Digging for data

The rise and fall of a Miocene mammal biodiversity hotspot in the Vallès-Penedès (Catalonia, Spain)

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Foreword

As a child I was the biggest Jurassic Park fan. Later on I gradually shifted my focus from the Mesozoic towards the Cenozoic, and from dinosaurs towards mammals. Graduating highschool at seventeen and being a minor still, I was not eligible for certain financial compensation for students. Furthermore, palaeontology as a study appeared non-existent in the Netherlands in 2002, driving me towards Archaeology. After two years of studying, I realised the most interesting part of excavations to me were mostly the pet burials. This led to a switch to Biology, where an internship at Naturalis Biodiversity Center guided me towards small mammal palaeontology, and later on to the location of the Iberian Peninsula, with the Vallès-Penedès as a study area.

After spending over a year in Barcelona, where my love for Catalunya grew, I became increasingly interested in the use of large databases within the field of palaeontology. Funnily enough, statistics were a struggle for me all through university, but as my involvement in the field expanded, so did my expertise. Nowadays colleagues at school sometimes even come to me for advice about this topic.

Even though working as a full time researcher was not the career path for me, helping students and teachers with developing their research skills feels like I found my place in the world. I love being able to guide people to question the world around them in a critical and structural manner and in that way contributing to a better society for future generations.

Anneke Madern

I won’t sit down,
And I won’t shut up,
And most of all I will not grow up.

Oh maturity’s a wrapped up package deal so it seems,
And ditching teenage fantasy means ditching all your dreams.
All your friends and peers and family solemnly tell you you will
Have to grow up, be an adult, be bored and unfulfilled.
Oh but no one’s yet explained to me exactly what’s so great
About slaving 50 years away on something that you hate,
About meekly shuffling down the path of mediocrity;
Well if that’s your road then take it, but it’s not the road for me.

Frank Turner - Photosynthesis

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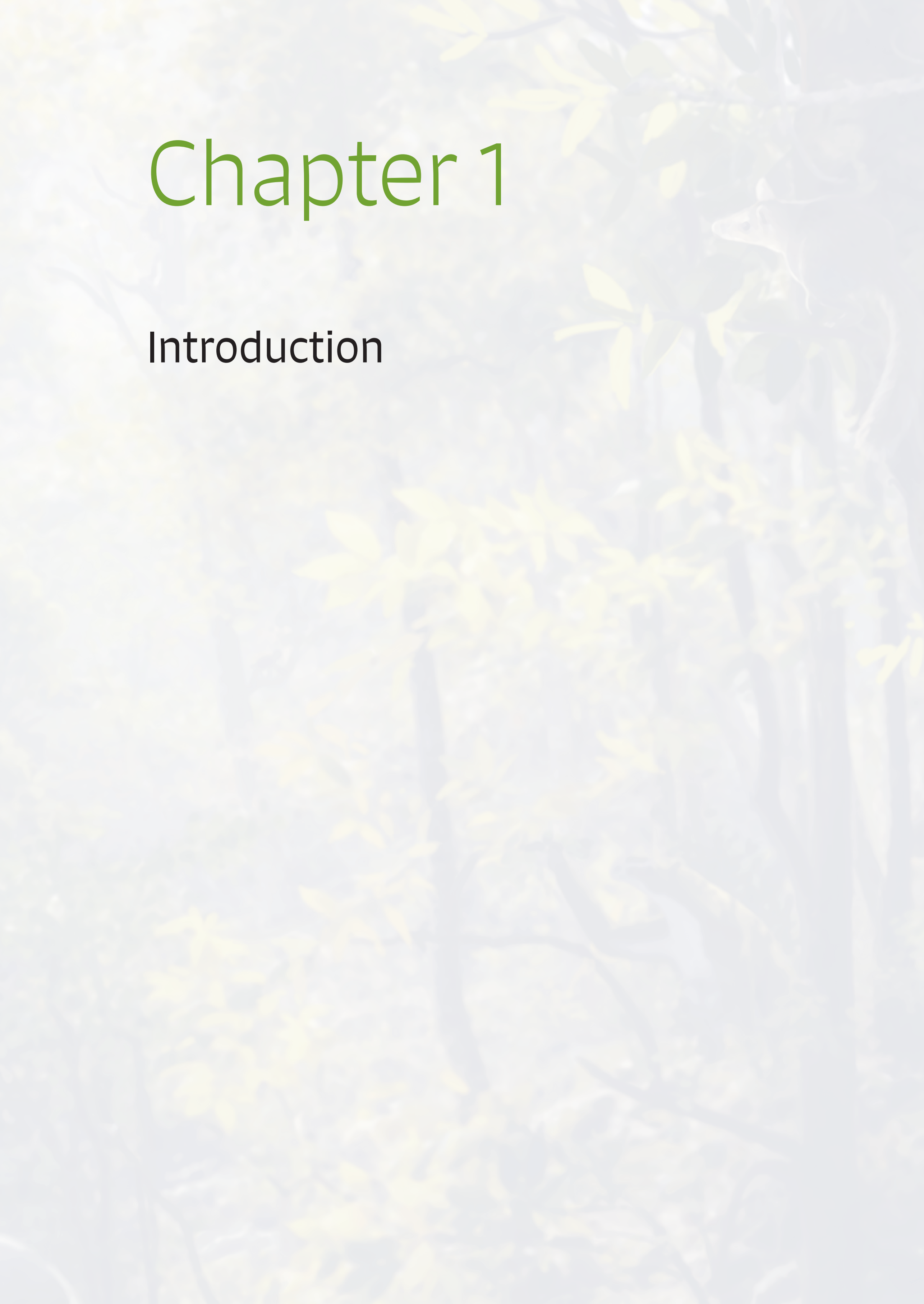

Chapter 1

Introduction

1. Introduction

> ***"A palaeontologist without a collection is lucky, […]***
> ***they are able to see the big picture."***
>
> *(Prof. Dr. Björn Kurten)*

1.1 Palaeontology: a world to explore

Ever since the Jurassic Park movie went into theatres in 1993, generations of kids have grown up loving dinosaurs. This interest in fossils and ancient animals has been solidified in the last decades, with an increasing amount of books and movies on the subject, for both young children and adults. Popular science is a first step towards scientific research and curiosity about the past. Palaeontology is the study of the history of life, leading to questions about the origins of current biodiversity.

Knowledge of the past can help us understand the present and even create expectations for the future of our planet. My nephews, both ages still in the single digits, already know more scientific names of dinosaurs than most people, and sometimes even correct me. Along with their love for animals of the past comes an interest for the world around them. As a highschool biology teacher, I witness the enthusiasm of children and young adolescents on a daily basis. They are inquisitive, curious, and relentless in their quest for knowledge. Students need to develop certain academic skills to be successful in their further studies and careers (Aarts et al. 2021a,b). There is too much focus on a central final exam, jeopardising other skills such as cooperation and learning critical thinking, while these are important for preparing students to become functioning members of society (Inspectie van het Onderwijs 2020).

Critical thinking is essential in today's information society. Being able to weigh different sources of information, discuss its meanings and implications, and coming up with solid conclusions are important abilities. Universities indicate that this critical, inquiring attitude is essential to teaching students other academic skills (Aarts et al. 2021a,b). Torenbeek et al. (2010) showed that different (pre-)academic skills can influence later study progress. A student's critical and inquiring attitude is particularly decisive in this regard.

An interest in palaeontology can be the first step into the right direction, the wrong one leading to science-deniers and ‘alternative facts’ supporters. As a research area, it is inherently multi- and even interdisciplinary, combining knowledge and methodology ranging from mathematics, history, chemistry, biology and computer science to engineering. The proponents of integrated education are convinced that it contributes to more meaningful and attractive education (Beane 1997; Lattuca et al. 2004). There are no defined disciplines in society; problems occur in an interdisciplinary context (Beane 1997; Spelt and Biemans 2007). Students worldwide indicate that they lack overall motivation to learn, while this is critical to learning success (OECD 2022). Lack of academic skills and motivation can result in study delays and dropping out of university (Rooij et al. 2017). Subject integration also provides more motivation for students, as it matches their interests and problems (Boxtel et al. 2009).

Palaeontology focuses on biodiversity through time and space, ultimately leading to a better understanding of evolution and ecology. It encompasses the effects of climate change on life in the past as well as the present and beyond. It illustrates how organisms on Earth are connected to both biotic and abiotic factors around them. Even ethics can be incorporated, when discussing our own impact on the environment.

Overall, a love for palaeontology can be a ‘gateway drug’ to science and ultimately a better understanding of the world and the role we play in it.

1.2 Miocene mammals in crisis

Palaeontology teaches us about biodiversity and the relationship between the biosphere and system Earth. In this thesis, I will focus on a remarkable mammal biodiversity hotspot of the past. Mammals are a representative link to recent ecosystems and thus a valuable object of study.

During the Miocene (23.0 to 5.3 Ma), Europe had a subtropical climate, populated by rhinoceros, forest giraffes, hyenas, tapirs, pandas, sabre-toothed cats and a plethora of unique insectivorans and rodents. It was an epoch with significant changes, both climatologically and biodiversity wise. It is these changes that fascinate most, particularly in a time when climate change and biodiversity crises are the big societal issues of the day.

Major faunal turnovers took place, while land masses gained their present form. Modern mammal groups arose during the Miocene, such as the first bears and dogs as well as antelope and deer (Behrensmeyer et al. 1992; Fortelius et. al 2014; Figueirido et al. 2012). During the Late Miocene, a little over eleven million years ago, the first hipparionine horse entered Eurasia from Northern America via the Bering land bridge, marking the beginning of the Vallesian (Bernor et al. 2021). The name Vallesian derives from its type area, the Vallès-Penedès Basin (near Barcelona, Catalonia, Spain). This time period consists of two Mammal Neogene (MN) units: MN 9, which is the early Vallesian, from 11.2 to 9.7 million years ago, and MN 10, the late Vallesian, from 9.7 to 8.9 million years ago (Casanovas-Vilar et al. 2016a,2016b; Garcés et al. 1996). It is then followed by the Turolian, named after the Spanish inland Teruel Basin (Crusafont Pairó and Truyols 1960; Hilgen et al. 2012).

In the Barcelona area, the Vallès-Penedès Basin has been excavated since the late 19th century, in a long tradition of trying to understand the mammal faunas in these Miocene outcrops. Systematic research started in the 1940's, with an increasing number of new sites being discovered in the basin. The Institut Català de Paleontologia Miquel Crusafont (ICP) in Sabadell currently holds a collection of thousands of vertebrate specimens, mostly mammals. This led to the Vallès-Penedès becoming the reference area for studying European Miocene faunas and the definition of the Vallesian land mammal age on its record, specifically on the locality of Can Llobateres 1 (Crusafont Pairó 1950,1964). Crusafont Pairó (1950) defined the Vallesian faunas as intermediate between the typical faunas of French Sansan and La Grive, and those of the Greek Pikermi fauna. They are characterised by Middle Miocene elements supplemented with the first presence of the extinct horse *Hipparion*, presenting a typical transition between the Aragonian (Middle Miocene) and the Turolian (Upper Miocene) mammal ages.

As the insight in Vallesian faunas increased, adding new sites and reviews of numerous mammal groups, a significant extinction event was recognised during the early Late Miocene (Agustí and Moyà-Solà 1990; Agustí et al. 1984). This 'Vallesian Crisis' was originally recognized by Jordi Agustí and Salvador Moyà-Solà in the 1980's as a local extinction event that coincided with the boundary of the early and late Vallesian, around 9.7 Ma. It is characterised by the disappearance of rodent groups, certain bovids, suids and cervids. At the same time typical Turolian taxa appear.

The Vallesian Crisis did not seem to be restricted to just the Vallès-Penedès and was recognised outside the basin (Agustí and Moyà-Solà 1990; Agustí et al. 1997,1999; Fortelius and Hokkanen 2001; Fortelius et al. 1996). The list of 'victims' of this crisis grew, with for example hominoid primates, certain carnivorans such as the amphicyonids and some perissodactyls, like tapirs. However, a direct climatic cause has proven difficult to identify and it has even been hypothesised that the event has more to do with the complex (and presumably delicate) structure of Vallesian faunas than with major environmental perturbations (Agustí et al. 2013). Casanovas-Vilar et al. (2014) cast some doubt on the severity of the event, demonstrating that for insectivorans and rodents, sampling bias in the Vallesian type area may have played an important role in the perceived drop in biodiversity between the early and late Vallesian.

1.3 Digging in databases (for a biodiversity hotspot)

All over the world, immense quantities of fossil data with their abiotic and biotic contexts are being stored in numerous databases. Some databases have wide scopes, such as the Paleobiology Database (PBDB). Others focus on a specific region or taxonomic group, such as the New and Old World (NOW) database, limiting its input to mammals (McClennen et al. 2017; The NOW Community 2022). Big databases like the NOW-database -celebrating its 25th-year anniversary-, give us the opportunity to recognise the larger patterns through time and space. This allows the reconstruction of dispersal patterns and correlations between certain groups and climatic or geologic events.
Palaeontologists traditionally focus on one specific area or taxonomic group. The risk of specialising in one taxonomic group is to lose sight of the big picture. When studying biogeographical and temporal distribution patterns, more data are needed. Combining all parts of the puzzle on a more meta level makes it possible to look at higher order phenomena in biodiversity, such as biodiversity hotspots. A biodiversity hotspot is a region with a markable high density of different taxa at the same time. In tropical marine ecosystems, for example, the richness and location of these hotspots have changed over time, following a 'Hopping Hotspots' model (Renema et al. 2008; Yasuhara et al. 2022). By tracking down non-random patterns in databases, we can detect these hotspots (Van Welzen et al. 2011) and the timing, location and scope of extinction and turnover events (Eronen 2009; Casanovas-Vilar et al. 2010,2014).

There have been numerous studies surrounding the causes and extent of the Vallesian Crisis. Notably, De Bruijn et al. (1996) and Franzen and Storch (1999) did not find evidence for a Late Miocene biodiversity crisis in Anatolia and Central Europe, respectively. Simultaneously different diversity trends were noted in other regions; during the late Vallesian diversity in fact increased in the eastern Mediterranean (Fortelius et al. 1996; Casanovas-Vilar et al. 2005). However, both studies agree on a severe Vallesian Crisis in at least southwestern Europe. This crisis would have mostly affected small- to medium-sized herbivores and omnivores, as well as small carnivorans (Fortelius et al. 1996; Fortelius and Hokkanen 2001).

This thesis aims to demonstrate the existence of a true biodiversity hotspot in the Vallès-Penedès during the Late Miocene. Even though the Vallesian was a very well sampled time period, this alone cannot explain the high number of taxa found. Therefore, the fossil record reflects a true peak in mammal diversity. Following the components of the hotspot through time and space gives us insight into how the diversity high came into existence. In addition, large data studies can resolve how and to what extent sampling influenced our understanding of the 'Vallesian Crisis', which marks the decline of the hotspot.

1.4 Methodology: biogeography through database analysis

Biodiversity is not simply a matter of the numbers of species. Calculations of sampling probability and richness require quantitative data. Originally focused on mammals of the Neogene of Eurasia, but now covering the Cenozoic worldwide, the NOW is the forerunner in its area, providing a basis for reconstructing biodiversity patterns of the past where mammals are concerned (Fortelius et al. 2002,2022). While previous studies reported a correlation between the observed richness and the number of localities based on various versions and subsets of the NOW database, its coverage is seen as good, especially for the Neogene of Europe (Peláez-Campomanes and Van der Meulen 2009). Thus, to closely approach a true overview of the dispersal patterns of European Miocene mammals, the NOW database is the best available repository.

In order to minimise sampling bias, the quality of the fossil record comes into play. Obviously, this quality is not the same for all mammal groups, with the small mammals being far more common and generally better known than the larger ones. Peláez-Campomanes and Van der Meulen (2009) showed that the coverage for micromammals is better than for the large species. Large mammals are not uncommon at all, but their record is more discontinuous, with important unsampled intervals between the major sites. Therefore, the analyses have to take into account differences in the quality of the record and need to be performed separately for large and small mammals (e.g. Casanovas-Vilar et al. 2010). Uneven distribution in time and space can lead to inflation of diversity peaks or perceived extinction events. The aforementioned Institut Català de Paleontologia is located in Sabadell (near Barcelona, Catalonia, Spain), aiming to expand and conserve Iberian palaeontological knowledge and collections since 1969. An important contribution of the research related to this thesis is that over the course of the last ten years, an extensive update of the ICP collections was carried out, including all large mammal Vallès-Penedès localities, together with contributions and updates of the NOW-database. The ICP will continue this work in the future leading up to establishing the Vallès-Penedès Miocene Vertebrates Paleobiodiversity Database (VPDB). This database will focus on Miocene continental vertebrates from the Vallès-Penedès Basin at the specimen level, making it possible to study palaeobiodiversity dynamics through time (Alba et al. 2022; Casanovas-Vilar et al. in press).

The analyses in this thesis are carried out at the genus level. This has been done for two main reasons: 1) it allows for the inclusion of taxa that are represented by very scarce material, insufficient to identify it to the species level; 2) for most sites comprehensive systematic descriptions have not been published, even though identifications at the genus level are readily available (Casanovas-Vilar et al. 2014). Besides these advantages, genus level analysis subsequently limits the conclusions to exclude patterns at the species level.

Various approaches have been used for this thesis' research. It alternates between focusing on one group of mammals, chronofauna (spatially and temporally restricted animal assemblages) and all mammals. It furthermore uses biodiversity variables such as genus richness or presence/absence data, first and last occurrences, a variety of similarity indices and zooming out to waxing and waning bioprovinces (zoogeographic areas). By alternating the focus it attempts to answer the questions about the nature and origin of the biodiversity hotspot, its composition and extent in order to determine the timing, range and extent of the Vallesian Crisis.

1.5.1 State of the art

This thesis aims to shed some light on the question whether the Vallesian Crisis is an example of the abrupt collapse of a diversity hotspot or a series of Late Miocene extinctions over a longer time interval. Research focusing on the micromammal record by Casanovas-Vilar et al. (2014) showed the potential of combining data from multiple localities through time.

The causes of this alleged crisis are controversial. It does not coincide with any environmental changes, the only thing that has been demonstrated is increased seasonality during the Late Miocene (Agustí et al. 2003; Van Dam 1997; Zachos et al. 2001). Böhme et al. (2008) argued that the transition from a hot and wet 'washhouse' climate to drier times between 9.7 and 9.5 Ma, together with an associated cooling episode, could have triggered faunal turnover (Böhme et al. 2008,2011).

The word 'crisis' suggests an abrupt event. Even though previous studies gave the appearance of exactly this abruptness, the image has become more clear that the late-Vallesian turnover event was more gradual than previously thought (Casanovas-Vilar et al. 2014) and moreso a localised event than a global one (Casanovas-Vilar et al. 2016b).

1.5.2 Going south: Latitudinal change in mammalian biodiversity in Miocene Eurasia

Chapter 2 explores the change of diversity in the Miocene throughout Europe. Many of the forest-adapted taxa present in Central Europe also occur in the Vallès-Penedès, making this basin a transitional zone between the forested environments of northern regions and the more arid landscapes of the inner Iberian Peninsula. By plotting Eurasian Miocene mammal genus richness in grids, we can get a helicopter view into the past and have a go at the origins of the Vallesian biodiversity hotspot. This hotspot appears to be the early Vallesian culmination of a southward trend of the region with the highest diversity, ending at the mid-Vallesian when diversity becomes more equitable over Europe.

1.5.3 The Miocene mammal record of the Vallès-Penedès Basin

Chapter 3 discusses an inventory of the hotspot by means of an updated review of the mammal succession in order to perform time series diversity analyses. Because the fossil record is very uneven, three types of diversity measures were used to assess 'real' diversity. First, just the data as is, the raw data, by using the maximum number of individuals and the number of observed genera. Secondly, we used rarefaction to compare the number of taxa in sites with different sample sizes. We rarified or impoverished the diversity to a minimum sample size of 50 and 100. Thirdly, we used the inferred diversity. We calculated the inferred ranges per genus, by calculating the probability of finding a certain taxon in a certain locality, taking into account the abundance of that genus and the sample size of that locality. Comparing these diversity measures, we tried to see whether the micromammals purported extinction event could be a sampling artefact. Indeed, the difference in abundance of early and late Vallesian localities played a role in our perception of the faunal turnover, which appears to be less abrupt than previously thought.

1.5.4 Iberian micromammals show local extent of Vallesian Crisis

Zooming in on the location of the Crisis, we tried to get a grasp of the severity of the faunal turnover event in chapter 4. As the small mammal record, especially the rodent and insectivoran data, has a much higher resolution than the large mammals, we use these groups to get a high definition look of the Vallès-Penedès basin just before, during and after the Crisis and comparing that to the record of the inland Teruel basin. In our study, we demonstrated that the range and extent of the Vallesian Crisis for this group was largely due to a sampling bias.

1.5.5 Variation in carnivoran distributional responses to the mid-Vallesian faunal turnover

This last chapter, chapter 5, uses a different approach to the genesis of the biodiversity hotspot and the Vallesian Crisis, by focusing exclusively on the carnivorans of Eurasia. Here, we aim to demonstrate whether carnivorans followed their food west or their habitats south.

By using Can Llobateres 1, the Vallesian reference locality, as the basis for a similarity analysis covering the Middle to Late Miocene (16-5.3 Ma) we can show that the origin of this carnivoran chronofauna lies to the north of the Iberian Peninsula, gradually making its way south. Many taxa disappear at the boundary of the early and late Vallesian, but others appear as transients, only appearing in the region during the (early) Vallesian before retracting the range northward. This approach can also be used for future analysis of different groups, to investigate whether they show similar biogeographical patterns.

1.5.6 In conclusion

The past can be fascinating and inspiring. While people might think nature strives for balance, our planet is continuously subject to change. This can teach us about our current and future world, and hopefully inspire generations to come to view nature as important and worthy to conserve and protect. By focusing only on a certain point in time and space, this thesis only makes a small contribution to science. I hope reading it might give you inspiration to ask questions, dig for information, give background to alleged known facts and that it piques your curiosity to explore other lost worlds. Curious, see chapter 6.

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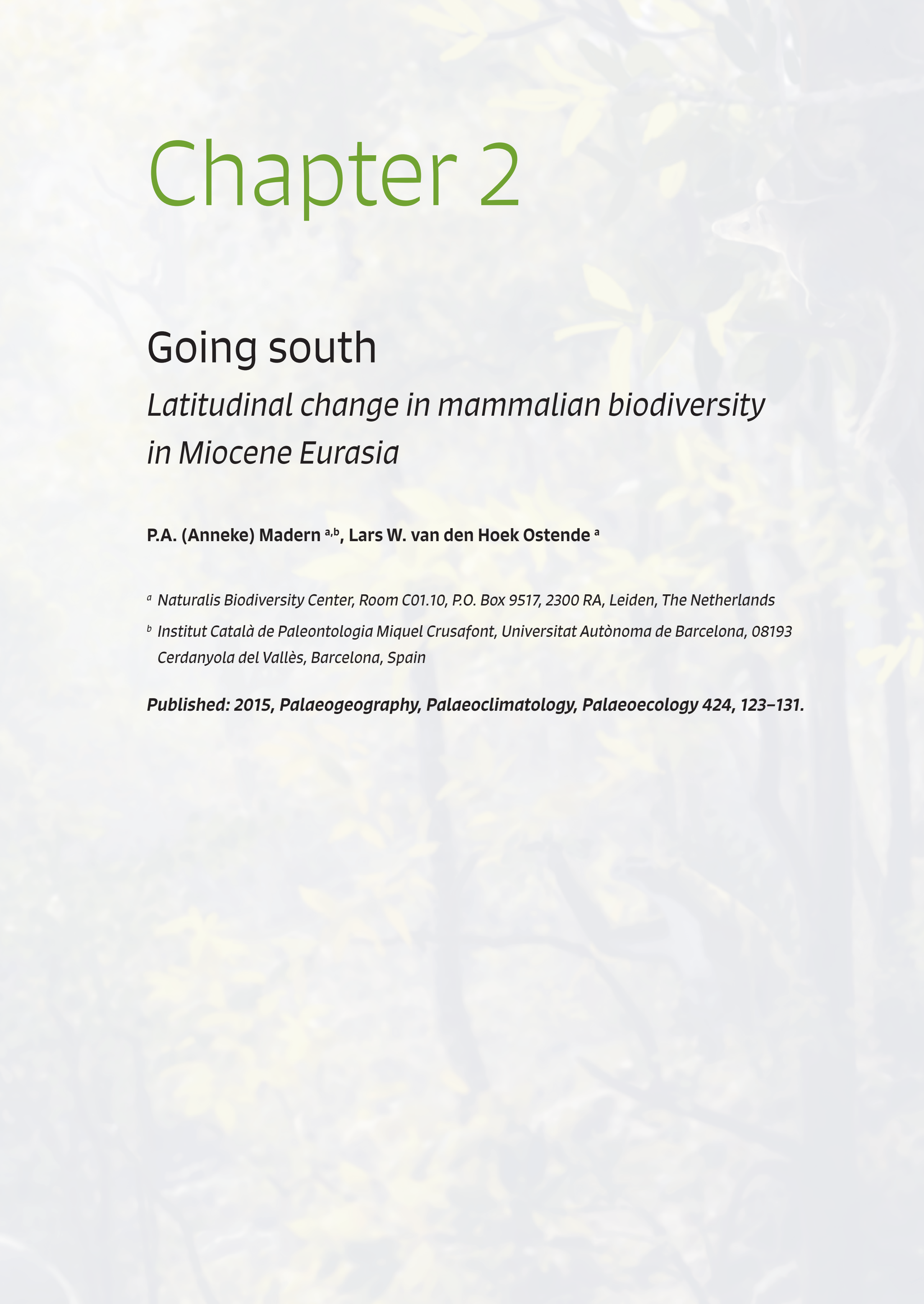

Chapter 2

Going south

Latitudinal change in mammalian biodiversity in Miocene Eurasia

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Abstract

For palaeontologists, the challenge is to reconstruct biodiversity patterns of the past. Mammal richness in grids is used to assess the stability of biodiversity hotspots and document changes over time in Europe for Mammal Neogene units 3 to 11 (19.5 to 7.6 Ma), Early to Late Miocene. The maps clearly show the patchiness of the fossil record. As the Miocene was an eventful epoch with severe environmental changes, Europe slowly became drier, and more seasonal, both in temperature and precipitation. From the Early to Middle Miocene an area of high biodiversity moved from higher to lower latitudes, culminating in one of the most remarkable hotspots in the history of mammals: the early Late Miocene (Vallesian mammal stage) faunas from the Vallès-Penedès (Catalonia, Spain). Remarkably, the surrounding areas did not exhibit similar richness. During the subsequent Vallesian turn over event (~9.7 Ma), the large and small mammal distribution became more equitable and the hotspots less prominent. The richest area was found in the periphery of the humid Miocene ecosystem, which experienced species influx from the drier south. The southward shift was a result of the expansion of the humid area with subsequent closed environments and related mixing of ecosystems, coming to a halt in the Late Miocene, when all of Europe became equally open.

Keywords: Neogene, Miocene, Vallesian, Mammals, Europe, Biodiversity, Biogeography

1. Introduction

Biodiversity is not equally distributed in time and space. While some areas contain only a few species, others have a remarkably high number of taxa. The latter are called biodiversity hotspots. These hotspots, however, are not stable (Renema et al. 2008). As the Earth and its climate change, so does the distribution of flora and fauna.

Relating to the current biodiversity crisis (IPCC 2007; Dirzo et al. 2014), a major goal for many palaeontologists is reconstructing past diversity. Enormous quantities of information about fossil animals and their environments are stored in numerous databases. The challenge is to recognize non-random patterns in these data. Biologists focus on areas with high species diversity, or high richness, and view these hotspots as the prominent places for nature conservation. Historical data can show how hotspots came to be and, more importantly in these days of crisis, how they came to their demise. To study these areas of high richness, they first have to be identified, followed by the reconstruction of dispersal patterns by tracking their movements. For a better understanding of the link between climatological and distributional changes in the Miocene, insight into the processes behind hotspot formation and termination is needed. In this paper, mammal diversity (genus richness) of the European Miocene is reconstructed.

The Miocene (23.0 to 5.3 Ma) was a turbulent time, marked by major faunal turnovers and climate changes. During this epoch, land masses assumed their present configuration and modern mammal groups were established. The first hyenas, bears and dogs arose, and primitive antelope, deer and giraffe appeared in Eurasia, together with the first modern horses and higher primates (Behrensmeyer et al. 1992). Temperatures were high during the Mid-Miocene Climatic Optimum, with a lower limit of the mean annual temperature (MAT) of 17.4 °C (Zachos et al. 2001; Böhme 2003; Mosbrugger et al. 2005; Sun and Zhang 2008; Merceron et al. 2012), followed by the Mid-Miocene Cooling, characterised by a dramatic drop in the MAT of probably more than 7 °C to temperatures around 15 °C. This drop can be attributed predominantly to a decrease of more than 11 °C of the minimum cold months' temperature (Van der Meulen and Daams, 1992; Zachos et al. 2001; Böhme 2003; Shevenell et al. 2004; Lewis et al. 2008).

Europe was also affected by major tectonic events, such as the uplift of the Alps and other mountain ranges. The uplift of the Tibetan Plateau changed atmospheric circulation, which caused increased seasonality in Eurasia in the later parts of the epoch (Agustí et al. 1997; Broccoli and Manabe 1997; Van Dam 2006; Jiménez-Moreno et al. 2010).

The closure of the Tethys Ocean in the east, at the end of the Early Miocene, provided a migration route to and from Africa, the so-called *Gomphotherium* landbridge (Rögl 1999; Harzhauser et al. 2007a). The palaeogeography of Europe continued to change, particularly as a result of the developments in the Paratethys (Rögl 1999; Popov et al. 2006; Harzhauser and Piller 2007; Harzhauser et al. 2007b). The last dramatic change in the Miocene map of Europe came at the Messinian (7.2 to 5.3 Ma), as most of the Mediterranean Basin disappeared during the salinity crisis (Rögl, 1999; Agustí et al. 2006; Popov et al. 2006; Van der Made et al. 2006; Krijgsman et al. 2010).

Due to changing palaeogeography, Europe experienced, besides the faunal exchange with Africa (e.g., Proboscidea), also exchange with both Asia (including Cricetodontinae, Murinae and Cricetinae) and North America (e.g., *Anchitherium*, *Hippotherium*). It has been long since recognized that Eurasia contains different bioprovinces, with a varying degree of similarity (Bernor 1984; Bernor et al. 1996; Maridet et al. 2007; Casanovas-Vilar et al. 2010). In addition, a latitudinal gradient influenced the distribution of at least some mammal orders, such as the insectivores (Furió et al. 2011).

The overall trend in the Miocene of Eurasia can be characterised as a long-term shift towards progressively drier, more seasonal conditions and open vegetation (Broccoli and Manabe 1997; Barry et al. 2002; Van Dam 2006; Van Dam et al. 2006; Stromberg et al. 2007; Eronen et al. 2012). According to Van Dam et al. (2006), this was the result of a southward extension of the moisture belt, followed by retreat to the north. Body weight distributions of late Early to Middle Miocene (ca. 17 to 14 Ma) mammalian communities indicate that a strong latitudinal gradient existed during this warm, almost subtropical, period (Costeur and Legendre 2008). The Iberian Peninsula had an arid climate and open environments at this time, whereas more closed to dense forest and a very humid climate progressively occurred towards the north (Maridet and Costeur 2010). Other studies have postulated a precipitation latitudinal gradient already present in the late early to early Middle Miocene (Jiménez-Moreno and Suc 2007; Furió et al. 2011). This means that, with the north–south humidity gradient, focusing on only higher or only lower latitudes will not show much change. In southern Europe it mainly continued to stay dry, while in northern Europe the wetness persisted (Böhme et al. 2006). Therefore, the focus of this study is Eurasia through time, to detect the subtle changes in the middle latitudes, which show the effects of changing distribution of the southern dry area.

The New and Old Worlds (NOW) database is the leading repository of information concerning Neogene age fossil mammals and provides a basis for reconstructing biodiversity patterns of the past (Fortelius 2013). Even though a correlation between the observed richness and the number of localities has been reported by previous studies based on various versions and subsets of the NOW database (Peláez Campomanes and Van der Meulen 2009), this resource gives the best coverage to get as close as possible to a true overview of the dispersal patterns of Miocene mammals in Europe.

The analysis of patterns and trends in past diversity always has to deal with the unwanted biases inherent to the nature of the fossil record and methodologies. A common bias is uneven sampling, where richer or more intensively sampled sites or time intervals contain more rare taxa and thus show a higher richness. A peak in data quality could lead to an overestimation of the recorded richness (Casanovas-Vilar et al. 2014). To assess such biases, robust diversity measures are needed, taking into account abundance, sample size and the probability of finding a certain taxon at a specific site (Barry et al. 2002,2013; Van Dam 2006; Casanovas-Vilar et al. 2014). The availability of deposits of a certain age also provides a bias, this is however an integral part of the fossil record.

Even though there is a good understanding of the development of mammalian communities in the Eurasian Miocene (Fortelius et al. 1996; Eronen et al. 2009; Ataabadi et al. 2013), less effort has been taken towards the quantification of mammalian faunal developments. With the present availability of better tools and information, now is the time to more precisely explore, quantify, and illustrate these patterns.

Here, the possibilities of presenting richness in grids were explored in order to examine the stability of biodiversity hotspots and document changes over time.

2. Material and methods

2.1. Dataset

In this paper, the terms biodiversity, mammal diversity and richness are defined as genus number. A single locality cannot give a complete overview of the biodiversity in a particular period. Therefore, in order to be able to combine data from an area, rather than from single localities, a large set of fossil mammal data was downloaded from the New and Old Worlds (NOW) database (Fortelius, 2013).

The dataset contains both large and small mammals and consists of over 13,000 specimens (4694 large and 8544 small) from 1219 localities. Small mammals encompass the orders Chiroptera, Chrysochloridea, Eulipotyphla, Hyracoidea, Lagomorpha, Macroscelidea and Rodentia as appearing in the NOW database. The large mammals encompass the orders Artiodactyla, Carnivora, Condylarthra, Creodonta, Embrithopoda, Marsupialia, Perissodactyla, Pholidota, Placentalia, Primates, Proboscidea, Ptolemaiida and Tubulidentata. All were identified to the genus level, with a total of 557 genera (307 large and 250 small).

Even though collection techniques for large and small mammals differ, as does the accuracy of taxonomic identification (Alroy 2003), they are expected to react to the same signals, for example in response to climatic or tectonic changes. Therefore, micro- and macromammals are analysed both separately and collectively. Compiling the dataset, several choices concerning taxonomic level, time control and (other) biases had to be made.

2.2. Taxonomic level

While ecological interpretations based on genera or higher taxonomic groups are said to be unreliable (Martín-Suárez et al. 2001), and ecological preferences may not have been the same for all species in a genus (Casanovas-Vilar and Agustí 2007), species level analyses are likely to introduce more noise. Biodiversity estimates based on species, for example, can be inflated because of false or unrecognised synonymies (Alroy 2002,2003). Alroy (1996,2003) compared genus and species level results of his diversity analysis of North American mammalian palaeofaunas, concluding that the genus level data are more taxonomically robust and preserve much of the same signal as the species level data. Genus is the lowest taxonomic level to which specimens are typically identified (Forcino et al. 2012), and genus assignments have more consensus than species determinations (Peláez Campomanes and Van der Meulen 2009).

A good indicator of how well the fossil data reflects the actual mammal community is completeness (“the proportion of taxa that have left some fossil record” (Foote and Raup 1996)) is not only higher for small mammals, but for genera as well (Alba et al. 2001). Alba et al. (2001) stated that the mammalian fossil record from the Neogene of the Iberian Peninsula is very complete, as their calculations showed it captured 77% at the specific, and more than 90% at the generic level. Although the large mammal record of the NOW database seems to be biassed by sampling effort at the metacommunity level, as well as at the locality level, the small mammal record is considered to be mostly homogeneous (Peláez-Campomanes and Van der Meulen 2009). Taking all of the above into account, all analyses were performed on the genus level.

