

# Spatial and temporal variation in European Neogene large mammals diversity

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Received 10 September 2007; received in revised form 7 January 2008; accepted 8 January 2008

## Abstract

Large mammals diversity (i.e., ungulates or hoofed mammals) is investigated over the whole European geographic area and through a period extending from the Late Oligocene, around 27 Ma ago, to the Early Pliocene, around 3 Ma ago. Qualitative and quantitative spatial and temporal patterns are discussed thanks to the analysis of a large dataset of localities (695) that yielded large mammals and distributed over this period and area. We show that the Miocene is a key period in the installation of modern faunas in Europe; modern ruminants (mainly cervids and bovines) largely develop during the period considered and replace the Oligocene-inherited dominant faunas. These replacements are triggered by different factors, often extrinsic and constitute the roots of the present situation. Indeed, a complex interplay between geographic (palaeogeographic reorganisations) and climatic factors (warming and cooling events) can be invoked to understand how faunas change. Geography seems to play a crucial role in the Early Miocene when it allows migration routes to open between Europe, Asia and Africa and in turn leads to a drastic increase of ungulate diversity that seems to be maintained in the Middle Miocene under the warm equable climates of the Miocene Climatic Optimum. The Late Miocene sees a global climatic deterioration leading to a decline in large mammals diversity and represents the root of the extant depleted situation. Regional comparisons indicate that endemism was already strong in the Miocene, especially in south-eastern Europe, and that strong climatic belts already seem to have an impact on mammal communities since the Late Miocene. The roots of the extant situation (endemism and low diversity) are therefore more complex and probably older than previously thought; they are to be looked for before the Quaternary Climatic Cycles and are the by-product of deep-time geographic and climatic events.

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**Keywords:** Neogenel; Europe; Palaeobiodiversity; Paleobiogeography; Ungulates; Mammals

## 1. Introduction

The European Neogene mammalian fossil record has largely been improved in the past decades thanks to intense sampling efforts. Consequently it has now become possible to investigate the spatial and temporal diversity evolution of the different groups of mammals for long periods of time within well-defined biochronological frameworks. In the European context, analysing past diversity bears strong implications as to whether the present day situation results from deep historical roots and/or from more recent factors such as the Quaternary climatic cycles (Baquero and Telleria, 2001).

Up to now, diversity analyses of the European Neogene mammals either focussed on rather small periods of time or on

large biogeographic regions (Fortelius et al., 1996) yielding interesting but incomplete indications on the controlling factors and on the fine-scale changes that can occur from region to region (Costeur et al., 2004). For instance, large-scale diversity gradients between western and eastern Europe (Fortelius et al., 1996) and punctual more regional patterns of faunal differentiations between eastern and central Spain (Agusti, 1989) are observed.

Recently, diversity and biogeographic analyses based on rodents (Van Dam et al., 2006; Maridet et al., 2007; respectively) from about 27 Ma to about 4 Ma (most of the Neogene) and either for the whole European continent or for smaller geographic areas have shown that climate was an essential factor controlling the diversity and distribution of these animals. This was to be expected as rodent diversity seems to be highly correlated to climatic proxies (Montuire et al., 1997; Aguilar et al., 1999; Legendre et al., 2005). Concerning large

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mammals, namely ungulates (hoofed mammals), much less correlation seems to hold between their raw diversity and climatic parameters (Heran, 2006). Preliminary studies have

shown that their diversity and distribution were controlled by large-scale climatic but also to a large extent by geographic changes (Costeur et al., 2004).

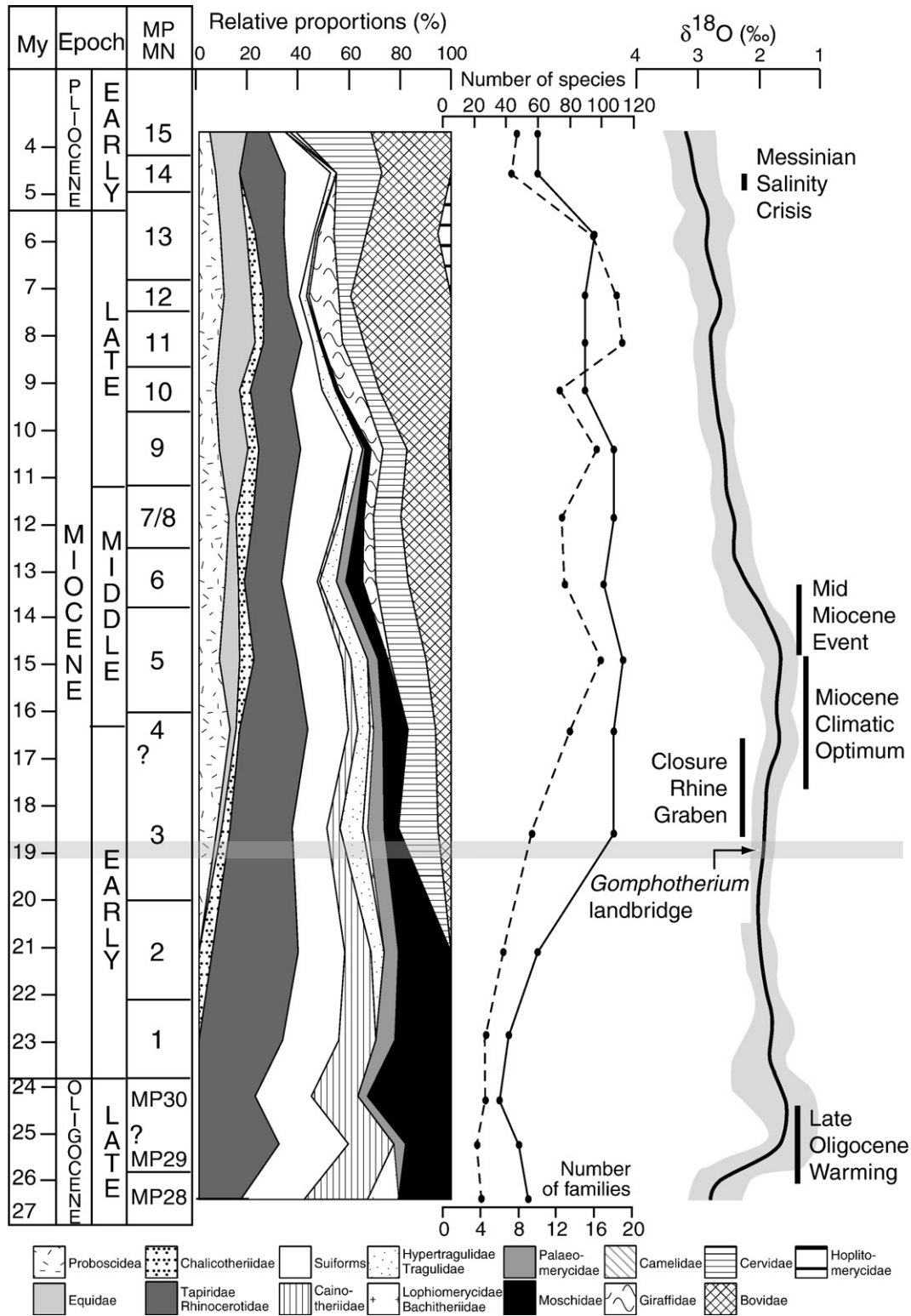


Fig. 1. Neogene time scale showing MP reference levels and MN zones (based on Aguilar et al., 1997 for MP and Agustí et al., 2001 for MN). Relative proportions of ungulates (families or larger groups such as sub-orders [e.g., Proboscidea]) are given at the European scale; ungulates raw family (solid line) and species (broken line) richness curves are given for the same geographic scale. The composite Oxygen isotopic curve of Zachos et al., 2001 is also provided along with diverse palaeogeographic and palaeoclimatic information on the left and right hand-side of the curve, respectively. Legends for families will be used later in Figs. 7–13.

The present diversity of European ungulates shows a rather depleted situation in a context of high endemism with diversity peaks in Central Europe (Baquero and Telleria, 2001). As reminded above, this has been said to result from the alternating Quaternary climatic cycles fracturing populations into refuge areas but also from the cul-de-sac morphology of the western European continent. Historically inherited continental morphology has often been invoked to explain animal diversity but many studies of the theoretical distribution of diversity over surfaces report that simple random spatial distribution models, in the absence of previous environmental or historical gradients, can explain the situation of low diversity towards borders and higher diversity in centres (mid-domain effect, Colwell et al., 2004), which is the actual case for western Europe today. In addition, Maridet et al. (2007) have shown that the extant endemic situation seen for rodents in Europe can also be explained by the long-term evolution of their biogeography before the onset of the northern hemisphere glaciations.

In this challenging context, we present a large-scale analysis of the diversity and distribution of large mammals for the European Neogene starting in the Late Oligocene (27 Ma) to understand the inheritance of the Neogene faunas and up to the Mid Pliocene (3 Ma) before the onset of northern hemisphere glaciations. We gathered a large amount of data from the literature, and after homogenisation and control for sampling biases (see below), we present the evolution of ungulates diversity in different geographic regions as well as for the whole European continent for the period considered. This study serves as a state-of-the-art and better understanding of to date only partly-known patterns and is a two-level analysis that helps better characterize the spatial and temporal evolution of large mammals diversity and distribution as well as the hierarchical factors that can act to modify it.

