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## The Messinian event: What happened to the peri-Mediterranean mammalian communities and local climate?

# L'événement messinien : quel impact sur les communautés de mammifères péri-méditerranéennes et sur le climat local ?

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#### Abstract

What truly happened in the terrestrial ecosystems in response to the famous Messinian salinity crisis is still the matter of extensive discussions. Did mammals record any faunal and/or a climatic or environmental fluctuation is a question that still remains open. Our objective is to investigate mammalian faunas before, during and after the crisis within different terrestrial basins surrounding the Mediterranean Sea. We therefore apply here two methods, the cenogram method and a transfer function based on murine (rodents) species richness to better understand if our proxies can record any qualitative or quantitative climatic or environmental change. The results indicate that mammal faunas do not record any particular shift in climate or environment at the scale of the whole peri-Mediterranean area. The trend is different at the regional scale of terrestrial basins as temperatures increase (Calatayud-Daroca-Teruel Basin) or decrease (Languedoc-Roussillon region) punctually occurs just after the crisis; stable conditions in different areas (e.g. Greece) contradict these trends. Biases in the fossil record or in the methodologies could produce such discrepancies.

#### Résumé

Le réel impact de la crise de salinité messinienne fait toujours l'objet de discussions soutenues. Dans ce contexte, une question reste toujours ouverte : les mammifères enregistrent-ils une quelconque fluctuation faunique et/ou climatique ou environnementale ? Notre objectif est d'étudier les faunes de mammifères avant, pendant et après la crise au sein des divers bassins continentaux entourant la mer Méditerranée. De fait, deux méthodes ont été choisies : la méthode des cénogrammes et l'application d'une fonction de transfert basée sur la richesse spécifique des Murinae (rongeurs). L'objectif étant de comprendre si les mammifères peuvent enregistrer des changements climatiques ou environnementaux qualitatifs ou quantitatifs. Les résultats n'indiquent aucune variation significative du climat ou de l'environnement à l'échelle de la région périméditerranéenne. La tendance est différente aux échelles locale et régionale où l'on peut distinguer ponctuellement juste après la crise soit une augmentation (bassin de Calatayud-Daroca-Teruel) soit une diminution des températures (localement dans le Languedoc-Roussillon) ; des conditions stables (e.g. en Grèce ou régionalement dans le Languedoc-Roussillon) viennent contredire ces tendances. Des biais évidents dans l'enregistrement fossile ou purement méthodologiques sont à l'origine de telles différences.

Keywords: Messinian salinity crisis; Mediterranean Sea; Mammalian communities; Palaeoenvironment; Palaeoelimate; Neogene

Mots clés : Crise de salinité messinienne ; Mer Méditerranée ; Communautés de mammifères ; Paléoenvironnement ; Paléoclimat ; Néogène

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#### 1. Introduction

The Messinian salinity crisis was a critical period in the European Neogene as the Mediterranean Sea almost entirely desiccated from 5.96 or 5.75 (according to two different hypotheses) to 5.32 Ma, upper part of Chron C3r (Clauzon et al., 1996; Cande and Kent, 1995; Krijgsman et al., 1999, 2002). This intensively studied event is still the matter of extensive debates as to how and exactly when the process of the Mediterranean Sea draw down happened (Hsü et al., 1973; Nesteroff, 1973; Rouchy and Saint Martin, 1992; Cornée et al., 1994; Gautier et al., 1994; Clauzon et al., 1996; Krijgsman et al., 1999; Roveri et al., 2001; Warny et al., 2003). Another question still unanswered about the crisis is whether or not it triggered, via a global or local event, a climatic or major environmental change that could have affected the floras and faunas in the Mediterranean realm.

Palaeoecological analysis of large data sets of mammalian faunas and communities has proved to be useful especially in the last two decades to decipher past environments and climates (Andrews et al., 1979; Janis, 1984, 1993; Legendre, 1986, 1989; Montuire et al., 1997; Montuire, 1999; Montuire and Marcolini, 2002; Fortelius et al., 1996, 2002). Several methods have been developed (see references cited above) with qualitative, quantitative, taxonomic or taxon-free approaches to investigate the relationships between faunas and their living environment and to evidence the factors responsible for the faunal changes well recognized long before. Consequently, scientists focussed on the well-recognized faunal changes and succeeded in identifying environmental or climatic fluctuations as controlling factors at global or local scale (Marshall et al., 1982; Legendre, 1986, 1989; Janis, 1989; Webb and Opdyke, 1995; Alroy, 1996). Our approach here is different as the Messinian salinity crisis was first geologically described (Hsü et al., 1973) and later we wondered if faunas and floras underwent its impact or, in other words, if the local climate and environment was sufficiently affected to leave identifiable marks in the palaeontological record.

