



Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations

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ABSTRACT

This paper analyses the relationship between the evolution of the Late Miocene and Early Pliocene rodent and insectivore assemblages from the Granada Basin (southern Spain) and climate changes. These climatic changes, in terms of humidity and temperature fluctuations, are inferred from variations of the relative abundances of taxa with definite ecological preferences. There is a general tendency towards a temperature increase from the latest Tortonian (Middle Turolian) to the Messinian (Late Turolian), and towards a decrease from the Mio-Pliocene boundary (latest Turolian–earliest Ruscinian) to the end of the Zanclean (Late Ruscinian). Dry conditions predominate in the latest Tortonian (Middle Turolian). At the beginning of the Messinian (Late Turolian) there was a significant increase in humidity, followed by an aridification throughout the end of the Messinian and Zanclean (Late Turolian and Ruscinian). These climatic variations are in accordance with the sedimentary evolution of the basin, and agree with the climatic interpretations inferred from the shallow-marine carbonate sediments (temperate/ tropical) deposited in the marine basins of southeastern Spain during the studied time interval.

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1. Introduction

The Neogene–Quaternary sediments of the Granada Basin (southern Spain) unconformably overlie a basement paleorelief constituted by rocks from the Internal and the External Zones of the Betic Cordillera (Fig. 1). The marine record of the Granada Basin extends from the Middle Miocene to the Tortonian, and the continental sedimentation from the latest Tortonian (Middle Turolian) to the Quaternary (Dabrio et al., 1982; Martín et al., 1984; Braga et al., 1990, 1996; García-Alix et al., *in press*). This paper deals specifically with the interval of the continental history spanning the latest Tortonian (Middle Turolian) through the Zanclean (Ruscinian), for which a high resolution biostratigraphy based on rodents has been established (García-Alix, 2006; García-Alix et al., *in press*). The chronology of the studied localities and sections from the Granada Basin, the equivalences between marine–continental terminology and the absolute ages of their boundaries, which have been followed in this paper are summarized in Fig. 2.

Mammals are good indicators of paleoclimatic conditions (Legendre, 1986; Avery, 1992; Andrews, 1995; Daams et al., 1999; van Dam and Weltje, 1999; Montuire, 1999; Martín-Suárez et al.,

2001b; Avery, 2001; López Antoñanzas and Cuenca Bescós, 2002; Legendre et al., 2005; among others). In this paper we propose some paleoclimatic interpretations for the Middle Turolian–Late Ruscinian interval (latest Tortonian–Zanclean interval) using only micromammal. Paleoclimatic and paleoclimatic reconstructions based on micromammals usually consider only rodents (van de Weerd and Daams, 1978; Daams et al., 1988; Daams et al., 1999; van Dam and Weltje, 1999; Martín-Suárez et al., 2001b; Casanovas-Vilar and Agustí, 2007; among others). We have used both rodents and insectivores because that combination provides better information about the environmental conditions in which the sediments were deposited (Reumer, 1999; Hernández Fernández, 2001; van den Hoek Ostende, 2003).

2. Materials and methods

Sixteen localities (see faunistic catalogues in Appendix A) from eight sections were included in our analysis (Figs. 1 and 2). They correspond to palustrine–lacustrine environments. Some laterally equivalent localities JUN-2 (2+2B+2C), PUR-25 (25+25A), DHS-4 (A+B), CLC-3 (3+3B) and BLS-1 (1+5A+6) have been fused together and considered as single localities. All the examined fossiliferous levels have very similar features: decimetric stratified levels of dark-coloured lutites with abundant organic matter, originated in a low-energetic sedimentary environment. These levels have been formed

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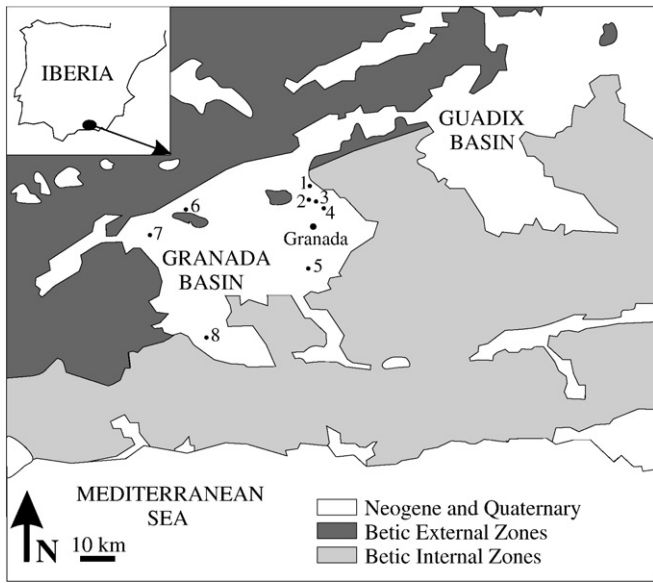


Fig. 1. Geologic and geographic context of the Granada Basin after Braga et al. (1990), and situation of the studied sections: 1, Calicasas; 2, Barranco del Purcal; 3, Cantera de Pulianas; 4, Canteras de Jun; 5, Otura; 6, Brácana; 7, Barranco de Blas; 8, Arenas del Rey.

by the same sedimentary processes and, therefore, the mammalian remains found in them have undergone the same biostratigraphic processes.

It is commonly accepted that the accumulation of small mammal remains in karstic fissures is mainly due to the action of nocturnal birds of prey (owls), which eject bones and teeth through pellets after digestion (Denys et al., 1996; Saavedra and Simonetti, 1998; Terry, 2004). Contrary to these karstic sites, formed by the action of a single species of avian predator near the nesting and roosting sites, remains found in lacustrine–palustrine localities may have different origins. Remains belonging to the preys of different predators (mainly nocturnal, but also diurnal birds of prey, besides mammalian carnivores), as well as bones and teeth of non-predated specimens, can be transported, mixed and finally deposited forming these lacustrine fossiliferous accumulations. Comparisons between karstic

and lacustrine small mammal localities have demonstrated that the latter ones do not reflect the diet of a single species of predator, but they include remains of different origins. Therefore, the biological bias introduced by the selective feeding behaviour of the predators is less in lacustrine localities, which reflect in a more reliable way the composition of the original community than karstic localities of scatological origin (Minwer-Barakat, 2005; Minwer-Barakat et al., 2007). This opinion is supported by other authors, who have pointed out that the fluvial–lacustrine accumulations of small mammal remains are more similar to the original community and, therefore, more useful for paleoecological reconstructions, than those originated by the action of predators in a specific place (Badgley, 1986; Behrensmeyer, 1991; Srivastava and Kumar, 1996).

For the paleoecological studies based on micromammals, Daams et al. (1999) suggested to use only rodent associations (excluding insectivores, chiropteres and lagomorphs), in which the number of m1 + m2 + M1 + M2 is 100 or more. Casanovas-Vilar and Agustí (2007) assumed that 50 cheek teeth is a sufficient number for a single sample. We chose all localities with more than 100 specimens (teeth) of rodents and insectivores, plus the localities DHS-15B (82 specimens), BRA-5B (71 specimens), PUR-3 (92 specimens) and BLS-1 (93 specimens) because of their biostratigraphical relevance.

Following Martín Suárez (1988), Martín-Suárez et al. (2001b) and Minwer-Barakat (2005), we use the total number of specimens (teeth) of each taxon in each locality, divided by its number of diagnostic elements; in this way, no taxon is over-represented. Identifiable fragments larger than half a tooth were counted too. The number of diagnostic elements of each family is: Muridae, Arvicolidae, Cricetidae and Trilophomyidae: 12 (molars); Gliridae and Sciuridae: 16 (P4 and molars); Castoridae and Soricidae: 20 (incisors, P4 and molars); Erinaceidae: 44 (all dental elements), but in *Parasorex ibericus* 42, because it lacks the I₃; Talpidae: 44 (all dental elements).