## 2. Material and methods

### 2.1. Dataset and time scale

The data set used here includes 695 fossil localities that yielded large mammals (detailed list available on request from

the authors). They are distributed within 17 successive biochronological units from the Late Oligocene (ca. 27 Ma; Paleogene reference-levels MP28 to MP30, Schmidt-Kittler, 1987; Aguilar et al., 1997) to the mid Pliocene (ca. 3 Ma; Neogene biozones MN1 to MN15, Mein, 1999). Fig. 1 shows the biochronological time-scale used here (from Agusti et al., 2001). The MP or MN zones are defined by the associations of diagnostic mammal species and a reference locality per zone is considered as giving the typical association of the lineages evolutionary stages. All the localities are relatively dated and assigned to a particular zone by comparison to these typical associations.

Over the whole period, about 600 species of ungulates are recorded after taxonomical standardization. Indeed, this dataset has been homogenised for systematics based on recently published systematic revisions (Rössner and Heissig, 1999) to remove any synonym that could artificially increase diversity counts. Indeterminate species (e.g., *Hipparion* indet.) were removed from the dataset when the genus was already present in a region considered (for instance if *Hipparion primigenium* was present in a region aside *Hipparion* indet., the latter was removed), they were kept when no record of the genus was already present. Sub-species were grouped within the species name to enable us to work at the same taxonomic level. Again, this is a conservative approach that prevent from artificially increasing raw diversity.

Local faunas were gathered into regional faunal lists to produce the regional scale level of analysis mimicking the relevant metacommunity level reached in ecological studies (Leibold et al., 2004). Regions considered here (Fig. 2, Table 1) are thus defined by sets of localities coming from homogeneous geological ensembles (sedimentary basins and/or geological formations) showing an environmental and ecological stability within each biozone (Damuth, 1985; Legendre, 1989). It was not always possible to separate the localities in regional pools and this mainly holds for eastern European countries. In that case, the name of the country is used for the name of the faunal list considered, but usually in a specific biozone, the localities gathered under a country name most often come

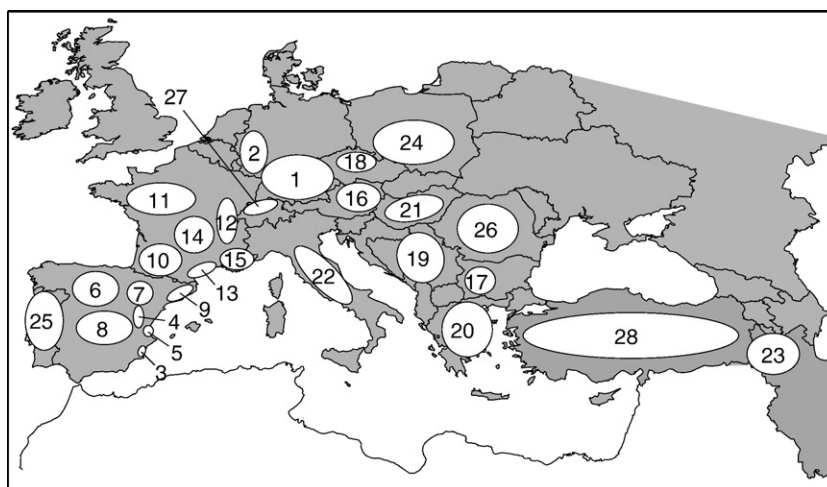


Fig. 2. Location of the European regions used in this study. Regions names are given in Table 1.

Table 1  
Regions names and numbers for Fig. 2

	Country	Region	Abbreviations
1	Germany	Bayern–Bade–Württemberg	BBdW-G
2	Germany	Rheinessen	Rh-G
3	Spain	Alicante Murcia	AM-S
4	Spain	Calatayud–Daroca–Teruel	CDT-S
5	Spain	Castillon–Valencia	CV-S
6	Spain	Duero	Du-S
7	Spain	Ebro	Eb-S
8	Spain	Guadalajara Madrid	GM-S
9	Spain	Valles Penedes	VP-S
10	France	Aquitainian Bassin	BA-F
11	France	Paris Basin	BP-F
12	France	Central Est	CE-F
13	France	Languedoc–Roussillon	LR-F
14	France	Massif Central	MC-F
15	France	Provence	Pro-F
16	Austria		Aus
17	Bulgaria		Bg
18	Czech Republic		CzRp
19	Former-Yugoslavia		Form-Yu
20	Greece		Gr
21	Hungary		Hg
22	Italy		It
23	Iran		Ir
24	Poland		Pol
25	Portugal		Por
26	Roumania		Ro
27	Switzerland		Sw
28	Turkey		Tk

Countries where regions are defined are also given. Regions defined follow Maridet et al., 2007. Abbreviations are used in Figs. 7–13.

from close deposits (e.g., Italy where the MN13 localities all come from the Tuscan geological formations, see also Maridet et al., 2007).

2.2. Spatial scales

Three spatial levels of analysis are developed in this study, each having its own necessity: the European, the bioprovincial and the regional levels. Fig. 2 shows the different regions for which faunal lists could be produced and as explained above some regions are larger (e.g., Turkey, Greece). Maridet et al. (2007) used regions often identical to those studied here (same dataset but they analysed small mammals) and they showed that the sizes of these regions were comparable to the resolution obtained in present-day ecological studies. This particular geographic size allows to enter in great details into the dynamics of diversity and to investigate smaller scale patterns that shape meta-communities, such as migrations, ecological exclusions, interspecific interactions or small scale ecological and environmental peculiarities.

To have a broader idea of the ungulates diversity that can help focus on large-scale controlling factors, we also compiled the data into a European dataset where we pooled all the data available per biozone over the whole European continent from the Iberian peninsula to Turkey (Iran is also included once in MN11) and as far North as the Polish record.

To identify specific diversity gradients, we also pooled data for larger areas (i.e., bioprovinces) to have a more complete record of specific families over several consecutive biochronological zones (which is rarely possible as very few regions have a continuous record over several million years) and to allow direct comparisons between large geographic ensembles. They were already used in a preliminary study (Costeur et al., 2004): south-eastern Europe (SW, Iberian Peninsula), north-western Europe (NW, France, Germany and Switzerland), central-eastern Europe (CE, Hungary, Romania, Former-Yugoslavia and Bulgaria) and south-eastern Europe (SE, mainly Greece and

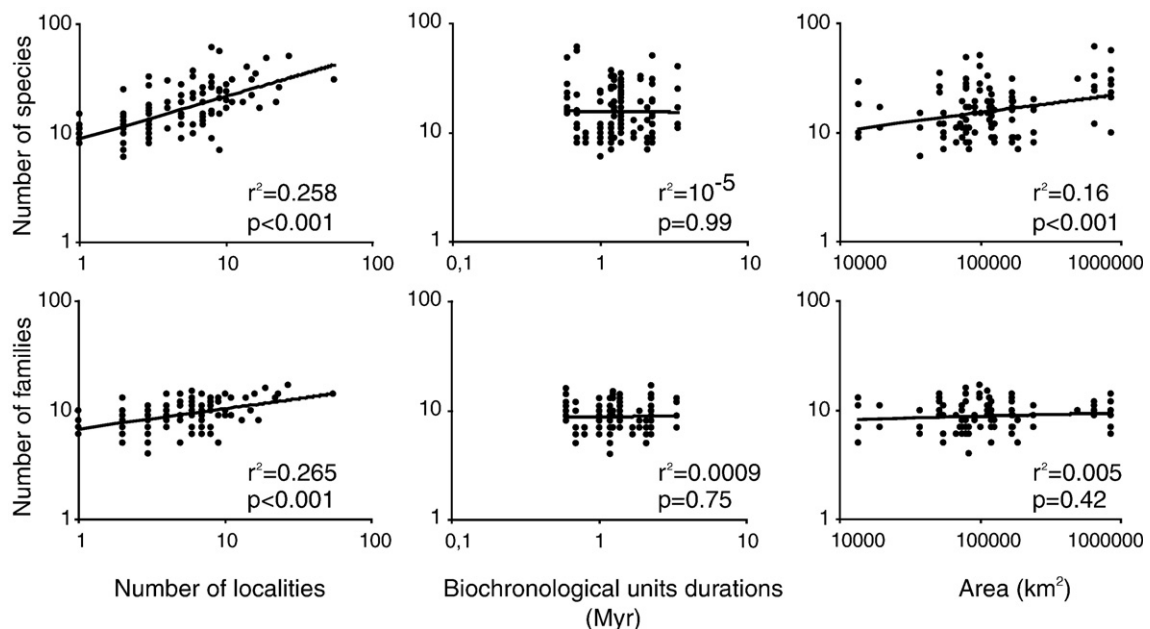


Fig. 3. Least squares regression analyses between diversity counts (species and families) and different potential biases: sample effort, units durations and regions areas. See text for details on significant or non-significant relationships.

Turkey plus Iran when present; the Greek–Turkish–Iranian province of Bonis et al., 1992).