2.3. Biogeography and chronology

Mammal point data at the genus level were divided into grid cells, squares of 1.5 × 1.5° (ca. 150 × 150 km at the equator) and plotted using both a GIS programme designed by the Naturalis Biodiversity Center, Leiden, namely NaturalisGrid, and R (R Core Team 2014), with packages 'raster' (Hijmans and van Etten 2012) and 'maptools' (Lewin Koh and Bivand 2012). Grouping in this manner makes the analysis more conservative, since multiple-locality complexes may otherwise bias the results (Jernvall and Fortelius 2002).

Since western Europe is one of the most intensively studied areas in mammalian palaeontology, this area was chosen and extended for a better overview of longitudinal (between 10° W and 50° E) and latitudinal (between 15° to 55° N) distribution changes (Fortelius et al. 1996,2002,2006).

This study encompasses eight successive biochronological units; Mammal Neogene units 3 to 11 (19.5 to 7.6 Ma) (Mein 1975). These MN units span the interval Early to Late Miocene, a period which has been sampled homogeneously and is well-studied (Peláez-Campomanes and Van der Meulen 2009). Mammal Neogene units represent varying time spans. The definition is based on (1) faunal associations, (2) first appearances and (3) last appearances of both large and small mammals (De Bruijn et al. 1992; Steininger et al. 1996; Mein 1999; Steininger 1999; Agustí et al. 2001).

2.4. MN system

The definition of the time intervals and therefore varying lengths is a complicating factor. The criteria for defining MN units are mainly based on the first or last appearance of certain taxa, which leads to higher origination and extinction rates at MN boundaries (Agustí et al. 2001; Casanovas-Vilar et al. 2010). The MN system contains 17 units of differ ent lengths, varying between 0.5 and 3.0 Myr (e.g., MN 3 is more than twice as long as MN 4). The different unit durations pose a problem for analyses of diversity because longer units are expected to contain more species than shorter units. However, MN 6, 7 + 8, 9 and 10 have similar lengths and obviously non-similar diversities. Differences between bioprovinces, relating the MN units to the marine record and spatial diachrony across Europe, further complicate matters (Van Dam et al. 2001; Gómez Cano et al. 2011; Van der Meulen et al. 2011,2012; Ataabadi et al. 2013).

There is need for a revision of the biochronological framework for the European Miocene (Costeur et al. 2007) or even for an independent chronology, excluding biochronology altogether (Domingo et al. 2007; Ataabadi et al. 2013). Unfortunately, this is not yet possible. A new (bio)chronology asks for better dated records in order to use absolute dating instead of a relative scale such as the MN system (Domingo et al. 2014).

A number of criteria for undertaking the analyses were applied. Localities were excluded when they (1) could not be assigned to the temporal span of a single MN unit or (2) lacked geographic positional data (such as coordinates). For the entry/exit events, that is, first or last occurrence of a taxon, the maximum or respectively minimum age was used. In addition, all age assignments were converted to their corresponding MN unit, i.e. Mammal Neogene Equivalents (MNEQs), which are based on the MN unit correlation scheme of the NOW database (Steininger et al. 1996; Ataabadi et al. 2013). Uncertain genus determinations were omitted from the study. No exclusions based on the number of taxa per locality were made, as, according to Ataabadi et al. (2013), the number of taxa used does not affect the spatial geographic patterns.

2.5. Bias

A common problem with palaeontological data is the unevenness of the fossil record. According to Alroy (2010), most counting methods have severe biases that can only be resolved using occurrence data rather than presence/absence data. However, data on relative abundances of taxa are only scarcely available for localities, as they have either not been recorded or are not comparable due to different sampling methods. Sampling biases could result in artificial hotspots. One can attempt to remove some of the bias by subsampling records. This has, however, a few disadvantages. Subsampling reduces the number of records and cannot correct for unsampled areas. Also, locally dense records might be a true reflection of the relative suitability of the habitat.

To assess the bias in the data, the correlation between diversity and sample size was computed for small and large mammals, both separately and combined. Barry et al. (2002) investigated the relationship between the number of specimens and the number of events, by calculating the correlation between sample size per interval and the number of events, that is, first (FO) and last (LO) occurrences. They found that a correlation between interval sample size and number of events indicates a bias, casting doubts on the truth of turnover events (Badgley and Gingerich 1988). To eliminate or at least minimise the bias' effects, the number of specimens should be taken into account. As the NOW provides presence–absence data, this is not exactly possible, consequently the number of genus records is taken as sample size. Relationships between the number of events, the sample size and the richness were calculated.

3. Results

3.1. Biogeography and biodiversity

The maps (Fig. 1a–h) show the patchiness of the fossil record during the Miocene. However, despite this irregularity, a pattern appears of an area of high richness moving from high to lower latitudes through time.

The shifting hotspot is best visible from the Early to Middle Miocene (MNEQ 3 to 7 + 8, Fig. 1a–e). Starting in the northern parts of Europe, it slowly travelled southwards. During MNEQ 3, the highest numbers per grid cell were in Germany and the Czech Republic, but maximum numbers did not exceed 65 genera. In MNEQs 4, 5 and 6, the biodiversity rose through Europe, in Germany, as well as France, but was still concentrated around Germany and Austria. After reaching a climax of 120 genera in MNEQ 7 + 8 in France, MNEQ 9 had the most southern hotspot in Catalonia, Spain, with 95 genera (Fig. 1f).

Following the Middle to Late Miocene faunal turnover that marks the beginning of the Vallesian mammal stage (Steininger et al. 1996), the diversity in the Vallès-Penedès basin increased. The biodiversity peak was relatively short-lived as the species number decreased dramatically halfway through the Vallesian. This drop in diversity is referred to as the Vallesian Crisis (Agustí 1981; Agustí et al. 2013). Richness of inland basins of the Iberian Peninsula was far lower than of the coastal basins. Moreover, apart from being brief in duration, the high richness appears to be rather local, which is consistent with Casanovas-Vilar et al. (2014) questioning the wide range and extent of the Crisis.

Furthermore, there was a southward shift of the richest latitude for the entire period (Fig. 2). While in Early to Middle Miocene (MNEQ 3 to 7 + 8; Fig. 2a–e) the maximum number of genera per grid cell was located in the higher latitudes with around 80 genera, the concentration of genus richness changed in the early Late Miocene. The change from MNEQ 7 + 8 to MNEQ 9 is a clear example of an area of high richness shifting from high (Fig. 2a–e) to low latitudes (Fig. 2f–g). In the Late Miocene, MNEQs 10 and 11 (Fig. 2g–h), mammal biodiversity was more homogeneously spread over Europe. The maximum numbers are much lower, not even reaching 70 genera per grid cell. Here, hotspots are less clearly identified and peaks in genus counts are less pronounced.

3.2. Large vs. small mammals

Despite the differences in dispersal abilities and other dynamics (Casanovas-Vilar et al. 2010; Maridet and Costeur 2010), the general pattern visible in both micro- and macromammals was expected to be the same, based on their similarities in the NOW database (Peláez Campomanes and Van der Meulen 2009). Even though Heikinheimo et al. (2007) stated that macromammal biodiversity is more related to environmental changes, the micromammals are expected to be more sensitive to changes, because of their smaller geographic ranges (Maridet et al. 2007). The large and small mammals indeed behaved in a comparable manner during the study interval, although the pattern of shifting hotspots was more pronounced in the small mammals (Fig. 2).

3.3. Bias

The correlation between diversity (Fig. 3a) and sample size was calculated (Fig. 3b) to test for bias in the data. Spearman rank correlation analysis per MNEQ unit showed that there is no significant correlation, as all have low rho-values and non-significant p-values (combined: rho2 = 0.09, p = 0.47; large: rho2 = 0.10, p = 0.46; small: rho2 = 0.15, p = 0.35). (Note that 'sample size' here is actually the matrix of recorded sites and species, for lack of abundance data.)

Following Barry et al. (2002), relationships between the number of events (first and last occurrences, that is, FOs and LOs), the sample size and the richness were calculated. After an initial decrease during MNEQ 6, there was an increase in entries in MNEQs 7 + 8 and 9

(Fig. 3c). However, there also was a high number of exits at the same time, indicating a period of faunal turnover. After MNEQ 9, the number of exits did not radically increase. In MNEQ 10 the number was lower than in MNEQ 7 + 8 and during MNEQ 11 it even declined further. While the number of events and sample size are not significantly correlated (combined: rho2 = 0.07, p = 0.53; large: rho2 = 0.15, p = 0.35; small: rho2 = 0.00, p = 0.91), the relationship between the number of events and the richness, the number of genera present per MNEQ, is highly significant for both large and small mammals (combined: rho2 = 0.81, p = 0.0024; large: rho2 = 0.66, p = 0.0149; small: rho2 = 0.51, p = 0.0465) (Fig. 3d).

As there is no significant relationship between the sheer number of finds (e.g., sample size) and the richness (e.g., number of genera), it is possible to distinguish between peaks in diversity that are artefacts and real diversity fluctuation. Hence, the richness signal here is not a direct function of sampling. An example is the hotspot in MNEQ 9, which still exists when the richest site, Can Llobateres 1, is excluded (Casanovas-Vilar et al. 2014).

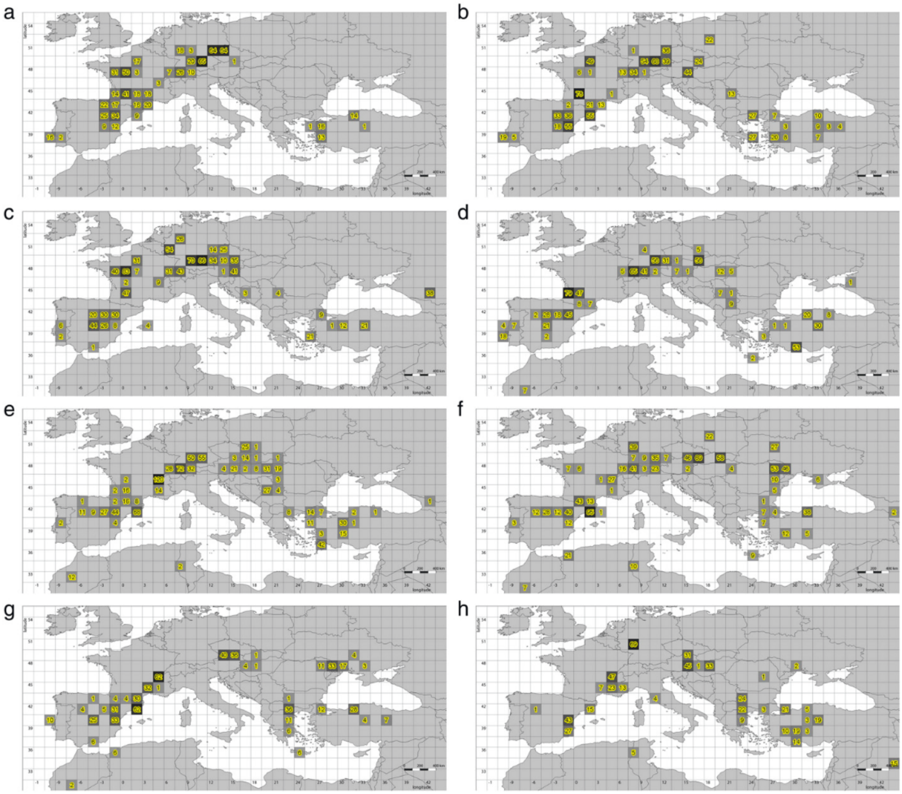

Fig. 1. a–h. Biodiversity per 1.5 × 1.5° grid cell for large and small mammals together, plotted per MNEQ.

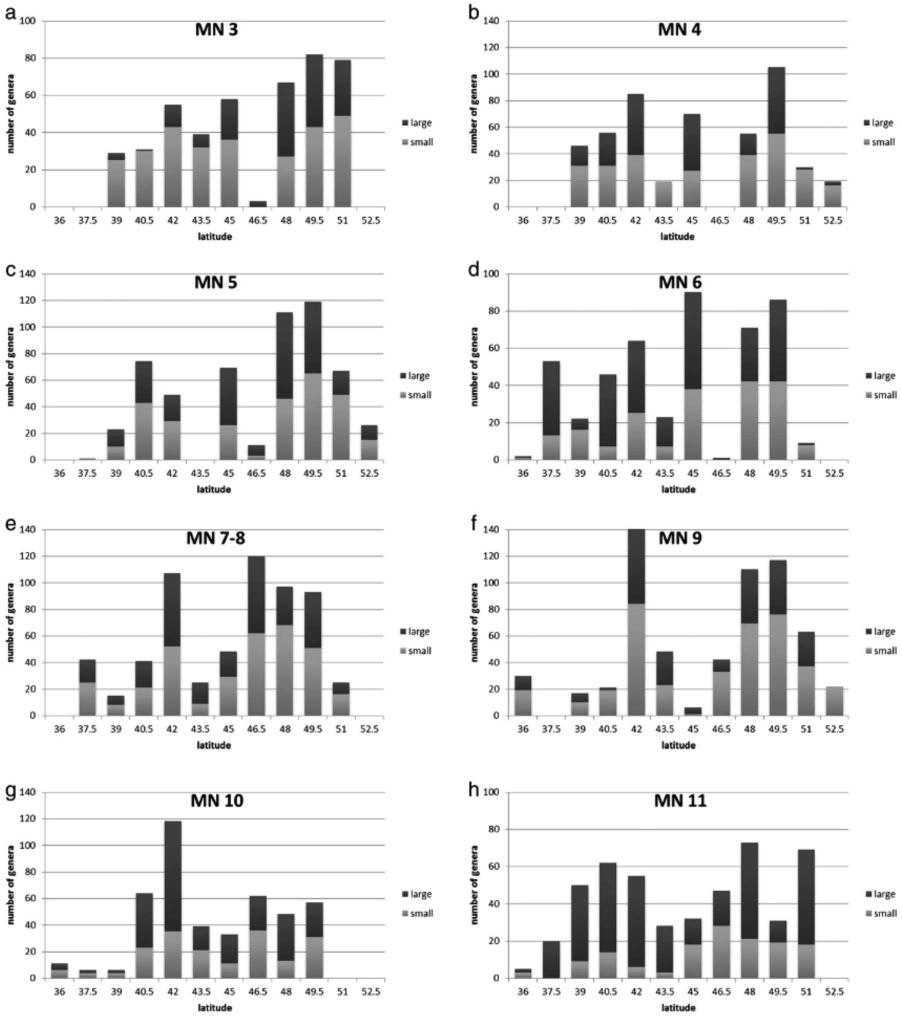

Fig. 2. a–h. Bar graphs showing the number of genera for the hotspots per latitude per MNEQ for large and small mammals (resp. dark and light colours in the bar graphs). The location of the richest latitude changes through time, going from rich higher latitudes in MNEQ 3 to MNEQ 7 + 8 to a more southern hotspot in MNEQ 9.

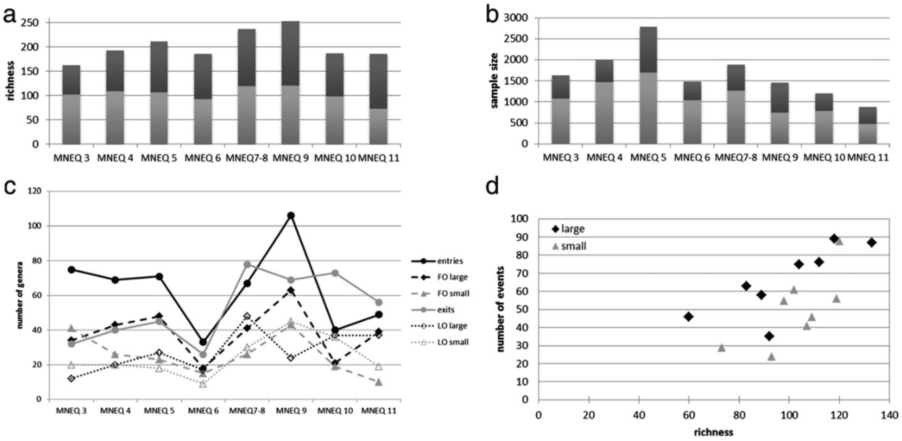

Fig. 3. Genus biodiversity explored through time (per MNEQ) for large and small mammals (resp. dark and light colours in the bar graphs), both separately and combined. (a) Richness in number of genera. (b) Sample size in number of data points. (c) Number of first (FO) and last (LO) occurrences. (d) Relationship between number of events (FO + LO) and richness per time interval.

While the sampling bias is considered negligible, there is still some geographic bias present in the data. During the Late Miocene, for instance, localities in the higher latitudes are lacking. This northern hiatus appears to be a conservation bias. Likewise, the patchiness is emphasised by empty spaces on the map (e.g., France, Croatia), as data from the various countries has not been entered equally into the NOW. Together, these amount to reservations to be kept in mind and not reasons to dismiss this type of comprehensive data.

4. Discussion

4.1. Data accuracy

Consistency of the data is a major difficulty of constructing a complete overview of all Eurasian Miocene mammals. Reconstructing ancient communities based on fossil assemblages depends on accurate and consistent identifications and the level of completeness as defined by Foote and Raup (1996).

The fossil record holds a great amount of information about the original living fauna (Alba et al. 2001). There is a high level of fidelity between modern bone assemblages and living populations, likewise changes in community structure can be accurately tracked in fossil assemblages (Western and Behrensmeyer, 2009). Furthermore, by comparing data from the NOW database with information about fossil communities with those from a database about recent populations, Saarinen et al. (2010) found that grid cell data from fossil localities give a good estimate of the total fauna and show ca. 60% of the total species diversity, implying that this percentage will be even higher for genus level biodiversity.

The differences within and between small and large mammal communities could be a problem, as they can vary greatly in completeness and dispersal ability. Previous studies of the NOW showed that the set of localities included in the database does not represent homogeneous sampling for the large mammals (Peláez-Campomanes and Van der Meulen, 2009). However, the NOW database is continuously being updated, and with numerous additions in the last few years (such as Casanovas-Vilar et al. 2010), the evolving dataset becomes more complete and accurate for new compilations (Fortelius 2013).

4.2. Spatial diachrony

The long-distance correlations commonly utilise Mammal Neogene (MN) biochronology (Mein 1999; Agustí et al. 2001), which is widely used in European mammal palaeontology. However, Van der Meulen et al. (2011, 2012) recently demonstrated the asynchrony of parts of this zonation by comparing long-term Miocene mammal sections from Spain and the North Alpine Foreland Basin of Germany and Switzerland that were correlated with the palaeomagnetical time scale (Van der Meulen et al. 2011). The observed diachrony by taxa entering the various areas at different times has strong biogeographical implications, as it shows the expansions and retractions of species distribution zones, and ultimately of ecosystems.

4.3. Pattern related to climate

In the Early to Late Miocene diversity hotspots drifted to lower latitudes, followed by a shift in diversity patterns from MNEQ 10 on. The changes in the Vallesian were characterised by the disappearance of certain mammal groups, in particular those adapted to stable humid or closed environments and specialised herbivores, that is, frugivores (fruit eaters) or folivores (leaf eaters) (Van der Made et al. 2003). New immigrants may have been more adapted to dry or open landscapes or less predictable environments. Numerous studies suggest the Late Miocene (after MNEQ 11) was becoming more dry, cold and seasonal (Agustí et al. 2003; Van der Made et al. 2003; Mosbrugger et al. 2005; Eronen et al. 2009,2010,2012). Vegetation patterns showed the development of continentality, where both temperature and precipitation seasonality increased (Bruch et al. 2011) together with the appearance of extensive grasslands (Stromberg et al. 2007).

Besides several groups declining and ultimately disappearing, the Late Miocene Vallesian Crisis also involved a change towards communities with a lower species richness (Casanovas-Vilar and Agustí 2007). Even though a small number of studies based on pollen records and stable isotopes do not show drastic changes in regional vegetation or climatic conditions on the Iberian Peninsula during the Vallesian (Jiménez Moreno et al. 2010), several others similarly link the Vallesian Crisis to changing climate. Maps based on mean hypsodonty (i.e., increased tooth height, used as a proxy of mean annual palaeoprecipitation) show increased aridification in south-west Europe (Fortelius et al. 2002). In addition, the transition from a hot and wet 'washhouse' climate sensu Böhme et al. (2008), with temperatures and precipitation higher than present to drier conditions timed between 9.7 and 9.5 Ma, and the associated cooling episode, seemed to have triggered faunal turnover (Böhme et al. 2008,2011).

However, the inland areas also experienced faunal transitions right at the beginning of the Vallesian and during the Vallesian Crisis (Van Dam et al. 2006). Astronomical forcing influenced the Earth's climate and in that way triggered faunal events. The Milankovic theory describes the cumulative effects of changes in the Earth's cyclic movements (orbital shape/eccentricity, axial tilt/obliquity and precession of the Earth's axis) on climate (Hays et al. 1976). Van Dam et al. (2006) argued that astronomical cycles could trigger analogous faunal events. At times when these different Milankovic cycles strengthen each other, they can change the climate to such a degree that the stability of ecosystems is affected. This, in its turn, may precipitate faunal events like migrations and extinctions.

Finding a pattern of southward movement of a diversity hotspot is one thing, recognizing the causes behind it quite another. In order to do so, the genera present in each diversity peak need to be evaluated, which is outside the scope of the present paper. It is possible, however, to speculate and attempt to draw up a working hypothesis for further research.

Insectivores are starting to become more widely recognized as good humidity indicators. Furió et al. (2011) showed that insectivore diversity is continuously higher in the north than in the south, and postulated a latitudinal humidity gradient across Europe throughout the late Early to early Late Miocene (ca. MN 2 to MN 10). As they analysed the data from the various MN units separately, they did not look at the development of this gradient through time. It is clear that the south of Europe was drier than the central parts. Van Dam noted this for the late Neogene, but showed (van Dam, 2006 fig. 9a) it also held true for the late Middle Miocene. According to Böhme et al. (2006), precipitation rates in the early Middle Miocene in Central Europe were about three times higher than those in the Iberian Peninsula. A southward movement of the more humid ecosystems in itself is not enough to explain the decreasing latitudes of the maximum diversity. Given a humidity gradient, one might expect the hotspot to remain in the most forested environments in the north. The pattern indicates a shift, particularly in MNEQ units 5 to 9, i.e., the Middle and early Late Miocene.

Similar to this study, the work of Furió et al. (2011) was based on data ordered in MN units. Van der Meulen et al. (2011,2012) noted that the system shows a certain amount of diachronicity, particularly in MN units 5, 6 and 7 + 8, the very period in which the area of high richness was moving in a southern direction. This implies that the correlation methods used would have impeded the recognition of the relation between the dry south and humid north, as MN units would in part have followed the ecosystem expansion, making them less suitable as a time frame (which may account also for the diachronicity found). The southward expansion culminated in the most southern hotspot in the Vallès-Penedès (MNEQ 9), when moist loving Eulipotyphla as heterosoricids and dimylids thrived in the area (Furió et al. 2011,2015), and the basin became one of the most important spots for hominoid diversity (Agustí et al. 2003; Casanovas-Vilar et al. 2011; DeMiguel et al. 2014).

The observed hotspots seem to have represented the fringes of a southward expanding humid ecosystem. Diversity was higher in the periphery, because of a spatial fragmentation of the environment, resulting in a mosaic where both southern and northern faunal elements lived in close proximity. In addition, this paper's methodology combines data from an area over an extended period of time. Minor oscillations in the position of the ecosystem boundaries would therefore lead to time averaging, leading to an even higher observed diversity.

Although diversity reached its acme in MNEQ 7 + 8, the most remarkable hotspot was arguably the one found in MNEQ 9. It represents the most southern one, and, moreover, it is somewhat paradoxical to have the highest diversity in Europe on a peninsula. Most important, however, is that here the southward movement ended. During MNEQ 10 diversity is far more equitable, which seems to indicate that ecosystems throughout Europe were more uniform.

5. Conclusions

These data reveal a trend of a southward moving area with the highest richness from the Early to Middle Miocene. This trend can be explained by an expansion of a humid ecosystem and subsequently closed environments from higher into lower latitudes, where high richness results from temporal and spatial mixing at the boundary of ecosystems. This trend culminated in the early Vallesian Iberian Peninsula. Notably, areas surrounding this most southern hotspot did not show the same richness.

During the late Vallesian and the Vallesian Crisis (at 9.7 Ma), the distribution of mammals in Europe became more even and areas of high richness not as sharply defined as before. This was the time of the disappearance of most humid-adapted and forest dwelling groups, meaning the end of the hominoids in Europe as well. The number of exits in MNEQ 10 is barely higher than in MNEQ 9 (Fig. 3c), which would be predicted if the Vallesian Crisis were more than a local event. Notably, the number of genera did not change in Eastern Europe. This is in line with the notion that the Vallesian Crisis was indeed local, not continent wide.

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Chapter 3

The Miocene mammal record of the Vallès-Penedès Basin (Catalonia)

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Abstract

The land mammal record of the Vallès-Penedès Basin (Catalonia, NE Spain) ranges from the early Miocene (Ramblian) to the late Miocene (Turolian), that is from about 20 to 7 Ma. Here we present an updated review of the mammal succession focusing on biochronology as well as on environmental and faunal changes. Based on faunal similarities with central Europe, we interpret this basin as a transitional zone between the forested environments of northern regions and the more arid landscapes of the inner Iberian Peninsula. The quality of the Vallès-Penedès record and its chronostratigraphic control is clearly better for the late Aragonian and the Vallesian (between 12.6–9.0 Ma), especially for small mammals. Therefore, we analyze small mammal diversity dynamics during this interval. Contrary to previous analyses, which found an abrupt extinction event coinciding with the early/late Vallesian boundary (the Vallesian Crisis), our results show that this pattern is due to uneven sampling. Instead, taxonomic richness slowly decreased since the late Vallesian as a result of a series of extinctions that mostly affected forest-dwelling taxa.

Keywords: Iberian Peninsula, Western Europe, Miocene, Magnetostratigraphy, Biostratigraphy, Paleodiversity

1. Introduction

The study of the mammal faunas of the Vallès-Penedès Basin (Barcelona, Catalonia) dates back to the late 19th century, when a few mammal remains were found in the short-lasting lignite mine of la Fontsanta (next to els Casots site, CS in Fig. 1) and the Molí Calopa brickyard in Rubí (MC, Figs. 1 and 2). These were reported by the priest and geologist Jaume Almera, from the Museum of Geology of Barcelona Seminary, who left the description of these remains (most of them currently lost) in the hands of renowned mammal palaeontologists of his time, including M. Boule, C. Depéret and A. Gaudry (Almera, 1898). In the following decades the outcrops of the Vallès-Penedès were surveyed by palaeontologists from the Barcelona Seminary resulting in the discovery of new sites, including the ones at els Hostalets de Pierola (Bataller, 1938).

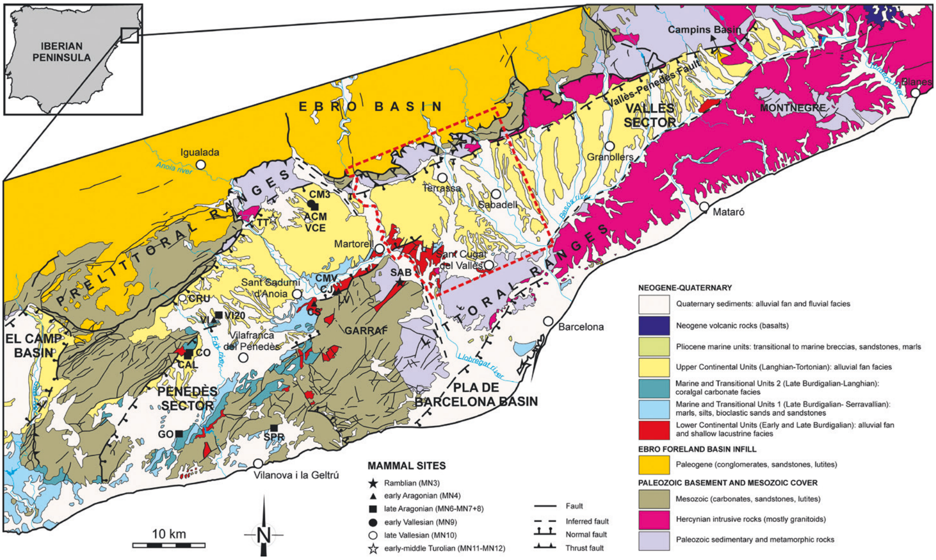

Fig. 1. Simplified geological map of the Vallès-Penedès Basin and major Miocene mammal sites (modified from Institut Cartogràfic i Geològic de Catalunya, 2015). The area enclosed by the dashed perimeter is shown in detail in Fig. 2. For locality acronyms, see Table 1.

However, the systematic sampling of the Miocene out crops did not start until the 1940s being led by Miquel Crusafont, Josep F. de Villalta and Jaume Truyols. This resulted in the discovery of tens of new sites and the collection of thousands of specimens, most of which are currently housed at the Institut de Paleontologia Miquel Crusafont (ICP) in Sabadell. Crusafont and Villalta focused on the study of mammals and occasionally other vertebrates (Crusafont et al. 1955; Crusafont Pairó, 1950; Crusafont Pairó and de

Villalta, 1951; de Villalta Comella and Crusafont Pairó, 1941a, 1941b), whereas Truyols mostly devoted his studies to the stratigraphical con text and regional geology of the area (Crusafont Pairó and Truyols Santonja, 1954, 1960; Crusafont et al. 1955). Thanks to their work, the Vallès-Penedès soon became a reference area for the study of European Miocene faunas, and eventually the Vallesian land mammal age was defined based on its record (Crusafont Pairó, 1950). The Vallesian age was quickly accepted and used in other regions of the Old World for the Late Miocene fossil faunas that are characterised by the entry of the first hipparionin horses.

During the 1970s and the 1980s the knowledge of the Vallès-Penedès mammal record improved with the addition of new sites and reviews of important mammal groups such as the rodents, insectivores and artiodactyls (for synthetic reviews, see Agustí et al. 1985 or Golpe-Posse, 1974). The publication of the first comprehensive palaeoecological and diversity analyses followed soon after (Agustí and Moyà-Solà, 1990; Agustí et al. 1984), resulting in the definition of a remarkable extinction event during the early Late Miocene. The Vallesian Crisis, as it was called, was also recognised in other European regions (Agustí and Moyà-Solà, 1990; Agustí et al. 1997, 1999; Fortelius and Hokkanen, 2001; Fortelius et al. 1996). Finally, during the last two decades, the construction of major works such as highways and landfills has allowed the discovery of hundreds of new sites, mostly of the latest Aragonian and Vallesian age. These new sites are placed in long and continuous series that have also been sampled for magnetostratigraphy (Alba et al. 2012a; Garcés et al. 1996;Moyà-Solà et al. 2009). The resulting correlations to the Geomagnetic Polarity Time Scale (GPTS) have allowed a high precision in the age estimation of many sites, which, coupled with the intensive sampling and study of the mammal faunas, open the way for more refined palaeoecological and diversity analyses. Here we provide an updated review of the Miocene mammal record of the Vallès-Penedès and its geological context, together with an analysis of the mammal diversity dynamics during the late Aragonian and the Vallesian, which is the best-sampled part of our record.

2. Geological setting

The northwestern Mediterranean was formed during the Latest Oligocene and the Miocene as a result of the subduction of the old oceanic crust of the Tethys Ocean under the Eurasian plate as the African plate progressively converged with it (Roca and Guimerà, 1992; Roca et al. 1999). At the Catalan Continental Margin, a widespread system of NE-SW and NNE-SSW oriented horsts and half-grabens was created, making up the northwestern margin of the Mediterranean (Bartrina et al. 1992; Cabrera and Calvet, 1996; Cabrera et al. 2004; Roca and Guimerà, 1992; Roca et al. 1999). The onshore zone of this continental margin includes the Vallès-Penedès and el Camp de Tarragona half-grabens that are bounded by the horsts defined by the Pre-littoral range to the northwest and the Littoral range to the southeast (Garraf-Montnegre horst).

The Vallès-Penedès Basin (Fig. 1) is an elongated half graben of about 100 km long by 12–14 km wide. Its northwestern margin is bounded by the Vallès-Penedès master fault and its basement dips gently towards this margin where it attains up to 4000 m in depth (Bartrina et al. 1992; Roca et al. 1999). Some major faults with a vertical slip larger than 1000 m, associated with minor faults with up to a few hundred metres of slip, occur at this margin. All these southeastern margin faults were overlapped by Early to Middle Miocene sedimentary sequences, which were affected by later minor fault reactivations (Cabrera, 1981a, 1981b; Cabrera and Calvet, 1996). The sedimentary infill of the Vallès-Penedès Basin started in the Early Miocene (Ramblian–early Burdigalian; Cabrera, 1981a; Cabrera et al. 1991, 2004; de Gibert and Casanovas-Vilar, 2011) and ended in the late Miocene (Turolian–Tortonian). Major features of the stratigraphic record in the Vallès-Penedès half-graben were closely controlled by the tectonic activity of its main bounding faults and the sea level changes in the western Mediterranean (Bartrina et al. 1992; Cabrera, 1981b; Cabrera and Calvet, 1996; Cabrera et al. 2004; Roca et al. 1999).

The Miocene record of the Vallès-Penedès Basin has been split into four main lithostratigraphical units dated by means of biostratigraphy and magnetostratigraphy (Agustí et al. 1985, 1990, 1997; Cabrera, 1981a, 1981b; Cabrera et al. 1991; Cabrera and Calvet, 1996; de Gibert and Casanovas-Vilar, 2011; Garcés et al. 1996). The oldest of these units is the Basal Breccia Unit, which crops out at a few points in the Littoral Range. It consists of time transgressive monogenic conglomerates and breccias. In the Vallès sector this unit dates back to the Ramblian (MN3), whereas in the Penedès sector its oldest record is early Aragonian (MN4) in age (de Gibert and Casanovas-Vilar, 2011).

The overlying Lower Continental Units (Figs. 1 and 3) crop out mainly near the southeastern basin margin and consist of intensely red alluvial fan and alluvial-lacustrine deposits corresponding to the Early Miocene (Ramblian–early Aragonian, MN3-MN4). Their oldest reported sedimentary record corresponds to small alluvial-fan facies sourced by local catchments from the southeastern basin margins. The overlying alluvial fan deposits covered wider areas and were also sourced from the northwestern reliefs. Shallow carbonate and evaporitic lacustrine systems developed in zones in the southeastern part of the basin, such as the La Costablanca, Molí de Can Calopa and Sant Andreu de la Barca areas (Cabrera, 1981a, 1981b; Cabrera et al. 1991). These lacustrine deposits are cyclically alternating with distal facies of alluvial fan systems, the latter bearing most of the mammal and plant sites of this age (Agustí et al. 1985; Casanovas-Vilar et al. 2011a).

During the latest Early Miocene and the Middle Miocene (17–15 Ma) several sea level changes took place in the context of the Mid-Miocene Climatic Optimum (Zachos et al. 2001). The faults that bounded the southeastern basin margin became inactive and the southern structural culminations were extensively onlapped and overlapped by the sedimentary infill (Cabrera and Calvet, 1996; Cabrera et al. 1991; Roca et al. 1999). At least three episodes of marine transgression and regression affected the Vallès-Penedès late Burdigalian, Langhian and early Serravalian (Cabrera and Calvet, 1996; Cabrera et al. 1991; de Gibert and Casanovas-Vilar, 2011; Roca et al. 1999). The sequences deposited at that time make up the Marine and Transitional Units (Figs. 1 and 3). Since the southwestern basin end and its southern margin in the Penedès were more directly connected and open to the sea, carbonate coral gal platform deposits, marine bay and transitional fan-delta siliciclastic systems occupied persistently that area. During Langhian times, the sea level was high enough and marine environments extended up to the Vallès sector with development of shallow marine and transitional deposits. The early Serravalian marine transgression only affected the southwestern basin sectors.