The purpose of this contribution is therefore to investigate the mammalian communities before, during and after the crisis (from the Late Miocene (Messinian) to the Early Pliocene (Zanclean)) with the aim of reconstructing the environmental and climatic evolution around this event from faunal data. Our objective involves two different analyses. The environmental evolution is documented from mammalian communities body weight distributions (cenograms) constructed for localities situated in different terrestrial basins in the Mediterranean area; and palaeotemperatures are quantified using species richness within several rodent sub-families through transfer functions.

#### 2. Methods

#### 2.1. Cenogram

A cenogram is a rank-ordered body weight distribution where terrestrial herbivorous and insectivorous nonvolant mammal species are plotted on a semi-log diagram. Legendre (1986, 1989)



Fig. 1. Relationships between cenograms' shapes and main environmental characteristics. 1: continuous shape and overall shallow slope (high species richness) in closed and humid conditions. 2: discontinuous shape, different slopes between large and small species (less large species), no break in the distribution in rather closed and arid conditions. 3: discontinuous shape, same slope between large and small species both being separated by a gap in the medium size category (low species richness in this category; large black arrow) in open and rather humid conditions. 4: discontinuous shape, different slopes between large and small species (much less large species), large gap in the medium size category (large black arrow) in open and arid conditions. Adapted from Legendre, 1989 and Aguilar et al., 1999.

Fig. 1. Relations entre l'allure des cénogrammes et les principales conditions environnementales. 1 : allure continue et pente d'ensemble faible (richesse spécifique élevée) pour les milieux fermés et humides. 2 : allure discontinue, pentes différentes selon les espèces de grande ou petite taille (moins de grandes espèces), pas d'interruption dans la distribution pour un milieu relativement fermé et aride. 3 : allure discontinue, même pente pour les espèces de grande ou petite taille toutes deux séparées par une interruption dans la catégorie de taille moyenne (faible richesse spécifique dans cette catégorie ; grande flèche noire) pour un milieu ouvert et assez humide. 4 : allure discontinue, pentes différentes selon les espèces de grande ou petite taille (encore moins d'espèces de grande taille), large interruption dans la catégorie de taille moyenne (grande flèche noire) pour un milieu ouvert et aride. Adapté de Legendre, 1989 et Aguilar et al., 1999.

extensively described the cenogram methodology and documented the relationships between extant mammalian communities and the main environmental characteristics prevailing in their habitat. The data used to estimate fossil mammals body masses are lower m1 length and width measurements as this tooth surface area proved to be allometrically strongly related to body mass (Gingerich and Ryan, 1979; Legendre, 1986, 1989). Fig. 1 briefly summarizes the relationships between a cenogram shape and the main environmental characteristics. In general, the overall cenogram shape used to infer environmental characteristics does not suffer from biases in the sampling record as shown by Legendre (1989: pp. 37–39) who performed simulations of randomly sample-biased assemblages based on extant faunas that did not reveal any significant difference in the environmental interpretations.

#### 2.2. Rodent species richness and climate

The reconstruction of past temperatures can be achieved using the relationship between extant rodents' species richness and extant mean annual temperatures. The methodology used is the linear least square regression technique performed on the distribution of present day rodent subfamilies as independent variable and mean annual temperature as dependant variable. Three equations have, to date, been developed to infer past temperatures using rodents' species richness. The first one has been developed on the arvicolines and is very powerful for the plio-pleistocene period when this subfamily flourished (Montuire et al., 1997). The second one is based on the New World sigmodontines as analogues for the Old World cricetines for the period spanning the late Early, Middle, to early Late Miocene (Montuire et al., 2006). Murines are an abundant rodent subfamily in the European Late Miocene and Early Pliocene and their relationship with temperature complements both above-mentioned equations. Michaux et al. (1995) and Aguilar et al. (1999) extensively explain the present day relationship and the limits of the method and already applied it to Pliocene and Middle to Late Miocene localities. It has also recently been used on the Pleistocene of Thailand where it yielded particularly sound results (Tougard and Montuire, 2006).