### 3. Methods

#### 3.1. Sampling biases

In diversity analyses it is always essential to test whether sampling efforts or other types of biases (e.g., duration of the time units taken into account, surfaces of the geographic divisions) significantly bias the interpretation of the data. In this study, regional species and family richness (basic counts of species and families per regions) were tested against sampling effort, i.e. number of localities per region, biozones duration (after Agusti et al., 2001) and regions surfaces (Fig. 3). We estimated the latter as the rectangle encompassing all known fossil localities, based on the minimum and maximum latitude and longitude coordinates recorded for the localities. It is noteworthy that some “regions”, namely Turkey, Greece and Italy are markedly overestimated in surface area (more than 400,000 km<sup>2</sup>, either because of particular present day geographical configuration very different from what was the actual case in the Neogene [Greece and Italy] or because of lack of finer regional subdivision [Turkey]) but this does not yield significant differences on the results. We tested the “richness vs. area” relationship by reducing these surfaces to the level of what is recorded in the other European regions and no significant change occurred (graphs not shown here).

We deliberately and arbitrarily removed regions that only yielded less than 5 species or 4 families postulating that they are not able to yield interpretable results; these are very often correlated to very low number of localities (mostly a single poor locality).

Species and family richness are significantly correlated to the number of localities per region ( $r^2=0.258$  and  $0.265$ , respectively with Spearman  $p<0.001$ , Fig. 3) but sampling effort only seems to explain not much than a fourth of raw diversity which makes the latter largely interpretable bearing in mind that particular time periods with few localities should be taken with caution. On the contrary, both diversity estimators are neither correlated to biozones durations (species richness:  $r^2=10^{-5}$ ,  $p=0.99$ ; family richness:  $r^2=0.0009$ ,  $p=0.76$ ) nor to regions areas (despite a significant but very low relationship between species richness and surface area:  $r^2=0.16$ ,  $p<0.001$ ; family richness:  $r^2=0.005$ ,  $p=0.42$ ; Fig. 3).

#### 3.2. Species and family counts, proportions and tests applied

Raw diversity is estimated through the compilation of species and family counts both at the regional and broader European levels. As said above, sampling biases although sometimes significant do not prevent to calculate both estimators as far as cases where very few localities exist are considered. We will stress this point when the results have to be taken with caution.

The non parametric Mann–Whitney test (Sokal and Rolf, 1998) calculated with PAST (Hammer et al., 1998) was applied to the proportions of different families during chosen periods. It allows to statistically compare two regions and/or bioprovinces together in order to evidence significant differences that can be related to diversity or compositional gradients.

#### 3.3. Raup and Crick biogeography index

Fig. 4 presents a biogeography index, the Raup and Crick index of similarity. The curve presented is the median (framed by its 1st and 3rd quartiles as colour-filled boxes) of this index calculated on a very similar dataset at the European scale and already published in Costeur et al. (2004). Too few data existing for the Oligocene, the curve starts in the Early Miocene. We will not re-enter into the explanation of this statistical probabilistic index and on the way it was processed (for detailed information, see Raup and Crick, 1979; Costeur et al., 2004 and Maridet et al., 2007) but we include this result here as it also gives an additional and interesting view of the homogeneity or heterogeneity of the spatial distribution (biogeography) of the Neogene ungulates. Note that high values of the index indicate a homogeneous situation (homogeneous biogeographic pattern or high faunal affinities between the different European regions) and vice versa.

### 4. Results

#### 4.1. European scale ungulate evolutionary history

##### 4.1.1. Proportions of ungulate families

The Late Oligocene (MP28, 29 and 30) is marked by a low diversity, less than 10 ungulate families and less than 30 species in total (Fig. 1). This period is dominated by 3 families, the Rhinocerotidae, Cainotheriidae and Moschidae all representing more than 20% each of the total ungulate species richness with

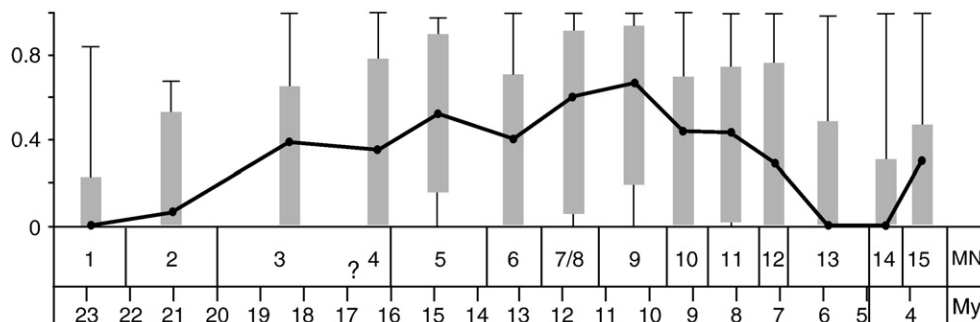


Fig. 4. Median of the Raup and Crick's similarity index values calculated between the European regions throughout the Neogene. From Costeur et al., 2004.

Table 2  
Raw numbers of species per families at the European scale from MP28 to MN15

Family	Late Oligocene			Early Miocene				Middle Miocene			Late Miocene				Pliocene		
	MP			MN				5	6	7/8	9	10	11	12	13	14	15
	28	29	30	1	2	3	4										
Gomphotheriidae						2	5	3	3	2	1	1	1				
Mammutidae				1	1			2	1	2	1	1	3	2	1	1	
Elephantidae									1	2	3	2	5	4	3	2	1
Deinotheriidae						1	4	2	3	2	2	1	1	2	2		
Equidae						1	2	8	4	2	11	7	16	12	1	4	7
Chalicotheriidae					2	2	1	6	2	5	4	3	4	5	3		
Tapiridae	1	2		3	5	3	1	1	1	1	2	1	2	2	2	2	1
Rhinocerotidae	3	5	6	6	8	11	21	16	1	1	14	11	15	9	9	6	3
Suidae	1	2	3	4	5	6	8	1	8	9	15	7	5	4	7	6	3
Tayassuidae	2	1			1	1	4	6	3	5	5	2					
Hippopotamidae															4	2	
Cainotheriidae	6	4	5	4	4	3	3	3	1	1							
Anthracotheriidae	3	3	3	2	1	1	1	2					1				
Hypertragulidae					2	2	1	1									
Tragulidae						3	3	6	5	2	4	4	3	3	1	1	
Bachitheriidae	2					1	1										
Lophiomerycidae	1																
Palaeomerycidae		1	1	2	2	4	3	4	3	3	1						
Moschidae	5	4	9	6	8	3	8	4	5	2	2	1	1				
Camelidae														1	1		1
Giraffidae								1	4	3	5	7	9	13	6		1
Cervidae					9	9	14	1	8	9	9	5	1	5	12	8	14
Bovidae					3	5	1	13	15	16	21	39	44	27	12	15	
Hoplitomerycidae											1				5		

about 5 species each for the different MP levels (Table 2). This result extends and confirms previous findings on French Oligocene large mammals (Blondel, 2001).

The Early Miocene (MN1 and 2) shows the same assemblage in Europe with the same dominant families. Despite the Late Oligocene warming evidenced by the global oxygen isotope record (Fig. 1, after Zachos et al., 2001), no particular change seems to occur in the western European large mammals communities at the Oligocene–Miocene boundary.

Zone MN3 sees an important increase in both the species and family diversity. The number of families almost doubles and 20 new species enrich the communities. This major reorganization is well known and is related to the establishment of land connections in south-eastern Europe. The so-called “*Gomphotherium* landbridge” (Rögl, 1999) links the Eurasian and African continents at this time and allows the immigration of several taxa in Europe. Proboscideans, equids, cervids and bovids arrive from Africa and Asia (Tassy, 1989; Van Der Made, 1999) significantly increasing the diversity levels. This event leads to a relative decrease in proportions of the Late Oligocene–Early Miocene dominant families (cainotheriids and moschids) to the benefit of the newly arrived groups but raw diversity (number of species) in both small ruminant families does not show a significant decrease in MN3 (Table 2).

Then a rather long period follows, from MN4 (around 17 Ma) to MN9 (around 10 Ma) with a high level of diversity, i.e. more than 17 families and more than 75 species. This time interval actually sees the progressive increase in proportions of the MN3 newly arrived families and especially of cervids and

bovids to attain up to a fifth of the total species richness in MN7/8 for the latter. This high level of diversity reached through the migration of new taxa in Europe is probably maintained in the late Early and early Middle Miocene by a period of favourable climatic conditions, the Miocene Climatic Optimum, a period of warm equable subtropical conditions throughout Europe (Böhme, 2003; Bruch et al., 2004).

Concomitantly, the Oligocene inherited cainotheriids and moschids drastically and significantly drop in diversity (Fig. 5), the former eventually goes extinct during this period while the latter finally is represented by a single species (*Micromeryx flourensianus*). Other Oligocene inherited families also disappear in this interval (Palaeomerycidae, Anthracotheriidae).

From the Early Miocene MN1 zone to MN9, suids show a more or less constant representation and do not seem to be affected by the deep reorganization seen in the small ruminant families. In the same way, from their appearance in Europe in MN3 onwards, proboscideans do not increase in proportions and always represent between a constant 5 to 10% of the total species richness. Finally, the early Late Miocene (MN9) is marked by the rapid immigration of hipparionine horses (Bernor et al., 1996, Agustí and Oms 2001) largely increasing the representation of the equid family (Fig. 1, Table 2) and continuing its significant development (Fig. 5).