3. Ecological requirements

The ecological requirements, habits or diet of a taxon, may be determined by different methods: by its dental pattern (like some cricetids and arvicolids), by the adaptive modification of some parts of the skeleton (like in talpids), by the phylogenetic relationships with extant species, by the association with taxons with known ecological

Section	Localities	Continental Age	MN Units	Marine Age	Absolute Age
Barranco de Blas	BLS-1	Late Ruscinian	MN 15		4.20
Barranco del Purcal	PUR-13			Zanclean	
Calicasas	CLC-3	Early Ruscinian	MN 14		
Barranco del Purcal	PUR-4 PUR-3				5.33
Brácana	BRA-5B				
Arenas del Rey	DHS-16, DHS-4 MNA-2, MNA-4, DHS-15B	Late Turolian	MN 13	Messinian	
Cantera de Pulianas	PUR-23, PUR-24A, PUR-25				
Otura	OTU-1				7.05
Canteras de Jun	JUN-2	Middle Turolian	MN 12	Tortonian	7.20

Fig. 2. Studied sections and localities. Age data from García-Alix et al. (in press): absolute ages of the marine stages according to GTS2004 (Gradstein et al., 2004); the age of the Middle–Late Turolian limit (MN12–MN13) is that of Garcés et al. (1998), Agustí et al. (2001) and Berger et al. (2005); the age of the Turolian–Ruscinian limit (MN13–MN14) is that of García-Alix et al. (in press); the age of the Early–Late Ruscinian limit (MN14–MN15) is that of Opdyke et al. (1997), Agustí et al. (2001) and Berger et al. (2005).

requirements, etc. According to Martín-Suárez et al. (2001b), taxa within the same anagenetic evolutionary lineage (linear evolution between two species) have equal preferences, but in vicariant speciation (two populations of a same species evolve in different ways due to changes in the physical environment) ancestor and descendant may have opposite ecological preferences; taxa with opposite frequency peaks have opposite ecological preferences; immigrants replacing taxa with highly similar dental pattern may have (or may not have) opposite preferences.

We have established the following groups of preferences: eurytopic (without preferences for a specific habitat), warm, cold, dry, wet, open/bare habitats (with scarce vegetation), open/herbaceous habitats, forested habitats, and (semi)aquatic habitats (Fig. 3); a supplementary group has been established for taxa of unknown ecological preferences.

Only three of the studied genera have extant representatives: *Micromys*, *Apodemus* (Muridae) and *Talpa* (Lipotyphla). We have summarized the ecological preferences of the studied taxa in Fig. 3,

	Climatic preferences					Habitat				Eurytopic		
	Unknown	Warm	Cold	Dry	Wet	Open / bare	Open / herbaceous	Forested	(Semi)aquatic	Temperature	Humidity	Habitat
<i>A. (aff.) gorafensis</i> *		X			X							X
<i>A. atavus</i>					X			X		X		
<i>A. aff. atavus</i>	X											
<i>Castillomys</i> *										X	X	X
<i>Castromys</i>			M'	M'								X
<i>Micromys paricioi</i>					D,S		X			X		
<i>Occitanomys adroveri</i>			M'	M'								X
<i>Occitanomys alcalai</i>		M'			M'							X
<i>Paraethomys meini</i>		M'		Re								X
<i>Paraethomys aff. abaigari</i>	X											
<i>Stephanomys</i> *										M',MB	M',MB	M',MB
Muridae indet.	X											
<i>Dipoides problematicus</i>					D,W,H				D,W,H	X		
<i>Apocricetus</i> *		M'					X				X	
<i>Blancomys</i> *							B,W,P			X	X	
<i>Hispanomys aff. adroveri</i>				W, B			W, B			X		
<i>Ruscinomys</i> *			M',G	D,D',W M',G			D,D',W M',G					
<i>Eliomys</i> *					W			W		X		
<i>Eliomys truci</i>					M,D,W			M,D,W		X		
<i>Muscardinus</i> *					W			W		X		
<i>Heteroxerus mariatheresae</i>		W,MB		W,MB		MB						
<i>Atlantoxerus</i> *		W,MB		W,MB		MB						
<i>Pliopetaurista pliocaenica</i>					W			W,C,B'		X		
Arvicolidae indet.			D,S,Rp F,MB		D,S,Rp F,MB		D,S,Rp F,MB					
<i>Trilophomys</i> sp.			A				P,MB				X	
<i>Archaeodesmana</i> *					Rü, M				Rü,M	X		
<i>Talpa minor</i>					X					X		X
<i>Desmanella</i> sp.					X					X		X
<i>Parasorex ibericus</i>										M'	M'	M'
<i>Asoriculus gibberodon</i>		R, K			R, K			R, K				
<i>Petenya</i> sp.					R',K'					X		X
<i>Paenelimoecus</i> sp.					R',K'					X		X
Soricidae (not Crocidurinae) indet.					R',K'					X		X
" <i>Myosorex meini</i> "							MB			X	X	
Crocidurinae indet.							MB			X	X	

A=Agustí et al. (2001)
C=Cuenca Bescós (1988)
B=de Bruijn et al. (1993)
B'=de Bruijn (1999)
D=van de Weerd and Daams (1978)
D'=Daams et al. (1988)
D*=Daams and Meulen (1984)
F=Fejfar and Repenning (1992)
G=García-Alix (2006)

H=Huguency (1999)
K=Rzebik-Kowalska (1994)
K'=Rzebik-Kowalska (1995)
M=Martín Suárez et al. (2001a)
M'=Martín Suárez et al. (2001b)
M*=Meulen and de Bruijn (1982)
MB=Minwer-Barakat (2005)
P=Hernández Fernandez and Pelaez-Campomanes (2003)

R=Reumer (1984)
R'=Reumer (1999)
Re=Renaud et al. (1999)
Rp=Repenning et al. (1990)
Rü=Rümke (1985)
S=Martín Suárez (1988)
W=van Dam and Weltje (1999)
X=This paper

Fig. 3. Summary of the ecological preferences of the studied taxa. *A. (aff.) gorafensis** includes *A. gorafensis* and *A. aff. gorafensis*; *Castillomys** includes *C. gracilis* and *C. cf. crusafonti*; *Stephanomys** includes *Stephanomys* sp., *S. ramblensis*, *S. dubari* and *S. donnezani*; *Apocricetus** includes *A. alberti* and *A. barrierei*; *Blancomys** includes *Blancomys* sp., *B. sanzi* and *B. aff. sanzi*; *Ruscinomys** includes *R. aff. schaubi*, *R. cf. lasallei*, *R. lasallei* and *R. cf. europaeus*; *Eliomys** includes *Eliomys* sp., *E. intermedius* and *E. aff. intermedius*; *Muscardinus** includes *M. cf. vireti* and *M. meridionalis*; *Atlantoxerus** includes *Atlantoxerus* sp., *A. cf. margaritae* and *A. margaritae*; *Archaeodesmana** includes *Archaeodesmana* sp. and *A. baetica*.

based on literature and on our own interpretations, which are justified below.

Martín Suárez and Mein (1998) proposed the phylogenetic line *A. gudrunae*–*A. gorafensis*–*A. mystacinus*. Martín-Suárez et al. (2001b) attributed to *A. gudrunae* warm preferences; *A. mystacinus* lives in the Balkans and the Middle East, in areas with relatively warm conditions (Grzimek, 2004). Therefore the line *A. gudrunae*–*A. aff. gorafensis*–*A. gorafensis*–*A. mystacinus* is thought to have had warm preferences. Martín-Suárez et al. (2001b) considered wet preferences for *A. gudrunae*, and we consider the same for its direct descendant *A. gorafensis*.

