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Palaeoenvironmental analysis of the Aragonian (middle Miocene) mammalian faunas from the Madrid Basin based on body-size structure

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Abstract

As a consequence of the growth of the Antarctic ice-sheet during the middle Miocene, a global decrease of temperatures and an associated increase in aridity provoked several environmental changes all around the world. Such environmental variations can be detected in the continental record of the mammalian prey community structure using a synecological approach. Because of the good quality of its faunas, the rich Aragonian vertebrate fossil record from the Madrid Basin (Spain) appears as a good candidate to explore these environmental changes. In order to analyse the climatic evolution of the Iberian Peninsula associated to the Global Cooling Event, two classic palaeosynecological methodologies (cenograms and body size diversity), based on body-size community structure, were applied to 6 fossil sites from the Madrid Basin, ranging over 2 million years (15.5 – 13.5 Ma). To establish a comparative framework, we used the ecological faunal data from 100 modern localities uniformly distributed all around the world. Our palaeoenvironmental inference is based on multivariate discriminant analysis of the dataset containing both modern and fossil mammals. Finally, we can conclude that the Aragonian mammalian assemblage from the Madrid Basin showed a predominance of semiarid environments with pulses of higher aridity in biozones Dc, E and F associated with the Global Cooling Event of the middle Miocene.

Keywords: Aragonian, Prey Mammal Community Structure, Madrid Basin, Body-size spectra, Cenograms, Climate

Resumen

Como consecuencia del crecimiento del casquete polar Antártico, durante el Mioceno medio, se produjo un descenso global de la temperatura asociado a un aumento de la aridez. Este tipo de cambios ambientales pueden ser detectados en el registro continental, siguiendo un modelo sinecológico para analizar la estructura de las comunidades de las faunas de mamíferos herbívoros. Debido a la calidad de sus faunas, el registro fósil de las faunas de vertebrados del Aragoniense de la Cuenca de Madrid se antoja como un buen candidato para explorar estos patrones de cambio ambiental. Con el objetivo de analizar la evolución climática de la Península Ibérica asociada al evento de enfriamiento global durante este lapso temporal, dos metodologías paleosinecológicas clásicas (cenogramas y espectros de diversidad de tamaño corporal), basadas en la estructura de tamaños corporales de las comunidades de mamíferos, han sido aplicadas a la fauna de herbívoros fósiles presente en seis yacimientos de la Cuenca de Madrid, abarcando aproximadamente 2 millones de años (15.5 – 13.5 Ma). Se ha establecido un marco comparativo usando los datos ecológicos de la fauna de mamíferos presente en 100 localidades uniformemente distribuidas por todo el planeta. Esta inferencia paleoambiental está basada en la aplicación de análisis discriminante multivariante sobre el conjunto de datos de las faunas actuales y fósiles. Finalmente, las faunas de mamíferos del Aragoniense de la Comunidad de Madrid mostraron una predominancia de ambientes semiáridos con varios pulsos de mayor aridez en las biozonas Dc, E y F asociados al evento de enfriamiento global del Mioceno medio.

Palabras clave: Aragoniense, Estructura de Comunidad de Mamíferos, Cuenca de Madrid, Espectros de Tamaño Corporal, Cenogramas, Clima

1. Introduction

The Miocene Climatic Optimum (MCO), recorded ~17 to 15 Ma, represents one of the warmest periods of the last 30 million years (Zachos *et al*., 2001; Shevenell *et al*. 2004). It lasted until 14 Ma, when a climatic change from warm and humid conditions to a more arid and cooler environment took place as a consequence of the growth of the Antarctic ice-sheet. This climatic change, known as Global Cooling Event, has been recorded in both marine and continental records using sedimentary and faunal data (e.g. Kennett and Barker, 1990; Böhme, 2003; Zachos *et al*., 2001; Lewis *et al*. 2008). Clift (2010) related changes in erosion rates across Eurasia, North America and Africa with climatic fluctuations during the last 33 Ma, peaking around 16 Ma ago. In Hauptvogel and Passchier's (2012) study, the analysis of heavy mineral composition of one drill core allowed them to define the Antarctic ice dynamics related to the climatic change during the early to middle Miocene (17 to 14 Ma). Faunal studies based on the evolution of hypsodonty in large herbivorous mammals from Asia (Liu *et al*., 2008), and modifications on ecophysiological structure of herpetological assemblages (Böhme *et al*., 2010), also detected a significant increase in aridity related to the Global Cooling Event. Finally, Larsson *et al*. (2011) investigated palynological composition of sediments from the Danish coast (lower to upper Miocene, 19 to 8 Ma) that also showed major climatic shifts during the Miocene.

As homeotherms and habitat-sensitive animals, mammals are one of the best proxies to detect these climatic changes in the continental record (Vrba, 1992; Barnosky, 2001). Variations in their ecological characteristics can be used to detect environmental constraints. In fact, shifts in their feeding habits (Domingo *et al*., 2009, 2012; De Miguel *et al*., 2011; Zhou *et al*., 2011), locomotor adaptations (Lewis, 1997; Samuels and Van Valkenburgh, 2009; Meloro, 2011), and body size or morphology (Legendre, 1986; Shepherd, 1998; Rodríguez, 2001) have been found to correlate to climate and ecological dynamics. Besides, body size has been traditionally related to climate via Bergmann's and Allen's rules (Bergmann, 1847; Allen, 1877), which stated a latitudinal variation pattern in mammal (and birds) body size and shape. These rules have been almost equally accepted (Mayr, 1956, 1963; Ashton *et al*., 2000; Ashton, 2001; Meiri and Dayan, 2003) and rejected (Scholander, 1954; McNab, 1971; Fuentes and Jaksić, 1979; Meiri *et al*., 2007). Although the original ideas expressed by Bergmann and Allen are not exactly supported, a relationship between climatic proxies and mammal body size can be established (Boyce, 1978; Wigginton and Dobson, 1999; Yom-Tov and Geffen, 2006) and confirms the value of this feature in climate inference.

