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Updated biochronology of the Miocene mammal faunas from the Madrid basin (Spain)

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New data on the mammal fossil record from the Madrid basin are presented. An updated biochronological arrangement of the Madrid basin faunas is proposed based on the results of similarity analyses. Similarity analysis was performed using either entire faunas, the large mammals, or the small mammals and the results are discussed and compared with other biochronologic and biostratigraphic European scales. New data on the relative abundance of mammal taxa from localities of the Madrid basin are presented and discussed.

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INTRODUCTION

Tertiary fossil mammals have been known from the Madrid area since the beginning of the nineteenth century (Ezquerra del Bayo 1837; Kaup 1840; Meyer 1844). After the first synthesis made by Prado (1864), these mammal faunas received little attention until the work of Royo Gómez & Menéndez Punget (1929). They carried out a paleontological study related to the elaboration of the first Geological Map (scale 1:50.000) of the Madrid Province. After a long period without paleontological work due to the Spanish Civil War, these faunas were then preliminarily studied by Crusafont & Villalta (1947), and more intensively in the 80's by Alberdi (1985). This date coincides with the promulgation of the Spanish Historical Heritage Law that included the paleontological record. Discoveries of new vertebrate localities in Madrid have recently multiplied due to paleontological surveys made during the construction of new public works. During the last ten years our knowledge of the mamma-

Table 1 Mammal fauna lists of Aragonian localities from the Madrid basin.

	Puente de Toledo	San Isidro	San Isidro 2	Cocheras	La Hidroeléctrica	Moratines	PAR Peñuelas	Estación Imperial	Paseo de las Acacias	Gasometro 6	Paseo de la Esperanza	Paseo de la Esperanza 7	Ciudad Pegaso	O'Donnell	Henares 2	Arroyo del Olivar	Puente de Vallecas	Cerro de Almodovar 1	Cerro de Almodovar 2	Henares 1	Paracuellos 5	Alhambra-Túneles	Paracuellos 2	Paracuellos 3	Moraleja de Enmedio
	Dc													Dd		E	F						G		
Tethytragus sp	X	X			X	X		X	X		X			X		X	X				X	X			
Tethytragus langai																								X	
Heteroprox moralesi																	X			X	X	X			
Heteroprox larteti																							X	X	X
Euprox furcatus																								X	X
Procervulus dichotomus	X				X		X		X		X														
Lagomeryx minimus					X																				
Triceromeryx pachecoi	X	X			X	X	X	X	X		X			X											
Amphitragulus sp.					X																				
Paleomeryx magnus																	X				X			X	
Hispanomeryx aragonensis																						X	X		
Micromeryx flourensianus					X									X		X				X				X	
Dorcatherium crassum									X		X														
Conohyus simorrense					X	X											X					X			
Bunolistriodon lockharti	X	X			X	X		X	X		X						X								
Listriodon splendens																				X	X			X	X
Suidae indet.																				X					
Caenotherium miocaenicum				X	X	X		X	X		X	X	X	X	X										
Hispanotherium matritense	X				X	X	X	X	X		X	X													
Alicornops simorrense																						X		X	X
Hoploaceratherium tetradactylum					X															X	X				
Hoploaceratherium sp.																	X								
Lartetotherium sansaniense																							X	X	
Rhinocerotidae indet						X											X								
Anchitherium sp.		X				X					X	X								X			X	X	X
Anchitherium alberdiae					X		X																		
Anchitherium matritense	X							X	X								X								X
Anchitherium cursor																X						X			
Anchitherium procerum																					X				
Gomphotherium angustidens	X	X			X		X								X	X	X				X	X	X	X	
Zygolophodon turiciensis					X																				
Chalicotherium grande																								X	
Magerictis imperialensis								X																	
Proputorios sp.					X			X	X																
Hemicyon sansaniensis																				X					
Hemicyoninae indet								X														X			X
Plithocyon armagnacensis																	X				X				
Amphicyon major					X			X	X								X							X	
Amphicyon giganteus																				X					
Pseudaelurus lorteti						X											X							X	
Pseudaelurus quadridentatus																	X				X	X		X	
Protictitherium crassum																					X			X	
Soricidae indet								X						X		X				X		X			
Galerix sp.			X										X		X	X					X	X		X	
Galerix exilis														X											
Crocidurinae indet																		X			X				
Amphechinus cf. intermedius																					X				
Lagopsis penai			X	X		X		X	X	X		X	X	X	X	X		X							
Lagopsis verus																				X	X	X		X	
Prolagus sp.																					X				
Democricetodon sp.								X	X	X		X													
Renzimys lacombai													X	X	X										
Fahlbuschia koenigswaldi													X	X	X										
Fahlbuschia darocensis																X				X	X	X		X	