The recent species *Apodemus sylvaticus* and *A. flavicollis* are descendants of *A. atavus* (Martín Suárez and Mein, 1998). These two recent species live in forested habitats, and *A. flavicollis* is restricted to areas of abundant rain fall (Schilling et al., 1987). Therefore *A. atavus* is thought to be linked to relatively wet and forested habitats. The phylogenetic relationships of *Apodemus* aff. *atavus* are unknown.

The lineage *C. gracilis*–*C. crusafonti*–*C. rivas* (Martín Suárez and Mein, 1991) is present from the Late Turolian to the Pleistocene in the Iberocitan province, in warm, cold, dry and wet epochs. It is an opportunist taxon without specific ecological preferences.

According to Martín-Suárez et al. (2001b) *Castromys littoralis* has cold and dry preferences.

The single recent representative of the genus *Micromys*, *M. minutus*, lives in wet regions with herbaceous vegetation (Grzimek, 2004). Van de Weerd and Daams (1978), and Martín Suárez (1988) consider *Micromys* an indicator of wet conditions.

Occitanomys adroveri indicates cold and dry conditions, and the immigrant taxon *O. alcalai*, warm and wet environments (Martín-Suárez et al., 2001b).

Paraethomys meini is an indicator of warm (Martín-Suárez et al., 2001b) and dry conditions (Renaud et al., 1999). In the latest Miocene, the desertization of the Sahara started (Diester-Haas and Chamley, 1978; Robert and Chamley, 1987), and *Paraethomys* and *Ctenodactylidae* (which at present live in arid or semiarid areas) coexisted there (Renaud et al., 1999). We do not agree with the interpretation of Hernández Fernández and Peláez-Campomanes (2003) that attributed wet and forested habitats to the Pliocene *Paraethomys* because of the similarities of its dental pattern with that of recent *Oenomys*. *Paraethomys* aff. *abaigari*, in our opinion, had unknown ecological preferences.

Some authors (van Dam and Weltje, 1999; Renaud et al., 1999; Renaud and van Dam, 2002; among others) attributed dry, herbaceous/open habitats and a diet based on fibrous plants to *Stephanomys*, because of its stephanodonty, large size and crown height; other authors (Fernández-Jalvo et al., 1998; Hernández Fernández and Peláez-Campomanes, 2003), comparing *Stephanomys* with recent taxa, attributed it a forested habitat. *Stephanomys* is present in almost all localities from the Late Turolian to the latest Pliocene, and its abundance seems to be independent of temperature and humidity, therefore it is considered an eurytopic taxon (Martín-Suárez et al., 2001b; Minwer-Barakat, 2005) and opportunist (Agustí and Llenas, 1996; Minwer-Barakat, 2005).

Castoridae have preferences for (semi)aquatic habitats and wet climates (van de Weerd and Daams, 1978; van Dam and Weltje, 1999; Hugueney, 1999), except some fossorial castorids that disappeared in the Lower Miocene (Hugueney and Escuillié, 1997; Hugueney, 1999). *Dipoides problematicus* is related to environments with large supply of water (García-Alix et al., 2007).

The studied genera of the family Cricetidae have no extant representatives, but *Apocricetus* is related to extant genera like *Crice-tus*, *Cricetulus*, *Mesocricetus*, *Allocricetulus* and *Phodopus* that live mainly in steppe open habitats (Grzimek, 2004). *Apocricetus alberti* and *A. barrierei* had preferences for warm conditions (Martín-Suárez et al., 2001b) and open/herbaceous habitats.

Blancomys has preferences for open/herbaceous habitats (de Bruijn et al., 1993; van Dam and Weltje, 1999; Hernández Fernández and Peláez-Campomanes, 2003).

Although Martín-Suárez et al. (2001b) considered *Hispanomys* as an eurytopic taxon, we agree with de Bruijn et al. (1993) and van Dam and Weltje (1999) considering preferences for open/herbaceous and dry habitats.

Ruscinomys has preferences for dry, open/herbaceous (van de Weerd and Daams, 1978; Daams et al., 1988; van Dam and Weltje, 1999; Martín-Suárez et al., 2001b; García-Alix, 2006) and cold habitats (Martín-Suárez et al., 2001b; García-Alix, 2006).

We have found two genera of Gliridae with recent representatives: *Eliomys* and *Muscardinus*. According to van Dam and Weltje (1999) *Eliomys* had wet and forested preferences. Although the extant *Eliomys quercinus* (descendant of *E. intermedius*) may live in zones with scarce trees, they are scansorial, they normally live in forested habitats, making nests in trees, and eat fruits of these trees (Saint Girons, 1973; Grzimek, 2004). According to Castells and Mayo (1993) the ideal habitat for *E. quercinus* is very humid. *Eliomys truci* had forested and moderate wet preferences too (van der Meulen and de Bruijn, 1982; Daams and van der Meulen, 1984).

The recent *Muscardinus avellanarius* is scansorial and lives in wet and forested zones of Europe and Asia (Corbet, 1978; Grzimek, 2004). The fossil species had wet and forested preferences too (van Dam and Weltje, 1999).

Three representatives of the family Sciuridae have been found: two Xerini and one Pteromyinae. *Atlantoxerus* and *Heteroxerus* (Xerini) have ground and diurnal habits (de Bruijn, 1999). Extant Xerini live in arid/semiarid and warm zones of Africa and Asia, in open habitats with scarce vegetation (Grzimek, 2004). Fossil Xerini had preferences for warm, dry (van Dam and Weltje, 1999; Minwer-Barakat, 2005) and open habitats with scarce vegetation (Minwer-Barakat, 2005).

Pliopetaurista is a flying squirrel with nocturnal habits that lived in forested/wooded zones (Cuenca Bescós, 1988; de Bruijn, 1999). Van Dam and Weltje (1999) suggested wet preferences and closed forest for Pteromyinae.

The Pliocene Arvicolidae had cold, wet and open/herbaceous preferences (van de Weerd and Daams, 1978; Martín Suárez, 1988; Repenning et al., 1990; Fejfar and Repenning, 1992; Minwer-Barakat, 2005). The extant species live in wet and open/herbaceous habitats. The maximum expansion of this family is observed in high latitude areas and in relation with global cooling periods (Repenning et al., 1990; Fejfar and Repenning, 1992).

Trilophomys (family Trilophomyidae) is a palearctic microtoid cricetid with preferences for cold (Agustí et al., 2001) and open/herbaceous habitats (Hernández Fernández and Peláez-Campomanes, 2003; Minwer-Barakat, 2005).

Three representatives of the family Talpidae have been found: *Desmanella*, *Archaeodesmana* and *Talpa*. *Desmanella* does not have a modified humerus, like Desmaninae (for swimming, Rümke, 1985; Martín-Suárez et al., 2001a), or like Talpinae (for burrowing in well-developed soils with lots of invertebrates), but we infer wet preferences, like in the majority of Talpidae.

Although *Parasorex* (family Erinaceidae) is considered as a taxon with unknown climatic preferences (van den Hoek Ostende, 2001; Van den Hoek Ostende and Doukas, 2003), we follow Martín-Suárez et al. (2001b) and Minwer-Barakat (2005), considering it eurytopic.

The representatives of the family Soricidae (except Crocidurinae), like *Petenya*, *Paenelimoecus* and Soricidae indet., have preferences for wet habitats (Reumer, 1999; RzebiK-Kowalska, 1995). *Asoriculus gibberodon*, relative of the extant *Episoriculus* from the forested/wooded, wet and warm regions of southern Asia, has wet, warm and forested/wooded preferences (Reumer, 1984; RzebiK-Kowalska, 1994).