However, the relationship between mammalian ecology and climate is not only reflected at the individual level, but also in the structure of the communities. During the last decades, the palaeoclimate from different periods and regions has been established based on the body size community structure of mammal fossils (Legendre, 1986, 1989; Montuire, 1999; Rodríguez, 1999; Croft, 2001; Storer, 2003; Hernández Fernández *et al*., 2006a; Palombo and Giovinazzo, 2006; Tougard and Montuire, 2006; Costeur *et al*., 2007; Travouillon and Legendre, 2009; Travouillon *et al*., 2009).

The well-studied mammalian groups from the Iberian Peninsula (Meulen and Daams, 1992; Fraile *et al*., 2000; Hernández Fernández *et al*., 2003, 2006a; Domingo *et al*., 2009, 2012), among the richest of the Neogene (Daams *et al*., 1977; Alba *et al*., 2001), represent a good opportunity to analyse ecomorphological aspects of fossil assemblages and their relationship to the climatic change that took place ~ 14 Ma ago. Particularly, the evolution of the body size community structure of the middle Miocene prey fauna from the Madrid Basin allows us to explore the connection between ecological community dynamics and macroenvironmental changes.

The Madrid Basin, originated by an endorheic lacustrine system (Calvo, 2000), is filled by detrital, evaporitic and carbonatic sediments. The age of the whole section ranges between 20 to 5.4 Ma, with three different lithostratigraphic units from the Madrid Basin defined (Alberdi, 1985; Calvo, 1989; Calvo *et al*., 1993): the Lower Unit (Ramblian to middle Aragonian), the Middle Unit (middle Aragonian to Vallesian) and the Upper Unit (Vallesian to Turolian). Several similar changes between humid and arid conditions have been also detected in this region for this short time in previous studies about the modifications in mammal body size community structure (Hernández Fernández *et al*., 2006a), the dietary evolution of herbivores (Domingo *et al*., 2009, 2012) or by changes in the mineral composition of the sediments present in the Somosaguas fossil site (Carrasco *et al*., 2008).

The aim of this research is to detect changes in the prey's community structure through time and to relate these changes to several major climatic fluctuations that took place during the middle Aragonian (middle Miocene). Thus, in order to evaluate the climatic evolution of the Madrid Basin before and after the middle Miocene Global Cooling Event, we applied two classic palaeo-synecological methodologies traditionally used for this purpose; cenograms (developed by Valverde (1964) and palaeoenvironmentally applied by Legendre in 1986 and 1989) and body size diversity (developed by Fleming (1973) and applied to the fossil record by Andrews *et al*., 1979) to the mammalian fauna from six different localities in the Madrid Basin. These localities are placed on the Lower or Middle Unit (Calvo, 2000; Montes *et al*., 2006; Domingo *et al*., 2009), covering local biozones Dc to G (15.5 to 13.5 Ma) according to the micromammal biozonation established by Daams *et al*. (1999) for the Calatayud-Daroca Basin and recognized in the Madrid Basin by Peláez-Campomanes *et al.* (2003). The analysed interval (2 million years) represents a good example to assess this environmental change, because it covers the end of the Miocene Climatic Optimum, together with the end of the Global Cooling Event (Zachos *et al*., 2001).