Table 1 Mammal fauna lists of Aragonian localities from the Madrid basin (continued).

	Puente de Toledo	San Isidro	San Isidro 2	Cocheras	La Hidroeléctrica	Moratines	PAR Peñuelas	Estación Imperial	Paseo de las Acacias	Gasometro 6	Paseo de la Esperanza	Paseo de la Esperanza 7	Ciudad Pegaso	O'Donnell	Henares 2	Arroyo del Olivar	Puente de Vallecas	Cerro de Almodovar 1	Cerro de Almodovar 2	Henares 1	Paracuellos 5	Alhambra-Túneles	Paracuellos 2	Paracuellos 3	Moraleja de Enmedio
	Dc													Dd		E	F						G		
Megacricetodon collongensis			X	X		X		X	X	X		X	X	X	X	X		X							
Megacricetodon gersii																			X	X	X	X			
Megacricetodon rafaeli																					X	X			
Megacricetodon crusafonti																								X	
Microdryomys sp.								X		X					X										
Microdryomys legidensis												X		X											
Microdryomys koenigswaldi									X					X							X			X	
Pseudodryomys simplicidens						X		X	X			X		X	X										
Armantomys jasperi									X	X		X													
Armantomys aragonensis			X			X		X	X	X		X	X												
Armantomys tricristatus														X	X	X				X	X	X		X	
Heteroxerus rubricati						X		X	X	X		X								X	X	X		X	
Heteroxerus grivensis														X	X	X		X				X		X	
Atlantoxerus blacki								X	X																
Spermophilinus sp.														X											

lian fossil record from Miocene deposits of the Madrid basin has especially increased (Herraez 1993; Morales *et al.* 2000).
The mammal fossil record from the Madrid basin ranges from the Upper Oligocene, e.g. the Sayatón faunas (Alvarez-Sierra *et al.* 1996), to the upper Turolian (Sesé *et al.* 1990), although many of the mammal faunas are dated as middle Aragonian (biozones Dc and Dd). Despite this uneven faunal preservation during the Aragonian, a relatively continuous sequence from biozone Dc to biozone G is well represented in the Madrid area. This new information of the fossil faunas allows us to establish a more precise biochronologic framework of the Madrid basin than that proposed in previous investigations (Alberdi 1985, López Martínez *et al.* 1987, Calvo *et al.* 1993).

The aims of this work are: (1) to present the new faunal data; (2) to present a biochronologic arrangement of Miocene mammal faunas from the Madrid Basin compared with other scales, such as the Mammalian Neogene (MN) zones (Mein 1975) or the local zonation proposed recently by Daams *et al.* (1999) for the Aragonian of the Calatayud-Daroca basin; and (3) to present quantitative data on the relative abundance of mammal taxa in the Madrid basin and its evolution through time.

MATERIAL AND METHODS

The database used to perform the present work comprises small and large mammals from several localities ranging from zone Dc to G of Daams *et al.* (1999). The revised taxonomic composition of the mammal associations from the Madrid basin (Table 1) shows several peculiarities when compared to faunas from other Aragonian Spanish basins. During the Middle Aragonian large mammals show some degree of endemism, e.g. the *Anchitherium* species from Madrid represent a clade that evolved independently during the Aragonian (Sánchez et al. 1998). On the contrary, the small mammal taxa from Madrid are identical to those recorded in other Spanish basins. The only difference is the low species richness in Madrid faunas, mainly due to the small number of glirid species and the absence of cricetids like *Cricetodon* and representatives of the *Megaricetodon minor-debruijni* lineage.