It is noteworthy that the coefficient of correlation is not very high for murines (R = 0.704, Aguilar et al., 1999) leading to rather large confidence intervals and thus constituting a methodological bias but correlation is highly significant (p < 0.0001) because of large sample size. Half of the variation in species richness ( $R^2 = 0.5$ ) can be explained by temperature witnessing a rather good dependence. Nevertheless this simple linear relationship between species richness and temperature probably implies that other climatic parameters (e.g., precipitation) can also partially control murine diversity; indeed, the extant murine distribution shows that this family presents a high diversity in tropical zones (and for instance in the tropical rainforest; Carleton and Musser, 1984) of South-East Asia where annual precipitations are also very high. A more complete data compilation on extant murine is under way (mostly adding these South-East Asian data that were absent from the first analysis of Aguilar et al., 1999) to improve this relationship and better understand the dependence of murine species richness to temperature as well as to other climatic parameters. Up to now, murines constitute the best mammal proxy for Late Miocene-Early Pliocene European palaeoclimatic reconstructions.

#### 3. Material

Concerning the cenogram analysis, 13 European localities around the Mediterranean realm can be used from 6.5 to 4 Ma, none being exactly dated from the Messinian salinity crisis episode (5.96/5.75-5.32 Ma). The best record comes from the Spanish Calatayud-Daroca-Teruel Basin with six localities, three before the crisis (Los Casiones, ca. 6.1 Ma, Van Dam and Weltje, 1999; El Arquillo, ca. 6 Ma; and Villastar, ca. ~6 Ma) and three after the crisis (La Gloria 4, ca. 4.5 Ma; La Calera, ca. 4.3 Ma, Aguilar et al., 1999; and Villalba Alta, ca. 4.2 Ma).

The Spanish Castillon-Valencia basin also tightly frames the salinity crisis with two localities (Venta del Moro, ca. 5.9 Ma; and Alcoy, ca. 5 Ma).

Southern France yielded two localities in the Early Pliocene (Montpellier, ca. 5 Ma and Perpignan, ca. 4 Ma, Aguilar et al., 1999) and none in the Messinian.

Southeastern Europe yielded one locality in Greece (Maramena, ca. 6.5 Ma, Sen and Leduc, 1996) and two in Turkey (Dinar-Akçaköy, ca. 4.5 Ma, Sen and Leduc, 1996; and Çalta, ca. 4 Ma, Sen, 1998).

As for the reconstruction of palaeotemperatures using murine species richness, 29 rodent-rich localities from MN13 to MN15 (6.8-3.2 Ma) are taken into account and detailed in Table 1. A subset of these localities is also included in Montuire et al. (2006). We have classified our localities in terrestrial basins and will discuss the evolution of the palaeoclimate inside the regions considered across the salinity crisis. To obtain a regional record of murine diversity and thus to approach temperatures with a regional perspective, we also grouped together 88 fossil-poor and fossil-rich localities and eventually built a "murine faunal list" at the regional spatial scale. We grouped the different species of the same lineage under the same taxon name to avoid working with "chrono-species" (two species of the same lineage can be reported from two sites of the same biochronological zone, virtually increasing species richness). At this regional scale, we obviously get a higher number of Murinae than at the single locality-based scale. We hypothesize that this higher number represents a closer level towards the actual regional murine species richness than does the richest localities on their own, as is the case in studies performed on present-day faunas (Ricklefs, 1987; Koleff and Gaston, 2002). We here reproduce the ecological "local versus regional sampling" of murine diversity. It is noteworthy that at such a regional scale, murine species richness is higher reflecting the local habitat-level endemicity within an environmentally homogeneous region. The higher diversity is not only a by-product of higher sample size (number of localities) as empirical results show that total regional species richness is almost entirely reached by sampling the two richest localities of the region, adding more localities do not significantly increase diversity. We empirically tested this on the Calatayud-Daroca-Teruel region and when only both richest localities are used, 80 to 100% of murine species richness is already sampled depending on the MN zone considered even if more than 10 localities containing murines exist (results not shown here but available on request from the corresponding author). We also understand that in doing so, we may sum localities of different ages but it dos not represent a major problem here as we work in the mammalian biochronological (MN Zones) framework. Table 1 gives the number of Murinae at the regional scale as well as the number of localities summed for each region.

All the data are available on request from the corresponding author.

