

Ecostratigraphy of micromammal faunas from the Neogene of Spain

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Daams, R., M. Freudenthal & A.J. van der Meulen. Ecostratigraphy of micromammal faunas from the Neogene of Spain. — *Scripta Geol.*, Spec. Issue, 1: 287-302, 5 figs., Leiden, May 1988.

The paleoecological analysis of Neogene rodent faunas in the Calatayud-Teruel Basin leads to the recognition of three relatively cool, and two relatively warm periods. The humidity curve reveals four wet and four dry periods. The results agree remarkably well with temperature and humidity curves obtained from other geological disciplines.

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Introduction

At the VII International Congress on the Mediterranean Neogene (Athens, 1979) it was felt that future research activities of the Regional Committee on Mediterranean Stratigraphy (R.C.M.N.S.) should concentrate on ecostratigraphy.

According to the definition given by Martinsson (1973) ecostratigraphy implies 'the construction of time planes with the greatest possible precision and frequency through environmentally-defined stratigraphic units'. This requires 'a far-reaching systematical and ecological knowledge of the organisms and communities involved'. Both statements illustrate the need to evaluate the principles of, and to develop methods applicable in paleoecological interpretations. It may lead to a better correlation between bio- and chronostratigraphic units from the marine realm on the one hand, and those from the continent on the other. It may also contribute to a better understanding of the depositional environment of various mineral resources in continental basins.

In the present paper we intend to put into practice the above-mentioned ideas using assemblages of small mammals from the Neogene of selected areas in Spain. During the chosen time interval ($\pm 20 - 1.5$ million years ago) drastic changes in the composition of the European mammal faunas are known to have occurred. Paleoclimatic and paleoecological factors, and tectonic events may have played an important role in these changes.

CURRENT STATE OF THE ART

During the past 25 years a great number of rich mammal localities have been sampled in various basins in Spain. This is particularly true for localities with so-called micromammals, i.e. Insectivora, Rodentia, Lagomorpha, and Chiroptera.

The existence of these localities lead the participants of the International Symposium on Mammalian Stratigraphy of the European Tertiary (München, April 1975) to propose formally that three Miocene 'Mammal Stages' were to be defined on the basis of type sections in Spain. One of these stages is the Aragonian, which has consequently been described by Daams, Freudenthal & van de Weerd (1977). In the summers of 1976 - 1983 many new faunas have been collected by Daams and Freudenthal and their team in the area of the type section, the Daroca-Calamocha area in the Calatayud-Teruel Basin. The resulting faunal succession covers the Lower Miocene (the Ramblian, recently defined by Daams, Freudenthal & Alvarez, 1987) and the Middle Miocene (the mentioned Aragonian), and it is the most detailed sequence of rodent assemblages in the world.

Daams and van de Weerd, who studied the rodents from the type area of the Turolian (around the city of Teruel), were the first to attempt a paleoecological interpretation of the Neogene rodents of Spain (van de Weerd & Daams, 1978). A more detailed study by Daams & van der Meulen (1984) resulted in the construction of humidity and temperature curves for the Early Miocene, mainly on the basis of changes in the composition of faunas from the Daroca-Calamocha area. The humidity curve resembles the one of van de Weerd & Daams (1978), but it is more refined. The temperature curve (the first one based on Miocene rodents) agrees remarkably well with the one constructed by Muller (1984), based on oxygen isotopes in planktonic organisms from the Miocene of the Atlantic and Mediterranean.

These promising results justify in our opinion the effort to substantiate further and to elaborate our paleoecological investigations. In the future a detailed ecostratigraphic scheme may be constructed, but more paleoecological data, like the ones mentioned above should be obtained.

METHODS

We intend to achieve our aims by the comparative study of the qualitative and quantitative changes in the composition of the micromammal faunas from coeval, densely sampled sections in various basins in Spain. In this paper we will only deal with the faunas from the Calatayud-Teruel Basin, ranging in age from the Early Miocene to the Ruscinian. The faunas originate from four areas (Fig.1): the Daroca-Villafeliche area, the Calamocha area, the Bañón area (Daams et al., 1987), and the Teruel-Alfambra area (van de Weerd, 1976).

