Ashraf M. T. Elewa

Editor

Migration of Organisms

CLIMATE · GEOGRAPHY · ECOLOGY

Springer

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Climate • Geography • Ecology

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(Editor)

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With 67 Figures

Springer

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Dedication

This book is dedicated to all people who

Believe in One God

Believe in Peace

Believe in Migration in the Way of God

To my father who died on Sunday, the 10th of April, 2005

Foreword

P. David Polly

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Evolutionary biology journals of the 1950s and 60s were filled with musings on the improbable. Disjunct distributions of related organisms on continents separated by hundreds of miles of open ocean or in seas divided by mountainous barriers were a historical challenge. Pregnant porcupines were rafted across the South Atlantic on mangrove trunks to explain the presence of Palaeogene hystricomorph rodents in Africa and South America. Limpets were lofted across the Isthmus of Panama in the talons of birds to connect latter day Caribbean descendants with their Miocene Pacific ancestors. By the 70s continental drift lumbered into the paradigms of palaeontology and vicariance inserted itself as the null hypothesis – the evolutionary hegira was redefined as abduction by subduction. Dramatic finds like the Triassic vertebrate *Lystrosaurus* on the Antarctic mountains that once lay within the genus's now disjunct African and Indian range confirmed the predictive power of vicariance. In some instances, the vicariant sword grew so sharp that scenarios of circuitous continental conveyers became even wilder than earlier tales of drifting diaspora. By the end of the century, however, ideological battles between migrationists and vicariants had given way to more dialectic mixed model of biogeographic history.

In the past decade, molecular phylogeography and geological isotope geochemistry have renewed interest in migration on much smaller temporal scales. Surveys of molecular diversity within species revealed that much geographic variation was phylogenetically structured. Pictures of species as panmictic gene pools have been redrawn so that speciation is no longer an event, but a never-ending narrative of the gradual breakdown in relationship. Rivers and hills, rather than oceans and mountains, separate subspecific clades. At the same time, geochemical evidence has revealed fine-scale wobbles in the Earth's climate. The Pleistocene, for example, is no longer the time when regal glaciers made stately advances and retreats across the continent, but a jumble of transient alternations of warm and cold overlain by more regular glacial and interglacial cycles. Warm spikes only hundreds of years long saw *Saiga* antelope sweep horde-like from Central Asia as far as England, only to be driven back just as quickly. Phylogeographers and palaeontologists alike now talk of putative refugia and post-glacial recolonization to explain the biogeographic history of populations of seemingly continuously distributed continental species.

The present collection by Dr Ashraf Elewa of Minia University contains papers about migration that are as timely as the subject is traditional. Migration, it seems, is an ever-moving subject, and Elewa presents us with a sampling of some of its current trajectories. Reyment discusses the interpretation, and misinterpretation, of distributions of fossil marine organisms in light of pre- and post-mortem movements. Elewa, in two papers, considers the distribution of tiny but biostratigraphically important ostracods in relation to the changing reaches of the shallow sea that periodically inundated what is now northern Africa. Petrakis and Legakis investigate problems of detecting and understanding insect migration in Mediterranean ecosystems. Longer-term migration and adaptation in cold water Pacific mollusc faunas are described by Amano. Thompson and Russell take a particularly elegant look at phylogeographic structuring in the mtDNA in salamanders in the Pacific Northwest. The Miocene Vallesian Crisis, a time when the subtropical forest faunas of Europe virtually disappeared during a cooling episode, is used by Casanovas-Vilar et al. to investigate the geographic restructuring of entire faunas and floras. The final paper of the book, by Hortal et al., contains a creative quantitative study of the provincializing effect of basin and range structures in Iberia on mammalian communities and an extrapolation by GIS modelling to see whether the same provincial structure existed in the Palaeogene. Readers will get a flavour of the latest quantitative analyses – GIS, faunal clustering, mtDNA phylogenetics – and a sense of the breadth of international research in migration and biogeography.

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1 Introduction

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Migration is commonly thought of as a mechanism by which organisms avoid unfavorable environments for more auspicious ones. Migration can be the seasonal movement of organisms from place to place or a more permanent dispersal from one region to another; either way, changing environmental conditions provide the impetus. But why do some organisms migrate and not others? How do the benefits of migration compare with the metabolic costs and hazards of the journey? Do differences between terrestrial and marine species in their interface with the environment have different effects on migration? What are the trade-offs between migration and evolutionary adaptation to local conditions?

Different species respond to environmental changes in different ways, partly based on their individual adaptations and range of tolerance. This phenomenon is most easily seen when comparing terrestrial and marine organisms, which have different relations to their environment. Terrestrial organisms are surrounded by low-density atmosphere and expend considerable energy moving and keeping themselves upright; marine organisms, in contrast, are surrounded by seawater, which has a density close to their own, making support and movement much less costly (Sverdrup et al. 2005). Thus, migration is likely to be more metabolically costly to a terrestrial animal than a marine one, all other things being equal. The factors affecting migration of land and sea species may therefore differ considerably, and one geologic episode may affect the two realms differently.

Terrestrial and marine organisms also differ in the environmental factors that affect them the most. Temperature and rainfall are major determinants on the land, but salinity is one of the most important in the sea. The difference in the salt content of seawater and bodily fluids affects the transport of water molecules through cell membranes in a process called osmosis; changes in salinity can have disastrous effects on the physiological balance of an organism. Temperature variation affects marine organisms also, but in different ways than terrestrial ones. Changes in temperature affect water density, and therefore buoyancy and the ability of an organism to maintain its optimal position in the water column, positions that are important in terms of ambient pressure and available nutrients. Pressure in deep waters is so great that organisms must avoid it or evolve special adaptations to survive. Most life in the marine realm requires carbon dioxide and oxygen, whose concentrations vary with depth. Oceans can be divided into an upper photic zone, where sufficient sunlight penetrates to support photosynthesis, and a lower aphotic zone, where the intensity of sunlight is low or does not penetrate at all, so inhibiting photosynthetic activity. The constant motion of water in the oceans affects the distribution of organisms and patterns of productivity in the seas, both by transporting the nutrients and gases necessary for life and by carrying floating or drifting organisms with the currents.

Migration often serves as a short-term solution to variable environments, but adaptation can provide a long-term solution. Adaptation can thus be viewed as a parallel way for organisms to survive. Some groups have evolved bioluminescence to bring their own light to ocean depths. Such adaptations will have evolved through selection on favourable chance variants. Because some individual organisms possess genetic combinations that are particularly valuable for survival in a local environment, they will find the environment less antagonistic than do others. For example, for many organisms living in, on, or near the sea floor, the properties of the bottom material, or substrate, are very important for survival. In the vast oceanic environment, both the water and the sea floor are divided into specific zones that have distinct characteristics and support different populations of organisms. Depending on the circumstances, selection may favour adaptations to one of these, or it may favour generalized adaptations that permit movement from one to another. As conditions change, the organisms will either cope or move, and some species will be geographically localized and others widespread. A challenge for migration studies, especially in the fossil record, is to distinguish widespread species from species that migrate between localized environments (Taylor in Boardman et al. 1987).

Since the classic works of Schmidt-Koenig (1975), Schmidt-Koenig and Keeton (1978), Gauthreaux (1980) and Adley (1981), which contain valuable information on migration and quantitative approaches for its study, no edited book, to my knowledge, has considered migration in its broadest sense across different groups of organisms. Moreover, the quantitative analyses in these other works are now aging, with many new approaches having been developed over the last decades. It is, however, worth noting that Dingle (1996) recently published an excellent textbook on migration, which covers all migratory organisms. The work focuses on the distinction between migration and dispersal and why the two should not be conflated. A second excellent book by Drake and Gatehouse (1995) is limited to insects and was an outgrowth of a symposium at the International Congress of Entomology in Beijing, China. A third recent book, was edited by Jones et al. (2004) with the title "Migrations and dispersal of marine organisms" and based on the proceedings of the 37th European Biology Symposium held in Reykjavík, Iceland, 5-9 August 2002. The main themes of the symposium were migrations and dispersal of marine organisms. Accordingly, no attention was paid to non-marine organisms.

To fill this gap, I have selected, in my opinion, a suitable collection of topics to explore migration in different groups of marine and non-marine organisms ranging from ostracodes and foraminifera (micro-invertebrates), then molluscs (macro-invertebrates), followed by insects, reptiles, amphibians, salamanders, birds, and finally mammals. Conceptually, these papers address a broad range of topics that have not been collected, I think, in any past single work:

1. The paleobiogeography and biogeography of organisms (both invertebrates and vertebrates);
2. The relation of ecological, paleoecological and other factors to migration;
3. The distinction between migration and species origination, extinction, and turnover;
4. Adaptability as a parallel way to migration for organisms to survive;
5. The ecological relation among species (predation, parasitism, commensalism, mutualism... etc.) and its effect on migration;
6. The application of modern quantitative techniques for constructing migration models.

This book should appeal to professionals and students at all levels. I hope this work represents an up to date summary of ideas in the field, as well as a useful summary of recent progress of the subject. In terms of authors, as in my previous book on morphometrics, I have invited a group of experts who present topics showing a broad diversity of organisms ranging from invertebrates to vertebrates, including popular groups such as insects, mammals, birds, reptiles and amphibians.

Additionally, as I am an ostracodologist, I have tried to highlight the importance of ostracodes for paleogeography. Pokorny in Haq and Boersma (1980) stated that marine ostracodes are not as well suited for interregional and intercontinental stratigraphic correlation as are other groups of planktonic microfossils, since benthic ostracodes have no planktonic larvae, therefore, the shallow, warm water species cannot easily cross geographic barriers (see also Keen et al. 1994; Elewa 2002). However, this limitation makes ostracodes excellent paleobiogeographical markers. Pokorny added that the deep-sea ostracodes of the Mediterranean province, studied by Benson and Sylvester-Bradley (1971), are of considerable paleogeographical interest. Examples are found in Paleocene to Middle Miocene and in Pliocene sediments from different areas of the Mediterranean province. Ostrocodes provided evidence that, in the Paleocene, there was a possibility in the southern Mediterranean for east-west migration through the Trans-Saharan Seaway (see Reyment and Reyment 1980; Reyment 1981; Elewa, chapter 3 of this volume). In the Late Miocene, the Mediterranean Sea was cut off from the Atlantic Ocean and transformed into a series of lagoons, as documented by endemic ostracode communities. At the beginning of the Pliocene, communication between the Mediterranean Sea and the Atlantic Ocean was re-established in the west, so that Atlantic euhaline species re-invaded the Mediterranean. Recent Mediterranean ostracodes are chiefly of Atlantic origin and differ from their Tertiary descendants. With the opening of the Suez Canal more than a hundred years ago, a migration route was established between the Indo-West Pacific and the Mediterranean. This is a special example of increasing human effect on the composition of naturally established regional faunas, as was emphasized by McKenzie (1973). Chapter 5 (this volume) by Elisabeth Brouwers presents valuable information about the migration of ostracodes along the northeast Pacific coast in response to temperature changes during glacial-interglacial cycles.

I would like to express my deep gratitude to all people who played an important role in the completion of this book. I especially acknowledge David Polly (UK) for writing the preface, as well as reviewing this introduction and two chapters for this book. The rest of the reviewers, an exceptional group of experts, are also thanked for their critical reviews of chapters in this book (Abdel Kireem and Bassiouni from Egypt; Blain from France; Rook from Italy; Tanabe from Japan; Campomanes, Hortal and Morales as well as an anonymous reviewer from Spain; Reyment and Savazzi from Sweden; Korner-Nievergelt from Switzerland; Whatley from UK; Cronin, Dodd, Finger and Peterson from USA; arranged alphabetically according to their countries). Thanks also to all of the contributors for devoting their time in preparing their chapters for this book. They have done excellent work and without their contributions this project would not exist. A special word of thanks is due to the publishers of Springer-Verlag for their continuous help during the several steps of editing this book. I also appreciate the great help of the staff at Minia University in Egypt.

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9 The geography of a faunal turnover: tracking the Vallesian Crisis

Isaac Casanovas-Vilar Salvador Moyà-Solà, Jordi Agustí and Meike Köhler

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9.1 Abstract

The configuration of emerged land masses as well as the distribution of suitable habitats are two important constraints for migration of land mammals. The evolution of late Miocene European land mammal faunas seems to be related to climatic change, which consisted in a general cooling and an increase in seasonality starting by the late Miocene. The pre-existing subtropical evergreen forests were replaced by mixed mesophytic ones at higher latitudes, while in the peri-Mediterranean regions the forest cover was fragmented. The Vallesian Crisis, which implied the disappearance of forest-adapted taxa and a general diversity decay in Western Europe by the beginning of the late Miocene, has been related to main climatic changes. This crisis is a well-established event in the Iberian Peninsula, however the response of mammal communities in other areas is still debated. The goals of present work are to refine chronologic and geographic limits of the Vallesian Crisis. Data input consists in a series of fossil mammal sites covering most of the middle and all the late Miocene (13.8 – 4.9 Ma). Provinciality has been studied using cluster analysis, and results indicate the maintenance of three main bioprovinces (Greek-Iranian, Iberian and Central European) during most of the time span. Diversity and origination and extinction rates have been calculated for all Europe and for each main bioprovince whenever possible. The results show that diversity increased during the late Vallesian and the Turolian in the Greek-Iranian bioprovince because of the development of open-country herbivore faunas while diversity remained stable in Central Europe. A decay in diversity started in the Iberian Peninsula by the early Vallesian and genera richness kept descending during the Turolian. Although the environment was rather similar in East and West, Turolian mammal faunas from the Iberian Peninsula are very poor and show few eastern immigrants. We suggest that mixed mesophytic forests covering most of Central Europe acted as an ecological filter, preventing the migration of open-country adapted taxa from Anatolia.

Keywords: Europe, Miocene, mammals, biogeography, paleoclimatology, faunal turnover, migration.

9.2 Climatic change and mammalian faunal dynamics

The influence of climatic change and its relation to major ecological and evolutionary transitions on fossil mammal faunas has been an extensively studied subject during the past decades. Detailed works have linked changes in species composition with climatic events (see for example Vrba 1985, 1995; Van der Meulen and Daams 1992; De Bonis et al. 1992; Fortelius et al. 1996; Agustí et al. 1999; Bobe and Eck 2001). However, as Alroy et al. (2000) have shown in the particular case of North American mammals, sometimes climatic shifts are correlated with ecological and evolutionary changes, while often other such transitions occur at time of little global climate change. The effect of global climatic change in mammal communities seems clear, but we should put more emphasis on the particular environmental conditions of the areas affected. Considering distribution of landmasses and past ecosystems can help us to understand better mammal turnovers and why sometimes they occur at moments of moderate climatic shifts.

Vrba (1985) proposed two mechanisms in order to explain turnover pulses as recorded in East African ecosystems: habitat tracking and ecologically induced genealogical events. Habitat tracking simply implies the expansion of the geographic ranges of pre-existing species. Otherwise climatic change may cause local speciation because habitat alteration and degradation leads to a more heterogeneous “patchy” environment. Nevertheless, Vrba (1985) notes that speciation does not occur in response to new empty niches, but fragmentation of species population. Distribution of emerged lands and particular ecosystems will evidently determine the principal kind of mechanism involved in a turnover event.

9.3 The Vallesian Crisis and the late Miocene faunal turnover

Within the Neogene the late Miocene is a complex moment which appears punctuated by several climatic and phisiographic events. This is the case, for instance, of the progressive closing of Eastern Mediterranean gateway during the late Serravallian – early Tortonian (Rögl 1999, 2001) and the uplift of the Tibetan plateau (Amano and Taira 1992), which led to a restructuration of atmospheric and marine circulation. These events resulted in the onset or intensification of monsoonal circulation in Asia and the appearance of a characteristic dry season in circum-Mediterranean regions (Kutzbach et al. 1993). At high latitudes temperatures decreased because of changes in position of polar ice fronts.

