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Late Miocene–Early Pliocene temperature estimates in Europe using rodents

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Abstract

Studies of mammal communities, and in particular of rodents, provide useful information on palaeoenvironments and palaeoclimates. Based on the relationship between species richness and climatic parameters, we propose three models, using arvicolines, murines or sigmodontines in order to quantify past temperatures. Based on rodents, temperatures are estimated here for Late Miocene–Early Pliocene (MN 9 to MN 15) European faunas at a regional scale. Two kinds of continental patterns in temperatures are observed with homogenous temperatures for MN 9 up to MN 11 or contrasted temperatures at the end of the Miocene. The onset of a latitudinal effect is also indicated during MN 15. Temperature estimates have also been used to infer past elevation for localities.

Keywords: Rodentia; Climate; Temperature; Neogene; Europe

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1. Introduction

Studies in paleoclimate reconstructions based on fossil material have been largely restricted to Quaternary sequences. Little has been done on older Pliocene times and very few studies relate to older Cenozoic periods. They are often based on diversity analysis of whole mammalian faunas (e.g., Andrews et al., 1979; Artemiou, 1984; Legendre, 1986, 1989; de Bonis et al., 1992; Gibernau and Montuire, 1996; Montuire and Desclaux, 1997; Montuire, 1999; Montuire and Marcolini, 2001), small mammals (e.g., Kowalski, 1971; van der Meulen and de Bruijn, 1982; Daams and van der Meulen, 1984; Horacek, 1985, 1990; Vianey-Liaud, 1991; Sesé, 1991; van der Meulen and Daams, 1992; Sesé, 1994; Popov et al., 1994; Chaline et al., 1995; Michaux et al., 1996, 1997; Montuire et al., 1997; Van Dam, 1997; Aguilar et al., 1999a; Van Dam and Weltje, 1999) or large mammals (e.g., Vrba, 1980; Janis, 1984; Van Valkenburgh, 1988). Attempts have been made to quantify climatic parameters based on pollen data (e.g., Guiot, 1990; Fauquette et al., 1998), on coleopterans (Atkinson et al., 1986), and mammals (Horacek, 1990; Montuire, 1996; Montuire et al., 1997; Aguilar et al., 1999b; Legendre et al., 2005).

Here we provide climatic estimates based on rodents for Late Miocene–Early Pliocene European faunas at a regional scale. Three methods have been developed for quantifying past climates: first with arvicolines, the Palearctic voles (Montuire, 1994; Montuire et al., 1997), second with murines, the Old World rats and mice (Aguilar et al., 1999b) and lastly with sigmodontines, the New World rats and mice (Legendre et al., 2005). This latter sub-family is used as an analogue for the European fossil cricetines.

2. Material

Species lists have been compiled from the literature for several rich Late Miocene–Early Pliocene rodents

Table 1
Neogene European localities from MN 9 to MN 15 with the number of cricetine (Cri), murine (Mur) and arvicoline (Arv) species

Zone	Country	Locality	Cri	Mur	Arv	References
MN9	Austria	Götzendorf	5	0	0	Bachmayer and Wilson (1985a,b), Rögl et al. (1993), Daxner-Höck (1996)
	France	Castelnou 1B (Languedoc–Roussillon)	5	1	0	Aguilar et al. (1999a)
		Lo Fournas 5 (Languedoc–Roussillon)	5	0	0	Aguilar et al. (1999a)
		Jujurieux (Provence)	5	0	0	Mein (1999)
	Germany	Hammerschmiede (Bayern)	5	0	0	Mayr and Fahlbusch (1975)
		Petersbuch 14 (Bayern)	5	0	0	Bolliger and Rummel (1994)
	Hungary	Rudabanya	5	0	0	Rabeder (1985)
	Spain	Nombrevilla (Teruel–Catalyud–Daroca)	5	0	0	Aguilar et al. (1979)
		Hostalets de Pierola (Vallés-Penedés)	6	0	0	Agustí and Gibert (1982)
MN10	France	Ambérieu 1 (Central East)	4	4	0	Farjanel and Mein (1984)
		Lo Fournas 6 (Languedoc–Roussillon)	2	4	0	Aguilar et al. (1999a)
		Lo Fournas 7 (Languedoc–Roussillon)	6	3	0	Aguilar et al. (1999a)
MN 11	Austria	Eichkogel	5	1	0	Bachmayer and Wilson (1985a,b), Rabeder (1989)
	France	Ambérieu 3 (Central East)	4	3	0	Farjanel and Mein (1984)
		Lobrieu (Provence)	2	5	1	Mein and Truc (1966), Mein (1999)
	Germany	Dorn–Dürkheim (Rheinhessen)	6	1	0	Franzen and Storch (1975)
	Spain	Crevillente 2 (Alicante–Murcia)	2	5	0	de Bruijn et al. (1992), Martín Suárez and Freudenthal (1993)
		Alfambra (Teruel–Catalyud–Daroca)	1	3	0	Alcalá et al. (1991), Van Dam (1997)
MN 12	France	Castelnou 1 (Languedoc–Roussillon)	4	6	0	Aguilar et al. (1999a)
	Spain	Aljezares de Teruel (Teruel–Catalyud–Daroca)	3	4	0	Adrover (1986), Alcalá (1987)
MN 13	France	Lissieu (Central–East)	2	4	0	Mein (1999)
		Castelnou 3 (Languedoc–Roussillon)	4	8	1	Aguilar et al. (1999a)
		La Tour (Provence)	4	5	0	Aguilar et al. (1982, 1989)
	Italy	Brisighella	2	4	0	Rook (1992), Kotsakis et al. (1997)
	Greece	Ano Metochi M1–3	2	5	0	de Bruijn (1989)
	Spain	Salobreña (Granada)	2	6	0	Aguilar et al. (1984)
		Casablanca-M (Castellon–Valencia)	3	5	0	Agustí and Galobart (1986)
MN 14	France	Vendargues (Languedoc–Roussillon)	1	5	1	Mein and Michaux (1970), Chaline and Michaux (1974), Bachelet (1990)
		Hautimagne (Provence)	0	6	0	Mein and Michaux (1970), Aguilar et al. (1983), Aguilar and Michaux (1984)
	Spain	Alcoy (Alcoy–Valencia)	4	6	0	Adrover (1969), Crusafont Pairó (1971), Brandy (1979)
		Gorafe 1 (Granada–Guadix–Baza)	3	5	0	Agustí and Martín Suárez (1987)
		Gorafe 4 (Granada–Guadix–Baza)	3	5	0	Agustí and Martín Suárez (1987)
		La Gloria 4 (Teruel–Catalyud–Daroca)	2	10	1	Adrover et al. (1993), Alcalá (1994)
	Greece	Maritsa (Rhodes Isl.)	3	5	0	de Bruijn et al. (1970)
	Hungary	Osztramos 1	5	0	1	Jánossy (1971)
	Poland	Podlesice	8	0	0	de Bruijn et al. (1992)
MN 15	France	Serrat-d'en Vaquer (Languedoc–Roussillon)	4	9	1	Bachelet (1990), Aguilar et al. (1991), de Bruijn et al. (1992)
		Mont-Hélène (Languedoc–Roussillon)	3	10	0	Aguilar and Michaux (1984), Aguilar et al. (1986), Bachelet (1990)
		Sète (Languedoc–Roussillon)	4	10	2	Aguilar et al. (1983), Bachelet (1990)
		Lo Fournas 13 (Languedoc–Roussillon)	3	8	1	Bachelet (1990), Bachelet and Castillo Ruiz (1990)
	Spain	Belmez (Córdoba)	4	10	0	Bachelet and Castillo Ruiz (1990), Castillo (1992)
		Moreda 1A (Granada)	0	8	1	Castillo Ruiz (1990)
	Slovakia	Ivanovce A	5	2	4	Fejfar and Heinrich (1985)
		Ivanovce B	5	2	3	Fejfar and Heinrich (1985)