The global Mid Miocene Event around 15–13 Ma marked by a strong decrease of deep water temperatures (positive shift of oxygen isotope values, see Flower and Kennett 1994 and Zachos et al., 2001; Fig. 1) seems to unequivocally act on rodents diversity distribution (Maridet et al., 2007) as well as on ectotherm diversity

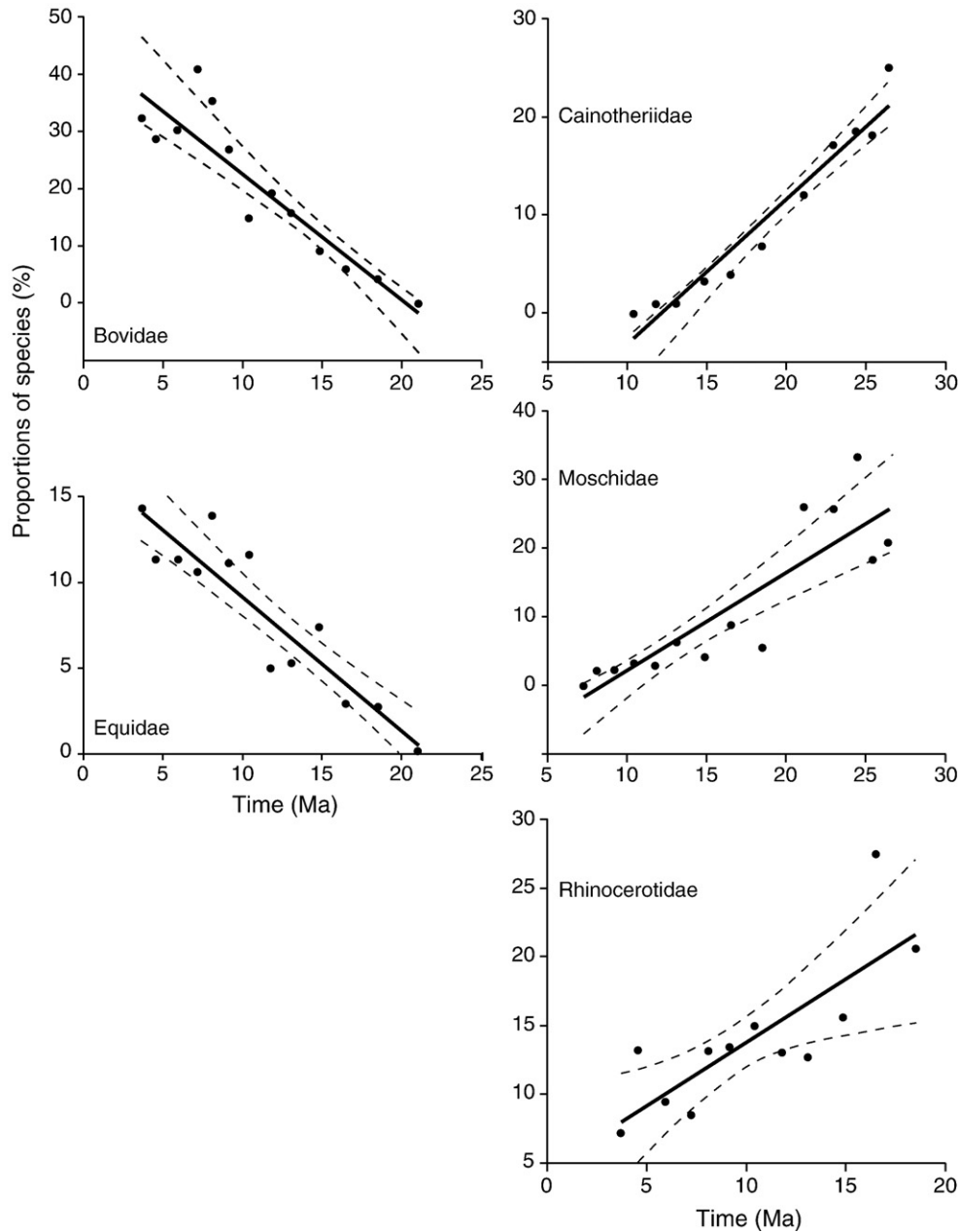


Fig. 5. Least squares regression analyses between family proportions and time (5 families are given here). 95% confidence intervals frame the regression line to show that relationships are significant.

(Böhme, 2003) but does not seem to produce the same effects on large mammals as no particular shift in community composition or decrease in diversity immediately follows this major event. This is somewhat in contradiction with the overall global mammalian record (Flower and Kennett, 1994) and this European peculiarity is still in need of explanation.

Later in the Late Miocene (MN11), moschids, one of the dominant components of the Late Oligocene and Early Miocene faunas, finally disappear. Modern ruminants continue to increase and dominate the faunas all over Europe (Fig. 1). Hipparionine horses also progressively increase in number while the diversity of rhinocerotids and other perissodactyls

(chalicotheres and tapirs) slightly but significantly decline (Fig. 5). Giraffids increase in proportions over the Late Miocene but with a restricted distribution as shown below. Camelids appear in Europe in the Late Miocene (MN12) and a peculiar ruminant family, the Hoplitomerycidae, is found restricted to the Italian fossil record in MN13 (Leinders, 1984). The general trend for ungulate family richness is a decrease from 15 families in MN10 to 10 in MN15 (Table 2). Species richness reaches a maximum around 110 species in MN11 and MN12 thanks to the large number of species (comprising 30 species or more of bovids) recorded in Greece and Turkey as well as to the addition of the Iranian fossil record in MN11 (see regional records below).

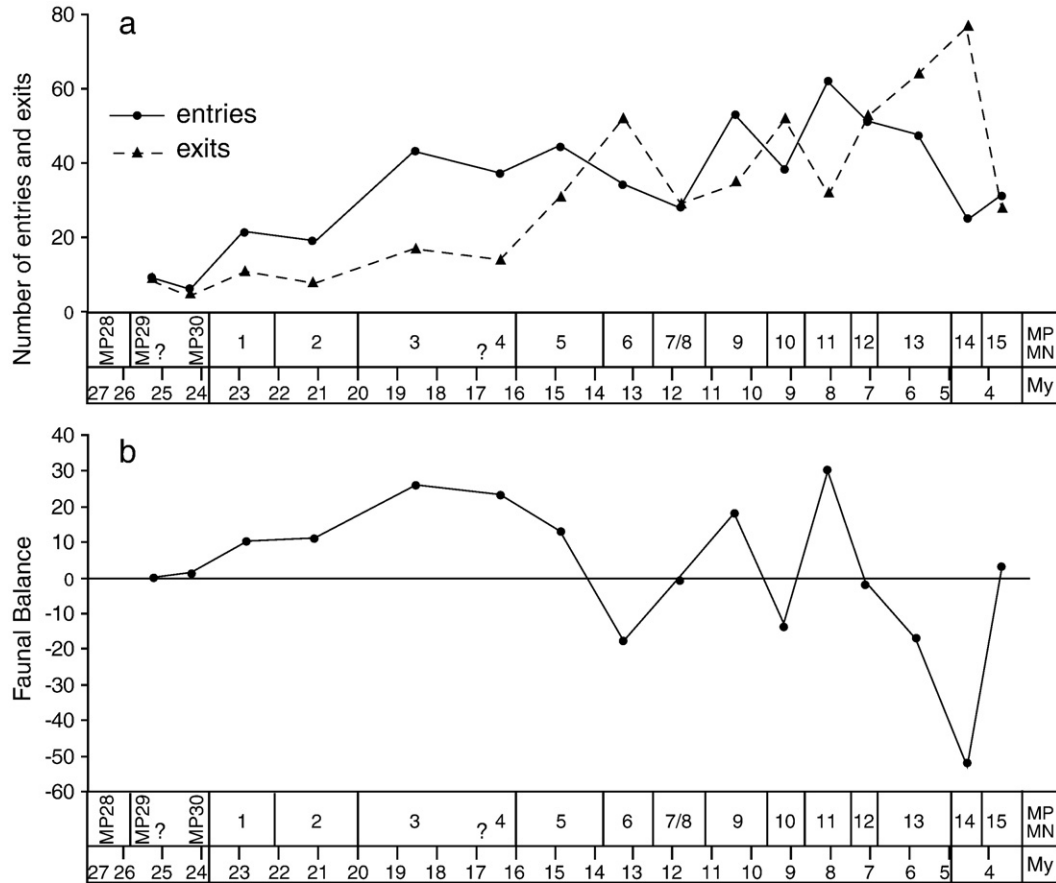


Fig. 6. a: top diagram, absolute number of entries and exits of ungulate species at the European scale. Solid line: entries; broken line: exits; b: bottom diagram, faunal balance calculated as entries — exists for each biozone at the European scale.

The Early Pliocene confirms the overall trends and cervids and bovinds now represent up to 60% of the total species richness. It is worth noting that bovinds proportions constantly and significantly increased in the last 20 Ma at the European scale (Fig. 5).