From Serravallian time onwards, sedimentation was again dominated by alluvial fan sediments, which constitute the Upper Continental Units (Figs. 1 and 2). The Vallès-Penedès main fault remained active until the Tor tonian, thus controlling the evolution of middle Aragonian to Middle Turolian alluvial fan systems sourced from the northwest reliefs (Fig. 3; Agustí et al. 1985, 1997; Cabrera and Calvet, 1996; Casanovas-Vilar et al. 2008; de Gibert and Casanovas-Vilar, 2011; Garcés et al. 1996; Roca et al. 1999). Thick, coarse-grained sequences were deposited near the northwestern margin of the basin, whereas finer grained, medial to distal-terminal sequences developed to the south and southeast. Large alluvial fan systems (e.g., Olesa-les Fonts fan) attained a radius of 10–15 km, while others were restricted to a few km of radial spread.

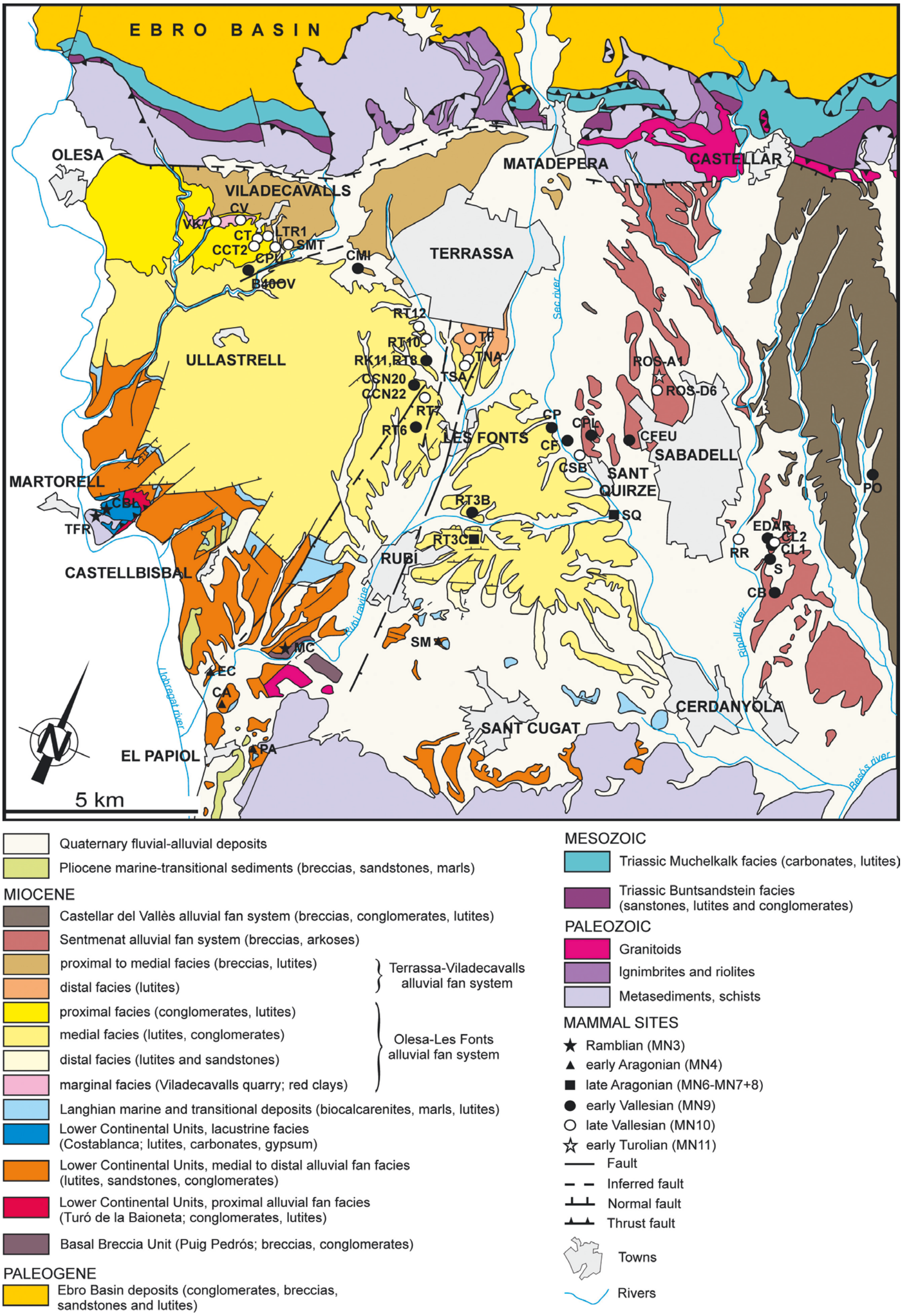

Fig. 2. Detailed geological map of the western Vallès sector (see Fig. 1) showing the position of the main mammal sites (modified after Garcés et al. 1996). For locality acronyms see Table 1.

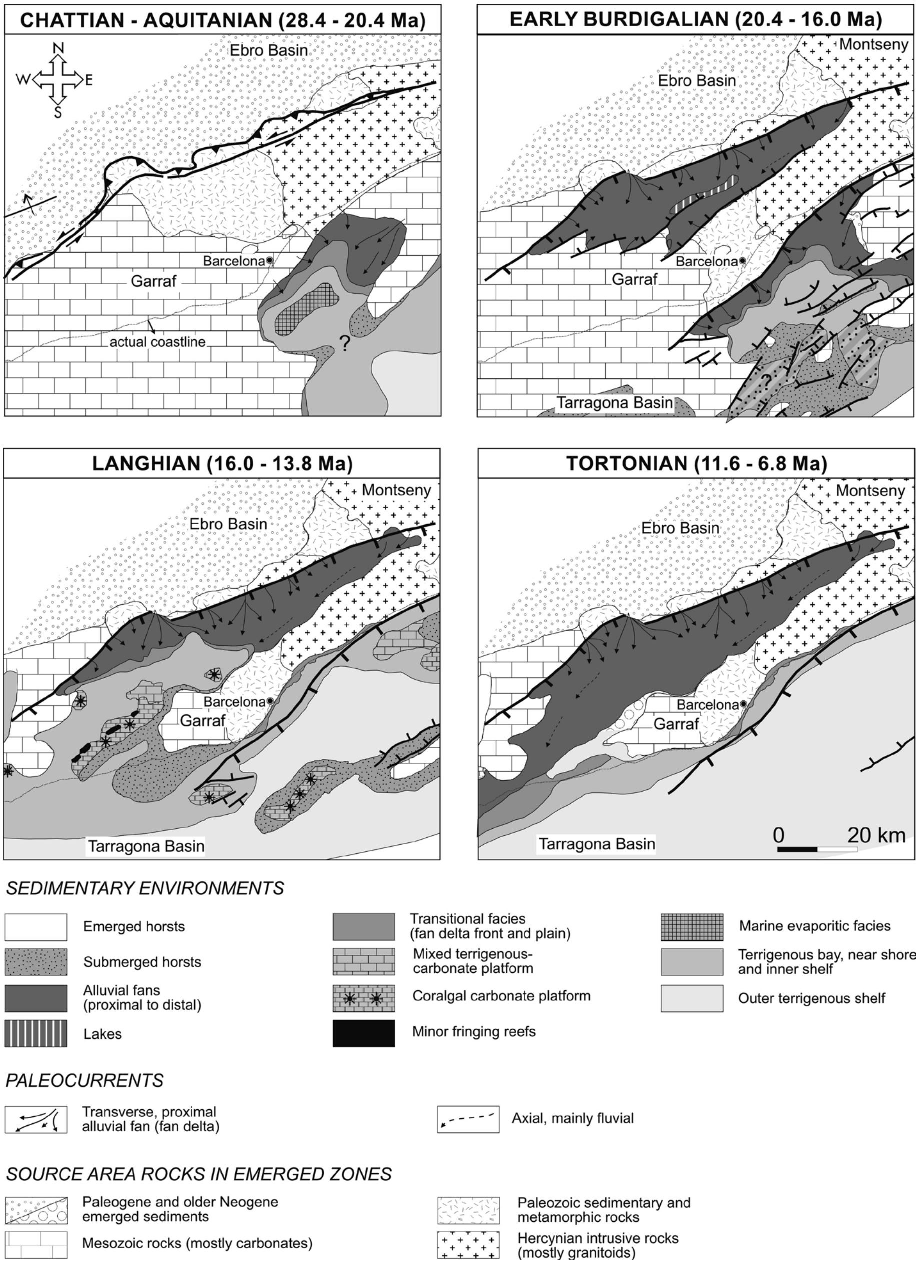

Fig. 3. Palaeogeographic schemes showing the evolution of the Vallès-Penedès Basin during the Late Oligocene and the Miocene: a: Chattian–Aquitanian (late Oligocene–earliest Miocene); b: early Burdigalian; c: Langhian; d: Tortonian. Note the extension of shallow marine environments and reef systems during the Langhian (see also Fig. 1). Modified after Cabrera et al. (2004).

The middle and distal areas of these fan systems interferred and coalesced with each other during their evolution. Most of the mammal sites oftheVallès-Penedès Basin are located in the distal to terminal, mudstone-dominated facies (Fig. 2).

The Messinian event resulted in a major interruption of the sedimentation as the Mediterranean sea level experienced a major lowering (Cabrera and Calvet, 1996). Later on, during the Early Pliocene, alluvial-fluvial (Gallart, 1981) and shallow marine deposits (Martinell, 1988) were deposited over deeply entrenched erosive surfaces affecting both the basement and earlier Miocene sequences. Finally, Pleistocene-Holocene terraced alluvial and colluvial sediments were deposited unconformably overlying the Neogene series.

3. Materials and methods

3.1. Collecting techniques

The Vallès-Penedès Miocene mammal record comprises more than 300 sites ranging from the Late Ramblian to the Middle Turolian, that is from about 19.6 Ma (Larrasoaña et al. 2006) to 7.4/6.8 Ma (Agustí et al. 2001; Hilgen et al. 2012). However, sampling is uneven and most of the sites correspond to the late Aragonian and early Vallesian. Regarding the localities, approximately two thirds of them have only small mammal remains, but a remarkable number has provided both small and large mammals. A list of the main sites and fossiliferous sections is given in Table 1. Finally, there are a few localities from which mostly large mammal remains have been recovered. Most of the old collections were assembled by the means of surface collecting as a result of quarrying activity at brickyards, where the workers often found mammal fossils during manual digging. The use of systematic collecting techniques increased since the late 1950s and early 1960s. These include planned excavations as well as systematic screen-washing of sediment samples of the major sites.

Table 1 Localities mentioned in the text and figures arranged alphabetically following the acronyms used in Figs. 1, 2 and 4. For each site we indicate its correlation to the local zones as well as to the MN units. In the case of long local sections that comprise several sites (ACM, ECM, EDAR) we give the acronym for the series but not individual acronyms for each site. In the case of the ACM series the whole biostratigraphic range covered by the series is given.

acronym	**site/series**	**local zone**	**local subzone**	**MN unit**
ACM	Abocador de Can Mata series (includes more than 250 sites)	*Hispanomys* assemblage	*M. crusafonti+D. larteti – D.crusafonti-Hippotherium* interval	MN6–MN7+8
B40OV	Autovia Orbital de Barcelona B40 Tram Olesa de Montserrat-Viladecavalls (includes 6 sites)	*Cricetulodon* range	*C. hartenbergeri*	MN9
CA	Can Canals	-	-	MN4
CAL	Can'Almirall	*Hispanomys* assemblage	*M. crusafonti+D. larteti*	MN6
CB	Castell de Barberà	*Hispanomys* assemblage	*Hippotherium–C. hartenbergeri* interval	MN9
CBL	la Costablanca	-	-	MN3
CCN20	Creu Conill 20	*Hispanomys* assemblage	*Hippotherium–C. hartenbergeri* interval	MN9
CCN22	Creu Conill 22	*Hispanomys* assemblage	*Hippotherium–C. hartenbergeri* interval	MN9
CCT2	Camí de Can Tarumbot 2	*Rotundomys* abundance	*R. montisrotundi*	MN10
CF	Can Sant Feliu (also known as Can Feliu)	*Hispanomys* assemblage	*Hippotherium-C. hartenbergeri* interval	MN9
CFEU	Can Feu (includes 2 sites)	*Cricetulodon* range	*C. hartenbergeri–P. hispanicus* interval	MN9
CJ	Can Julià	-	-	MN4
CL1	Can Llobateres 1	*Cricetulodon* range	*C. hartenbergeri–P. hispanicus* interval	MN9
CL2	Can Llobateres 2	*Cricetulodon* range	*C. sabadellensis+P. hispanicus*	MN10
CM1	Can Mata 1	*Hispanomys* assemblage	*D.crusafonti-Hippotherium* interval	MN9
CM3	Can Mata 3	*Hispanomys* assemblage	*Hippotherium-C. hartenbergeri* interval	MN7+8
CMI	Can Missert	*Hispanomys* assemblage	*Hippotherium–C. hartenbergeri* interval	MN9

Table 1 *(Continued)*

acronym	site/series	local zone	local subzone	MN unit
CMV	Can Martí Vell (includes 2 sites)	-	-	MN4
CO	les Conilleres	*Hispanomys* assemblage	*M. crusafonti+D. larteti*	MN6
CP	Can Poncic 1	*Cricetulodon* range	*C. hartenbergeri*	MN9
CPL	Can Pallars de Llobateres (includes 2 sites)	*Cricetulodon* range	*C. hartenbergeri–P. hispanicus* interval	MN9
CPU	Can Purull	-	-	MN10
CRU	Can Cruset (includes 2 sites)	*Rotundomys* abundance	*R. bressanus*	MN10
CS	els Casots	-	-	MN4
CSB	Can Casablanca	*Rotundomys* abundance	*R. montisrotundi*	MN10
CT	Can Turu	*Rotundomys* abundance	*R. bressanus*	MN10
CV	Ceràmiques Viladecavalls	*Rotundomys* abundance	*R. montisrotundi*	MN10
EC	el Canyet	-	-	MN4
ECM	Ecoparc de Can Mata series (includes 12 sites)	*Hispanomys* assemblage	*Hippotherium-C. hartenbergeri* interval	MN9
EDAR	Estació Depuradora d–Aigües Residuals del Riu Ripoll (includes 15 sites)	*Cricetulodon* range	*C. hartenbergeri*	MN9
GO	La Gornal	-	-	MN6?
LTR1	La Tarumba 1	*Rotundomys* abundance	*R. montisrotundi*	MN10
LV	les Cases de la Valenciana	-	-	MN4
PA	les Escletxes del Papiol	-	-	MN4
PO	Polinyà (includes 4 sites)	-	-	MN9
RK11	Autopista de Rubí-Terrassa K11	*Hispanomys* assemblage	*D. crusafonti–Hippotherium* interval	MN7+8
ROS-A1	Ronda Oest de Sabadell A1	*H. vireti* range	-	MN11

Table 1 *(Continued)*

acronym	**site/series**	**local zone**	**local subzone**	**MN unit**
ROS-D6	Ronda Oest de Sabadell D6	*Rotundomys* abundance	*R. bressanus*	MN10
RR	Riu Ripoll	*Rotundomys* abundance	*R. montisrotundi*	MN10
RT10	Autopista de Rubí-Terrassa 10	*Rotundomys* abundance	*R. montisrotundi*	MN10
RT12	Autopista de Rubí-Terrassa 12	*Cricetulodon* range	*C. sabadellensis+P. hispanicus*	MN10
RT3B	Autopista de Rubí-Terrassa 3B	*Cricetulodon* range	*C. hartenbergeri*	
RT3C	Autopista de Rubí-Terrassa 3C	*Hispanomys* assemblage	*M. crusafonti+D. larteti*	MN6
RT6	Autopista de Rubí-Terrassa 6 (includes 4 sites)	*Cricetulodon* range	*C. hartenbergeri*	MN9
RT7	Autopista de Rubí-Terrassa 7 (includes 2 sites)	*Cricetulodon* range	*C. sabadellensis+P. hispanicus*	MN10
RT8	Autopista de Rubí-Terrassa 8	*Cricetulodon* range	*C. sabadellensis+P. hispanicus*	MN10
SAB	Sant Andreu de la Barca	-	-	MN4
SM	Sant Mamet	-	-	MN4
SMT	Sant Miquel de Toudell	-	-	MN10
SPR	Sant Pere de Ribes (includes the sites: Viñedos and Pedrera C1)	-	-	MN6? MN7+8?
SQ	Sant Quirze (includes several classical sites plus 3 microvertebrate sites)	*Hispanomys* assemblage	*D. crusafonti–Hippotherium* interval	MN7+8
TF	Torrent de Febulines (includes 6 sites)	*Rotundomys* abundance	*R. bressanus*	MN10
TFR	Turó de les Forques (also known as Costablanca II)	-	-	MN3
TNA	Trinxera Nord Autopista (includes 2 sites)	*Rotundomys* abundance	*R. bressanus*	MN10

Table 1 *(Continued)*

acronym	**site/series**	**local zone**	**local subzone**	**MN unit**
TSA	Trinxera Sud Autopista (includes 4 sites)	*Rotundomys* abundance	*R. bressanus*	MN10
TT	Torrentet de Traginers (also known as Piera)	*O. adroveri* range	-	MN12
VI	Vilobí	-	-	MN4
VI20	Vilobí 20	-	-	MN5? MN6?

During the early 1980s screen-washing techniques were improved, with the introduction of sieving equipment capable of processing huge sediment samples (Daams and Freudenthal, 1988). Therefore, larger micromammal samples, comprising between fifty to a few hundreds of individuals, could be gathered for many known sites. During the 1990s and the 2000s, most of the mammal sites known to date were discovered as a result of emergency campaigns coinciding with major construction projects. Macromammal remains were mostly collected after systematic excavation, whereas screen-washing was used for the micromammals. Thus, most of the material has been obtained using standardised collecting methods. The material is kept in the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP) at Sabadell, except for part of the old collections, which are curated in the Geology Museum of the Barcelona Seminary and in the Museum of Natural Sciences of Barcelona.

3.2. Magnetostratigraphy

Magnetostratigraphic sampling in the Vallès-Penedès Basin started during the mid 1990s (Garcés et al. 1996) and focused on the Vallesian successions. More recent studies have complemented these data with those from long sections covering the Late Aragonian and its transition to the Vallesian (Alba et al. 2012a; Moyà-Solà et al. 2009). The sequences studied for magnetostratigraphy include four main sections: Abocador de Can Mata, Les Fonts, Mon tagut and Viladecavalls, plus a few shorter ones (Fig. 4). These sequences contain abundant mudstone beds, which allowed a tight sampling resolution of 1–2 m/site. Routine stepwise demagnetization of the natural remanence magnetization revealed the presence of a stable magnetization carried by iron oxides such as magnetite and hematite. Since magnetostratigraphy relies on the demonstrably primary character of the rock magnetization, a number of stability tests (Opdyke and Channel, 1996) were performed. In the Vallès-Penedès sequences, the relative uniformity of bedding dip attitudes made the fold test insignificant, but a northerly directed mean direction after tilt correction suggests a pre-folding magnetization. A positive conglomerate test further supported a primary, synsedimentary origin. More significantly, magnetostratigraphic results could be cross-checked with biostratigraphy along multiple composite sections of Montagut, Les Fonts, Terrassa and Viladecavalls (Fig. 4), thus indicating that the retrieved magnetic zonation bears chronostratigraphic significance.

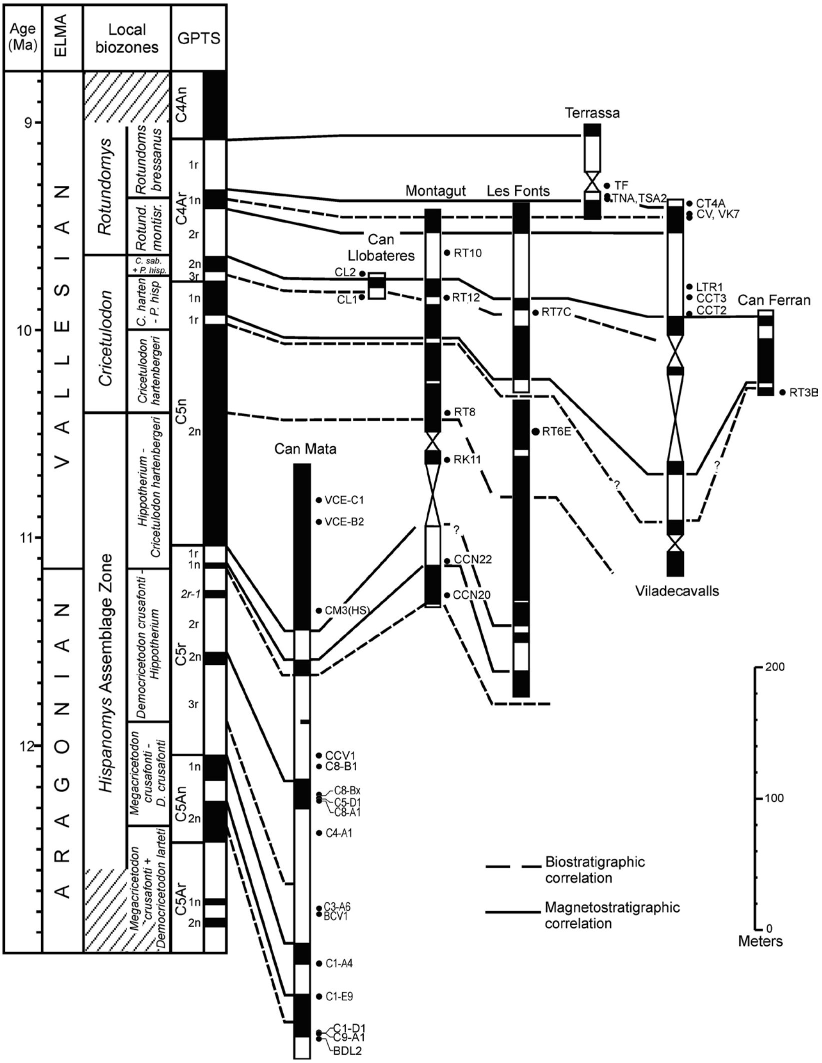

Fig. 4. Correlation of the key local magnetostratigraphical sections of the Vallès-Penedès Basin to the Geomagnetic Polarity Time Scale (GPTS). The European Land Mammal Ages (ELMA) and local biozones of the Vallès-Penedès are also indicated.We have indicated some of the major sites in the Can Mata composite series. Abbreviations in the Can Mata composite series refer to different sectors of the landfill and nearby farm houses as follows: ACM: Abocador de Can Mata [Can Mata landfill]; BCV: Barranc de Can Vila [Can Vila ravine]; BDL: Bassa de Decantació de Lixiviats [setting pond of leachates]; C1–C9: ACM cells 1 to 9; CCV: Camí de Can Vila [Can Vila road]; CM: Can Mata. For other locality acronyms, see Table 1. Neogene time scale and boundaries after Hilgen et al. (2012). GPTS after Ogg (2012).

3.3. Calculation of sampling probability and taxonomic richness

Time series diversity analyses require a great accuracy in the dating of individual sites as well as a well-resolved taxonomy (see Badgley et al. this issue). Considering the quality of our data, diversity analyses can only be performed for the late Aragonian and early Vallesian, for which most of the sites have associated bio- and magnetostratigraphical data of high quality. Regarding the taxonomic data, the quality of the record is not the same for all mammal groups. Small mammals, and in particular the orders Rodentia and Eulipotyphla, are more abundant and have a more continuous record than large mammals. Furthermore, they have been thoroughly reviewed and genus-level identifications are available (Casanovas-Vilar et al. research in progress). Between the late Aragonian (12.6 Ma) and the end of the Vallesian (9.0 Ma) these orders are represented by more than 20,000 specimens from nearly 200 different sites. Our calculations are carried out at the genus level, excluding all the material that could not be identified to this taxonomic rank.

The calculation of sampling probability and generic richness requires the use of quantitative data. In this regard, we used the maximum number of individuals of each taxon, since this information is routinely written down in our collection inventories. Sampling probability was calculated using the method devised by Barry et al. (2002) (see also Badgley et al. and Flynn et al. this issue) as modified by Van der Meulen et al. (2005) and Van Dam et al. (2006). This method considers the probability of finding a given taxon based on its abundance and sample size:

$$p = 1 - (1 - q)^{r}$$

where q is the relative abundance of the taxon in the interval where it was first (or last) recorded and r is the additional number of specimens sampled. A genus is considered to be absent when the cumulative probability of finding it over preceding or succeeding time intervals is greater than 0.9. Not surprisingly, the inferred range for a given taxon may extend beyond its last observed record and earlier than its first observed record. This is ultimately related to its abundance, so that rare taxa tend to have long inferred ranges unless sample size is large enough to reject that they were present. We used a range-through assumption, so we consider a genus to be continuously present between its first and last appearances. This assumption is in contrast with Van der Meulen et al. (2005) who interpreted discontinuous ranges as local extinctions followed by subsequent migrations. In our case only a few very rare taxa show discontinuous ranges, so we rather attribute their absence to sampling biases. The studied time span (12.6–9.0 Ma) was divided into 0.1 Myr bins, and observed and inferred genera ranges were used to calculate generic richness for each bin (Fig. 7). Considering that the typical extent of time-averaging for terrestrial vertebrate assemblages in fluvial systems and surface accumulations oscillates between 100 and 100,000 years (Behrensmeyer, 1982; Behrensmeyer et al. 2000), shorter time bins are not recommended. Finally, we have evaluated the effects of sample size in the calculation of these richness measures using the Spearman's rank order correlation test.

4. Chronological framework and locality age estimation

The chronostratigraphic framework of the Vallès-Penedès Basin is based on a combination of magneto- and biostratigraphic data. Unfortunately, magnetostratigraphic studies are still in progress for the older part of the record (Ramblian–middle Aragonian), so for this interval the age of the sites and main bioevents can only be constrained on the basis of biostratigraphy. The same applies to the Turolian sites. In contrast, most of the Late Aragonian and Vallesian sites are placed in the composite magnetostratigraphic framework, which have a total thickness of approximately 700 m (Fig. 4). The overall record results in a long pattern of polarity reversals, which allows a correlation with the GPTS (Ogg, 2012) using the unambiguous identification of chron C5n, a distinctly long normal chron that characterises the Early Tortonian as a reference point. This chron is recognized both in the Vallès sector (Garcés et al. 1996) and in the Can Mata composite series of els Hostalets de Pierola (Moyà-Solà et al. 2009), in the Penedès sector. The overall magnetostratigraphic sequence represents a time span of approximately 3.6 Myr, from 12.6 to 9.0 Ma (Fig. 4). Shorter sections, such as Terrassa or Can Llobateres, cannot be directly matched to the GPTS, but can be reliably correlated to longer sections on the basis of biostratigraphical and magnetostratigraphical data. An absolute age up to the 0.1 Myr bin could be assigned to most of these sites. Finally, approximately 35% of the sites (mostly older collections) of this period lack associated magnetostratigraphical data. Therefore, their correlation relies entirely on local biostratigraphy, which usually implies an age uncertainty not higher than 0.3 Ma (see below and Fig. 5). However, our analyses require that each site is assigned an absolute age, so a random age between its maximum and minimum possible ages is given to the sites with only biostratigraphical data.

Concerning the sites with associated magnetostratigraphical information, an absolute age can be estimated using the methods of Barry et al. (2002). The calculations are based on the stratigraphic position of a given site in the local magnetostratigraphic series. The interpolation must be done between two points of known ages, namely polarity changes in the section that correspond to chron boundaries. Then age is calculated as follows:

$$Age = UAge + \left(\frac{(LAge - UAge)}{T} \cdot SD \right)$$

where Age is the estimated absolute age of the locality; UAge and LAge are the ages of the upper and lower boundaries of the geomagnetic chron, respectively; T is the stratigraphic thickness of that magnetozone in the local section; and SD is the stratigraphic distance between the locality and the top of the magnetozone in the same section. When one of the chron boundaries is not recorded in the section, Age is calculated using the composite sections that do record the chron boundaries. This method assumes constant sedimentation rates within each magnetozone, a condition which strictly speaking will not be fulfilled because the sedimentation in alluvial fan systems is episodic and there are short periods of erosion, leading to the existence of many short hiatuses (Sadler, 1981). However, if these hiatuses are randomly distributed within the sections and their duration is not large compared to the duration of an interval, this approach will give reliable results (Badgley et al. 1986; Barry et al. 2002; Johnson et al. 1988). In our study case, the relative stratigraphic thickness of the corresponding geomagnetic intervals is comparable between sections, implying similar sedimentation rates. Furthermore, no major hiatuses are known during the late Aragonian and the Vallesian.

5. The Miocene mammal succession: biostratigraphy, main bioevents and palaeoenvironmental reconstruction

Throughout the text, the Vallès-Penedès record is cor related to the European Land Mammal Ages as well as to the MN zonation. We have used the mammal ages that are customarily used for the Iberian record. This implies some differences for the Early and Middle Miocene, since the Aegenian, Orleanian and Astaracian ages are replaced by the Ramblian and the Aragonian ages (see Steininger, 1999). For the internal subdivision and boundaries of these ages, the reader is referred to Daams and Freudenthal (1989), Agustí et al. (2011) and Larrasoaña et al. (2006) for the Ramblian, and to Daams et al.

(1999), Agustí et al. (2011), Van der Meulen et al. (2011, 2012) and García Paredes et al. (this issue) for the Aragonian. As far as MN zones are concerned, we follow the more 'biostratigraphical' concept of the MN zones (see Hilgen et al. 2012; Van Dam, 2003) and use the boundaries for western Europe. The MN boundaries for central Europe are significantly older, particularly for the Early Miocene; the reader is referred to Van der Meulen et al. (2011, 2012) for a comparison. MN zone boundaries are based on different sources: for the Ramblian, zone boundaries follow Larrasoaña et al. (2006), Agustí et al. (2011) and Hilgen et al. (2012); for the Argonian, they are mostly based in Daams et al. (1999), Agustí et al. (2011) and Van der Meulen et al. (2011, 2012); those of the Vallesian follow Agustí et al. (2001) and Hilgen et al. (2012); and finally, for the Turolian we follow Van Dam et al. (2001, 2006) and Hilgen et al. (2012).

5.1. The Ramblian (ca. 20.4–16.8/17 Ma)

The Early Miocene successions of the Vallès-Penedès Basin have produced relatively few sites, and many of them, particularly the older ones, are very poor. Crusafont et al. (1955) systematically surveyed this part of the record and found about fifteen mammal-bearing sites, although many of them have since been destroyed (Casanovas-Vilar et al. 2011b). In recent years, some classical sites (such as Costablanca or Molí Calopa) have been surveyed again in order to sample microvertebrates, which had been overlooked by earlier researchers. The correlation of these localities is entirely based on biostratigraphy. Magnetostratigraphical studies are now in progress.

The oldest site in the Vallès-Penedès Basin is Turó de les Forques (TFR, Figs. 1 and 2), which is located in a small outcrop of the Basal Breccia Unit. This site contains scarce macromammal remains and a richer rodent assemblage that includes the cricetid *Melissiodon*, the eomyid *Ligerimys* cf. *fahlbuschi*, the glirid *Pseudodryomys ibericus*, and scarce remains of the cricetodontine Democricetodon. The first common occurrence of Democricetodon marks the beginning of the Aragonian, but this genus is already recorded in the latest Ramblian, though it is very rare (Van der Meulen et al. 2012; García-Paredes et al. this issue). Therefore, this site is correlated with the late Ramblian zone A, which according to the latest data from the Ebro Basin would range between 19.6 and 16.8–17 Ma (Larrasoaña et al. 2006). The Ramblian is chronologically equivalent to zone MN3 and its upper part corresponds to the so called "cricetid vacuum" (Daams and Freudenthal, 1989), that is, the time interval between the last occurrence of the old Oligocene cricetids of the genus *Eucricetodon* and the earliest cricetodontines of the genus *Democricetodon*. During this time *Melissiodon*, a peculiar genus showing a unique "honeycomb" molar morphology, is the only cricetid present in western Europe.

The remaining Ramblian sites of the Vallès-Penedès show a similar rodent fauna dominated by the glirid genera *Pseudodryomys* and *Simplomys*, as well as eomyids of the genus *Ligerimys*. Relatively rich Ramblian macromammal faunas are known from Molí Calopa, Costablanca and Sant Andreu de la Barca (MC, CBL and SAB in Figs. 1 and 2). These include abundant remains of the minute artiodactyl *Cainotherium miocaenicum*, although the cervid *Procervulus dichotomus* is also common (Casanovas-Vilar et al. 2011a, 2011b). The equid *Anchitherium* and the felid *Styriofelis* are present at various sites, whereas the first gomphotheres (*Gomphotherium*) are recorded at Sant Andreu de la Barca (Agustí and Galobart, 1997). Mein (1975a) used the earliest record of proboscideans in Europe to characterise the MN4 zone (16.8/17–16/16.4 Ma), but for Western Europe the first common occurrence of *Democricetodon* is now used as diagnostic criterium for the base of this zone and the beginning of the Aragonian (Hilgen et al. 2012; Van der Meulen et al. 2011, 2012). In the Vallès-Penedès (Sant Andreu de la Barca) and France (Navère; Bulot and Ginsburg, 1993) the record of proboscideans precedes that of *Democricetodon*, and is therefore placed in the late MN3, with an age ranging from 19.6 to 16.8/17 Ma. This age is congruent with recent dating of the proboscidean dispersal event in Central Europe at ca. 17.5 Ma (Pálfy et al. 2007). However, the appearance of this order in other areas of Eurasia is substantially older, with deinotheres present at the Pakistan Siwaliks at around 23 Ma (Flynn et al. 2013) and an unidentified elephantoid having been reported from the Latest Oligocene of the Bugti Hills (Antoine et al. 2003, 2013).

Macroplant remains are abundantly reported from the shallow lacustrine levels of the Costablanca series and offer a detailed picture of the local palaeoenvironment surrounding the humid areas (Sanz de Siria Catalán, 1993, 2001). The recovered flora points to a tropical to subtropical climate with rainfall seasonality (Sanz de Siria Catalán, 1993, 2001). This reconstruction is congruent with the small mammal fauna, which is dominated by glirids with a simple dental pattern that purportedly preferred more arid environments than most of their relatives (Van der Meulen and De Bruijn, 1982). However, the large mammal fauna, which includes basal pecorans (*Amphitragulus*), cervids (*Procervulus*) and small browsing equids (*Anchitherium*), is more consistent with forested environments (Casanovas-Vilar et al. 2011a).

5.2. The early Aragonian (16.8/17–16/16.4 Ma)

The early Aragonian is chronologically equivalent to the MN4. The sites are located in facies of small lacustrine systems or in distal facies of alluvial fans (Figs. 1 and 2). Most of the known localities were first reported by Crusafont et al. (1955). The richest sites belong to the Subirats unit, in the Penedès sector, which is defined by an alternation of lutites and carbonates that correspond to shallow lakes and the distal facies of alluvial fans (Agustí and Cabrera, 1980; Cabrera, 1981a, 1981b). These include les Cases de la Valenciana, Can Martí Vell, and more importantly Els Casots (LV, CMV and CS, Fig. 1). Els Casots was excavated during the 1990s and has produced a rich collection of micro and macromammals in a remarkable state of preservation (Casanovas-Vilar et al. 2011c). In the Vallès sector,the early Aragonian sites are located in red lutites corresponding to the distal facies of major fan systems. Some sites, such as les Escletxes del Papiol or Sant Mamet (PA and SM, Fig. 2) are just a few metres below the Langhian marine units. The Vallès sites have mostly micromammals.