Table 2
Parameters of the least square regression between the number of species of Arvicolinae, Murinae, and Sigmodontinae and annual temperatures (after Montuire et al., 1997; Aguilar et al., 1999a,b; Legendre et al., 2005)

Annual temperature	*N*	R^2	Slope ± SE	Intercept ± SE	SE estim.
Arvicolinae	253	0.8485	−2.84334 ± 0.07584	20.27902 ± 0.39201	3.55036
Murinae	114	0.4962	1.14783 ± 0.10928	9.15367 ± 0.73521	4.81156
Sigmodontinae [a]	261	0.8820	0.04395 ± 0.00100	2.42411 ± 0.00083	0.00472

[a] Equation with Log_{10} (*N* sp. + 1) and Log_{10} of temperature in Kelvin, Log_{10} (θ °C + 273.15).

faunas (from MN 9 to MN 15 zones), especially for cricetines, murines and arvicolines.

The older localities, dated from MN 9 zone are: Götzendorf in Austria (Bachmayer and Wilson, 1985a,b; Rögl et al., 1993; Daxner-Höck, 1996); in France, Castelnou 1B and Lo Fournas 5 in Languedoc–Roussillon (Aguilar et al., 1999a) and Jujurieux in Provence (Mein, 1999); in Germany (Bayern), Hammerschmiede (Mayr and Fahlbusch, 1975) and Petersburch 14 (Bolliger and Rummel, 1994); in Hungary, Rudabanya (Rabeder, 1985); and in Spain, Nombrevilla in the Catalyud–Teruel–Daroca basin (Aguilar et al., 1979) and Hostalets de Pierola in Vallés-Penedés (Agustí and Gibert, 1982).

For the MN 10 zone, only three French localities are documented: Ambérieu 1 in the East Central region (Farjanel and Mein, 1984) and Lo Fournas 6 and Lo Fournas 7 in Languedoc–Roussillon (Aguilar et al., 1999a).

The localities for the MN 11 zone are widely distributed in Europe: Eichkogel in Austria (Bachmayer and Wilson, 1985a,b; Rabeder, 1989); in France, Ambérieu 3 in East Central (Farjanel and Mein, 1984), Lobrieu in Provence (Mein and Truc, 1966; Mein, 1999); in Germany, Dorn–Dürkheim in Rhein–Hessen (Franzen and Storch, 1975); and in Spain, Crevillente 2 in Alicante–Murcia region (de Bruijn et al., 1992; Martín Suárez and Freudenthal, 1993) and Alfambra in the Teruel–Catalyud–Daroca basin (Alcalá et al., 1991; Van Dam, 1997).

Only two localities are documented for the MN 12 zone: one in France, Castelnou 1 from Languedoc–Roussillon (Aguilar et al., 1999a), and one in Spain, Aljezares de Teruel in the Teruel–Catalyud–Daroca basin (Adrover, 1986; Alcalá, 1987).

Table 3
Mean annual temperatures (Annual ± SE) for Arvicolinae (for *N* species from 0 to 12) and Murinae and Sigmodontinae (for *N* species from 0 to 20)

N sp.	Arvicolinae	Murinae	Sigmodontinae	
	Annual ± SE	Annual ± SE	Annual ± SE	Annual (°C)
0	20.28 ± 3.572	9.15 ± 4.867	2.424113 ± 0.004787	−7.6 (−10.5/−4.7)
1	17.44 ± 3.566	10.30 ± 4.856	2.437345 ± 0.004748	0.6 (−2.4/3.6)
2	14.59 ± 3.561	11.45 ± 4.846	2.445084 ± 0.004734	5.5 (2.5/8.6)
3	11.75 ± 3.559	12.60 ± 4.839	2.450576 ± 0.004727	9.1 (6.0/12.2)
4	8.91 ± 3.557	13.74 ± 4.835	2.454836 ± 0.004725	11.8 (8.8/15.0)
5	6.06 ± 3.558	14.89 ± 4.833	2.458316 ± 0.004724	14.1 (11.0/17.3)
6	3.22 ± 3.560	16.04 ± 4.833	2.461258 ± 0.004725	16.1 (13.0/19.3)
7	0.38 ± 3.563	17.19 ± 4.836	2.463807 ± 0.004726	17.8 (14.6/21.0)
8	−2.47 ± 3.569	18.34 ± 4.842	2.466056 ± 0.004728	19.3 (16.1/22.5)
9	−5.31 ± 3.576	19.48 ± 4.849	2.468067 ± 0.004730	20.7 (17.5/23.9)
10	−8.15 ± 3.584	20.63 ± 4.860	2.469886 ± 0.004732	21.9 (18.7/25.1)
11	−11.00 ± 3.594	21.78 ± 4.872	2.471547 ± 0.004734	23.0 (19.8/26.3)
12	−13.84 ± 3.606	22.93 ± 4.888	2.473075 ± 0.004736	24.1 (20.8/27.3)
13		24.08 ± 4.905	2.474490 ± 0.004739	25.0 (21.8/28.3)
14		25.22 ± 4.925	2.475807 ± 0.004741	25.9 (22.7/29.2)
15		26.37 ± 4.947	2.477039 ± 0.004744	26.8 (23.5/30.1)
16		27.52 ± 4.972	2.478196 ± 0.004746	27.6 (24.3/30.9)
17		28.67 ± 4.998	2.479287 ± 0.004749	28.3 (25.1/31.7)
18		29.81 ± 5.027	2.480319 ± 0.004751	29.1 (25.8/32.4)
19		30.96 ± 5.059	2.481298 ± 0.004753	29.7 (26.5/33.1)
20		32.11 ± 5.092	2.482230 ± 0.004756	30.4 (27.1/33.7)

For the MN 13 zone, the localities cover southern Europe. There are three localities in France, Castelnou 3 in Languedoc–Roussillon (Aguilar et al., 1999a), Lissieu in East Central (Mein, 1999) and La Tour in Provence (Aguilar et al., 1982, 1989). One locality comes from Italy, Brisighella (Rook, 1992; Kotsakis et al., 1997) and one from Greece, Ano Metochi M1–3 (de Bruijn, 1989). In Spain, there are two karstic localities, Salobreña in Granada (Aguilar et al., 1984) and Casablanca-M in Castellon (Valencia; Agustí and Galobart, 1986).