In the terrestrial realm, these events must have influenced the pattern of dispersal and turnover among the mammalian faunas, according to the ideas of turnover pulses exposed above. In fact, the late Miocene, that is the period covered by continental mammal stages Vallesian and Turolian, coincides with several faunal dispersals, induced either by climatic events, intercontinental relationships or interplay between both causes. Particularly, the Vallesian stage (between 11.1 Ma and 8 Ma) is characterized by the overall dispersal at 11.1 Ma of three-toed hipparionine horses, which entered Eurasia from North America via the Bering Strait (Bernor et al. 1993; Garcés et al. 1997). This event was possible because of an important sea level fall of about 100 m (Haq et al. 1987) coinciding with a major shift in δ^{18} O (Mi 5) (Miller et al. 1991) indicating general cooling. However, this climatic event seems to have had few effects over land mammal communities, and in fact diversity increased continuously during the Vallesian (at least in Spain, see Agustí et al. 1999).

This scenario changed abruptly at 9.7 Ma, when a significant mammal turnover, known as the Vallesian Crisis, deeply altered the composition of the Western and Central European terrestrial ecosystems. This point marks the boundary between the early and late Vallesian at 9.7 Ma (Garcés et al. 1996). The Vallesian Crisis (sometimes also cited as Mid or Late Vallesian Crisis) was recognized for the first time in the Vallès-Penedès Basin (northeastern Spain) and involved the disappearance of most of the middle Miocene elements adapted to the warm wet-subtropical environments (Agustí and Moyà-Solà 1990; Moyà-Solà and Agustí 1990). The diversity and number of forest-adapted rodents decreased significantly coinciding with the entry and widespread of murids that completely outnumbered the cricetids, major elements of the rodent communities until the late Vallesian (Agustí 1982; Van Dam 1997). Among the large mammals the crisis specially affected perissodactyls (tapirids and the rhinoceroses *Lartetotherium sansaniense* and "*Dicerorhinus*" *steinheimensis*), artiodactyls (the suid *Conohyus*, the cervid *Amphiprox*, the moschid *Hispanomeryx*, the bovids *Miotragocerus* and *Protragocerus*), hominoids (*Dryopithecus*) and the large carnivores of the families Nimravidae and Amphycionidae (Moyà-Solà and Agustí 1990; Agustí et al. 2003). It has also been suggested that the Vallesian Crisis extended to the Central European mammal faunas (Fortelius et al. 1996; Franzen and Storch 1999). The effects of the crisis there would have been less marked, and some middle Miocene relics persisted in Germany, Austria and Hungary during the late Vallesian. On the other hand the Vallesian Crisis is not observed in the Rhône Valley (Mein 1999), while in southeastern Europe coincides with an increase in diversity and turnover. The crisis coincides with a minor isotopic event, Mi 7 (Miller et al. 1991), even weaker than previous Mi 6 although this time the shift in δ^{18} O is accompanied of a noticeable sea level lowering (Haq et al. 1987). The Vallesian Crisis has been related to this event (Agustí et al. 1999), which would have implied the onset of a late Miocene glaciation in the Arctic zones (Zubakov and Borzemkova 1990). This scenario of high latitude cooling and low latitude drying continued during the Turolian. This stage records the progressive extension to the west of the bovid and giraffid dominated faunas that characterized Anatolian communities (Fortelius et al. 1996; Koufos 2003).

As exposed above, after decades of work, a general picture of the climatic changes taking place during the late Miocene and their effect over European mammal faunas is emerging. However, problems appear when focusing in concrete events, areas, or time spans. For example, the effects of the Vallesian Crisis and the existence of such event in some areas are still debated. The absence of a reasonably complete record in many countries may obscure the effects of the crisis in these areas, or simply the crisis did not occur there. There seems to be a diversity loss in Spain and Central Europe, but in Anatolia diversity increased during the crisis as result of the entry of new taxa. To what extend are we dealing with an extinction or a turnover event? And why the response of mammal communities is different depending on the area? The aim of this work is to find the temporal and geographic limits of the Vallesian Crisis, and to construct a late Miocene picture of Europe consistent with them.

9.4 Material and methods

9.4.1 The database

We have focused in the western part of the Old World, covering a latitudinal range from 35 to 55 degrees and from –10 to 40 degrees of longitude. Northern Africa and the British Islands are not included. We have selected a time span covering nearly all the late Miocene, ranging from the late Aragonian (middle Miocene) until the end of the epoch (13.8-4.9 Ma, datings after Agustí et al. 2001). This time span includes seven MN zones ("Mammal Neogene" biozones): MN 6 (late Aragonian, 13.8-12.5 Ma) MN 7 + 8 (late Aragonian, 12.5-11.1 Ma); MN 9 (early Vallesian, 11.1-9.7 Ma); MN 10 (late Vallesian, 9.7-8.7 Ma); MN 11 (early Turolian, 8.7-7.5 Ma); MN 12 (middle Turolian, 7.5-6.8 Ma); and MN 13 (late Turolian, 6.8-4.9 Ma) (datings are after Agustí et al. 2001).

Data source for this chapter is the version of the NOW (Neogene Old World) database, which is available at the following site: http://www.helsinki.fi/science/now/data.html, realized in July 2003. This database has been completed with data from many Spanish localities. We have included localities dated at the MN zone level of resolution at least and ignored those inaccurately dated. Finally a genera occurrence by localities database has been written using the data compiled. For this second database we have selected only the localities from the first one that included at least five genera. If more than one species of the same genus is present in the locality the genus is counted only once. Taxa identified to a suprageneric level are counted as an additional genus only if there are no identified genera of the same suprageneric level. For instance, if in a locality the genus *Deinotherium* is present and we have also recorded Proboscidea indet., we only count one genus: *Deinotherium*. If in another site only Proboscidea indet. is recorded, it counts as a genus in our database. Macromammals and micromammals have been recorded in separate databases because they are recovered using different field methods. As a result we have obtained a database that includes a total of 341 sites: 145 macromammal sites and 196 micromammal sites. A total of 442 taxa are recorded in the studied time span: 253 macromammals and 189 micromammals. In order to study the geographic trends in mammal assemblages through time we have divided the western Old World in 40 squares of the same area. These squares are defined by the intersection of latitude and longitude lines each one equally separated 5° from their nearest neighbors. Thus the side of the squares is also 5°. Each site is assigned the to one square numbered from 1 until 40 (see Fig. 1 and Table

1). Of course, some squares will include land and sea, and the ratio land to sea will not always be the same. Although we consider that this fact will not affect the results in an important way, it must not be forgotten. Appendix shows the localities used in the cluster analysis of Figs 2-8 (see below) as well as the square in which each one is included.

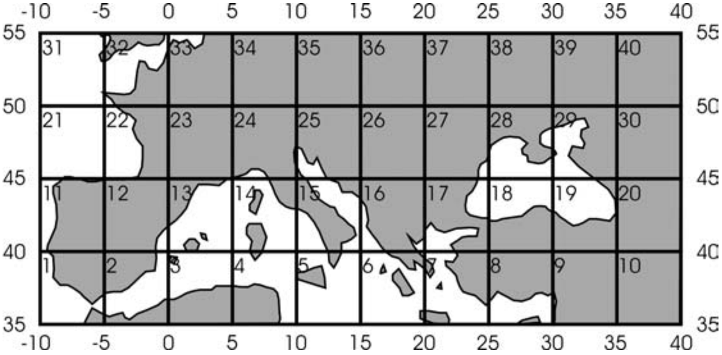

Fig. 1. Map of the study area. The western Old World is divided in 40 squares of the same area defined by the intersection of latitude and longitude lines, each one equally separated 5° from their nearest neighbors. Each square is numbered from 1 until 40

9.4.2 Provinciality

We have considered sites in each MN zone and constructed taxa occurrence by locality matrices. Macromammals and micromammals are considered separately resulting in two different matrices for each MN zone, thus fourteen matrices. Cluster analysis has been performed on each matrix. We have used unweighted pair-group average algorithm (UPGMA) to join clusters, while distance matrix has been computed using Raup-Crick index for presence / absence data (Raup and Crick 1979). This index uses randomization procedure, comparing the observed number of genera co-occurring in two associations with the distribution of co-occurrences of 200 random replicates. Calculation was carried out using the program PAST 1.27 (Hammer et al. 2001).

Table 1. Per-square (see Fig. 1) percent of the total number of macromammal and micromammal sites recorded in each MN zone. The higher proportion of both micro and macromammal localities comes from central and northeastern Spain, so it is expected that Spanish results will clearly bias calculations when Europe is considered as a whole

	MACROMAMMALS (% of total number of localities in each MN)							MICROMAMMALS (% of total number of localities in each MN)						
square	MN 6	MN 7 + 8	MN 9	MN 10	MN 11	MN 12	MN 13	MN 6	MN 7 + 8	MN 9	MN 10	MN 11	MN 12	MN 13
1	0	0	0	0	0	0	0	8	0	0	7	0	0	0
2	0	0	0	0	7	7	11	0	0	0	0	4	4	15
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	5	0	0	0	0	0	0	0
7	0	0	0	0	0	10	0	0	4	0	0	0	0	0
8	0	6	3	0	14	13	0	0	4	0	0	0	0	0
9	11	6	0	6	7	3	0	4	4	0	0	0	0	0
10	0	0	0	0	0	0	0	0	4	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	3	0	0	4
12	22	0	7	18	21	27	37	50	23	43	64	46	81	56
13	17	56	31	24	7	3	5	4	35	26	18	12	0	7
14	0	0	0	0	0	3	0	0	0	0	0	0	4	4
15	0	0	0	0	0	10	16	0	0	0	0	4	4	7
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	6	0	0	24	21	0	21	0	4	0	0	4	0	7
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	7	3	0	0	0	0	0	0	4	0
20	0	0	0	6	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	5	8	0	0
24	11	6	31	6	7	0	0	17	8	4	5	15	0	0
25	11	13	3	0	0	0	0	4	4	0	0	0	0	0
26	17	0	7	0	7	0	5	4	4	9	3	8	0	0
27	0	6	0	0	0	0	0	0	4	4	0	0	0	0
28	0	0	17	18	0	13	0	0	0	9	0	0	4	0
29	0	0	0	0	0	3	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	6	0	0	0	0	0	0	8	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	6	0	0	0	0	0	0	4	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	4	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	3	0	0	0	0	0	0	0	0

However, there is an important pitfall in our provinciality analysis: all sites included in an MN zone are not of the same absolute age. This would not be a great problem if the MN zones consisted in relatively short time spans, but some zones, such as MN 7 + 8 and MN 9 last nearly 1.5 Ma. Then, differences expressed by clusters could not correspond to real ecological or biogeographical differences between sites at a specific time just because the localities compared are not necessarily contemporary. Unfortunately accurate datings are not available for most of the sites, so an analysis at a finer level than an MN zone as a whole is not possible with our data set. The cases when differences expressed by cluster analysis seem to be explained by a temporal factor will be discussed.

9.4.3 Diversity

We have computed diversity for each MN zone in all the study area and in each latitude and longitude rank in order to explore geographic trends in diversity through time. We have calculated total diversity in each interval (N_{tot}) as:

$$N_{tot} = N_{FL} + N_{bL} + N_{Ft} + N_{bt} \qquad (10.1)$$

Where N_{FL} is the number of genera confined to the interval (singletons sensu Foote 2000); N_{bL} is the number that cross the bottom boundary only; N_{Ft} is the number that cross the top boundary only; and N_{bt} is the number that cross both boundaries. N_{bt} also includes taxa known before and after the time span but not during. These quantities are calculated for each latitude and longitude rank, considering only the genera present in this single rank and discarding those present in adjacent ranks. Thus they are different in each latitude and longitude rank. N_{tot} is the total number of taxa that existed during the interval. This diversity measure is strongly affected by the duration of the time span considered: the longer time interval the higher number of N_{FL}. Diversity measures that estimate standing diversity at a point in time express better the number of taxa susceptible to origination or extinction at an instant in time (Van Valen, 1984). One of this second kind of diversity measures is the estimated mean standing diversity (N_{st}):

$$N_{st} = (N_b + N_t) / 2 \qquad (10.2)$$

Where,

$$N_b = N_{bL} + N_{bt} \qquad (10.3)$$

and similarly,

$$N_t = N_{Ft} + N_{bt} \tag{10.4}$$

N_b and N_t are the bottom-boundary and top-boundary crossers respectively. Thus, N_{st} estimates the diversity as their average. Because its definition N_{st} cannot be calculated for our first and last intervals (i. e. MN 6 and MN 13). Foote (2000) has shown the advantages and pitfalls of this and other diversity measures. Modeling shows that this measure becomes progressively worse as the length of the interval increases overestimating mean standing diversity if origination rate is different to extinction rate. The advantage of this measure is that singletons are simply irrelevant. Singletons are especially sensitive to variation in preservation and interval length, so basing diversity measures in estimated number of taxa partly removes this undesirable effects. Unfortunately there is not any measure of absolute diversity independent of temporal variation in preservation and interval length.

We have also estimated changes in diversity using the ratio (Foote, 2000):

$$\ln (N_t / N_b) \tag{10.5}$$

Normalized by interval length (Δt), which gives the proportional change in diversity through an interval. This measure is directly derived from the difference between origination and extinction rates (see below) and is particularly useful because all differences in species richness that may exist between areas (many of them resulting from the quality of their record) are leveled of. The proportional change in diversity is calculated for the study area as a whole and for selected squares. As the previous measure it cannot be calculated for the first and the last interval in the studied time span.

9.4.4 Origination and extinction rates

We have calculated estimated per-capita origination ($\hat{p}$) and extinction ($\hat{q}$) rates (Foote, 2000) for the study area as a whole and for selected squares:

$$\hat{p} = -\ln (N_{bt} / N_t) / \Delta t \tag{10.6}$$

$$\hat{q} = -\ln (N_{bt} / N_b) / \Delta t \tag{10.7}$$

As modeling has shown (Foote 2000) these estimates are unaffected by interval length. The ratios N_{bt} / N_t and N_{bt} / N_b decay exponentially with time if rates are constant within the interval; thus the logarithm of each ratio declines linearly with time. Even if true origination and extinction rates (o and e respectively) are not constant, $\hat{p}$ and $\hat{q}$ provide unbiased estimates of the mean rate within an interval. In contrast to other rate this rates do not rely on counting events within the interval and normalizing by a diversity measure. Thus $\hat{p}$ is not affected by extinction rate, while $\hat{q}$ is unaffected by origination rate. Singletons are irrelevant for these rate measures, so they are expected to be less sensitive to variation in preservation rates. The ratio ln (N_t / N_b) used here to estimate relative changes in diversity derives from substracting $\hat{q}$ from $\hat{p}$. These measures were intended for analyzing the whole fossil record of animal groups, rather than studying small areas and concrete time intervals. So in our case it is accurate to refer to $\hat{p}$ and $\hat{q}$ as per-capita entry and exit rates respectively because true origination and extinction may have taken place outside the area considered. Then $\hat{p}$ and $\hat{q}$ include not only true originations and extinctions but also immigration and regional disappearance of taxa.

9.4.5 Distinguishing variation in origination and extinction rates from variation in rates of preservation

A singular increase in preservation rate in one interval will cause an increase in both rates in this interval (see Foote 2000, Fig. 15). The number of genera that would have made their last appearance in preceding intervals is reduced because they now appear last in the interval with better preservation. The same is true for first appearances in succeeding intervals. Metrics underestimate extinction before the pulse in preservation, and underestimate origination afterwards. The measures are also affected by a singular decrease in preservation in an opposite way. A pulse in extinction will not affect origination, and a pulse in origination will not affect extinction (see Foote 2000, Fig. 12). Then we will be able to distinguish variation in taxonomic rates from variation in preservation rates but we will have to analyze the variation in apparent taxonomic rates that is potentially attributable to variation in preservation rates.