The beginning of the Aragonian is marked by the first abundant occurrence of the cricetodontines *Democricetodon* and, slightly later, *Megacricetodon* (Daams and Freudenthal, 1988, 1989; Daams et al. 1999; Van der Meulen et al. 2012; García-Paredes et al. this issue). These cricetids originated in Asia (Flynn and Wessels, 2013; Maridet et al. 2011) and soon after their earliest record in Western Europe they became major components of the Aragonian and earliest Vallesian faunas (e.g., Daams et al. 1988). In the Aragonian type area, the Calatayud-Montalbán Basin, the presence of *Megacricetodon* distinguishes local zones B and C, both covering the early Aragonian (Daams and Freudenthal, 1988; Daams et al. 1999; Van der Meulen et al. 2012; García-Paredes et al. this issue). In the Vallès-Penedès, *Democricetodon* (*D. hispanicus*) and *Megacricetodon* (*M. primitivus*) coexist in all the studied localities but in Sant Mamet. However, the absence of *Megacricetodon* may be due to insufficient sampling. Furthermore, the paracricetodontine *Eumyarion* (*E. weinfurteri*) is also present in this site (Agustí, 1981), and its first appearance in other Spanish basins is in zone C (Daams and Freudenthal, 1974; Ruiz-Sánchez et al. 2003; Van der Meulen et al. 2012; García-Paredes et al. this issue). Even though *D. hispanicus* and *M. primitivus* dominate the rodent assemblages in most sites, the eomyid *Ligerimys ellipticus* and the glirids *Pseudodryomys ibericus* and *Simplomys simplicidens* are common components as well (Agustí, 1981, 1983; Agustí and Llenas, 1993; Casanovas-Vilar et al. 2011c). None of the known sites in the Vallès-Penedès could be correlated to the lowermost Aragonian (zone B), where characteristically *Democricetodon* is the only cricetid genus present. Interestingly, the Calatayud-Montalbán local zones could be extended to the Ramblian and Early Aragonian record of the Vallès-Penedès (Casanovas-Vilar et al. 2011a, 2011b), a situation contrasting with that of the late Aragonian and especially the Vallesian, when the rodent succession shows marked differences between these areas.

Most of our data on the Early Aragonian large mammal faunas of the Vallès-Penedès come from the site of els Casots (Casanovas-Vilar et al. 2011c and references therein). The suid *Eurolistriodon*, the early bovid *Eotragus* and the tragulid *Dorcatherium* appear for the first time (Agustí et al. 1985; Casanovas-Vilar et al. 2011a, 2011c). At this time, deinotheres are first recorded, being scarcely represented at Els Casots and Les Escletxes del Papiol.

Cainotherium persists, but is rarer than in earlier sites. The suoids (*Eurolistriodon*, *Taucanamo*), palaeomerycids (*Ampelomeryx*) and some rhinoceroses (*Plesiaceratherium*) are common among the large mammal faunas. The most abundant carnivores are the amphicyonids (*Amphicyon*) and ursids (*Hemicyon*, *Plithocyon*).

5.3. The middle Aragonian (16/16.4–13.8 Ma)

During the Langhian (15.97–13.65 Ma), great parts of the basin were covered by a shallow sea embayment, so it is not surprising that no mammal sites are correlated to the approximately time-equivalent middle Aragonian, which equals to MN5. However, some portions of the Vallès sector were exposed at that time, so they might potentially yield sites of this age. On the other hand, there are numerous palaeobotanical sites around the towns of Martorell and Sant Sadurní d'Anoia. These have produced a rich collection of macroflora, indicating that the environment was slightly more arid than during the Ramblian (Sanz de Siria Catalán, 1993, 2001). In addition, palynological samples have been collected from marine sediments close to the small reef systems of Sant Pau d'Ordal, located just a few kilometres to the south of Sant Sadurní d'Anoia (Bessedik and Cabrera, 1985). The pollen assemblage indicates the presence of Avicennia mangroves in the coastline.

5.4. The late Aragonian (13.8–11.2 Ma)

The late Aragonian is one of the best represented time intervals in the Vallès-Penedès Basin. Most of our knowledge of this period derives from the study of the intensively-sampled Can Mata composite series at els Hostalets de Pierola (Penedès sector; Fig. 1). This series (Fig. 4) comprises the sections of the Abocador de Can Mata landfill (ACM), the Ecoparc de Can Mata (ECM), and a few nearby classical sites (Can Mata 1 and 3), which together include more than 200 mammal sites that have produced tens of thousands of specimens (Alba et al. 2011). The Can Mata composite series ranges from about 12.5 Ma to 10.6 Ma, the age of the sites being well constrained thanks to a combination of detailed litho-, bio- and magnetostratigraphical data (Fig. 4; Alba et al. 2011; Casanovas-Vilar et al. 2011d; Moyà-Solà et al. 2009). In addition to the Can Mata series, there are a number of other sites that have been correlated to the Late Aragonian. These include the classical Sant Quirze sites (SQ, Fig. 2), Can Almirall and Les Conilleres (CAL and CO, Fig. 1; Agustí et al. 1985). The latter two are placed in the upper transitional facies of the Marine and Transitional Unit and in palustrine facies related to fluvial sequences in the Penedès sector. Agustí et al. (1985) reported the presence of the cricetids *Cricetodon* aff. *jotae*, *Eumyarion medium* and *Megacricetodon crusafonti*, which would indicate a correlation to MN6. However, the fauna has not been studied in detail, so other correlations can not be ruled out. On the other hand, certain sites that had been traditionally placed in the Late Aragonian, namely Can Missert and Castell de Barberà (CM and CB, Fig. 2), are here correlated to the Early Vallesian because scarce hipparionin remains were identified during a recent review of the collections (Robles et al. 2011; Rotgers and Alba, 2011).

A high-resolution biozonation for the late Aragonian and Vallesian has been devised on the basis of the rodent fauna (Casanovas-Vilar et al. 2011d and research in progress). The late Aragonian rodent assemblages are characterized by the dominance of the cricetids *Hispanomys*, *Democricetodon* and *Megacricetodon*. Usually, *Hispanomys* is the most abundant taxon, being represented by several different species during this time interval. This allows defining a long *Hispanomys* Assemblage Zone that covers the late Aragonian and earliest Vallesian (c. 12.5–10.3 Ma, Fig. 5). The coexistence of different species of *Megacricetodon* and *Democricetodon*, as well as the first record of the equid *Hippotherium*, allow the subdivision of the *Hispanomys* zone into four subzones (Fig. 5): *M. crusafonti + D. larteti* Concurrent Range Subzone (?–12.4 Ma); *M. crusafonti - D. crusafonti* Interval Subzone (12.4–11.9 Ma); *D. crusafonti-Hippotherium* Interval Subzone (11.9–11.2 Ma); *Hippotherium - Cricetulodon hartenberger* Interval Subzone (11.2–10.3 Ma). The last corresponds to the earliest Vallesian, whereas the previous three correlate to the late Aragonian. Even though the faunal succession is not the same, these subzones can be correlated with the local zones of the Calatayud-Montalbán Basin (Daams et al. 1999). Subzone G2 from Calatayud Montalbán would be approximately equivalent to the *M. crusafonti + D. larteti* subzone, whereas the subzone G3 would be equivalent to the *M. crusafonti - D. crusafonti* and the *D. crusafonti-Hippotherium* interval subzones in the Vallès-Penedès. Similarly, our zones can be correlated to the MN units, with the three Late Aragonian subzones being equivalent to the MN 7 + 8 (Hilgen et al. 2012). Nevertheless, if one follows the definition of the MN zones of Agustí et al. (2001) or Mein (1999), the older subzone (*M. crusafonti + D. larteti*) would be equivalent to the uppermost part of the MN6.

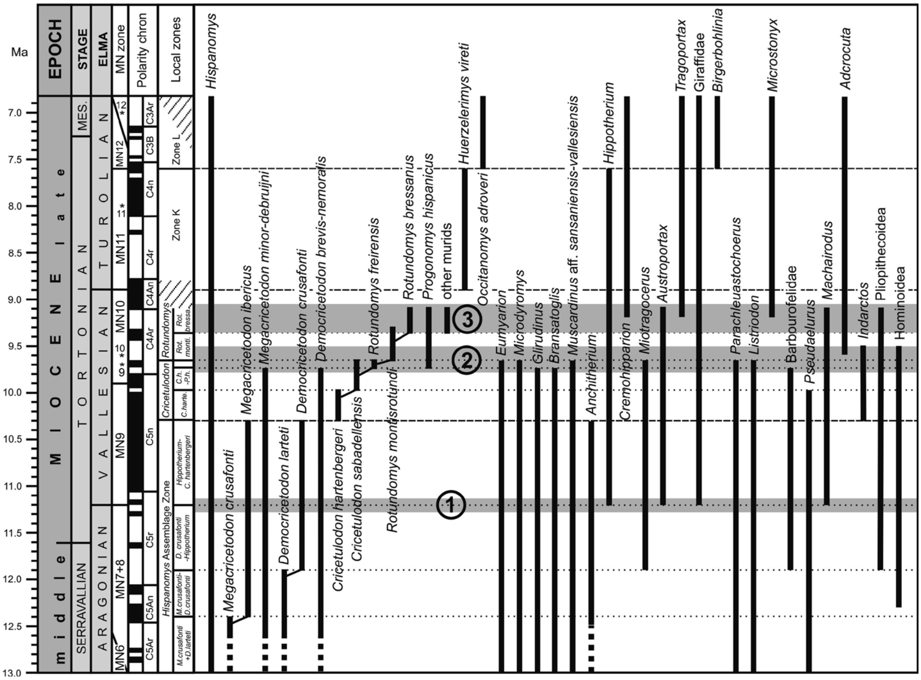

Fig. 5. Local biozonation of the Vallès-Penedès Basin for the late Aragonian to the middle Turolian. The observed ranges of the biostratigraphically important taxa are indicated. The shadowed time intervals highlight the times of major faunal turnover: 1) dispersal of hipparionin horses and some eastern faunal elements (*Machairodus*, Giraffidae) at the Aragonian/Vallesian boundary; 2) Vallesian Crisis, implying the disappearance of many forest elements of Middle Miocene origin and coinciding with the first record of murids (*Progonomys hispanicus*) and the cricetines of the genus *Rotundomys*; 3) diversification of the murids and dispersal of the first 'Pikermian' elements such as the bovid *Tragoportax* and the hyaenid *Adcrocuta*. See main text for details. In the case of the MN zones, asterisks indicate the chronological position of their reference sites, whereas their boundaries are defined on the basis of selected appearance events (see Hilgen et al. 2012). Neogene time scale and boundaries after Hilgen et al. (2012). GPTS after Ogg (2012).

As explained above, the late Aragonian small mammal faunas are dominated by *Hispanomys*, *Democricetodon* and *Megacricetodon*. The paracricetodontine *Eumyarion* may be very common at certain sites, such as ACM/BCV1 (see Fig. 4). The glirids are diverse though not abundant and include mostly purported forest-dwelling genera (*Bransatoglis*, *Muscardinus*, *Glirudinus*, *Myoglis*). The small eomyids *Keramidomys* and *Eomyops* as well as the flying squirrels (*Albanensia*, *Miopetaurista*) are first recorded in the *M. crusafonti* + *D. larteti* subzone, ca. 12.5 Ma. Castorids (*Chalicomys*) are first recorded ca. 11.9 Ma, but are very rare. The hypsodont cricetid *Anomalomys*, appears for the first time at ca. 11.8 Ma. The eulipotyphlan faunas are diverse (e.g., Furió et al. 2011, 2015) and include talpids (*Desmanella*, *Talpa*), dimylids (*Plesiodimylus*), heterosoricids (*Dinosorex*), abundant erinaceids (*Galerix*, *Parasorex*) and crocidosoricine soricids.

The large mammal faunas are also diverse (Alba et al. 2011). The megaherbivores include two different genera of proboscideans (Gomphotherium, Deinotherium), rare chalicotheres (*Anisodon*) and diverse rhinos (*Alicornops*, *Hoploaceratherium*, *Lartetotherium*). The suoids (*Albanohyus*, *Conohyus*, *Listriodon*, *Propotamochoerus*) are also diverse and common, whereas the cervid *Euprox* may be common at some sites. There is a remarkable diversity of carnivorans, including mustelids, hyaenids, felids (*Pseudaelurus*, *Styriofelis*) and false sabertooths (the barbourofelid *Albanosmilus*). The suid *Listriodon splendens*, the small and short-legged rhino *Alicornops* and specially the moschid *Micromeryx* are the most abundant large mammals in the Can Mata composite series. Hominoids (*Anoiapithecus brevirostris*) are first recorded at around 12.3–12.4 Ma (Alba et al. 2013). This group shows a remarkable diversity around 11.9–12 Ma (*M. crusafonti–D. crusafonti* Interval Subzone), being represented by the genera *Dryopithecus*, *Anoiapithecus* and *Pierolapithecus* (Casanovas-Vilar et al. 2011d). Pliopithecoids first occur slightly later, at around 12 Ma (Alba et al. 2012b), but are mostly recorded between 11.8–11.7 Ma (*D. crusafonti-Hippotherium* Interval Subzone), being represented by the genus *Pliopithecus*. The cervid *Euprox furcatus*, a common component of the fauna, is first recorded during the *M. crusafonti* + *D. larteti* subzone. Other ruminant groups, such as the bovids and the tragulids, are generally rare. Amongst the bovids, *Miotragocerus* and *Tethytragus* first occur during the *D. crusafonti-Hippotherium* Interval Subzone. *Tethytragus*, an abundant genus in the inner Iberian basins, is restricted to this zone, being represented by scarce remains only.

Overall, the late Aragonian faunas of the Vallès-Penedès Basin stand out by their high diversity due to the presence of a number of taxa that are extremely rare or not recorded at all in other Iberian Basins (Agustí, 1989; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al. 2008; DeMiguel et al. 2011). These taxa are traditionally recognized as forest dwellers, shared by the Vallès-Penedès and other European regions such as France and Germany, but absent from inner Spain. Amongst the small mammals these include certain eulipotyphlans (dimylids, talpids), arboreal glirids, pteromyinins, eomyids, andcertaincricetids such as *Eumyarion* and *Anomalomys*. The large mammal faunas are congruent with the occurrence of more forested environments, since certain taxa such as hominoids, pliopithecoids or chalicotheres are not recorded from elsewhere in the Iberian Peninsula. Others, such as suoids and rhinocerotids, are more abundant and usually more diverse in the Catalan basins. Unfortunately, there is no time-equivalent palaeobotanical data that could provide a more complete picture of the Late Aragonian palaeoenvironments in the basin.

5.5. The early Vallesian (11.2–9.73 Ma)

The Vallesian mammal successions have been the subject of multiple reviews, given that the Vallès-Penedès is the type area for this mammal age (Agustí and Moyà Solà, 1990; Agustí et al. 1985, 1997; Casanovas-Vilar et al. 2011a, 2011d; Moyà-Solà and Agustí, 1987, 1989). Most of the Vallesian sites are placed near the towns of Sabadell and Terrassa, in the Vallès sector of the basin (Fig. 2), and have associated magnetostratigraphical data (Fig. 4; Agustí et al. 1997; Garcés et al. 1996).

Crusafont Pairó (1950) defined the Vallesian on the basis of the coexistence of the first hipparionin horses with faunal elements that were characteristic of the forest faunas of the Middle Miocene, such as certain rhinos, cervids, suoids and chalicotheres. Previously, hipparionins were thought to be characteristic of the so-called Pikermian faunas, after the Turolian site of Pikermi, near Athens (Greece). The Pikermian faunas are dominated by open country herbivores, such as antelopes, giraffes and horses, whereas forest elements, such as deer, are rare (Bernor et al. 1996; Eronen et al. 2009; Solounias et al. 1999). Such faunas represent a rather uniform mammal community from the standpoint of their ecological characteristics, not necessarily at the taxonomic level of genera and species. The Pikermian fauna expanded its range into Western Europe during the Turolian (Bernor, 1983, 1984; Eronen et al. 2009). However, Crusafont Pairó (1950) showed that some ‘Pikermian’ taxa such as the earliest hipparionins dispersed earlier. Currently this dispersal is placed within chron C5r.1n in the Vallès-Penedès Basin, with an estimated age of 11.2 Ma (Garcés et al. 1996, 1997; dates recalculated taking into account the latest version of the GPTS after Ogg, 2012). This age is not inconsistent with the record of the Calatayud Montalbán Basin, where the entry could be placed between 11.2 and 10.8 Ma (Garcés et al. 2003; Van Dam et al. 2014; García-Paredes et al. this issue).

It is also congruent with the data from Central Europe (Bernor et al. 1988; Woodburne, 2009; Daxner-Höck et al. this issue), but it is somewhat older than age estimates for this event in other areas (Sinap Formation, Siwaliks), which range from 10.8 to 10.3 Ma (Barry and Flynn, 1989; Barry et al. 1982, 1985, 2002; Flynn et al. 2013; Kappelman et al. 2003). The oldest occurrence of hipparionins (*Hippotherium*) is recorded at the lowermost part of the Montagut composite section (Fig. 4). However, the Aragonian/Vallesian transition is documented in the Can Mata composite series, the sites belonging to the ECM section and the classical locality of Can Mata 3 (CM3) being correlated to the Vallesian (Fig. 4). CM3 has numerous hipparionin remains, which would be slightly younger than the ones of the Montagut section. On the other hand, these equids are not recorded in any of the ECM sites. The earliest Vallesian rodent faunas cannot be distinguished from those of the Latest Aragonian and are placed within the *Hispanomys* Assemblage Zone (Fig. 5). Only the presence of the equid *Hippotherium* confirms their Vallesian age. The *Hippotherium-Cricetulodon hartenbergeri* Interval Subzone defines the Earliest Vallesian. In some rodent faunas, the cricetodontine *Megacricetodon ibericus* may be extremely abundant, such as Creu Conill 22 or Can Feliu (CCN22, CF, Fig. 2).

The rest of the Vallesian subzones are defined on the basis of the evolution of the cricetine genera *Cricetulodon* and *Rotundomys*. The species present are members of a well-known anagenetic lineage (*C. hartenbergeri–C. sabadellensis–R. montisrotundi–R. bressanus*), characterised by its increasing hypsodonty coupled with a simplification of the molar pattern into a continuous sigmoidal crest (Freudenthal, 1967; Freudenthal et al. 1998; Mein, 1975b). The *Cricetulodon* Range Zone (Fig. 5) covers most of the early Vallesian (MN9) and the beginning of the late Vallesian (MN10). This zone is divided into three subzones depending on the *Cricetulodon* species present: *C. hartenbergeri* Range Subzone (10.3–10 Ma); *C. hartenbergeri–Progonomys hispanicus* Interval Subzone (10–9.7 Ma); and the short-lasting *C. sabadellensis* + *P. hispanicus* Concurrent Range Subzone (9.7–9.6 Ma). *Cricetulodon* is the most common element in these subzones and it may define up to 70% of the recovered remains. The genera *Democricetodon* and *Megacricetodon* are rare and only represented by the small-sized species. The castorids (*Chalicomys*, *Euroxenomys*) and the paracricetodontine *Eumyarion* are common at certain sites such as Can Llobateres 1 (CL1, Fig. 2). The micromammal faunas of this subzone are diverse in forest elements, particularly glirids. Eulipotyphlans reach their highest diversity, with at least three genera of erinaceids, two genera of dimylids and talpids, and four of soricids (Van den Hoek Ostende and Furió, 2005). The hitherto persisting heterosoricid *Dinosorex* is still a common element, but suddenly disappears from the micromammal assemblage at the very beginning of the Vallesian (Furió et al. 2015). The first occurrence of murids in Western Europe defines the boundary between Early and Late Vallesian, or between MN9 and MN10 (Agustí et al. 1997, 2001; Hilgen et al. 2012). *Progonomys hispanicus* is the earliest murid in the Vallès-Penedès, being recorded at several sites in the uppermost part of chron C4Ar.3r (Figs. 4 and 5), with an estimated age of 9.7 Ma. This rodent family evolved in the Middle Miocene in Pakistan (Jacobs, 1977), while the genus *Progonomys* first appeared in that area around 12 Ma (Barry and Flynn, 1989; Barry et al. 1982, 2002; Flynn et al. 1995, 2013; Wessels, 2009). Updated stratigraphic correlations attained in the Calatayud-Montalbán Basin (Van Dam et al. 2014; García-Paredes et al. 2015) show a very rare presence of *Progonomys* during the Early Vallesian, at 10.4 Ma, and a common occurrence of this form after 10.0–9.9 Ma. In Turkey, its first record is slightly older, at 10.1 Ma (Kappelman et al. 2003). In our study area, the dispersal of *Progonomys* coincides with the first appearance of *Rotundomys* (*R. freirensis*), although *C. sabadellensis* is still the dominant rodent in most assemblages. At the same time, a number of taxa are no longer recorded, including the cricetids *Democricetodon*, *Megacricetodon*, *Eumyarion* and the glirids *Microdyromys*, *Glirudinus*, *Bransatoglis* and *Muscardinus vallesiensis*. Castorids and pteromyines become rarer. This set of local extinctions is part of the Vallesian Crisis (see below).

Regarding the large mammals, the early Vallesian faunas retain large numbers of Late Aragonian components, so that the immigration of *Hippotherium* did not coincide with any noticeable extinction event (Agustí et al. 1997). Giraffids, the felid *Machairodus* and the bovid *Austroportax* immigrated at the same time (Casanovas-Vilar et al. 2011a; Fig. 5). The long-ranging felid *Pseudaelurus* is last recorded within the *C. hartenbergeri* subzone. The hominoid *Hispanopithecus* is recorded at several sites from the *Cricetulodon* zone (Casanovas-Vilar et al. 2011d). Overall, the Early Vallesian faunas are extremely diverse, including a high diversity of medium to large-sized herbivores and carnivore species (Agustí et al. 1997, 2001; Casanovas-Vilar et al. 2011a). Bovids became more diverse and abundant. This assemblage is very similar to that of contemporaneous sites from Central Europe (Casanovas Vilar et al. 2008, 2010), such as Rudabánya in Hungary (Bernor et al. 2005), which on the other hand has also produced great ape remains. Finally, the Early/Late Vallesian transition witnessed the extinction of several large mammal taxa of Middle Miocene origin in the context of the Vallesian Crisis (see below). These include the barbourofelid and amphycionid carnivorans, the suids *Listriodon* and *Parachleuastochoerus*, and the bovid *Miotragocerus*.

5.6. The Late Vallesian (9.7–8.9 Ma)

Even though the murids are continuously present in the Vallès-Penedès Basin, they remain usually rare components of the mammal faunas. This contrasts with the late Vallesian assemblages of other Iberian basins, such as the Teruel Basin, where murids are dominant and define the basis for local biostratigraphy (Van Dam, 1997; Van Dam et al. 2001). By contrast, the genus *Rotundomys* is the most abundant component of the faunas in the Vallès-Penedès, defining the *Rotundomys* Abundance Zone that covers most of the late Vallesian (Fig. 5). This is divided into two sub zones according to the member of the anagenetic lineage present: *R. montisrotundi* Lineage Subzone (9.6–9.4 Ma) and the *R. bressanus* Lineage Subzone (9.4–8.9 Ma). As the upper boundary for this zone we take the Vallesian/Turolian age boundary in the Teruel Basin (Krijgsman et al. 1996; Van Dam et al. 2001), since it is not recorded in any of the magnetostratigraphical sections of the Vallès-Penedès. The rodent faunas are less diverse than during the early Vallesian, although a number of forest elements are present in low numbers (Agustí et al. 1997, 1999; Casanovas-Vilar et al. 2011a; 2014). In the *R. montisrotundi* subzone, *Progonomys hispanicus* is the only murid species present, whereas in the *R. bressanus* subzone the murid assemblage is enriched with the appearance of *P. cathalai* and *P. woelferi* as well as the genera *Parapodemus* and *Huerzelerimys*. *Rotundomys montisrotundi* coexists for some time with its putative descendant, *R. bressanus*. The large mammal faunas record a number of new eastern immigrants, particularly during the *R. bressanus* subzone (Agustí et al. 1997; Casanovas-Vilar et al. 2011a; 2011d). These include the suids *Schizoporcus* and *Microstonyx*, the equid *Cremohipparion* and the bovid *Tragoportax*, which will later become major components of the Turolianfaunas.Amongst the carnivorans, the hyaenid *Adcrocuta* is first recorded within the *R. montisrotundi* subzone, whereas the ursid Indarctos is last recorded at the same time. Finally, hominoid primates (*Hispanopithecus*) are last recorded within this subzone, at the site of La Tarumba 1 (LTR1, Fig. 2), which has an estimated age of about 9.6 Ma (Casanovas-Vilar et al. 2011d). Pliopithecoids survived into the *R. bressanus* subzone, being last recorded at 9.1 Ma at Torrent de Febulines (TF, Fig. 2; Moyà-Solà et al. 2001).

The Vallesian biozonation of the Vallès-Penedès can be recognized in other Catalan basins, such as La Seu d'Urgell or the Empordà basins (Casanovas-Vilar et al. 2011b). However, it is different from that in other areas of Spain, such as the Calatayud-Montalbán Basin (Daams and Freudenthal, 1988; Daams et al. 1999) or the Teruel basins (Van Dam et al. 2001; Van de Weerd, 1976). While the order and timing of the main bioevents, such as the first record of *Cricetulodon* and *Progonomys*, are roughly the same, the major components of the faunas that are the basis for the local biozonations differ. For example, *Rotundomys* is not recorded in Teruel, and in the Vallès-Penedès the murids are too rare to be considered for the definition of local biozones. Casanovas-Vilar and Agustí (2007) emphasised these differences and related them to the occurrence of more humid and forested environments in the Vallès-Penedès, particularly during the Late Vallesian. Such an interpretation is supported by the distribution of other mammal taxa such as certain glirids, the flying squirrels, chalicotheres and hominoid primates, to name just a few examples.

Regarding the Vallesian palaeoenvironment, the diverse mammal fauna, rich in forest elements, has been interpreted as indicative of subtropical to warm-temperate humid forest environments (Agustí and Moyà-Solà, 1990; Agustí et al. 1984, 1999; Casanovas-Vilar and Agustí, 2007; Morales et al. 1999). Unfortunately, the palaeobotanical information of this period is very scarce, and has to be complemented with data from other Catalan basins (Empordà, Cerdanya). These show that the zonal vegetation consisted of a warm-temperate mixed forest defined by evergreen laurels, together with leguminous trees and shrubs as well as a significant proportion of deciduous elements (Sanz de Siria Catalán, 1993, 1994). The subtropical taxa would have been mostly restricted to the humid areas in the lowlands (Marmi et al. 2012). The rich Late Vallesian macroflora from Trinxera Sud Autopista 2 near Terrassa (TSA2, Fig. 2) indicates the presence of a warm-temperate mixed forest with up to 40% of deciduous taxa (Agustí et al. 2003).

5.7. The Turolian (8.9–5.3 Ma)

Only two Turolian sites are well known from the Vallès-Penedès: Ronda Oest de Sabadell A1 in Sabadell and Torrentet de Traginers in Piera (ROS-A1 and TT, Figs. 1 and 2). However, some fossiliferous areas, particularly around Viladecavalls and Piera, might potentially yield new Turolian sites. Furthermore, the Vallesian/Turolian transition could be recorded at the Ronda Oest de Sabadell succession (Fig. 2), although these faunas and their stratigraphic context have not been studied in detail yet. ROS-A1 has a relatively rich small mammal sample dominated by the murid *Huerzelerimys vireti*, which would indicate an early Turolian (MN11 or zone K) age (Agustí et al. 2001;Van Damet al. 2001, 2006). The large mammals are insufficiently known, but the faunas are significantly impoverished with bovids and *Hippotherium* dominating the assemblage. In contrast, Torrentet de Traginers (also known in the literature as Piera) has produced a rich large mammal fauna that includes more than 2700 specimens. Its diversity is remarkably low, far below that of the Vallesian assemblages. The fauna is overwhelmingly dominated by the bovid *Tragoportax gaudryi*, with the equid *Cremohipparion mediterraneum* and the giraffid *Birgerbohlinia schaubi* as major components (Fig. 6).

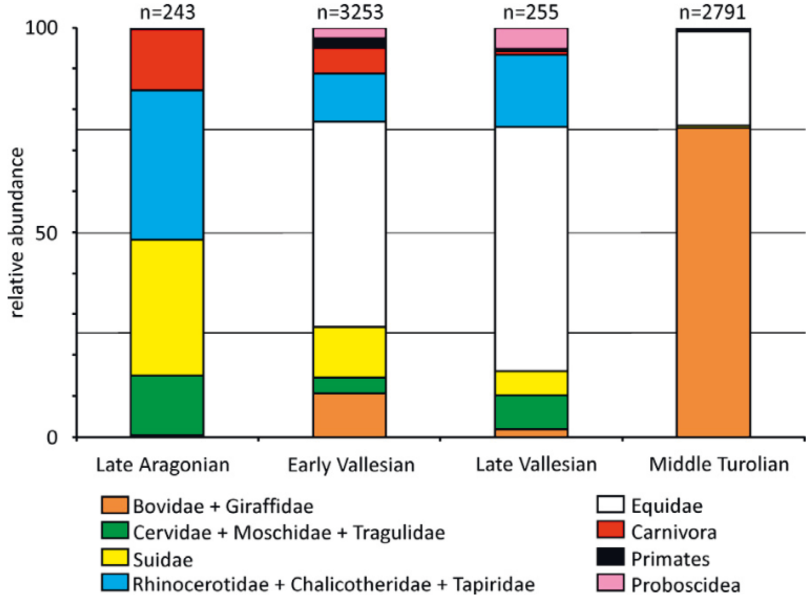

Fig. 6. Composition of the large mammal faunas from the Late Aragonian to the middle Turolian. n stands for the maximum number of individuals identified to the genus level. The late Aragonian faunas are represented by the Sant Quirze sites; the early Vallesian includes Creu Conill 20, Can Missert, Castell de Barberà, Can Poncic, Santiga and Can Llobateres 1; the late Vallesian includes Trinxera Sud Autopista, Trinxera Nord Autopista and Torrent de Febulines; finally, the Middle Turolian is solely represented by Torrentet de Traginers. Note the evenness of the late Aragonian faunas, the abundance of equids during the Vallesian, and the dominance of bovids during the middle Turolian. See text for further details.

The remaining taxa include the suid *Microstonyx* and the hyaenid *Adcrocuta*, amongst others. Forest elements are extremely rare, but chalicotheres (*Anisodon*) and rhinoceroses (*Aceratherium*, *Dihoplus*) are still present. Intensive screen-washing has not been carried out at this site, so the small mammal sample size is very limited, consisting of just twenty molars belonging to the murid *Occitanomys adroveri*, which indicates a Middle Turolian (MN12 or zone L) age (Agustí et al. 2001; Van Dam et al. 2001; 2006). This contrasts with previous correlations, which mostly on the basis of the large mammal fauna had correlated this site to MN11 (Agustí et al. 1985; 1997; Casanovas-Vilar et al. 2011a). The composition and structure of the mammal fauna are very similar to those of contemporaneous sites of the Teruel Basin (Alcalá, 1994; Alcalá et al. 2000), pointing to a similar arid and warm environment in both regions. This is in sharp contrast with the situation seen during the Vallesian, when the environment was clearly more humid and forested in the Vallès-Penedès Basin. Furthermore, although biostratigraphical data are preliminary, the Teruel rodent-based local zonation can apparently be extended to the Vallès-Penedès Basin.

6. Late Miocene diversity dynamics and a re-evaluation of the Vallesian Crisis

Agustí and Moyà-Solà (1990) were the first to recognize the Vallesian Crisis, an important turnover coinciding with the Early/Late Vallesian boundary (around 9.7 Ma), which implied the abrupt extinction of most of the forest-adapted elements that had characterised the Middle Miocene. These authors had previously recognized that some rodent and artiodactyl taxa seemed to be missing during the Late Vallesian (Agustí, 1981; Agustí et al. 1984, 1985; Moyà-Solà and Agustí, 1987, 1989), but later found that other mammals, including certain carnivorans and the primates had disappeared at the same time. The event was initially recognized in the Vallès-Penedès Basin, although they suggested that it had also occurred in other European regions (Agustí and Moyà-Solà, 1990). Later studies supported this conclusion, leading many authors to consider the Vallesian Crisis as a European or even Eurasian event (Agustí et al. 1997, 1999; Fortelius and Hokkanen, 2001; Fortelius et al. 1996). However, the potential causes of the Vallesian Crisis are elusive, since the main climatic (Zachos et al. 2001) and vegetational changes (Mossbrugger et al. 2005) had already started during the Middle Miocene, almost six million years earlier. Therefore, the crisis has been related to a complex interplay of climatic factors which would have increased the temperature latitudinal gradient along Europe and, in particular, rainfall seasonality in the peri-Mediterranean area (Agustí et al. 1997, 1999, 2003). In the Vallès-Penedès, the crisis would have been triggered by an increase in temperature seasonality that implied a significant increase of deciduous trees in the zonal vegetation (Agustí et al. 2003). However, deciduous elements were already major components of the floral assemblages in Central Europe (Mossbrugger et al. 2005) and other areas of Catalonia and the Iberian Peninsula (Barrón et al. 2010). More recently, Agustí et al. (2013) admitted the lack of correlation of the Vallesian Crisis with any major climatic perturbations and proposed a rather ad hoc new model calling for internal causes. The Vallesian faunas were highly diverse because of the entry of new immigrants and the persistence of most Middle Miocene taxa. According to these authors, this resulted in a sort of self-organised climax assemblage that was highly sensitive to environmental changes, so that just small perturbations could make the whole system collapse like a 'House of Cards'.

However, it has been recently shown that previous evaluations of the Vallesian Crisis in the Vallès-Penedès had not taken into account the effects of uneven sampling on diversity estimates (Casanovas-Vilar et al. 2014). Here we present an updated summary of those analyses that incorporates the latest data from the late Aragonian sites of the Can Mata composite series as well as some Vallesian sites that had not been included in previous work (Fig. 7). Only rodents and eulipotyphlans are taken into account. However, rodents in particular are considered to be highly affected by the Vallesian Crisis (Agustí and Moyà-Solà, 1990; Agustí et al. 1997, 1999). For the sake of comparison, we have included sample size in Fig. 7. The quality of the record is clearly better during the late Argonian and the early Vallesian, with sample size decreasing markedly during the late Vallesian. It is important to note that there is a sampling peak just before the early/late Vallesian boundary, thus immediately preceding the crisis. Genus richness tracks sample size and both variables are significantly correlated, even if a range-through approach is used as in Agustí et al. (2013) (rs = 0.418; P [no correlation] = 0.012). Therefore, the decrease in richness during the Late Vallesian is explained by the poorer quality of the record. Furthermore, the sampling peak in the time interval before the Early/LateVallesian boundary also helps to distort the pattern. As data simulations have shown (Foote, 2000), quality peaks will artificially inflate diversity and overestimate extinction rates because many taxa that would have last occurred in a preceding time interval are then last recorded in the interval with the better record. When we use inferred-range diversity estimates, which are uncorrelated with sample size (rs = 0.191; P [no correlation] = 0.270), the Vallesian Crisis changes from an abrupt extinction event to a gradual decrease in genus richness during the late Vallesian (Fig. 7).