Recent Crocidurinae have preferences for open/herbaceous habitats, and they are less bound to humidity than other soricids (Rathke and Bröring, 2005); therefore, and according to Minwer-Barakat (2005) we attribute to Crocidurinae, like *Myosorex meini*, preferences for open/herbaceous habitats.

4. Results and interpretation

In all localities rodents are much more abundant than insectivores; the family Muridae is the most abundant one, with values of relative abundance higher than 60% of the total (García-Alix et al., 2008). Cricetidae is the next most abundant family of rodents; it is present in all localities except in OTU-1. Gliridae are present in all localities, except in four of the Arenas del Rey localities and BRA-5B. Sciuridae and Castoridae are scarce. Trilophomyidae and Arvicolidae only appear in some of the Late Ruscinian localities (Fig. 4; Appendices A, B and C).

The order Lipotyphla, with the families Soricidae, Erinaceidae and Talpidae, is present in all localities. Talpidae are absent in the Middle Turolian and Upper Ruscinian localities, and Erinaceidae are absent in the Upper Ruscinian localities (Fig. 4; Appendices A, B and C).

4.1. Evolution of the associations and their inferred habitats

During the Middle–Late Turolian transition the micromammal associations are composed mainly of *C. littoralis* and/or *O. adroveri*. In this interval taxa with preferences for herbaceous/open, forested habitats and bare/open habitats are present; those with preferences for bare/open habitats are scarce.

In the Late Turolian the most abundant taxa are *Apodemus*, *Stephanomys*, *Occitanomys*, *Archaeodesmana*, and *P. meini*. *Archaeo-*

desmana and *Dipoides*, that indicate (semi)aquatic habitat, appear for the first time in the basin. During the Late Turolian indicators of herbaceous/open, (semi)aquatic, forested and bare/open habitats are present, but those of herbaceous/open and (semi)aquatic habitats are the most abundant. Although taxa with forested preferences are poorly represented, they occur in four localities. Indicators of bare/open habitats are very scarce, only present in one locality (PUR-24A). The presence of *Dipoides* and *Archaeodesmana* indicates the existence of significant water courses.

The main association in the Early Ruscinian is composed of *Paraethomys* and *Stephanomys*. Taxa with preferences for herbaceous/open, forested, (semi)aquatic and bare/open are present. The presence of *Archaeodesmana* and *Dipoides* indicates relevant water courses.

In the Late Ruscinian there is a change with respect to the previous associations. The locality BLS-1 is widely separated in time from the rest of the Ruscinian localities. The main association is composed of *Stephanomys*, *Arvicolidae* indet., *Castillomys* and *Ruscinomys*; *Stephanomys* is the most abundant taxon. In this locality, only indicators of forested and herbaceous/open habitats are present.

4.2. Evolution of temperature

The relative abundances of taxa with cold and warm preferences show a drastic change in temperature at the beginning of the Late Turolian: a dominance of taxa with cold preferences yields to a dominance of taxa with warm preferences (Fig. 5).

In general, an increase in temperature can be observed, starting at the beginning of the Late Turolian, and a subsequent decrease, starting at the end of the Late Turolian (from DHS-4). The temperature at the Middle Turolian–Late Turolian boundary might be characterized as cold–temperate. In the Late Turolian it was tropical to warm–temperate. In detail, however, there are significant variations in the relative abundances of warm indicators throughout the Late Turolian. At the Turolian–Ruscinian transition there was a slight decrease in temperature, associated with a lesser abundance of warmth indicators, with a minimum in PUR-13. This decrease in temperature was more marked in the Late Ruscinian (BLS-1), where only taxa with cold preferences are present. In general, the Ruscinian may be characterized as temperate, with higher temperatures in the earliest Ruscinian than in the Late Ruscinian (Fig. 5; Table 1).

4.3. Evolution of humidity

The localities from the Middle–Upper Turolian transition show high abundances of taxa with dry preferences, and low abundances of taxa with wet preferences, therefore, we interpret this as a dry period. At the beginning of the Late Turolian, there was a drastic change with a clear predominance of wet taxa. The maximum abundance of wet taxa is found in MNA-2. From this point onwards until PUR-13 (Early Ruscinian) there is a tendency to aridification. The relative abundance of wet indicators decreases, with small oscillations that sometimes are coupled with variations of dry indicators. In the Lower Ruscinian localities there is a decrease of both wet and dry indicators, and an increase of eurytopic taxa. However, the relative abundance of taxa with dry preferences is larger than in the localities from the Late Turolian. In the Late Ruscinian the relative abundances of taxa with wet and dry preferences are smaller than in the Early Ruscinian, but wet indicators dominate slightly (Fig. 5; Table 1).

4.4. Temperature vs humidity

The temperature and humidity indicators show a drastic change at the beginning of the Late Turolian. During the Middle–Late Turolian transition the estimated conditions are cold and dry; these conditions may be called cold–temperate. At the beginning of the Late Turolian

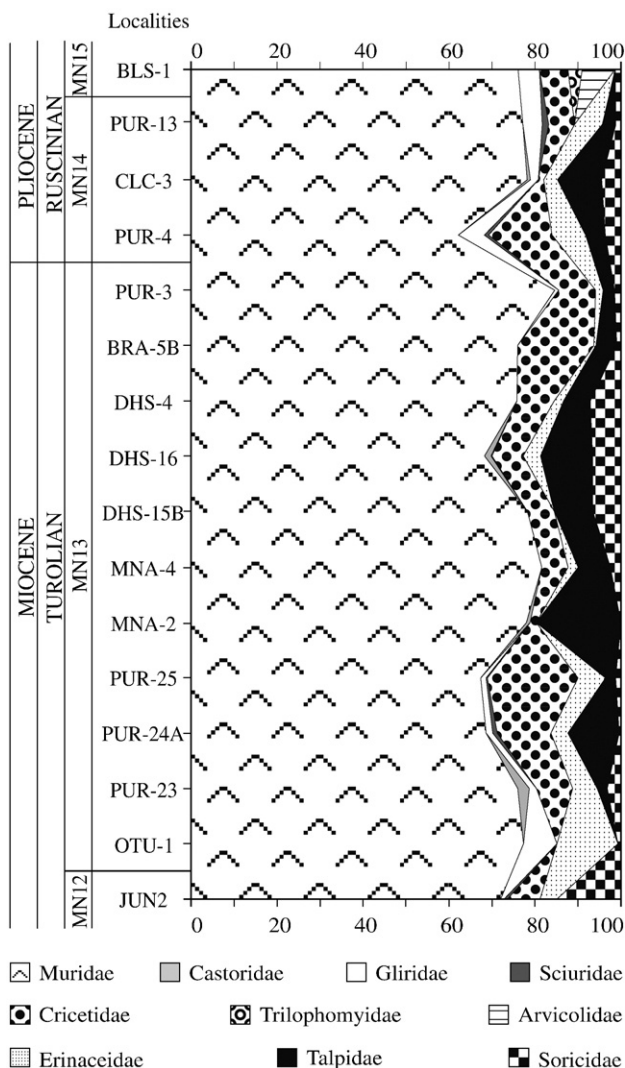


Fig. 4. Relative abundances of the studied families.