#### 4. Results

#### 4.1. Cenogram analysis

The fauna of Los Casiones in the Spanish Calatayud-Daroca-Teruel Basin at ca. 6.1 Ma (MN13, Fig. 2) is quite rich (more than 30 species) and presents a discontinuous shape with two segments having more or less the same slope and separated

Table 1

Localities and	l regions	used in	this	study	and	associated	temperature	estimates
Tableau 1								

	MN Zone	T°C estimates	per region		T°C estimates per locality				
Region		No Murinae (localities)	$T^{\circ}C$	Confidence interval	Locality	No Murinae	T°C	Confidence Interval	
Calatayud-Daroca-Teruel	MN13	9 (14)	19.5	14.6-24.3	Celadas 9	6	16	11.2-20.9	
	MN14	15 (8)	26.4	21.6-31.2	Lomas de casares	7	17.2	12.4-22	
					Peralejos E	9	19.5	14.6-24.3	
					La Gloria 4	10	20.6	15.8-25.5	
	MN15	7 (3)	17.2	12.4-22.0	Moreda 1A	8	18.3	13.5-23.2	
					Villalba alta	7	17.2	12.4–22	
Granada	MN13	11(10)	21.8	17.0-26.6	Salobreña	6	16	11.2-20.9	
					Purcal 13	7	17.2	12.4-22	
	MN14	9 (4)	19.5	14.6-24.3	Gorafe 1	5	14.9	10.1-19.7	
					Gorafe 4	5	14.9	10.1-19.7	
	MN15	17 (10)	28.2	23.9-33.5	Belmez	10	20.6	15.8-25.5	
Castillon	MN13	7 (2)	17.2	12.4-22.0					
Valencia	MN14	7 (2)	17.2	12.4-22.0	Alcoy 2	6	16	11.2-20.9	
Duero	MN15	7 (1)	17.2	12.4-22.0	Layna	7	17.2	12.4–22	
Languedoc-Roussillon	MN13	8 (3)	18.3	12.3-23.2	Castelnou 3	8	18.3	13.5-23.2	
	MN14	9 (8)	19.5	14.7-24.3	Vendargues	5	14.9	10.1-19.7	
	MN15	13 (6)	24.1	19.3-28.9	Serrat-d'en Vaquer	9	19.5	14.6-24.3	
					Mont-Hélène	10	20.6	15.8-25.5	
					Sète	8	18.3	13.5-23.2	
					Lo Fournas 13	8	18.3	13.5-23.2	
					Nîmes	5	14.9	10.1–19.7	
Greece	MN13	9 (6)	19.5	14.6-24.3	Monasteri	4	13.7	8.9–18.6	
					Anno Metochi M1,2,3	5	14.9	10.1-19.7	
					Maramena	4	13.7	8.9-18.6	
	MN14	9 (5)	19.5	14.6-24.3	Ptolemaïs 1	4	13.7	8.9-18.6	
					Marites	5	14.9	10.1-19.7	
					Kardhia	4	13.7	8.9–18.6	
Turkey	MN14	10 (4)	20.6	15.8-25.5	Develi	4	13.7	8.9–18.6	
	MN15	6 (4)	16.0	11.2-20.9	Calta	4	13.7	8.9–18.6	

They are classified in their MN zone. Temperature estimates and associated confidence intervals are given according to murine species richness.

Elles sont classifiées selon leur zone MN. Les estimations de température et les intervalles de confiance associés sont donnés en fonction de la richesse spécifique des murinés.

by a large gap in the medium sizes. This cenogram is typical of an open and not very arid environment (Fig. 1, schematic shape no. 3). This result for this region is emphasized by the two other faunas, El Arquillo (ca. 6 Ma, MN13, Fig. 2) and Villastar (ca.  $\sim$ 6 Ma, MN13, Fig. 2), yielding the same body weight distributions.

After the salinity crisis, the fauna of la Gloria 4 (ca. 4.5 Ma, MN14, Fig. 2) gives a somewhat similar environmental interpretation that is open and perhaps slightly more humid conditions (higher number of small species). Continuing into the Pliocene (MN15), the faunas of La Calera (ca. 4.3 Ma, Fig. 2) and Villalba Alta (ca. 4.2 Ma, Fig. 2) yield again the same results with the large gap in the medium size category documenting open conditions, La Calera being probably slightly more humid than Villalba Alta as the latter shows a steeper slope in the large species.