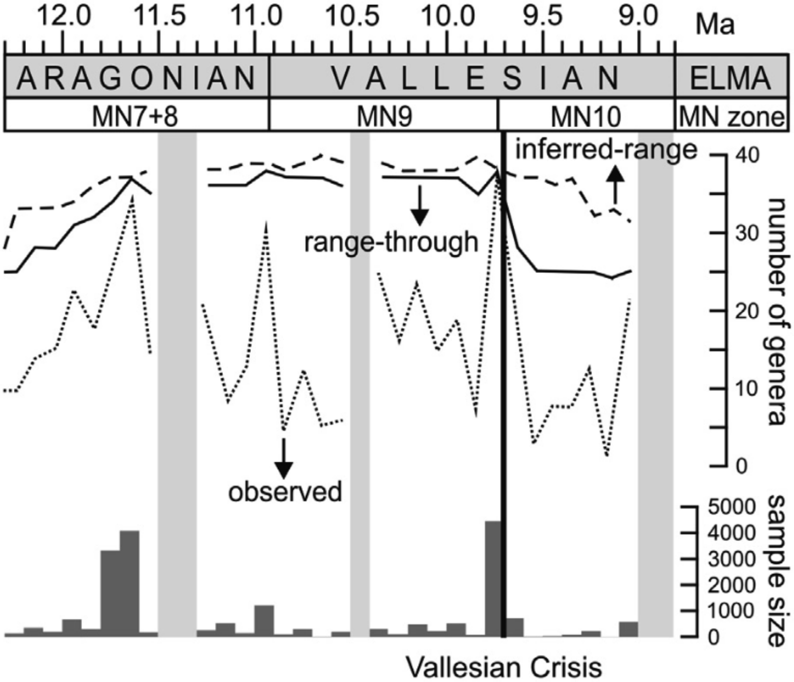

Fig. 7. Small mammal (Rodentia and Eulipotyphla) observed generic richness, sample size (maximum number of individuals) and richness measures for the Late Aragonian and the Vallesian. All the parameters are calculated for 0.1 Myr bins and a range-through approach is used for all richness measures. The light grey areas indicate gaps in the record. Note that 'observed richness' fluctuates importantly with sample size and is strongly correlated with it (rs = 0.864; P [no correlation] = 2.21 × 10–11). 'Range-through richness' is based on raw specimen counts but uses a range-through approach. Nevertheless, it is also highly correlated with sample size (rs = 0.418; P [no correlation] = 0.012). Therefore, note that the decrease in richness after the Vallesian Crisis is explained by the smaller sample size as compared to the early Vallesian. 'Inferred-range richness' estimates consider the probability of recording a given taxon given sampling effort and are uncorrelated with sample size (rs = 0.191; P [no correlation] = 0.270). Inferred richness shows a gradual decrease during the Late Vallesian instead of an abrupt crisis. See text for further details.

The 'victims' of the 'Vallesian Crisis' have two things in common: they are mostly purported forest-dwellers of Middle Miocene origin; and, perhaps more importantly, they are generally rare. Amongst the rodents, they mostly include the glirids, which, although diverse in many sites, rarely account for more than 10% of the recovered specimens. The same can be said of certain sciurids, such as the pteromyines, beavers, and the paracricetodontine *Eumyarion*, which are only common at certain sites. Therefore, sample size during the Late Vallesian would not be sufficient to record these rare taxa. This is further supported by our data from a few richer late Vallesian sites, such as Torrent de Febulines. Some of the 'Vallesian Crisis' 'victims' still have been recovered at this site, including a diverse dormice fauna (*Bransatoglis*, *Myoglis*, *Glirudinus*, *Paraglirulus*), flying squirrels (*Miopetaurista*), beavers (*Chalicomys*) and the eomyid *Eomyops*. Not surprisingly, pliopithecoids, represented by the endemic genus *Egarapithecus*, are also present at Torrent de Febulines (Moyà-Solà et al. 2001). However, some local disappearances seem to have occurred during the Early/Late Vallesian transition, including those of the cricetids *Eumyarion*, *Democricetodon* and *Megacricetodon*, the small castorid *Euroxenomys* and the heterrerosoricid *Dinosorex*.

The large mammal record of the Vallès-Penedès is not as continuous as that of small mammals and, furthermore, a taxonomic review of certain groups should be carried out before a similar diversity analysis is attempted. However, we can already see that the faunal composition of the Vallesian and, especially, the Turolian large mammal assemblages differs markedly from that of the late Aragonian (Fig. 6). In general, the late Aragonian assemblages consist of an even mixture of rhinocerotids, suoids, cervids and moschids. During the Vallesian, the bovids increase their abundance and hipparionin horses become dominant components of the faunas. Finally, the Turolian assemblages (solely represented by Torrentet de Traginers) are the least diverse and are overwhelmingly dominated by the bovid *Tragoportax*, followed by the equid *Cremohipparion* and the giraffid *Birgerbohlinia* as major components. The remaining taxa, which include some forest elements, are very rare. The dominance of savanna-like herbivores is characteristic of the Turolian faunas, but the earlier change in evenness seen in the Vallesian assemblages may indicate that some of the changes that would later shape the Turolian had already started in the Vallesian.

As we have seen, the uneven quality of the record overemphasises the severity and abruptness of the 'Vallesian Crisis' in the Vallès-Penedès Basin. Some extinctions did occur, but apparently they were merely part of a more protracted turnover event extending into the Turolian. Therefore, it is not surprising that the crisis did not coincide with any remarkable climatic event at 9.7 Ma. The analysis of the geographical range of the 'Vallesian Crisis' is beyond the scope of this paper. However, we must note that, although some disappearances occur, one discrete event is not recognized in other Iberian basins, such as the Teruel Basin, although rodent extinction rates are higher between 10–9.5 Ma in this area (Van Dam et al. 2006). In Central Europe, some forest-adapted taxa (such as chalicotheres, moschids and certain rodents) survived well into the Early Turolian, being recorded in some Austrian (Kohfidisch, Eichkogel; see Daxner-Höck et al. this issue) and German sites (Dorn-Dürkheim 1; Franzen et al. 2013). Finally, the small mammal record of the eastern Mediterranean (Greece, Turkey) does not record significant extinctions (De Bruijn et al. 1996) and indeed large mammal diversity increased continuously during the Vallesian, peaking at the Early Turolian (Fortelius et al. 1996).

Summary and conclusions

After more than seventy years of systematic survey, the mammal record of the Vallès-Penedès Basin stands out as one of the best Miocene records in Europe, comprising hundreds of sites and tens of thousands of specimens. It includes both large and small mammals and ranges from the Early Miocene (Ramblian) to the Late Miocene (middle Turolian). However, the quality of the record is uneven and the Late Aragonian and Vallesian successions have been more intensely sampled during the last years. Moreover, a magnetostratigraphical study of the major mammal-bearing successions has been carried out and hence accurate age estimates are available for many of these sites. During most of the Miocene, the Vallès-Penedès represented a transitional area between the Iberian and Central European mammal faunas, so that many of the forest-adapted taxa present in the latter also occur in this basin. By contrast, the faunas of other Spanish basins are indicative of more arid environments that apparently prevented the dispersal of some taxa, such as hominoids, chalicotheres or certain rodents and insectivores, into inner Spain.

As a case study, we have analysed small mammal diversity dynamics during the late Aragonian and the Vallesian (from 12.6 to 9.0 Ma), which represents our best-sampled interval. Previous studies had recognized a major extinction event, the Vallesian Crisis, characterised by the abrupt disappearance of most forest-adapted taxa at the early/late Vallesian boundary (9.7 Ma). We show that previous diversity analyses were greatly influenced by sampling, so that the decrease in diversity during the late Vallesian is correlated with a decrease in the quality of the record. Clearly, sample size is too poor to record the rare taxa, which mostly turn out to be purported forest dwellers. Nevertheless, diversity slowly decreased during the Late Vallesian as a part of a more gradual extinction event, likely extending into the Turolian. Such analyses cannot be applied to the large mammal faunas yet, although the known Turolian assemblages show a lower diversity than the Vallesian ones, being clearly dominated by a few taxa. Our future goal consists of expanding the temporal and taxonomic range of these analyses, in order to better understand faunal dynamics in this region.

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Chapter 4

Iberian micromammals show local extent of Vallesian Crisis

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Abstract

Once perceived as a continent-wide extinction event, doubts have been raised as to the severity and extent of the Vallesian Crisis. In this paper, we use the high-resolution late Aragonian to middle Turolian micromammal record from both the coastal Vallès-Penedès Basin and inland Calatayud-Teruel Complex to determine geographic extent of this Late Miocene turnover event and its effects within the reaches of the Iberian Peninsula. Differences in faunal composition between the two regions confirm that the event was much less severe than previously thought. Surprisingly, the diversity peaks in the two areas do not coincide. Whereas at the coast highest diversity is found in the early Vallesian (just before the turnover), in the inland it peaks in the late Vallesian. Several taxa never made it inland as reflected by the low similarity between both areas during the early Vallesian, suggesting that the Vallès-Penedès was indeed unique and consistently showed higher affinities with northern regions. The large differences even at relatively short distances support the idea that the 'Vallesian Crisis' was a local event.

Keywords: late Miocene, paleobiogeography, rodents, insectivores, Vallesian turnover event

1. Introduction

Originally considered a local bioevent within the Vallès-Penedès (Agustí et al. 1984; Moyà-Solà and Agustí 1987), the notion of a 'Vallesian Crisis' during the early Late Miocene has been considered to be a continent wide event by some (e.g., Agustí and Moyà-Solà 1990; Agustí et al. 2003; Agustí et al. 2013; Casanovas-Vilar et al. 2005; Van der Made et al. 2003). A renewed interest in the Vallès-Penedès mammal succession led to recent excavations of both classical and new sites, as well as a review of the vast collections assembled throughout decades. This has produced a rich dataset that allows for a state-of-the-art evaluation of the Vallesian Crisis. In recent studies, doubts have been cast upon the scope and severity of this event (Casanovas-Vilar et al. 2014,2015). Fortelius et al. (2014) argued that environment and subsequent biotic interaction can drive evolutionary change, where novelties arise under harsh environmental conditions, and mild environments in contrast give relics a chance of survival. While most Mediterranean environments at the start of the Late Miocene became drier and harsher, the Vallès-Penedès Basin (Catalonia, Spain) continued to remain humid and forested-adapted faunas until around 9.6 Ma, including the last hominoids of western Europe (Agustí et al. 2003; Casanovas-Vilar et al. 2011; Marmi et al. 2012).

The Iberian Peninsula has an outstanding Miocene mammal fossil record, with long continuous sections from numerous basins, that permit detailed studies of spatial and temporal biogeographical processes (Alba et al. 2001; Casanovas-Vilar et al. 2015,2016; García-Paredes et al. 2015; Van Dam et al. 2001). For the Spanish inland, the Calatayud-Montalbán, Daroca-Calamocha and Teruel-Alfambra basins are well-studied, from now on referred to as the Calatayud-Teruel complex. Among the coastal basins, the Catalan Vallès-Penedès Basin is the most extensively studied (Casanovas-Vilar, 2016 and references therein). The Vallès-Penedès (V-P) Basin and Calatayud-Teruel (C-T) complex, separated by only 300 km, each hold an impressive record of micromammals (Fig. 1). These long-term records allow us to test whether or not the Vallesian Crisis was a local phenomenon within the confinements of the Iberian Peninsula. Madern and Van den Hoek Ostende (2015) noted that the biodiversity in the V-P preceding the turnover event was considerably higher than in the inland basins. Many mammal species from the Catalan basin are not known from the inland (Agustí 1990; Casanovas-Vilar and Agustí 2007; Furió et al. 2011), with the primates, purported victims of the Vallesian Crisis, as the best-known example (Agustí et al. 2003; Casanovas-Vilar et al. 2008; DeMiguel et al. 2014).

Herein, the regional differences in micromammal diversity within the Spanish Miocene are explored, comparing the coastal high species richness predating the Vallesian Crisis with the Iberian inland. By comparing diversity and faunal composition dynamics between the coastal V-P basin and inland C-T complex during the latest Middle and early Late Miocene (late Aragonian to middle Turolian), this research aims to provide a better understanding of the extent and severity of this faunal turnover.

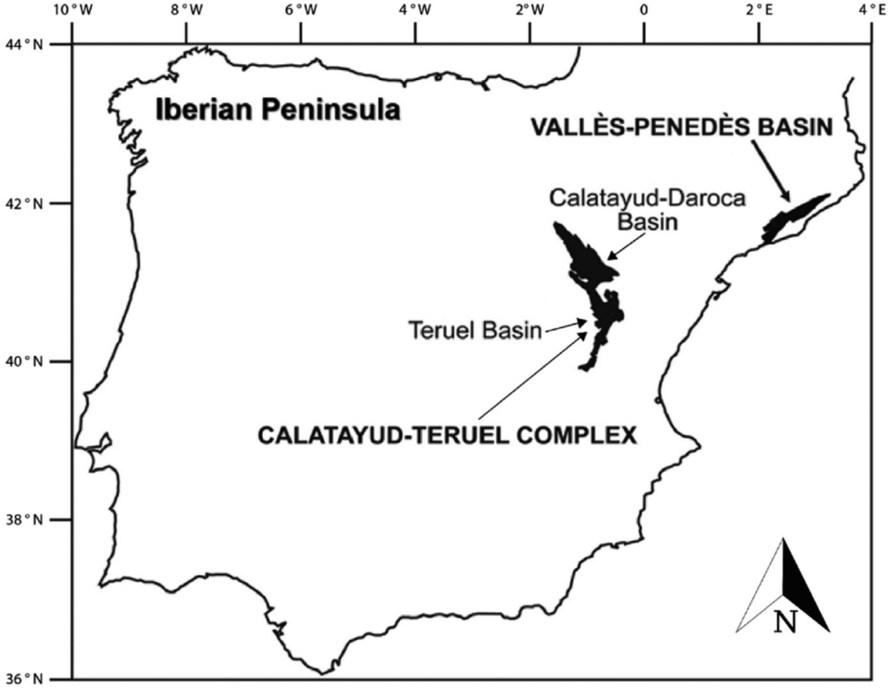


Figure 1. Map of the Iberian Peninsula with the Calatayud-Teruel and Vallès-Penedès basin indicated. Adapted from Casanovas-Vilar and Agustí (2007), Table 1, their p. 175.

2. Material and methods

2.1. Dataset

The micromammal dataset is limited to the orders Rodentia and Eulipotyphla. For the C-T, micromammal data were downloaded from the NOW database (Fortelius 2015). These were complemented with published information not yet entered into the NOW

(López-Guerrero et al. 2011; Van den Hoek Ostende et al. 2012). For the V-P, the data are taken from Casanovas-Vilar et al. (2016) and have since also been entered into the NOW database.

The studied time interval covers four successive biochronological units; Mammal Neogene (MN) units 7+8 to 11 as re-defined by Hilgen et al. (2012). Therefore, this comprises a period from 13.1-12.6 to 7.6 Ma (Hilgen et al. 2012). The turnover took place at the transition of the early to late Vallesian, thus around 9.6 Ma (Agustí and Moyà-Solà 1990). For both areas, high-quality bio- and magnetostratigraphic data are available (Agustí et al. 2001; Casanovas-Vilar et al. 2016; Domingo et al. 2007; Garcés et al. 1996; Moyà-Solà et al. 2009; Van Dam et al. 2001,2014; Van der Meulen et al. 2011,2012), allowing for a firm correlation of most sites with the Geomagnetic Polarity Timescale (Ogg 2012). Furthermore, considering the position of the sites within the local magnetostratigraphic sections an absolute age can be interpolated for each one of them (see Casanovas-Vilar et al. 2014 and Barry et al. 2002, for a description of the methods used to do so). For those few sites lacking associated magnetostratigraphic data we followed Casanovas-Vilar et al. 2014 in assigning to these localities a random age within the age range of the biozone to which they belong. To perform the analyses (see section 2.3), the studied time frame is divided in 0.5 Myrs time bins and each locality is assigned to a single interval. Bin size was empirically determined to hold sufficient localities in both basins while having as high a time resolution as possible. Analyses were performed at the genus level (64 genera from 278 localities), where all uncertain genus identifications were considered as certain. Taxa identified at the suprageneric level only were not included.

2.2. Geographical range

The areas of interest within the Iberian Peninsula are three basins, the coastal Vallès-Penedès Basin (V-P) near Barcelona and the inland Calatayud-Teruel complex (C-T), consisting of the Calatayud-Daroca and Teruel-Alfambra Basins (Fig. 1). The V-P is the type area for the Vallesian (Crusafont Pairó 1950), Calatayud-Montalbán for the Aragonian (Daams et al. 1999) and Teruel for the Turolian European land mammal ages (Crusafont Pairó and Truyols 1960). Sequences of both regions are long, well-calibrated and densely sampled, with rich Miocene mammal successions (Casanovas-Vilar et al. 2016, submitted; García-Paredes et al. 2016). Daroca has very poor MN 10 and 11 layers, and the younger Teruel lacks late Aragonian, but this can be (partly) compensated by combining the record of both basins (Fig. 2).

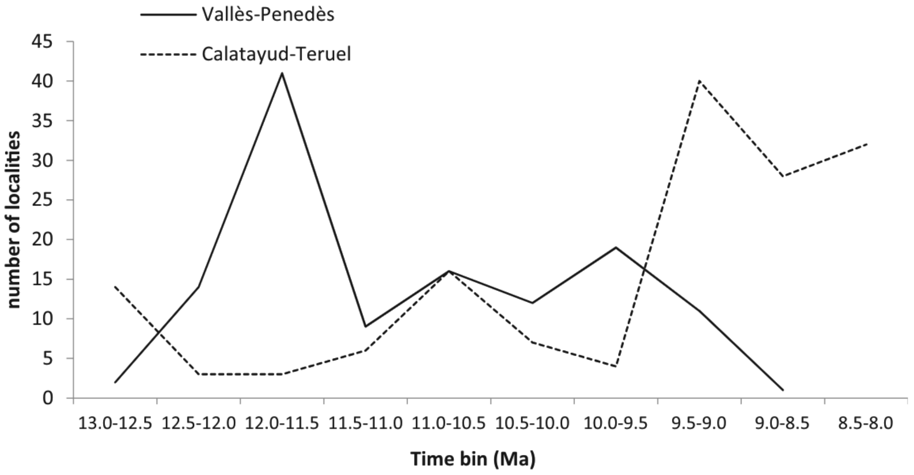


Figure 2. Number of localities per region.

The final dataset contains 125 localities from the V-P and 153 from the C-T, where layers within excavations were handled as separate localities when ages were available. As far as the V-P is concerned, the middle Turolian record of this basin is not comparable to those of the late Aragonian and Vallesian. Only two Turolian micromammal sites are known and these have delivered a very limited sample, with only one locality contributing to our database (Ronda Oest de Sabadell A1).

2.3. Data analysis

In both areas, only part of the fauna has been described and identified to the species level. However, genus-level identifications are routinely compiled and those data are easily available for all the sites. Furthermore, genus-level determinations have more consensus than species (Peláez-Campomanes and Van der Meulen, 2009).

After transforming the occurrence data to a presence-absence matrix in R 3.1.2 (R Core Team 2015), the rest of the analyses were conducted both in R and in PAST 3.14 (Hammer et al. 2001).

One-way PERMANOVAs (Permutational MANOVA; Anderson, 2001) were performed to test whether the genus compositions and presence-frequencies between regions and time bins were different. In order to explore the differences within regions, the time intervals were tested with one-way pairwise PERMANOVAs. All tests use the Raup-Crick coefficient as a similarity measure with 9999 random permutations (Raup and Crick

1979). The Raup-Crick (dis)similarity measure was chosen as it was specifically developed for analysing palaeontological presence-absence data using randomization and probabilistic measures (Shi 1993).

Simpson, Dice (or Sørensen) and Jaccard similarity indices were calculated separately for rodents and insectivores between basins per time bin (Dice 1945; Jaccard 1912; Simpson 1943).

The Simpson similarity index (Lennon et al. 2001; Simpson 1943) is defined as:

$$S_S = \frac{a}{a + min(b, c)}$$

, the Jaccard similarity (Jaccard 1912) is calculated as:

$$S_J = \frac{a}{a + b + c}$$

, and Dice's similarity index (Dice 1945; Sørensen 1948) as:

$$S_D = \frac{2a}{2a + b + c}$$

All depend on both matches and mismatches of taxa between two communities. Following the notation of Krebs (1999), in both formulas a stands for the number of taxa (or taxon presences) shared by two communities (i.e., matches), b the total number of taxa unique for one community and c the total number of taxa present solely in the other community (i.e., b+c is the number of mismatches between two communities). The computed similarities S_S, S_J and S_D range between 0 (no overlap of taxa) and 1 (full overlap of taxa). Although Dice and Jaccard are calculated in comparable fashions, Dice similarity has extra weight put on matches, represented by the product 2a, and is hence more based on taxon overlap between two communities. Because of this, the formulas imply that Dice similarities will always have higher values than the Jaccard similarities in case of overlapping taxon presences. In the Simpson similarity measure, the smaller number of unique taxa of separate communities is chosen, such that it corrects for differences in species richness between the two communities (Jaccard or Dice could be highly dominated in case of a high local taxon richness; Lennon et al. 2001). All three calculate the similarity of two samples based on absence/presence data and all can be expressed as percentages after multiplication with 100 (Harper 1999).

3. Results and discussion

3.1. Ecological changes/community structure within regions

Table 1 summarises rodent and eulipotyphlan richness during the considered time span in the two regions. The V-P held the highest total number of genera or genus richness, except for the Late Miocene. While the inland basins have a good post-Vallesian record, Turolian localities in the V-P are, unfortunately, rare, making it difficult to see changes after the Vallesian. During the late Vallesian, there was a sharp decline in rodent genera and richness in the V-P, but not in the number of rodent families (Table 1). Conversely, the inland richness, especially of the rodents, increased considerably in the late Vallesian. While insectivore richness was higher in the V-P than the C-T basin during the Middle Miocene, for coastal insectivores the number of genera in the Late Miocene was very low, with the inland exceeding at least twofold.

We analysed the changes within regions with a pairwise PERMANOVA with Raup-Crick similarity index, comparing V-P and C-T fauna composition per 0.5 Myr age bin, with 9999 permutations (Table 2). For the C-T, almost all show significant differences through time. Within the V-P, there is less significance, meaning that the basin experienced fewer dramatic changes in faunal composition over time. Pairwise comparison of age bins shows the largest differences for both the rodents and the insectivores between 12.5 and 9 Ma. This makes sense, given these are the two best sampled time bins separated in time. It is noteworthy that genus compositions and frequencies within the inland localities differ significantly for every pair. Interestingly, the majority of the p-values of pairs of subsequent time bins do not show significant differences, indicating the faunal transition was a gradual one.

Table 1. Taxon counts per time bin (13-8 Ma) comparing the inland basin complex Calatayud-Teruel to coastal basin Vallès-Penedès.[a]

epoch	**Middle Miocene**			**Late Miocene**						
stage	**late Aragonian**			**early Vallesian**				**late V.**	**early Turolian**	
age bin	**13-12.5**	**12.5-12**	**12-11.5**	**11.5-11**	**11-10.5**	**10.5-10**	**10-9.5**	**9.5-9**	**9-8.5**	**8.5-8**
Rodentia										
Families V-P	4	6	6	9	7	9	9	8	4	
Families C-T	3	1	4	3	5	6	5	8	5	7
Genera V-P	10	19	18	23	20	19	26	18	4	
Genera C-T	13	11	17	8	13	12	11	10	9	12
Eulipotyphla										
Families V-P	2	5	5	5	5	5	5	3	4	
Families C-T	2	2	2	2	3	2	2	3	3	3
Genera V-P	2	11	14	8	14	11	13	5	6	
Genera C-T	3	4	3	4	5	5	3	6	6	8

[a] Total number for all micromammal taxa and counted separately per order.

When comparing genus richness between both regions, the diversity peaks do not seem to overlap (Fig. 3). Moreover, the extinction from the Vallesian mammal turnover displays an offset when comparing the inland to the coastal basins. The genus richness in the C-T is mostly stable, while the V-P experiences more fluctuations. Relating the richness to the number of localities per region (Fig. 2), there is no observed correlation.

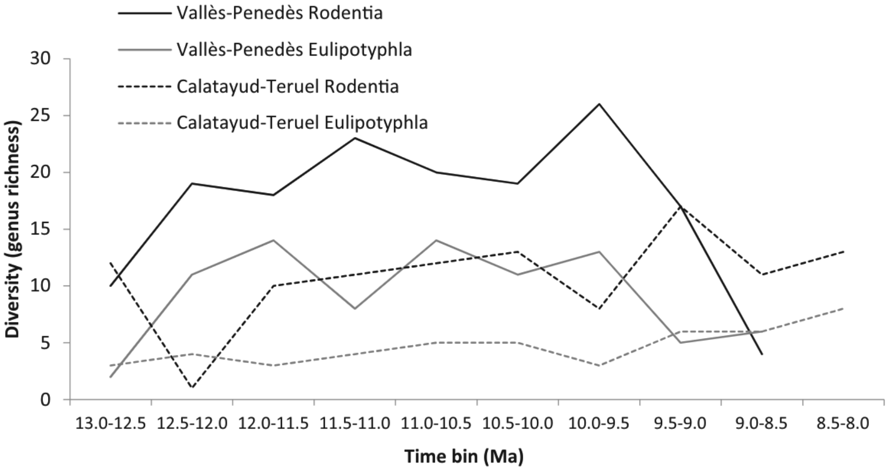


Figure 3. Observed genus richness (number of genera per time bin) per region and order.

Table 2. PERMANOVA pairwise comparison of fauna composition between regions.

	13-12.5	12.5-12	12-11.5	11.5-11	11-10.5	10.5-10	10-9.5	9.5-9	9-8.5	8.5-8
2a. Rodentia Vallès-Penedès										
13-12.5		-0.1172	0.0137	0.3391	0.7898	2.277	1.176	3.744	4.863	
12.5-12	0.8368		-0.29	0.2702	5.922	16.31	6.986	12.75	46.43	
12-11.5	1	0.8938		0.1009	4.772	10.23	5.426	7.737	29.24	
11.5-11	0.8325	0.6712	0.7183		-0.4027	1.299	1.852	0.64	5.354	
11-10.5	0.5673	0.0146*	0.0255*	0.9199		5.601	2.376	1.511	5.312	
10.5-10	0.3267	0.0011**	0.002**	0.391	0.0051*		3.995	4.859	10.68	
10-9.5	0.3008	0.0038**	0.0113*	0.1974	0.1087	0.0318*		0.292	1.648	
9.5-9	0.1991	0.008*	0.0295*	0.5806	0.2599	0.0175*	0.8042		1.15	
9-8.5	0.1649	0.0075*	0.0077*	0.0289*	0.0274*	0.0074*	0.251	0.4003		
8.5-8										
2b. Eulipotyphla Vallès-Penedès										
13-12.5		2.527	3.744	8.506	1.757	0.4593	1.655	0.365	0.2271	
12.5-12	0.0593		1.614	2.056	-0.4994	0.1173	3.549	1.215	4.653	
12-11.5	0.0229*	0.2343		0.6686	0.5724	2.131	5.496	1	8.359	
11.5-11	0.0383*	0.1548	0.5739		1.635	3.1	3.838	2.431	9.362	
11-10.5	0.1672	0.9772	0.6207	0.2661		-0.03563	0.8045	0.3688	1.837	
10.5-10	0.7494	0.7933	0.1338	0.0862	0.8268		1.216	-0.7294	1.925	
10-9.5	0.2496	0.0364*	0.0043**	0.0412*	0.509	0.3729		0.9421	1.126	
9.5-9	1	0.3478	0.4304	0.125	0.7467	1	0.4462		0.1287	
9-8.5	0.6149	0.0101*	0.0002**	0.0023**	0.2352	0.2225	0.393	0.8555		
8.5-8										

Table 2. *(Continued)*

	13-12.5	12.5-12	12-11.5	11.5-11	11-10.5	10.5-10	10-9.5	9.5-9	9-8.5	8.5-8
2c. Rodentia Calatayud-Teruel										
13-12.5		0.7756	6.955	39.29	115.6	49.27	196.5	145.6	204.3	411.40
12.5-12	0.4992		0.4236	0.5847	3.338	0.1843	0.8519	5.067	4.481	6.42
12-11.5	0.1377	1		13.46	18.16	8.845	56.51	25.63	28.51	36.39
11.5-11	0.0035**	0.5949	0.0657		4.046	2.443	33.64	27.87	49.29	100.90
11-10.5	0.0004**	0.1067	0.0207*	0.0692		-0.1337	6.533	22.88	37.86	98.70
10.5-10	0.0029**	1	0.0665	0.2852	0.828		1.929	15.23	29.52	71.35
10-9.5	0.0295*	1	0.3236	0.0686	0.0223*	0.1326		3.87	13.5	40.95
9.5-9	0.0001**	0.088	0.0025**	0.0002**	0.0001**	0.0002**	0.0708		14.83	150.20
9-8.5	0.0001**	0.0661	0.0064*	0.0002**	0.0001**	0.0003**	0.0075*	0.0001**		44.18
8.5-8	0.0001**	0.0513	0.0066*	0.0001**	0.0001**	0.0004**	0.0061*	0.0001**	0.0001**	
2d. Eulipotyphla Calatayud-Teruel										
13-12.5		4.416	3.159	5.575	17.25	30.68	29.4	20.94	41.28	187.20
12.5-12	0.0534		0.4379	2.19	5.731	3.128	17.6	9.984	16.37	72.77
12-11.5	0.2433	1		1	2.125	0.9008	7.625	4.104	6.446	26.64
11.5-11	0.0269*	0.334	1		0.8589	1.289	1.936	2.606	4.476	16.14
11-10.5	0.0003**	0.0215*	0.1094	0.577		3.761	0.9131	4.928	4.818	14.79
10.5-10	0.0097*	0.0937	0.4922	0.2994	0.0554		4.349	10.18	13.6	52.54
10-9.5	0.0305*	0.3404	0.3301	0.3381	0.4691	0.2057		2.026	5.417	20.07
9.5-9	0.0001**	0.0057*	0.0508	0.1248	0.0079*	0.0007**	0.1205		5.069	18.34
9-8.5	0.0001**	0.0088*	0.07	0.0258*	0.0101*	0.0017**	0.0289*	0.0104*		3.57
8.5-8	0.0001**	0.0095*	0.0708	0.0099*	0.0002**	0.0022**	0.0075*	0.0001**	0.042*	

PERMANOVA pairwise testing, Raup-Crick index as similarity measure, comparing fauna composition over time within V-P and C-T basins, 9999 permutations. P-values under diagonal, above F-values. Significance is indicated with stars: *p<0.05, **p<0.005.

Table 3. Percentage of localities per basin where a certain family was recorded.

Rodents	V-P	C-T	Insectivores	V-P	C-T
(M) Anomalomyinae	20	1	Dimylidae	37	0
(M) Cricetinae	63	22	Erinaceidae	78	89
(M) Cricetodontinae	81	83	Heterosoricidae	40	0
(M) Murinae	31	69	Soricidae	51	73
Castoridae	20	8	Talpidae	46	39
Dipodidae	0	16			
Eomyidae	22	18			
Gliridae	74	63			
Pteromyini	22	0			
Other Sciuridae	70	24			

3.2. Rodent palaeobiogeography

Rodents are a highly diverse mammal group, with varying morphological types, size, diet and habitats. Here, the changes in rodent palaeobiogeography are discussed for all found rodent families separately, as variations in climate and environment have differential effects within such a diverse order.

Castoridae, the beavers, include both fossorial and semi-aquatic taxa, but all the European Miocene species are semi-aquatic (Hugueney 1999). This family occupied only a fraction of the inland localities in the various time bins (recorded in 8% of the sites, see Table 3), but was much more common in the V-P (20%). The beavers do not seem to have been extremely affected by the Vallesian mammal turnover (Fig. 4).

Dipodidae, the family including jumping mice, are represented by only one genus of the subfamily Zapodinae. *Eozapus* first appeared in the inland basins around 9 Ma (Fig. 4), and is present in 16% of C-T localities (Table 3). As yet, they have not been recorded in the coastal basins. Dipodids are small mammals with hind legs and tails that are modified for saltatorial locomotion, but they can also be scansorial. Their diet consists mainly of fruits, seeds and can include insects. Extant dipodids occupy a wide variety of habitats (Daxner-Höck 1999). Zapodinae are typically found in wooded areas, grasslands and meadows (Nowak 1999).

The Eomyidae are an extinct family that was once greatly diverse. At least one species presented gliding adaptations (Franzen and Storch 1999), while others were more generalised terrestrial quadrupeds (Engler and Martin 2015). After the high Eomyidae diversity up until the Middle Miocene, *Eomyops* and *Keramidomys* were the only surviving genera, always associated with humid faunas (Daams et al. 1988), they preferred temperate climates (Casanovas-Vilar and Agustí 2007; Van Dam 1997; Van Dam and Weltje 1999) and were probably forest dwellers. They occurred in low numbers in the V-P throughout the Miocene. During the Early Miocene, eomyids are widespread throughout Europe, as in the C-T, where the genus *Ligerimys* is a major biostratigraphical tool (Van der Meulen and Daams 1992). During the late Aragonian and Vallesian, in the Iberian Peninsula the family is only continuously present in the V-P (Casanovas-Vilar and Agustí 2007), though *Eomyops* is scarcely represented in two sites in the C-T, in bins 10-9.5 and 9.5-9 Ma (Fig. 4).

Gliridae (dormice) are mainly arboreal and scansorial animals, and their presence in certain areas is linked to forested environments (Daams et al. 1988). Starting in the late Middle Miocene, both the diversity and the relative abundance of glirids in fossil record assemblages declined (Daams 1999; Gómez Cano et al. 2014; Hartenberger 1994). In the analyses of this study, glirids in both regions were taxonomically quite diverse, but more so in the V-P. Also, both regions had most genera in common. Still, many genera were rare and only recovered in one or two localities. The V-P glirids were the second most diverse group in the late Aragonian (Fig. 4). These high numbers do not indicate a dominating abundance in the fossil record, but mostly result from the presence of numerous rare genera resulting in high numbers of occurrences of mostly rare rodent fauna components, such as *Glirudinus*, *Glirulus*, *Microdyromys* or *Eliomys* (Casanovas-Vilar et al. 2014). The glirids declined in diversity in the V-P from late Vallesian onwards. In the Aragonian and Vallesian inland localities, the glirids were actually frequently present in the faunas, though less diverse, and more prominent than in the V-P (Table 3). Following the V-P, in the C-T the glirid ratio dropped in the Turolian (from 9 Ma onwards). Overall, the glirids are very diverse but consistently represent a minor portion of the fauna. Based on ecomorphology of dental characteristics (Van der Meulen and De Bruijn 1982), forest-dwelling glirids (e.g., *Eliomys*, *Glirulus*, *Myoglis* and *Paraglis*) preferentially occur in the V-P, but the ground-dwellers (mainly *Armantomys*, *Myomimus*, *Tempestia*) seemed to be more numerous in or even restricted to the inland. The forest-dweller *Muscardinus* is regularly found in both areas and stands out as one of the most frequently present glirids (Casanovas-Vilar and Agustí 2007; Van Dam et al. 2001).

The Muridae comprise the largest family with four subfamilies: Anomalomyinae, Cricetodontinae, Cricetinae and Murinae. The subfamilies are marked '(M)' in the figures and tables. 'Cricetids' is used here as a collective name for both the Cricetodontinae and the Cricetinae. During the Late Miocene and particularly the Vallesian, many significant changes involved occurred within the cricetids and murids, as discussed below. Distinction is made between ancient hamsters (Paracricetodontinae, solely including *Eumyarion* here), old hamsters (Cricetodontinae) and modern hamsters (Cricetinae).

Anomalomyinae are considered descendants of the paracricetodontine muroids (Bolliger 1999; De Bruijn 2009). The only genus present is *Anomalomys*, which was adapted to a fossorial lifestyle (Bolliger 1999). In the V-P it is first recorded during the late Aragonian and it is continuously present from then on, in the C-T it occurs just once in bin 9.5-9 Ma (Fig. 4).

Cricetodontinae comprise the group of the old hamsters. In the Middle and Late Miocene these were quite diverse in Central Europe (Rummel 1999) and abundant in the earliest Vallesian faunas (Casanovas-Vilar and Agustí 2007). The data reflect this, with Cricetodontinae being both diverse and present in most localities during the late Aragonian and early Vallesian in both C-T and V-P, followed by a strong decline in the number of localities in which it was found from the late Vallesian onwards in the V-P. In the C-T, conversely, they continue to occur commonly in the Turolian faunas of our analyses, being represented by *Hispanomys* (Fig. 4). Overall, the Cricetodontinae decrease in diversity coincided with the Vallesian mammal turnover. However, it is remarkable that the number of occurrences of cricetodontines in the inland Turolian still supersedes the recorded number of modern hamsters (cricetines).