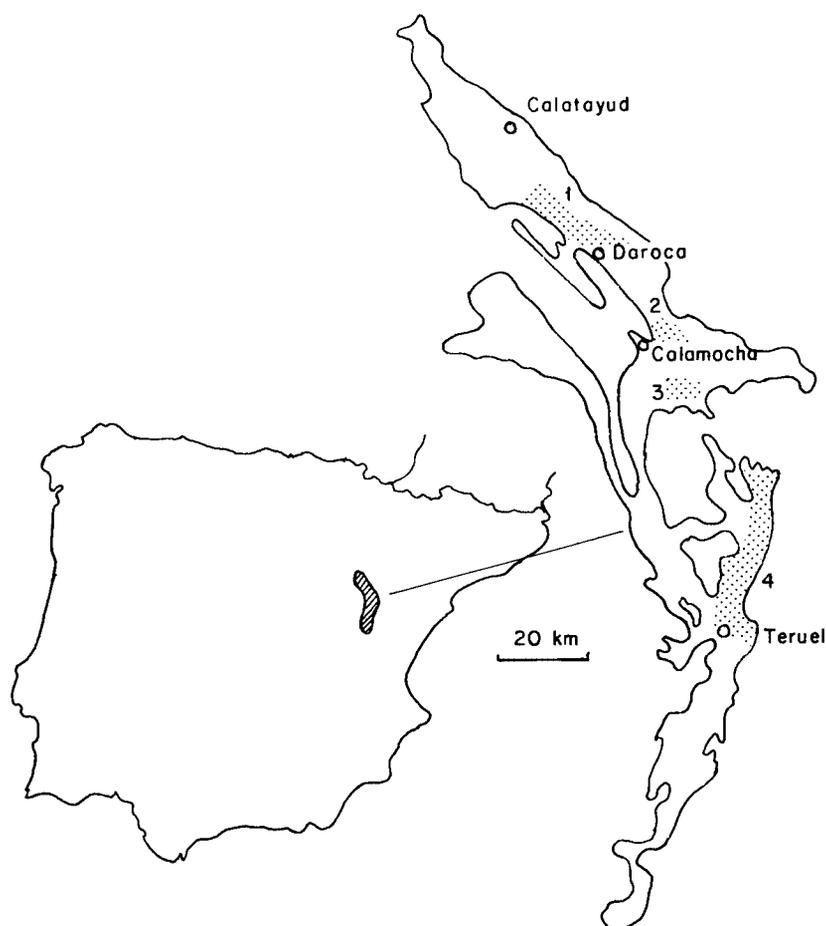


Fig. 1. Sketch of Spain and situation of the Calatayud-Teruel Basin. The dotted areas indicate major concentrations of fossiliferous sites.

Working hypothesis

Before starting a paleoecological interpretation, we made a number of basic assumptions on habitat preferences of various rodent groups. The ecology of living representatives was extrapolated to the fossil ones, whenever possible:

Castoridae (beavers) require streams with a continuous flow of water.

Sciurinae (squirrels) in our faunas belong to the ground-squirrels, which prefer dry, open country.

Gliridae: van der Meulen & de Bruijn (1982) grouped living and fossil glirid species (dormice) on the basis of characteristic features of the upper first and second molars and extrapolated the ecology of the living representatives to the fossil species. Their grouping, slightly changed by Daams & van der Meulen (1984), will be used in the present paper.

Petauristinae (flying squirrels) require forests.

Eomyidae: this is an extinct rodent family and an actualistic interpretation of their ecology is not possible. Nevertheless we think that all representatives of this family were forest-dwellers. Firstly, in localities where Eomyidae are relatively frequent, they are associated with forest-dwelling Gliridae, as for instance in Daams & Freudenthal's (1981) zone A and in the localities Las Planas 5K (Aragonian zone G, Spain) and Aliveri (Greece). Secondly, in localities where Eomyidae are the predominant group, lignite beds are often well-developed (Aliveri; Cetina de Aragón, zone Y). In Aliveri the Eomyidae are also associated with a relatively large number of flying squirrels (de Bruijn et al., 1980), and in Cetina de Aragón and Agreda (zone A) they concur with beavers.

Table 1 gives the habitat preferences of the rodents, as assumed in this paper. The habitat preference of Muridae is unknown, and has been omitted from Table 1. However, it is probable that *Parapodemus* and *Occitanomys* are rather indifferent. The faunas of Teruel on the one hand, and Crevillente (Alicante, de Bruijn et al., 1975) on the other obviously represent quite different environments; the *Parapodemus* and *Occitanomys* species from both areas are identical.

Changes in humidity

Two glirid peak zones, alternating with two eomyid peak zones (Fig. 2), are present in the Z-A-B-C interval. Eomyidae are thought to have been forest-dwellers, the Myomiminae, which constitute the large majority of the Gliridae in this interval, preferred an open country biotope. We, therefore, interpret the increase and decrease in the relative numbers of the eomyids in zones Z to C as expansion and shrinking respectively of the forest area. These changes are in turn controlled by changes in the humidity of the climate. Thus, in the Z-C interval zones Z and B are relatively dry, and zones A and C relatively humid.

In zones D, E, and F *Heteroxerus* and *Atlantoxerus* (Sciurinae, ground-squirrels) are relatively well represented. Myomiminae, although less frequent than in the preceding zones, still constitute the majority of the Gliridae in zone D. Both groups are supposed to have been open country dwellers. Representatives of forested biotopes are practically absent in the D-F interval.