Preservation probability (R_i) can be estimated as:

$$R_i = X_{bt,\ samp} / X_{bt} \qquad (10.8)$$

Where X_{bt} is the number of genera known both before and after the interval and $X_{bt,\ samp}$ is the number of these genera actually sampled during the interval. Preservation rate r_i is estimated as (Foote 2000):

$$r_i = -\ln (1 - R_i) / \Delta t \qquad (10.9)$$

If variation in apparent taxonomic rates were dominated by variation in preservation rates, then the correlation between both kinds of rates would be large and positive. We will calculate r_i for the study area as a whole and for selected squares. We will test for correlation between two variables by calculating Kendall's τ. As in previous calculations, preservation rates cannot be calculated for our first and last time intervals.

9.5 Results

9.5.1 Provinciality

Cluster analysis (see Figs. 2 to 8) show the existence of a high degree of provinciality. Although there are some incongruences (MN 6, see Fig. 2 and MN 7+8, see Fig. 3) the same bioprovinces can be recognized in the case of micro and macromammals. Results clearly show the maintenance of three main bioprovinces during most of the time span. Those are an eastern province (also mentioned as Greek-Iranian province), a Central European province and an Iberian (including southern France) province. The existence of two distinct provinces (Eastern and Western Europe) occurring synchronously in the late Miocene was first recognized by Tobien (1967), while the distinction of an Iberian province by the same time (although never recognized) seems evident in the results presented by Fortelius et al. (1996, Fig. 31. 6 p. 422).

In MN 6 three main bioprovinces can be recognized: the Greek-Iranian province, the Central European province and the Iberian province (Fig. 2). The distinction between Central European province and Iberian province is clear considering the macromammals, while in the case of micromammals, localities from Germany, Slovakia and Switzerland appear close to Spanish and Portuguese ones. These localities are characterized by a high diversity of insectivores, dormice and mid-Miocene cricetids. Three Swiss sites cluster apart, due to a higher diversity of flying squirrels and Eomyidae. This fact may reflect the existence of a certain differentiation between Iberia and Central Europe starting at MN 6, although both provinces are very similar.

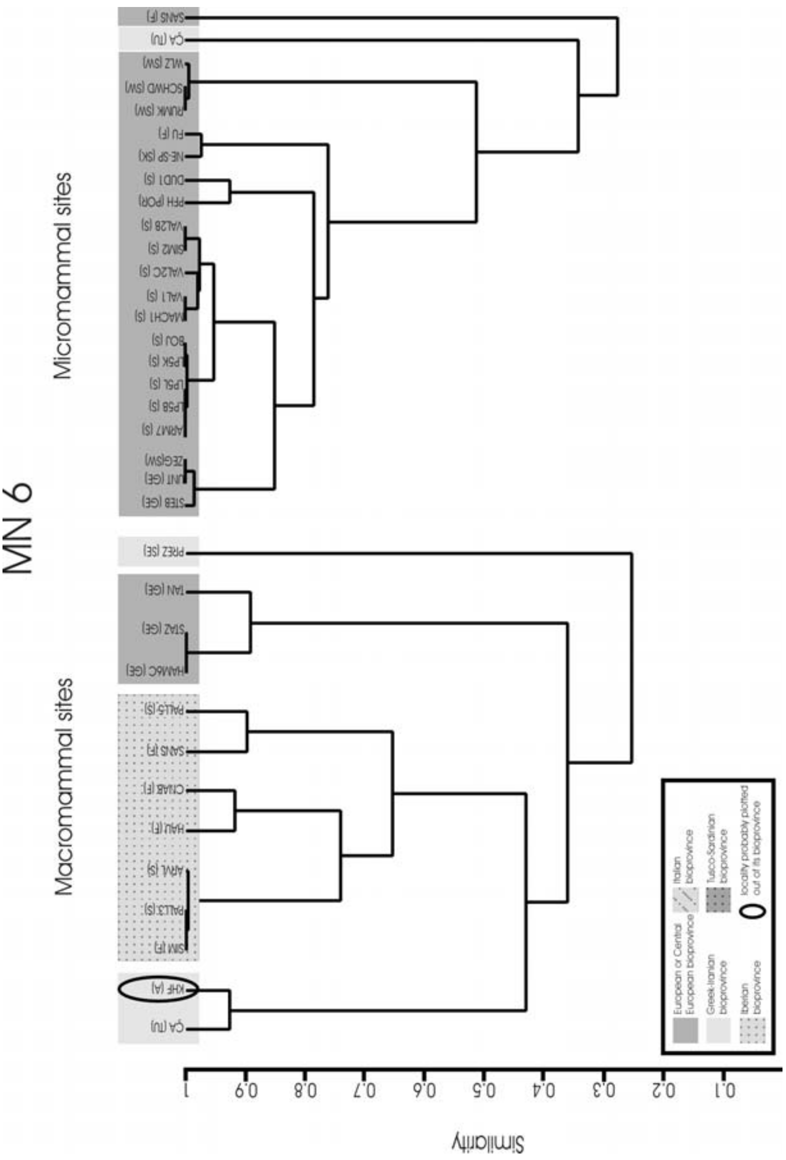

Fig. 2. Dendrogram displaying the results of cluster analysis for MN 6 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

Table 2. Key to country codes used in clusters from Figs. 2 to 8

Country	Country code	Country	Country code
Austria	A	Portugal	POR
France	F	Romania	RO
Germany	GE	Serbia	SE
Greece	GR	Slovakia	SK
Hungary	HU	Spain	S
Italy	IT	Switzerland	SW
Moldova	MO	Turkey	TU
Poland	PO	Ukraine	U

The locality of Sansan in France (SANS (FR) in Fig. 2) appears as very different of the other sites because of its exceptionally rich fauna, but it should be included in the Central European-Iberian province. The single micromammal fauna from the Greek-Iranian province (Çandir, Turkey; ÇA (TU) in Fig. 2) also appears isolated from the rest of sites. This fauna is characterized by the absence of many western cricetid genera, and by the presence of Spalacidae. Considering the macromammals, eastern faunas (Turkey, Serbia) are clearly separated from western ones, except from the site of Kohfidisch (Austria), which seems close to Çandir (Turkey). The eastern faunas are characterized by a higher bovid diversity including many exclusively eastern genera, although others reached Central Europe (*Turkoceras*, *Hypsodontus*). This fact results in a higher similarity between southeastern Europe and some Central European sites. Central European faunas are characterized by the presence of the rhinos *Alicornops*, *Plesiaceratherium* and *Hoploaceratherium*, together with more diverse Suidae and Cervidae. Macromammal faunas in Spain included less Cervidae genera and appear somewhat different from Central European ones.

In MN 7 + 8 the situation remains unchanged (Fig. 3), and again the three bioprovinces are clearly different if we attain to macromammals, while some confusion between Iberian and Central European provinces occurs in the micromammal sites cluster. Considering micromammals, the Greek-Iranian province is clearly recognized and it is characterized by a relatively lower diversity of dormice and squirrels. Cricetids also differ, so different forms lived in East and West of Europe. An illustrative example is the different lineages of hypsodont cricetids (Cricetodontini) which are represented by the genus *Byzantinia* in the East and *Hispanomys* in the West. Both genera arose from *Cricetodon* (although from different species) and followed a parallel evolution during the late Miocene (for a recent review of the evolutionary history of the Cricetodontini see De Bruijn et al. 1993; De Bruijn and Ünay 1996). Some differentiation can be seen between Central European micromammal faunas and those from inner Spanish basins. The differences expressed by the analysis are due to the presence of less dormice genera in assemblages dominated by few species of cricetids. Other Spanish sites, placed in the northeastern margin of the peninsula (Castell de Barberà and Sant Quirze (CB (S) and SQ (S) in Fig. 3), both from the Vallès-Penedès Basin), cluster with Central European

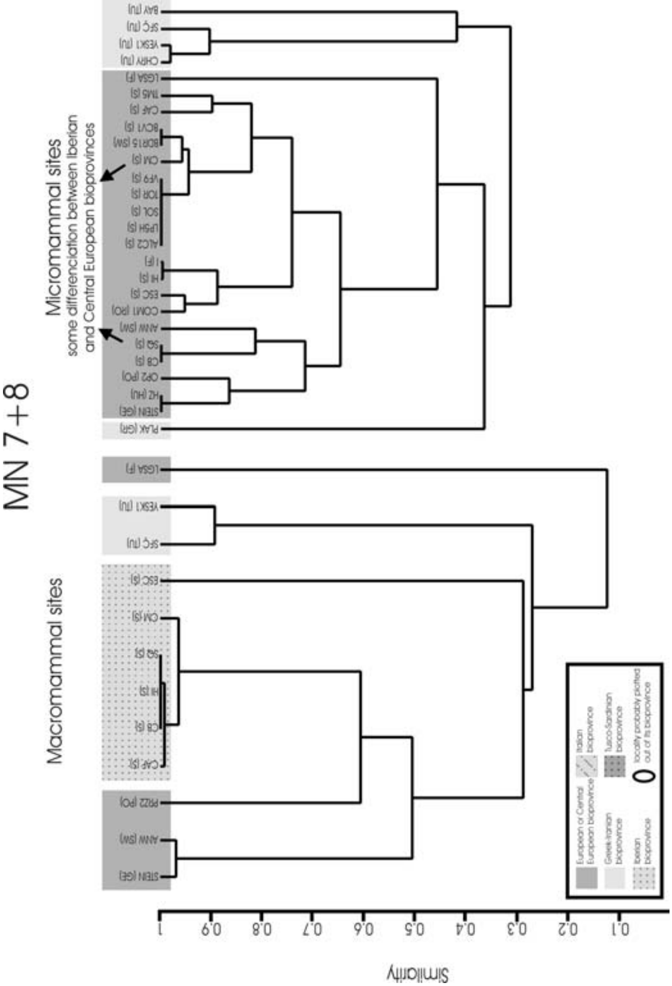

Fig. 3. Dendrogram displaying the results of cluster analysis for MN 7 + 8 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

because of their more diverse rodent faunas including many dormice species andalso some beavers and Eomyidae, very rare in the inner peninsula. However, other sites from the same basin (Hostalets Inferior (HI (S)), Can Missert (CM (S)) and Barranc de Can Vila 1 (BCV1 (S))) appear closer to the remaining Spanish sites. This fact may reflect that the boundary between both bioprovinces may fluctuate in time due to climatic changes (it must not be forgotten that the time span covered by MN 7 + 8 lasts nearly 1.5 Ma). An important bovid radiation occurred in the Eastern Mediterranean by this time, so Turkish sites include more than six bovid species. The occurrence of these elements explains why the sites appear so different from the rest of the European ones in the macromammal cluster. La Grive Saint Alban (France, LGSA (FR) in Fig. 3) also seems very different (a situation also observed in the micromammal cluster), but this is an undesirable taphonomical effect, because it is a karstic site (as well as Escobosa (ESC (S)), which appears as very different too). La Grive Saint Alban must be part of the Central European bioprovince, characterized by the less diverse bovid fauna and the presence of certain rhinos (*Dicerorhinus steinheimensis*), suids (*Albanohyus*) and primates. The sites from Spain cluster all together because of the presence of Boselaphini, while this bovid tribe is absent from many Central European sites. However, these sites do not seem very different from Central European ones and similarity between the two provinces (or should we say subprovinces?) is higher than in MN 6.

The MN 9 recorded the dispersal of hipparionine horses in the Old World. Some other taxa (the sabertoothed cat *Machairodus* and the hyaenid *Thalassictis* for instance, the giraffid *Palaeotragus* forms part of an older migration wave by the end of MN 7 + 8) extended their range from the East and accompanied the hipparions in their dispersal into Western Europe. This event coincided with a rhino turnover in Eastern Europe (appearance of *Ceratotherium* and *Chilotherium*) while bovid diversity continued rising. There seems not to have been any turnover in macromammal faunas in central and southwestern Europe, and the new immigrants are simply incorporated to the pre-existing faunas. The degree of similarity between the Central European and the Iberian bioprovinces (Fig. 4) is close to the one recorded in MN 7 + 8, but in MN 9 the localities from each province do not cluster in separate (although closely related) groups, and in Fig. 4 the Spanish sites appear altogether with German, Swiss and Hungarian ones showing few differences. The locality of Los Valles de Fuentidueña (VFÑ (S) in Fig. 4) appears close to Moldavian sites, clustered out of its province. Other sites such as Rudabánya (Hungary) and Nombrevilla (RUD (HU) and NOM (S) in Fig. 4) may also cluster out of their respective provinces. The Moldavian sites are clearly different from European ones, thus belonging to the Greek-Iranian province, but they also differ a little from the Turkish site Esme Akçaköy (EAKY (TU) in Fig. 4) because bovid diversity in Moldova was lower. The micromammal cluster shows the three main provinces. The Greek-Iranian province (represented only by Moldavian sites) is completely split from a great cluster including Central Europe and the Iberian Peninsula. These later provinces are more dissimilar than they were in previous analysis. Southwestern Europe (Iberian Peninsula and Southern France) is characterized by cricetid-dominated assemblages, while rest of rodent families are less diverse. The genus *Cricetulodon* appears in Spain at the beginning of the Vallesian and will be a major component of the MN 9 rodent faunas. This genus is an eastern immigrant (recorded in the Turkish MN 7 + 8 site Bayraktepe 1 (BAY (TU) in Fig. 3)), which is absent from Central European sites. Another eastern immigrant is the ground dormouse *Myomimus*, which are the most abundant dormice in the faunas of the inner Peninsula. Central European faunas were similar to those of the MN 7 + 8, with high levels of diversity and several genera of Eomyidae, dormice, ground and flying squirrels and beavers. The site of Vösendorf (Austria, VOS (A) in Fig. 4) appears closer to the Spanish ones because the poor fauna recovered lacks Gliridae. The late Vallesian (MN 10) seems to be a time of increasing similarity between East and West (see macromammal cluster of Fig. 5). For the first time Greek sites cluster with French and Spanish ones, although the differences are still important. The Greek-Iranian province (maybe the gentilice “Greek” should not be used to define the name of the bioprovince during MN 10) includes Moldavian and Turkish sites characterized by open-country Bovidae and Giraffidae plus a high diversity of the Bovoidea genera that are going to characterize the Turolian. Furthermore, there was a vicariant evolution of hipparionine horses that led to the origin of *Cremohipparion* in the Eastern Mediterranean, and to *Hipparion* s. s. in the West (Bernor and Armour-Chelo 1999). Western faunas include less Bovoidea and a higher diversity of Cervidae, Suidae and Tragulidae plus some eastern immigrants such as the hyaena *Adcrocuta* and the Boselaphini *Tragoportax*. The clustering of Greek localities with western ones may reflect the diachronous dispersal of open-country eastern herbivores. In the micromammal cluster we can only detect two groups: the Iberian province and the Central European province, which is mainly integrated by French sites. The presence of a still diverse dormice and squirrel fauna in Central Europe characterizes these sites. Another major component of the rodent faunas is *Rotundomys* and hypsodont cricetid that appears in few Spanish sites and many French ones.