Most parts of Europe are represented for the MN 14 zone: in France, there is one locality in Languedoc–Roussillon, Vendargues (Mein and Michaux, 1970; Chaline and Michaux, 1974; Bachelet, 1990) and one locality in Provence, Hautimagne (Mein and Michaux, 1970; Aguilar et al., 1983; Aguilar and Michaux, 1984). In Spain, three basins are documented: the locality of Alcoy in the Alcoy Basin (Adrover, 1969; Crusafont Pairó, 1971; Brandy, 1979), Gorafe 1 and 4 in Guadix–Baza (Agustí and Martín Suárez, 1987) and La Gloria 4 in Teruel–Catalyud–Daroca (Adrover et al., 1993; Alcalá, 1994). The locality of Maritsa (de Bruijn et al., 1970) in Greece (Rhodes Island) is also dated to the MN14 zone. In the eastern part of Europe, two localities are present, one in Hungary, Osztramos 1 (Jánossy, 1971) and one in Poland, Podlesice (de Bruijn et al., 1992).

For France, Perpignan (Serrat-d'en-Vaquer), Mont-Hélène, Lo Fournas 13 and Sète all located in Languedoc–Roussillon (Aguilar et al., 1983; Aguilar and Michaux, 1984; Bachelet, 1990; Aguilar et al., 1991; de Bruijn et al., 1992), are dated from the MN 15 zone. In the same time unit, in Spain, there are two karstic localities, one in Córdoba, Belmez (Bachelet and Castillo Ruiz, 1990; Castillo, 1992) and one in Granada, Moreda 1A (Castillo Ruiz, 1990). In the eastern part of Europe, Ivanovce A and B (Fejfar and Heinrich, 1985) in Slovakia are also from MN 15 zone.

Table 1 summarizes species richness for all localities from MN 9 to MN 15 units. Lists of species are given in the Appendix.

3. Methods

Several studies have shown that the geographical distribution of mammals, and especially rodents is controlled and correlated closely with climate (Hokr, 1951; Kowalski, 1971; Horacek, 1985, 1990). New methods of quantifying climatic parameters have been developed and they are based on the relationship between species richness and climatic parameters (Montuire et al., 1997; Aguilar et al., 1999b; Legendre et al., 2005). This relationship is analysed using a linear least square regression technique (see, for example: Campbell, 1989; Neter et al., 1990) with species richness as the independent variable (=X) and climatic parameter as the dependent one (=Y). Species richness of arvicolines, murines and sigmodontines has been compiled from mainly literature data for

Table 4
Temperature estimates in Europe from zones MN 9 to MN 15

Zone	Locality	Annual temperature (°C)
MN9	Götzendorf	14.1 (11.0–17.3) — Cri
	Castalnou 1B	14.1 (11.0–17.3) — Cri
	Lo Fournas 5	14.1 (11.0–17.3) — Cri
	Jujurieux	14.1 (11.0–17.3) — Cri
	Hammerschmiede	14.1 (11.0–17.3) — Cri
	Petersbuch 14	14.1 (11.0–17.3) — Cri
	Rudabanya	14.1 (11.0–17.3) — Cri
	Nombrevilla	16.1 (13.0–19.3) — Cri
	Hostalets de Pierola	16.1 (13.0–19.3) — Cri
MN10	Ambérieu 1	13.7 (8.9–18.6) — Mur
	Lo Fournas 6	13.7 (8.9–18.6) — Mur
	Lo Fournas 7	16.1 (13.0–19.3) — Cri
MN11	Eichkogel	14.1 (11.0–17.3) — Cri
	Ambérieu 3	12.6 (7.8–17.4) — Mur
	Lobrieu	14.9 (10.1–19.7) — Mur
	Dorn–Dürkheim	16.1 (13.0–19.3) — Cri
	Crevillente 2	14.9 (10.1–19.7) — Mur
	Alfambra	12.6 (7.8–17.4) — Mur
MN12	Castelnou 1	16.0 (11.2–20.9) — Mur
	Alj. De Teruel	13.7 (8.9–18.6) — Mur
MN13	Lissieu	13.7 (8.9–18.6) — Mur
	Castelnou 3	18.3 (13.5–23.2) — Mur
	La Tour	14.9 (10.1–19.7) — Mur
	Brisighella	13.7 (8.9–18.6) — Mur
	Ano Metochi M1–3	14.9 (10.1–19.7) — Mur
	Salobreña	16.0 (11.2–20.9) — Mur
	Casablanca-M	14.9 (10.1–19.7) — Mur
MN14	Vendargues	14.9 (10.1–19.7) — Mur
	Hautimagne	16.0 (11.2–20.9) — Mur
	Alcoy	16.0 (11.2–20.9) — Mur
	Gorafe 1	14.9 (10.1–19.7) — Mur
	Gorafe 4	14.9 (10.1–19.7) — Mur
	La Gloria 4	20.6 (15.8–25.5) — Mur
	Maritsa	14.9 (10.1–19.7) — Mur
	Osztramos 1	14.1 (11.0–17.3) — Cri
	Podlesice	19.3 (16.1–22.5) — Cri
MN15	Serrat–d'en Vaquer	19.5 (14.6–24.3) — Mur
	Mont-Hélène	20.6 (15.8–25.5) — Mur
	Sète	20.6 (15.8–25.5) — Mur
	Lo Fournas 13	18.3 (13.5–23.2) — Mur
	Belmez	20.6 (15.8–25.5) — Mur
	Moreda 1A	18.3 (13.5–23.2) — Mur
	Ivanovce A	14.1 (11.0–17.3) — Cri
	Ivanovce B	14.1 (11.0–17.3) — Cri

Mean annual daily temperatures (prediction error interval) are given using cricetines (Cri) or murines (Mur).