Cricetodontines are a very diverse and widespread rodent group and its members are of different sizes (Casanovas-Vilar and Agustí 2007), with a variety of different dentitions, adapted to different kinds of diets. Medium-sized to small old (*Democricetodon* and *Megacricetodon*) and ancient hamsters (*Eumyarion*) were brachyodont and bunodont and fed on a wide variety of food sources (Oliver and Peláez-Campomanes 2013). *Hispanomys*, a descendant from *Cricetodon* (López-Guerrero et al. 2013,2015), developed hypsodonty and consequently most likely fed on tougher vegetation (De Bruijn and Ünay 1996). This may have given it an advantage of being able to process the plants of the upcoming open woodland vegetation of the Late Miocene. It was one of the few cricetodontine genera that did not go extinct after the early Vallesian in both C-T and

V-P, and remained prevalent in later time periods, ultimately evolving into the genus *Ruscinomys*, which made it into the Pliocene (Van Dam 1997).

The genus *Megacricetodon* was very abundant in the Middle Miocene (Kälin 1999; Oliver and Peláez-Campomanes 2013,2014). It is hypothesised that the larger species might have preferred dry and open environments (Daams and Freudenthal 1988), while the smaller species would have dwelled in more humid environments during late Aragonian and early Vallesian. A habitat preference is assumed for the smaller species of *Democricetodon*, also frequently recorded during the Middle Miocene, which are associated with wet and wooded habitats. Small-sized species of *Democricetodon* and *Megacricetodon* survive until the early/late Vallesian boundary (9.7 Ma), but they are rare components of the faunas. By contrast, larger-sized species (such as *Megacricetodon ibericus* and *Democricetodon crusafonti*) disappear earlier, during the first half of the early Vallesian (Agustí et al. 1997; Casanovas-Vilar and Agustí 2007; Casanovas-Vilar et al. 2015,2016).

Cricetinae are the ‘modern’ hamsters, represented by *Cricetulodon* (brachyodont), its descendant *Rotundomys* (hypsodont and lophodont, though earliest species are brachyodont) and *Neocricetodon* (brachyodont) (Casanovas-Vilar and Agustí 2007; Fejfar 1999; Kälin 1999). The Cricetinae are first recorded in the Calatayud-Teruel Basin around 10.6 Ma (Van Dam et al. 2014) and slightly later, at 10.3 Ma, also make their appearance in the Vallès-Penedès (Fig. 4). Replacing the cricetodontines by cricetines was virtually completed by the end of the early Vallesian (9.7 Ma), when *Cricetulodon* dominated the assemblage in both regions. The murids are recorded from 10.5 Ma on in the C-T (Van Dam et al. 2014), but bloom during the late Vallesian, when they are recorded for the first time in the V-P (Casanovas-Vilar et al. 2016).

Murinae, or the family Muridae in a restricted sense, derived from the old cricetid hamsters (Jacobs and Downs 1994; Kimura et al. 2013; Wessels 2009). This is the most diversified mammal subfamily and present-day murines occupy a wide range of habitats, ranging from forests to grasslands, with some semi-aquatic species as well. Murines are herbivorous or omnivorous and sometimes even predominantly carnivorous (Freudenthal and Martín-Suárez 1999; Nowak 1999; Gómez Cano et al. 2013). In both regions, murids first occurred in the early Vallesian (Fig. 4). In the V-P, the true mice *Progonomys* (rare in early, abundant in late Vallesian), *Huerzelerimys* (two occurrences in the two last age bins) and *Parapodemus* (a single occurrence in Ronda Oest de Sabadell D6) were present. By the end of the Late Miocene the Muridae had become one of the dominant taxonomic groups. Especially inland, almost every locality contained true murids. Notably, *Progonomys* was very commonly found in the C-T from 10 Ma onwards till 8.5 Ma. Contrasting *Occitanomys*, which was just found in two sites in time bin 9-8.5 Ma and more often from 8.5 Ma on. While *Parapodemus* was exclusively recorded in one locality in the V-P (8.5-8 Ma), it was more frequently present in the C-T. However, it is recorded later inland, its appearance marking the start of the early Turolian. Even though the murids were rare in early Vallesian, together with cricetids and glirids they were the largest group of the late Vallesian and eventually even dominated the rodent fauna of the Turolian, being recorded in 31% of all V-P and 69% of all C-T localities (Table 3). Whereas Murinae numerically dominate the late Vallesian rodent faunas of the C-T (Casanovas-Vilar and Agustí 2007; Van Dam and Weltje 1999), the V-P the faunas of this period are dominated by the cricetine *Rotundomys* with the murines only being extremely rarely recorded in some sites. This has been previously considered as evidence for the existence of different environmental conditions in both areas, with the V-P being more humid than the inland basins (Casanovas-Vilar and Agustí 2007; Gómez Cano et al. 2013).

The Sciuridae are divided into two subfamilies, the Pteromyini is a tribe within the tree squirrels. These Pteromyini, the flying squirrels, are mostly restricted to forested environments (e.g., Daams et al. 1988; Thorington et al. 2012; Van de Weerd and Daams 1978). A high diversity of Pteromyini is only found in subtropical and tropical forest (Thorington et al. 2012). They were only present in the V-P and represented a small fraction of the rodent fauna throughout most of the studied period (Fig. 4). Two genera were regularly recorded: *Albanensia* and *Miopetaurista*, both persisting until time bin 10-9.5 Ma. The rich locality of Can Llobateres 1 adds rare finds of *Pliopetaurista* and *Blackia*, whereas in Abocador Can Mata even *Neopetes* was present (Casanovas-Vilar et al. 2015,2016).

The remaining genera of the Sciuridae from the Vallesian and adjacent periods were tree climbers (Sciurini) or ground squirrels (Xerinae). They lived in dry and open country (Daams et al. 1988; Van de Weerd and Daams 1978), but are also found in wet environments (Van Dam and Weltje 1999). Here, they also seem ubiquitous, as members of these two subfamilies were present in both regions during every time interval (Fig. 4). During the late Aragonian, sciurids were relatively common in the inland basins, but the number of localities where they were recorded decreased from the Vallesian onwards. There were no Sciurini recorded in the V-P, meaning all sciurids which are not flying squirrels belong to the ground squirrels; the Xerinae. In the V-P, however, this subfamily was rare in the late Aragonian and more abundant during the entire Vallesian (Fig. 4). One genus, ground squirrel *Spermophilinus*, was a Lazarus taxon in the C-T, only being present until time bin 11.5-11 Ma, to later pop up in Peralejos D, two million years later.

3.3 Dice, Jaccard and Simpson diversity/similarity indices

Low Dice or Jaccard values imply less overlap and hence differences in genus compositions between the two regions. Low similarity is due to one of the two regions having notably high genus diversity. This is the case on the Iberian Peninsula, as the V-P rodent genus richness exceeds that of the C-T rodents (Table 1). This relates to why Simpson yields higher values. The Simpson index corrects for one area having a higher richness than the other one, as it takes the less diverse region as a benchmark, meaning the region with higher diversity has a relatively high overlap in genera as the unique taxa of the richer genus are not considered.

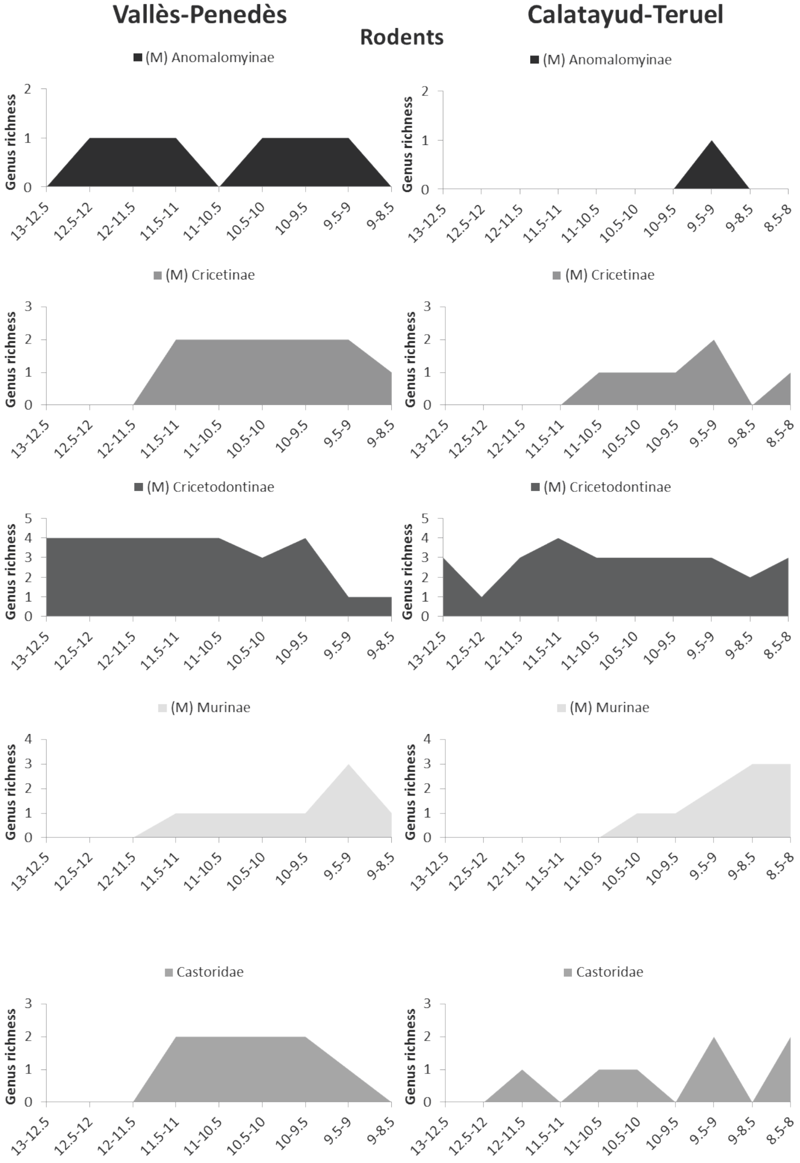
Dice and Jaccard similarity between regions is low throughout the studied period. The Simpson's index, however, shows high similarity occasionally as a result of the way it deals with sample subsets. For example, the high rodent similarity in time bin 12.5-12 Ma is due to the low number of sites and identified specimens. As a result, the single *Democricetodon* in the C-T basin is interpreted as a subset of the V-P assemblage, leading to a high Simpson similarity of 1, while the basins were indeed very different (Fig. 5a). The patterns of all three measures are more consistent with each other for the Insectivores (Fig. 5b). This can be attributed to the overall much lower Eulipotyphla genus diversity, leading to less dominance of richness of one of the localities.

Remarkably, the increased genus richness of the C-T in the Turolian suggests the landscape became more diverse at that time. Similarity between the inland and the coast is constantly 0.5 or below, albeit for the Simpson's index when comparing rodent assemblages between regions (Fig. 5). This suggests the V-P, probably due to its connections with Central Europe, was indeed unique within the Iberian Peninsula. Analogous changes in similarity between regions for both Rodentia and Eulipotyphla, such as the change from high to low similarity comparing early to late Vallesian show a local similarity change, implying not all changes in biodiversity were long-reaching.

Table 4. PERMANOVA comparing fauna composition between regions.

	13-12.5	**12.5-12**	**12-11.5**	**11.5-11**	**11-10.5**	**10.5-10**	**10-9.5**	**9.5-9**	**9-8.5**
p-values									
Rodentia	0.1268	0.509	0.0646	0.3625	0.1228	0.0024**	0.0555	0.003*	0.0046**
Eulipotyphla	0.0294*	0.0092*	0.0208*	0.0374*	0.0094*	0.0073*	0.0227*	0.0065*	0.0002**
F-values									
Rodentia	3.827	0.7826	22.39	1.387	2.624	14.7	2.942	6.189	7.92
Eulipotyphla	48.62	9.017	5.248	6.616	4.753	11.16	3.421	7.162	14.68

PERMANOVA results, with Raup-Crick similarity index, comparing fauna composition per time bin between V-P and C-T basins, 9999 permutations. Significant values are indicated with stars (*p<0.05, **p<0.005).


Vallès-Penedès
Rodents
Calatayud-Teruel
■ (M) Anomalomyinae
■ (M) Cricetinae
■ (M) Cricetodontinae
■ (M) Murinae
■ Castoridae
Genus richness
0
1
2
3
4
5
13-12.5
12.5-12
12-11.5
11.5-11
11-10.5
10.5-10
10-9.5
9.5-9
9-8.5
8.5-8

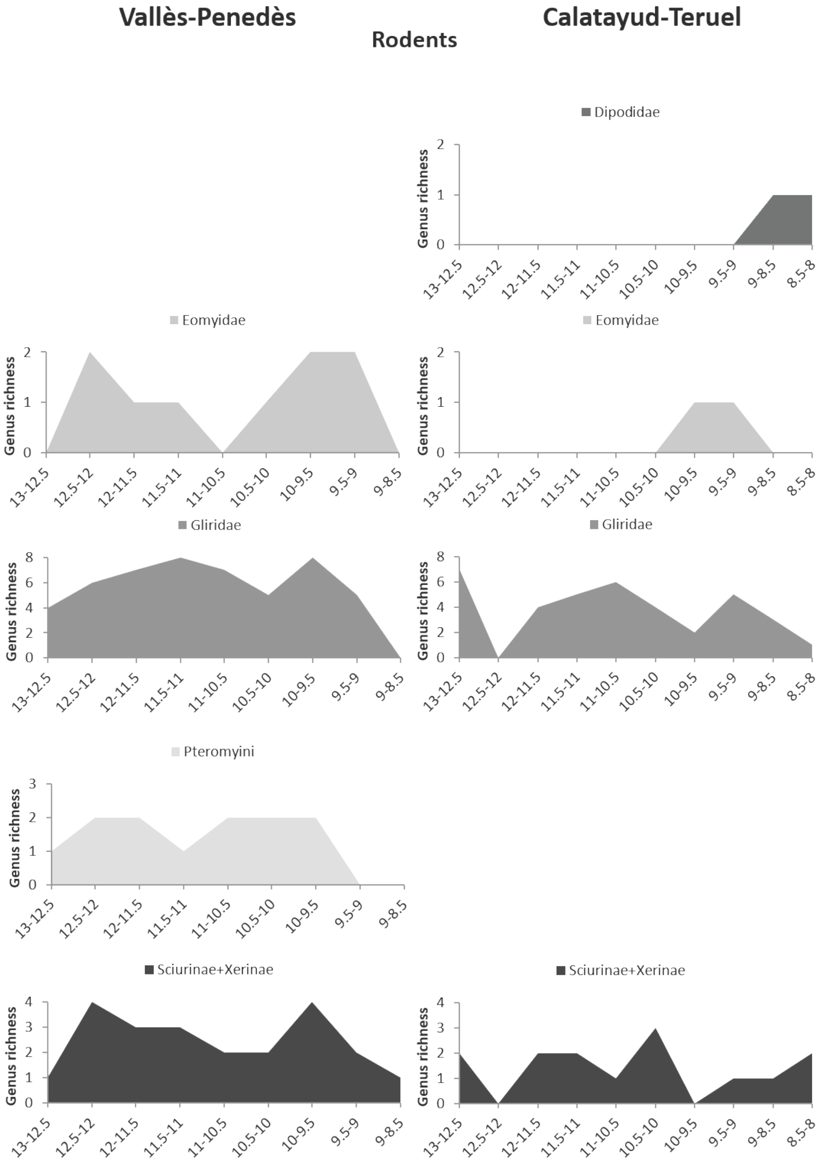
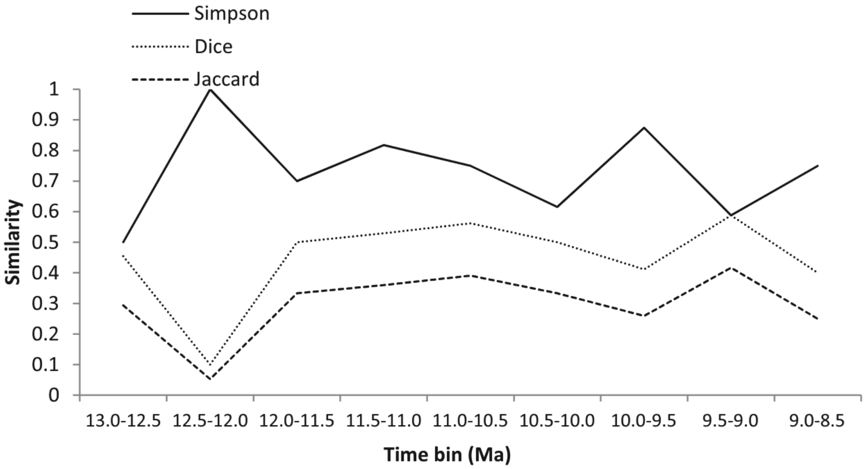


Figure 4. Rodent richness trends compared between regions. Area charts per family displaying genus diversity per time bin.

a)



b)

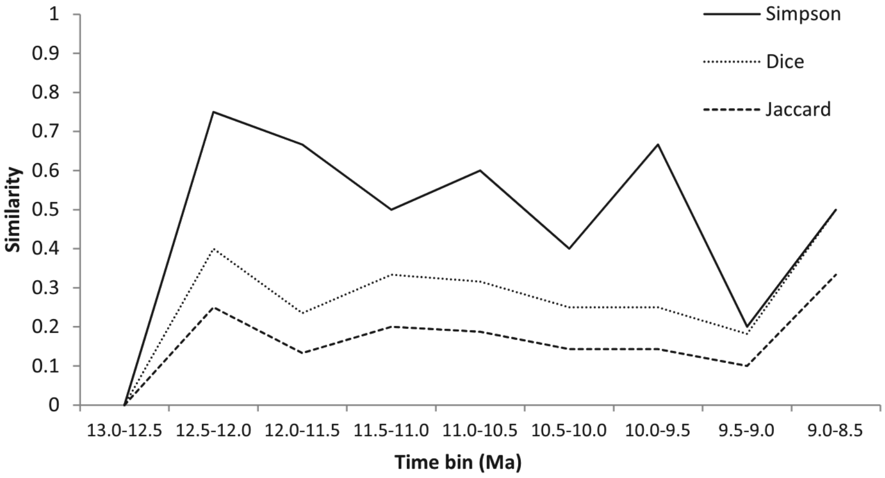


Figure 5. Similarity (Simpson, Dice and Jaccard) between basins through time, with a) rodent and b) insectivore similarity per time bin.

3.4. Insectivores

Eulipotyphla, commonly known as insectivores, are an anatomically diverse mammalian order of animals which are thriving in humid environments with lush vegetation, while some can cope with drier conditions (Furió et al. 2011; Merritt 2010; Ziegler 1999). Insectivores occupy various niches: they live in terrestrial or (semi-) aquatic environments and are fossorial, scansorial or ground-dwelling in their foraging ways. They are mostly nocturnal with a diet consisting of insects and other arthropods, although they can be omnivorous or carnivorous (Ziegler 1999). This group, like other non-rodent small mammals, is less diverse and has fewer recordings in the fossil record compared to the rodents (Furió et al. 2011). Some families are extinct (Dimylidae, Heterosoricidae), while others are extant (Erinaceidae, Soricidae and Talpidae).

The Erinaceidae is the widespread family of the hedgehogs, with a variable habitat range which can even be extended to desert and steppe environments (Ziegler 1999). The hedgehogs were present in both regions during every studied time interval. In the inland C-T, they were very consistent, while starting off as a smaller group in the V-P (Fig. 6). At the coast, they became the most prevalent group in the late Vallesian. The Erinaceidae in the C-T make up a small percentage of the fauna; however, this is relative due to the increase in soricid and talpid occurrences at that time. The most frequently recorded genera were the gymnures (moon rats) *Galerix* and *Parasorex*. *Galerix* was commonly found in inland localities during the Aragonian, but rare in the subsequent time bins there. In contrast, *Parasorex* started as a small group, yet became the most prevalent erinaceid genus from the Vallesian on. According to Van den Hoek Ostende (2001), these two genera were the most frequently recorded Miocene insectivores, and probably generalists concerning their diet and habitat. In this family, there was one ostensible Lazarus genus: the spiny hedgehog *Amphechinus* was only present in a few localities between 13-12 Ma to reappear in one locality in time bin 8.5-8 Ma. In between it was absent, which is probably due to the confusion in erinaceine taxonomy. Notably, the younger localities show various occurrences of another spiny hedgehog, *Postpalerinaceus*, between 8.5-8 Ma. The gymnure *Lantanotherium* is an example of a typical Central European taxon. This genus was only present in the coastal V-P basin, but not inland (Van den Hoek Ostende et al. 2015). It seems to have preferred humid habitats (Furió et al. 2011) and appeared more often in late than in early Vallesian localities.

Talpidae, the mole family, has some extant representatives which are found in temperate parts of Holarctic region. They are adapted to burrowing and live underground.

The desman group of this family however, are mainly (semi-)aquatic, albeit they sometimes burrow as well (Rumke 1985; Ziegler 1999). Uropsiline moles have a lifestyle more comparable to that of shrews, hence their common name shrew-moles (Van den Hoek Ostende and Fejfar 2006). Besides these uropsilines, moles are dependent on moist environments that provide suitable soils (Furió et al. 2011). In the studied periods, there were almost opposite appearance trends of talpids in C-T and V-P. While talpids occurred in a large portion of coastal localities during the Aragonian, albeit in low numbers, they were absent inland until 11 Ma (Fig. 6). In the late Vallesian the talpids became more prevalent in the C-T and just as diverse in number of genera as the other insectivore families. After the turnover in the V-P, the frequency of talpid occurrence declined relative to the erinaceids and soricids. For the entire studied period, with the exception of the last time bin, the uropsiline mole *Desmanella* was the only talpid genus in the C-T. This mole is associated with relatively humid environments (Freudenthal et al. 2014; García-Alix et al. 2011). Between 8.5-8 Ma, two new talpid (non-uropsiline) genera appeared, *Archaeodesmana* and *Talpa*. In contrast to the inland localities, *Talpa* was at that time the most frequently recorded genus in the V-P.

Soricidae, the shrews, inhabit terrestrial or aquatic places and sometimes resort to (litter) burrowing (Ziegler 1999). The diversification of shrews is favoured by humid climates (Reumer 1995; Van Dam 2006). In the inland basins, shrews were the most diverse insectivore family between 10.5-9 Ma (Fig. 6). From 9-8 Ma their prevalence declined as that of the talpids increased. The soricids do not appear to be particularly diverse in the V-P (Fig. 6). In contrast to inland basins, where *Miosorex* was prevailing, in the V-P only two genera (*Crusafontina*, *Miosorex*) were identified. *Crusafontina*, a shrew believed to have thrived in humid environments (Ziegler 1999), first appeared in V-P during time bin 12-11.5 Ma, became more widespread in the late Vallesian and was from then on found in the inland basins.

The Dimylidae were an extinct family of insectivores, with a particular type of dental morphology, specialised for eating snails and other animals with exoskeletons (Furió et al. 2011; Müller 1967). The dimylids appear to have never reached the inner Iberian Peninsula as they were only found in the V-P (Fig. 6). *Plesiodimylus*, the most widespread genus of this family and characteristic of Central Europe and humid environments, was present from the late Aragonian and survived into the Turolian (Van den Hoek Ostende et al. 2016). While *Plesiodimylus* was the less-specialised dimylid, *Metacordylodon*, a form with a strongly amblyodont dentition (Ziegler 1999), was also present during the early Vallesian but it is restricted to the V-P and only sporadically recorded.

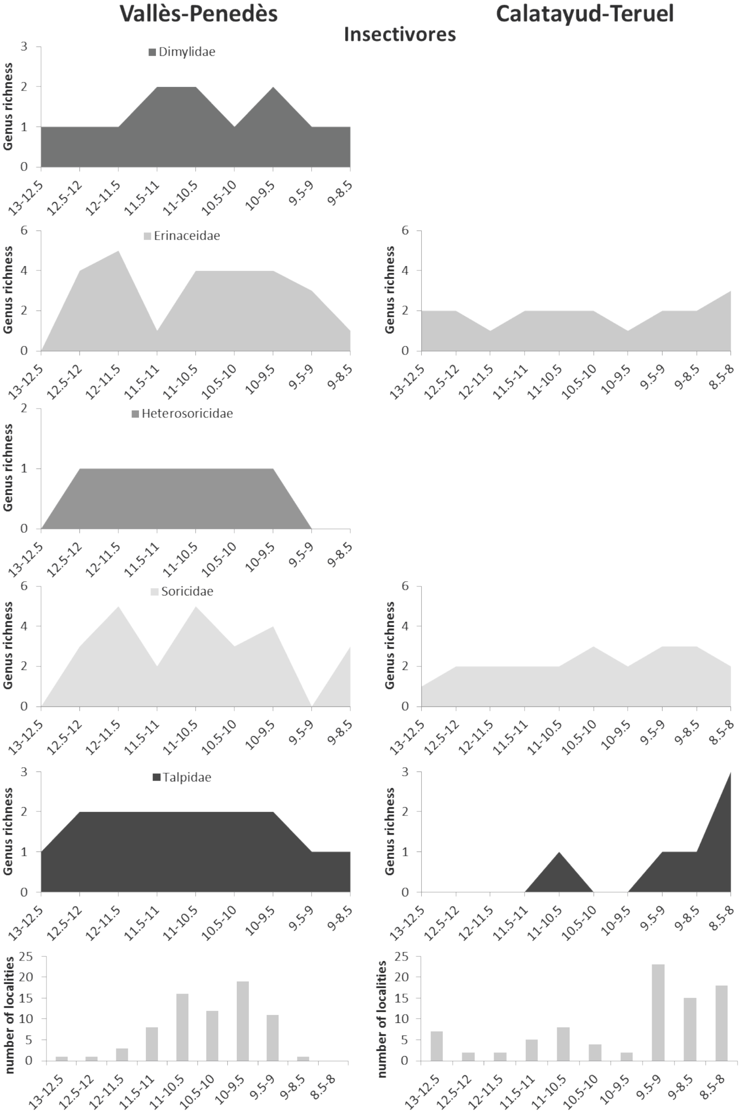


Figure 6. Insectivore richness trends compared between regions. Area charts per family displaying genus diversity per time bin. Bar charts below indicate sample size for rodents and insectivores combined (number of localities per time bin).

The last family is the Heterosoricidae, the ancient shrews. The only genus that represented this family was *Dinosorex*. These shrews preferred humid conditions and are mainly present in Central Europe during the Miocene (Furió et al. 2011). Heterosoricidae in the Iberian Peninsula were only ever found in the V-P until the turnover event and did not reach inland (Furió et al. 2015). They encompassed the least frequently recorded of the insectivore families and were gone by the end of the Vallesian faunal turnover event (Table 3).

Similar to the rodents, insectivores show a consistent low similarity for all indices except the Simpson's, again due to the C-T occasionally being a mere subset of the V-P assemblage (Figs. 3, 5b). Overall, the trends in Eulipotyphla diversity do not appear to differ that much between the inland and the coastal basins.

3.5. Micromammal differences within the Iberian Peninsula

Highest genus richness occurred in the early Vallesian of the V-P (Madern and Van den Hoek Ostende 2015). Within-region changes, especially inland, can mostly be explained by how many localities contained certain genera, and thus, how frequently a genus occurred. Some trends appeared less local and were visible in both the inland and at the coast. Both regions showed a high diversity of both glirids and old hamsters (Cricetodontinae), as well as erinaceids, throughout the studied time period. For many cricetid lineages (both cricetodontines and cricetines) there seemed to be a trend in evolving hypsodonty from brachyodont teeth or developing a tendency to hypsodonty. Fejfar et al. (2011) described the development of hypsodonty in various Miocene cricetine lineages and related these developments to presumably be adaptations to the consumption of tougher plant material, including grasses. This could explain why the cricetodontine lineage that also developed hypsodonty, namely the *Cricetodon-Hispanomys-Ruscinomys*, survived into the Pliocene.

Numerous differences were observed between the Miocene micromammal faunas of the inland C-T complex and the coastal V-P basin. Generally, the V-P had richer, more diverse faunas, which fits the notion of a more forested and humid coastal area versus a relatively open and more arid inland, indicated (amongst other evidences) by the localised presence of hominoids at the coast (Casanovas-Vilar et al. 2008,2011).

The coastal faunas contained a high number of Central European components, such as: *Heteroxerus, Tamias, Spermophilinus, Albanensia, Miopetaurista, Chalicomys, Glirudi-*

nus, Muscardinus, Myoglis, Paraglirulus, Tempestia, Eomyops, Lartetomys, Eumyarion, Democricetodon, Kowalskia, Megacricetodon, Anomalomys, Parasorex, Postpalerinaceus, Amphechinus, Atelerix, Schizogalerix, Lanthanotherium, Galerix, Desmanodon, Desmanella, Paenelimnoecus, Lartetium, Dinosorex, Plesiodimylus (Casanovas-Vilar et al. 2008). These taxa are not endemic and usually associated with humid environments. Furthermore, there are notable absences of Central European taxa in the V-P as well, such as *Deperetomys*, *Collimys*, *Forsythia* and a number of talpids. Most of the Central European taxa are intermittently present in the V-P, being only recorded when sample size is large enough (Casanovas-Vilar et al. 2014). This indicates a stronger connection with Central Europe than inner Spain, with the V-P being the area with taxa from both sides coexisting, resulting in higher diversity. The reasons for this are yet unclear, and may be linked to a higher environmental heterogeneity than the C-T, with the occurrence of more or less restricted humid environments. The higher rodent diversity in the V-P was due to the presence of many typical forest-dwellers, already indicating a difference in climatic conditions between the two regions of the Iberian Peninsula (Gómez Cano et al. 2011,2014).

The PERMANOVA results show the differences between the two areas per time interval (Table 4). The Eulipotyphla exhibit significant differences between both regions for all time bins within the studied period. The rodents show a slightly different picture. For this order, differences became more marked during the Vallesian, especially the late Vallesian. This demonstrates that faunal composition between both regions was generally fairly similar before. The Vallesian Crisis event apparently had a differential effect on the faunal composition of the coastal localities versus the inland ones, as was already suggested by Casanovas-Vilar and Agustí (2007). After the Vallesian the differences were more evident among these regions. A major difference between the regions can be seen in the Gliridae; their genus diversity was highest in the V-P, while they were more frequently recorded in the C-T.

One of the big differences between the inland and the coast was (and still is) the climate (Quézel and Médail 2003). Palaeoclimatic reconstructions show, from the Middle Miocene onwards, a latitudinal climatic gradient between the south and the north (Jiménez-Moreno et al. 2010). During the early to late Vallesian, the Iberian Peninsula experienced a change to arid and more seasonal conditions, which in the V-P led to the extinction of some forest-dwellers and the old hamsters (Bruch et al. 2011).

In conclusion, overall genus diversity was higher in the V-P than in the C-T, with the V-P also containing more Central European taxa. This is in accordance with Furió et al. (2011), who observed higher insectivore richness in more humid Central Europe and Casanovas-Vilar et al. (2008) for most micromammals.

3.6. Dynamics of the Vallès-Penedès small mammal faunas

Overall, the Vallès-Penedès contained mixed faunas including both taxa with preferences for arid habitats as well as ones with preferences for humid and forested environments during the late Aragonian and early Vallesian. Micromammal biodiversity was high between 12.5 and 9.5 Ma (Table 1). This confirms the development of a climax in Vallesian mammal richness. Notably, not one family, not even the typical forest-dwellers, declined within the V-P during the early Vallesian, just before the Vallesian mammal turnover took place. After the dispersal of new subfamilies into the area, such as the Murinae and Cricetinae, these became common in the rodent assemblage, found in most localities. The forest-dwelling taxa (Gliridae, Eomyidae and Pteromyini) were not too diverse during the Aragonian, while the Cricetodontinae simultaneously diversified (Fig. 4). This type of rodent assemblage, where forest-dwellers appear together with dominating cricetids, as seen in the first part of the studied period until the turnover event, is thought to be associated with humid warm to temperate forest environments, indicating the V-P was relatively more humid than other Iberian areas (Casanovas-Vilar and Agustí 2007; Casanovas-Vilar et al. 2008,2010; Gómez-Cano et al. 2011).

The cricetodontines experienced a decrease in occurrences, with only two genera, *Democricetodon* and *Megacricetodon*, disappearing after the Vallesian Crisis event. Furthermore, the glirids reduced in both frequency and diversity at the same time. These observations are in accordance with previous studies on Vallesian micromammal faunal dynamics (Agustí et al. 2003,2013). In contrast to the major changes in glirids, cricetodontines and murines, changes in other families were more subtle, as several taxa (including other forest-dwellers) at the early to late Vallesian boundary did not disappear instantly, but rather became less abundant (Casanovas et al. 2014). The changes in the local environment were probably relatively mild; Crusafont Pairó (1950) noted that the Vallesian faunas of the V-P reflected gradual change in the Late Miocene. Moreover, the persistence of early Vallesian forest-dwellers until the Vallesian/Turolian boundary indicated the environmental conditions at the coast continued to stay humid for a longer time until 9 Ma, or that at least some locally humid patches persisted (Casanovas-Vilar et al. 2014). On the other hand, some taxa might have been more sensitive to these gradual environmental changes than others and the boundary of early to late Vallesian (9.6 Ma) appeared to be the tipping point of their demise. This might be similar to the 'House of Cards' effect described by Agustí et al. (2013), where biodiversity levels strongly increased due to stable circumstances and then suddenly collapsed after passing a critical threshold. According to these authors, Vallesian faunas would have evolved into a self-organised, highly diverse ecosystem that because of its very nature was very sensitive to minor perturbations. In this 'House of Cards' model the demise of the Vallesian fauna is partially related to internal causes.

The fluctuations in the insectivores were more prominent. The Erinaceidae and Soricidae came to be more diverse during the late Vallesian, whereas the talpids exhibited the opposite. It is unclear what could have triggered these changes. Even though Eulipotyphla diversification is supposed to be favoured by humidity (Furió et al. 2011), the soricids here were not very diverse. As the shrews are the least humid dependent group, the moist conditions could actually have been limiting. At the end of the early Vallesian the disappearance of the Heterosoricidae was the most evident effect of climate change on the Eulipotyphla. The insectivores remained diverse and numerous after the turnover event, but there were some shifts in relative ratios of insectivore families. Consequently, the climatic and environmental transitions may have had their effect on the insectivores, but, except for the local extinction of *Dinosorex* (Furió et al. 2015), did not trigger a significant turnover event in this group.

3.7. Dynamics of the Calatayud-Teruel small mammal faunas

The overall micromammal diversity inland was lower than that at the coast (Fig. 3), with the exception of the earliest time bin and 9.5-8.5 Ma, although this might be an artefact due to the much poorer V-P record at that time (Fig. 2). While in the V-P some Middle Miocene mammals became extinct after the turnover event, these elements persisted in the C-T. *Democricetodon*, for example, persevered until the Turolian (Van Dam, 1997). Generally, the changes were subtle for every order, but PERMANOVAs show the frequencies in which localities contained certain genera changed significantly between successive time bins (starred values in Table 4).

The insectivores in the C-T, consisting of only three families, were less diverse than those of the V-P. The Talpidae re-appeared during the early Vallesian (Van den Hoek Ostende et al. 2012). The talpid ratio in the Turolian increased as the Soricidae decreased, in part because of the appearance of two new talpid genera. The proportion of erinaceids remained constant.

In the early Vallesian, the number of recorded Castoridae rose (and many more castorids are awaiting identification) at a time when more rodent families emerged. Overall, rodent diversity increased. Glirids, murines and cricetids in particular were present frequently. The murines were not rich in genera, but their appearance in numerous localities of the C-T shows they became increasingly more common elements of faunas during the Late Miocene.