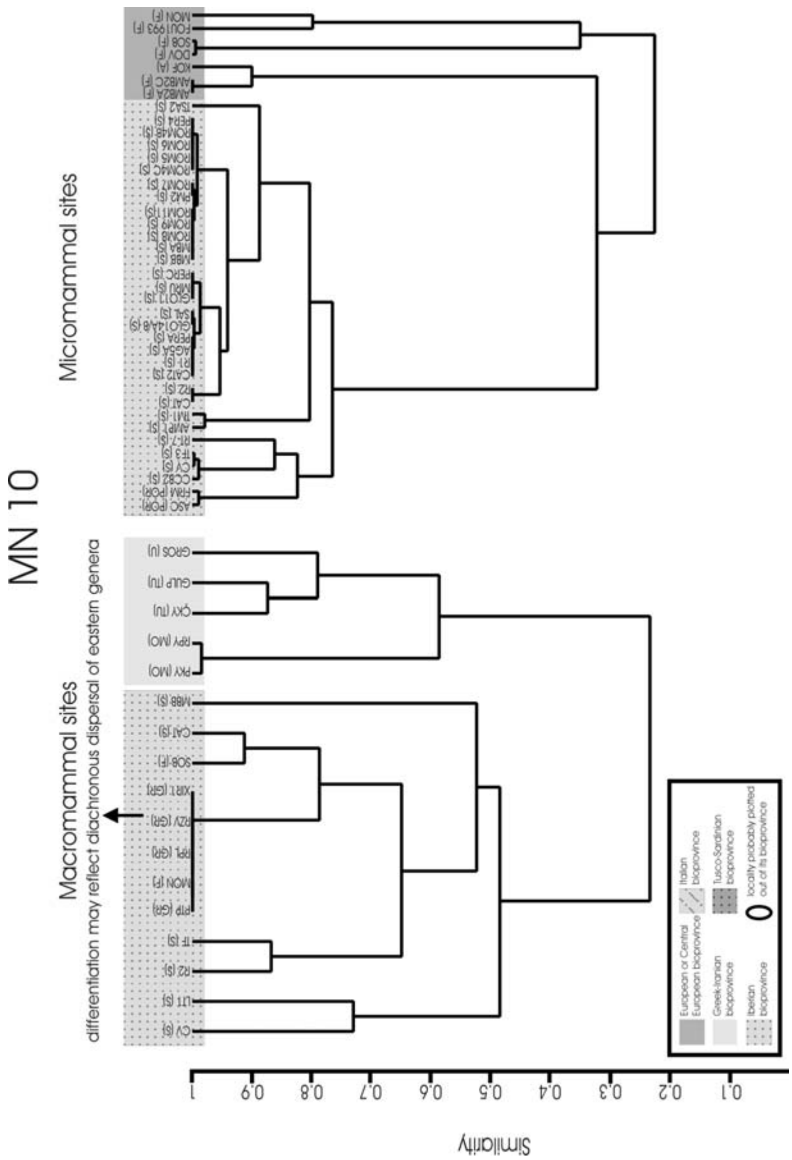

Fig. 4. Dendrogram displaying the results of cluster analysis for MN 9 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

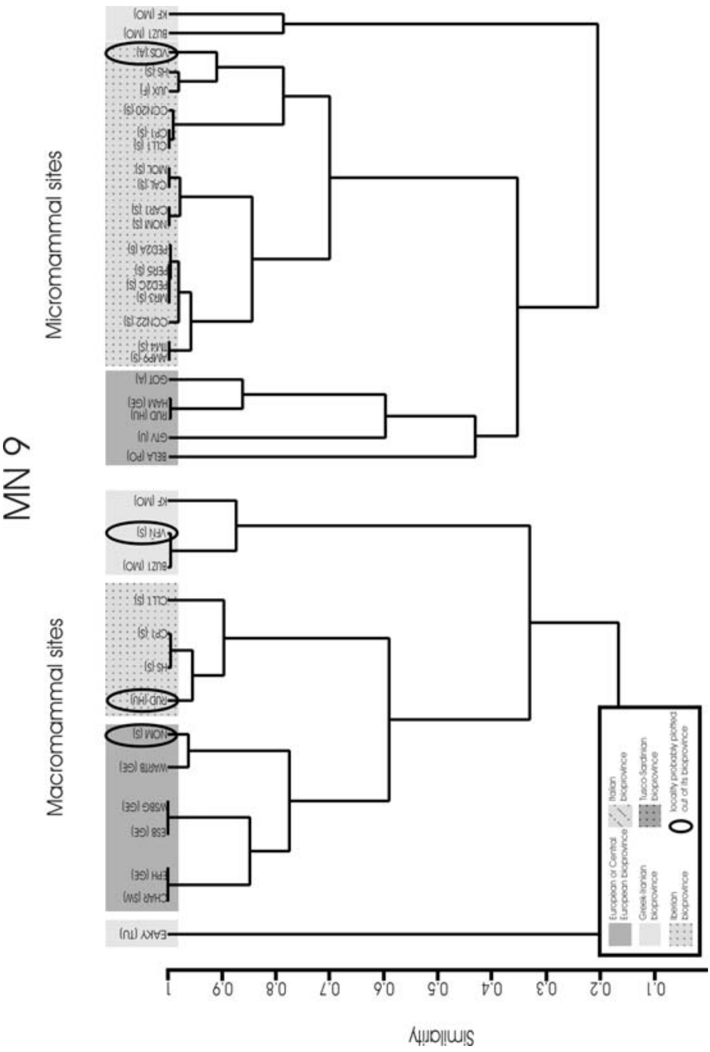

Fig. 5. Dendrogram displaying the results of cluster analysis for MN 10 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

Rodent faunas in the Iberian province are very poor and mice (Muridae) have replaced cricetids being the most abundant rodents in the majority of the sites. The Muridae evolved during the mid-Miocene in Asia, and entered Europe by MN 9. The first occurrence of the Muridae *Progonomys* in Turkey is dated at 10.135 Ma (Kappelman et al. 2003), but it needed about 0.4 Ma to reach Spain (it appears at 9.7 Ma in the Vallès-Penedès Basin (Garcés et al., 1996)). After their arrival in Spain the mice will characterize the rodent assemblage and evolve into several endemic genera during the Vallesian and the Turolian.

Similarity between Greek and Turkish macromammal assemblages increased during MN 11 (Fig. 6) with the arrival into Greece of open-country Bovoidea and Giraffidae. The cercopithecid monkeys (*Mesopithecus*) and the proboscidean *Choerolophodon* accompanied these artyodactyls in their dispersal. These open-country faunas will be characteristic of the Greek-Iranian province during the whole Turolian. The analysis clearly distinguishes an Iberian province with impoverished macromammal faunas. There is a third province very different from the remaining, the Central European one. The persistence of many forest-adapted families (tragulids, tapirids) and the absence of open-country Bovoidea is the main criterion to distinguish its faunas. Considering micromammals, the Greek-Iranian province is represented by the poor fauna of Lefkon (Greece, LK in Fig. 6) including exclusively eastern genera. The faunas of Central Europe appear as clearly different from the Iberian ones and are characterized by a still diverse fauna including several Gliridae and Sciuridae, plus some mice, beavers and cricetids with prismatic teeth. The faunas from Dorn Dürkeheim (Germany) and Sümeg (Hungary) (DDURK (GE) and SUG (HU) in Fig. 6) may appear so different because of their very diverse faunas including many forest-adapted genera. The rodent faunas of the Iberian province are very poor and characterized by the murids *Parapodemus*, *Occitanomys* and *Huerzelerimys*. Minor components of the fauna include modern cricetids (Cricetinae of the genus *Kowalskia*) and the Cricetodontini (*Hispanomys*). A new fourth group appears, the Tusco-Sardinian province, which presents bizarre insular faunas (for recent synthesis see Rook et al. 1999; Moyà-Solà et al. 1999a; Bernor et al. 2001) and cluster apart of all other sites.

The highest degree of similarity in macromammal faunas from the Greek-Iranian and the Iberian provinces is attained at MN 12 (Fig. 7), when eastern faunas attain their maximum range. However, some differences still exist, and the bovid diversity in Western Europe is much lower. The insular fauna from the Tusco-Sardinian province continued evolving isolated from the continent. The micromammal sites cluster shows the same provinces recognized in MN 11, Iberian rodent faunas being still very poor. The Central European record disappears at MN 11, so the persistence of a Central European province cannot be confirmed.

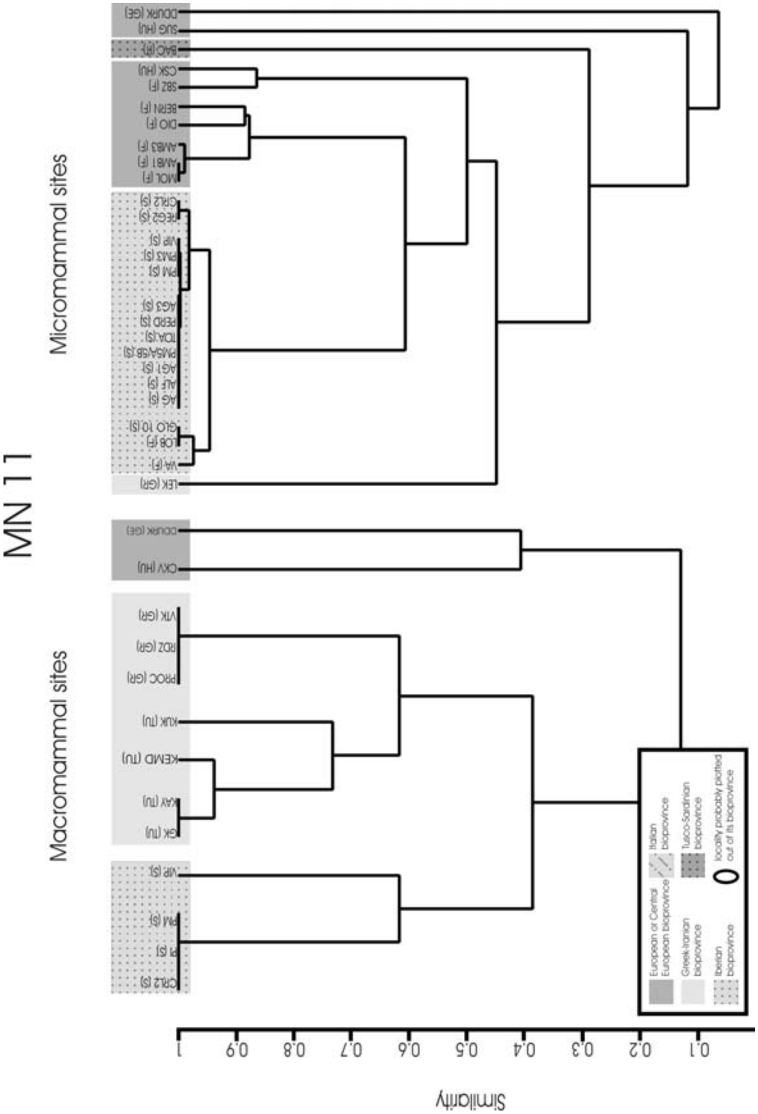

Fig. 6. Dendrogram displaying the results of cluster analysis for MN 11 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

The situation is going to change in the Messinian (MN 13, Fig. 8) and provinces will increase their differences. The macromammal cluster clearly shows three provinces: Iberian, Greek-Iranian and a new Italian province. The Iberian province is characterized by its low diversity, except in the case of the locality of Venta del Moro (VMOR (S) in Fig. 8) which is slightly differenced from the others. This site records the dispersal into Spain of the canids of the genus *Nyctereutes* and camelids (*Paracamelus*) from North America. The relatively poor fauna from Gravitelli (Italy, GRA (IT) in Fig. 4) may explain well why it appears so close to Spanish sites. The Greek-Iranian province is only represented by Greek sites with a diverse bovid and giraffid fauna inherited from the Turolian. The Italian faunas appear rather different from the ones of the remaining sites. The Tusco-Sardinian province and its bizarre insular faunas disappeared when Italy became part of the continent during the Messinian, so the differences observed are not an insularity effect. The Italian province includes three sites (four if we consider that Gravitelli is not plotted in its province) showing a clear Central European influence, so they include many taxa present in Central Europe during MN 11, but absent from rest of provinces since MN 10 (*Tapirus*, *Euprox*, Moschidae) as well as the exclusively Central European proboscidean *Zygolophodon*. The macromammal community is completed with few immigrants from other areas such as *Mesopithecus* and elements that are going to characterize the Pliocene (*Parabos*, *Korynochoerus* (= *Propotamochoerus*), *Nyctereutes*). The presence of many MN 11 relicts may support the existence of a Central European province at least until the end of the Miocene. Many genera from Central Europe would have arrived into Italy when it became part of main land. The micromammal faunas also show the existence of an Italian province, characterized by the presence of some Gliridae (*Muscardinus*), beavers and mice. By MN 13 the rabbits and hares (Leporidae) appear in all micromammal faunas of Europe. The Leporidae evolved in North America and dispersed into Eurasia during the Messinian, but they did not replace the Ochotonidae (the Lagomorph family including pikas) since the Pleistocene. It should be noted that the French micromammal fauna of Lissieu (LIS (FR) in Fig. 8) includes a considerable diversity of cricetids with prismatic teeth, Muridae, Eomyidae, Zapodidae and dormice, that seems closer to the Italian sites than Spanish ones. However the assignment of this site to the Italian province is doubtful. A Greek-Iranian province is also recognized by the cluster, characterized by the absence of some Western mice genera and by the presence of gerbils, beavers, ground and flying squirrels, absent in most of Western sites.

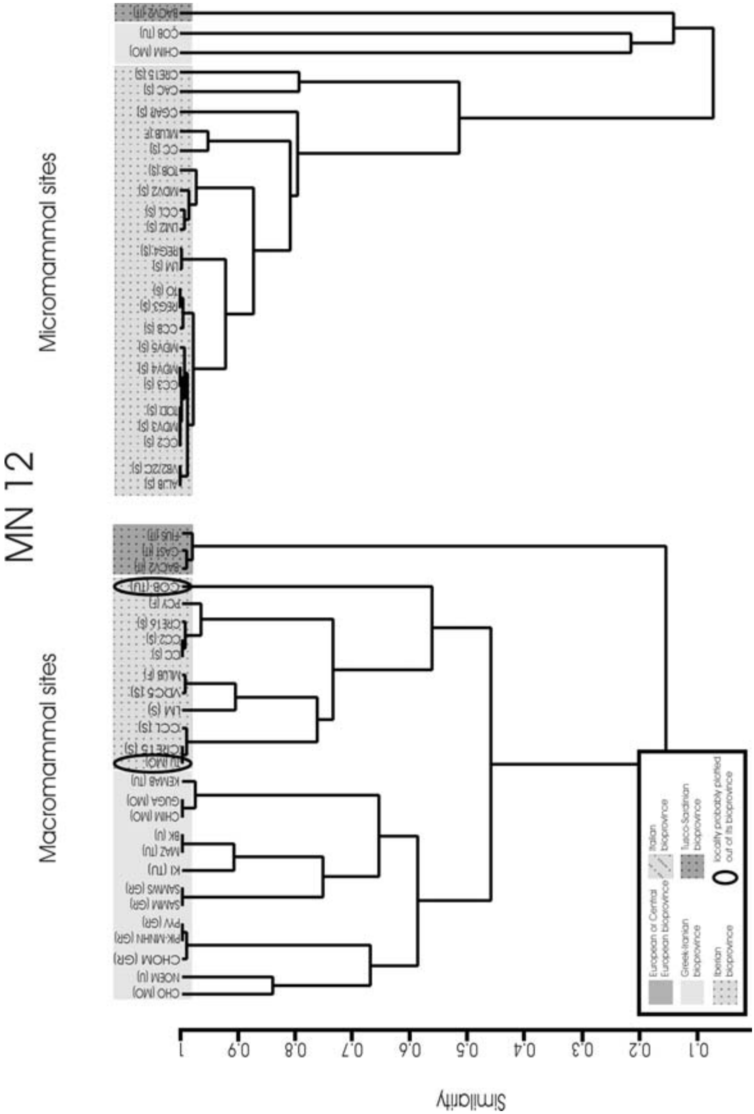

Fig. 7. Dendrogram displaying the results of cluster analysis for MN 12 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