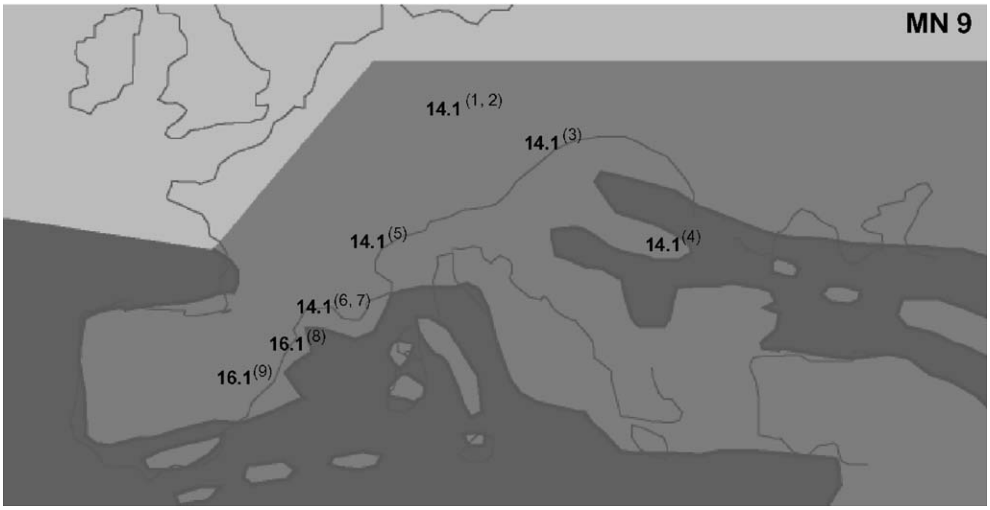

Fig. 1. Mean annual daily temperature estimates for European localities from the MN 9 zone. 1,2 Hammerschmiede, Pertersbuch 14 (Germany, Bayern); 3 Götzendorf (Austria); 4 Rudabanya (Hungary); 5 Jujurieux (France, Provence); 6, 7 Castelnou 1B, Lo Fournas 5 (France, Languedoc–Roussillon); 8 Hostalets de Pierola (Spain, Vallés-Penedés); 9 Nombrevilla (Spain, Teruel–Catalyud–Daroca).

extant local faunas. Arvicolines are widespread in Old and New World and they are numerous in Northern areas whereas they are absent from Tropics. More than 250 arvicoline faunas have been compiled for the Palearctic and Nearctic realms. Murines are only present in the Old World and they are highly diversified in tropical areas. Around 115 local to regional murine faunas have been compiled, excluding commensal species. Sigmodontines corresponding to the New World rats and mice and used here as analogous of Old World fossil cricetines, have been compiled for more than 280 faunas. Climatic data are taken from Wernstedt (1972) and from the Global Climate Perspectives System database (NOAA, National climatic data center; http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/).

The coefficient of determination is very high for arvicolines and sigmodontines ($R^2 \approx .85$) whereas it is lower for murines ($R^2 \approx .50$).

Richness data or temperatures values are either raw data or log-transformed. Regression parameters for predicting mean annual temperatures are provided in

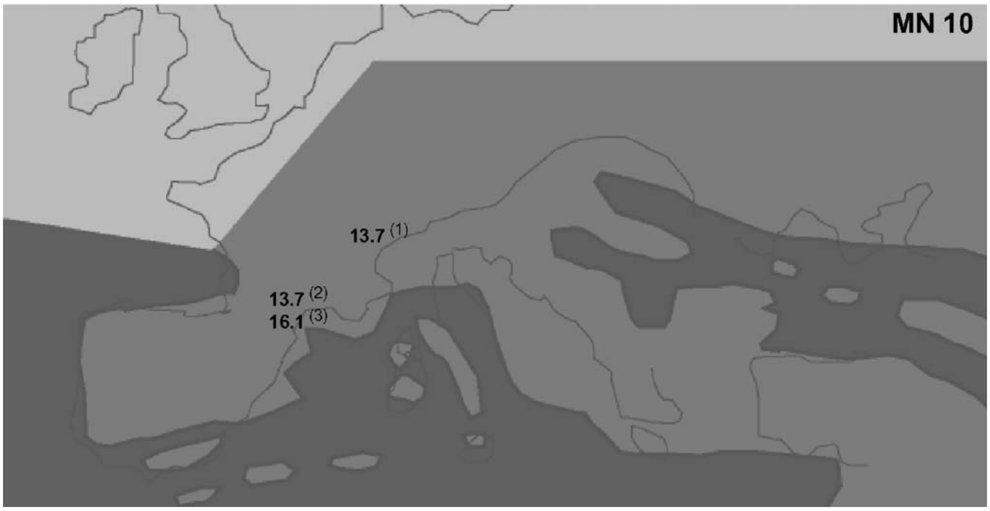

Fig. 2. Mean annual daily temperature estimates for European localities from the MN 10 zone. 1 Ambérieu 1 (France, East Central); 2 Lo Fournas 6 (France, Languedoc–Roussillon); 3 Lo Fournas 7 (France, Languedoc–Roussillon).

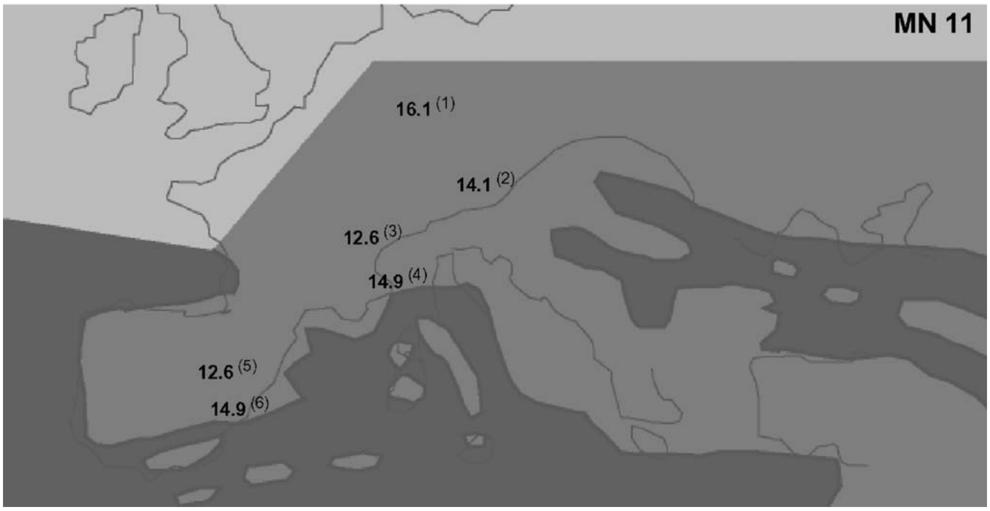

Fig. 3. Mean annual daily temperature estimates for European localities from the MN 11 zone. 1 Dorn-Dürkheim (Germany, Rheinhessen); 2 EichKögel (Austria); 3 Ambérieu (France, East Central); 4 Lobrieu (France, Provence); 5 Alfambra (Spain, Teruel–Catalyud–Daroca); 6 Crevillente 2 (Spain, Alicante–Murcia).