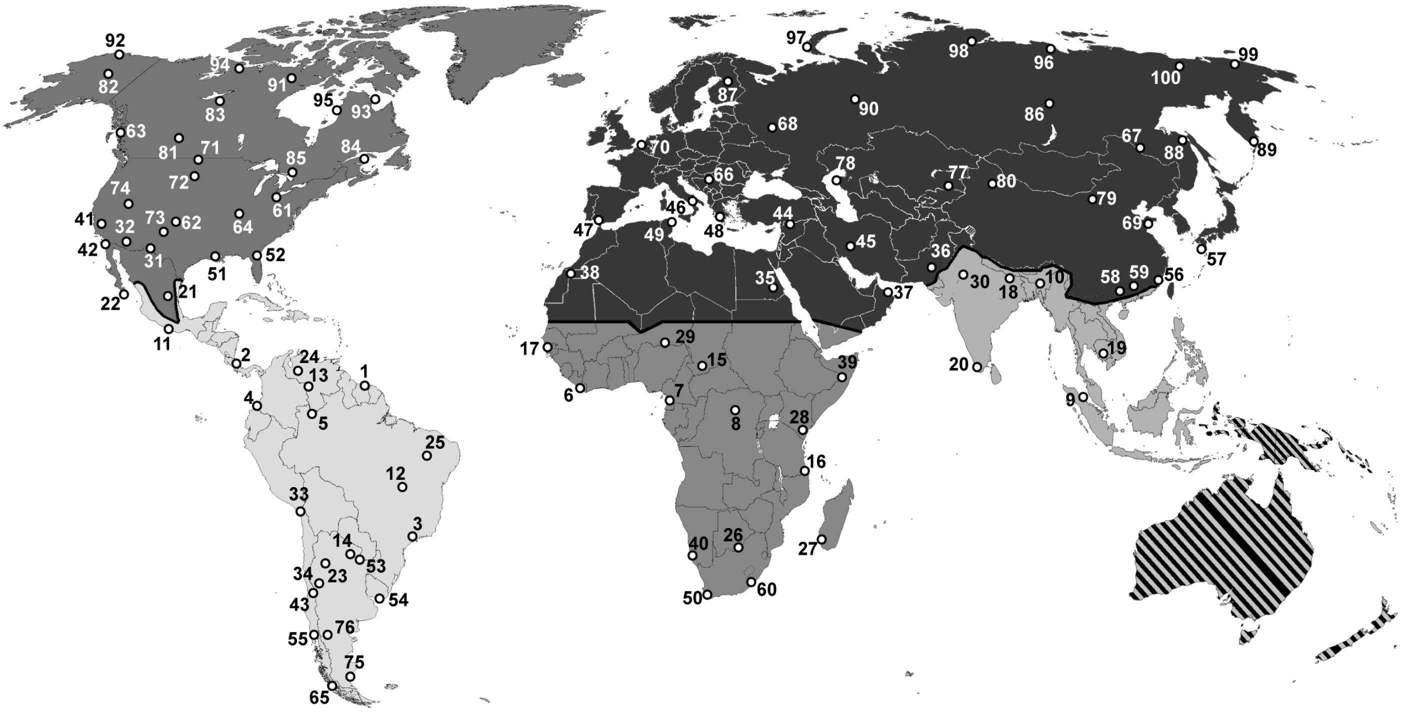

Fig. 1.- Distribution of the 100 modern communities studied in this work. Numbering as in supplementary data I. The different grey shades indicate the different biogeographical realms (light black: Palearctic; dark grey: Nearctic; grey: Afrotropic; silver: Indomalaysia; light grey: Neotropic)

Additionally, in order to generate a comparative framework to assign a specific biome to each fossil assemblage, we described the body size community structures for mammalian prey of 100 modern localities. Finally, since the geological and environmental histories of the continents determine the faunal composition of the different regions (Pickford and Morales, 1994; Moreno Bofarull *et al*., 2008) and are relevant factors for the mammalian community structure (Croft, 2001; Nieto and Rodríguez, 2003; García Yelo *et al*., 2009), the influence of biogeography on the relationships was also analysed.

2. Material and Methods

2.1. Extant and fossil faunas

In order to establish our comparative framework and to test the relationship between body size community structure and climate, we used the climatic data (type of biome) and the mammalian prey faunal data from 100 extant localities (Fig. 1, supplementary data I) uniformly distributed around the world (excluding Australia). Here we followed the biome characterization from Walter (1970), and modified by Hernández Fernández (2001), which represents the 10 climate types present in the Earth today (I: evergreen tropical rainforest; II: tropical deciduous woodland; II/III: savannah; III: tropical desert; IV: sclerophyllous woodland; V: temperate evergreen forest; VI: nemoral broadleaf-deciduous forest; VII: steppe; VIII: taiga; IX: tundra). Marine and flying mammals, as well as the species introduced by anthropic action, were excluded from our analysis. Nevertheless, those species that were extinct during historic times were incorporated in the database. Taxonomy was standardized to Wilson and Reeder (1993). The body size data for modern species were obtained from Smith *et al*. (2003). For the few species with no body size information, the mean of the genera was calculated (Rodríguez, 1999; Croft, 2001; Hernández Fernández *et al*., 2006a). Here we use the concept prey mammals as any terrestrial species, excluding the Australian ones, not belonging to the order Carnivora (Orders Didelphimorphia, Paucituberculata, Microbiotheria, Tubulidentata, Macroscelidea, Hyracoidea, Proboscidea, Xenarthra, Scandentia, Dermoptera, Primates, Rodentia, Lagomorpha, Insectivora, Pholidota, Perissodactyla, and Artiodactyla).

In order to evaluate the climatic evolution of the Madrid Basin before and after the middle Miocene Global Cooling Event, we analysed the body size community structure of prey from six middle Miocene fossil sites from the Madrid Basin (Fig. 2). These localities are: Estación Imperial; Paseo de las Acacias; Arroyo del Olivar-Puente de Vallecas; Somosaguas; Paracuellos 5 and Paracuellos 3. The faunal list of the six localities, together with the body size for fossil species were obtained from Peláez-Campomanes *et al*. (2003), Hernández Fernández *et al*. (2006b), Perales *et al*. (2009) and Hernández-Ballarín *et al*. (2011), and are detailed in supplementary data II. These fossil sites are among the most completely sampled of the Madrid Basin for this period, with a total of 54 species represented and more than 18000 pieces recuperated in successive field works (supplementary data II).

2.2. Body size Community Structure and Discriminant Analysis

We used two palaeo-synecological methodologies, cenograms (Legendre, 1986, 1989) and body size spectra (Andrews *et al*., 1979), to describe the community structure of the mammals present in each locality. Originally, these methodologies were used to visually compare fossil community structure patterns with those from recent mammalian communities and then try to assign a particular habitat to the fossil community.