4.2. Turnover

Fig. 6a shows entries and exits per biozone and Fig. 6b a faunal balance calculated as (entries – exists) following Legendre (1987) at the European scale. These curves allow to draw interesting conclusions on the dynamics of appearances and extinctions in the Neogene. Three large periods characterize this dynamics, the first one from the Late Oligocene (MP28) to the early Middle Miocene (MN5) shows more entries than exits (faunal balance is positive) confirming the pattern of immigration from Asia and Africa; the second one from the Middle Miocene (MN6) to the early Late Miocene (MN11) is quite chaotic with alternating periods where either appearances or extinctions dominate evidencing the extinctions of Oligocene inherited taxa and the appearances of new species (in particular new hipparionine horses, cervids or bovinds); and then the Late Miocene to very Early Pliocene period (MN12–MN14) is characterized by extinctions in excess.

Raw appearances and extinctions are rather high in each biozones especially after MN3 where 30 to 75 species either

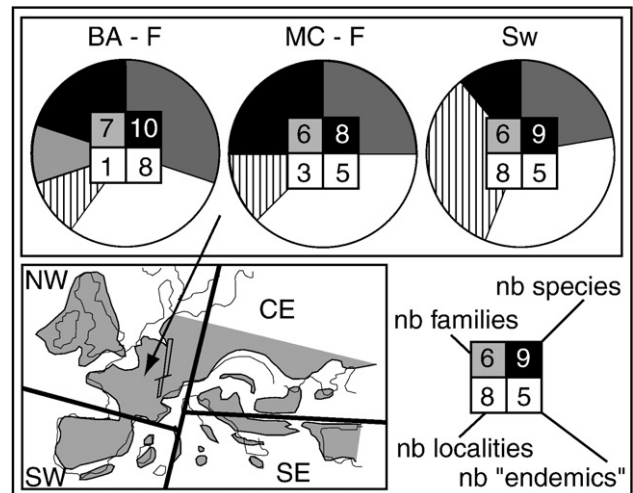


Fig. 7. Regional pie diagrams showing the relative proportions of ungulate families for period MP28–MN1. Pie diagrams of reference level MP29 represent this period. Legends can be found on Fig. 1. Regions abbreviations can be found in Table 1. Palaeogeographic maps after Rögl, 1999. Europe is divided in four bioprovinces: NW, north-western; SW, south-western; CE, central-eastern and SE, south-eastern such as defined in the text. The bottom right hand-side of the figure indicates what is given in the boxes inside pie diagrams, namely number of families, species, localities and “endemics”. Note that number of “endemics” is the number of species only found in a given region for a given time period.





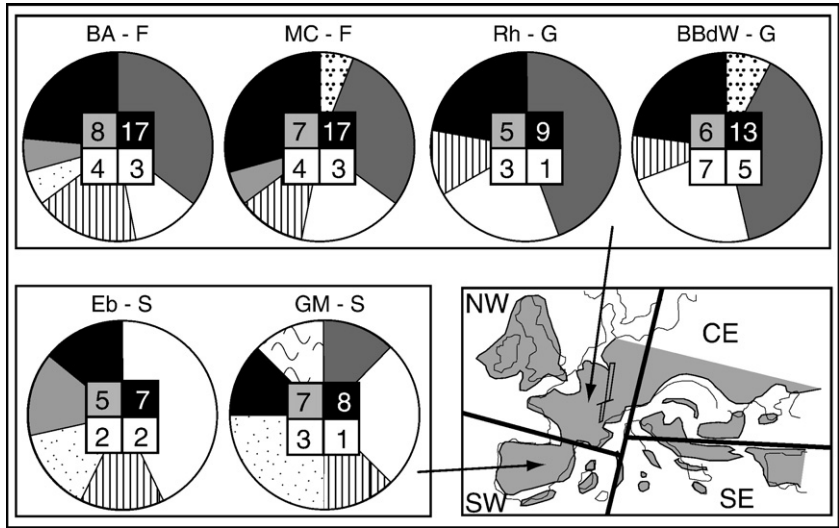


Fig. 8. Regional pie diagrams showing the relative proportions of ungulate families for period MN2. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

situation, especially in the Late Oligocene, shows at least 50% of species restricted to a single region.

4.6. *Early Miocene (MN2)*

The MN2 fossil record for large mammals is more consistent; species diversity is slightly higher in French regions.

The same families as for the former period still dominate ungulate communities. Tapirs and chalicotheres are now present in north-western regions and absent in the Iberian Peninsula. This differentiation seems to be also visible in the proportions of moschids (in general higher on the diagrams for northern regions, Fig. 8) but a closer look at the data through statistical comparisons using Mann–Whitney tests fails to evidence a

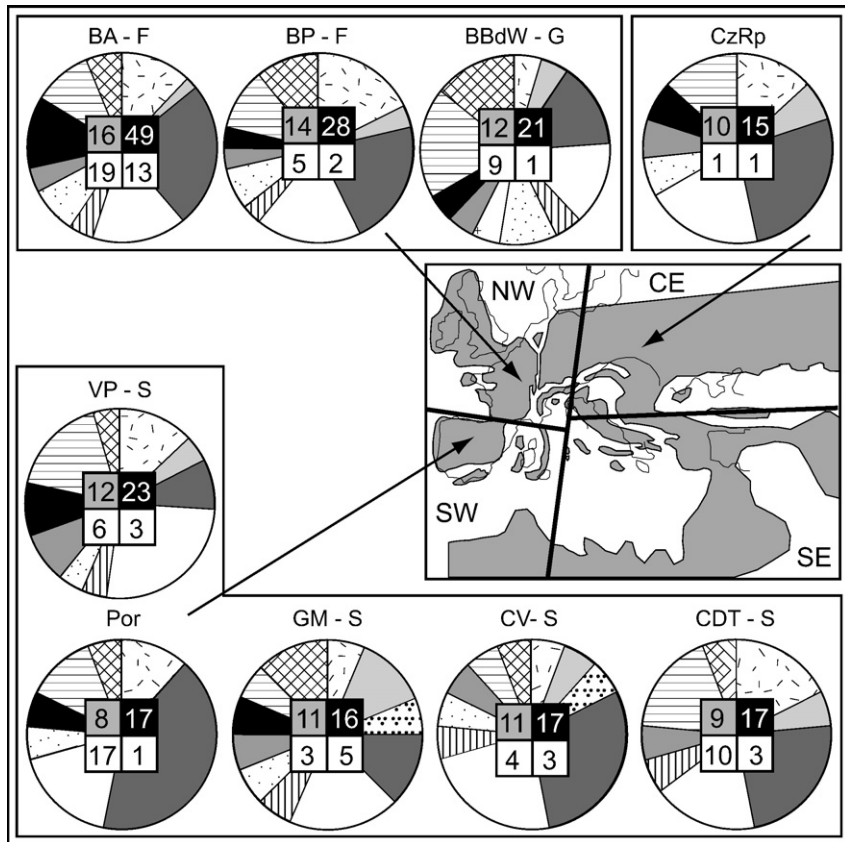


Fig. 9. Regional pie diagrams showing the relative proportions of ungulate families for period MN3–4. Pie diagrams of zone MN4 represent this period. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

significant diversity gradient for this family (at the regional scale when individual north-western regions are compared to south-western ones and again at the bioprovincial scale when all the data pooled for NW are compared to data pooled for SW:  $p \gg 0.01$ ).

4.7. Late Early Miocene (MN3-4)

The change in large mammals communities is important here with a drastic increase in both species and family diversity in every regions (up to 49 species and 16 families in the French Aquitanian Basin in MN4). Proboscideans (three families appear in Europe: Gomphotheriidae, Mammutidae and Deinotheriidae), equids, tragulids, cervids and bovids now enrich previous assemblages (Fig. 9). Oligocene-inherited families are still present but obviously proportionally less dominant except for rhinocerotids.

4.8. Middle Miocene (MN5-6)

This period here represented by the MN5 pie diagrams (Fig. 10) still presents a high regional diversity (up to 51 species

and 17 families only in the French Paris Basin). Several species are largely distributed (e.g., *Gomphotherium angustidens*, *Anchitherium aurelianense*, *Bunolistriodon lockharti*, *Procervulus dichotomus*) giving the more homogeneous biogeographic situation seen on Fig. 4. South-eastern Europe represented by the Greek region is now recorded and shows a faunal affinity with the other regions with no particular endemism. Nevertheless it already shows the presence of giraffids and of choerolophodontids (proboscideans that will only be recorded in SE Europe). From MN6 (graphs not shown here), this SE province becomes largely endemic with always more than 50% of endemic species. MN6 also shows the drastic decline (either extinction or geographic range contraction) of some of the oldest families: cainotheriids, anthracotheriids and hypertragulids.