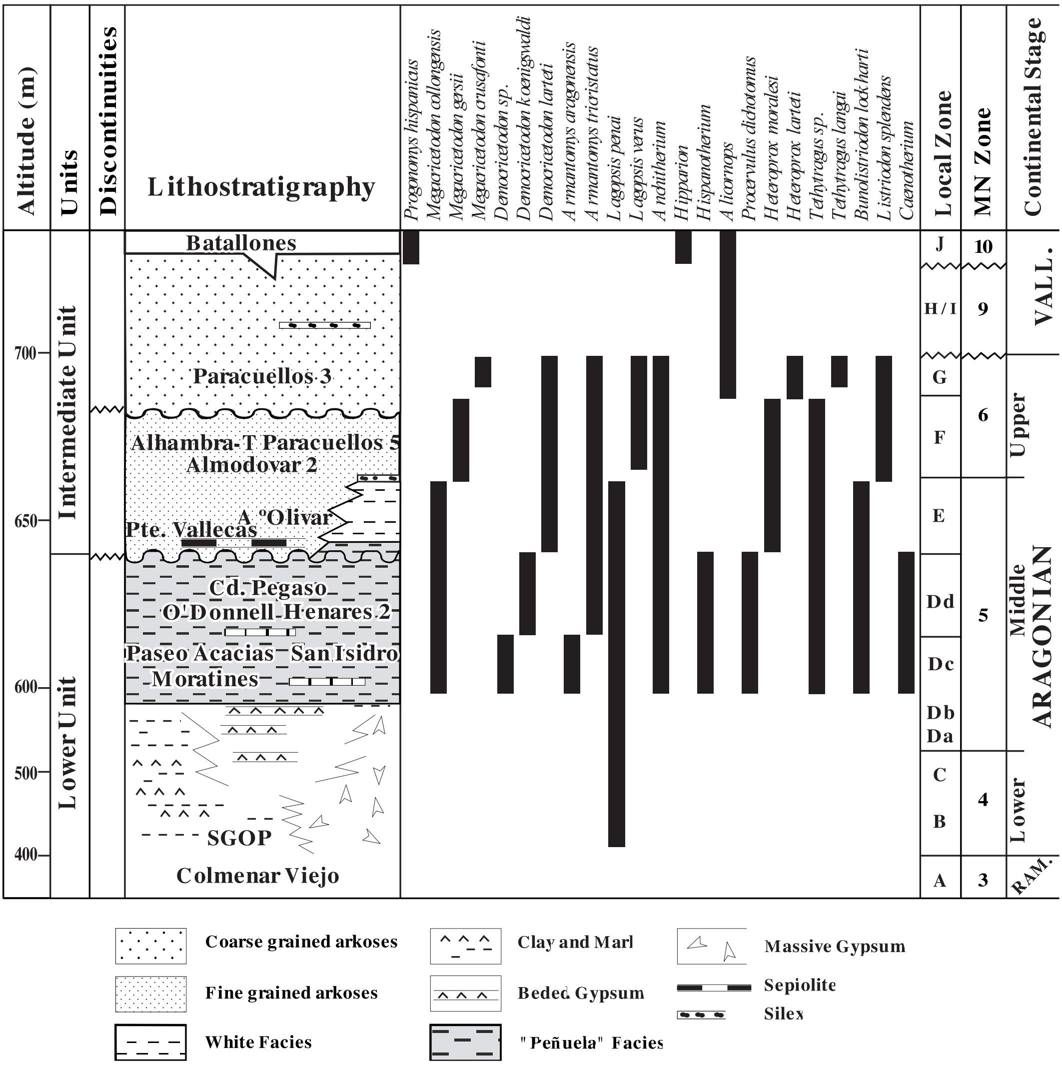

Figure 1 Biostratigraphy of the middle and late Miocene localities from the Madrid Basin. Lithostratigraphic scheme, distribution of selected large and small mammals and proposed correlations with the local zonation of Daams *et al.* (1999) and Mein (1975).

