimplified on the geological map of Daams *et al.* (1999a).

Artesilla has been placed between marker beds N1 and N2 (Table A1). However, the sandy sediments, which contain the large as well as the small mammals, are not in normal continuation with the surrounding sediment of the Valdemoros-Vargas unit. According to Azanza *et al.* (1993) the peculiar situation resembles that of a fissure filling. Therefore, Van der Meulen and Daams (1992) used a biostratigraphical correlation to fit the locality in

**TABLE I** | Comparison between the sequences of localities proposed by Freudenthal (2006) and the one used in this paper, which is indicated by the numerical ages, to show their incompatibility. Note, for instance the positions of VA8A and VA8C, two localities without *Ligerimys***,** amid Zone C localities with *Ligerimys* according to Daams and Freudenthal (1988**)**

| Numerical age | Locality | Biozone (This paper) | Marker bed (Freudenthal, 2006) | Biozone (Daams and Freudenthal, 1988) |
|---|---|---|---|---|
| 14.32 | LUM4 | Dd | U | |
| 14.33 | VA7D | Dd | U | |
| 14.37 | LUM3 | Dd | U | |
| 14.39 | VR11 | Dd | U | |
| 14.41 | LUM2 | Dd | N11-U | |
| 14.43 | LUM1 | Dd | N11-U | |
| 15.51 | VL4A | Dc | N11-U | D2 |
| 14.52 | VA3F | Dd | S11-U | |
| 14.55 | VA3E | Dd | S11-U | D3 |
| 14.83 | VA3D | Dc | S11-U | D2 |
| 14.85 | VA3B | Dc | S10-11 | D2 |
| 14.4 | VA6B | Dd | S10-11 | |
| 14.56 | VA6A | Dd | S10-11 | |
| 14.73 | VR8C | Dd | N9-10 | |
| 14.75 | VR8B | Dd | N9-10 | |
| 15.20 | VA11 | Dc | S8-9 | |
| 14.82 | VR7 | Dd | N8-9 | |
| 15.35 | VA9 | Dc | S8-9 | |
| 15.25 | VR6 | Dc | N7-8 | |
| 15.32 | VR5 | Dc | N7-8 | |
| 14.58 | VA7C | Dd | S7-8 | |
| 15.85 | FTE4 | Db | N7-8 | |
| 14.62 | VA7B | Dd | S6-7 | |
| 15.92 | FTE3 | Da | N6-7 | |
| 15.93 | FTE2 | Da | N6-7 | |
| 15.95 | OR9 | Da | N6-7 | D1 |
| 15.96 | VR2B | Da | N6-7 | |
| 14.64 | VA1A | Dd | S5-6 | D1 |
| 14.65 | VA7A | Dd | S5-6 | |
| 14.69 | VA8B | Dd | S5-6 | |
| 15.87 | COL-D | Db | S5-6 | |
| 15.89 | COL-C | Da | S5-6 | |
| 15.91 | COL-B | Da | S5-6 | |
| 15.97 | COL-A | Da | S5-6 | |
| 15.98 | VR2A | Cb | N5-6 | |
| 15.99 | OR8 | Cb | N5-6 | C |
| 16.13 | VR3 | Cb | N5-6 | |
| 16.00 | FTE1 | Cb | N5-6 | |
| 16.14 | VR1A | Cb | N5-6 | C |
| 16.16 | VR4B | Cb | N5-6 | |
| 15.70 | VA8A | Db | S4-5 | |
| 14.71 | VA8C | Dd | S4-5 | |
| 16.02 | OR5 | Cb | N4-5 | C |
| 16.18 | VR4A | Cb | N4-5 | |
| 16.35 | SR3 | Ca | N3-4 | |
| 16.32 | OR4A | Ca | N3-4 | |
| 16.64 | VL2A | B | N2-3 | B |
| 16.65 | OR3 | B | N2 | B |
| 16.66 | SR5 | B | N2 | |
| 16.67 | SR2 | B | N2 | B |
| 16.7 | SAM | B | N2 | |
| 16.51 | ART1 | Ca | N1-2 | |
| 16.73 | OR2 | B | N1 | B |
| 16.76 | OR1 | B | N1 | B |
| 16.78 | SR1 | B | N1 | B |
| 17.01 | SR4A | A | N1 | |