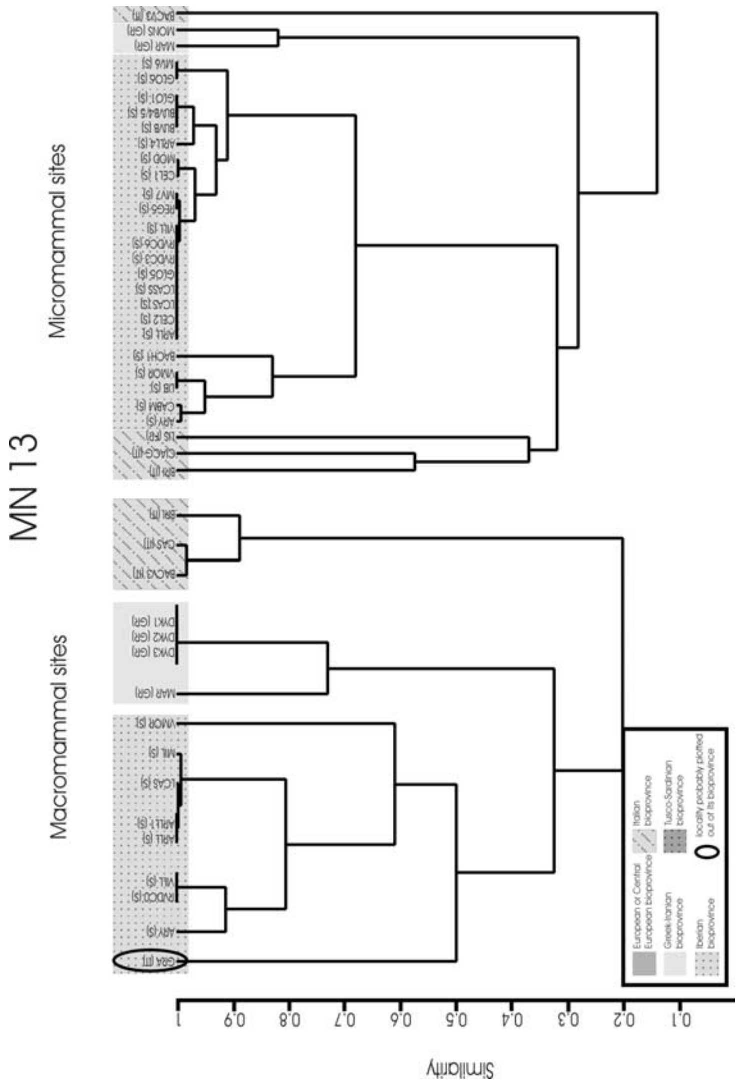

Fig. 8. Dendrogram displaying the results of cluster analysis for MN 13 micro and macromammal sites. Key to locality codes is given in the appendix, whereas key to country codes is given in Table 2

The Iberian bioprovince still persists but it is divided in two biogeographic regions (Levant and Central Iberia). Levant sites (Venta del

Moro, Casablanca M, Librilla, etc.) exhibit a diverse fauna including several Muridae, Gerbillidae (of Asian or African origin, see Agustí 1989; Geraads 1998) ground squirrels and (in a few cases) beavers. The sites from central Spain are characterized by poor faunas dominated by mice (*Castillomys*, *Stephanomys*, *Apodemus*, *Occitanomys*, *Castromys*) and very hypsodont endemic Cricetodontini (*Ruscinomys*), while beavers and squirrels are very rare and gerbils are absent.

9.5.2 Diversity

We have estimated diversity as well as origination and extinction rates for the whole study area and for selected squares. We have only selected squares containing a moderately rich mammal record covering at least five MN zones without temporal gaps in the range. Only three squares suit the criteria (see Fig. 1 and Table 1): 12, 13 and 24. Thus we could only consider Northern Spain plus Southern France and Central Europe. In order to include SE Europe we have summed squares 8 and 9 to obtain a moderately rich macromammal record ranging from MN 6 to MN 12. However, we would like to compare areas of the same surface, so if we take two squares for SE Europe, we would have to take also two squares for the other areas compared. We have summed squares 12 and 13 and obtained a continuous record including both macromammals and micromammals covering the whole time span. Note that squares 12 and 13 include most of European localities in every MN zone. We have also considered square 24, and added the adjacent square 25. This results in a rather complete Central European micro and macromammal record that lasts until the MN 11.

Total number of genera (N_{TOT}) in Europe is shown in Fig. 9A. Macromammals show two diversity peaks: MN 9 and MN 12. These peaks are also associated with an abrupt increase in the number of singletons (N_{FL}), especially in the case of the MN 12. MN 13 shows a moderate decrease although N_{FL} keeps increasing. The lowest values of diversity are attained at MN 6 and MN 10 representing the loss of about 30 genera. MN 10 minimum coincides with a decrease in N_{FL}, whereas this is not the case in the MN 6 lowest. Micromammals increase diversity until their optimum at MN 7 + 8 and afterwards a fall in diversity starts. This loss is moderate until MN 11 but at MN 12 N_{TOT} abruptly falls to its minimum values. Micromammals would have lost close to 30 genera from MN 7 + 8 to MN 12. A moderate recover takes place at MN 13, and N_{TOT} reaches values similar to those of MN 11. Decrease in N_{TOT} coincides with a progressive decrease in N_{FL} and the abrupt fall observed in MN 12 is associated with the absence of singletons in this zone.

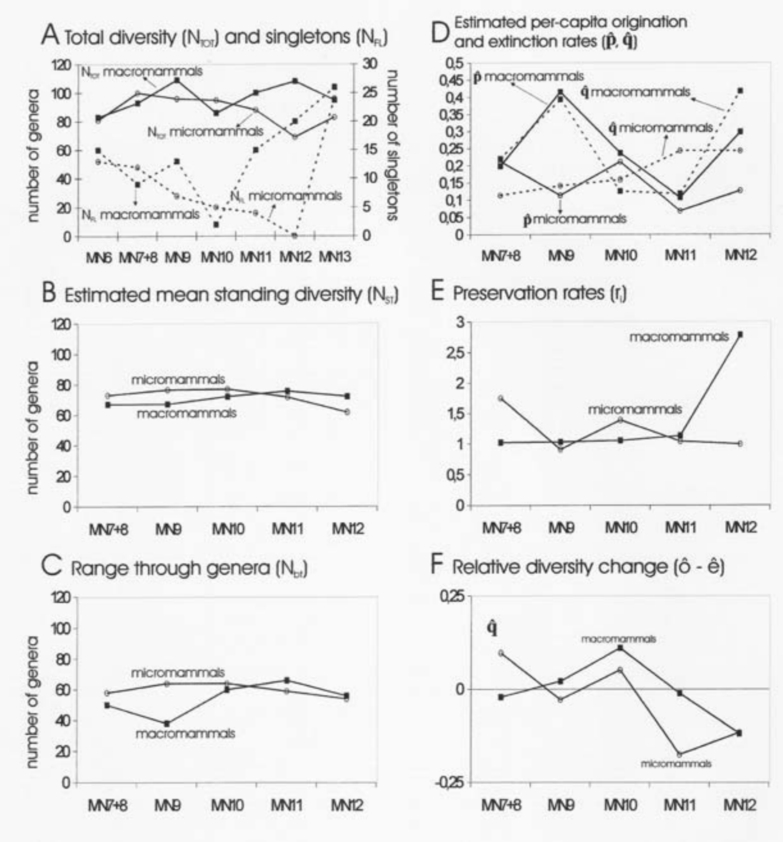

Fig. 9. Diversity and taxonomic and preservation rates plots for the whole study area (see text for details). A) Total diversity (N_{TOT}) and singletons (N_{FL}); B) Estimated mean standing diversity (N_{ST}); C) Range through genera (N_{bt}); D) Estimated per-capita origination and extinction rates ($\hat{p}$, $\hat{q}$); E) Preservation rates (r_i); F) Relative diversity change ($\hat{p}$ minus $\hat{q}$). Plots display results for macromammals and micromammals. For results of correlation test between N_{ST}, $\hat{p}$, $\hat{q}$ and r_i see Table 2

The apparent recovery in MN 13 coincides with a spectacular increase in $N_{FL.}$ If we exclude singletons from our calculations and estimate mean standing diversity, the situation changes considerably (see Fig. 9B). The apparent diversity crisis that affected macromammals at MN 10 disappears, and their diversity gradually increases until a peak in MN 11. Afterwards N_{ST} remains approximately the same. The loss of genera concerning to micromammals appears less marked but still exists. Micromammal diversity reaches its maximum at MN 9 – MN 10, and afterwards decreases until a minimum at MN 12. Thus, a diversity crisis seems to have affected micromammal genera in Europe although it occurred in the Turolian rather than in the Vallesian. Nevertheless, as we have seen, Spanish sites represent most of the European micromammal record, so we should consider to what extent these results are affected by this fact.

Figure 10A show N_{TOT} and N_{FL} of macromammals and micromammals respectively for the selected squares 8 + 9 (labeled as Turkey), 12 + 13 (labeled as SW Europe), and 24 + 25 (labeled as Central Europe). In SW Europe, N_{TOT} of micro and macromammals has its higher values at MN 7 + 8 and MN 9 respectively. Afterwards diversity starts a moderate decrease in the case of macromammals while micromammals loose genera faster. Macromammal N_{TOT} keeps falling until MN 13 with a slight recover at MN 12. Micromammals had lost about 30 genera since MN 7 + 8, but an important recover took place at MN 13 and N_{TOT} attained values similar to those of MN 9. Increases in N_{TOT} in micromammals are associated with increases in the number of singletons, while in the case of macromammals this pattern is not so clear and only the extreme low values of N_{TOT} at MN 11 coincide with extreme low values of N_{FL}. When considering N_{ST} in SW Europe (see Fig. 10B) the picture changes only a little. Macromammals loose diversity gradually from MN 7 + 8 until they reach a minimum at MN 10, afterwards there is a slight recover at MN 11 to continue falling during MN 12. Micromammals were very diverse at MN 9 and afterwards diversity decreased gradually at higher rate than macromammals during the whole time span.

The existence of a diversity crisis starting at MN 10 (or maybe earlier in the case of macromammals) seems clear in SW Europe. This crisis affected all land mammal communities but its effects were probably more severe on micromammals. Central Europe and Turkey show lower values of diversity than SW Europe, but this is almost certainly and effect of the quality of the record, which is clearly best in SW Europe. Central European record unfortunately disappears in MN 11, but if the Vallesian Crisis at MN 10 affected all Europe it should be detected. This crisis is apparent, and N_{TOT} of macromammals shows an abrupt decrease in MN 10, while micromammals reduced their diversity earlier, at MN 9. In both cases there is a quick recover afterwards.

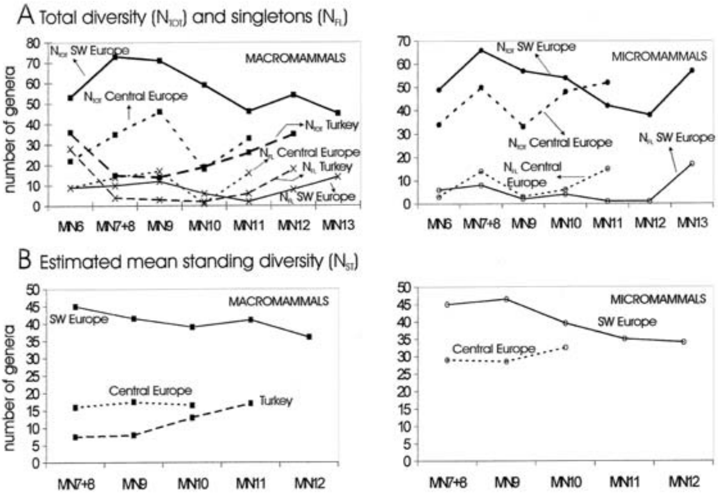

Fig. 10. Diversity calculated for selected squares: SW Europe (squares 12 + 13), Central Europe (squares 24 + 25) and Turkey (squares 8 + 9) (see text for details). A) Total diversity (N_{TOT}) and singletons (N_{FL}); B) Estimated mean standing diversity (N_{ST}). Plots display results for macromammals and micromammals. For results of correlation test between N_{ST} and r_i see Table 2

Changes in N_{TOT} are clearly associated with changes in N_{FL} during the same zones. Moreover the decrease in the number of singletons observed at MN 9 and MN 10 is related with a decrease in the number of localities relative to previous time spans. Thus, these apparent falls are most probably an effect of completeness and should be removed if singletons are excluded from the analysis. This is what we have done by computing N_{ST} (see Fig. 10B), and results evidence these undesirable effects of a poor record.

Macromammal diversity remains more or less stable, while micromammals even increase their diversity during MN 10, showing opposite trends than SW Europe. We could only consider macromammals in the case of Turkey, but the trends observed in this area are very different from those seen in SW and Central Europe. N_{TOT} has high values at MN 6 but abruptly falls to its minimum at MN 7 + 8, afterwards diversity gradually recovers until a new maximum at MN 12. Note that the trends show by N_{TOT} clearly follow those of N_{FL} (Fig. 10A) but in this case they are not associated with a significant decrease in the number of sites. Removing the singletons we obtain the same pattern: diversity in Turkey is low during MN 7 + 8 and MN 9 and afterwards gradually increases. It seems that a diversity crisis could have occurred in Turkey, but it happened during the late Aragonian, about 3 Ma earlier than in SW Europe.

We have tested for correlation between N_{ST} and preservation rate (r_i) in Europe and the selected areas (see Figs. 9E and 11C respectively) using Kendall's τ (see Table 3). In every situation the effects of r_i over N_{ST} are not statistically significant but the probability of correlation is high (about 0.4 in all cases). When considering the whole macromammal record in Europe this probability increases to 0.9. So in any case effects of preservation and quality of the record should be taken on account.

9.5.3 Origination and Extinction rates

Figure 9C shows the number of genera that range through the entire MN zone (N_{bt}) for all Europe. Macromammal N_{bt} is surprisingly low during MN 9, and quickly recovers afterwards. Micromammal N_{bt} decay gradually from MN 10 onwards. These patterns are also observed in all squares (results not presented), and this fact points to the existence of an important macromammal turnover at MN 9 in contrast to a more gradual micromammal turnover starting at MN 10. Figure 9D shows origination and extinction rates for Europe, and both rates increase spectacularly during MN 9 in the case of macromammals. Then an important decrease in both rates follows and they rise again in MN 12, although this time extinctions outnumber originations and reach their higher values. Micromammal originations reach their maximum values at MN 7 + 8 and MN 10, but there is a first minimum at MN 9. Afterwards a gradual increase in extinctions occurred until MN 11, when there is an abrupt rise associated with a decrease in originations. In MN 12 extinctions stopped their increase and the origination rate rose. We have tested for correlation between rates and r_i (see Fig. 9E and Table 3) in every situation and results show that both variables are not correlated in any case. For macromammals in both situations Kendall's τ is 0, so variables are totally uncorrelated.

Table 3. Results of correlation test between standing diversity (N_{ST}), origination ($\hat{p}$) and extinction ($\hat{q}$) rates with preservation rate (r_i). Kendall's τ and probability of being uncorrelated is given for macromammals and micromammals in each area and the whole continent (see text for details)

Area		N_{ST}		ô		ê	
		τ	p(unc.)	τ	p(unc.)	τ	p(unc.)
Europe	macromammals	0.67	0.10	0.00	1.00	0.00	1.00
	micromammals	0.10	0.79	0.60	0.14	-0.20	0.62
SW Europe	macromammals	-0.20	0.62	0.20	0.62	0.40	0.33
	micromammals	-0.20	0.62	0.60	0.14	0.00	1.00
Central Europe	macromammals	-0.33	0.60	0.33	0.60	0.33	0.60
	micromammals	0.00	1.00	0.33	0.60	1.00	0.00
Turkey	macromammals	0.18	0.71	-1.00	0.00	0.33	0.50

However, these surprisingly good results are probably an effect of the few points included in the calculations: the fewer points the test finds perfect no correlation if the two variables are not very correlated. On the contrary if variables are strongly correlated, few data points will result on perfect positive or negative correlations and an absolute value of 1 for τ. In our particular situation we assume that our variables are nearly uncorrelated. In the case of micromammals there is no statistically significant correlation between $\hat{p}$ and r_i but results are not so good and probably origination peaks of MN 7 + 8 and MN 10 are partly due to an increase in r_i. In the case of micromammal $\hat{q}$ correlation is negative ($\tau = -0.2$). If variation in $\hat{q}$ was dominated by changes in r_i, τ should be large and positive, so in this last situation we also conclude that micromammal preservation and extinction rates are nearly uncorrelated.