Spain also recorded the Miocene-Pliocene transition in the Castillon-Valencia Basin. Venta del Moro (ca. 5.9 Ma, MN13, Fig. 2) just preceeds the salinity crisis and interestingly the same environmental interpretations as for the Teruel Basin can be proposed from that fauna even though it yielded less small species. It therefore is characteristic of an open and not very arid environment. The other fauna in that region, Alcoy (ca. 5 Ma, MN14, Fig. 2) yielded more small and less large species but the cenogram shape is not particularly different except a slightly steeper slope for large than for small species that would characterize rather arid conditions, there is again a large gap in the medium sizes signing the open environment and the overall shape is between schematic shapes nos. 3 and 4 (Fig. 1).

Southern France only yields faunas suitable for a cenogram analysis in the Early Pliocene. Both faunas (Montpellier and Perpignan, Fig. 2) have been described in Michaux et al. (1995) and Aguilar et al. (1999). Montpellier (ca. 5 Ma, MN14) is typical of a closed and humid environment (schematic shape no. 1, Fig. 1) whereas Perpignan (ca. 4 Ma, MN15) gives still rather closed conditions (a small gap in the medium sizes indicates adjacent open areas) in a less humid climate.



Fig. 2. Sequence of cenograms of 13 Mio-Pliocene peri-Mediterranean mammalian localities before and after the Messinian salinity crisis (M.S.C.). The stratigraphic position of the localities is indicated by the black triangles.

Fig. 2. Séquence de cénogrammes de 13 faunes de mammifères mio-pliocènes du pourtour méditerranéen précédant et suivant la crise de salinité messinienne. La position stratigraphique des localités est indiquée par des triangles noirs.

The southeastern European record is quite fragmentary as only a single locality, suitable for cenogram analysis, of Late Miocene age and two of Early Pliocene age are available. The Greeck locality of Maramena (ca. 6.5 Ma, MN13) is interesting as it characterizes a rather closed and humid environment (continuous shape, shallow slope and no important gaps in the distribution, Fig. 2). The Turkish record (Dinar-Akçaköy, 4.5 Ma, MN14, and Calta, ca. 4 Ma, MN15, Fig. 2) tells a totally different story as both faunas characterize rather open and arid conditions (very large gap in the medium sizes even though the slopes of large and small species are not very different).

#### 4.2. Climatic quantifications

Table 1 gives paleotemperature estimates and confidence intervals for the localities used in this study.

The overall temperature range at the locality scale observed in Europe does not particularly increase nor decrease over the Messinian salinity crisis. Indeed, the estimated temperature range for MN13 is 13.7 to  $18.3^{\circ}$ , 13.7 to  $20.6^{\circ}$  for MN14 and 13.7 to  $20.6^{\circ}$  for MN15. Temperatures estimates at the regional scale are higher as the number of murine species is higher in good concordance with the established relationship: 17.2 to  $21.8^{\circ}$  for MN13, 17.2 to  $26.4^{\circ}$  for MN14 and 17.2 to  $28.7^{\circ}$  for MN15. A variation of about  $10^{\circ}$  is recorded for MN zones 14 and 15 and it might be the result of specific regional climatic conditions or to the difference in number of localities from region to region. Temperatures are thus quite heterogeneous throughout Europe and no real difference is found before and after the crisis although a slight tendency to higher temperatures can be detected.

If we look in close details at the regions, temperature estimates tell a different story. The Calatayud-Daroca-Teruel Spanish Basin shows a strong increase in temperature across the Messinian salinity crisis. Indeed, inside this basin, mean temperatures range from 16 to  $19.1^{\circ}$  from MN13 to MN14, this increase is still recognised in MN15 with mean temperatures of about  $17.7^{\circ}$ . The same increase is recorded when all the localities are summed in the basin: temperatures increase from 19.5 to  $26.4^{\circ}$ , a decrease then follows in MN15.

The Granada-Guadix-Baza Basin does not record such an increase across the Messinian salinity crisis and temperatures stay rather homogeneous: 16 to  $17.2^{\circ}$  in MN13,  $14.9^{\circ}$  in MN14; they sharply increase in MN15 ( $20.6^{\circ}$ ). When all localities are summed, temperatures estimates are very high,  $21.8^{\circ}$  for MN13,  $19.5^{\circ}$  in MN14 and  $28.7^{\circ}$  in MN15.