In zones F and G the glirid fauna is quantitatively strongly impoverished, but not qualitatively. Various species of the forest-dwelling Glirinae are present, Eomyidae are

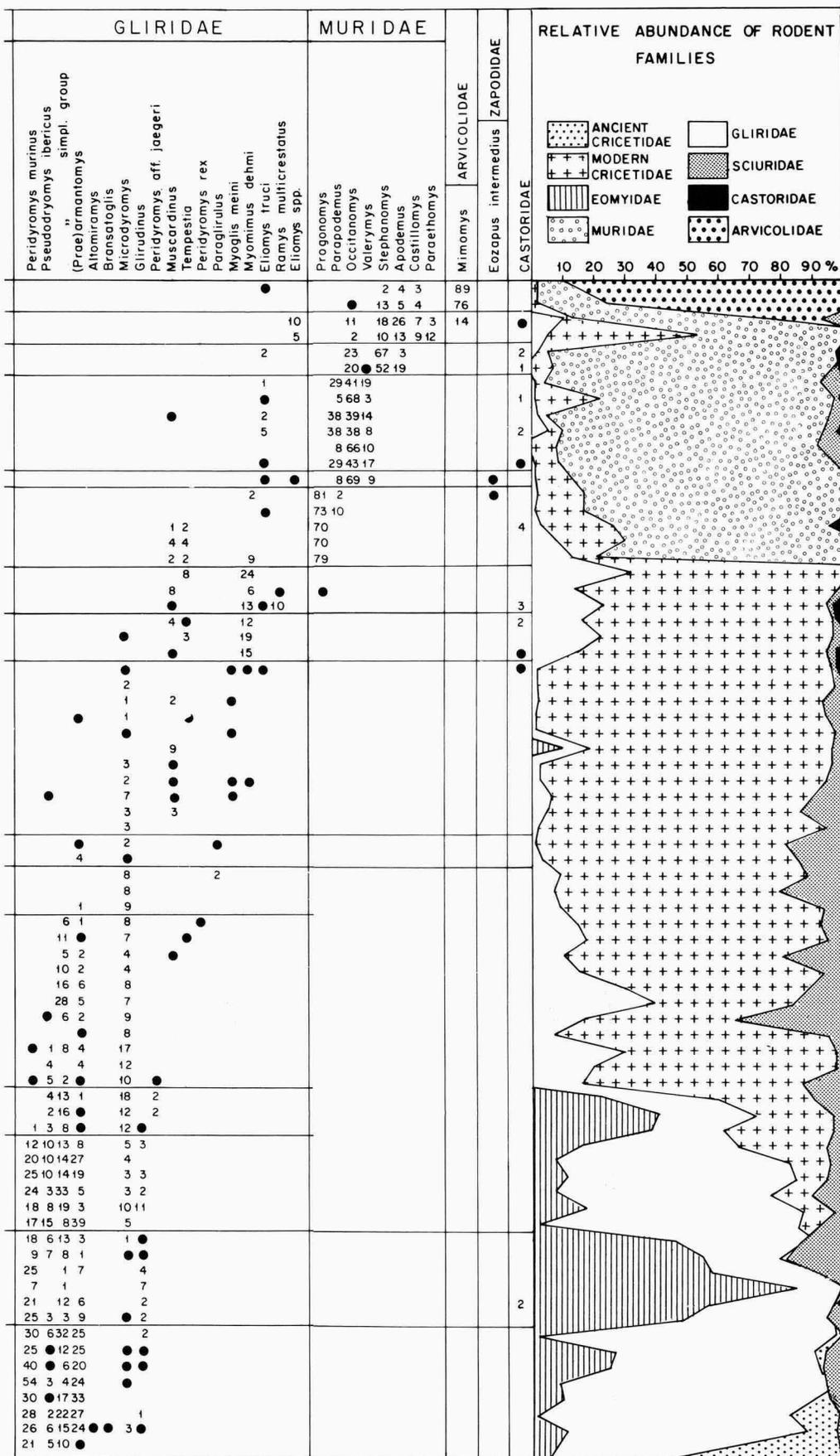
Table 1. Habitat preference of the Neogene rodents of the Calatayud-Teruel Basin.

	Cricetidae	Gliridae	Various
	<i>Melissiodon</i>	<i>Glirudinus</i>	Castoridae
W	<i>Eumyarion</i>	<i>Muscardinus</i>	Eomyidae
E	<i>Megacricetodon minor</i>	<i>Myoglis</i>	Arvicolidae
T	<i>Megacricetodon debruijni</i>	<i>Ramys multicrestatus</i>	Petauristinae
	<i>Democricetodon gaillardi</i>	<i>Branssatoglis</i>	
	<i>Neocricetodon</i> (=Cricetulodon)	<i>Peridyromys</i> aff. <i>jaegeri</i>	
		<i>Paraglrululus</i>	
C			
A			
T	<i>Megacricetodon primitivus</i>	<i>Microdyromys</i>	
H	<i>Megacricetodon collongensis</i>		
O	<i>Megacricetodon crusafonti</i>		
L	<i>Megacricetodon ibericus</i>		
I			
C			
	<i>Ruscinomys</i>	<i>Peridyromys murinus</i>	<i>Heteroxerus</i>
		<i>Pseudodryomys ibericus</i>	<i>Atlantoxerus</i>
		<i>Pseudodryomys simplicidens</i> group	
D		<i>Altomiramys daamsi</i>	
R		<i>Tempestia</i>	
Y		<i>Peridyromys rex</i>	
		<i>Myomimus dehmi</i>	
		<i>Eliomys truci</i>	
		<i>Eliomys</i> spp.	
	<i>Eucricetodon</i>		
U	<i>Democricetodon hispanicus</i>		
N	<i>Fahlbuschia</i>		
K	<i>Renzimys</i>		
N	<i>Pseudofahlbuschia</i>		
O	<i>Cricetodon</i>		
W	<i>Hispanomys</i>		
N	<i>Cricetus</i>		
	<i>Blancomys</i>		

present in two localities, and in one a flying squirrel has been found. Although the representatives from forested biotopes occur in low numbers, the decrease in number of Sciurinae also indicates that these zones must have had a more humid climate than the D-E interval. This is supported by the presence (return) of beavers in the uppermost locality of zone G (Solera).