Table 2. Table 3 gives the predicted values with prediction error intervals for species number ranging from 0 to 20 for murines and sigmodontines and ranging from 0 to 12 for arvicolines.

4. Results

Evolution of mean value for annual temperature is followed during the studied period comparing the different regions where data are available at the European continental scale. Estimates are given in Table 4. These data are synthetically presented on palaeogeographical maps (Jones, 1999; Rögl, 1999; Solsona et al., 2000) in Figs. 1–7.

For the MN9 zone (Fig. 1), the temperatures, around 14 °C, are quite homogenous over most part of Europe, except for Spain where temperatures are slightly warmer. For the MN10 zone (Fig. 2), estimates are similar to those for the MN9 zone. For the MN 11 zone (Fig. 3), temperatures are not homogenous, with a

Fig. 4. Mean annual daily temperature estimates for European localities from the MN 12 zone. 1 Castelnou 1 (France, Languedoc–Roussillon); 2 Aljezares de Teruel (Spain, Teruel–Catalyud–Daroca).

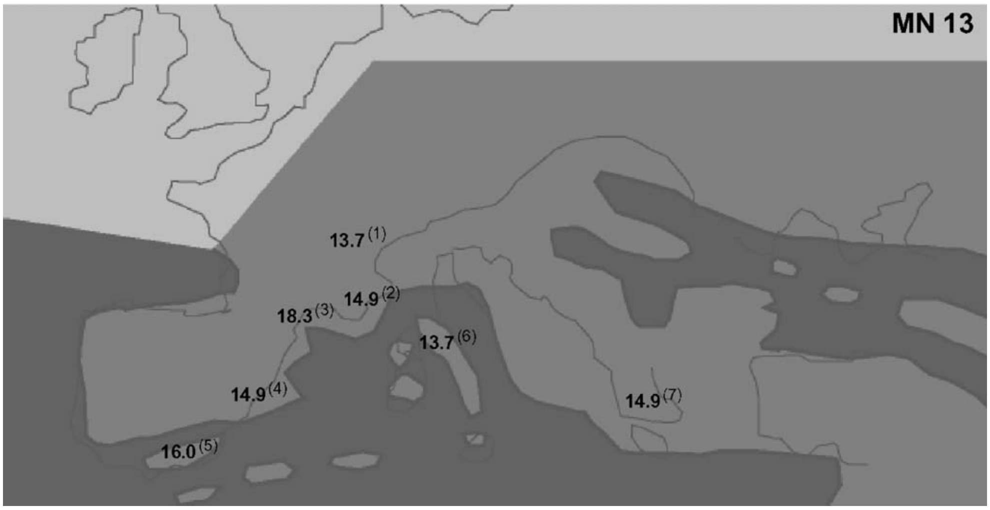

Fig. 5. Mean annual daily temperature estimates for European localities from the MN 13 zone. 1 Lissieu (France, East Central); 2 La Tour (France, Provence); 3 Castelnou 3 (France, Languedoc–Roussillon); 4 Casablanca-M (Spain, Castellon–Valencia); 5 Salobreña (Spain, Granada); 6 Brisighella (Italy); 7 Ano Metochi M1–3 (Greece).

mean around 15 °C (from 12.6 to 16.1 °C). For the MN 12 zone (Fig. 4), only two localities are documented, one locality in France is relatively warm, with 16 °C, and one in Spain is colder, with only 13.7 °C in the Teruel area. At MN 13 (Fig. 5), temperatures are not homogenous in Europe and vary between 13.7 and 18.3 °C similar to or slightly warmer than in MN 11 and MN12 zones. For the MN14 zone (Fig. 6), just after the Messinian crisis, there is a slight temperature increase. The minimum in the mean annual temperature is found in Hungary (14.1 °C), and the maximum in Spain (20.6 °C). At MN15 (Fig. 7), temperatures are homogenous, warmer and characteristic of this period of the Pliocene for the southern part of Europe with a mean temperature around 21 °C.

Generally, murines are more diversified in the Late Miocene in southwestern Europe whereas cricetines

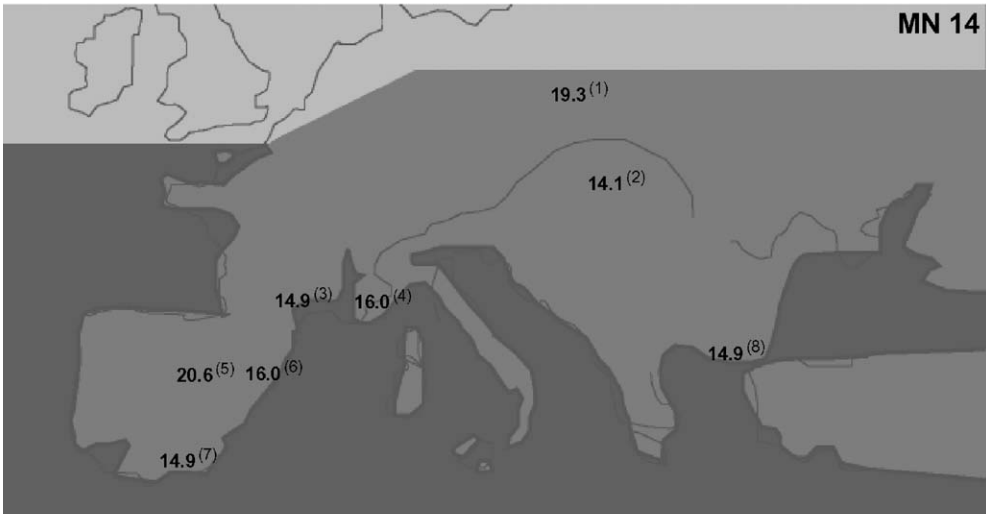

Fig. 6. Mean annual daily temperature estimates for European localities from the MN 14 zone. 1 Podlesice (Poland); 2 Osztramos 1 (Hungary); 3 Vendargues (France, Languedoc–Roussillon); 4 Hautimagne (France, Provence); 5 La Gloria 4 (Spain, Teruel–Catalyud–Daroca); 6 Alcoy (Spain); 7 Gorafe 1, 4 (Spain, Guadix–Baza); 8 Maritsa (Greece, Rhodes Island).