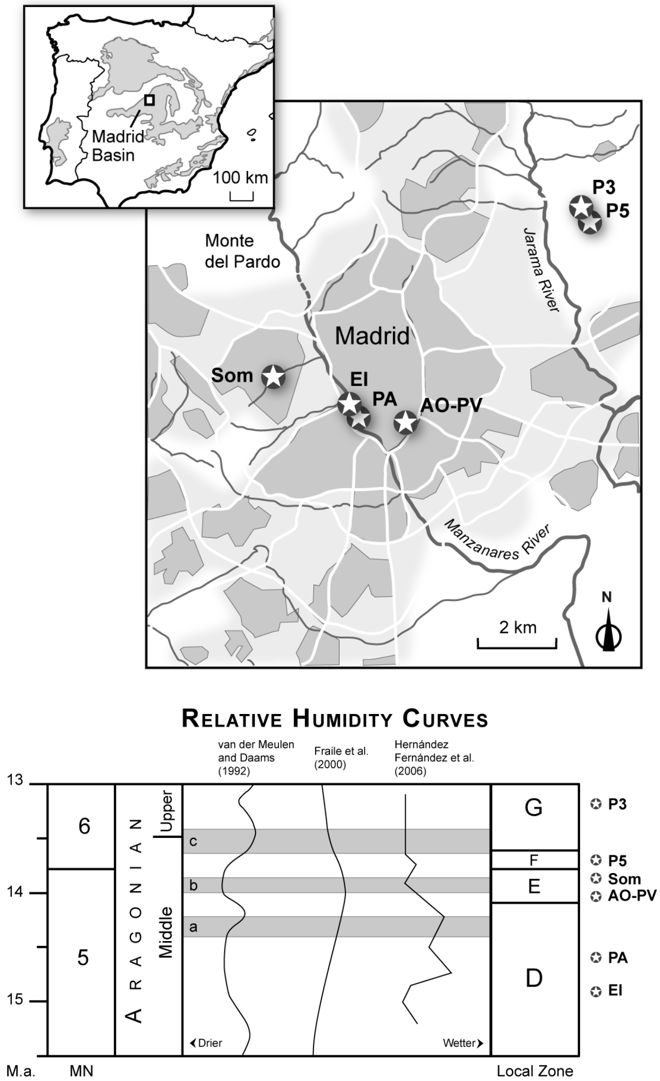

Fig. 2.- Temporal and geographical situation of the six fossil sites used in this analysis. The relative humidity curves of van der Meulen and Daams (1992), Fraile *et al*. (2000) and Hernández Fernández *et al*. (2006) are also included to compare with our results. The grey lines indicate the pulses of changes in the aridity conditions. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3)

BODY SIZE SPECTRA CATGORIES

Category	Weight range (g)
A	0 - 100
B	100.1 - 1000
C	1000.1- 10000
D	10000.1 - 45000
E	45000.1 - 90000
F	90000.1 - 180000
G	180000.1 - 360000
H	> 360000

Table 1. Body size categories defined to determine the body size spectra of the mammalian communities used in our study (Andrews *et al*., 1979; Hernández Fernández *et al*., 2006).

In body size spectra, every prey mammal from a particular community is assigned to one of the body size categories defined in table 1 (Andrews *et al*., 1979; Hernández Fernández *et al*., 2006a). Once each species of the prey community was classified in one of the body size categories and the final sum for each category converted to a percentage, the body size spectrum of the community was obtained. For Legendre's methodology, rank ordered taxa *vs*. body size graphs were plotted. Species were then separated according to body size in four categories, small prey (< 500 g), medium prey (500 g - 8 Kg), large prey (8 - 1000 Kg) and mega-prey (≥ 1000 Kg) (Legendre, 1986, 1989; Rodríguez, 1999; Hernández Fernández *et al*., 2006a). Rodríguez (1999) stated that these body-size thresholds, defined by previous authors (Legendre 1989; Gingerich 1989), respond to trophic and physiological constraints. As mega-prey species are restricted to a few tropical localities, they were excluded from the analysis in order to make the results more comparable among the different communities. Finally, twelve cenogram variables (Fig. 3, Table 2) were defined to describe the mammalian body size structure of the communities. Both Rodríguez (1999) and Hernández Fernández *et al*. (2006a) selected these variables because of their ecological significance. Although the limits between categories are fixed, the number of species present in those categories can vary as a consequence of the predator pressure (Valverde 1967). Thus, while the different mean weight or body mass (Wx) reveals the more suitable size to avoid predator pressure in each category, the magnitude of the different gaps (G, mG and MG) and its position on the cenogram (WG, WmG and WMG) depict exactly the opposite. Finally the slopes in the cenogram were defined in order to state the species-richness in each category (Gingerich 1989).

Taphonomic biases might have affected mammalian diversity and structure of the fossil communities, making a rarefaction analysis necessary. Nevertheless, as previous studies have revealed, a high number of species have to be lost to significantly affect the structure of a community (Gómez Cano *et al*. 2006). Due to the high sample size of the fossil sites used in this study, the possibility of taphonomic biases may be discarded.

CENOGRAM VARIABLES	
Variables	Description
W1	Mean weight or body mass of all small prey (< 500 g) (in logarithmic units)
W2	Mean weight or body mass of all medium prey (500 g – 8 Kg) (in logarithmic units)
W5	Mean weight or body mass of all medium-large prey (500 g – 1000 Kg) (in logarithmic units)
P1	Slope of the line segment determined by small prey (< 500 g)
P5	Slope of the line segment determined by medium-large prey (500 g – 1000 Kg)
P5-P1	Difference in slope between the line segments determined by medium-large and small prey
G	Magnitude of the gap between small and medium-large prey (in logarithmic units)
mG	Magnitude of the major gap between two consecutive species of medium-large prey (in logarithmic units)
MG	Magnitude of the major gap between two consecutive species of all prey (in logarithmic units)
WG	Mean weight or body mass of the two species that define G (in logarithmic units)
WmG	Mean weight or body mass of the two species that define mG (in logarithmic units)
WMG	Mean weight or body mass of the two species that define MG (in logarithmic units)

Table 2. Cenogram variables defined to describe the mammal community structure based on the cenogram methodology (Valverde, 1964, 1967; Hernández Fernández *et al*., 2006)