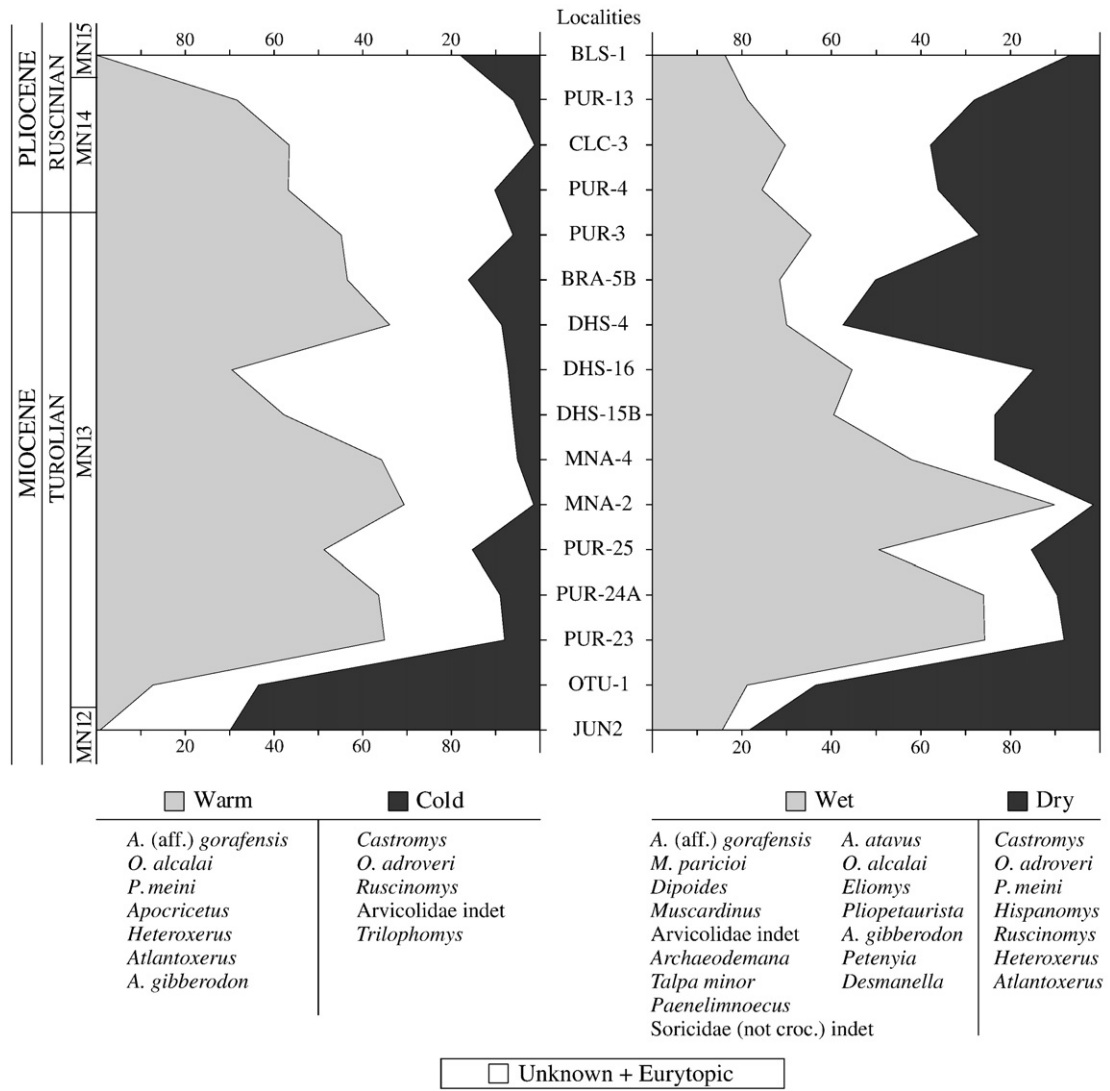


Fig. 5. Relative abundances of taxa with warm/cold preferences (left) and those with wet/dry preferences (right).

these change to warm and wet. Some early Late Turolian localities represent the highest temperature and humidity, and may be related to tropical conditions. Towards the Turolian–Ruscinian boundary conditions change to dryer and slightly cooler, and may be characterized as warm–temperate. The estimated conditions for the Late Ruscinian are cooler than those of the Late Turolian and Early Ruscinian (Fig. 5; Table 1).

During the Middle–Late Turolian transition and the first part of the Late Turolian, increases in warm and wet indicators were coupled with decreases in cold and dry indicators. During the Ruscinian, warm and wet indicators had a positive correlation, which is not observed between cold and dry indicators. Therefore, we cannot conclude that variations in temperature and humidity are in general correlatable (Fig. 5). Hernández Fernández et al. (2007), noted warm and dry, warm and

Table 1

Climatic evolution and correlation for the studied interval between Granada Basin and SE Spain basins compared with global temperature evolution. Note the difference between global and local temperature

Continental scale	Granada Basin			SE Spain Basins (sea-surface temperature)	Global evolution (temperature)	Marine scale
	Climate	Humidity	Temperature			
Upper Ruscinian	Temperate				General warming	Zanclean
Lower Ruscinian	Warm–temperate	+	+	Cold		
Upper Turolian	Warm–temperate	++	++	Warm	General cooling	Messinian
	Tropical	+++	+++	Cold Warm Warm		
Middle Turolian	Cold–temperate	---	---	Cold		Tortonian

pluvial, cool and dry, and cool and pluvial periods throughout the Plio-Pleistocene; and they indicated that the positive correlation between humidity and temperature is typical of tropical environments, which agrees with our interpretation for the Late Turolian.

5. Paleoenvironmental conditions

The paleoclimatic interpretations from the Middle Turolian to the Late Ruscinian agree with the paleogeographical evolution of the Granada Basin, where fluvio-lacustrine systems evolved through time. Around a lake and in flood plain areas there existed zones with vegetation (forested or herbaceous) and more peripherally, open areas with scarce vegetation (bare habitats).

5.1. Middle–Late Turolian transition

There was a braided fluvial system in the eastern sector of the basin flowing into a lake in the central and western sector (García-Alix et al., in press). The studied localities are situated in the flood plain. Dry and cold conditions are inferred for this interval. In this context, the herbaceous/open habitats predominated; forested environments, more scarce, may have existed in some zones near the water reservoirs, and bare/open habitats probably were far away from the lacustrine or palustrine zones (Fig. 6). Braided fluvial systems, with a very irregular discharge, are related to zones of scarce vegetal cover, and are typical in semiarid areas (Ramos, 1992). Probably this discontinuous water flow made the conditions not suitable for taxons with (semi)aquatic habitats, like *Dipoides* or *Archaeodesmana* that need large and constant water courses (they were present in later periods, when the humidity conditions and the supply of water were optimum for these taxons). Although some possible (semi)aquatic habitats were present, they were not occupied by micromammals.

5.2. Late Turolian

At this time almost the entire basin was occupied by a large lake, fed by two main fluvial systems (one in the northeast and the other one in the southwest) that developed two small deltas (García-Alix et al., in press) (Fig. 6). Our fossiliferous localities are situated in these two deltaic complexes and in lacustrine sediments. Deltaic complexes develop in fluvial systems that receive moderate to abundant precipitations (Arche, 1992). This fact agrees with the high humidity conditions interpreted for these deposits. The main conditions of the area were wet and warm, with some oscillations. There was a progressive decrease in humidity during the Late Turolian, which agrees with the observed reduction of the lacustrine system (García-Alix et al., in press). The main habitats during this interval were (semi) aquatic and herbaceous; forested habitats had medium importance and, only occasionally, bare/open habitats developed (Fig. 6).

5.3. Latest Turolian–Ruscinian

Two independent alluvial–lacustrine systems developed in the eastern and western part of the basin respectively. Our latest Turolian–Early Ruscinian localities are situated in the eastern sector; the only Late Ruscinian locality (BLS-1) is from the western sector of the basin (García-Alix et al., in press).