Origination rates have their maximum values at MN 10 for SW Europe and Turkey in the case of macromammals (Fig. 11A) and decrease to a minimum in MN 11. A moderate increase is seen in SW Europe during MN 12. Central Europe shows a peak in originations at MN 9 coinciding with the peak seen when considering Europe as a whole, which otherwise is not evident in Turkey and SW Europe. The existence of this peak of macromammal $\hat{p}$ in the European record is due to the existence of high rates in Central Europe plus moderately high rates in Turkey and SW Europe. The decrease seen in MN 11 is mostly due to the decay in $\hat{p}$ seen in these two areas during this zone. Micromammal $\hat{p}$ reached its maximum values at MN 7 + 8 in SW Europe, and decrease significantly during MN 9. Finally it recovered at MN 10. Central Europe shows the same trends than lower latitudes but the increase in originations in MN 10 was more marked. The Central European record disappears at MN 11 but in Spain data show that $\hat{p}$ decreased during the following intervals.

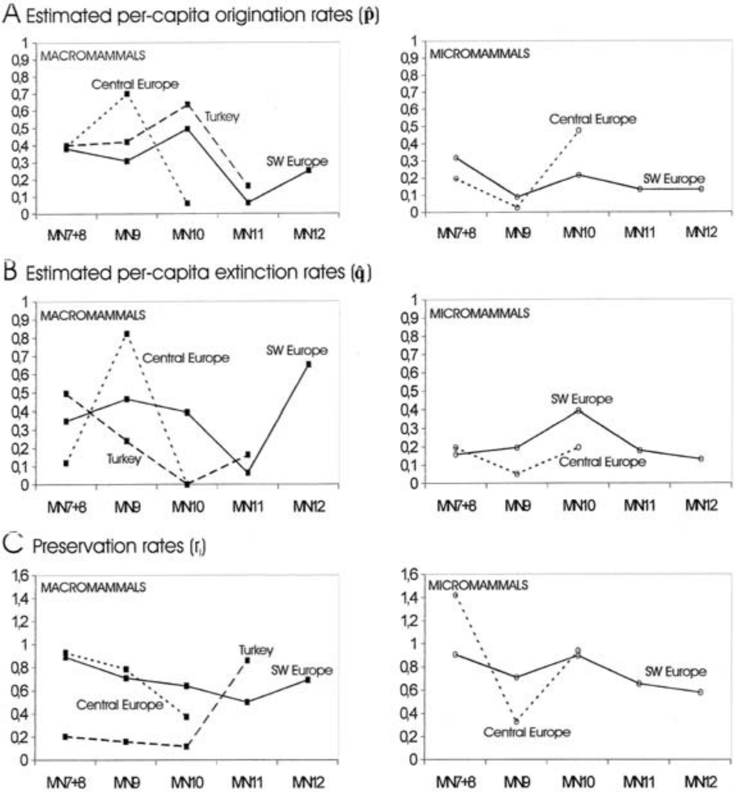

Fig. 11. Taxonomic and preservation rates calculated for selected squares: SW Europe (squares 12 + 13), Central Europe (squares 24 + 25) and Turkey (squares 8 + 9) (see text for details). A) Estimated per-capita origination rate ($\hat{p}$); B) Estimated per-capita extinction rate ($\hat{q}$); C) Preservation rates (r_i). Plots display results for macromammals and micromammals. For results of correlation test between $\hat{p}$, $\hat{q}$ and r_i see Table 2

The pulse in macromammal $\hat{p}$ seen in Europe in MN 9 (Fig. 9D) is associated with a pulse in $\hat{q}$. As Fig. 11B shows, this pulse in $\hat{q}$ only occurred in Central Europe, and only a moderate increase in $\hat{q}$ took place in SW Europe. $\hat{q}$ decreased in Turkey. However, the values of this rate were rather high in all regions, so they result in a peak when the whole of Europe is considered. $\hat{q}$ fell to 0 in Turkey and Central Europe during MN 10, while in SW Europe there was only a slight decrease. In SW Europe extinctions have their minimum at MN 11, when Turkish macromammal $\hat{q}$ increase again. In MN 12 $\hat{q}$ increase abruptly in Spain having a maximum of 0.65. Note that most of macromammal data from MN 12 and MN 13 are from central Spain, so the increase in $\hat{q}$ seen in Europe in MN 12 partly results from the local increase in $\hat{q}$ in Spain during this interval. In the case of micromammals (Fig. 11B) plots for Central Europe $\hat{q}$ are depressed at MN 9, and in MN 10 rise to approximately the same value they had before. In SW Europe there was an abrupt increase in $\hat{q}$ in MN 10 and a decrease immediately afterwards. The increase in $\hat{q}$ seen in Europe during MN 11 and MN 12 may be attributable to the absence of other micromammal records in other areas than SW Europe. As in previous calculations we have tested for correlation between $\hat{p}$, $\hat{q}$ and r_i using Kendall's τ (see Table 3). Correlation is not statistically significant in any case except for macromammal $\hat{p}$ in Turkey (0.04) and micromammal $\hat{q}$ in Central Europe where test detects perfect positive correlation ($\tau = 1$). In Turkey correlation is negative ($\tau = -1$), and if changes in $\hat{p}$ where related to variations in r_i these value should be high and positive, so significant correlation has to be ruled out.

9.5.4 Biogeographical stability and its consequences during the late Miocene mammal turnover

The Spanish record is the most complete mammal record for the late Miocene (Alba et al. 2001, calculated the completeness of the Spanish Neogene mammal record in the means of Foote and Raup (1996) and showed that completeness was even higher than some marine records), so this fact is going to influence the whole European record. The graphs for diversity and rates in Europe (Fig. 9) resemble those of southwestern Europe (Figs. 10 to 12), especially in the case of micromammals. Thus, events taking place only in the Iberian Peninsula may also be expressed when considering Europe as a whole.

There are three main bioprovinces maintained during most of the time span: Iberian (plus southern France), Central European and Greek-Iranian provinces (see Figs. 2-8). The existence of the Greek-Iranian province is well known (Tobien 1967), but the division of western Europe in two bioprovinces is a new point of view (althoug Fortelius et al. 1996) recognized some degree of differentiation in southwestern Europe during the late Miocene). During the middle Miocene the two western provinces were not very different and they even may constitute a single province characterized by a high diversity of forest-adapted mammals. Levels of diversity during MN 7 + 8 (see Fig. 10B) are the highest of the considered period (the differences of diversity between central and southwestern Europe are probably an artifact of completeness). In contrast the faunas from Turkey exhibit low levels of diversity (Fig. 10B).

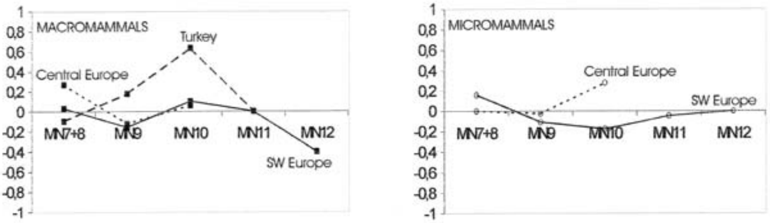

Fig. 12. Relative diversity change ($\hat{p} - \hat{q}$) calculated for selected squares: SW Europe (squares 12 + 13), Central Europe (squares 24 + 25) and Turkey (squares 8 + 9) (see text for details)

The Iberian province is hardly distinguished from the Central European one in the macromammal cluster (Fig. 2), evidencing a similar environment in both areas. During the late middle Miocene the Central European paleovegetation record shows a progressive decrease in evergreen woody taxa and an increase in deciduous ones, resulting in associations comparable to modern mixed mesophytic forests (Kovar-Eder 2003). The progressive cooling during the early Middle Miocene led to the disappearance of megathermic taxa and the *Avicennia* mangrooves of southwestern Europe (Bessedik et al. 1984). Palynological data from the Duero Basin (Spain) dated as MN 7 + 8 (after García-Moreno 1987) indicates the presence of a moderately open woodland and also wet areas including many hydrophilous elements (*Typha*, *Sparganium*, *Magnolia*) (Rivas-Carballo and Valle 1986). Thus, the environment was relatively warmer and more opened in Spain than in Central Europe. The vegetation of the Greek-Iranian province was more similar to Central Europe during the early / early-middle Miocene (on the Balkan Peninsula and Evia Island, see Kovar-Eder 2003). As the Western Mediterranean it included some sclerophyllous taxa together with some evergreen genera present in Central Europe in preceeding periods (*Platanus neptuni*, *Calocedrus*). So the biogeographic pattern shown by mammals (see biogeographical map of the Serravallian in Fig. 13) is also observed when the vegetation is considered. Fortelius et al. (2002, 2003) used mean hypsodonty in Eurasian macromammal sites as a proxy of mean annual precipitation. Their maps for the Middle Miocene show the existence of two areas of different mean hypsodonty corresponding to the two well known Greek-Iranian and Western European province, while the Iberian province cannot be distinguished (Fortelius et al. 2003).

During MN 7 + 8 taxonomic rates in the case of macromammals were moderate in Western Europe ($\hat{q}$ in Central Europe is very low, see Fig. 11B), while in the case of micromammals were rather high. Originations exceeded extinctions resulting in an increase in micromammal diversity (Fig. 10B). This fact may be explained because of the minor environmental change affecting forest environments all over Europe. These small changes would have created new microhabitats and fragmented the populations favoring ecologically induced genealogical events (sensu Vrba 1985). Regarding the macromammals, habitat heterogenity was not so important as to induce any turnover. The macromammal extinction rates in Turkey are considerably high (Fig. 11B), while originations (Fig. 11A) equal those of the other provinces. This fact explains the relatively low diversity recorded in the area, and may reflect some opening of the mid Miocene forests, which led to an important turnover in herbivore faunas.

The beginning of the late Miocene (MN 9) is characterized by a progressive decrease in the $\hat{p}$ rates in all the provinces (except for macromammals in Central Europe, see Fig. 11 A), while extinctions increased in central and southwestern Europe (Fig. 11 B). The moderate decrease in $\hat{p}$ and the increase in $\hat{q}$ in southwestern Europe (mainly Spain) resulted in a decline in macromammal diversity. This did not occur in the case of micromammals, which maintained their diversity (althoug extinctions were also high). The macrofloral remains recovered in the Vallès-Penedès Basin and adjacent areas (Spain) records the appearance of broad-leafed deciduous taxa such as *Acer tricuspidatum* and *Platanus leucophylla* (Sanz de Siria 1993, 1994). However some subtropical genera (*Ficus*, *Sabal*) survived during the latest MN 9 in the same area. The environment in Spain may have been less forested during the lowermost Vallesian (Fortelius et al. 1996; Casanovas-Vilar and Agustí submitted). A brief recovery in humidity is seen prior to the early/late Vallesian boundary (Van der Meulen and Daams 1992; Casanovas-Vilar and Agustí submitted).

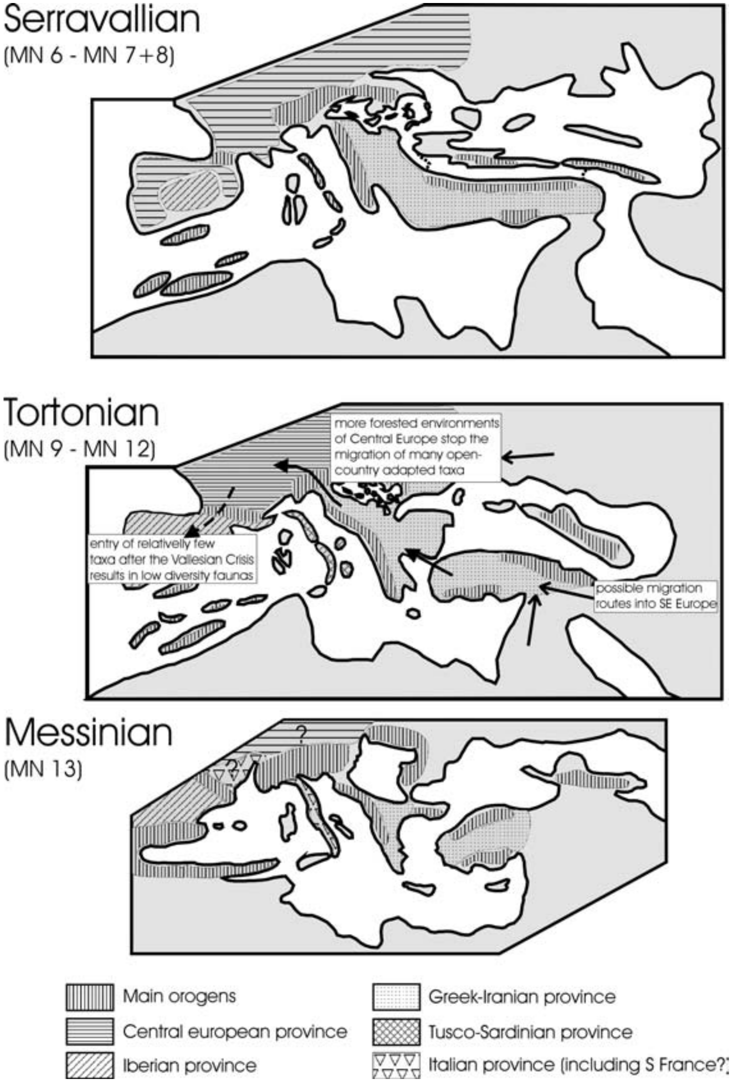

Fig. 13. Paleogeographical maps for the Serravallian, Tortonian (after Rögl 1999, 2001; modified) and Messinian (after Ghetti et al. 2002; modified) showing evolution of the Mediterranean Basin during the studied time-span. Distribution of main orogens and the area covered by identified bioprovinces is also shown (see text for details)

A clear effect of the reduction of the forest cover during the earliest Vallesian is the disappearance from the Spanish record of many forest dwelling rodents, while they are still present in Central Europe where dense mixed mesophytic forests persist (Bernor et al. 1987) (many genera will temporally re-appear by the latest MN 9 in the Vallès-Penedès Basin). The beginning of the fragmentation of forest cover in Spain started at MN 9, coinciding with a major isotopic event (Mi 5) (Miller et al. 1991; also recorded in the Mediterranean by Turco et al. 2001) and a sea level fall of nearly 100 m (Haq et al. 1987). These events, as well as the Tibetan uplift would have produced a high-latitude cooling and a mid-latitude drying, with an increase in wet / dry seasonality in the Mediterranean regions. The increase of seasonality would have favored the development of opened areas, especially in the inner Iberian Peninsula (Casanovas-Vilar and Agustí submitted). The habitat of some micromammals would have been reduced to “patches” of the old middle Miocene forests, while other genera inhabited the new opened areas. In Turkey extinction rates kept lowering while originations remain stable. Bovid diversity continued increasing with both browsing and grazing adaptations being represented, indicating the beginning or the break-up of the forest environments in the region (Bernor et al. 1996).