4.9. Late Middle Miocene–early Late Miocene (MN7/8–9)

This period marks the last age of high diversity in Europe except in the south-eastern regions. Regional endemism is low to very low except in the SE. The most remarkable faunal evolution that starts in this period is indeed a regional differentiation of the south-eastern province. Bovids drastically develop there and

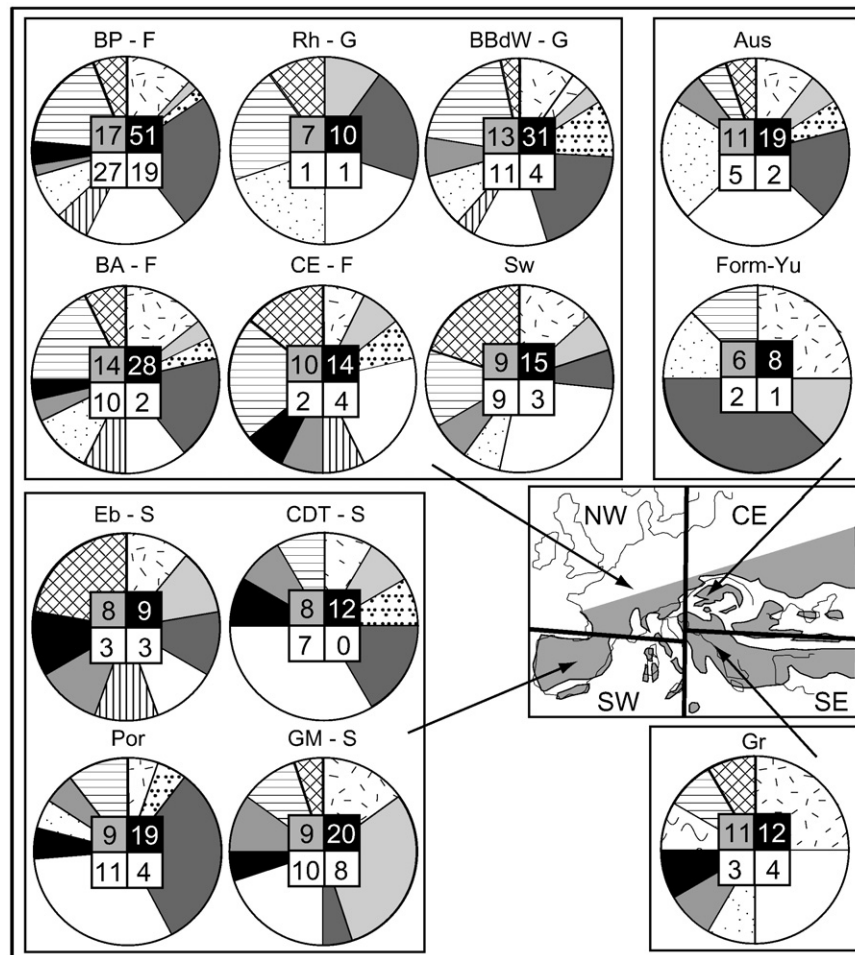


Fig. 10. Regional pie diagrams showing the relative proportions of ungulate families for period MN5–6. Pie diagrams of zone MN5 represent this period. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

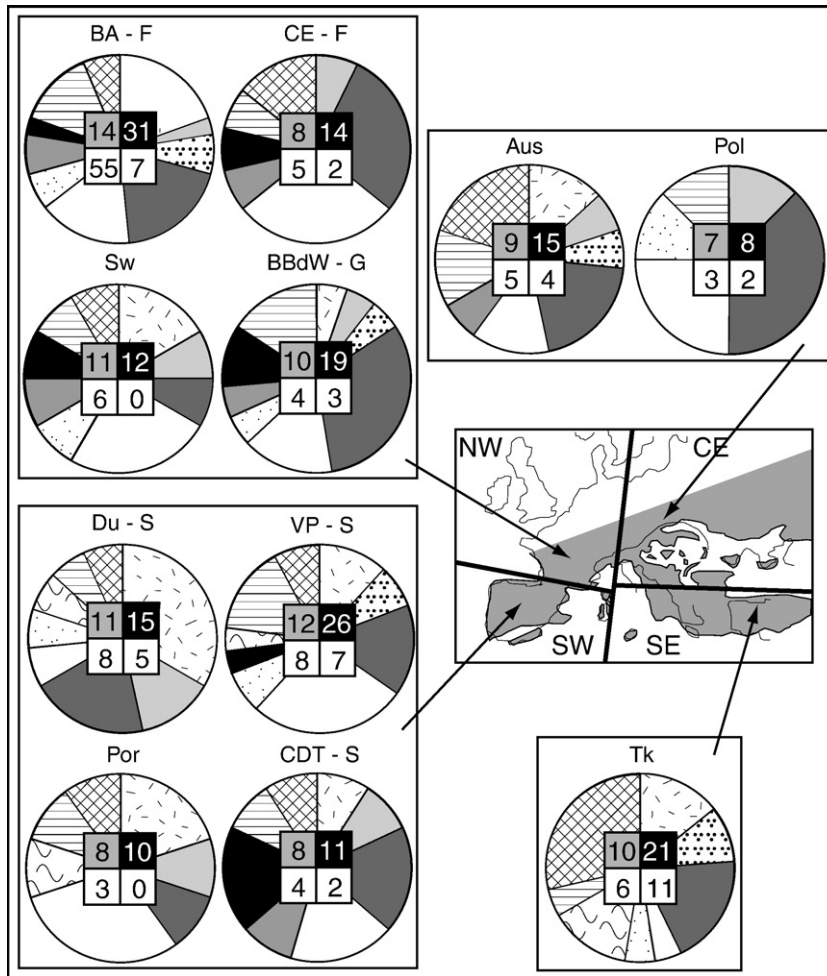


Fig. 11. Regional pie diagrams showing the relative proportions of ungulate families for period MN7/8–9. Pie diagrams of zone MN7/8 represent this period. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

constitute 40% or more of total species richness, cervids on the contrary seem to be less abundant than elsewhere (Fig. 11). The overall situation however still is represented by a biogeographic homogeneity (highest Raup and Crick's index values, Fig. 4) as cosmopolitan species are still well developed. MN9 is marked by the rapid dispersion in Europe of the hipparionine horses (especially *Hippotherium primigenium*) participating to the biogeographic pattern.

#### 4.10. Late Miocene (MN10–13)

The trend separating the south-eastern province with the others continues and bovids and giraffids largely expand there in comparison with the other European regions. Species diversity in this province can reach up to 61 species (Greece, MN12) with the classic Pikermian biota (Solounias et al., 1999), family richness decreases with no more than 12 families at most. In the other regions, species diversity is lower than before (maximum 31 in Italy, MN13 but lower than 25 in general, Table 3) and family richness decreases with most often less than 10 families per region (Fig. 12, Table 3). Oligocene inherited families finally disappear (last appearance of moschids in MN11) and less and less species show large geographic ranges (e.g.,

*Deinotherium giganteum* or *Microstonyx major*). Camelids appear in Europe in the Late Miocene (MN13) and this zone shows high endemism also in the islands of what is now Italy (almost 2/3 of endemic species).

#### 4.11. Pliocene (MN14–15)

Fewer regions are recorded in the Pliocene for large mammals and species and family diversity are smaller. Again, very few species now have a large geographic distribution (*Anancus arvernensis*) participating to the low values of the biogeographic index (Fig. 4). The dominant families are bovids, cervids, equids and suids among a few others less diversified (Fig. 13, Table 3).

#### 4.12. Diversity gradients at provincial scale

Mann–Whitney tests comparing the proportions of certain families of ungulates in different bioprovinces for different periods of time were calculated to see if significant differences existed. It is a way to evidence significant diversity gradients that can be related to geographic and/or climatic factors, both recorded from other sources. Four large bioprovinces described

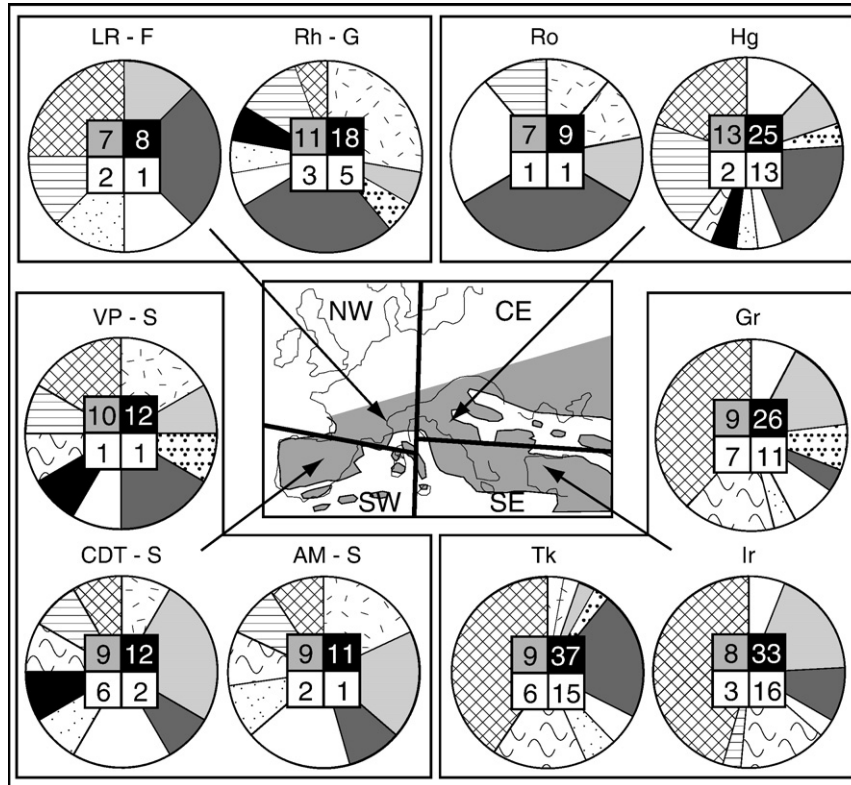


Fig. 12. Regional pie diagrams showing the relative proportions of ungulate families for period MN10–13. Pie diagrams of zone MN11 represent this period. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

above (i.e., SW, NW, CE and SE) were compared as they are characterized by a large geographic coverage yielding enough raw data for such comparisons, i.e., many localities spread over long time-periods. When smaller geographic areas are compared (regions such as defined in this study), Mann–Whitney tests can rarely evidence significant differences because too few data exist over long-enough time periods yielding too few differences in proportions between two regions (i.e., only when

bovids are considered between the Turkish region and the Calatayud–Daroca–Teruel basin during MN6–12 [ $p=0.03$ ]). Results are given in Table 4. The 95% confidence level is the