In the eastern sector a system of alluvial fans developed, changing laterally into a fluvial system converging into a reduced lake. The conditions for this interval are colder and dryer than those of the Late Turolian. The localities are situated in alluvial/fluvial and lacustrine sediments. The presence of these three sub-environments in a reduced space implies a very diverse habitat: forested, herbaceous/open, bare/open and (semi)aquatic. Indicators of the forested and (semi)aquatic habitats are better represented in the lacustrine locality

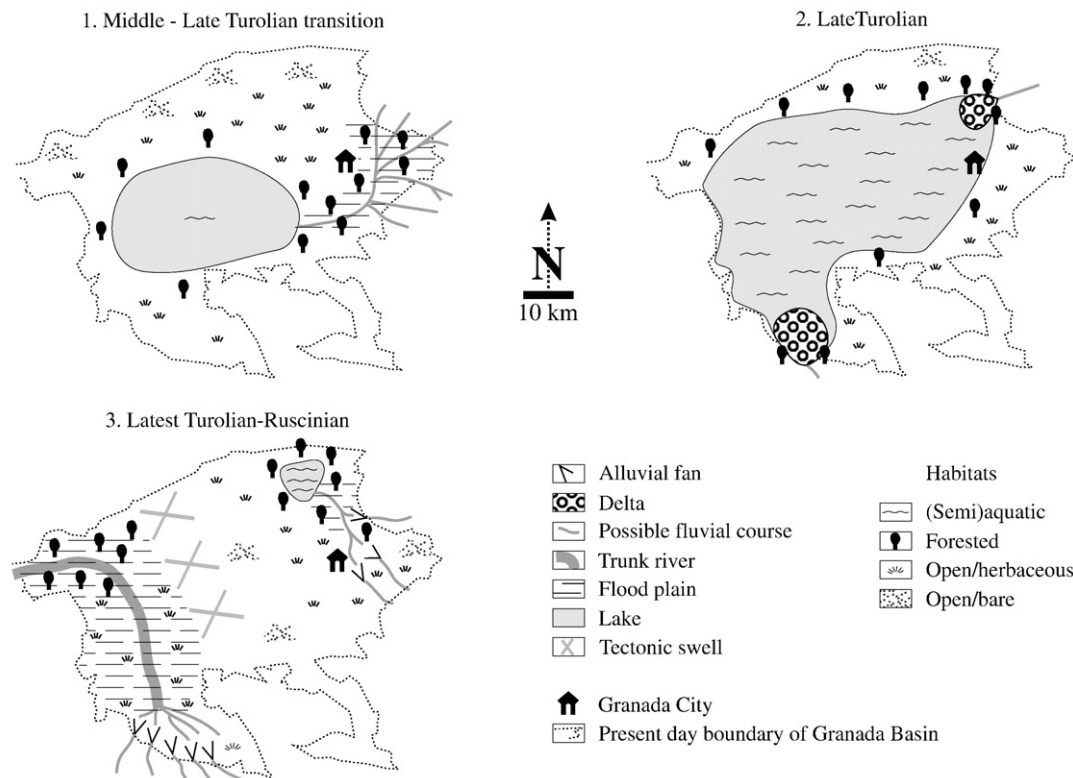


Fig. 6. Paleoenvironmental reconstruction of the Granada Basin from the Middle Turolian to the Late Ruscinian, and relation with the sedimentary evolution (modified from García-Alix et al., in press).

(CLC-3), and in the localities situated in the alluvial/fluvial zone indicators of herbaceous/open habitats and bare/open habitats are more important (Fig. 6).

In the western sector there was a fluvial braided system with a wide flood plain with a subaquatic, or palustrine/ephemeral lacustrine zone to the north. Apparently the conditions are dryer than in the previous period. This fluvial system at times exited to the west and at times was endorreic (Fernández and Soria, 1987). Our localities are situated in the subaquatic flood plain, and only herbaceous/open and forested habitats are represented. There is not a continuous lake; therefore, taxons that indicate (semi)aquatic conditions are not represented (Fig. 6).

6. Climatic evolution of the studied interval

The global climatic evolution for the studied interval is based mainly on interpretations of the isotopic record, basically from the Atlantic Ocean. The isotopic interpretations of Zachos et al. (2001) show a general trend of gradual cooling from the Middle Miocene to around 6 Ma (Messinian), and a subtle warming trend during Early Pliocene (Table 1). High resolution isotopic curves for the Late Miocene and Early Pliocene indicate a gentle decrease in temperature during the Messinian without changes during the Mio-Pliocene transition, followed by a short warm phase in the Early Pliocene (Shackleton, 1995; Hodell et al., 2001; Billups, 2002; Vidal et al., 2002) (Fig. 7).

The palynological record of the Messinian–Early Pliocene in the Mediterranean area is very scarce, and it notes a warm phase during the Early Pliocene and one episode of temperature decrease at around 4.5 Ma (Suc et al., 1995b; Fauquette et al., 1998). Suc et al. (1995a,b) proposed that in SW Europe open habitats predominate from the Mio-Pliocene transition (5.3 Ma) to 4.5 Ma, with abundance of herbaceous vegetation and scarce forested habitats. The cooling episode at 4.5 Ma did not cause large changes in the vegetation of SW Europe (Fauquette et al., 1998).

Our localities show drastic variations in the associations, which indicate climatic changes with a tendency to temperature increase from the Middle Turolian (cold–temperate) to the Late Turolian (tropical), and a slight decrease from the Turolian–Ruscinian boundary (warm–temperate) to the Late Ruscinian (temperate). These temperature variations do not fit ideally with the global climatic evolution. However, they correlate well with the estimated climatic conditions inferred for southern Spain from isotopic studies carried out in contemporaneous marine deposits (see below) (Table 1).

The cold–temperate conditions of the Middle–Late Turolian transition agree with a general cooling, linked to a global glaciation, at around 7.0 Ma (Jansen and Sjøholm, 1991; Larsen et al., 1994; Thiede et al., 1998). The isotopic curve of Shackleton (1995) shows an increase in the δO^{18} (cooling) around 5.8 Ma, which coincides with a decrease in warm faunas in the Granada Basin (Fig. 7). In the latest Turolian there is a slightly increase in temperature, deduced by a decrease in δO^{18} , which matches our interpretations (Fig. 7).

Although the palynological and isotopic records indicate, in general, a warm phase in the Early Pliocene (Table 1), our interpreted warm–temperate conditions of the Early Ruscinian agree with a slight increase in δO^{18} at the beginning of Zanclean, which is reflected in a slight decrease in temperatures, more accentuated around 4.8 Ma (Shackleton, 1995), which coincides with the decrease in warm taxa in the locality PUR-13 (Fig. 7).

Although Shackleton (1995) proposes in general high temperatures for the Zanclean (low δO^{18}), there is a peak of increase in δO^{18} around 4 Ma (cooling), which is very near to our locality of the Late Ruscinian (without warm taxa), related to a temperate climate (Fig. 7).

6.1. Comparison with other Mio-Pliocene continental basins

The sequence of paleocommunities of micromammals in the Calatayud–Teruel Basin (Daams et al., 1988; van Dam and Weltje, 1999; among others) is very complete from the Vallesian to the Turolian. However, the time interval studied in this paper is poorly represented, due to the existence of an important sedimentary hiatus not recognized by these authors, according to Martín Suárez and Freudenthal (1998) and Martín-Suárez et al. (2001a). The paleoclimatic and paleoenvironmental interpretations for Calatayud–Teruel Basin from Daams et al. (1988) and van Dam and Weltje (1999) show a positive correlation between warm and dry conditions on the one hand, and cool and wet on the other. Daams et al. (1988) proposed a warm and dry climate for the Middle and Late Turolian that became cold and wet during the Ruscinian. Van Dam and Weltje (1999) proposed cold and wet conditions around 7 Ma, changing to warm and dry, and around 6 Ma, becoming cold and wet again. This temperature curve agrees, in general, with our data (Fig. 7). However, our humidity evolution is very different from that of van Dam and Weltje (1999).