Despite those differences, correlations with the Calatayud-Daroca local zonation of Daams *et al.* (1999) have been tentatively established using the stratigraphic relationships and the faunal composition of several localities from the Madrid basin. The results as well as the biochronologically most indicative taxa are presented in Figure 1. While the latter local scale is based mainly on rodent faunas, our biochronologic analysis includes all the mammal information available from the Madrid basin in order to test how well it correlates with the most widely used scales for the European Miocene, the MN units and the Calatayud-Daroca local biozonation.

In order to recognize a sequence of biochronologic units of the Aragonian mammal faunas from the Madrid basin, we have performed several cluster analyses using the computer program NTSYS-PC version 1.8 (Rohlf 1993) and the UPGMA method (Unweighted pair-group method, arithmetic

Table 2 Relative abundance of selected large mammal groups in Aragonian localities from the Madrid basin.

	Proboscidea	***Anchitherium***	**Rhinocerotidae**	**Suidae**	**Palaeomerycidae**	**Cervidae**	**Bovidae**	**Tragulidae**	**Other**
PARACUELLOS 3			43,0	2,0	1,0	7,0	39,5		7,0
PARACUELLOS 5	10,0	50,0	5,0	2,0		18,0	8,0		7,0
PUENTE DE VALLECAS	3,0	55,0		3,0		16,0	23,0		
PASEO DE LAS ACACIAS		32,5	25,3	1,5	5,8	12,1	5,5	1,7	15,6
ESTACIÓN IMPERIAL	1,0	52,2	6,0	10,6	12,2		1,7		16,4
MORATINES	3,0	37,0		10,0	35,0		8,0		7,0

average). The latter method keeps the same weights on all grouping levels, and therefore, a smaller bias concerning the similarity matrix (Hazel 1970; Shi 1993). Among the vast spectrum of similarity indices, we have selected the Jaccard index because it does not consider the shared absences. Shared absences do not imply a higher similarity between faunas, but may indicate higher taphonomic, ecological or geographic bias, given the special characteristics of the continental fossil record (Alberdi *et al.* 1997). In addition, the Jaccard index is particularly adequate to our analysis because its values are positive and range between 0 and 1. It is also metric, symmetric, and insensitive to sample size and shows a linear relationship with the number of shared taxa (Shi 1993).

We have tested the goodness of fit of the cluster analysis with the similarity matrix using the cophenetic correlation coefficient (CCC). This was obtained by comparing the

Table 3 Relative abundance of rodent taxa in Aragonian localities from the Madrid basin.

	LOCAL ZONE	*Megacricetodon collongensis*	*Megacricetodon gersii*	*Megacricetodon rafaeli*	*Megacricetodon crusafonti*	*Fahlbuschia koenigswaldi*	*Renzimys lacombai*	*Fahlbuschia darocensis*	*Democricetodon sp.*	*Pseudodryomys simplicidens*	*Armantomys jasperi*	*Armantomys aragonensis*	*Armantomys tricristatus*	*Microdyromys legidensis*	*Microdyromys koenigswaldi*	*Microdyromys sp*	*Heteroxerus rubricati*	*Heteroxerus grivensis*	*Atlantoxerus blacki*	*Spermophilinus sp.*	*Lagopsis penai*	*Lagopsis cf. penai*	*Lagopsis verus*	*Prolagus sp.*
PARACUELLOS 3	**G**				73			3,3					13		1,4		3,8	0,5					4,8	
PARACUELLOS 5	**F**		40	6,7									5,3		1,8		11						33	3,5
TUNELES			51	19				7,5					4,7				7,5	0,9					9,3	
HENARES 1			73					9,1					4,5				9,1						4,5	
ARROYO DEL OLIVAR	**E**	19						30					24					1,3			25			
HENARES 2	**Dd**	39				4,3	5,7			7,1			10			1,4		16			17			
O'DONNELL		25				25	1,6			1,4			4	3,8	0,2			6,4		0,2	32			
ESPERANZA 7	**Dc**	53							5,3		16	11		5,3			5,3				5,3			
GASOMETRO 6		63							2		2	12				3,9	14				3,9			
PASEO DE LAS ACACIAS		39							2,7	6,4	1,8	24		0,9	5,5		4,5		0,9		15			
ESTACIÓN IMPERIAL		14							8,1	8,1		49				2,7	11		2,7			5,4		
MORATINES		20								10		20					40					10		

original clustered similarity matrix with the cophenetic value matrix calculated on the basis of the obtained cluster.