In zones H and I the trend towards a more humid biotope continues. This is reflected by the frequency increase of the *Megacricetodon minor* – *debruijni* group, the entry of *Cricetulodon*, and the presence of forest-dwelling Gliridae such as *Ramys multicrestatus* and *Muscardinus hispanicus*.

A remarkable change in the fauna is noted at the base of the *Progonomys hispanicus* zone. The expansion of the Muridae coincides with the disappearance of various Cricetidae, but the hypsodont *Hispanomys*, supposedly a dry, open country dweller, continues and it is well represented. These events have been interpreted as a change towards a relatively dry climate, continuing during the Turolian. The increase of Sciurinae in the Middle Turolian would also point to this trend; macromammal faunas of



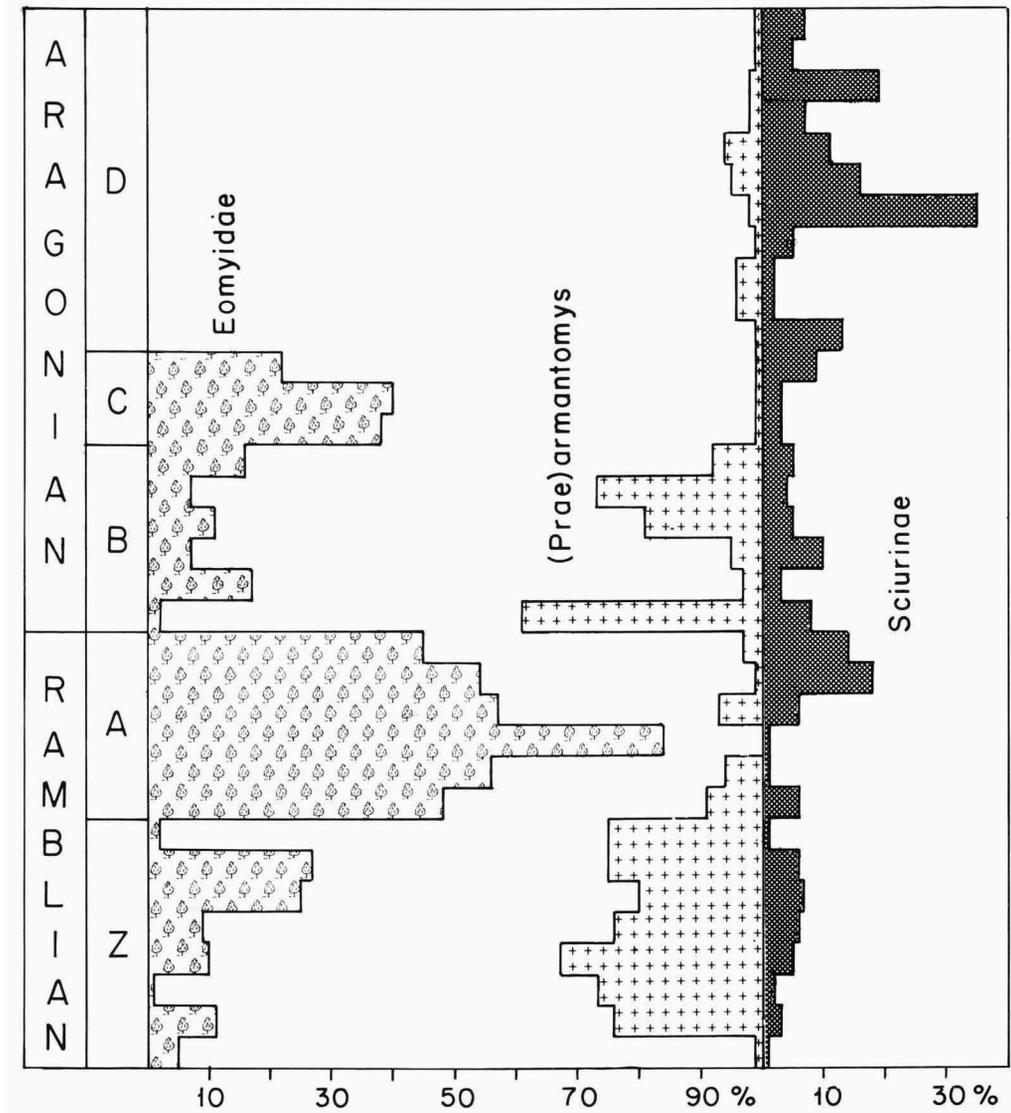


Fig. 3. Distribution pattern of Eomyidae, (Prae)Armantomys and Sciuridae in the zones Z to D.