Once the community structure and biome of modern faunas were defined in each locality, we tried to establish a statistical relation between the type of biome and a specific community structure pattern. Following Hernández Fernández *et al.* (2006a) we performed a multivariate discriminant analysis of the dataset containing modern faunal information in order to assess the statistical capability of both methodologies to distinguish between biomes. In a second analysis the different biogeographic histories of the continents were taken into account; thus, the test was repeated independently with localities grouped by their respective biogeographic realms. Conceptually, this forced us to remove from the study those localities that belong to biomes represented by only one community in a biogeographic realm. Consequently, only tropical biomes are represented in the tropical realms of the Old World, and the Indomalaysian region only included evergreen tropical rainforest and tropical deciduous woodland biomes. Additionally, due to a likely Palaeotropical origin of the Miocene mammals from the Iberian Peninsula (Pickford and Morales, 1994) and the climatic similarities between the modern tropical realms and the Iberian Peninsula during the Miocene (Hernández Fernández *et al*., 2006a), we carried out a new analysis where the localities within the Afrotropical and Indomalaysian realms were grouped together. Thus, the biomic inference for the fossil sites was based on the Afrotropical, Indomalaysian and Palaeotropical discriminant models.

3. Results

Discriminant analyses applied to body size spectra and cenogram variables from the modern fauna have shown a low biome discriminant capability of both methodologies at the global scale (47% and 55.7% of correctly classified localities respectively). However, our results were significantly improved when the analyses were repeated separating communities by biogeographic realms (Table 3), indicating a noteworthy influence of the evolutionary history on prey community structure based on their body size distributions.

In order to examine which body size variables made the strongest contribution to discriminate biomes in every analysis, the principal components that discriminate biomes in our study have been studied (supplementary data III). While for

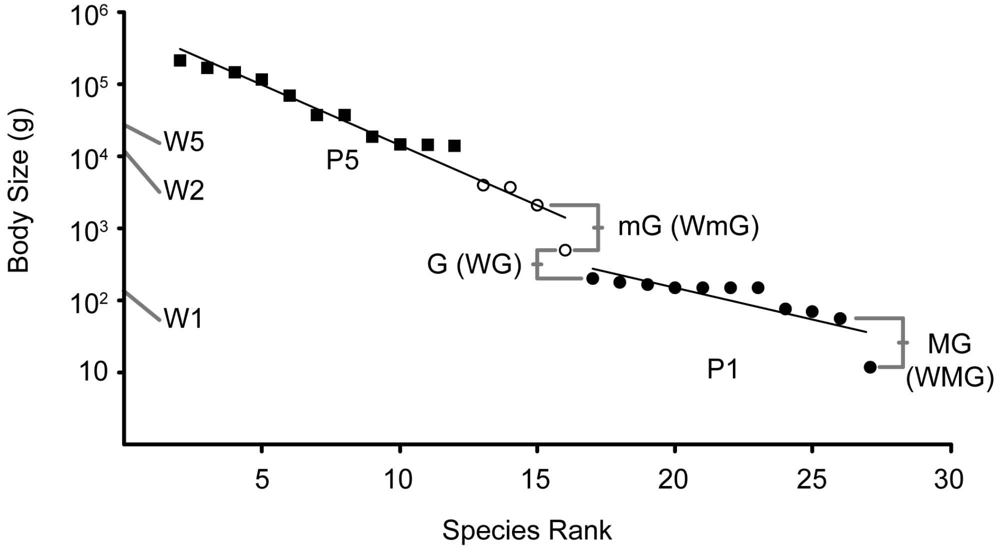

Fig. 3.- Cenogram associated with the mammal community of Patna (India). Black circles, small prey; white circles, middle-size prey; black blocks, large prey. Variables of the cenogram as in table 2.