In order to avoid overrepresentation of taxa, the original database (Table 1) was revised such that: (1) taxa denominated as *confer* were included in their nominal taxon and (2) taxa identified as sp. or indet. were eliminated from the database. In addition to the fauna list used for the biochronologic study, data on the relative abundance of large and small mammals from well-represented faunas are presented and compared with the fossil mammal record from other Spanish basins. Data for large mammals are presented in Table 2 and small mammals in Table 3. Data on relative abundance were independently calculated for large and small mammals because the sampling methods were different, and in some of the localities even the sampling effort was different. Furthermore, there are numerous localities where just large or small mammals were recorded.

SIMILARITY ANALYSIS

Three cluster analyses were performed to study the relationships among the different local faunas based on the presence of shared taxa (Q-mode). A first cluster analysis was calculated using the complete faunal database, and two others were calculated using just micro mammals or macro mammals. The reason for these three cluster analyses is the fact that there are faunas from which either macro mammals or micro mammals were recorded, or one of these groups is poorly represented.

The obtained dendrograms are shown in Figures 2, 3 and 4. It is evident that the resulting arrangement of localities is somewhat different in each of the cluster analyses. These differences are mainly due to the fact that the representation of large and small mammals is not equivalent at each of these localities. Localities with few specimens may be arranged differently depending on the particular distribution of the records from them.

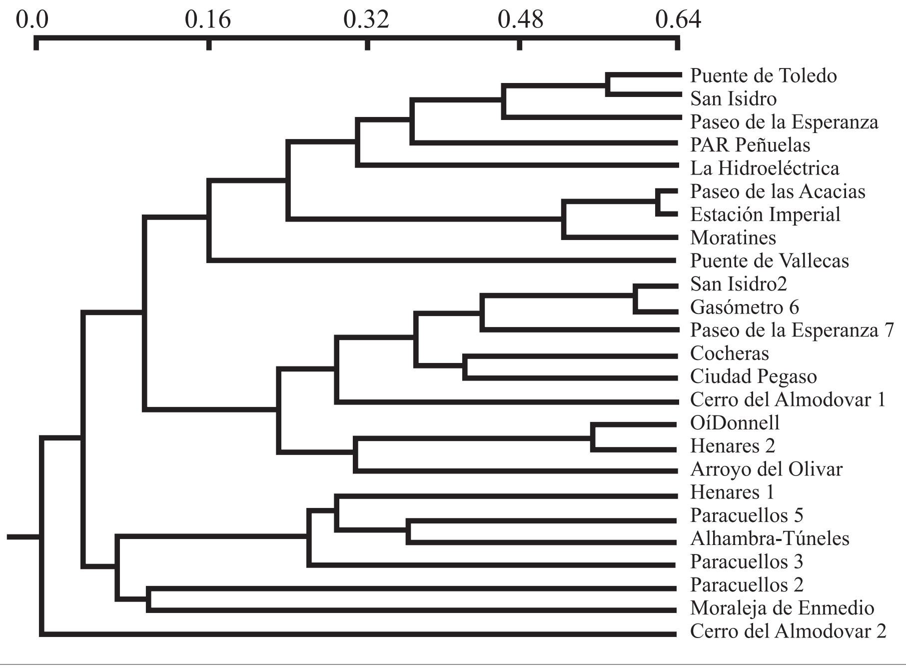

Figure 2 Similarity dendrogram (Q mode) of Aragonian localities from the Madrid basin, based on whole mammal faunas. CCC=0,83407.

Cluster analysis of the complete mammal faunas (Fig. 2):

The dendrogram shows a clear differentiation between faunas dated as middle Aragonian and those dated as late Aragonian. This differentiation corresponds to the MN zonation proposed by Mein (1975). The localities from the middle Aragonian are correlated with MN 5 while all localities from the late Aragonian correlate with MN 6. Nevertheless, the dendrogram does not reveal other, more detailed, zonations proposed by other authors, such as that of Daams *et al.* (1999), built on the basis of local faunas from the Aragonian type area in Spain. As has been pointed out previously, the results shown in Figure 1 could be explained by preservational bias because there are localities that have exclusively macro mammals or micro mammals, while some have both groups represented, often in different proportions. Therefore, the arrangement of localities within the different zones could be an artefact that has no biochronologic meaning.