← Fig. 2. Range chart of rodent genera and species from the Neogene of the Calatayud-Teruel Basin. Explication of partial range zones (van de Weerd, 1976): M.s. = *Mimomys stehlini* Zone; C.c.g. = *Castillomys crusafonti gracilis* Zone; S.r. = *Stephanomys ramblensis* Zone; P.g.b. = *Parapodemus gaudryi barbarae* Zone; P.l. = *Parapodemus lugdunensis* Zone; P.h. = *Progonomys hispanicus* Zone.

the Middle Turolian, such as Venta del Moro (Morales, 1984), contain many savannah dwellers as well.

The Turolian shows a general resemblance to the E and F zones of the Aragonian. The Sciurinae are relatively frequent, the Gliridae fauna is impoverished, the Cricetidae are well represented in the E and F zones, and the Muridae are abundant in the Turolian. Strongly impoverished faunas are characteristic for dry biotopes (Mares, 1980).

In the Ruscinian a trend towards a more humid climate is indicated by the immigration of *Trilophomys*, Arvicolidae and *Pliopetaurista* (flying squirrel).

Distribution of the Gliridae

We have calculated the relative frequencies of the genera and species of the Gliridae (Table 2); they have been grouped morphologically according to Daams & van der Meulen (1984). The relative frequency curves of the categories (open country dwellers, forest-dwellers and ubiquitous) are given in Fig. 4.

The following changes are apparent (Table 2):

- 1) *Peridyromys murinus* decreases considerably in frequency in the zone A to C interval and disappears in D.
- 2) The relative frequency of *Microdyromys* increases strongly in C and again in E and F, and it decreases in H.
- 3) The glirid assemblages of zones E and F are poorly diversified.
- 4) The glirid assemblages change in composition in the G-H interval.
- 5) The frequency of *Myomimus dehmi* increases strongly from G to H, and it decreases gradually afterwards until its disappearance in the Turolian.
- 6) The frequency increase of *Eliomys truci* from zone I to the Turolian.
- 7) The frequency increase of *Tempestia* from zone G to the *Progonomys hispanicus* Zone, followed by its decrease in the Turolian.
- 8) The frequency increase of forest-dwelling Gliridae from zones E and F to zone I, followed by its decrease in the Turolian.

We shall discuss these observations below and first consider the fluctuating frequencies of the Myomiminae in the Z-C interval. It appears that the fluctuations shown by this subfamily are mainly due to the relative frequency changes of (*Prae*)*Armantomys* (Fig. 3). This high-crowned glirid is supposed to have lived in dry, open country (Daams & van der Meulen, 1984). Faunas with abundant Eomyidae (zones A and C) show low percentages of (*Prae*)*Armantomys*, whereas the faunas from zones Z and B with few Eomyidae show high percentages. We conclude that during the wetter phases, indicated by the abundance of the Eomyidae, the biotope occupied by (*Prae*)*Armantomys* decreased relatively more in area than that of the other Myomiminae (*Peridyromys murinus* and *Pseudodryomys* spp.). We therefore assume that (*Prae*)*Armantomys* lived in the driest parts of the open country.

In Fig. 4 the relative frequencies of the Gliridae are given without counting the (*Prae*)*Armantomys* molars, following Daams & van der Meulen (1984, pp. 253-254): 'Since we are dealing with percentages, the large fluctuations in the relative frequency of the *Armantomys* - *Praearmantomys* subgroup directly influence the relative frequency patterns of all other glirid species: the squeezing effect (Drooger, 1982)'. In order to investigate possible significant changes in the frequency patterns of these other dormice,