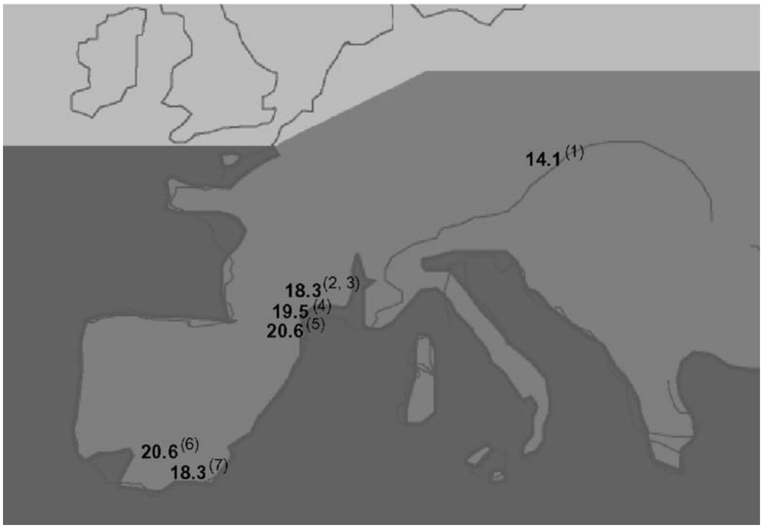

Fig. 7. Mean annual daily temperature estimates for European localities from the MN 15 zone. 1. Ivanovce A, B (Slovakia); 2 Sète (France, Languedoc–Roussillon); 3 Perpignan Serrat-d'en-Vaquer (France, Languedoc–Roussillon); 4 Mont-Hélène (France, Languedoc–Roussillon); 5 Belmez (Spain, Córdoba); 6 Moreda 1A (Spain, Granada).

remain well diversified in northeastern Europe. Arvicolines only radiated during the Late Pliocene and thus do not help in climatic reconstructions in our time sequence.

Two rather complete sequences are available in our data set: the Teruel–Catalayud–Daroca basin in Spain, and the Languedoc–Roussillon region in France; data are combined with values obtained from neighbouring basins. Evolution of mean daily annual temperatures from MN 9 to MN 15 for France and Spain is illustrated in Fig. 8.

From MN10 to MN13, there are some slight fluctuations around a mean annual temperature of 15 °C for France and Spain. During the Messinian (MN 13), temperatures are between 13.7 and 16 °C, except for Castelnou 3 (18.3 °C). After the salinity crisis, after the Miocene–Pliocene boundary, a slight warming is observed in the two areas (14.9 to 16 °C) except for La Gloria 4 (20.6 °C). Later in the Early Pliocene (MN 15), as previously shown by Aguilar et al. (1999a,b), a temperature maximum is reached in southern France as well as in Spain.

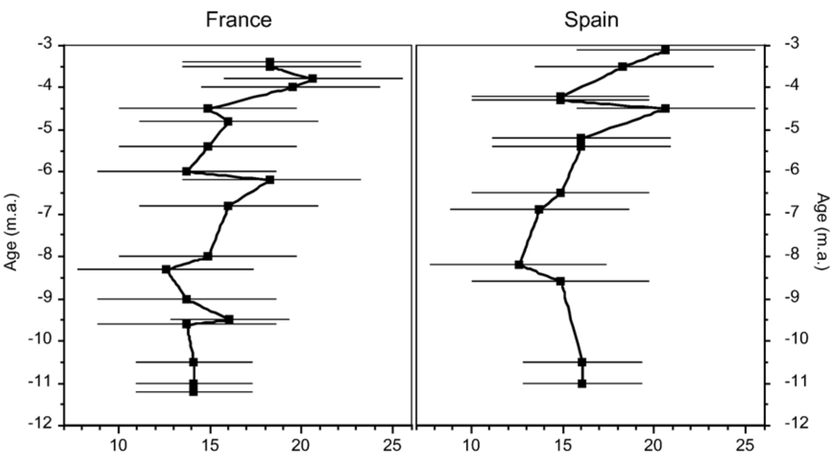

Fig. 8. comparisons in the mean annual temperatures (given with the statistical prediction error) between France and Spain from zones MN 9 to MN 15.

5. Discussion

There are two kinds of continental patterns in temperatures. Temperatures are quite homogenous for the MN9 to MN 11 zones, with temperatures generally ranging from 13.7 to 16.1 °C. MN 12 is poorly documented. By contrast, temperatures begin to be more regionally variable at the end of the Miocene during MN 13 (with temperatures between 13.7 and 18.3 °C). During MN 15, we record the onset of a latitudinal effect: temperatures in Slovakia (14.1 °C) are much colder than French and Spanish ones (18.3 to 20.6 °C). MN 14 shows a very heterogenous situation (14.1 °C in Hungary, 19.3 °C in Poland, 14.9 to 20.6 °C in Spain). But, there is no obvious trend, increase or decrease in the temperatures during the transition between the Miocene and the Pliocene, i.e., during the Messinian salinity crisis between MN13 and MN 14 zones.

In a similar way to that recently proposed by Fauquette et al. (1999) who used temperature estimates from vegetational data to assess paleoaltitude, our temperature estimates can be used to infer past elevation for localities. For example, during MN14, surface temperatures are 14.9 °C for Vendargues and 20.6 °C for La Gloria 4. The elevation of Vendargues during MN 14 was close to the sea-level and the latitude difference between Vendargues and La Gloria 4 was close to 3°. Using the present thermic elevation gradient (0.6 °C for 100 m elevation) and considering that one degree in latitude corresponds to 110 m in altitude (Ozenda, 1989), and supposing that the Mio-Pliocene gradient was close to the extant one (Fauquette et al., 1999), the paleoaltitude for La Gloria 4 should have been about 620 m.

This example illustrates the interest, beyond climatic reconstructions, of quantified estimates in the terrestrial realm.

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Appendix A. Species lists

MN 9

Austria

Götzendorf (Bachmayer and Wilson, 1985a,b; Rögl et al., 1993; Daxner-Höck, 1996)
- *Anomalomys* cf. *gaillardi*
- *Democricetodon* sp.
- *Eumyarion* sp.
- *Kowalskia* sp.
- *Microtocricetus* sp.

France

Castelnou 1B (Aguilar et al., 1999a)
- *Cricetodon* sp.
- *Democricetodon affinis*
- *Hispanomys* sp.
- *Megacricetodon gregarius*
- *Megacricetodon similis*
- *Progonomys* cf. *hispanicus*

Jujurieux (Mein, 1999)
- *Anomalomys* cf. *gaudryi*
- *Democricetodon* cf. *nemoralis*
- *Eumyarion* cf. *latior*
- *Hispanomys bijugatus*
- *Megacricetodon* cf. *freudenthali*

Lo Fournas 5 (Aguilar et al., 1999a)
- *Democricetodon* sp.
- *Fahlbuschia larteti*
- *Hispanomys bijugatus*
- *Megacricetodon gregarius*
- *Megacricetodon minor*

Germany

Hammerschmiede (Mayr and Fahlbusch, 1975)
- *Anomalomys gaudryi*
- *Democricetodon brevis*
- *Democricetodon freisingensis*
- *Megacricetodon* aff. *debruijni*
- *Microtocricetus molassicus*