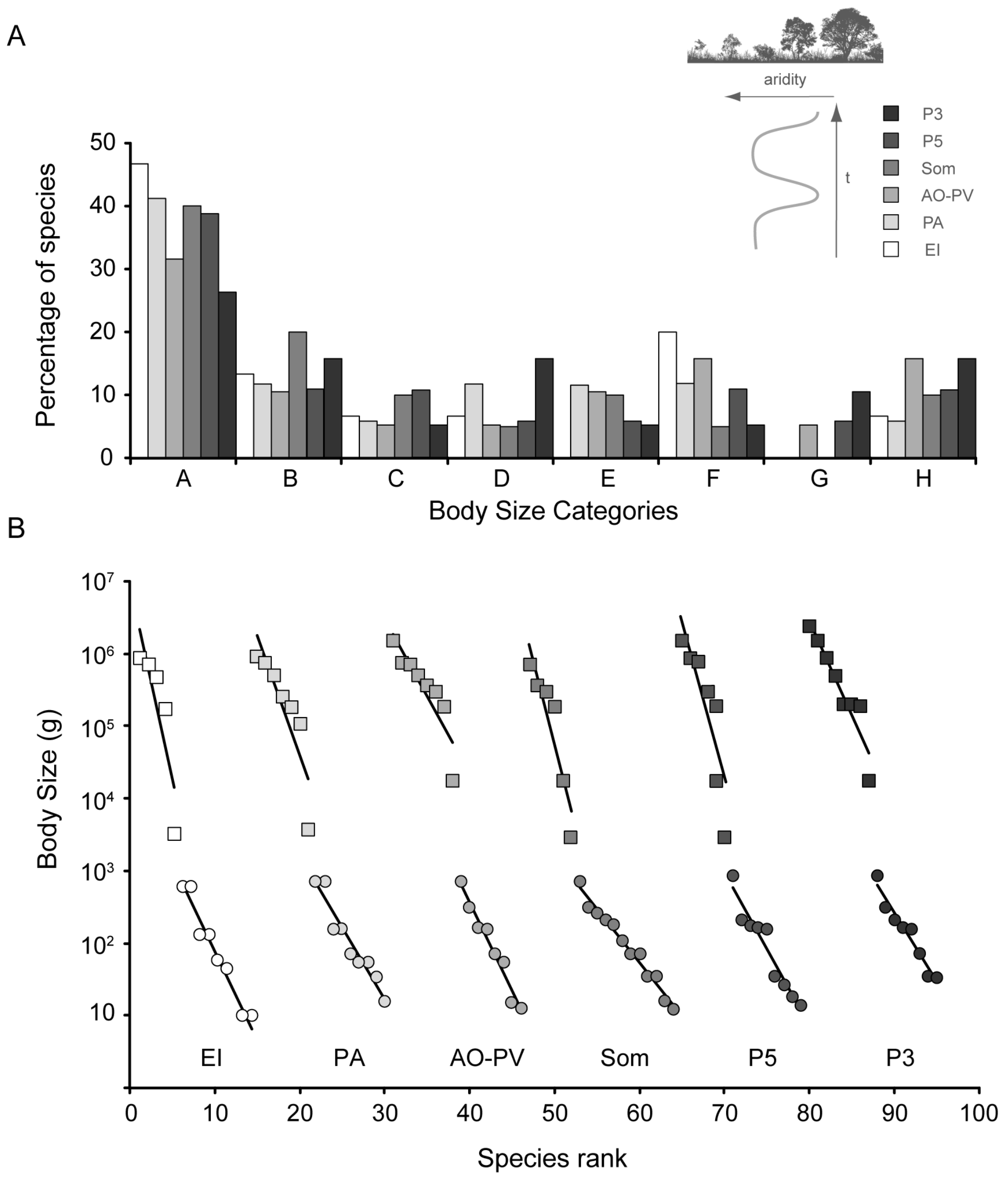

Fig. 4.- Resume figure with a compendium of the six body size spectra (A) and the cenograms (B) obtained for the Aragonian palaeocommunities. A schematic aridity curve is provided for the analysis interval. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3)

cenogram global analysis are the slope variables (P5, P5-P1, G, W1 and WG) the principal ones that contribute to discriminate biomes, for the biogeographic realms analyses different variables contribute to separate biomes in every region. While for the Indomalaysian realm the mean weight variables (W1, W2 and W5) are the ones that discriminate biomes, for the Afrotropic and the Palaeotropic most of the cenogram variables seem to help to discriminate biomes. In the body size spectra case, body size categories A and E are the main contributors to the global discrimination of biomes. Nevertheless, when the discriminant analyses are repeated by biogeographic realms, different categories separate biomes in each biogeographic region, with all body size categories being represented (supplementary data III).

Once the discriminant models for the Afrotropical, Indomalaysian and Palaeotropical realms were performed, the biomic inference for the six fossil sites were obtained (Table 4). Given a particular biogeographic region (e.g., Afrotropic), the inferred biome for the same fossil locality (e.g., Estación Imperial) is different using each methodology (tropical deciduous woodland and tropical desert). All predicted biomes, excluding the evergreen tropical rainforest detected by the Indomalaysian realm, are arid and warm.

These results are complex and make the use of both methodologies to infer biomes complicated. Nevertheless, a common pattern can be asserted. Changes in the aridity and forest density through time can be detected by cenograms (for all realms analysed) and the body size spectra (for the Palaeotropical realm). It is worth mentioning that most of these changes are detected synchronously by both methods in most of the cases (Table 4). The studied period started with an arid/semiarid and scarcely forested environment (II or III biomes were obtained for Estación Imperial and Paseo de las Acacias) that was followed by a climatic change to relative more wooded-humid conditions between biozones D and E (I, II, II/III biomes for Arroyo del Olivar-Puente de Vallecas). After

Table 3. Results of the discriminant analyses for the extant communities at global level and by biogeographic realms (biome clasification as in the text). *The N (numbers of localities) noted with an asterisk reflects those cases where the localities included in the analysis are not the same for both methodologies (given number refers to the BBS method). The number of included localities for cenogram method is: 97 (for global analysis), 15 (for Neotropic) and 32 (for Palaearctic) **The double asterisk indicates that the number of biomes included in the Neotropics is also different in both methods, being the given biomes those for the BBS method, while for cenogram method are I, II, II/III and V.

		N (INCLUDED BIOMES)	CORRECTLY CLASSIFIED COMMUNITIES	
			BSS	CENOGRAMS
GLOBAL		100* (I-IX)	47.0%	55.7%
BIOGEOGRAPHIC REALM	NEARCTIC	26 (II/III-IX)	65.4%	96.2%
	NEOTROPIC	19* (I,II,II/III,V,VII)**	73.7%	100.0%
	PALEARCTIC	33* (III-IX)	72.7%	84.4%
	AFROTROPIC	12 (I-III)	91.7%	100.0%
	INDOMALAYSIA	5 (I-II)	100.0%	60.0%
PALEOTROPIC		18 (I-III)	77.80%	100.0%

Table 4. Inferred biomes for the six fossil sites included in the analysis. The grey colours mean different trends in the hydric gradient; relatively more humid climates are marked with dark grey and relatively more arid biomes with light grey. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3)

		EI	PA	AO-PV	Som	P5	P3
BODY SIZE SPECTRA	AFROTROPIC	II	II	II	II	II	II
	INDOMALAYSIA	I	I	I	I	I	II
	PALAEOTROPIC	III	III	II	II/III	II/III	II
CENOGRAM	AFROTROPIC	III	III	II/III	III	II/III	II/III
	INDOMALAYSIA	II	II	I	II	II	I
	PALAEOTROPIC	III	II	II	III	III	II

a short lapse of time (still inside biozone E), arid and less forested conditions returned (II, II/III or III for Somosaguas and Paracuellos 5). Finally, a new environmental change to more forested and humid conditions (I, II, II/III biomes for Paracuellos 3) took place between biozones F and G.