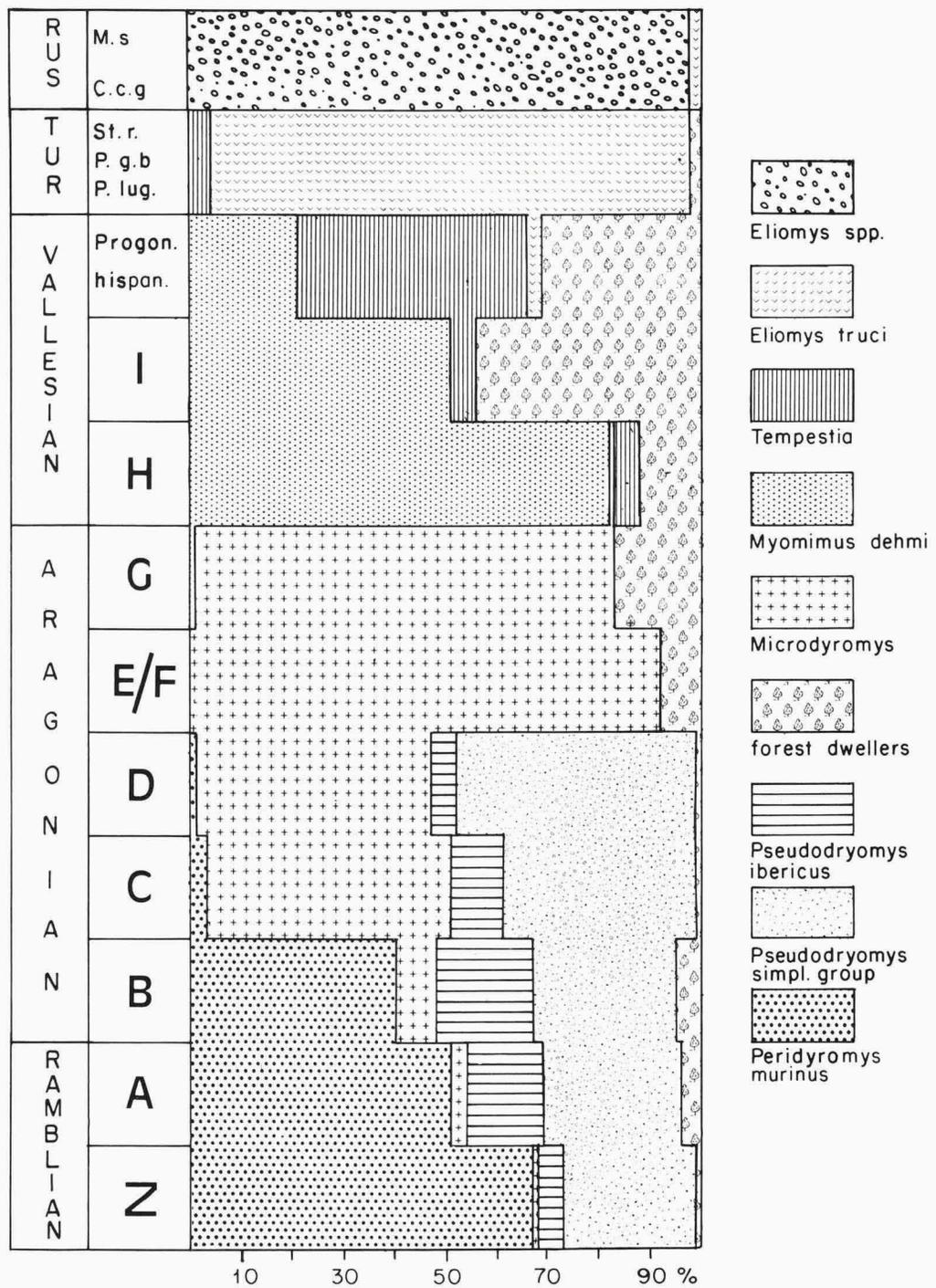


Fig. 4. Distribution and relative frequency of genera and species of the Gliridae, except (*Prae*)*Armantomys*, from the Neogene of the Calatayud-Teruel Basin. The forest-dwellers in this figure are the Glirinae *Peridyromys* aff. *jaegeri*, *Branssatoglis*, *Paraglrulus*, and *Ramys multicrestatus*.

Table 2. Distribution and relative abundance (in percentages) of genera and species of Gliridae in the Neogene of the Calatayud-Teruel Basin. The (*Prae*)*Armantomys* group is omitted. Asterisks indicate a frequency of under 1 %. See also explication of Fig. 2.

	Z	A	B	C	D	E/F	G	H	I	P.h.	S.r.	M.s.
											P.g.b.	C.c.g.
											P.l.	C.c.g.
<i>Altomiramys daamsi</i>	*											
<i>Branssatoglis</i>	*											
<i>Glirudinus</i>	1	4	5	1								
<i>Peridyromys murinus</i>	67	51	40	3	1							
<i>Microdyromys</i>	1	3	8	48	46	91	80	1				
<i>Pseudodryomys robustus</i>	24	28	28	36	48							
+ <i>simplicidens</i>												
<i>Pseudodryomys ibericus</i>	5	15	19	10	5							
<i>Peridyromys</i> spp.				3	*							
<i>Muscardinus</i>					*		13	16	25	31	4	
<i>Tempestia</i>							*	1	2	45	2	
<i>Paraglrulus</i>						9						
<i>Myoglis meini</i>							4					
<i>Myomimus dehmi</i>							1	82	49	21		
<i>Eliomys truci</i>							*		1	3	94	2
<i>Ramys multicrestatus</i>									24			
<i>Eliomys</i> spp.											*	98

we calculated the relative frequencies for zones Z-D, leaving *Armantomys* and *Praearmantomys* out of the total sum of the Gliridae molars. It appears that *Peridyromys murinus* and *Microdyromys* show opposite trends in this interval, the former decreasing in relative frequency, the latter increasing. These changes are supposed to represent a single signal, which is independent of the cyclic humidity signal. Since the trends in the frequency patterns of *P. murinus* and *Microdyromys* continue over several zones, we looked for a gradual and longlasting change in the environment. We assume that this change reflects a climatic factor, and as this factor cannot be humidity, we attribute this signal to temperature. Our assumption is based on the following arguments:

- 1) In Spain *Pseudodryomys ibericus* has its maximum frequency in zone B (lower MN 4), in Southern France its peak is found in a higher part of MN zone 4 which can be correlated to zone C, and in Bavaria it is only present in MN zones 5 and 6 (Mayr, 1979).
- 2) In Spain *Pseudodryomys simplicidens* does not occur above zone D (MN 4b), in Bavaria it is present only in MN 6 (Mayr, 1979).