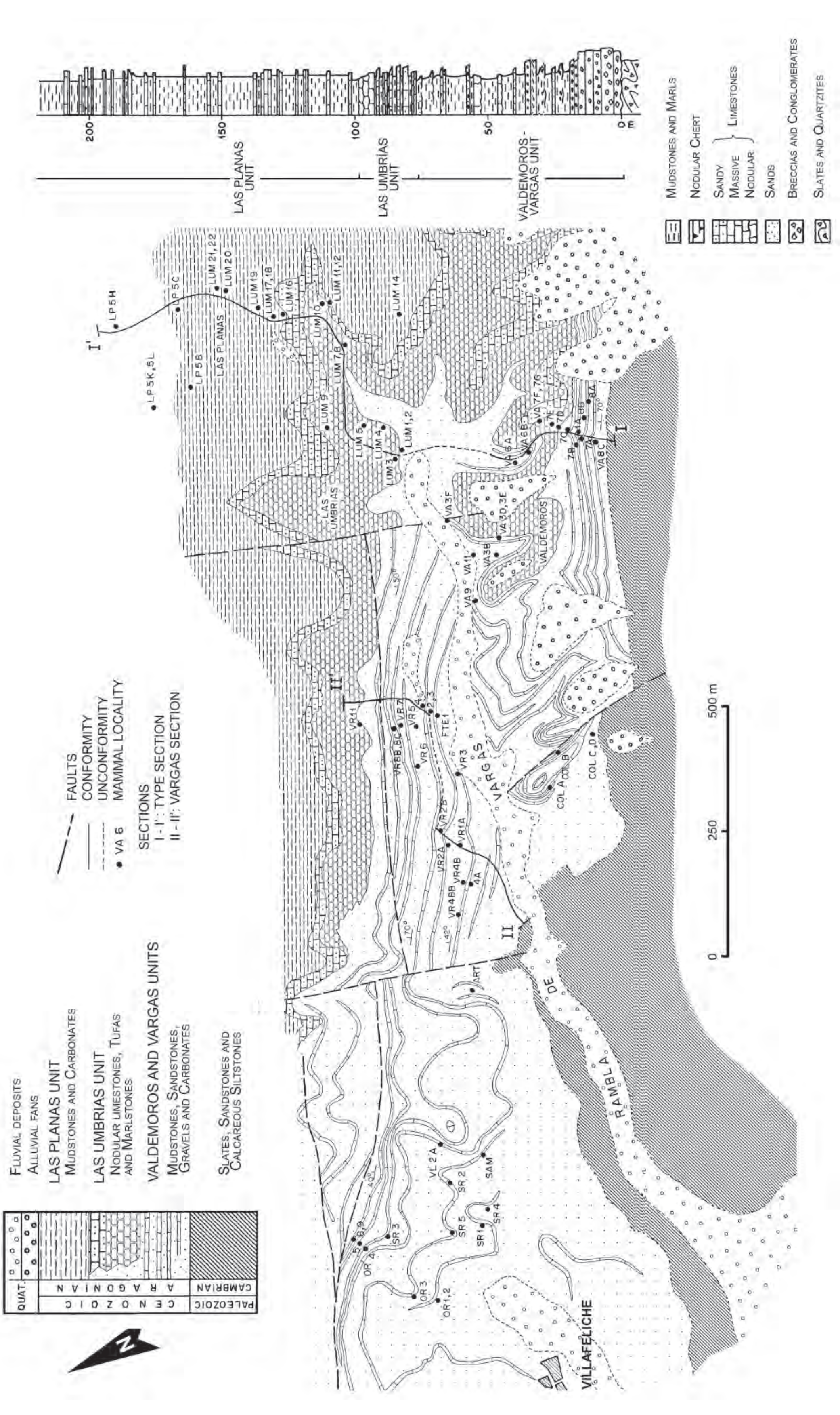

**FIGURE 1** Geological Map, showing the situation of localities and stratigraphic sections, and synthetic lithostratigraphic log of the Aragonian Type area. Modified from Daams et al. (1999a).