The third region that records the Miocene-Pliocene boundary is the Languedoc-Roussillon Basin in southern France; in this area, temperatures seem to drop from MN13 to MN14 and then increase in MN15 (temperature estimates:  $18.3^{\circ}$ ,  $14.9^{\circ}$  and  $14.9-20.6^{\circ}$ , respectively). The drop after the Messinian partly accounts for the single poor murine record (locality Vendargues) in MN14. At the regional scale, when all murine-bearing localities available are taken into account, no significant temperature change is recorded from MN13 to MN14 (18.3 to  $19.5^{\circ}$ , respectively), then a large increase up to  $24.1^{\circ}$  occurs in MN15.

Greece also provides a record across the Messinian salinity crisis and the temperatures are homogeneous before and after the crisis: 13.7 to  $14.9^{\circ}$  in MN13 and MN14 for the locality based analysis. When all localities are summed, the same homogeneity is recorded with higher temperatures:  $19.5^{\circ}$  in MN13 and MN14.

Other basins yield fragmentary records, in Spain (Duero Basin) and Turkey; the temperature estimates either agree with the other estimations in the richer basins or are a little lower due to a lower number of localities that biased the record towards a lower species richness.

#### 5. Discussion

Both methods give similar results. Either qualitative or quantitative estimates of the palaeoenvironment and of palaeotemperatures converge towards the same conclusions.

It is important to note that cenograms probably better reflect the aridity/humidity rather than the warm/cold climatic component. The effect of warm temperatures on a cenogram structure might well be merged with the effect of a high humidity. It is worth noting here that in extant communities, the warmest and most humid regions yield the longest and shallowest cenogram shapes (Legendre, 1989). Cold places are usually rather arid as well and arid places can also be very warm thus in any case (cold or warm), cenograms will be short and have steep slopes. Bearing this in mind, the Calatayud-Daroca-Teruel Basin records an important increase of temperatures across the Messinian salinity crisis, and cenograms record slightly more humid conditions in MN14 probably signing a warmer climate also (Table 1). It is noteworthy that increasing temperatures and aridity could have been expected from the drying of Mediterranean Sea rather than the increasing humidity recorded here.

Southern Spain does not show any temperature fluctuation through the crisis. The Granada locality-based record is constant around  $15^{\circ}$ , no cenogram can be drawn for this area to confirm this result. At the regional scale, a small temperature drop occurs, but is below the resolution power of the method (Table 1).

In southern France, the Languedoc-Roussillon region yields a single murine-rich locality in the Messinian giving a high temperature estimation (18.3°). Early Pliocene records are poorer in rich localities and give lower estimates and MN15 yields higher temperatures such as for the Granada region. Cenograms are only available in the Pliocene and the MN15 Perpignan body weight structure also probably indicates warmer conditions (Aguilar et al., 1999) than in MN14. Temperature estimates and cenogram shapes agree on the conditions that prevailed in this area. At the regional level, when all localities are considered, no temperature evolution occurs from MN13 to MN14.

Southeastern European (Greece) temperature estimates are constant throughout the crisis and, unfortunately, no cenogram can confirm this trend for the Pliocene.

Our results rather point to a limited impact of the Messinian salinity crisis on the local Mediterranean climate. Three hypotheses can be put forward to explain this:

- the Messinian salinity crisis did not actually trigger any particular local climatic change;
- a poor fossil record could limit these results but 88 localities have been taken into account in the region-based climatic quantifications yielding a large number of fossil murines, eventually showing no major climatic fluctuations and corroborating the results of the locality-based estimates;
- discrepancies inherent to the quantitative method could also limit the results. It is probable that two factors hamper the power of the murine diversity-temperature relationship: first, few extant Asian localities have been integrated in the present-day model; increasing sampled geographical areas and the number of extant faunas will probably give better results. Second, the murine species richness-temperature relationship is probably not as direct as that of the other rodent subfamilies (i.e. arvicolines and sigmodontines) and humidity also seems to play an important role in controlling murine diversity (Aguilar et al., 1999).