Cluster analysis including only micro mammals (Fig. 3):

The obtained dendrograms show, as in the one for the whole fauna, a clear separation between localities from the middle and late Aragonian, hence between localities correlated with MN 5 or MN 6 respectively. The main differences between these two periods are the presence of the lagomorph *Lagopsis* in the former versus the cricetids *Megacricetodon gersii* and *M. rafaeli* or *M. crusafonti* in the late Aragonian localities. In this case, contrasting with the cluster analysis of the whole mammal faunas, in this analysis the clustering within the main division has a biochronological meaning. Compared with the local zonation proposed by Daams *et al.* (1999) on the basis of rodents, there is a clustering of localities that can be correlated with the zones Dc, Dd and E of the middle Aragonian, and with the zones F and G of the late Aragonian.

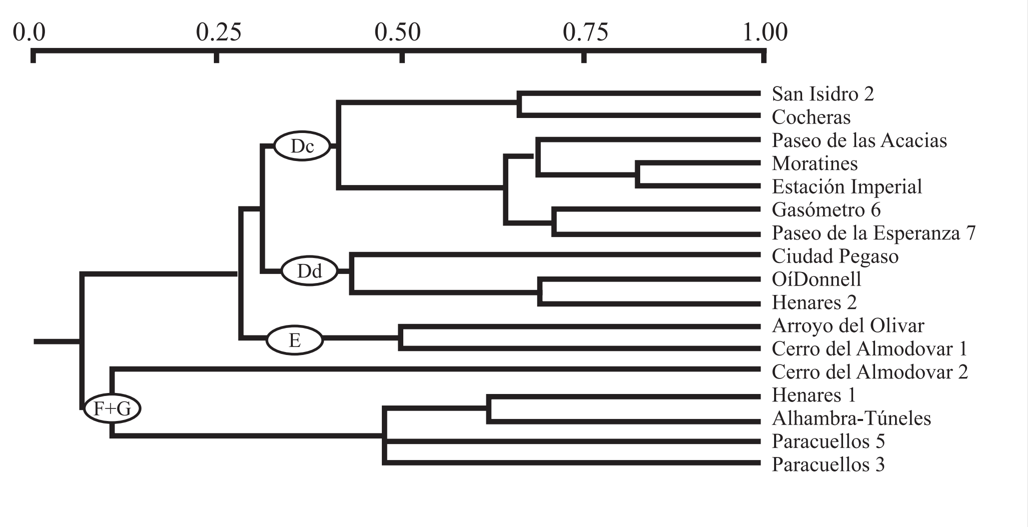

Figure 3 Similarity dendrogram (Q mode) of Aragonian localities from the Madrid basin, based on small mammal faunas. CCC=0,93528.