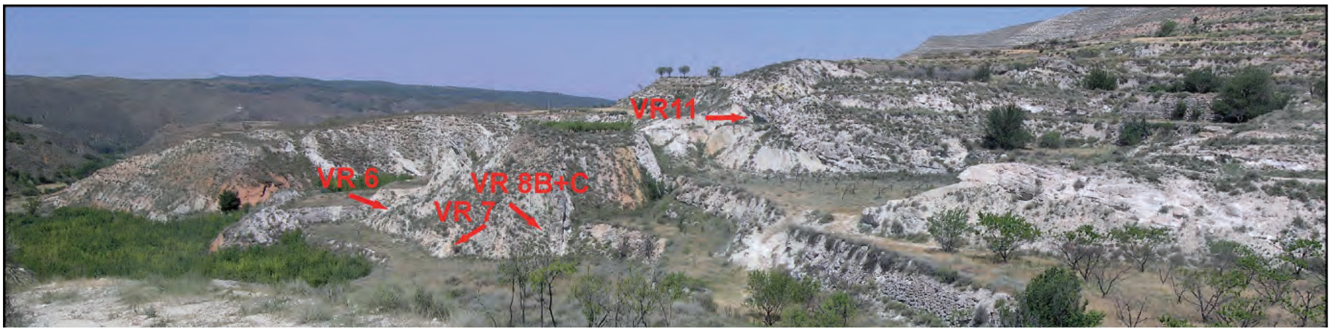

**FIGURE II** | Panoramic view of the Vargas section (Aragonian Type Area, Zaragoza, Spain) showing the tilting of Las Umbrias unit.

the sequence, and not a lithological one. We maintain the assignment to Zone Ca, and place it above Villafeliche 2A.

Freudenthal's comments and his Figure 3 on the magnetostratigraphy of the area include unacceptable alterations of, and correlations between, the Vargas and the Aragon sections of Krijgsman *et al.* (1994, 1996). He disregards the important role of the Armantes section that was unambiguously correlated to the GPTS, as a result of which the type section could be calibrated with the aid of biostratigraphy (Krijgsman *et al.*, 1994, 1996; Daams *et al.*, 1999a). Commenting on the estimated locality ages based on magnetostratigraphy, he writes (Freudenthal, 2006): "In the corrected sequence [*i.e.* the sequence of his Table 2, and our Table A1] the supposed ages jump up and down almost randomly, *but of course one might recalculate them on the basis of that sequence*" (the italics are ours). Magnetostratigraphers, however, base their research on continuous sections, not on a spatial patchwork of sediments found in between presumed marker beds.

Freudenthal (2006) emphasizes that the many new localities published by Daams *et al.* (1999a) should be placed in the sequence of Daams and Freudenthal (1988). In fact, this is exactly what Daams *et al.* (1999a) did, except for the relative position of Valdemoros 3B (formerly Zone D2, now Dc) and Valdemoros 1A (formerly Zone D1, now Zone Dd). By taking the opposite relative position of these two localities as his starting point, his marker-bed sequence results in a complete jumble of the whole Lower to Middle Aragonian biozonation mixing the Zone Dd faunas from the type section with Zone Cb, Da, Db, and Dc faunas from other sections. This is in complete disagreement with the superpositional sequences from the Vargas (see above), La Col and other sections, which form the basis of the biostratigraphy of Daams *et al.* (1999a). Its correctness does not depend on the position of the Valdemoros 3 section. Finally, the top of the Valdemoros-Vargas unit in the small Valdemoros 3 section yields a paleomagnetic pattern that differs from the continuous part of the type section, into which Freudenthal wants to insert it. (Krijgsman *et al.*, 1994, 1996; Daams *et al.*, 1999a). Since the locality sequence of Freudenthal (2006) is based on arguable grounds, and is not compatible with the sequence derived from superposition in the various sections, and leads to biostratigraphical and magnetostratigraphical inconsistencies, we dismiss his comments and maintain that the sequence of Daams *et al.* (1999a) is the correct one.

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