Nevertheless, it is also worth mentioninig that the results given by the body size spectra for the Indomalaysian realm show an homogeneous climate during most of the sequence excepting at the end, where a climatic change between humid to arid conditions (from biome I to II) was produced, showing an inversion of the pattern (table 4). Finally, regardless of the high inference potential of the body size spectra for the modern localities of the Afrotropical region, this method does not detect any environmental change for the whole sequence of the fossil sites under study.

4. Discussion

Our results show changes in climate during the middle Miocene in the Madrid Basin, with a fluctuation between arid and relatively more humid conditions. All the climates inferred for the different fossil sites in this research are tropical, and most of them show aridity at some level. Previous studies also found a tropical warm and arid climate for the Iberian Peninsula during this time span. Amezua *et al*. (2000) used several palaeo-synecological methodologies (ecological diversity spectra, cenograms, diversity indexes, quantitative species composition and presence/absence of environmental indicative species) to analyse the environmental evolution of the Madrid Basin over the middle Aragonian. They found very homogeneous conditions for the Madrid Basin through the middle Miocene, with warm and arid environments with slight variations in the humidity. Hernández Fernández *et al*. (2006a) also used ecological diversity and cenograms to recognise aridity peaks, by means of biome characterization, through the middle Aragonian of Spain. All fossil sites were classified as tropical deciduous forest (II), savannah (II/III) or tropical desert (III) (excluding three of them classified as temperate evergreen forest by the trophic diversity model), which are warm and relatively arid biomes. Costeur and Legendre (2008) analysed the mammalian body-weight structure of 17 fossil communities from middle Miocene (17-14 M.a.)

from Spain and Germany, finding a southwest-northeast latitudinal environmental gradient, from a warm, arid and open environment in Spain to a warm, closed and humid environment in Germany.

In most of the discriminant models a common pattern can be detected. At the beginning (coincidently with the Miocene Climatic Optimum) and the middle of the sequence (after the Global Cooling Event), two lapses of time corresponding to local zones Dc and E-F (including Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5 fossil sites), the prey community structures of the fauna present in the Madrid Basin reflect more open and arid conditions (desert, tropical deciduous woodland or savannah) than the rest of the sequence in the different discriminant models. The rest of the sequence (Arroyo del Olivar-Puente de Vallecas and Paracuellos 3 fossil site communities) represents more humid and closed environments (evergreen tropical rainforest, tropical deciduous woodland or savannah). Although the same biome classification was estimated for some sites of both environment types, arid and relatively humid localities, such overlap is rarely obtained within the same discriminant model. Our results suggest that three environmental fluctuations took place during this period. The first and third climatic changes (between Paseo de las Acacias and Arroyo del Olivar-Puente de Vallecas, and between Paracuellos 5 and Paracuellos 3) were toward relatively more humid and forested conditions. The second one (between Arroyo del Olivar-Puente de Vallecas and Somosaguas) coincided with the middle Miocene Global Cooling Event and reflects more arid conditions. The relative humidity curves given by Meulen and Daams (1992) and Hernández Fernández *et al*. (2006b), based in changes in the structure of rodent faunas, depict aridity peaks that match in time with the climatic change towards more open and arid environments detected in the present study (Fig. 2). Fraile *et al*. (2000) also detected these changes in mammal faunas from the Madrid Basin although they noticed small differences on the time limits between arid and humid environments (Fig. 2). Finally, isotopic analysis of tooth enamel of middle Miocene ungulates from the Madrid Basin also shows similar results, with fluctuations between arid and relatively humid periods (Domingo *et al*., 2012).

When the six body size spectra and cenograms from the fossil communities are represented together (Fig. 4), further interpretations can be made. James (1970) found that birds in cold and dry environments were smaller than their relatives in warm and humid ones, so the relative large *vs.* small birds ratio should grow from dry to humid environments. If we extrapolate this concept to mammalian communities, the proportion of small species should decrease from dry environments to humid ones, whereas large species would become more frequent as the aridity of the environment decreases. Analysing the body size spectrum of the different extinct communities (Fig. 4a), different ratios of large *vs.* small mammals can be noticed. In dryer localities (Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5), small mammals (characterized by body size category A) are over represented (above the 40%; $\overline{X}$=42.25%), and the large *vs*. small mammals (categories G and H; cat[G+H]/catA ratio) ratio is small ($\overline{X}$=0.24). On the other hand, in relatively more humid localities (Arroyo del Olivar-Puente de Vallecas and Paracuellos 3), small mammals are drastically reduced (in both cases under the 32%; $\overline{X}$=28.95%) and the large *vs*. small mammals ratio is higher ($\overline{X}$=0.83). These differences in the body size diversity structure between arid and relatively humid fossil communities are statistically significant (small mammals: T=-4.816, ρ=0.009; large *vs*. small mammals ratio: T=4.122, ρ=0.015). Nevertheless, these differences have not been found in the modern fauna (small mammals: $\overline{X}_{humid}$=48.94%, $\overline{X}_{arid}$=43.92%, T=1.783, ρ=0.078; large *vs*. small mammals ratio: $\overline{X}_{humid}$=0.08, $\overline{X}_{arid}$=0.12, T=-1.538, ρ=0.128), maybe as a consequence of the interaction of some other climatic factors, such as temperature, over the body size of mammals (Bergmann rule).