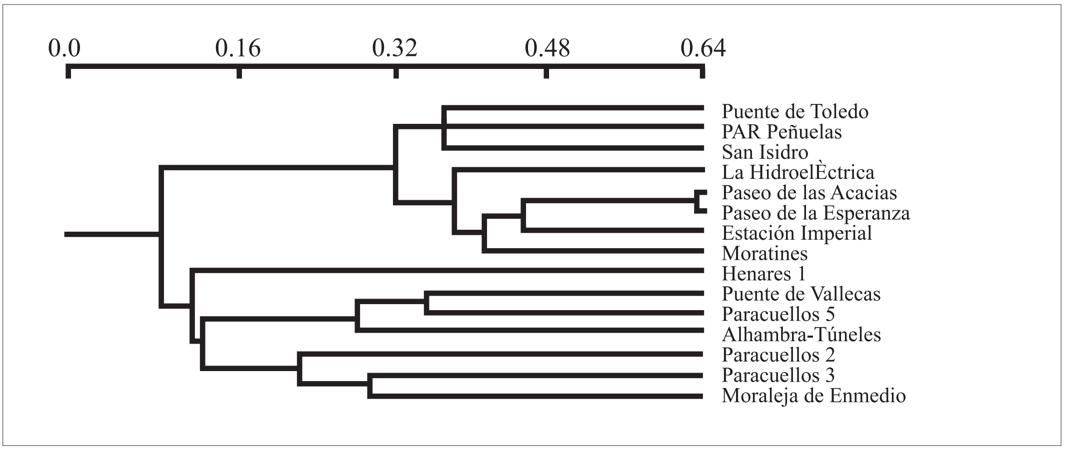

Figure 4 Similarity dendrogram (Q mode) of Aragonian localities from the Madrid basin, based on large mammal faunas. CCC=0,935.

Cluster analysis including only macro mammals (Fig. 4): Considering exclusively the large mammals, the obtained clustering appears more ambiguous when trying to find a correspondence with the established zonations. Again, two groups, representing the middle Aragonian and late Aragonian are easily discernible. Inside the latter, localities of biozones F and G can be distinguished. The Puente de Vallecas locality, however, is incorrectly placed within the late Aragonian cluster. The similarity of the fauna from this site with those recorded in upper Aragonian sediments were pointed out by Morales & Soria (1985). These authors recognized that the only dissimilarity between the faunas is the presence of different taxa of suids. The similarity between Puente de Vallecas and the late Aragonian faunas can be explained by the clustering shown in Figure 3. However, in our opinion, it is also important to note that there is an under-representation of large mammal localities in zone Dd of the Madrid Basin. Therefore, the differences between Dc and E faunas may be exaggerated.

RELATIVE ABUNDANCE

Large mammals

Table 2 shows the relative abundance of primary large mammals groups from the Aragonian of the Madrid basin. Evidently, there is a general trend towards a decrease of Palaeomerycidae. The decrease is more or less gradual from localities with a high percentage of palaeomerycids such as La Hidroeléctrica. In the beginning, the decrease may have been due to a climatic trend to more arid environments, but later, from Paseo de las Acacias, it could be interpreted as the result of competition with the cervids, since both groups can be considered as bunodont herbivores of medium to large body size. During zone Dc an increase of the Perissodactyla is observed which, depending on the locality, could be due either to the predominance of *Anchitherium* (bunodont) or *Hispanotherium* (hypsodont). These differences in faunal composition can be interpreted as the result of differences in local landscape structure, more closed or open, instead of climatic change. Finally, in zone G there is a relative increase in the abundance of bovids.

Small mammals

The rodents from the Madrid basin show a relative abundance distribution (Fig. 5) that differs clearly from other Spanish basins such as Calatayud-Daroca (Freudenthal 1988, van der Meulen & Daams 1992) and Loranca (Morales *et al.* 1999). Although the main