Petersburch 14 (Bolliger and Rummel, 1994)
- *Anomalomys gaudryi*
- *Democricetodon* aff. *brevis*
- *Democricetodon* cf. *freisingensis*
- *Eumyarion* cf. *latior*
- *Megacricetodon* aff. *minor*

Hungary

Rudabanya (Rabeder, 1985)
- *Anomalomys gaudryi*
- *Democricetodon* cf. *gaillardi*
- *Eumyarion latior*
- *Microtocricetus molassicus*
- *Prospalax petteri*

Spain

Hostalets de Pierola (Agustí and Gibert, 1982)
- *Anomalomys gaudryi*
- *Cricetodon lavocati*
- *Cricetulodon hartenbergeri*
- *Fahlbuschia crusafonti*
- *Hispanomys dispectus*
- *Megacricetodon ibericus*

Appendix A (*continued*)

MN 9
Spain
Nombrevilla (Aguilar et al., 1979)
Democricetodon minor
Fahlbuschia sp.
Hispanomys nombrevillae
Megacricetodon debruijni
Megacricetodon gregarius
Megacricetodon similis
MN 10
France
Ambérieu 1 (Farjanel and Mein, 1984)
Hispanomys cf. *mediterraneus*
Neocricetodon cf. *fahlbuschi*
Rotundomys bressanus
Prospalax petteri
Apodemus lugdunensis
Occitanomys clauzoni
Parapodemus sp.
Progonomys cf. *cathalai*
Lo Fournas 6 (Aguilar et al., 1999a)
Hispanomys mediterraneus
Rotundomys montisrotundi
Apodemus cf. *lugdunensis*
Parapodemus pasquieri
Progonomys cf. *hispanicus*
Progonomys clauzoni
Lo Fournas 7 (Aguilar et al., 1999a)
Anomalomys cf. *gaillardi*
Cricetulodon sp.
Democricetodon sulcatus
Hispanomys mediterraneus
Neocricetodon sp.
Rotundomys montisrotundi
Huerzelerimys vireti
Occitanomys faillati
Progonomys castilloae
MN 11
Austria
Eichkogel (Bachmayer and Wilson, 1985a,b; Rabeder, 1989)
Anomalomys gernoti
Collimys primus
Epimeriones austriacus
Neocricetodon cf. *fahlbuschi*
Prospalax petteri
Apodemus lugdunensis
France
Ambérieu 3 (Farjanel and Mein, 1984)
Apocricetus cf. *plinii*
Epimeriones cf. *austriacus*
Neocricetodon cf. *occidentalis*
Prospalax petteri
Apodemus lugdunensis
Huerzelerimys vireti
Occitanomys sondaari
Lobrieu (Mein and Truc, 1966; Mein, 1999)
Arvicolidae indet.
Hispanomys cf. *peralensis*
Neocricetodon sp.
Apodemus lugdunensis

Appendix A (*continued*)

MN 11
France
Lobrieu (Mein and Truc, 1966; Mein, 1999)
Huerzelerimys vireti
Occitanomys clauzoni
Parapodemus pasquieri
Muridae indet.
Germany
Dorn–Dürkheim (Franzen and Storch, 1975)
Collimys cf. *primus*
Cricetulodon indet.
Epimeriones austriacus
Neocricetodon cf. *lavocati*
Prospalax petteri
Pterospalax indet
Apodemus lugdunensis
Spain
Alfambra (Alcalá et al., 1991; Van Dam, 1997)
Neocricetodon fahlbuschi
Apodemus lugdunensis
Occitanomys sondaari
Valerymys vireti
Crevillente 2 (de Bruijn et al., 1992; Martín Suárez and Freudenthal, 1993)
Hispanomys peralensis
Neocricetodon occidentalis
Apodemus lugdunensis
Huerzelerimys vireti
Occitanomys sondaari
Parapodemus sp.
Valerymys vireti
MN 12
France
Castelnou 1 (Aguilar et al., 1999a)
Cricetus cf. *kormosi*
Cricetus sp.
Hispanomys cf. *mediterraneus*
Neocricetodon seseae
Apodemus barbarae
Huerzelerimys turoliensis
Karnimata cf. *intermedia*
Occitanomys faillati
Occitanomys sp.
Rhagapodemus primitivus
Spain
Aljezares de Teruel (Adrover, 1986; Alcalá, 1987)
Kowalskia indet.
Ruscinomys schaubi
Ruscinomys sp.
Apodemus barbarae
Occitanomys adroveri
Parapodemus sp.
Valerymys turoliensis
MN 13
France
Castelnou 3 (Aguilar et al., 1999a)
Promimomys sp.
Apocricetus barrierei
Hispanomys cf. *mediterraneus*
Myocricetodon sp.

Appendix A (*continued*)

MN 13

France

Castelnou 3 (Aguilar et al., 1999a)
Ruscinomys cf. *lasallei*
Apodemus cf. *gudrunae*
Apodemus cf. *jeanteti*
Apodemus dominans
Occitanomys adroveri
Occitanomys sp.
Paraethomys cf. *anomalus*
Rhagapodemus primaevus
Stephanomys dubari

La Tour (Aguilar et al., 1982, 1989)
Blancomys sp.
Cricetus cf. *kormosi*
Trilophomys cf. *pyrenaicus*
cf. *Trilophomys* indet.
Apodemus cf. *dominans*
Occitanomys sp.
Paraethomys cf. *anomalus*
Rhagapodemus primaevus
Stephanomys ramblensis

Lissieu (Mein, 1999)
Epimeriones cf. *austriacus*
Neocricetodon lavocati
Apodemus gudrunae
Occitanomys cf. *adroveri*
Rhagapodemus primaevus
Stephanomys ramblensis

Italy

Brisighella (Rook, 1992; Kotsakis et al., 1997)
Apocricetus cf. *barrierei*
Ruscinomys cf. *lasallei*
Apodemus cf. *gudrunae*
Centralomys benericettii
Paraethomys anomalus
Stephanomys debruijni

Greece

Ano Metochi M1–3 (de Bruijn, 1989)
Neocricetodon lavocati
Cricetus sp.
Apodemus dominans
Apodemus gudrunae
Micromys bendai
Occitanomys adroveri
Rhagapodemus hautimagnensis

Spain

Casablanca-M (Agustí and Galobart, 1986)
Cricetus cf. *kormosi*
Myocricetodon cf. *parvus*
Ruscinomys sp.
Apodemus gudrunae
Castillomys crusafonti gracilis
Occitanomys sp.
Paraethomys aff. *miocaenicus*
Stephanomys ramblensis

Salobreña (Aguilar et al., 1984)
Cricetus cf. *kormosi*
Myocricetodon sp.