Martín-Suárez et al. (2001b) reinterpreted the climatic curves from Teruel and compared them with those from Crevillente. They reached

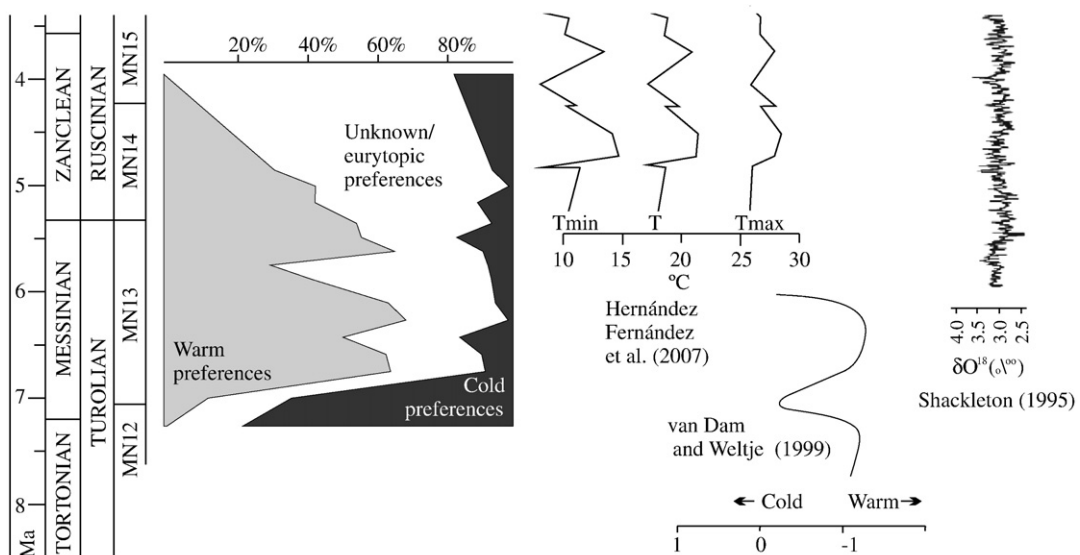


Fig. 7. Correlation of the variation of warm and cold associations from the Granada Basin, the paleotemperature curve of van Dam and Weltje (1999), the paleotemperature curves (maximum, minimum, and mean temperatures) of Hernández Fernández et al. (2007), and the isotopic curve of Shackleton (1995).

the conclusion that the curves show different climatic evolution mainly because of their different geographical position: Crevillente is located in the coastal plain of the Mediterranean Sea and Teruel on the Central Spanish Plateau. The (paleo)geographical context of the Granada Basin, where the sea retreated in the Latest Tortonian and that is at present separated less than 20 km from the Mediterranean Sea, is more similar to that of the Crevillente area than that of the Calatayud–Teruel Basin. In this respect it is not surprising that the deduced climatic conditions for the Granada Basin are similar to those inferred for the Crevillente area: cold and dry during Middle Turolian–Late Turolian transition, and warmer and more humid for the Late Turolian. However, the conditions seem to be slightly wetter during this interval in the Granada Basin, possibly due to the presence of the Sierra Nevada Mountain range that constituted an important relief in the Late Tortonian (Braga et al., 2003). These conditions differ from those of the Calatayud–Teruel Basin, which are dryer and cooler according to Martín-Suárez et al. (2001b).

The data of different Spanish basins from Hernández Fernández et al. (2007) assign warm climate to the Early Ruscinian, slightly warmer conditions for this age than our interpretations; they assign to the locality PUR-4 a temperate climate, which agree with our warm-temperate climate. They propose a cooling trend during the Plio-Pleistocene, which begins to be more accentuated from the Villafranchian onwards. Hernández Fernández et al. (2007) divide the Ruscinian in four phases; two warm, and two temperate. The first temperate phase coincides with our data from the earliest Ruscinian, and the second one matches with the interpretation of temperate conditions from our Upper Ruscinian locality (Fig. 7).

The Guadix Basin, situated around 25–30 km to the west of the Granada Basin, had warm and dry conditions during the Late Turolian (Martín Suárez, 1988; Sesé, 1991; Minwer-Barakat, 2005). These interpretations are based on scarce and isolated localities with *Parathomys*, which may be correlated with similar localities from the latest Turolian of the Granada Basin, like DHS-4 or BRA-5B. However, the dry conditions for this interval seem to be more pronounced in the

Guadix Basin: in the scarce localities from the Late Turolian and Early Ruscinian of the Guadix Basin African gerbillids are present (Minwer-Barakat, 2005), whereas they are absent in the Granada Basin, where thirty-seven localities have been sampled (García-Alix, 2006; García-Alix et al., in press). Costeur et al. (2007) suggested warmer conditions in the Late Ruscinian than in the Early Ruscinian in the continental southern Spanish basins; however, the Late Ruscinian locality BLS-1 in the Granada Basin shows a large number of taxa with cold preferences, marked by the arrival of arvicolids, and few warmth indicators. It coincides, in general, with the interpretations of Agustí et al. (2001), Minwer-Barakat (2005) and Martín Suárez (1988), which indicated that there is an arrival of cold fauna to the Guadix Basin in the Late Ruscinian, contemporaneous with a radiation of arvicolids, related with a global cooling period (Repenning et al., 1990; Fejfar and Repenning, 1992). In this respect it does not agree with the suggestions of Costeur et al. (2007).

At present, the Guadix Basin has semiarid conditions. It is more arid than the Granada Basin, mainly because of the “rain-shadow” effect of the Sierra Nevada and the Sierra de los Filabres mountains to the south of the basin. Present rainfall in the Granada Basin ranges between 150 and 700 l per year; areas with 350–500 l are most abundant (located at the center of the basin). In the Guadix–Baza Basin rainfall in most areas oscillates between 150 and 350 l per year; areas with precipitations between 350 and 500 l are scarce (<http://www.mapa.es>). Probably, this situation also occurred in the past, since the Sierra Nevada and Sierra de los Filabres constituted important reliefs in the Late Miocene and Pliocene too (Braga et al., 2003).

Montuire et al. (2006) noted that the temperatures become more regionally variable at the end of the Miocene (Late Turolian) in the continental European basins, which is in accordance with our conclusions.

In summary, the climatic interpretations based on mammals, are doubtlessly affected by the geographic (orographic) features of the region, therefore the climatic interpretations of some areas may be different, even in two nearby regions as Casanovas-Vilar and Agustí (2007) suggested in a comparable example from Miocene of northern Spain.