The Vallesian Crisis is though to coincide with early / late Vallesian boundary (or the boundary between MN 9 and MN 10), but the results (Fig. 10 B) do not show a decrease in diversity in all areas. In fact, diversity only decreased in the Iberian province, especially in the case of the small mammals. In Central Europe remained stable (with an slight increase in the case of micromammals) and in Turkey diversity start increasing. In southwestern Europe the important micromammal turnover implies a rising in $\hat{p}$ and $\hat{q}$, but the increase in the number of extinctions was higher (Fig. 11 A and B). The per-capita macromammal origination rates in this region rose following the pattern seen in Turkey, so large mammal diversity stopped decreasing. The Vallesian Crisis also coincides with an isotopic event (Mi 7 in Miller et al. 1991), although it is not so marked as the preceding Mi 5 and Mi 6. However, during the late Vallesian global temperature kept decreasing while the changes in atmospheric circulation due to the Tibetan uplift (Kutzbach et al. 1993) intensified wet / dry seasonality at low latitudes. The rodent record from different basins of Spain shows this increase in seasonality that would have led to the onset of the characteristic dry season of the Mediterranean climate (Van Dam and Weltje 1999; Casanovas-Vilar and Agustí submitted). This change in seasonality would have favored the replacement of cricetids by murids in the inner Peninsula (Van Dam 1997).

However, in the northern basins rodent communities were rather different and this seasonality in humidity was accompanied by an increase in the seasonality in temperature (Casanovas-Vilar and Agustí submitted). The late Vallesian floras from the Vallès-Penedès Basin (NE Spain) (Sanz de Siria 1997; Agustí et al. 2003) include a 45 % of deciduous trees (*Acer*, *Alnus*, *Fraxinus* and others) and a 15 % of drier, sclerophyllous pre-Mediterranean elements (*Quercus ilex*, *Quercus praecursor*) confirming the presence of the two kinds of seasonality. However, these floras record the persistence of a "hard core" of evergreen trees (close to 33 %). Pollen from deciduous trees is also the most abundant in the palynological record of the Duero Basin (NW Spain) (Rivas-Carballo and Valle 1986). The "patches" of the Middle Miocene forest would have reduced even more, and the composition of this forest would have changed, evergreen trees being outnumbered by deciduous ones. The forest-adapted mammals would have been confined to this "patches", but finally those became too small and the mammals could not maintain their populations, thus being locally extinct. The effects would have been greater in the small mammals, because of their reduced migration capability, while many large mammals migrated to more suitable environments. The fauna of Dorn Dürkheim (MN 11, Germany) includes a number of forest-adapted forms that migrated from the Greek-Iranian and the Iberian provinces (Franzen and Storch 1999) Figures 10B, 12 show a sharp decrease in micromammal diversity and a moderate decrease and recovery in macromammals. Some macromammals, unable to tolerate a seasonality in temperature would have disappeared. This is the case of the hominoid primate *Dryopithecus* and the pliopithecids. These primates needed whole-year availability of fruits, so they could not migrate to higher latitudes and were trapped in the "patches" of southern forests (Andrews 1992; Fortelius and Hokkanen 2001; Agustí et al. 2003), the combinated effect of the increasing reduction of those and the progressive substitution of evergreen by deciduous trees brought hominoids to the extinction in Europe. The survival of the hominoid *Oreopithecus bambolii* in the Turolian faunas of Tuscany and Sardinia is consequence of the insular conditions of this geographic area at that time. The peculiar trophic adaptations of this primate, consequence of the peculiar selective pressures of insular ecosystems, allowed this hominoid to tolerate the effect on vegetation trophic resources of seasonality (Köhler and Moyà-Solà 1996; Moyà-Solà et al. 1999b; Köhler and Moyà-Solà 2003).

The same events that caused the Vallesian Crisis in southwestern Europe affected extensive areas of the Old World, but their effects on the land mammal communities were different. In Turkey diversity started increasing as a result of a minimum in extinction rates (Fig. 11B) and a maximum in originations (Fig. 11A). This fact reflects the radiation of open-country bovids and giraffids that is going to characterize the Turolian in the Greek-Iranian province. The reduction of forest in southeastern Europe, had opposite effects than in the Iberian Peninsula, allowing the migration of many taxa of Asian or African origin. Why did many of those genera not arrive into Spain? Migrations of some large mammals into all European regions, such as the hipparionine horses or the bovid *Tragoportax*, were quick events taking no more than 1 million years length. In contrast, many eastern open-country mammal taxa failed to disperse into Western Europe (Koufos 2003). Large areas of southwestern and Eastern Europe (De Bonis et al. 1992) were covered by open woodlands, then why we do not find the same open-country mammals in both areas? One hypothesis might be that some orogens such as the Alps or the Pyrenees acted as important barriers for migration. However, palynologic data have shown that the high of these reliefs was much lower during the Miocene (Pérez-vila et al. 2001), thus they would not have constituted effective barriers. It seems more logical that the persistence of humid and forested environments in Central Europe (Fortelius et al. 2002, 2003) may have acted as an ecological filter, so only ubiquist taxa (for instance *Tragoportax*, *Microstonyx*) could cross it and successfully arrive into the Iberian Peninsula (see the biogeographical map for the Tortonian on Fig. 13). This situation would persist during the Turolian.

By the Turolian, mammal diversity in the Iberian province keeps declining (Figs. 10, 12), this was first caused by a decay in $\hat{p}$ and $\hat{q}$, but in MN 12 extinctions exceed originations (Fig. 11A, B). Again this is an effect of the impossibility of eastern faunas to disperse to southwestern Europe (only few taxa as for example sivatherine giraffids, some species of *Gazella* and *Protoryx*, probably ubiquist taxa, reached the Iberian Peninsula during the Turolian), plus the extinction of the last forest-dwelling relicts (*Dorcatherium*, *Micromeryx*, *Lucentia*). It is surprising that an endemic open-country fauna did not develop in the Iberian Peninsula during the Turolian. This could be because macromammal populations were not deeply fragmented, so ecologically induced genealogical events (as exposed by Vrba 1985) did not occur. However, the situation was not the same in the case of micromammals, and a characteristic fauna of mice and hypsodont cricetids developed in the inner basins (although it was not very diverse). The macromammal clusters on Figs. 6 and 7 show an increasing degree of similarity between the Iberian and the Greek-Iranian province during the Turolian. The eastern open-country faunas, covered their maximum geographic range during MN 12. The high similarity results may reflect some degree of aridification of

Central Europe, allowing the dispersal of more eastern herbivores than in preceding periods. Cerling et al. (1997) have provided impressive isotopic evidence for a global vegetational change starting at 8-7 Ma (thus coinciding with the Turolian) and given by the transition from C3 to C4 vegetation. This event presumably occurred earlier at lower latitudes and, although there are no data, C3 vegetation might have appeared in Central Europe by the mid Turolian.

Restoration of the level of provincial diversity is observed again by the end of the Turolian (MN 13, see Fig. 8) when an Iberian, Greek-Iranian and a new Italian province is observed. Italy was a small archipelago during the lower and middle Turolian inhabited by bizarre insular faunas. The connection to main land during the MN 13 led to the extinction of these faunas, and the migration into the new peninsula of faunas showing clear Central European affinities (see previous section). The Messinian (MN 13) records an important recovery of the environmental conditions in the Mediterranean. Floras from the lower part of Komnina Formation (Ptolemais Basin, Greece) generally indicate continuously humid and warm climatic conditions (Kloosterboer-van Hoeve et al. 2000). The early Messinian deposits of the Velona Basin (central Italy) have yielded a palynological record interpreted as unstable shallow lacustrine/marshy environment, rich in aquatic vegetation, surrounded by swamps dominated by Taxodiaceae and uplands dominated by warm temperate deciduous forest (Ghetti et al. 2002). However, the Iberian Peninsula is still characterized by a low diversity of macromammals (including few immigrants, such as *Paracamelus* and few African forms such as *Hexaprotodon* and *Macaca*), suggesting that the Central European forest filter kept working until the Pliocene (see the biogeographical map for the Messinian on Fig. 13). Fortelius et al. (2002, 2003) have shown the persistence of a high mean annual precipitation zone in Central Europe during the Pliocene, which would explain the maintenance of the forest filter. However, Iberian micromammal fauna was enriched with the entry of some immigrants of Asian or African origin, during the “Messinian Salinity Crisis”. This event led to the dessecation of the Mediterranean because of the tectonic closing of its western gateway during the latest Miocene.

Although open, savanna-like environments persisted in southeastern Europe, no new occurrences are recorded in Greek sites by MN 13. Furthermore, many of the taxa that characterized the Turolian in the province (the giraffids, *Adcrocuta*, *Choerolophodon*, *Microstonyx*, *Tragoportax*, *Prostrepsiceros*) will not cross the Miocene / Pliocene boundary and will be replaced by a new macromammal comunity including *Parabos*, *Sus*, *Paracamelus* and *Korynochoerus* (= *Propotamochoerus*) amongst others (Koufos 2003).

9.5.5 Epilogue: This view of the European late Miocene

The several climatic and phisiographic events that punctuated the late Miocene (Mi 6, Mi 7 peaks, Himalayan and Tibetan uplift, intensification of seasonality, decrease of mean global temperatures because of first Artic glaciations), had different effects depending on the area. For instance, the Vallesian Crisis (as defined by Agustí and Moyà-Solà 1990) was not a continent-wide event, and it only affected southwestern Europe. In the Iberian bioprovince we see an evident decrease of mammal diversity from MN 9 to MN 10, which is especially evident in the case of micromammals (Fig. 10B). However mammal diversity started to decline earlier (see Fig. 12), in MN9, when extinctions exceed originations (Fig. 11A, B). Then the crisis is not an abrupt event marking a boundary between early (MN 9) and late Vallesian (MN 10), instead it reflects a more gradual process of environmental deterioration. The main climatic change was the onset of seasonality in both humidity and temperature. This crisis coincided with an increase in diversity in Turkey, with the entry of many open-country Bovoidea and Giraffidae, while in Central Europe is little changed, and micromammals even increased their diversity (Fig. 10B). Fortelius et al. (1996) and Franzen and Storch (1999) identified the Vallesian Crisis in Central Europe, but there is no evidence of it when mean standing diversity is considered, so we think that this identification is an undesirable effect of using absolute countings of taxa in their calculations (as we have shown, the number of records in Central European MN 10 is very low compared with MN 9 and MN 11).

The only phenomenon we detect is a diversity crisis in the Iberian province product of its geographical position at the southwestern margin of Europe, and the persistence of forested environments in Central Europe acted as an ecological filter for eastern open-country mammal faunas (which would have prospered in the Iberian environments, probably fairly close to Greek and Turkish ones, that are situated in similar latitudes, if they had arrived). The Iberian Peninsula did not become a "small species factory" and did not developed an autochthonous open-country herbivore fauna. This situation persisted during the Turolian, thus explaining the low diversity of the Iberian faunas (Fig. 10B). Diversity increased in southeastern Europe as a result of the entry of many eastern taxa. The eastern immigrants attained their maximum geographical range to the west during the Turolian, coinciding with the transition from C3 to C4 vegetation (Cerling et al. 1997), which could have resulted in some opening of the canopy in Central Europe. Provinciality increased again in the Messinian, with a higher segregation of the three provinces. Italy, which had been a small archipelago during most of the Turolian, was joined to the continent and a mammal community with clear Central European affinities replaced the bizarre insular faunas.

As we have shown, climatic changes, correlate well with main faunal changes in Europe. This was not the case in the North American mammal record (Alroy et al. 2000), where some climatic changes are correlated with mammal turnovers while others are not. On the other side of the Atlantic, Central Europe is characterized by overall stability, while on the Mediterranean region climatic changes especially affected mammal faunas. This difference can be explained because of the different geography of both continents, the complex distribution of emerged lands in Europe prevented habitat tracking. The presence of the Paratethys at the East, and the Mediterranean at the South, increased the probability for taxa of being trapped in one of the Mediterranean peninsulas. The only connection with Africa was through Anatolia (except in the MN 13 interval), so when climate changed, many taxa preferring warm forest environments could not migrate to lower latitudes because they had to cross Central Europe which stopped their dispersal. By its side, Anatolia was invaded for new Asian and African immigrants, resulting in an increase in diversity in that area. The situation in North America is very different, because habitat tracking is not stopped by barriers such as the Mediterranean. The connections of North America with other continents during the late Miocene occurred during important climatic changes (such as the sea level lowering of 100 m at the mid / late Miocene boundary), but were brief and most of the time the continent was isolated, implying the entry of fewer immigrants in the area.

9.5.6 Data availability

The whole database used in this work is available from the first author under request. Additional tables and calculations (diversity, taxonomic rates) are also available.

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Appendix

Key to localities included in the clusters from Figs. 2 to 8. Most of the localities and their respective ages are taken from the NOW database. Presence of micro or macromammals is indicated by “X”. Each locality is assigned to one of the squares that appear in Fig.1.

Locality code	Locality	Country	Age	Macrom.	Microm.	Square
AG(S)	Los Aguanaces	Spain	MN11		X	12
AG1(S)	Los Aguanaces 1	Spain	MN11		X	12
AG5(S)	Los Aguanaces 5	Spain	MN11		X	12
AG5A(S)	Los Aguanaces 5A	Spain	MN10		X	12
ALC2(S)	Alcocer 2	Spain	MN7+8		X	12

ALF(S)	Alfambra	Spain	MN11		X	12
AMB1(F)	Ambérieu 1	France	MN11		X	23
AMB2A(F)	Ambérieu 2A	France	MN10		X	23
AMB2C(F)	Ambérieu 2C	France	MN10		X	23
AMB3(F)	Ambérieu 3	France	MN11		X	23
AMP1(S)	Ampudia 1	Spain	MN10		X	12
AMP9(S)	Ampudia 9	Spain	MN9		X	12
ANW(SW)	Anwil	Switzerland	MN7+8	X	X	24
ARLL(S)	Arquillo	Spain	MN13	X		12
ARLL1(S)	Arquillo 1	Spain	MN13	X	X	12
ARLL4(S)	Arquillo 4	Spain	MN13		X	12
ARM7(S)	Armantes 7	Spain	MN6		X	12
ARVL(S)	Arroyo del Val	Spain	MN6	X		12
ARY(S)	Arenas del Rey	Spain	MN13	X	X	2
ATVK(MO)	Atavaska	Moldova	MN9	X		28
BAC(IT)	Baccinello V0	Italy	MN11		X	15
BACH1(S)	Bacochas 1	Spain	MN13		X	2
BACV2(IT)	Baccinello V2	Italy	MN12	X	X	15
BACV3(IT)	Baccinello V3	Italy	MN13	X	X	15
BAL(HU)	Baltavas	Hungary	MN13	X		26
BALL(S)	Ballestar	Spain	MN9	X		13
BAY(TU)	Bayraktepe 1	Turkey	MN7+8		X	10
BCV1(S)	Barranc de Can Vila 1	Spain	MN7+8		X	13
BDR15(SW)	Bois de Raube 15	Switzerland	MN7+8		X	24
BELA(PO)	Belchatow A	Poland	MN9		X	37
BERN(F)	Bernardière	France	MN11		X	24
BK(U)	Belka	Ukraine	MN12	X		39
BOJ(S)	Borjas 1	Spain	MN6		X	12
BRI(IT)	Brisighella	Italy	MN13	X	X	15
BUV4/5(S)	Bunker de Valdecebro 4/5	Spain	MN13		X	12
BUVB(S)	Bunker de Valdecebro B	Spain	MN13		X	12
BUZ1(MO)	Buzhor 1	Moldova	MN9	X	X	28
Ç0B(TU)	Çobanpinar	Turkey	MN12	X	X	19