Table 4  
Mann–Whitney tests on ungulate proportions for 6 families for which such comparisons were possible

Families	Provinces compared	Time-period considered	$p$	Significant difference (Yes/No)
Bovidae	SE–NW	MN5–12	0.008	Y
	SE–NW	MN5–9	0.04	Y
	SE–NW	MN9–12	0.03	Y
	SE–SW	MN9–13	0.012	Y
	SE–CE	MN11–13	0.08	Y★
	SW–NW	MN9–12	0.88	N
	SW–CE	MN11–13	0.83	N
Cervidae	NW–CE	MN11–12	0.21	N
	NW–CE	MN5–9	0.68	N
	SW–CE	MN5–9	0.29	N
	SE–NW	MN6–12	0.005	Y
Equidae	SE–SW	MN6–13	0.005	Y
	SE–SW	MN11–13	0.08	Y★
	SW–NW	MN3–7/8	0.016	Y
	SW–NW	MN9–12	0.47	N
	SE–SW	MN9–12	0.19	N
Giraffidae	SE–NW	MN9–12	0.88	N
	SE–SW	MN9–12	0.03	Y
Rhinocerotidae	SE–NW	MN9–13	0.06	Y★
Moschidae	SE–SW	MN9–12	0.03	Y

The tests compare 2 bioprovincial records together for periods where a given family occurs. The difference between 2 bioprovinces is considered as highly significant at the 95% confidence level ( $p<0.05$ ). Stars indicate a lower level of confidence (90%) nonetheless signing particularly high differences.

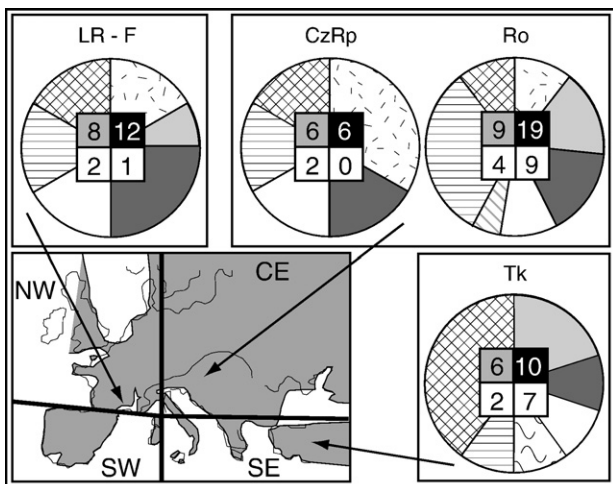


Fig. 13. Regional pie diagrams showing the relative proportions of ungulate families for period MN14–15. Pie diagrams of zone MN15 represent this period. Legends can be found on Fig. 1. Palaeogeographic maps after Rögl, 1999. For the rest, same caption as in Fig. 7.

rule here but a few of the results are significant at the 90% confidence level such as shown in Table 4.

The main result arising from these statistical comparisons concerns the south-eastern bioprovince. It emerges as a very different area mostly during the whole or parts of the Middle and Late Miocene with several families for which proportions are significantly different from the other provinces: bovids, moschids and giraffids always show higher proportions in the SE, and cervids always show lower proportions in the SE. Late Miocene rhinocerotids proportions are always higher in the NW province, when compared to the SE province, but level of confidence is lower here (90%, i.e., Mann–Whitney,  $p=0.06$ ). The other significant difference concerns the Equidae family which shows higher proportions in the SW province, when compared to the NW province, during the late Early to late Middle Miocene. All the other combinations comparing the different provinces and the other families together always give non-significant differences.

Consequently, two gradients can be recognized from the communities' composition, the first concerns the fairly strong faunal isolation of the SE bioprovince confirming the endemism level evidenced above during the Middle and Late Miocene. The second is a North–South gradient between north-western and south-western Europe during the Late Miocene and mainly evidenced here on the proportions of Equids.

## 5. Discussion

### 5.1. Diversity, geography and climate

The Neogene large mammals' diversity evolution can largely be related to two kinds of parameters that are recorded by other sources: geography and climate. It is not surprising that both parameters control mammals' spatial and temporal diversity dynamics as previous studies already emphasized their active role. Indeed, Maridet et al. (2007) already showed that Neogene rodents diversity dynamics mostly resulted from climatic controls and Costeur et al. (2004) emphasized the role of geography over Early Miocene ungulates diversity. Following this preliminary analysis, it becomes now evident that geographic factors partly participated to the building of the European large mammals biodiversity over the deep time. Several tectonic events and geographical changes occur throughout the European Late Oligocene and Neogene geological history. The overall tectonic evolution is driven by the Alpine Cycle, triggering the convergence of the European and African–Arabian plates (Meulenkamp and Sissingh, 2003). During the Late Oligocene and very Early Miocene it resulted in the European Cainozoic Rift System (Rhine and Rhone grabens) being largely flooded, what probably constituted an important geographic barrier to dispersal explaining the high level of endemism in regions separated by this system (French basins to the West and South-German and Swiss basins to the East, i.e., both with more than 50% of endemic species, Fig. 7). The continued development of the Alpine cycle in the Early Miocene had a dramatic impact on the European large mammals diversity through the establishment of the “*Gomphotherium* landbridge” (Rögl, 1999) that physically

bridged previously existing water barriers between three continental domains (Europe, Asia and Africa). This well-known event led to the arrival in Europe of numerous ungulate species and families from Asia and Africa (Tassy, 1989, Agustí and Antón, 2002; Mein, 2003) drastically increasing their diversity (Fig. 1). It is worth noting that new taxa (e.g., proboscideans, equids, cervids, bovids) enriched the Oligocene-inherited European faunas without replacing their constituent species and families. In addition, their arrival generated higher affinities between regional assemblages such as evidenced on the high Raup and Crick faunal similarity index values (Fig. 4). This result is mainly driven by the migration in Europe of species with large geographic range sizes (e.g., *Gomphotherium angustidens*, *Anchitherium aurelianense*, *Procervulus dichotomus*). Gaston (2003) and many other studies evidenced the positive relationship between geographic range size and species body mass indicating that large species have larger distribution areas; and when one adds that large-size species tend to have higher dispersal abilities than small-size species because of lower population densities (Damuth, 1981), it is reasonable to expect that the arrival of large mammals in Europe after a situation dominated by regional endemic faunas produces higher regional faunal affinities (Fig. 4). This result is emphasized by the higher number of entries than exists (positive faunal balance) during the whole Early Miocene (Fig. 6a–b). Again it is worth noting that the situation is logically different when rodents are considered (Maridet et al., 2007); regional faunal affinities tend to decrease at this time period following the same rule than for ungulates.

Later geographic changes affecting the European continent do not seem to have significant impacts on ungulate biodiversity. Indeed, climatic factors seem to be preponderant to control mammals diversity and distribution. When the Early and Middle Miocene are considered, it seems difficult always to separate geographic from climatic controlling factors. If geography seems to play a major role in the Late Oligocene and around 19–18 Ma as explained above, climate already probably plays a significant part in controlling ungulate diversity. The “*Gomphotherium* landbridge” easily explains the immigrations and the increasing diversity in the Early Miocene but the fact that ungulate diversity stays high during a quite long time period after this event (up to the end of the Middle Miocene) most probably finds explanations in a long-term favourable climatic context. The end of the Early Miocene and the Middle Miocene are characterized by a warm and humid equable subtropical to warm-temperate climate in the European mid-latitudes. Several regional palaeoenvironmental analyses attest to this assumption. Daams and Van Der Meulen (1984) indicate high temperatures in the Spanish Calatayud–Daroca–Teruel basin for this period. Besse-dik (1984) also records from plants high mean annual temperatures (MAT, more than 20 °C) in southern France and northern Spain. Stuchlik et al. (1999), Ivanov et al. (2002) and Jiménez Moreno et al. (2005) confirm the presence of a warm and humid subtropical-like climate in eastern Europe from plant assemblages (mean annual temperatures around 18°–20 °C and mean annual rainfall around 1200–1400 mm). Utescher et al. (2000) also record in northern Germany the warmest interval of the last 25 Ma in the Late Burdigalian–Langhian period (ca. 17–14 Ma) with plant-based MAT ranges from 15.5 to 21 °C, classifying the

climate as “extratropical”. Böhme (2003) sets a lower limit for MAT estimations based on Central European ectothermic vertebrates to 17.4 °C. In the same area, paleobotanical estimations give MATs of about 20 °C (Schweigert, 1992; Bruch et al., 2004). Such a climate favours high animal diversity by increasing habitat diversity as well as the availability of ecological niches (Blondel, 1995).