These northward shifts corroborate a trend towards increasing temperature (see Fig. 5) during zones B-E. It then follows that *P. murinus* tolerates lower and *Microdyromys* higher temperatures.

A comparable trend of replacement is present in the Vallesian and Turolian: *Myomimus dehmi* decreases in frequency and it is absent in the Turolian, whereas *Eliomys truci* is poorly represented in the Vallesian and relatively abundant in the Turolian. We attribute this trend to a change in temperature too, but in the opposite direction: *M. dehmi* tolerates lower and *E. truci* higher temperatures. In zone H, where *M. dehmi* is the predominant dormouse, *Microdyromys* is very scarce, indicating that temperatures were relatively low in that interval.

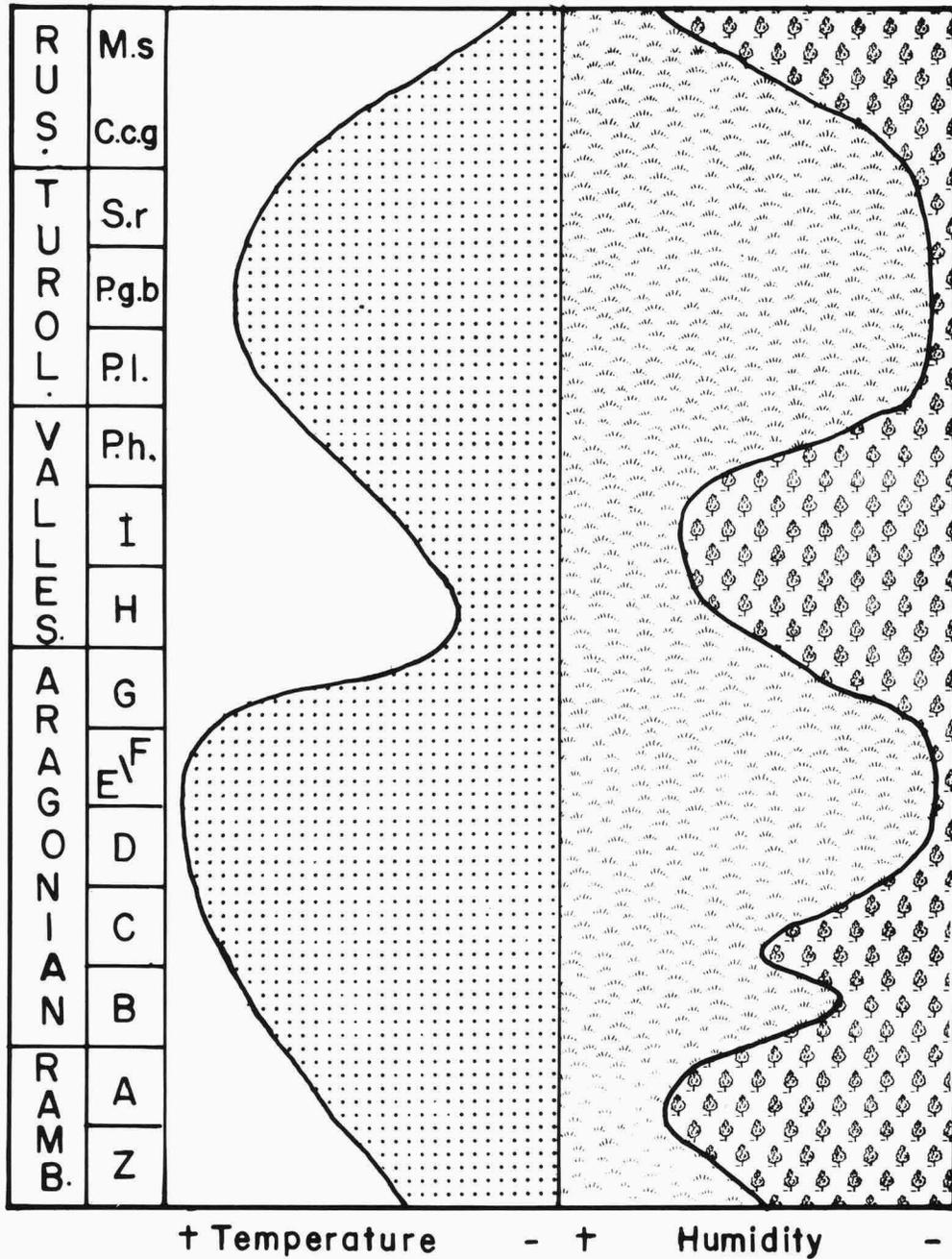


Fig. 5. Temperature and humidity curves based on rodent associations from the Neogene of the Calatayud-Teruel Basin.

Although the A and C intervals are thought to have had a humid climate, relatively few forest-dwelling Gliridae are present. The Vallesian on the other hand, has been a humid period as well, and the forest-dwelling Gliridae are relatively well represented. Perhaps these differences are due to differences in the type of forests.

Comparison with events in continental and marine realms in other areas

At the R.C.M.N.S. Interim-Colloquium on Mediterranean Neogene Continental Paleoenvironments and Climatic Evolution (Montpellier, April 1983) many contributions on ecostratigraphy were submitted from various fields of investigation. A comparison of the paleoenvironmental events in the Calatayud-Teruel Basin with events in other areas shows striking resemblances.