The continuing presence of beavers in the C-T indicates there must have been flowing water present. Furthermore, the appearance of the talpids (*Desmanella*) in the early Vallesian strengthens the indication for an increase in wet conditions during the Vallesian (Garcia-Alix et al. 2011). This has been confirmed by Van den Hoek Ostende et al. (2012), who reported a higher proportion of insectivore versus rodent fossils, and concluded that the circumstances of the late Aragonian were slightly humid, but became wetter in the Vallesian. Central Spain was unique during the Aragonian and early Vallesian, with much lower rainfall levels and stronger warming than the rest of Europe (Van Dam 2006; Van Dam and Reichart 2009). Low humidity levels could explain the lack of forest-dweller abundance; as such environments did not extend inland.

Counterintuitively, the insectivores were most diverse in the Turolian, even though the conditions were supposedly dry or seasonal (Van Dam and Reichart 2009). Talpid genera *Archaeodesmana*, *Desmanella* and *Talpa* co-occurred in Teruel, indicating that wetter conditions might have (temporarily) returned to the Iberian inland during that time, perhaps after the increased seasonality around 8.5 Ma dry seasons were interspersed with wetter environments.

There is no clear evidence for an abrupt period of faunal change in the C-T, contrary to what has been reported about the coastal basin. The number of forest-adapted taxa present inland was low during the entire studied period. Moreover, the initial environment was open and less forested than in the V-P (Van der Meulen and Daams 1992). And as the C-T was probably less humid than the V-P during the late Aragonian and early Vallesian, the transition to an arid and seasonal climate was not as extreme and probably had effects of a lesser magnitude on the local faunas.

4. Conclusions

In spite of the many similarities in genus composition, the coastal Vallès-Penedes and inland Calatayud-Teruel basins were significantly different throughout the Vallesian and Turolian. Both had cricetid-dominated faunas during most of that time, with murids taking over in the late Vallesian and especially the Turolian. However, in the V-P, the cricetid rodents coexisted with many forest-adapted taxa and a high insectivore richness, indicating more wooded habitats with higher humidity levels. Genus counts were lower in the C-T and the 50% diversity drop in the V-P at the transition from early to late Vallesian was not mirrored inland. Instead, the number of rodents in the C-T increased, with the insectivores following at the beginning of the Turolian. Comparing the faunal composition and occurrences of the different families between regions highlight the differences. Not only did the community structure of the V-P differ significantly from the inland C-T basin, but the coastal basin also contained more Central European taxa. Several taxa never made it inland and, surprisingly, the diversity peaks in the two areas do not coincide. Whereas the greatest diversity along the coast is found in the early Vallesian (just before the turnover), the inland's peaks in the Turolian. Where the C-T gradually aridified, the V-P was humid, illustrated also by the high Eulipotyphla diversity and presence of Middle Miocene forest-dwellers. In both the C-T and V-P the true mice (Murinae) became dominant, taking over the role of the old hamsters (Cricetodontinae). The insectivores were apparently less susceptible to these changes. From the late Vallesian onwards, the climate became drier with increased temperature seasonality in both regions, which in the V-P led to the extinction of some forest-dwellers and the old hamsters. However, there is no indication that the coastal basin became more similar to the inland basin complex.

Our study confirms that large faunal differences, which should be linked to different environments, existed between the coastal area and the inlands of the Iberian Peninsula. Moreover, it shows that the Vallesian faunal turnover, while having a key impact in the V-P, did not cause major changes even within the confinement of the Iberian Peninsula. Through time, it seems that most genera did not actually disappear; indeed many of the purported victims of the Vallesian Crisis (certain glirids, the flying squirrels or a few cricetodontines) are sporadically recorded after this event, indicating that micromammal genera went extinct over longer periods of time. Their survival in the coastal basins / at higher latitudes is consistent with the theory that regions with milder environments function as so-called 'oases in the desert', where relict species survive longer. The large differences even at relatively short distances support the idea the 'Vallesian Crisis' was at most a local event.

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Chapter 5

Where's dinner?

Variation in carnivoran distributional responses to the mid-Vallesian faunal turnover

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Abstract

The Catalan locality of Can Llobateres 1 (early Vallesian, MN9) shows a remarkably rich diversity just prior to the mid-Vallesian crisis, including 23 species of Carnivora. Similarity maps using the Raup-Crick index and covering the Middle to Late Miocene (16–5.3 Ma) show that the origin of this carnivoran chronofauna lies to the north of the Iberian Peninsula, gradually making its way south. The chronofauna built up through migrations during the Aragonian, but shows a major influx during the early Vallesian, leading to a biodiversity hotspot. At the end of MN9, the mid-Vallesian turnover, the chronofauna collapses. This is mainly because of the extinction of parts of the fauna, and the retraction of some species to the north, disappearing from Spain. Thus, the rich fauna is an amalgamation of persisting older elements, northern elements having a brief temporary presence and new elements coming in. All these were supported by the unique rich ecosystem of the Vallès-Penedès Basin during the early Vallesian.

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Keywords: Late Miocene, palaeobiogeography, Carnivora, Vallesian Crisis, mammals, Iberian Peninsula

Introduction

Large carnivorans, like lions, leopards, bears, and wolves, have some of the widest distributions among mammals (Nowell and Jackson 1996), although they have been greatly reduced by anthropogenic influence. Only a few decades ago, leopards, for instance, still roamed the hills of Anatolia (Baskaya and Bilgili 2004), and lions survived in the Atlas Mountains well into the last century (Black et al. 2013). Mythology and folklore make it clear that in historical times large carnivorans have disappeared from various areas. One only has to consider the role of the wolf in European fairy tales or the presence of lions in the Middle East and southern Europe, which were featured in classical mythology (Hercules) and the Bible (David, Daniel). Nowadays, particularly the large cats like the Asian lion and tiger, are severely threatened, and various subspecies have already gone extinct (IUCN 2021).

When considering the late Pleistocene record, the distributions of the large carnivorans are even more impressive. (Sub)species of lion and spotted hyena roamed throughout Eurasia, the former even reaching the Americas (e.g., Argant and Brugal 2017; King and Wallace 2014; Rohland et al. 2005). Moreover, these large carnivorans were found during both glacial and interglacial cycles. Combined with the sizable present-day distribution, this suggests that these carnivorans are able to cope with a wide range of habitats and climatic conditions and hunt a wide variety of prey species. Even though some research suggests that hypercarnivorans may be more prone to extinction (Van Valkenburg et al. 2004; DeSantis et al. 2012), we may hypothesise that such ecological plasticity makes carnivorans more resilient than other groups to environmental changes and major faunal turnovers. To test this hypothesis, this paper focuses on the carnivorans during one of the most important faunal changes in the European Miocene, the mid-Vallesian faunal turnover.

Originally identified in the Vallès-Penedès Basin, the mid-Vallesian turnover known as the 'Vallesian Crisis' (Agustí and Moyà-Solà 1990; Moyà-Solà and Agustí 1990) started to be recognised throughout Europe and was considered as marking the change towards more seasonal climates and more open landscapes in Eurasia. The mid-Vallesian faunal turnover was also identified by Morales et al. (2015) as one of the major extinction events affecting Iberian Carnivora. However, recently the magnitude of the 'crisis' has come under scrutiny. Casanovas-Vilar et al. (2014, 2016) showed that, at least for the micromammals, the proposed sudden drop in diversity could be explained in part by sampling bias. Additionally, the geographic range of the Vallesian Crisis seems to be more limited than posed by some authors. Already within the confines of the Iberian Peninsula, inland basins show a quite different pattern of small mammal diversity change than the Vallès Penedès (Madern et al. 2018), the coastal basin that holds the type sections for the Vallesian European mammal age and in which the faunal turnover was first recognised. At the beginning of the Late Miocene the Vallès-Penedès hosted a remarkably rich mammal fauna (Madern & Van den Hoek Ostende 2015). This is particularly evident at the most famous of its fossil sites, the extensively sampled locality of Can Llobateres (Crusafont 1964; Begun et al. 1990; Moyà-Solà and Köhler 1995; Alba et al, 2011a, 2011b).

In this paper, we compare the carnivoran assemblage of Can Llobateres (Table 1) with the other European assemblages of the Middle and Late Miocene. We compute faunal similarity to assess to what extent the assemblage was part of the southward diversity trend noted by Madern and Van den Hoek Ostende (2015) or that it was a unique assemblage in itself.

Table 1. Fauna list Can Llobateres 1 (CL1); carnivoran chronofauna.

FAMILY	GENUS	FAMILY	GENUS
Ailuridae	*Protursus*	Mephitidae	*Mesomephitis*
Amphicyonidae	*Magericyon*	Mephitidae	*Promephitis*
Amphicyonidae	*Thaumastocyon*	Mustelidae	*Circamustela*
Barbourofelidae	*Albanosmilus*	Mustelidae	*Eomellivora*
Felidae	*Machairodus*	Mustelidae	*Marcetia*
Hyaenidae	*Protictitherium*	Mustelidae	*Martes*
Ursidae	*Indarctos*	Mustelidae	*Sabadellictis*
Ursidae	*Ursavus*	Mustelidae	*Trocharion*
Viverridae	*Semigenetta*	Mustelidae	*Trochictis*

Material and Methods

Palaeobiogeography

The methods used stem from the concept of chronofauna developed by Olson (1952). A chronofauna refers to a regionally limited assemblage of animal populations that has maintained its structure over a significant period of time. Analytically, the chronofaunas are represented by a set of localities distinguished by its similarity to a locality of interest (here Can Llobateres 1) (Ataabadi 2013).

The basis of this palaeobiogeographic analysis is a dataset downloaded from the New and Old World database of fossil mammals (NOW) on February 19th, 2023 (NOW Community 2023). The area under investigation for the Vallesian carnivoran chronofauna ranges from Europe to Anatolia and excludes North Africa; longitude between 10° W and 50° E; latitude between 15° and 55° N. Before filtering, the dataset contained 1434 specimen records (occurrences), from 332 Miocene localities. From the initial dataset, we applied several thresholds to filter out most single occurrences. We follow the updated Mammal Neogene units (MN) by Hilgen et al. (2012). We acknowledge the possible diachrony in MN unit boundaries (Van der Meulen et al. 2011, 2012), but since the biogeographic analysis relies on non-overlapping time bins, they are recognized as the best option. Localities with greater accuracy than MN unit level are lumped into the corresponding MN unit. Localities that cannot be confidently assigned to a unique MN unit are omitted from the dataset.

All analyses in this paper are carried out at the genus level. Genus-level data are considered more taxonomically robust than species-level data (Alroy 1996, 2003; Madern & Van den Hoek Ostende 2015), albeit these may introduce generalised assumptions about the ecology of the species within a genus (Martín-Suárez et al. 2001). Use of genus-level data holds more consensus (Peláez-Campomanes and Van der Meulen 2009) and is a widely-used taxonomic level at which specimens are identified (Forcino et al. 2012).

The biogeography of the Carnivora present in the early Vallesian Vallès-Penedès is analysed using the faunal resemblance index (GFRI) to Can Llobateres 1 based on Raup-Crick similarity indices (Raup & Crick 1979; Eronen 2009). The data was transformed into a presence-absence matrix using the sample2matrix function (Webb et al. 2008) from the picante library (Kembel et al. 2010) in R (R Core team, 2023). Can Llobateres 1 was chosen as a reference locality, being the best documented fauna in the Vallès-Penedès (Alba et al. 2011) and, additionally, the reference locality for MN9 (De Bruijn et al. 1992; Hilgen et al. 2012). Similarity indices were calculated using the vegan library (Oksanen 2023) in R (R Core team 2023). These were computed using the raupcrick function with 1000 randomizations of the dataset (Chase et al. 2011). An advantage of the Raup-Crick similarity index is that it takes the genus frequencies into account. Thus, localities sharing rare genera will score a higher similarity than communities sharing the same number of common genera. Calculated GFRI values per locality are given in the Supplementary Material.

Because the study addresses a terrestrial ecosystem, marine genera (Pinnipedia) were excluded. Occurrences of marine carnivorans are generally restricted to coastal areas and therefore do not contribute to the expected signal.

From the initial dataset, genera that were present in less than 10% of the sites in each MN unit were filtered out. The filtering threshold was empirically determined, by running analyses with a 0%, 5% and 10% filter, the latter providing the most consistent results (Braumuller 2019). Out of 332 localities and 133 genera, a total of 283 localities and 50 genera were retained, covering European mammal units MN4 to MN13 (around 17 to 5.3 Ma). In order to work out the relationship between distribution and extinction, carnivoran similarity was mapped.

The analysis and visualisation were performed in QGIS 3.26, using the IDW interpolation tool featured in the Spatial Analyst toolbox (QGIS.org 2023). The GFRI Raup-Crick values per locality were analysed separately for each MN unit with an inverse distance weighted distance coefficient P set at 3.0 (~300km) and pixel size 0.005. The interpolation areas were masked with an influence radius of 3 degrees buffer zone around each point (again ~300km) and plotted on the map per MN unit.

Results

Similarity maps

The map of MN4 (Fig. 1a) shows still little overall similarity with the Vallesian chronofauna. The highest similarity is found in the Swiss locality of Ober Schriberschwändili (0.66), but this is based on its sole carnivoran, *Trochictis*, being part of the chronofauna. Well-defined French carnivoran assemblages from the MN unit, like Bézian (twelve genera) and Artenay (15 genera), show much lower similarities (0.16 and 0.29, respectively), and have respectively three and four taxa in common with the chronofauna. One of these is *Martes*, a genus name that has been used as a waste-basket for many Miocene mustelids (Valenciano et al. 2022), and therefore should be treated with caution. Notably, it is also the only taxon of the chronofauna that is recorded from the Iberian Peninsula in MN4 and only in two out of the ten localities, El Canyet (also in the Vallès-Penedès, 0.45) and Artesilla (0.11).

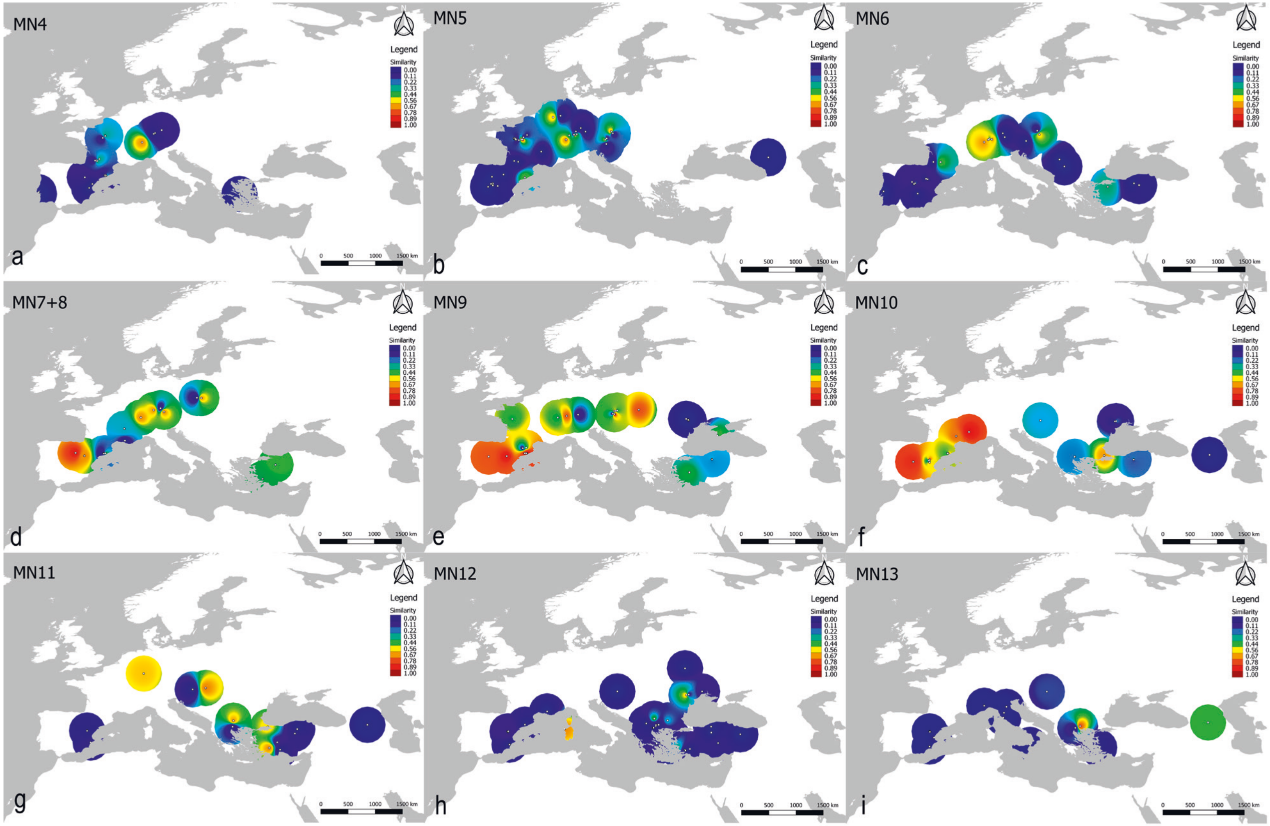

Figure 1 a) MN4, b) MN5, c) MN6, d), MN7+8, e) MN9, f) MN10, g) MN11, h) MN12, i) MN13. Maps of Eurasia, colours indicate Genus Faunal Resemblance Index (GFRI), based on Raup-Crick similarity per locality to Vallesian locality Can Llobateres 1, in order to identify the carnivoran Vallesian chronofauna.

In MN5 (Fig. 1b), the highest similarity is again found north of Spain, but this time it is much higher, reaching over 0.95. The assemblages with the highest indices are clustered in the Loire region. Most evident is Contres, France, (0.96), which shares four out of six genera with the Vallesian chronofauna. Contres is, however, an exception. Seven central European localities have a similarity between 0.55 and 0.75. This includes well-defined carnivoran assemblages such as Noyant-sous-le-Lude (5 out of 12 chronofauna genera shared; 0.68) and Pontlevoy (6/15; 0.67). Other larger assemblages from central Europe have much lower similarities, such as those from Göriach (1/9; 0.05) and Sandelzhausen (1/9; 0.02). Only two out of twelve Iberian MN5 assemblages in our analysis contain elements from the chronofauna, viz. La Retama (1/6; 0.06) and els Casots (2/7; 0.47).

The MN6 map (Fig. 1c) suggests relatively high similarities with central Europe, but this is caused by the three closely set Swiss localities of Oeschgraben, Uzwil-Nutzenbuech, and Sagentobel, which all represent single occurrences of *Trocharion*, resulting in the highest similarities in MN6 (0.65-0.68). Overall, similarities are somewhat lower than in the preceding unit, but more equitably distributed. This more equitable distribution is also evident from the higher proportion of the Iberian assemblages containing elements from the chronofauna, namely four out of ten. The highest similarity on the peninsula is found in the assemblage of Arroyo del Val (3/9; 0.36). A notable feature of the MN6 map is the very low similarity of the reference locality of the unit, Sansan (2/20; 0.01), in southernmost France.

MN7+8 (Fig. 1d) is the first unit with the highest similarity found inside Spain, in the assemblages of Escobosa de Calatañazor (3/5; 0.89) and Sant Quirze (3/5; 0.89). Even though the latter is located in the Vallès-Penedès Basin, in the *Democricetodon crusafonti - Hippotherium* interval zone, representing the latest part of MN unit 7+8, the basin appears as an area of low similarity on the map. The low value of the small assemblage of Barranc de Can Vila 1 (0/2; 0.0) visually obscures the highest similarity of the MN unit at San Quirze, in fact one of the highest overall similarities overall (Fig. 1d). Apart from having the highest similarity, the Iberian Peninsula shows for the first time a majority of assemblages containing an element from the chronofauna (five out of nine).

Similarities for well-defined assemblages in central Europe are moderate, such as those from La Grive M (0.63; 6/18), Steinheim am Albuch (0.65; 5/15), and Anwil (0.67; 3/6). The latter two display as areas of higher similarity in southern Germany and Switzerland, but, as was the case in the Vallès-Penedès, the area of La Grive in southwestern France appears as an area of low similarity. Here, the value of La Grive M is overshadowed by those of other La Grive fissures, with similarities ranging from 0.00 (La Grive CD 14; 0/1) to 0.50 (La Grive L3; 5/14).

As the analysis is based on the MN9 (Fig. 1e) chronofauna of the Vallès-Penedès, it is not surprising that the highest similarities are found in that basin. Apart from the reference fauna of Can Llobateres 1, with a similarity of 1 per definition, four other carnivoran assemblages (Can Ponsic I (7/11), Can Poncic (6/11), Castell de Barberà (4/5), and Santiga (3/3)) have similarities exceeding 0.95. All 15 Iberian assemblages except for one, that of la Teuleria del Firal (0/1), contain elements of the chronofauna. Unfortunately, this single occurrence causes, together with the nearby assemblage from Bellestar (0.18; 1/4) an apparent spot of low similarity in the north of Catalonia on the map (Fig. 1e).

Similarities in central Europe are generally higher than in other MN units. The highest scores are found for the localities of Götzendorf (0.90; 3/5) and Rudabánya (0.76; 5/12). Notably, the overlap with the reference fauna Can Llobateres is not that large, and the high similarity is presumably based on shared rare taxa, such as *Mesomophitis* in the former and *Protursus* in the latter. In fact, Can Llobateres and Rudabánya are the only two localities that have a record of *Protursus*.

Similarities on the Iberian Peninsula remain high during MN10, but overall, they seem to be more localised (Fig. 1f). Ten out of the twelve highest Raup-Crick values are located in Spain, the other two being the localities of Soblay (0.91; 4/7) and Montredon (0.71; 3/7), both in southern France. In fact, only one locality in Spain has no similarity to the chronofauna, and this concerns a single occurrence in Masía del Barbo 2B (0/1). The map shows that there is a clear separation, with similarities in the west being higher than those in the east. The only light spot in the east on the map is caused by the Turkish locality of Yulafli (CY), which is again based on a single similar genus, in this case of *Indarctos*.

The map of MN11 (Fig. 1g) shows a marked decrease in similarities. Notably, only 16 carnivoran assemblages are available for this unit, with the two larger assemblages (Csákvár, (0.69; 4/11) and Dorn-Dürkheim (0.61; 7/18) suggesting the highest similarities with central Europe. Within the Iberian Peninsula, similarities are markedly low (Crevillente 2, 0.10; 1/5; Puente Minero, 0.07; 1/7). As on the map of MN10, lighter spots in the east are mainly caused by single occurrences (Kemiklitepe D in Anatolia and Kocherinovo 1 in Bulgaria), although the locality of Küçükçekmece also gives a relatively high similarity (0.58; 2/6).

Similarities remain low in MN12 (Fig. 1h). Out of the 50 carnivoran assemblages, 29 have no elements from the chronofauna. Higher similarities all concern assemblages with one or two carnivorans only, the highest being Samos (PMAS) (0.90; 2/2). Because of its isolated position, Fiume Santo (0.68; 1/1) creates a light spot on Sardegna/Corsica, but this is clearly an artefact. Large carnivoran assemblages such as those of Pikermi (0.06; 3/17) and Los Mansuetos (<0.01; 1/13) confirm the general lack of similarity with the Vallesian fauna. In MN13 (Fig. 1i), only four out of twenty-one assemblages contain elements from the chronofauna. The higher similarity for Maramena (0.75; 2/5), giving a peculiar light spot to the east, can be attributed to the presence of *Promephitis*, a rarer element in the Late Miocene assemblages, and a species of *Martes*, which we already recognized as a contentious taxon for the Miocene.

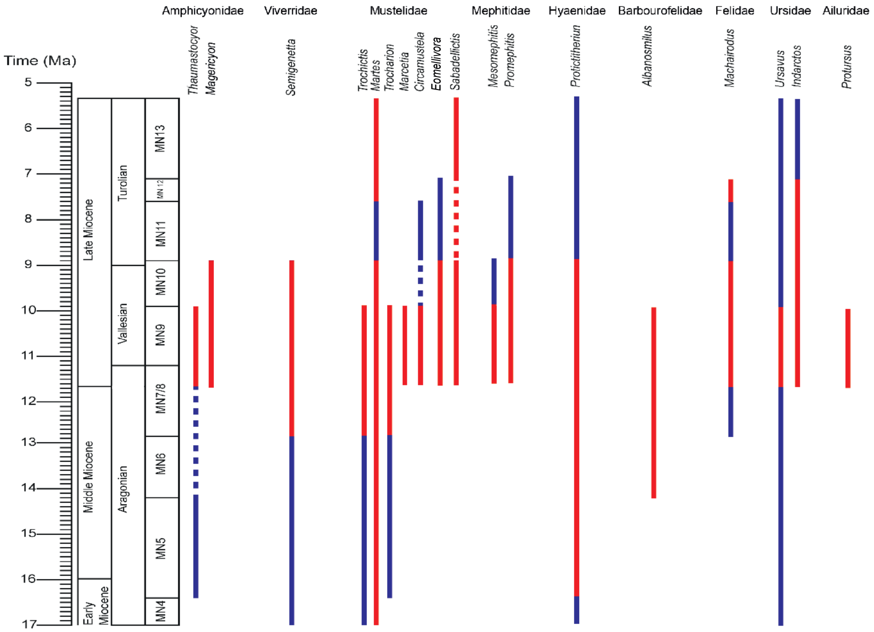

Figure 2. Temporal ranges per genera in Europe (blue) and in Iberia (red) per MN unit.

Rise and fall of the chronofauna

Figure 2 shows the temporal ranges of Carnivora genera of the chronofauna in Eurasia, first (FO) and last occurrences (LO), as well as their FO/LO on the Iberian Peninsula.

Only a few elements of the Vallesian carnivoran chronofauna appeared in Europe as early as MN4, accounting for the low similarities in western Europe and the Aegean region. The carnivorans that are already present are the hyenid *Protictitherium*, the viverrid *Semigenetta*, the ursid *Ursavus* and the mustelids *Trochictis* and *Martes*. One has to bear in mind, however, that the latter genus name is used as a waste basket for multiple Miocene species (Valenciano et al. 2022). Therefore, we should not attach much value to *Martes* being the only element of the chronofauna present on the Iberian Peninsula in MN4.

Not counting *Martes*, *Protictitherium* is the first element to enter the Iberian Peninsula in MN5. *Thaumastocyon* and *Trocharion* make their first appearance in Europe, bringing the total number of chronofauna elements up to seven. In MN6, only one element is added, the barbourofelid *Albanosmilus*, which immediately also appears in Spain. However, there are no records of *Thaumastocyon* as of yet in that unit.

Three small carnivorans make their first appearance on the Iberian Peninsula during MN7+8; the viverrid *Semigenetta* and the mustelids *Eomellivora*, *Trochictis* and *Trocharion* (Alba et al. 2021). The major pulse comes in MN9. The ursid *Ursavus,* already present in Europe, now makes its way onto the Iberian Peninsula, as does the felid *Machairodus*. The entrance date of *Thaumastocyon* cannot be determined by the lack of records from MN6 and MN7+8, but it is also present on the Iberian Peninsula in MN9. Eight taxa appear for the first time: the amphicyonid *Magericyon*, the mustelids *Marcetia*, *Circamustela*, and *Sabadellictis*, the mephitids *Mesomephitis* and *Promephitis*, the ursid *Indarctos*, and the ailurid *Protursus*.

While nine taxa of the chronofauna make their first appearances in MN9, the unit records the last occurrences of six. Four of these are elements that were already present in the Middle Miocene, the amphicyonid *Thaumastocyon*, the barbourofelid *Albanosmilus*, and the mustelids *Trochictis* and *Trocharion*. The two other taxa, *Marcetia* and *Protursus*, are, in fact, restricted to MN9. In addition, both the mephitid *Mesomephitis* and the ursid *Ursavus* have their last occurrence on the Iberian Peninsula. This holds also true for the mustelid *Circamustela*, but, in the absence of an MN10 record, the true time of its extirpation in Spain is unclear.

Two of the surviving genera into MN10, *Magericyon* and *Semigenetta* disappear during that unit. The presence of *Martes* and *Machairodus* on the Iberian Peninsula is interrupted during MN11, but as we noted above, fewer assemblages are available for this time unit, which may account for the temporary regional absence. All in all, eight taxa from the chronofauna are present in the Turolian, half of which are only found north of Spain. Notably, five out of the eight Turolian taxa made their first appearance at the beginning of MN9, representing true Late Miocene elements. *Protictitherium* and *Ursavus* are long ranging taxa. *Martes* also appears as such, but, as mentioned above, there are doubts to what extent the Miocene representatives can truly be attributed to the extant genus (Valenciano et al. 2022).

Discussion

Methodology

Similarities between localities and the early Vallesian chronofauna for the carnivorans from the Vallès-Penedès were calculated using the most complete fauna from the basin: Can Llobateres 1. Out of the four highest similarities found, three are from MN9 localities in the Vallès-Penedès (all >0.98), which indicates that Can Llobateres 1 is indeed a representative fauna for that time and region. However, some of the faunas from the basin in our analysis gave low similarities. This shows that we have to be careful with our interpretation of the maps, since particularly small faunas may show a similarity deviating from the overall pattern. Whereas the low similarities in the Vallès-Penedès can be considered a false negative, poor faunas in the Turolian and early Middle Miocene, particularly single occurrences, can lead to false positives. They appear like dots of high similarity in a region of low similarity. This is enhanced if the single occurrence happens to be a rarer element, even in larger assemblages such as the MN13 locality of Bazaleti. The relatively high number of deviant values is doubtlessly related to the general rarity of carnivorans in mammal assemblages. This enhances the effect of chance occurrences.

Although the carnivorans of Can Llobateres 1 are clearly representative of the early Vallesian fauna of the Vallès-Penedès, it is important to realise that they do not comprise the entire faunal community of the time and region. The chronofauna is clearly dominated by mustelids (Tab. 1, Fig. 2), but contains only one hyaenid, *Protictitherium*, and one felid, *Machairodus*. However, two more felids, *Styriofelis* and *Pseudaelurus,* and two more hyaenids, *Hyaenictitherium* and *Thalassictis*, were present in the early Vallesian of the Vallès-Penedès (e.g., Robles et al., 2013). As such, our analyses are partly influenced by the local conditions at Can Llobateres, and the similarities of localities containing these faunal elements would be higher when considering the Vallès-Penedès MN 9 carnivoran assemblage as a whole.

Biogeography

The Miocene is a period with large climatic changes, including the Mid Miocene Climatic Optimum, the Mid Miocene Cooling, and the increased seasonality in the Late Miocene (Zachos et al. 2001; Dam 1997; Steinthorsdottir et al. 2021). Together with large-scale geographic changes, such as the closing of the Mediterranean and the gradual retreat of the Parathetys, these climatic events resulted in the shift of the distribution of mammals. Pickford and Morales (1994) already noted that changes in faunal similarity are connected to latitudinal shifting of zoogeographic realms. The southward trend of the area of highest diversity through the Middle and early Late Miocene, as suggested by Madern and Van den Hoek Ostende (2015), might represent the shifting of the border between two such realms. The Iberian Peninsula was open and arid during the Middle Miocene (Meulen and Daams 1992; Maridet and Costeur 2010), a situation that started to change towards the beginning of the Late Miocene. According to Van der Meulen and Daams (1992), humidity started to increase at the end of the Aragonian towards the humid conditions of the early Vallesian. This is, for instance, clear from the reappearance of beavers in the inland basins of the Iberian Peninsula, and supported by palaeobotanical evidence (e.g., Barrón et al. 2010; Jiménez-Moreno et al. 2010).

MN7+8 sees a marked increase in similarity between the Iberian faunas and the chronofauna (Fig. 1d). As discussed above, the apparent low similarity in the Vallès-Penedès in the figure is a mapping artefact, the highest similarity of the unit actually being found in this basin. Morales et al. (2015) identified the late Aragonian as a period in which many carnivorans migrated to the Iberian Peninsula. Abella et al. (2014) linked the migration of the Ursidae into Iberia to these humid conditions and the dense forests of the early Vallesian. Indeed, Ailuridae and Ursidae enter only at the beginning of the Vallesian, with *Indarctos* being the only genus that remains after MN9. *Ursavus*, by contrast, is only present in Spain during MN9. As such, the taxon is a transient in the sense of Van der Meulen et al. (2005). However, it is not the only genus that only appears in MN9 in Spain.

Marcetia and *Protursus* have a range restricted to MN9, the former even being known from Can Llobateres 1 only, the latter only appearing in Rudabánya in our dataset, and recently identified in Hammerschmiede (Kargopoulos et al. 2022). Like *Ursavus*, possibly amphicyonid *Thaumastocyon* has a more northern occurrence before entering Spain in MN9 and becomes extinct at the mid-Vallesian turnover. The mustelids *Sabadellictis*, and *Circamustela*, as well as the skunks *Promephitis* and *Mesomephitis*, have their first overall occurrence. Of these four, only *Sabadellictis* continues into the Spanish Turolian. *Circamustela* and *Promephitis* seem to retract their ranges to the north, although the latter continues in Spain in the late Vallesian. *Mesomephitis* is no longer found in Spain after MN9, and becomes extinct at the beginning of the Turolian. As such, *Circamustela*, *Promephitis* and *Mesomephitis* should also be considered Vallesian transient taxa on the Iberian Peninsula.

All in all, the Vallesian turnover event for the carnivorans is an amalgamation of Aragonian relics, an influx of new taxa in late MN7+8/early MN9, combined with extinctions in MN9 (Fig. 1e; Casanovas et al. 2010; Morales et al. 2015). The build-up of the chronofauna on the Iberian Peninsula was apparently gradual, with two elements being present in MN4, one entering in MN5, one in MN6 and three in MN7+8 (Fig. 2). However, the time of entrance of *Thaumastocyon* is uncertain because of the lack of latest Middle Miocene records both inside and outside the Iberian Peninsula.

We also noted that the chronofauna lacks two hyaenids and two felids that are present in other early Vallesian localities in the basin. Of these, *Hyaenictitherium* is indeed an MN7+8 immigrant, whereas the other hyaenid, *Thalissictis*, enters only in MN9. Both genera continue into the Turolian. By contrast, the two felids are long-term residents on the Iberian Peninsula and were already present in the early Aragonian. Neither survives into the Turolian, *Pseudaelurus* having its last Iberian record in MN9 and *Styriofelis* in MN10 (Robles et al. 2013).

Conclusions

Plotting the similarity of carnivoran assemblages to that of our MN9 reference fauna, Can Llobateres 1, reveals a southward trend with the highest similarities in the Middle Miocene, accumulating in Spain in the early Vallesian, followed by a collapse in MN10. Whereas our study confirms the plotting of Raup-Crick values as a valuable tool for recognizing patterns, it also shows the importance of looking behind the data. Anomalies in the pattern can be as important as the pattern itself. Although many of these anomalies are, even after filtering, the result of single occurrences or small sample sizes, larger assemblages may not fit the pattern. In our case, this could in part be traced back to some of the early Vallesian genera from the Vallès-Penedès not appearing in the reference fauna, namely the hyaenids *Hyaenictitherium* and *Thalassictis*, and the felids *Pseudaelurus* and *Styriofelis.* A second caveat that became clear from our analyses, is that high similarity may be obscured on the map, stressing the importance of looking beyond the visualisation and considering the data itself.

The stratigraphic ranges of the individual elements of the chronofauna show that older elements entered Spain gradually throughout the Middle Miocene. Their earlier presence at higher latitudes accounts for the higher similarities being found to the north of the Iberian Peninsula. The early Vallesian sees an increased influx of northern elements, the most notable of which are the bears, in line with the forested, humid conditions of the period. At the same time, new elements arrive, including the Mephitidae and Machairodontines.

The extinction of several lineages in the chronofauna, including the mustelids bearing the heaviest of the loads, marks the end of MN9 as a true turnover. However, a number of genera appear to be Vallesian transients, only appearing in Spain at a time when conditions were optimal, but retracting their ranges to the north afterwards.