Appendix A (*continued*)

MN 13

Spain

Salobreña (Aguilar et al., 1984)
Apodemus aff. *gudrunae*
Castillomys crusafonti
Dendromys sp.
Occitanomys adroveri
Paraethomys cf. *anomalus*
Stephanomys ramblensis

MN 14

France

Hautimagne (Mein and Michaux, 1970; Aguilar et al., 1983)
Apodemus dominans
Apodemus gorafensis
Occitanomys brailloni
Paraethomys meini
Rhagapodemus ballesioi
Rhagapodemus hautimagnensis

Vendargues (Mein and Michaux, 1970; Chaline and Michaux, 1974; Bachelet, 1990)
Polonomys insuliferus
Apocricetus barrierei
Apodemus dominans
Apodemus jeanteti
Apodemus gorafensis
Occitanomys brailloni
Rhagapodemus hautimagnensis

Spain

Alcoy (Adrover, 1969; Crusafont Pairó, 1971; Brandy, 1979)
Blancomys sanzi
Cricetus aff. *kormosi*
Neocricetodon polonica ?
Ruscinomys lasallei
Apodemus gorafensis
Castillomys gracilis
Occitanomys montheleni
Paraethomys abaigari
Paraethomys meini
Stephanomys medius

Gorafe 1 (Agustí and Martín Suárez, 1987)
Apocricetus cf. *barrierei*
Ruscinomys cf. *lasallei*
Trilophomys castroi
Apodemus gorafensis
Castillomys gracilis
Occitanomys sp.
Paraethomys meini
Stephanomys cf. *medius*

Gorafe 4 (Agustí and Martín Suárez, 1987)
Apocricetus barrierei
Ruscinomys indet.
Trilophomys castroi
Apodemus gorafensis
Castillomys gracilis
Occitanomys indet.
Paraethomys meini
Stephanomys medius

La Gloria 4 (Adrover et al., 1993; Alcalá, 1994)
Polonomys insuliferus

Appendix A (*continued*)

MN 14

Spain

La Gloria 4 (Adrover et al., 1993; Alcalá, 1994)

Apocricetus barrierei
Ruscinomys lasallei
Apodemus aff. *gorafensis*
Apodemus barbarae
Apodemus cf. *dominans*
Castillomys crusafonti
Huerzelerimys cf. *turoliensis*
Occitanomys alcalai
Paraethomys anomalus
Paraethomys meini
Rhagapodemus hautimagnensis
Stephanomys medius

Greece

Maritsa (de Bruijn et al., 1970)

Cricetulus sp.
Cricetus lophidens
Mesocricetus primitivus
Apodemus aff. *jeanteti*
Apodemus cf. *dominans*
Castillomys crusafonti
Paraethomys anomalus
Pelomys europaeus

Hungary

Osztramos 1 (Jánossy, 1971)

Polonomys sp.
Baranomys kowalskii progressus
Neocricetodon magna
Neocricetodon polonica
Rotundomys sp.
Prospalax kretzoi

Poland

Podlesice (de Bruijn et al., 1992)

Cricetus sp. 1
Cricetus sp. 2
Epimeriones progressus
Microtodon kowalskii
Neocricetodon magna
Neocricetodon polonica
Bjornkurtenia canterranensis
Anomalomys sp.

MN 15

France

Lo Fournas 13 (Bachelet, 1990; Bachelet and Castillo Ruiz, 1990)

Kislangia cappetai
Cricetus angustidens
Ruscinomys europaeus
Trilophomys pyrenaicus
Apodemus dominans
Apodemus jeanteti
Castillomys crusafonti
Occitanomys brailloni
Occitanomys montheleni
Paraethomys jaegeri
Paraethomys meini
Stephanomys cf. *donnezani*

Appendix A (*continued*)

MN 15

France

Mont-Hélène (Aguilar and Michaux, 1984; Aguilar et al., 1986; Bachelet, 1990)

Blancomys neglectus
Cricetus angustidens
Trilophomys pyrenaicus
Apodemus dominans
Apodemus gorafensis
Apodemus jeanteti
Castillomys gracilis
Occitanomys montheleni
Paraethomys cf *jaegeri*
Paraethomys. meini
Rhagapodemus ballesioi
Rhagapodemus hautimagnensis
Stephanomys donnezani

Perpignan (Serrat d'en Vacquer) (Bachelet, 1990; Aguilar et al., 1991; de Bruijn et al., 1992)

Mimomys davakosi–occitanus
Blancomys neglectus
Cricetus angustidens
Ruscinomys europaeus
Trilophomys schaubi
Apodemus dominans
Apodemus gorafensis
Castillomys crusafonti
Micromys praeminutus
Occitanomys montheleni
Occitanomys brailloni
Paraethomys jaegeri
Paraethomys meini
Rhagapodemus hautimagnensis
Stephanomys donnezani

Sète (Aguilar et al., 1983; Bachelet, 1990)

Dolomys occitanus
Kislangia cappeta
Blancomys neglectus
Cricetus angustidens
Ruscinomys europaeus
Trilophomys pyrenaicus
Apodemus jeanteti
Apodemus dominans
Apodemus gorafensis
Castillomys crusafonti
Occitanomys brailloni
Paraethomys jaegeri
Paraethomys meini
Rhagapodemus hautimagnensis
Stephanomys donnezani
Valerymys ellenbergeri

Spain

Belmez (Bachelet and Castillo Ruiz, 1990; Castillo, 1992)

Blancomys neglectus
Hispanomys cf. *adroveri*
Ruscinomys cf. *europaeus*
Trilophomys cf. *pyrenaicus*
Apodemus dominans
Apodemus jeanteti
Castillomys crusafonti

Appendix A (*continued*)

MN 15

Spain

Belmez (Bachelet and Castillo Ruiz, 1990; Castillo, 1992)

Castillomys gracilis

Occitanomys brailloni

Occitanomys sp.

Paraethomys belmeznsis

Rhagapodemus frequens

Stephanomys calveti

Stephanomys thaleri

Moreda 1A (Castillo Ruiz, 1990)

Mimomys occitanus

Apodemus dominans

Apodemus jeanteti

Castillomys crusafonti

Castillomys gracilis

Occitanomys brailloni

Rhagapodemus frecuens

Stephanomys donnezani

Stephanomys minor

Slovakia

Ivanovce A (Fejfar and Heinrich, 1985)

Dolomys occitanus

Germanomys parvidens

Germanomys weileri

Mimomys gracilis

Allocricetus cf. *bursae*

Baranomys loczyi

Neocricetodon intermedia

Trilophomys depereti

Prospalax priscus

Apodemus sp.

Rhagapodemus frequens

Ivanovce B (Fejfar and Heinrich, 1985)

Dolomys occitanus

Germanomys weileri

Mimomys gracilis

Allocricetus cf. *bursae*

Baranomys loczyi

Neocricetodon intermedia

Trilophomys depereti

Prospalax priscus

Apodemus sp.

Rhagapodemus frequens

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