1) The trend from a moist to dry biotope in the C-F interval. A similar trend has been observed in various other areas that may be correlated by generally accepted criteria: Tagus Basin in Portugal (Pais, 1979); flora and large mammals. NW Mediterranean area (Bessedik & Suc*; Aguilar & Michaux*); flora and micromammals.

Southern Germany (Fahlbusch*); mammals and flora.

Northern Perimediterranean area (Tobien*); large mammals.

Central Spain (Alberdi et al., 1984; López*); large mammals and Lagomorpha.

Vallés-Penedés, Catalonia, NE Spain (Agustí*); rodents.

2) The subsequent trend from a dry to a humid climate in the Late Aragonian/Early Vallesian has been observed in the following areas:

NW Mediterranean area (Aguilar & Michaux*); rodents.

Southern Germany (Fahlbusch*); mammals and flora.

Northern Perimediterranean area (Tobien*); large mammals.

3) The dry climate of the Turolian has been recognized in the following areas:

Nile Delta (Poumot*); pollen.

NW Mediterranean area (Aguilar & Michaux*); rodents.

Northern Perimediterranean area (Tobien*); large mammals.

Vallés-Penedés, Catalonia, NE Spain (Agustí*); rodents.

4) The subsequent wet period in the Ruscinian has been recognized in the following areas:

NW Mediterranean area (Bessedik & Suc*; Aguilar & Michaux*); flora and rodents.

Northern Perimediterranean area (Tobien*); large mammals.

5) Our relative temperature peak in the late Medial Aragonian and the subsequent cooling trend into the Vallesian have been observed in the following areas:

Rhone Valley and Western Tethys (Demarcq*); marine macrofaunas.

SE France (Cappetta*); selachians.

Portugal, Tagus Basin (Antunes*; Pais, 1979); marine evidence and flora.

Lyon region, France (Mein*); mammals.

Southern Germany (Fahlbusch*); mammals and flora.

6) The Turolian as a relatively warm period has been observed by Riedl (1984) on the basis of geomorphological features in Greece.

*) Reference taken from the compilation charts Neogene faunal and floral changes, *Paléobiol. Continent.*, 14, 2 (R.C.M.N.S. Interim-Coll. Mediterranean Neogene continental paleoenvironments and paleoclimatic evolution, Montpellier, 1983): 485.

The relative temperature curve on the basis of microplankton from the Mediterranean and the Atlantic (Muller, 1984) is strikingly similar to our curve: the relatively warm period of the middle/early Late Aragonian, the relatively cool Vallesian, the warm Turolian and the cooler Ruscinian.

Paleoclimatic conditions of the Mediterranean area were inferred from an integrated study of clay minerals, planktonic foraminifera and stable isotopes in marine Neogene sections in Sicily (Italy) by Chamley et al. (1986). The long-term cooling period and the increase of humidity after the Middle Aragonian is seen both in Sicily and in Spain. This period is characterized by the inflow of cold water in the Mediterranean. The short-term warming in the early Tortonian of Sicily may coincide with our trend during the Vallesian. Our data indicate, however, that the warming-up trend continues until the middle Turolian, whereas the Sicilian data point at a cooling trend from the early Turolian on. This discrepancy may be caused either by correlation errors or by insufficiency of our data. The trend towards increasing humidity after the middle Turolian coincides in both areas. On the whole, it is remarkable that interpretations of data obtained through different disciplines and from distant areas in the Mediterranean agree so well. This corroborates the value of further quantitative and qualitative analysis of mammal faunas.

Discussion

The Ramblian – Ruscinian interval in the Calatayud-Teruel Basin covers approximately 18 million years according to the stratigraphic framework of Rögl & Steininger (1983). In this interval three relatively cool and two relatively warm periods may be distinguished. In the same interval four relatively humid and four relatively dry periods may be recognized. The temperature and humidity curves are not parallel ones. Although the middle/early Late Aragonian and the Turolian warmth peaks coincide with draught peaks, fluctuations of humidity occur in the Ramblian and Early Aragonian regardless of the temperature trend. The cold peak in the Vallesian does not coincide with a humidity peak either.

The climatic trends shown in this paper are due to large scale events. Possibly small scale events are obscured by a relative incomplete record, and by averaging our data per biozone. In order to detect small scale events, it is necessary to have denser documentation of the mammal faunas in various sections in the same area with good lithostratigraphic control. For instance, the fauna of Las Planas 5K houses a relatively high number of rodents from moist biotopes (*Eomyops catalaunicus* – 10 %; *Muscardinus thaleri* – 9 %; *Democricetodon gaillardi* – 5 %; *Megacricetodon minor* – 7 %), whereas the other faunas in zone G represent much drier biotopes. We do not know if this fluctuation is due to a small scale climatic event, or to different taphonomical circumstances only. Denser sampling with good lithostratigraphic control is possible in the Aragonian of the Daroca-Villafeliche area, enabling us to establish a more detailed ecostratigraphic framework.

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