ÇA(TU)	Çandir	Turkey	MN6	X	X	9
CABM(S)	Casablanca M	Spain	MN13	X	X	13
CAC(S)	Casa del Acero	Spain	MN12		X	12
CAF(S)	Can Feliu	Spain	MN7+8	X	X	13
CAL(S)	Casas Altas	Spain	MN9		X	12
CAR1(S)	Carrilanga 1	Spain	MN9		X	12
CAS(IT)	Casino	Italy	MN13	X		15
CAST(IT)	Casteani	Italy	MN12	X		15
CAT(S)	La Cantera	Spain	MN10	X	X	12
CAT2(S)	La Cantera 2	Spain	MN10		X	12
CB(S)	Castell de Barberà	Spain	MN7+8	X	X	13
CC(S)	Concud	Spain	MN12	X	X	12
CC2(S)	Concud 2	Spain	MN12	X	X	12
CC3(S)	Concud 3	Spain	MN12		X	12
CCB(S)	Concud B	Spain	MN12		X	12
CCB2(S)	Can Casablanques 2	Spain	MN10		X	13
CCL(S)	Concud Barranco	Spain	MN12	X	X	12
CCN20(S)	Creu Conill 20	Spain	MN9	X	X	13
CCN22(S)	Creu Conill 22	Spain	MN9		X	13
CEL1(S)	Celadas 1	Spain	MN13		X	12
CEL2(S)	Celadas 2	Spain	MN13		X	12
CGAR(S)	Cerro de la Garita	Spain	MN12	X	X	12
CHAR(SW)	Charmoille	Switzerland	MN9	X		24
CHIM(MO)	Chimishlija	Moldova	MN12	X	X	28
CHO(MO)	Chobruchi	Moldova	MN12	X		28
CHOM(GR)	Chomateres	Greece	MN12	X		7
CHRY(GR)	Chrysavgi	Greece	MN7+8		X	17
CIACG(IT)	Ciabot Cagna	Italy	MN13		X	14
CKV(HU)	Csakvar	Hungary	MN11	X	X	26
ÇKY(TU)	Çorak Yerler	Turkey	MN10	X		20
CLL1(S)	Can Llobateres 1	Spain	MN9	X	X	13
CM(S)	Can Missert	Spain	MN7+8	X	X	13
CNAB(F)	Castelnau-d'Arbieu	France	MN6	X		13
COM1(RO)	Comanesti 1	Romania	MN7+8		X	27
CP1(S)	Can Ponsic 1	Spain	MN9	X	X	13

CRE15(S)	Crevillente 15	Spain	MN12	X	X	2
CRE16(S)	Crevillente 16	Spain	MN12	X		2
CRL2(S)	Crevillente 2	Spain	MN11	X	X	2
CV(S)	Ceràmiques Viladecavalls	Spain	MN10	X	X	13
DDURK(GE)	Dorn Dürkheim	Germany	MN11	X	X	24
DIN(GE)	Dinotheriensande	Germany	MN9	X		24
DIO(F)	Dionay	France	MN11		X	24
DOV(F)	Douvre	France	MN10		X	24
DUD1(S)	Duredos 1	Spain	MN6		X	12
DYK1(GR)	Dytiko 1	Greece	MN13	X		17
DYK2(GR)	Dytiko 2	Greece	MN13	X		17
DYK3(GR)	Dytiko 3	Greece	MN13	X		17
EAKY(TU)	Esme Akçaköy	Turkey	MN9	X		8
EPH(GE)	Eppelsheim	Germany	MN9	X		24
ESB(GE)	Esselborn	Germany	MN9	X		24
ESC(S)	Escobosa	Spain	MN7+8	X	X	13
FIUS(IT)	Fiume Santo	Italy	MN12	X		15
FOU1993(F)	Lo Fournas 1993	France	MN10		X	13
FRM(POR)	Freiria do Rio Maior	Portugal	MN10		X	11
FU(F)	Four	France	MN6	X	X	13
GBG(A)	Gaiselberg	Austria	MN9	X		26
GK(TU)	Garkin	Turkey	MN11	X		8
GLO1(S)	La Gloria 1	Spain	MN13		X	11
GLO10(S)	La Gloria 10	Spain	MN11		X	12
GLO11(S)	La Gloria 11	Spain	MN10		X	12
GLO14A/B(S)	La Gloria 14A/B	Spain	MN10		X	12
GLO5(S)	La Gloria 5	Spain	MN13		X	11
GLO6(S)	La Gloria 6	Spain	MN13		X	11
GOT(A)	Götzendorf	Austria	MN9	X	X	26
GRA(IT)	Gravitelli	Italy	MN13	X		6
GROS(U)	Grossulovo	Ukraine	MN10	X		28
GTV(U)	Gritsev	Ukraine	MN9		X	28
GUGA(MO)	Gura-Galben	Moldova	MN12	X		28

GULP(TU)	Gülpinar	Turkey	MN10	X		9
HAM(GE)	Hammerschmiede	Germany	MN9	X	X	24
HAM6C(GE)	Hambach 6C	Germany	MN6	X	X	34
HAU(F)	Haulies	France	MN6	X		13
HI(S)	Hostalets de Pierola inferior	Spain	MN7+8	X	X	13
HOW(GE)	Höwenegg	Germany	MN9	X		24
HS(S)	Hostalets de Pierola superior	Spain	MN9	X	X	13
HZ(HU)	Hasznos	Hungary	MN7+8		X	26
I(F)	Isere	France	MN7+8		X	13
JUX(F)	Jujurieux	France	MN9		X	14
KAY(TU)	Kayadibi	Turkey	MN11	X		8
KEMAB(TU)	Kemiklitepe A-B	Turkey	MN12	X		8
KEMD(TU)	Kemiklitepe D	Turkey	MN11	X		9
KF(MO)	Kalfa	Moldova	MN9	X	X	28
KHF(A)	Klein Hadersdorf	Austria	MN6	X		26
KI(TU)	Kinik	Turkey	MN12	X		9
KOF(A)	Kohfidisch	Austria	MN10		X	26
KUK(TU)	Küçükçekmece	Turkey	MN11	X		19
LCAS(S)	Las Casiones	Spain	MN13	X	X	12
LCASS(S)	Las Casiones superior	Spain	MN13		X	12
LCAT(S)	La Cantera	Spain	MN11	X		12
LEK(GR)	Lefkon	Greece	MN11		X	17
LGSA(F)	La Grive St. Alban	France	MN7+8	X	X	13
LIB(S)	Librilla	Spain	MN13		X	2
LIS(F)	Lissieu	France	MN13		X	13
LM(S)	Los Mansuetos	Spain	MN12	X	X	12
LM2(S)	Los Mansuetos 2	Spain	MN12		X	12
LOB(F)	Lobrieu	France	MN11		X	13
LP5B(S)	Las Planas 5B	Spain	MN6		X	12
LP5H(S)	Las Planas 5H	Spain	MN7+8		X	12
LP5K(S)	Las Planas 5K	Spain	MN6		X	12
LP5L(S)	Las Planas 5L	Spain	MN6		X	12
LT1(S)	La Tarumba 1	Spain	MN10	X		13

MACH1(S)	Manchones 1	Spain	MN6		X	12
MAR(GR)	Maramena	Greece	MN13	X	X	17
MAZ(TU)	Mahmutgazi	Turkey	MN12	X		8
MBA(S)	Masía del Barbo A	Spain	MN10		X	12
MBB(S)	Masía del Barbo B	Spain	MN10	X	X	12
MDV2(S)	Masada del Valle 2	Spain	MN12		X	12
MDV3(S)	Masada del Valle 3	Spain	MN12		X	12
MDV4(S)	Masada del Valle 4	Spain	MN12		X	12
MDV5(S)	Masada del Valle 5	Spain	MN12		X	12
MIL(S)	Milagros	Spain	MN13	X		12
MLUB(F)	Mt. Luberon	France	MN12	X	X	14
MOD(S)	Modorras	Spain	MN13		X	12
MOL(F)	Mollon	France	MN11		X	24
MOL(S)	Molina de Aragón	Spain	MN9		X	12
MON(F)	Montredon	France	MN10	X	X	13
MONS(GR)	Monasteri	Greece	MN13		X	17
MR3(S)	Masía la Roma 3	Spain	MN9		X	12
MRU(S)	Masada Ruea	Spain	MN10		X	12
MV6(S)	Masada del Valle 6	Spain	MN13		X	12
MV7(S)	Masada del Valle 7	Spain	MN13		X	12
NE-SP(SK)	Neudorf-Spalte	Slovakia	MN6	X		26
NOEM(U)	Novaja Emetovka	Ukraine	MN12	X		29
NOM(S)	Nombrevilla	Spain	MN9	X	X	12
OP2(PO)	Opole 2	Poland	MN7+8		X	36
PALL3(S)	Paracuellos 3	Spain	MN6	X		12
PALL5(S)	Paracuellos 5	Spain	MN6	X		12
PCY(F)	Puy Courny	France	MN12	X		13
PED2A(S)	Pedregueras 2A	Spain	MN9		X	12
PED2C(S)	Pedregueras 2C	Spain	MN9		X	12
PER4(S)	Peralejos 4	Spain	MN10		X	12
PER5(S)	Peralejos 5	Spain	MN9		X	12
PERA(S)	Peralejos A	Spain	MN10		X	12
PERC(S)	Peralejos C	Spain	MN10		X	12

PERD(S)	Peralejos D	Spain	MN11		X	12
PFH(POR)	Pero Filho	Portugal	MN6		X	1
PI(S)	Piera	Spain	MN11	X		13
PIK-MNHN(GR)	Pikermi-MNHN	Greece	MN12	X		7
PKY(MO)	Poksheshty	Moldova	MN10	X		28
PLAK(GR)	Plakia	Greece	MN7+8		X	7
PM(S)	Puente Minero	Spain	MN11	X	X	12
PM2(S)	Puente Minero 2	Spain	MN10		X	12
PM3(S)	Puente Minero 3	Spain	MN11		X	12
PM5A/5B(S)	Puente Minero 5A/5B	Spain	MN11		X	12
POSAT(POR)	Póvoa de Satarém	Portugal	MN6		X	1
POU-CAY(F)	Poudenas-Cayron	France	MN7+8	X		13
PREZ(SE)	Prebreza	Serbia	MN6	X		17
PROC(GR)	Prochoma	Greece	MN11	X		17
PRZ2(PO)	Przeworno 2	Poland	MN7+8	X		36
PTP(GR)	Pentalophos	Greece	MN10	X		17
PYV(GR)	Pyrgos Vassilissis	Greece	MN12	X		7
R1(S)	La Roma 1	Spain	MN10		X	12
R2(S)	La Roma 2	Spain	MN11	X	X	12
RDZ5(GR)	Ravin des Zouaves 5	Greece	MN11	X		17
REG2(S)	Regajo 2	Spain	MN11		X	12
REG3(S)	Regajo 3	Spain	MN12		X	12
REG4(S)	Regajo 4	Spain	MN12		X	12
REG5(S)	Regajo 5	Spain	MN13		X	12
ROM11(S)	Masía de la Roma 11	Spain	MN10		X	12
ROM4B(S)	Masía de la Roma 4B	Spain	MN10		X	12
ROM4C(S)	Masía de la Roma 4C	Spain	MN10		X	12
ROM5(S)	Masía de la Roma 5	Spain	MN10		X	12
ROM6(S)	Masía de la Roma 6	Spain	MN10		X	12
ROM7(S)	Masía de la Roma 7	Spain	MN10		X	12
ROM8(S)	Masía de la Roma 8	Spain	MN10		X	12
ROM9(S)	Masía de la Roma 9	Spain	MN10		X	12

RPL(GR)	Ravin de la Pluie	Greece	MN10	X		17
RPY(MO)	Respopeny	Moldova	MN10	X		28
RT-7(S)	Rubí-Terrassa 7	Spain	MN10		X	13
RUD(HU)	Rudabánya	Hungary	MN9	X	X	27
RUMK(SW)	Rümikon	Switzerland	MN6	X	X	24
RVDC0(S)	Rambla de Valcecebro 0	Spain	MN13	X		12
RVDC3(S)	Rambla de Valcecebro 3	Spain	MN13		X	12
RVDC6(S)	Rambla de Valcecebro 6	Spain	MN13		X	12
RZV(GR)	Ravin des Zouaves 1	Greece	MN10	X		17
SAL(S)	La Salle	Spain	MN10		X	12
SAMM(GR)	Samos Main Bone Beds	Greece	MN12	X		8
SAMWS(GR)	Samos White Sands	Greece	MN12	X		8
SAN(S)	Santiga	Spain	MN9	X		13
SANS(F)	Sansan	France	MN6	X	X	12
SBZ(F)	Saint Bauzille	France	MN11		X	13
SCHWD(SW)	Schwamendingen	Switzerland	MN6		X	24
SFÇ(TU)	Sofça	Turkey	MN7+8	X	X	9
SGAUVAL(F)	Saint-Gaudens(Valentine)	France	MN7+8	X		13
SIM(F)	Simorre	France	MN6	X		13
SIM2(S)	Simancas 2	Spain	MN6		X	12
SOB(F)	Soblay	France	MN10	X	X	24
SOL(S)	Solera	Spain	MN7+8		X	12
SQ(S)	Sant Quirze	Spain	MN7+8	X	X	13
STAZ(GE)	Stätzling	Germany	MN6	X		25
STEB(GE)	Steinberg	Germany	MN6		X	34
STEIN(GE)	Steinheim	Germany	MN7+8	X	X	25
STSPH(A)	St. Stephan im Lavanttal	Austria	MN7+8	X		25
SUG(HU)	Sümeg	Hungary	MN11		X	26
TF(S)	Torrent de Febulines	Spain	MN10	X		13
TF3(S)	Torrent de Febulines 3	Spain	MN10		X	13
THAN(GE)	Thannhausen	Germany	MN6	X		25
TM1(S)	Torremormojón 1	Spain	MN10		X	12
TM4(S)	Torremormojón 4	Spain	MN9		X	12

TM5(S)	Torremormojón 5	Spain	MN7+8		X	12
TO(S)	Tortajada	Spain	MN12		X	12
TOA(S)	Tortajada A	Spain	MN11		X	12
TOB(S)	Tortajada B	Spain	MN12		X	12
TOC(S)	Tortajada C	Spain	MN12		X	12
TOD(S)	Tortajada D	Spain	MN12		X	12
TOR(S)	Toril	Spain	MN7+8		X	12
TSA2(S)	Tal·lús Sud Autopista 2	Spain	MN10		X	13
TU(MO)	Tudorovo	Moldova	MN12	X		28
UNT(GE)	Unterneul	Germany	MN6		X	25
VA(F)	Valréas	France	MN11		X	13
VAL1(S)	Valalto 1	Spain	MN6		X	12
VAL2B(S)	Valalto 2B	Spain	MN6		X	12
VAL2C(S)	Valalto 2C	Spain	MN6		X	12
VAR(MO)	Varnitsa	Moldova	MN9	X		28
VB2/2C(S)	Villalba Baja 2/2C	Spain	MN12		X	12
VDC5(S)	Valdecebro 5	Spain	MN12	X		12
VF9(S)	Vilafeliche 9	Spain	MN7+8		X	12
VFÑ(S)	Valles de Fuentidueña	Spain	MN9	X		12
VILL(S)	Villastar	Spain	MN13	X	X	12
VIP(S)	Vivero de Pinos	Spain	MN10	X	X	12
VMOR(S)	Venta del Moro	Spain	MN13	X	X	2
VOS(A)	Vösendorf	Austria	MN9	X	X	26
VTK(GR)	Vathylakkos	Greece	MN11	X		17
WARTB(GE)	Wartenberg	Germany	MN9	X		25
WHF(GE)	Westhofen	Germany	MN9	X		24
WLZ(SW)	Wiesholz	Switzerland	MN6		X	24
WSBG(GE)	Wissberg	Germany	MN9	X		24
XIR1(GR)	Xirochori 1	Greece	MN10	X		17
YESK1(TU)	Yeni Eskihisar 1	Turkey	MN7+8	X	X	8
ZEG(SW)	Zeglingen	Switzerland	MN6		X	24