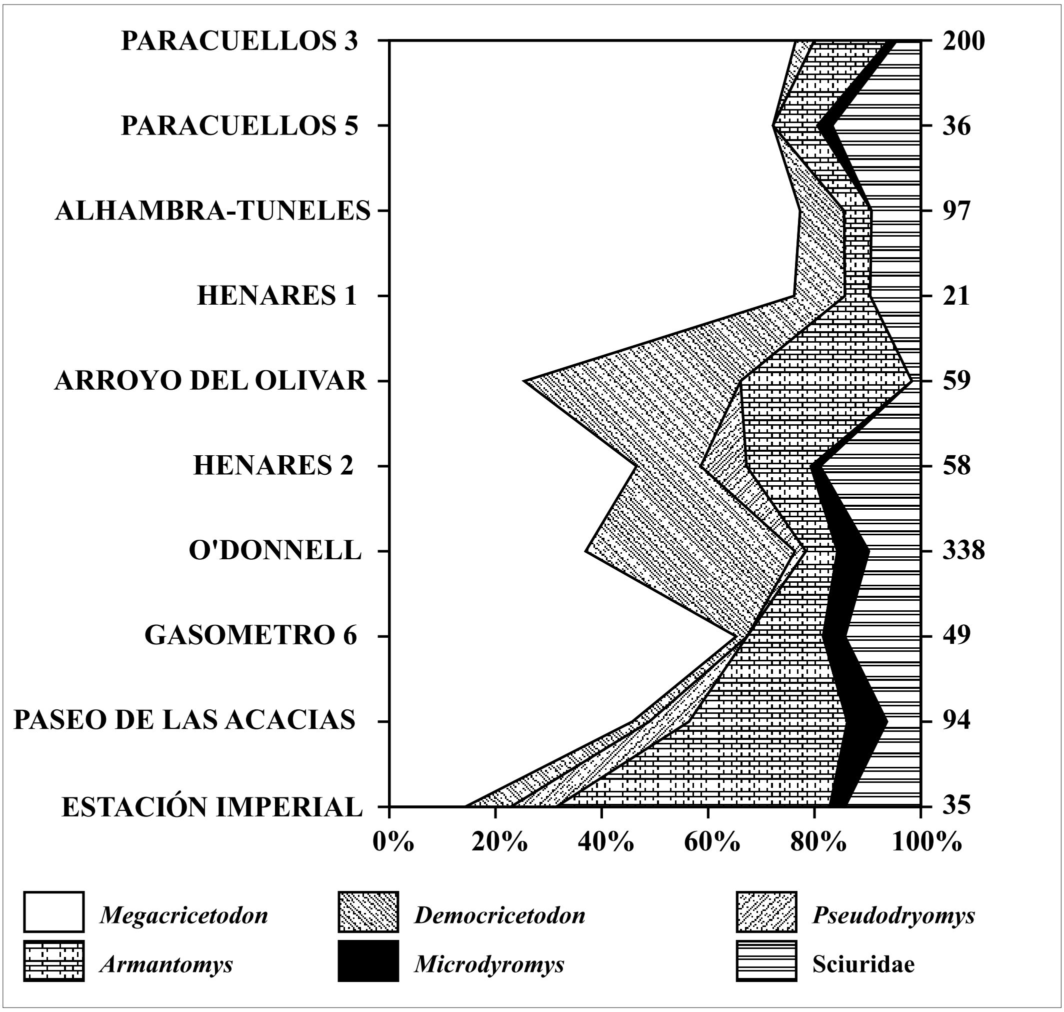

Figure 5 Relative abundance of rodent genera of Aragonian localities from the Madrid basin. The numbers on the right side represent the frequency of upper and lower first and second molars.

rodent groups in all the basins display a similar trend towards an increase in the relative abundance of cricetids during zone Dc, the relative abundance within each genus is different. The rodent record from Madrid always shows a high relative abundance of the glirid *Armantomys*, which is a rare species in the other basins. There is also a low abundance of other glirid taxa. The cricetids from Madrid are represented mainly by *Megacricetodon*, while in the other basins during most of zone D the most frequent cricetid is *Democricetodon*. In addition to this, it is important to note the absence of cricetodontine rodents and representatives of the lineage *Megacricetodon* minor-debruijni.

The general trend observed in abundances of the main rodent groups is interpreted as consequence of a global climatic change because it is observed in all the basins. However, the differences among species composition and their abundances may be due to regional differences in landscape. Probably the high number of *Armantomys* and sciurids recorded in the Madrid basin can be explained by a more open landscape in this area.

CONCLUSIONS

Based on similarity analyses, it is possible to establish a biochronologic arrangement of mammal fossil localities in the Madrid basin. In the analyses there is a clear differentiation between faunas correlated with MN5 and those with MN6. When trying to establish a more detailed biochronologic subdivision, it is obvious that the best results are obtained from the micromammal record. Similarity analysis using exclusively small mammals allows us to recognize the subdivisions proposed by Daams *et al*. (1999) for the Aragonian type area. Despite some obvious differences, it is possible to correlate Madrid basin faunas with other European and Spanish biochronologic zonations.

The corrected correlations presented here allow study of faunal changes that occurred during the Aragonian in the Madrid basin from both a taxonomic and ecological perspective. We conclude that the landscape in the Madrid basin was probably relatively more open and perhaps more arid than in other areas, although, on the whole, the climatic conditions were similar throughout the Iberian Peninsula during the study period.

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