To sum up, the early Vallesian carnivoran community of the Vallès-Penedès is an amalgamation of varying signals. It is a culmination of Middle Miocene elements entering Spain at various times, combined with new elements and northern taxa making a temporary appearance on the Iberian Peninsula. The optimal conditions in the basin led to a short-lived, real biodiversity hotspot. The role of the transient taxa certainly has bearing on the discussion about the range and extent of the 'Vallesian Crisis', as their disappearance from Spain enhanced the regional signal. The carnivorans thus emphasise the unique conditions of the early Vallesian in its type area.

Supplementary Material

1. GFRI Raup-Crick similarity values per locality
2. Presence/absence matrix genera per locality
3. Maps per MN unit with locality labels

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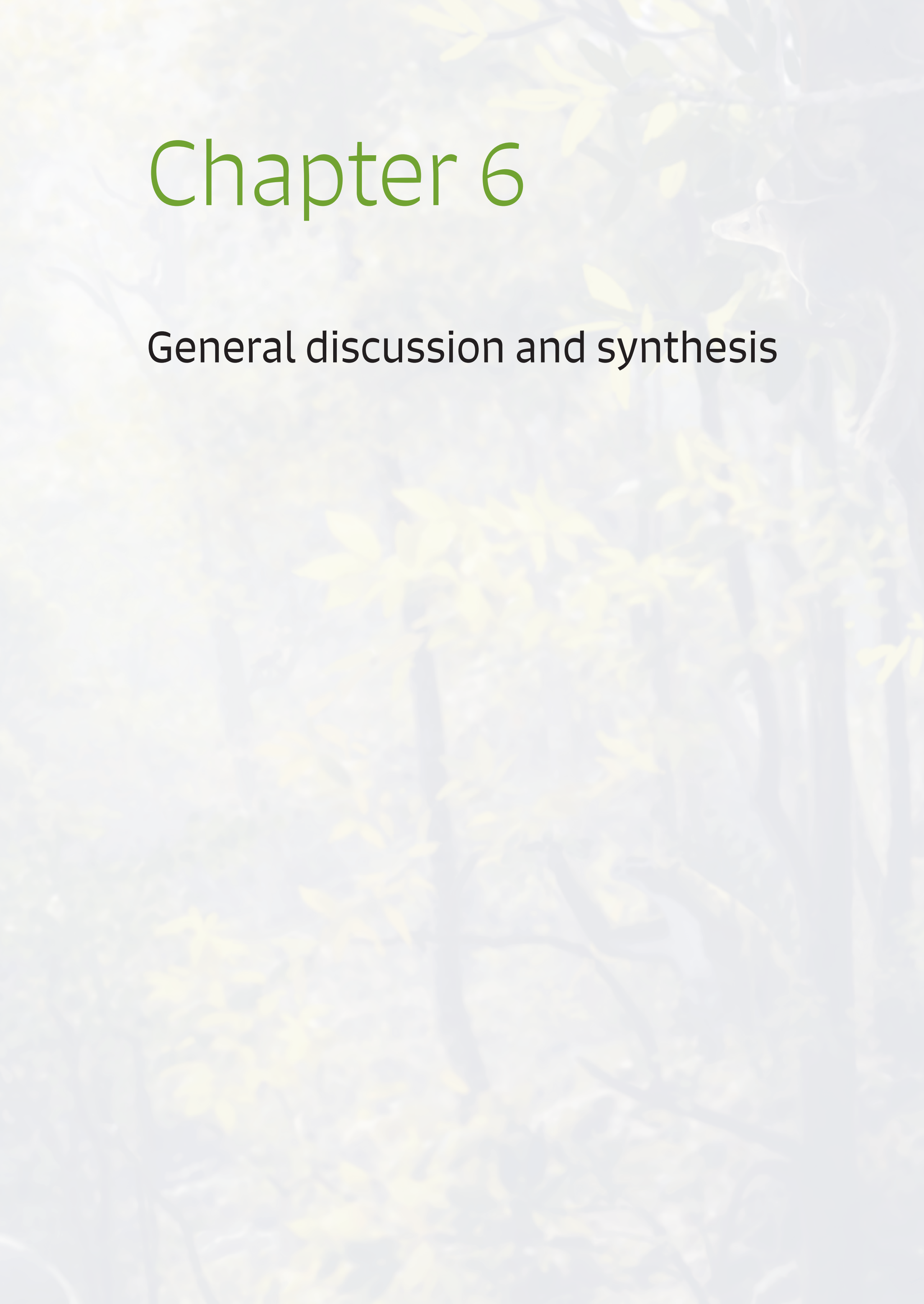

Chapter 6

General discussion and synthesis

6. General discussion and synthesis

This thesis aims to determine whether the Vallesian Crisis is an example of the abrupt collapse of a diversity hotspot or a series of Late Miocene extinctions over a longer time interval. As Stephen Jay Gould already noted last century: "Paleontologists are [...] historians at heart and by profession", working to infer "the processes we cannot see from results that have been preserved."

In the history of mammalian palaeontology, the Iberian Vallès-Penedès Basin plays an important role. It was here that one of the founders of Spanish mammal palaeontology, Miquel Crusafont Pairó, started his research and discovered many classical localities (Crusafont Pairó 1950; Crusafont Pairó and Truyols 1960; Alba & Casanovas-Vilar 2022); the most famous of these sites is doubtlessly the locality of Can Llobateres 1 (Crusafont Pairó 1964).

The early work mainly focused on large mammals, small mammals being at most by-catch. Nonetheless, when the study of micromammals took flight around half a century ago, again the Vallès-Penedès showed its remarkable richness, also for these tiny fossils (e.g. Agustí 1981,1982,1990; Agustí et al. 1985,1997; Casanovas-Vilar et al. 2010,2011,2014,2016b; Furió et al. 2011; Hartenberger, 1965,1966; Hartenberger & Thaler 1963).

Whereas the richness in the number of sites and multitude of fossils was clear from the beginning, the realisation of the rich diversity of the Vallès-Penedès grew gradually. In hindsight, it can already be recognized in the definition of the Vallesian by Crusafont Pairó as an admixture of old elements and Late Miocene immigrants. Chapter 2 not only shows that the Vallès-Penedès was indeed a hotspot in Miocene mammal diversity, but also that this diversity peak is the culmination of a southward dispersal trend (Madern & Van den Hoek Ostende 2015).

Following this biodiversity peak came a drastic drop in richness during the early Late Miocene, recognized as the 'Vallesian Crisis' (Agustí and Moyà-Solà 1990; Agustí et al. 1984). However, the remarkable diversity of the Vallès-Penedès can only be recognised when compared to that of other areas, as already noted by Agustí (1990). This comparison was further facilitated by the introduction of databases in palaeontology. The NOW database has proven itself to be a particularly valuable tool for interregional comparisons, as shown in chapter 4 (Madern et al. 2018).

6.1 The hotspot and sampling bias

In general the small mammal record is fairly continuous, in contrast to the large mammal record, which has major hiatuses between the major sites. There are important effects of uneven sampling over diversity dynamics in the Vallès-Penedès mammal record, as outlined by Casanovas-Vilar et al. (2014,2016b). Because the sample size is much larger during the late Aragonian and early Vallesian, computing richness by simply counting the number of specimens present will always result in a higher diversity. The result is an abrupt collapse of species richness, the so-called 'Vallesian Crisis'. This decrease in diversity in fact reflects a decrease in sample size, and implies that many uncommon taxa are not recovered during the late Vallesian simply because sampling is insufficient. The pattern is even more pronounced because one of the better sampled intervals, between 9.7 and 9.8 Ma, immediately precedes the 'Vallesian Crisis'. This interval includes the site of Can Llobateres 1, which with more than 70 mammal species, has the highest richness in the entire European early Vallesian period (Alba et al. 2011; Casanovas-Vilar et al. 2014; Madern et al. in press). Despite the fact that ongoing, extensive excavations have an impact on how biodiversity is perceived, genus richness is far less affected than relative abundance, making it a better measure for analysis (Madern & Van den Hoek Ostende 2015).

The quality of the fossil record in the Vallès-Penedès Basin differs before and after 9.7 Ma, with the richest site of Can Llobateres 1 right before the boundary 'inflating' diversity even further. Because of uneven sampling, diversity prior to the crisis is exaggerated. The presence of such sampling peaks immediately increases richness as well as the number of originations and extinctions during this interval (Foote 2000). In terms of extinctions, a number of taxa that would have been last recorded in preceding intervals now appear in the interval with the better record, implying an abrupt extinction event.

When comparing the victims of the Vallesian Crisis, three characteristics stand out. First, they are mostly forest-dwellers, second, they are of Middle Miocene origin, and last, very important, they are rare during the early Vallesian. These rare taxa have discontinuous distributions and are mostly, and sometimes only, recorded in rich sites, such as Can Poncic and Can Llobateres 1 (e.g. Alba et al. 2011; Casanovas et al. 2015; DeMiguel et al. 2011).

As far as micromammals are concerned, some of the purported victims of the Vallesian Crisis were actually recorded during the late Vallesian in well-sampled sites, although very rare (Casanovas-Vilar et al. 2014,2016a). The smaller sample size of the early Turolian sites is probably insufficient to record more rare taxa.

For the large mammals the Turolian sites have a substantially lower genus richness than the Vallesian ones (Madern & Van den Hoek Ostende 2015). Many Vallesian taxa seemingly had already gone extinct by the middle Turolian, and with the absence of early Turolian records this results in an artificial extinction peak during the latest Vallesian. Clearly, continental-scale analyses of the Vallesian Crisis should account for the potential bias introduced by sampling and critically evaluate its effects on diversity patterns. Given the poor Turolian record, this is especially important for Central Europe. In order to quantify these patterns, analysing bioprovinces or chronofauna are tools for which databases can be very useful. Obviously, the pattern changes considerably if specific rich sites were excluded from the analyses. In fact, the Vallès-Penedès represents a diversity hotspot during the early Vallesian (Madern & Van den Hoek Ostende 2015), mainly because of Can Llobateres 1. Without this locality diversity remains high but much more comparable to that of other European regions, such as Austria and eastern Hungary (Casanovas-Vilar et al. 2014).

Agustí et al. (2013) recognized the lack of correlation between the Vallesian Crisis and any major global climatic perturbation. They advocated internal mechanisms and coined the 'House of Cards' effect as an explanation. Early Vallesian assemblages are enriched with new immigrant taxa while simultaneously retaining most of the typical Middle Miocene forest-adapted faunal elements. According to Agustí et al. (2013), the increased diversity following prolonged times of environmental stability resulted in overly complex and saturated mammal communities highly sensible to perturbation. Only a minor perturbation, such as environmental change, could have caused the whole system to collapse. However, this is a rather 'ad hoc' hypothesis that implicitly assumes that sampling is complete and even, while Casanovas-Vilar et al. (2014) clearly showed this was not the case.

It must be noted that while current status of the Vallesian Crisis as an abrupt and drastic extinction event affecting early Late Miocene mammal communities has been questioned as partly deriving from sampling bias (Casanovas-Vilar et al. 2014,2016b), the 'Vallesian diversity hotspot' does not fall within this category. Indeed early Vallesian communities were enriched with new immigrant taxa but at the same time retained most older, late Aragonian, residents although many of these were rare and hence are not represented if sample size is not large enough. Intensively sampled sites such as

Can Llobateres 1 allow for the recovery of such rare taxa (for an example regarding the extremely rare flying squirrels see Casanovas-Vilar et al. 2015) and provide an accurate picture of true diversity.

6.2 The turnover event

6.2.1 Composition of the Vallesian chronofauna

The term chronofauna was introduced halfway during the last century by Olson (1952) “defined as a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time” (Van der Meulen et al. 2005; Van der Meulen & Peláez-Campomanes 2007). The Turolian large mammal faunas of the Iberian Peninsula are notably different from the Vallesian ones. They reflect the expansion of the so-called Pikermi chronofauna (Solounias et al. 1999; Eronen et al. 2009), characterised by the abundance and diversity of more savanna-like herbivores. Eronen et al. (2009) and Casanovas-Vilar et al. (2010) linked their expansion into western territories to the noted aridification of the Mediterranean region. As early as the Aragonian the first eastern immigrants entered the Vallès-Penedès, while more followed during the Vallesian, such as felids like *Machairodus*, bovids like *Tragoportax* and giraffids such as *Palaeotragus* and *Decennatherium* (Alba et al. 2019,2022; Robles et al. 2011). The horse *Hippotherium* originally dispersed from North America, with the oldest occurrence in the Vallès-Penedès dating back to 11.2 Ma (Bernor et al. 2021; Garcés et al. 1997).

Late Miocene Pikermi faunas from Greece represent an open country assemblage and were characterised by hipparionine horses (*Hipparion* and *Cremohipparion*), together with bovids and giraffids (Bernor 1984; Bernor et al. 1979,2021; Eronen et al. 2009; Fortelius et al. 1996; Solounias et al. 1999; Tobien 1967). Central-European Middle Miocene faunas were different. They were dominated by cervids, suids and had more humid and forested environments (Madern & Van den Hoek Ostende 2015). The Middle Miocene of inland Iberia is quite dry and presumably had more open-country dwellers (Bernor et al. 1996; Casanovas-Vilar et al. 2005; Eronen et al. 2009; Solounias et al. 1999). The Vallesian large mammal assemblages were intermediate between those two faunas. They contained immigrants from the East, coexisting with Middle Miocene forest faunas (Agustí et al. 2013; Madern & Van den Hoek Ostende 2015).

Concerning small mammal faunas, the early Vallesian records the dispersal of the modern cricetine *Cricetulodon*, which is recorded by the latest Middle Miocene in Anatolia (de Bruijn et al. 2013) and appears in the Calatayud-Montalbán basin at 10.6 Ma (Van Dam et al. 2014) and in the Vallès-Penedès at 10.3 Ma (Agustí et al. 1997; Casanovas-Vilar et al. 2016a). The dispersal of *Cricetulodon* coincided with the decline in abundance and the extinction of some species of the older cricetid genera *Democricetodon* and *Megacricetodon*, dominant in Middle Miocene Iberian faunas, but did not imply any other noticeable changes in rodent assemblages. Another important rodent dispersal was that of the early murine *Progonomys*, first recorded in Pakistan at 11-12 Ma (Wessels 2009, Flynn et al. 2020), and which were already present in very low numbers in Calatayud-Montalbán and Teruel basins at 10.4 Ma (Van Dam et al. 2014). *Progonomys* is recorded later in the Vallès-Penedès, at 9.7 Ma (Agustí et al. 1997; Casanovas-Vilar et al. 2016a). During the entire Vallesian the Vallès-Penedès faunas are consistently characterised by a higher diversity of rodents and insectivorans as compared to Iberian inland basins (see Casanovas-Vilar & Agustí, 2007; Furió et al. 2011; Madern et al. 2018), with the persistence and/or greater abundance of late Aragonian elements adapted to more humid and forested environments. This distinguishes the coastal areas of Catalonia as a separate biogeographic region and is also evidenced by some macromammals, such as primates, which indeed do not occur in inland basins. During the late Vallesian the differences between the small mammal assemblages are particularly striking, those of Teruel for example being overwhelmingly dominated by murines and those of the Vallès-Penedès including murines but being instead dominated by the cricetine *Rotundomys* (a descendant of *Cricetulodon*) and still retaining several, although rare, forest elements such as flying squirrels and eomyids (Casanovas-Vilar & Agustí 2007; Casanovas-Vilar et al. 2016a,2016b; Madern et al. 2018).

While most Mediterranean environments at the start of the late Miocene became drier and harsher, the coastal Vallès-Penedès Basin (Catalonia, Spain) continued to remain humid, with faunas such as Can Mata which were dominated by suids, rhinos and small pecorans (*Micromeryx*, *Dorcatherium*). Forest-adapted faunas roamed until around 9.6 Ma, including the last hominoids of western Europe, while pliopithecoids lasted even a little longer, until 9.1 Ma at Torrent de Febulines (Agustí et al. 2003; Casanovas-Vilar et al. 2011; Marmi et al. 2012). The late Vallesian macrofloral data from the Vallès-Penedès Basin show the persistence of warm-temperate forest environments, although they would include a remarkable proportion of deciduous trees (Agustí et al. 2003).

The environment during the late Vallesian was spatially fragmented, resulting in a biodiverse mosaic at the fringes where both southern and northern faunal elements co occurred. The low biodiversity in the Turolian and ultimate disappearance of the hotspot could be attributed to a shift in the humidity gradient (Madern & Van den Hoek Ostende 2015).

6.2.2 Geographical and temporal patterns

The environment and subsequent biotic interactions can drive evolutionary change, which happened in the Neogene as well (Behrensmeyer et al. 1992; Fortelius et al. 2014). Harsh environmental conditions lead to extinctions or the appearance of novelties, and mild environments like in the Vallès-Penedès give long ranging taxa a chance of survival and in a sense act as a refugium (Madern et al. in press).

After the Vallesian, the Turolian faunas show lower diversity than before. The persisting humid and forested environments of Central Europe could have prevented the dispersal of open-country specialists, resulting in a poor fauna with only a small number of Pikermian immigrants, numerous extinctions and no additional endemics (Casanovas-Vilar et al. 2005; Madern & Van den Hoek Ostende 2015; Madern et al. 2018;in press).

Comparing faunal composition between both the coastal Vallès-Penedès Basin and inland Calatayud-Teruel Complex confirms the local scale of the turnover event (Madern and Van den Hoek Ostende 2015). Shifting bioprovinces can explain that the diversity peaks in the two areas do not coincide (Madern et al. 2018). When zooming out yet again and looking at the similarities between the mammal assemblage of type locality Can Llobateres 1 and other Miocene localities, we see a clear waxing and waning of bioprovinces through time and space. Highest Vallesian similarity is found during MN 9 and highest Pikermi similarity between MN11-MN12, demonstrating the gradual but relatively rapid turnover of faunal assemblages; the replacement of one chronofauna by another one. The Vallès-Penedès stands out mainly as the area where the fringes of bioprovinces overlap, leading to strikingly higher genus richness and thus a biodiversity hotspot moving through time and space.

Our study confirms that large faunal differences, which should be linked to different environments, existed between the coastal area and the inlands of the Iberian Peninsula.

6.3 Conclusions

One of this thesis' aims is to confirm the Vallès-Penedès biodiversity hotspot during the Late Miocene. It is established that this diversity hotspot indeed exists. The Vallesian Crisis abrupt drop off however, is probably overemphasised by sampling, creating the illusion of a drastic and sudden event, instead of a longer, more gradual turnover. The richest site immediately precedes the early/late Vallesian boundary, causing the severity of the event to be overestimated. For both micro- and macromammals there would have been a gradual species loss during the late Vallesian and the early Turolian rather than an abrupt extinction event at the early/late Vallesian boundary. Unfortunately, the lack of a good Turolian record in the Vallès-Penedès does not allow to confirm this hypothesis. Casanovas-Vilar et al. (2014) and Domingo et al. (2014) have come to similar conclusions.

It would be more accurate to refer to the Vallesian Crisis as a turnover event because of the timing and magnitude being caused by the sampling bias. This Late Miocene mammal turnover would have two main causes: a change in the vegetation associated with a decrease in the mean annual temperatures and a gradual increase in aridity. The Vallesian faunas show remarkable changes during this period of relatively rapid turnover, particularly in the case of large mammals, and even when zooming in on the carnivores we see numerous genera disappear from MN 9 to MN 10 (Madern et al. in press).

Crusafont noted back in 1950 that the final extinction of these forest-dwelling Middle Miocene taxa and the arrival of new eastern immigrants did not occur until the Turolian. The Vallesian faunas and environments would reflect that the changes that occurred during the Late Miocene were gradual. Surely, he was right. Therefore, the Vallesian Crisis should be better referred to as the Vallesian mammal turnover event marking the replacement of the typical Middle Miocene forest faunas of Western Europe by a different mammal assemblage that included a set with more open country elements. In the Iberian Peninsula this turnover coincided with the expansion of more arid ecosystems with rainfall seasonality in the inner basins (Barrón et al. 2010; Böhme et al. 2008,2011; Jimenéz-Moreno et al. 2010; Postigo Mijarra et al. 2009). This favoured the expansion of the open country Pikermian mammal faunas in the region during the Turolian.

This thesis demonstrates that after the biodiversity hotspot, the late Vallesian crash in the Vallès-Penedès was not the result of a continent-wide extinction event, but rather the result of the retreat of certain taxa's ranges. Not all genera went extinct; numerous supposed victims of the Vallesian Crisis were found sparingly after the event, indicating that at least micromammal genera went extinct over longer periods of time. There is no reason to believe that macromammals would behave differently, as shown by the carnivores.

Despite being in the midst of shifting bioprovinces caused in part by local climate change, the Vallesian faunal turnover did not result in major changes even within the Iberian Peninsula. The Vallès-Penedès served as a local refugium for transients, long-ranging species from the Middle Miocene. The large disparities at even relatively short distances indicate that the 'Vallesian Crisis' was at most a local event.

6.4 Implications and concluding remarks

The Vallès-Penedès basin has an incredible record for the Miocene, especially around the Aragonian/Vallesian transition (Middle/Late Miocene; ~12.5–11 Ma); and the Vallesian Crisis (early/late Vallesian, Late Miocene; ~10–9 Ma). Furthermore, between 18-16 Ma it has already greatly improved (Casanovas-Vilar et al. 2021,2022a,2022b). The NOW database has been vastly updated and refined throughout the course of these meta-analyses. Despite being a heavily researched area, the possibilities for gaining a better understanding of Miocene faunas are far from exhausted.

Spatial diachronicity has implications for the expansions and retractions of species distribution zones and thus of ecosystems (visible in chronofauna assemblages and shifting bioprovinces) (Madern & Van den Hoek Ostende 2015). Shifting from relative to absolute dating is a continuing process, leading to a temporal higher resolution. Furthermore, this eliminates the circular reasoning inherent to using biodiversity based time unit capturing communities and gives the opportunity to use equal sized bins, which is already possible for micromammals.

To substantiate the local scale of the event, the spatial resolution of the fossil record is essential to fill in the gaps and support the theory that rare species are a main cause of an apparent biodiversity loss. After extensive work on the large mammal collections of the Iberian Peninsula, it would be imminent to analyse the large mammals in a manner similar to the small ones. The use of presence/absence data and first/last occurrences when lacking abundance data, is out of urgency, not ambition. Again, compensation for sampling bias will show the true dimensions of the Vallesian turnover event.

As more scientists contribute to databases and their information becomes freely available over time, palaeontological research can take new steps toward filling in the bigger picture, with the added hope of attracting new enthusiastic future scientists.

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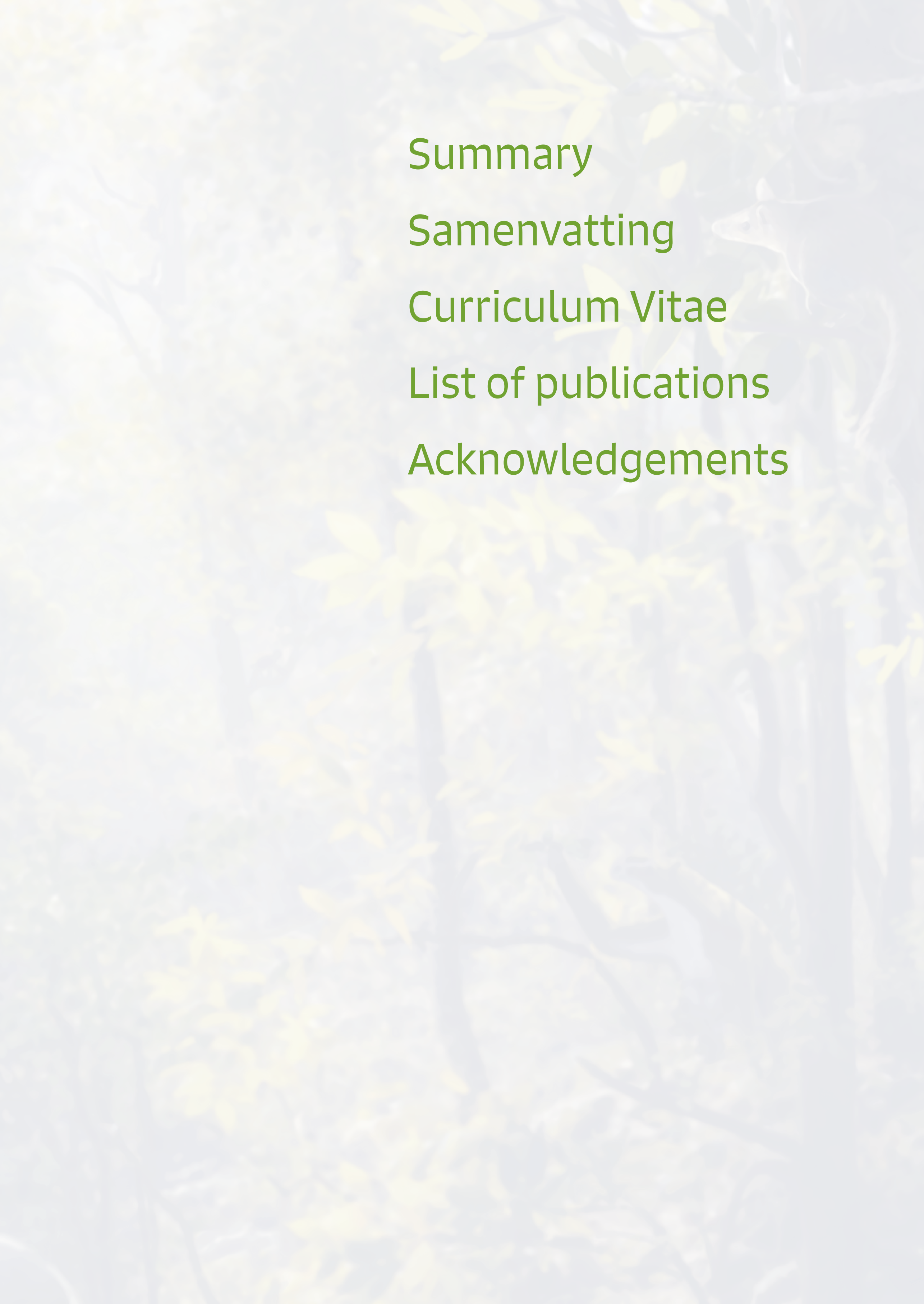

Summary

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Summary

Palaeontology studies biodiversity across geological time and space, as well as the effects of climate change on current and past life. This thesis focuses on the Late Miocene biodiversity hotspot and subsequent 'Vallesian Crisis'. The Vallès-Penedès Basin is located near Barcelona (Catalonia, Spain). During the Miocene (23.0 to 5.3 Ma), Europe experienced a subtropical climate with giraffids, tapirs, and hyeanids.

Database research is an important part of analysing biogeographical and temporal distribution patterns, including biodiversity hotspots, which are areas with unusually high taxon density. This allows for the recreation of migration patterns and the establishment of links between specific populations and climatic or geological events. The NOW (New and Old Worlds) fossil mammal database contains information about Cenozoic land mammal taxa and localities and is currently the best tool for reconstructing historical patterns of biodiversity. This thesis assesses the quality of the fossil record for both large and small mammals, with the goal of eliciting the bigger picture.

The thesis seeks to determine whether the Vallesian Crisis was a sudden collapse of a biodiversity hotspot or a series of extinctions that occurred over time. It alternates between focusing on a specific group of mammals, chronofauna (spatially and temporally constrained animal assemblages), and all mammals. It uses biodiversity indicators such as genus richness, presence/absence data, first and last occurrences and similarity indices, and zooming out to waxing and waning bioprovinces (zoogeographic areas). The Miocene mammal record from the Vallès-Penedès Basin was used to assess 'true' diversity, and determine the role of sampling bias in the disparity between the abundance of early and late Vallesian fossil record.

Can Llobateres 1 is used as the basis for a similarity analysis to discuss the history of the Vallesian Crisis and the biodiversity hotspot. Its chronofauna originated to the north of the Iberian Peninsula and gradually spread southward. The Vallesian Crisis is the result of a biodiversity peak and subsequent sampling bias in the Vallès-Penedès Basin mammal record. Instead of a continent-wide extinction event, the late Vallesian crash in the Vallès-Penedès was brought on by the retraction of some taxa's geographic ranges. There were significant faunal differences between the coastal region and the inland of the Iberian Peninsula. Mammal genera went extinct over extended time periods, while the Iberian Peninsula was not significantly altered by the Vallesian faunal turnover.

The expansion and contraction of species distribution zones and ecosystems are affected by spatial diachronicity. The geographical resolution of the fossil record is crucial to fill in the blanks. Rare species are a major factor in apparent biodiversity loss and support evidence for the local scale of the event.

The victims of the crisis share three characteristics: they are mostly forest dwellers, they are Middle Miocene in origin, and they are uncommon during the early Vallesian. Whereas the Vallesian Crisis' current status as a sudden and severe extinction event affecting early Late Miocene mammal groups has been called into question and has been linked in part to sampling bias, the 'Vallesian diversity hotspot' does not fall under this category. New immigrant taxa enriched early Vallesian communities, while the majority of older, late Aragonian occupants remained.

Samenvatting

Paleontologen richten zich op veranderingen in biodiversiteit in tijd en ruimte, evenals de effecten van klimaatverandering op het leven vroeger en nu. Dit proefschrift zoomt in op een biodiversiteitshotspot in het late Mioceen en de daaropvolgende 'Vallesiaanse Crisis'. Locatie: het Vallès-Penedès Basin, in de buurt van Barcelona (Catalonië, Spanje). Tijdstip: het Mioceen (23.0 tot 5.3 miljoen jaar geleden). Europa genoot op dat moment een subtropisch klimaat, met onder andere giraffen, tapirs en hyena's.

Onderzoeken van databases is een cruciaal onderdeel van het analyseren van biogeografische en temporele distributiepatronen, waaronder hotspots van biodiversiteit (gebieden met een bijzonder hoge taxon-dichtheid). Hierdoor wordt het mogelijk om migratiepatronen te recreëren en connecties te maken tussen bepaalde populaties en klimatologische of geologische gebeurtenissen. De NOW (New and Old Worlds) database bevat informatie over taxa en vindplaatsen van fossiele landzoogdieren, en deze database is op dit moment het best beschikbare middel voor het reconstrueren van historische patronen van biodiversiteit. Dit proefschrift evalueert de kwaliteit van de fossiele waarnemingen voor zowel grote als kleine zoogdieren en heeft tot doel het grotere plaatje in beeld te krijgen.

Het doel van dit proefschrift is om te bepalen of de Vallesiaanse Crisis een dramatische ineenstorting was van een biodiversiteitshotspot, of bestond uit een reeks uitstervingen die zich over een langere periode hebben voorgedaan. De hoofdstukken schakelen tussen de focus op één groep zoogdieren, de chronofauna (dieren die enkel op een specifieke tijd en plek voorkomen), en het richten op alle zoogdieren met behulp van biodiversiteitsindicatoren zoals genusrijkdom, aanwezigheid / afwezigheidsgegevens, eerste en laatste voorkomens, gelijkenisindices, en uitzoomen naar groeiende en krimpende bioprovincies (zoögeografische gebieden). De database met de Miocene zoogdierwaarnemingen van het Vallès-Penedès Basin werd gebruikt om de 'ware' diversiteit vast te stellen, en om de rol van steekproefvooroordelen te bepalen in de discrepantie qua hoeveelheid fossiele vondsten tussen het vroege en late Vallesien.

De geschiedenis van de Vallesiaanse Crisis en de hotspot worden besproken met behulp van de vindplaats Can Llobateres 1 als basis voor een vergelijkingsanalyse. De chronofauna had haar oorsprong in het noorden van het Iberisch schiereiland, en trok geleidelijk naar het zuiden. De Vallesiaanse Crisis is het directe resultaat van een biodiversiteitspiek en daaropvolgend steekproefvooroordeel in de zoogdierwaarnemingen van de Vallès-Penedès..

In plaats van een continentale extinctie, werd de late Vallesiaanse ineenstorting in de Vallès-Penedès veroorzaakt door de terugtrekking van de verspreiding van een aantal taxa. Er waren aanzienlijke faunaverschillen tussen de kustregio en het binnenland van het Iberisch schiereiland. Zoogdiergenera zijn over een langere tijd uitgestorven, terwijl het Iberische schiereiland niet aanzienlijk is veranderd door de verschuiving in de Vallesiaanse fauna. De expansie en krimp van distributiezones en ecosystemen werd beïnvloed door ruimtelijke diachroniciteit. De geografische resolutie van de fossiele waarnemingen is cruciaal om hiaten te vullen. Zeldzame soorten zijn een belangrijke factor in een ogenschijnlijk verlies van biodiversiteit en ondersteunen het bewijs voor de lokale omvang van het evenement.

De slachtoffers van de crisis werden geïdentificeerd en hebben drie dingen gemeen: ze zijn voornamelijk bosbewoners, ze zijn van Midden-Miocene oorsprong, en ze zijn zeldzaam tijdens het vroege Vallesien.

Terwijl de huidige positie van de Vallesiaanse Crisis als een gebeurtenis van plotseling en ernstig uitsterven, van invloed op de vroeg late Miocene zoogdiergroepen, in twijfel is getrokken en gedeeltelijk is gekoppeld aan steekproefvooroordeel, past de biodiversiteitshotspot niet onder deze paraplu. Nieuwe immigranten verrijkten vroege gemeenschappen in het Vallesien, terwijl de meerderheid van de oudere, late Aragonese groepen behouden bleef.

Curriculum Vitae

Anneke Madern was born on October 26th, 1983, in Vlaardingen, the Netherlands. She started out studying Archaeology in Leiden, but switched to Biology and received her bachelor's degree in biology at Leiden University in 2007.

Her thesis was focused on fossil island micromammals, supervised by Lars van den Hoek Ostende. For this work, she collaborated with high school student Jelle Zijlstra, which led to the publication of a new genus of Pleistocene oryzomyines with the poetic name of *Agathaeromys praeuniversitatis.*

After obtaining her bachelor's, she moved on to Utrecht University for a Master of Biogeology. However, due to organisational difficulties there, she quickly returned to Leiden to receive her Master of Biology there in 2010, following the master track Biodiversity in Time and Space. During her research master's, she combined her interests in data science and palaeontology with an internship at the National Herbarium with Niels Raes about Species Distribution Modelling and conservation, and an internship at Naturalis Biodiversity Center studying fossil mammal biodiversity.

While working at the collection department of Naturalis in 2011, she was accepted as a PhD candidate with a joint affiliation: Leiden University through Naturalis and Universitat Autònoma de Barcelona via the ICP; Institut Català de Paleontologia Miquel Crusafont. Her supervisors were Lars van den Hoek Ostende and Isaac Casanovas-Vilar, with Peter van Welzen as promotor. From 2012 to 2016, she spent over twelve months near Barcelona, at the ICP museum in Sabadell, and doing fieldwork at Can Llobateres. She followed courses in Frankfurt and Sydney, and presented her research in London, Berlin, Los Angeles, Istanbul, Madrid, Turin, Vienna, and Dallas. She taught courses at Leiden University, supervised bachelor and master students and even set up a Naturalis PhD council, which still exists today.

Following her work at Naturalis, she got accepted into a traineeship for ‘excellent academics’ to become a high school teacher; EerstdeKlas. Since 2016 she has been working at the Odulphuslyceum in Tilburg, teaching Biology, STEAM (Science, Technology, Engineering, Art and Mathematics) and Big History. Together with colleagues at her school, other high schools and higher education institutions, she developed a so-called ongoing learning curriculum from secondary to higher education. Additionally, she published articles in NVOX, a Dutch journal for science teachers. She is the research coordinator at the Odulphuslyceum and part of its educational committee.

The museum world still beckons, leading her to volunteering at Het Natuurhistorisch, the Natural History Museum Rotterdam, to prepare mammal study skins for the scientific collection.

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Alles blijft
Alles gaat voorbij
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