Differences between regions reflect the normal evolution of the European climate through the Late Miocene and Early Pliocene towards strengthened climatic belts and overall cooler and more temperate conditions. This evolution is global and linked to the development of permanent Antarctic Ice Sheets (Flower and Kennett, 1994; Zachos et al., 2001) inducing reorganisations of deep-sea cold water and palaeoatmospheric circulations. Palaeotopographic developments (Himalayas and Tibetan Plateau) also played an important role in controlling palaeoatmospheric features such as the Asian monsoon and its deep impact on Eurasian climates. Its onset related to further uplift of Tibet 8 Myrs ago (Wang et al., 1999) and to northward shift of Africa and then its regular functioning (and particularly the northward monsoonal component) triggered the development of more humid conditions (Zeit Wet Phase) during the Messinian in the southeastern mediterranean region (Northeastern Africa); in turn, the Mediterranean draw down probably emphasized this wet phase in creating a zone of low atmospheric pressure strengthening the monsoon (Griffin, 2002). But apparently, the wet phase was restricted to northeastern Africa and the western edges of the Mediterranean Sea did not receive this moisture (Griffin, 2002). Our results confirm these considerations. Some authors yet postulate that the Messinian salinity crisis maintained a slight global cold phase up to 5.55 Ma through reduced outflow of saline waters from the Mediterranean Sea to the Atlantic (Vidal et al., 2002).

Several plant-based analyses confirm that no true climate change occurred in response to the Crisis. Bertini (1994) and Ghetti et al. (2002) investigated the climate in central and northern Italy during and after the Messinian. They documented, from pollen assemblages, a vegetation characteristic of a sub-tropical to warm temperate climate before the crisis and of a warm temperate to temperate climate after. Suc and Bessais (1990) recorded non-changing thermo-xeric conditions in Sicily before, during and after the salinity crisis and concluded that the climatic context favoured the Mediterranean drying which in turn did not change it. No extraordinary climatic conditions led to the crisis (Blanc, 2000). Suc et al. (1999) later indicated that the evolution of the Late Miocene vegetation reflected a southern European aridification and the loss of the previous subtropical character, the Messinian salinity crisis not affecting this long term ongoing process. The crisis triggered the disappearance of mangrove taxa (Avicennia) but not as a response to a particular climatic shift and rather to ecological conditions such as an increase of salinity (Quézel and Médail, 2003). Additionally, Utescher et al. (2000) quantitatively estimated palaeoprecipitations in Northwestern Germany in the past 25 My from the palaeobotanical record of megafloras and argued that the precipitation levels remained constant during the whole Messinian.

All these lines of evidence indicate that climate did not change across the salinity crisis. It therefore also supports the idea that the Mediterranean draw down was caused by tectonic uplift in the Alboran Sea as supposed by Duggen and Hoernle (Duggen and Hoernle, 2003, 2004) rather than by a global glacio-eustatic sealevel fall (Adams et al., 1977; Hodell et al., 1986, 2001).

It therefore seems that, up to the present knowledge, faunas and floras do not record any particular climatic evolution in response to the Messinian salinity crisis (Agustí and Anton, 2002).

#### 6. Conclusions

We applied two methodologies to the mammalian fossil record spanning the Messinian and the Zanclean. Our goal was to test if the Messinian salinity crisis had an impact on the mammalian community structure and on the local climate.

The cenogram method was conducted on 13 rich localities and a transfer function between murine species richness and temperature was applied to 28 rodent-rich faunas and to regional sums of 88 murine-bearing faunas. Both methods point to the same conclusions:

- the structure of local mammalian communities remained unchanged through the crisis, only African immigrants entered southern Europe via emerged corridors and slightly enriched the faunas;
- consequently, the environments deduced from the cenogram analysis remain constant before and after the crisis, but are different in the five regions considered;
- the overall temperatures, at the level of the Mediterranean realm, are not homogeneous but are quite stable through the crisis;
- at the locality-based scale, different problems (taphonomic and methodological issues) punctually bias the temperature estimates either giving increases (Calatayud-Daroca-Teruel Basin), decreases (Languedoc-Roussillon region) or stable conditions (Greece) from the Late Messinian to the Early Zanclean. For regional temperature estimates less problems subsist and estimates point to rather stable conditions (e.g. Languedoc-Roussillon, Greece).

Our results are consistent with several plant-based analyses that do not record any significant climate or environmental change in response to the Messinian salinity crisis; southern Europe documenting thermo-xeric (Suc and Bessais, 1990; Suc et al., 1999) conditions and towards northern Europe progressively more humid, temperate-like conditions being inferred (Bertini, 1994; Utescher et al., 2000).

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