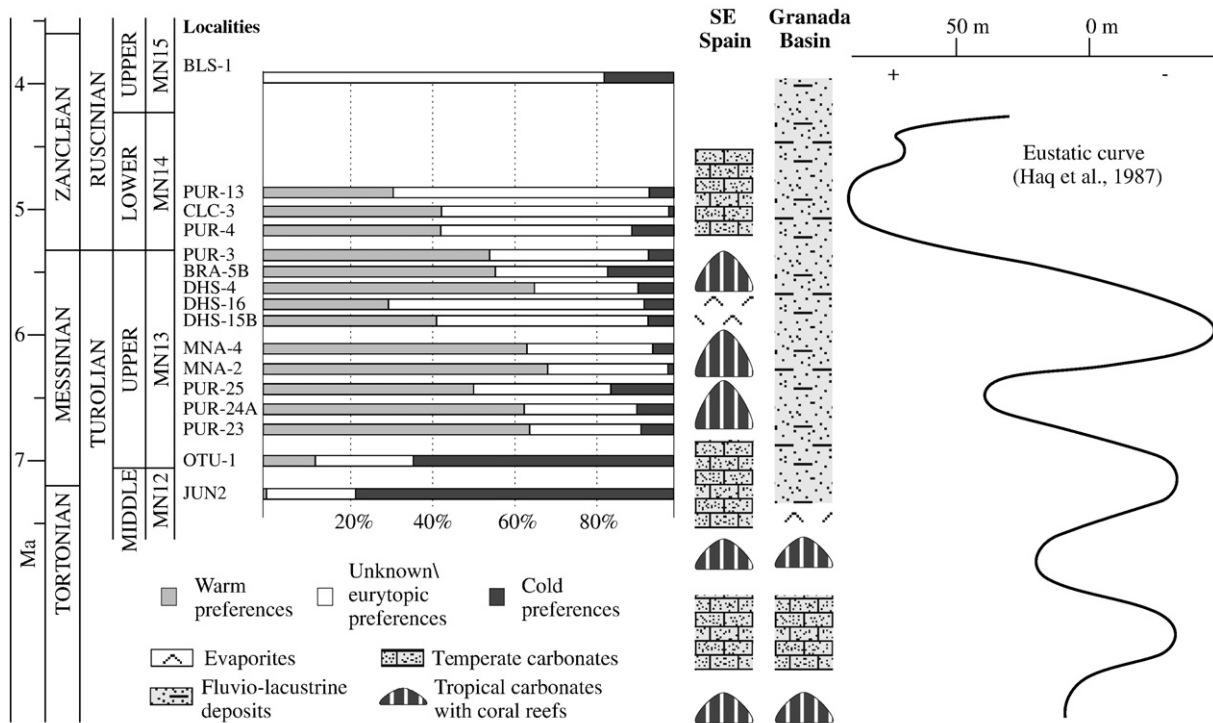


Fig. 8. Temperature variations (deduced from relative abundance of taxa with warm/cold preferences) and correlation with eustatic sea-level curve (Haq et al., 1987), shallow-marine temperate and tropical shelf carbonate sedimentary-events in SE Spain (data from Martín et al., in press), and sediment-types found in the Granada Basin (data from Martín et al., 1984; Braga et al., 2003; García-Alix et al., in press).

6.2. Correlation between marine and continental deposits

The observed variations in the relative abundances of taxons with specific climatic preferences agree with the climatic oscillations interpreted from contemporaneous marine deposits in SE Spain basins. In these basins there is a complete record of coastal sediments, ranging in age from the Tortonian to the Pliocene, showing an alternation of temperate and tropical carbonates (Fig. 8) (Martín and Braga, 1994; Brachert et al., 1996; Esteban et al., 1996; Martín et al., 1999; Martín and Braga, 2001; Sánchez-Almazo et al., 2001; Martín et al., in press). These alternations are linked to variations in the sea-surface water-temperature, as the stable isotopes studies ($^{16}\text{O}/^{18}\text{O}$) demonstrate (Martín et al., 1999; Sánchez-Almazo et al., 2001; Martín et al., in press). The presence of coral reefs in the tropical deposits (Esteban et al., 1996) indicates winter mean sea-surface water-temperatures of at least 20 °C; when temperate carbonates were deposited, this temperature was lower, usually ranging from 14 to 18 °C (Martín et al., 1999; Sánchez-Almazo et al., 2001; Martín et al., in press).

A correlation can be established between some deposits in the Granada Basin and those of other areas of SE Spain during the Late Miocene and earliest Pliocene. In the Tortonian the Granada Basin was still marine and underwent one episode of temperate carbonates and two tropical ones with coral reef development (Braga et al., 1990, 1996; Rivas et al., 1999), which are correlatable with similar, contemporaneous episodes in other SE Spain basins (Esteban et al., 1996). Marine–continental transitional deposits (Martín et al., 1984) are found overlying the marine deposits in the Granada Basin (Fig. 8).

The studied continental deposits of the Middle–Upper Turolian transition (localities JUN-2 and OTU-1) may be partially correlated with the temperate carbonate episode of the so-called “Azagador Member” (Puga-Bernabéu et al., 2007a,b) in the basins of Almería (SE Spain). Martín et al. (1999) and Sánchez-Almazo et al. (2001), using isotopic analyses, indicated that sea-surface water-temperature during the deposition of the “Azagador Member” was similar to present-day Mediterranean sea-surface water-temperature, corresponding to a temperate climate. This agrees with our interpretation of a temperate-cold climate for this interval inferred from the micromammal associations in the localities of the Granada Basin (Fig. 8).

The Upper Turolian (Messinian) localities in the Granada Basin show variations in the relative abundances of warm associations, and they may be correlated with different episodes of carbonate deposition in the SE Spain basins (Fig. 8). The localities PUR-23, PUR-24A, PUR-25, MNA-2 and MNA-4, where warm indicators dominate, may be correlated with the Messinian “Bioherms” and “Fringing Reef” units of Martín and Braga (1994) from SE Spain (Fig. 8). The presence in MNA-4 of *Paraethomys*, whose arrival in the Iberian Peninsula is dated around 6.1 Ma (Garcés et al., 1998), indicates that this locality is slightly younger than 6.1 Ma. This date coincides with the time of development of the “Fringing Reef unit” in Almería (Sánchez-Almazo et al., 2001, 2007). The beginning of the “Messinian Salinity Crisis”, estimated around 5.9–5.8 Ma (Gautier et al., 1994; Garcés et al., 1998; Krijgsman et al., 1999a,b), is correlated with a eustatic sea-level fall linked to a glacial episode (Abreu and Haddad, 1998; Hardenbol et al., 1998). There is an important decrease of warm associations in the next two localities after MNA-4, which may be correlated with the beginning of the “Salinity Crisis” and with gypsum deposition in the Almería basins. Coral-reef carbonates occur again in Almería after this episode, during the latest Messinian (Riding et al., 1991, 1998). Their presence agrees with the relatively high abundance of warm indicators in our latest Turolian localities (DHS-4, BRA-5B and PUR-3).

As pointed out by Martín et al. (in press) in the earliest Pliocene there was a significant change in the Atlantic–Mediterranean connection, with the opening of the Gibraltar Strait immediately after the closing of the Rifian Strait, that caused an influx of cold Atlantic water into the Mediterranean Sea. As a consequence, a

decrease of sea-surface water-temperature of the Mediterranean Sea (as isotopic data demonstrate: Martín et al., in press) occurred. This new paleogeographical configuration was probably responsible for the deposition of temperate carbonates in the marginal basins of SE Spain in the Early Pliocene and the absence of tropical reefs, still present in the latest Messinian (Martín et al., in press). This fact coincides with a decrease in warm taxons in the lowermost Pliocene localities PUR-4, CLC-3 and PUR-13, and a warm–temperate phase with temperatures slightly lower than in the Late Turolian (Fig. 8). Probably the cooling of the surface-water of the Mediterranean Sea that inhibited the development of tropical reefs (Martín et al., in press), affected in some way the nearby terrestrial ecosystems.

Costeur et al. (2007), noted that the Messinian “Salinity Crisis” did not actually trigger any particular local climatic change. This affirmation seems to be incorrect, in view of our results. These authors mainly used data from sediments deposited before and after the crisis, specially in the Spanish basins. Although the interpretations of our record and those from Costeur et al. (2007) agree in that the general tendency of temperatures has not changed before and after the crisis; the data of the Granada Basin, show an important decrease in warm taxa in two consecutive localities coinciding with the crisis (Fig. 8). It agrees with a punctual cooling, according to the isotopic record of Shackleton (1995), which may be linked to a glacial episode (Abreu and Haddad, 1998; Hardenbol et al., 1998). Therefore, we do not agree in full with Costeur et al. (2007), who related the “Salinity Crisis” with tectono-eustatic phenomena only, without climatic/glacioeustatic influence as Abreu and Haddad (1998), and Hardenbol et al. (1998) proposed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2008.04.005](https://doi.org/10.1016/j.palaeo.2008.04.005).

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