This pattern is also reflected for macromammals in the cenogram structure of the different fossil communities (Fig. 4b), where the slope of the line that defines medium-large prey (P5) is statistically different between arid and relatively humid fossil sites (T=-3.078, ρ=0.037), being more pronounced in arid localities ($\overline{X}$=-0.88) than in the relatively humid ones ($\overline{X}$=-0.47). Furthermore, these differences are also detected in the modern fauna ($\overline{X}_{humid}$=-1.02; $\overline{X}_{arid}$=-0.695; T=2.099, ρ=0.039). Interestingly, the cenograms for these fossil sites contradict one of the most accepted rules for aridity and cenogram structure. As Legendre defined (1986, 1989), the magnitude of the gap between small and medium-large prey is related to the aridity of the environment; the more arid the climate is, the larger the gap. But in our results statistically larger gaps are present in the humid localities (T=-9.729, ρ=0.001; $\overline{X}_{humid}$=2.70; $\overline{X}_{arid}$=1.28). Again, these differences are also detected in the modern fauna ($\overline{X}_{humid}$=1.32; $\overline{X}_{arid}$=0.93; T=-2.092, ρ=0.040). In the fossil sites, this is a consequence of the absence in Arroyo del Olivar-Puente de Vallecas and Paracuellos 3 of the species *Cainotherium miocaenicum* or a member of the genus *Amphechinus*, the latter showing a clear preference for arid environments (Furió *et al*., 2011). This fact could be a consequence of taphonomic bias against the preservation of small mammals in closed environments (Cantalapiedra *et al*., 2012), but since this difference is also detected in the modern fauna, we suggest that this pattern could be a consequence of the higher hydric constrictions of large prey mammals. Water is an environmental conditioning factor that forces large animals to inhabit preferentially more closed and humid environments (Robertshaw and Taylor, 1969; McNab, 2002) and consequently, smaller species would find benefits in get adapted to arid environments in order to avoid competition.

Also the species composition of the fossil sites corroborates our results. An important proportion of the species of our fossil communities are typically arid-adapted taxa, as inhabitants of arid localities. However, the presence of a few taxa allows us to assess further details of the environment (more arid and open, or more humid and close). For example, arid conditions are reflected in the presence of *Hispanotherium matritense* or *Anchitherium cursor*, two perissodactyls with hypsodont dentition and relatively gracile limbs that are adapted to open and arid conditions (Cerdeño and Nieto, 1995; Soria *et al*., 2000; Salesa *et al*., 2001; Hernández Fernández *et al*., 2003), or several members of the order Rodentia, such as *Armantomys*, *Microdyromys*, *Democricetodon* or *Cricetodon* (Weerd and Daams, 1978; Meulen and de Bruijn, 1982; Daams and Meulen, 1984; Mein, 1983; Sesé *et al*., 1985). This supports the idea of a more arid an open environment for Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5 fossil sites. On the contrary, all these taxa are absent in Arroyo del Olivar-Puente de Vallecas and Paracuellos 3, whereas other forest-adapted dwellers are found, pointing to a more closed and less arid environment. Some examples of such forest-adapted faunas are *Chalicotherium grande*, a perissodactyl with longer forelimbs and a brachiodont dentition (Sánchez, 2000); cervids such as *Euprox furcatus*, a browser with preferences for arboreal vegetation (Soria *et al*., 2000), or the rhinoceros *Lartetotherium sansaniense* with shorter and slightly more robust limbs than *Hispanotherium* (Sánchez-Chillón and Cerdeño, 2000).

Additionally, the presence of thermophile species, such as *Lagopsis penai, Lagopsis verus, Microdyromys koenigswaldi, Microdyromys monspeliensis* (López Martínez, 1977; Meulen and de Bruijn, 1982; Daams and Meulen, 1984; Mein, 1983; Sesé *et al*., 1985; Luis and Hernando, 2000) in all the fossil localities confirms the warm conditions of the Madrid Basin during the sequence.

5. Conclusions

While at the global scale body size spectra and cenogram methodologies seem to have low capability to discriminate biomes from the data in modern localities, when the biogeographic histories of modern faunas are considered, body size community structure of prey mammals emerges as a good proxy for inferring biomes. Nevertheless, when the method is applied to the fossil record, the biome inferences may appear inaccurate, although fluctuations in climate and environments are precisely recovered.

Compared with the extant mammals from the Palaeotropics, the body size community structures of the Aragonian mammals present in the Madrid Basin allowed us to infer a predominance of semiarid environments between 15.5 and 13.5 Ma. Additionally, the methodologies used here allowed us to clearly distinguish several pulses of distinctive aridity throughout the whole sequence. A phase of arid climate and open environments was detected at the beginning of the sequence (Estación Imperial and Paseo de las Acacias fossil sites), which was followed by an environmental change towards a more humid and forested phase (Arroyo del Olivar-Puente de Vallecas). Arid conditions and grass-dominated habitats returned to central Iberia associated to the Global Cooling Event of the middle Miocene (coinciding with Somosaguas fossil site age). At the end of the sequence (Paracuellos 3 fossil site) the landscape returned to a more covered and humid scenario.

When the body size community structure of the fossil faunas was deeply analysed, a positive influence of the aridity over the relative percentages of small prey was recovered. Nevertheless, this influence is masked by other climatic factors (e.g. temperature) in the actual faunas. Nonetheless, cenogram methodology also detects this influence, not only in fossil sites, but also in the extant mammalian communities. The slope of the line that defines medium to large prey (P5) is more marked in arid environments than in relatively more humid ones. The magnitude of the gap between small and medium-large (G) prey also shows this influence, having bigger gaps in humid localities. This contradicts Legendre's more accepted rules over cenograms, which stated that the more arid the environment is, the larger the gap between small and medium-large prey. Nevertheless, our methodology uses a macro-scale approach to analyse climatic evolution, and some differences are expected if a smaller geographical scale is taken into account.

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