This warm interval, the second warmest after the Palaeocene–Eocene Thermal Maximum, is directly followed by a strong climatic cooling (Miocene Climatic Event) reflected by a large increase of benthic and planktonic foraminifera  $\delta^{18}\text{O}$  (>1‰) from about 15 to 13 Ma and recorded worldwide (Fig. 1; western Pacific: Woodruff et al., 1981; North Atlantic: Miller et al., 1991; Kerguelen Plateau: Wright and Miller, 1992; South-West Pacific: Flower and Kennett, 1993; Colombian basin: Mutti, 2000; South China Sea: Zhao et al., 2001; South Tasman Rise: Shevenell et al., 2004). This drastic increase represents the second major step towards cooling in the Cenozoic history. It also is associated to short and important relative sea-level fluctuations around 14 Ma with a global lowering around 14.2 Ma (Haq et al., 1987). It is also noteworthy that the Carbon isotopic record covaries with the Oxygen isotopic record indicating the burial of huge quantities of organic Carbon mainly in marginal basins of the Californian Monterey formation (Vincent and Berger, 1985; Flower and Kennett, 1994; Zachos et al., 2001) leading to the “Monterey Hypothesis” to explain this global Miocene Climatic Cooling. Nevertheless, growth and installation of a permanent East Antarctic Ice Sheet (EAIS) constitutes the main hypothesis to explain  $\delta^{18}\text{O}$  increase and thus global cooling.

On the continental realm, this cooling is also recorded worldwide by different palaeoclimatic proxies (Flower and Kennett, 1994): In Europe, palaeobotanical data record a shift from subtropical environments to more arid conditions (references cited above, see also Bruch et al., 2004); the ectothermic vertebrate record is also congruent with the flora cooling pattern.

Böhme (2003), indeed, deduced from the diversity of ectotherms that a cooling of about 7 °C most likely occurred around 13.5 Ma in Central Europe; likewise, Legendre et al. (2005) document a decrease in temperature of ca. 7 °C in the central-eastern French region from rodents diversity that they ascribe to this global cooling. This event triggers the appearance of more seasonal and more latitudinally-organized climates in mid-latitudes worldwide during the Late Miocene and has a strong impact on mammal faunas. The European ungulate diversity responds to the Miocene Climatic Cooling and climatic deterioration that follows. Number of exits is indeed high in the Late Middle Miocene (MN6, Fig. 6a) indicating an impact of the global climatic deterioration on faunal diversity. This was already shown by Daams and Van der Meulen (1984) on rodents. As shown in this study, the number of species and families of ungulates gradually decrease from the very early Late Miocene onwards to reach half of the Middle Miocene diversity. This is also reflected in the increasing pattern of exits often higher than entries yielding a negative faunal balance (Fig. 6a–b). Again, the turnover pulse around the MN9–10 can be related to the well-described Vallesian Crisis (Agusti et al., 1997; Agusti et al., 2003)

probably linked to pulses evidenced on the marine oxygen-isotope records (Mi6 and Mi7 in Miller et al., 1991) following the major mid-Miocene event. Later on in the Late Miocene, taxa that are adapted to more open and more temperate conditions (e.g., equids, giraffids, bovids, cervids) dominate the faunas at the expense of forest-dwellers that previously were well represented (e.g., cainotheriids, moschids, certain species of rhinocerotids). This Late Miocene drop in diversity is accompanied by the appearance of significant gradients in the proportions of certain families, notably bovids, moschids and giraffids which always are more diversified in south-eastern European regions than elsewhere, a situation already emphasized for bovids by Bonis et al. (1992) and later by Fortelius et al. (1996), Costeur et al. (2004) and Eronen (2006) but never firmly quantified before. On the contrary, cervids and to a lesser extent rhinocerotids are more abundant in northern provinces evidencing the same gradient probably related to more open and arid conditions in south-eastern European areas (Zazzo et al., 2002; Costeur, 2005; Merceron et al., 2005; Strömberg et al., 2007). Well-defined latitudinal climatic belts were therefore already present by the late Middle Miocene just after the Miocene Climatic Cooling and mainly represent strengthened belts already forming in the late Early–early Middle Miocene (Böhme, 2003; Costeur and Jimenez-Moreno, 2004; Casanovas-Vilar and Agustí, 2007; Jimenez-Moreno and Suc, 2007; Costeur and Legendre, in press).

### 5.2. Deep time roots of diversity and endemism

The present situation concerning mammalian diversity in Europe shows a rather depleted state with a hot spot in central-eastern regions and decreases towards northern, southern and western boundaries (Baquero and Tellería, 2001). The authors explain that this particular configuration mostly results from the peninsular form of the European continent leading to a decline of the surface of inhabitable zones towards coastal areas. Other factors related to the Quaternary climatic, environmental and biogeographic history probably also had a significant impact (see Hewitt, 1996, 1998). This peninsular shape already existed during the Miocene and it is noteworthy that certain of the westernmost regions (Aquitainian and Paris basins) constituted areas of highest biodiversity all along the Early and Middle Miocene (Figs. 9 and 10). The « cul-de-sac » shape of the European continent thus cannot explain on its own the present situation. Simple random spatial models of species distributions under no-existing-gradient conditions yield a pattern of diversity that closely resembles the European situation with hot-spots in the area's centres; this is the mid-domain effect (Colwell et al., 2004). Often simple combinations of geographic mid-domain effects and basic biotic or abiotic constraints may explain empirical patterns of diversity distribution (Brayard et al., 2005). Consequently great care must be taken before interpreting the present European mammalian diversity distribution with purely climatic or geographic factors.

The present depleted European large mammals diversity seems to have deep historical roots beyond the time of the Quaternary climatic cycles as diversity was already decreasing from the beginning of the Late Miocene, some 12 Ma ago. The

same result is found on small mammals (rodents and lagomorphs, Maridet et al., 2007) evidencing a general pattern of diversity dynamics.

Concerning endemism, Baquero and Tellería (2001) also indicate that present high endemism areas are situated in the southernmost European regions: The Iberian Peninsula, south-eastern Europe (i.e., Balkans pro parte). They explain that this situation is inherited from Pleistocene climatic cycles. Pleistocene biogeographic factors would have allowed genetic diversification of populations forced to contract their geographic ranges to refugia in southern Europe and thus would have allowed numerous allopatric speciations yielding the highly endemic pattern now known there (Avisé and Walker, 1998). The work presented here indicates that south-eastern Europe (e.g., Greece, Turkey) is a zone of high species richness and high provincialism since at least the Middle Miocene. The origin of this strong endemism is to be found largely before the numerous speciations related to the Pleistocene biogeography. The intermediate geographic position of this zone between Europe, Asia and Africa lead numerous species to meet there favouring a high diversity. At the opposite, the Iberian Peninsula was not really a centre of endemism as for Miocene ungulates are concerned and the present biogeography can certainly be more directly explained by the action the Quaternary climatic cycles (Hewitt, 1998). Future studies in progress will help clarify the complex pattern of endemism over the whole European Neogene.

## 6. Conclusions

This study of a large dataset of European ungulate species and families over more than 20 Ma yields particularly interesting results on the temporal and spatial dynamics of their diversity and biogeography. Contrary to what was known to date, the roots of the present situation are to be found before the Quaternary Climatic Cycles. Indeed, European ungulate diversity was already largely decreasing since the Late Miocene, some 12 Ma ago. In addition present endemic areas often simply regarded as the result of Pleistocene climatic variability were already firmly present in south-eastern Europe in the Miocene; hence the history of endemism in Europe seems to be much more complicated than previously thought.

Concerning factors that control ungulate diversity, a more complex pattern than what is now accepted for small mammals (rodents and lagomorphs, Maridet et al., 2007) seems to arise. If climate appears to play a crucial role in determining levels of diversity and its spatial distribution through limiting factors (e.g., temperature and precipitation) and gradients, geography also has a major role in that it allows large isolated continental areas to meet. This triggers migration episodes that in turn produce large scale community changes (such as the major enrichment occurring in the Early Miocene through the connection of Europe, Asia and Africa). It is worth noting that small mammals respond differently to geographic reorganisations (Maridet et al., 2007) probably partly because of their lower dispersal abilities.

Finally, integrating spatial scales from region to continent allowed us to produce a precise spatial evolutionary history for Neogene ungulates and gave us the opportunity to under-

stand differential changes over the whole European geographic area.

## Acknowledgements

We thank both anonymous reviewers for their interesting comments that helped improve our manuscript. We acknowledge financial support from the “Institut Français de la Biodiversité” and from the ESF-sponsored EEDEN scientific program “Environment and Ecosystem Dynamics of the Eurasian Neogene”). L.C. was financed by the French Ministry of Education and Research through a PhD grant.

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