Early Miocene cricetids from the Vallès- Penedès Basin (Catalonia): taxonomy, biostratigraphy and paleoecological implications

Sílvia Jovells Vaqué

Ph.D. Thesis
Doctorate in Biodiversity

Early Miocene cricetids from the Vallès-Penedès Basin (Catalonia): taxonomy, biostratigraphy and paleoecological implications

Sílvia Jovells Vaqué

Universitat Autònoma de Barcelona

Institut Català de Paleontologia
Miquel Crusafont

Supervisor: Dr. Isaac Casanovas-Vilar
Tutor: Prof. Jacint Ventura Queija

Institut Català de Paleontologia
Miquel Crusafont
Universitat Autonòma de Barcelona

2020

ICP
Institut Català de Paleontologia
Miquel Crusafont

Ph.D. Thesis 2020

UAB
Universitat Autònoma
de Barcelona

Early Miocene cricetids from the Vallès- Penedès Basin (Catalonia): taxonomy, biostratigraphy and paleoecological implications

Sílvia Jovells Vaqué

Dissertation presented by Sílvia Jovells Vaqué in fulfillment of the requirements for the degree of Doctor by the Universitat Autònoma de Barcelona, Doctorate Program in Biodiversity of the Departament de Biologia Animal, Biologia Vegetal i d'Ecologia. Under the supervision of:

Director: Dr. Isaac Casanovas Vilar, Researcher at Institut Català de Paleontologia Miquel Crusafont. Head of the Paleoecology and Biochronology Research Group.

Tutor: Prof. Jacint Ventura Queija. Professor from Departament de Biologia Animal, Biologia Vegetal i d'Ecologia from Universitat Autònoma de Barcelona.

Doctoral candidate
Sílvia Jovells Vaqué

Supervisor
Dr. Isaac Casanovas Vilar

Tutor
Prof. Jacint Ventura Queija

Abstract

The early and early middle Miocene (late Ramblian to middle Aragonian; ca. 19-15 Ma) rodent record of the Vallès-Penedès Basin (Catalonia, north-eastern Spain) is far richer and more continuous than previously thought. This thesis is centered in the description of the cricetid fauna from this time interval and its biostratigrahical, paleobiogeographical and paleoenvironmental implications.

The systematic study of the cricetid fauna of all known early and early middle Miocene sites from the Vallès-Penedès Basin defines the main body of this work. The studied material comprises nearly 1,000 isolated molars as well as some mandibular fragments and even a partial skull. Four cricetid genera occur in the early to early middle Miocene (late Ramblian-middle Aragonian, MN3-MN5) record of the Vallès-Penedès Basin. The archaic cricetid *Melissiodon dominans* is common during Ramblian zone A (ca. 19.3-17.2 Ma) a before the dispersal of the so-called 'modern cricetids' of the genera *Democricetodon* and *Megacricetodon*. Modern cricetids are dominant components ofAragonian zone C and early zone D faunas (ca. 16.5-15 Ma) and include four species of the genus *Democricetodon* (*D. hispanicus*, *D.* cf. *decipiens*, *D. gracilis*, *D.* sp. 4) and one of the genus *Megacricetodon* (*M. primitivus*). The paracricetodontine *Eumyarion weinfurteri* and the last *Melissiodon dominans* complete the cricetid assemblage, but both species are generally rare. Overall the early Miocene cricetid succession shows several affinities with that from the Aragonian type area, the Calatayud-Montalbán Basin (Aragon, east-central Spain) allowing the use of the same high-resolution local biostratigraphy, with only minor differences. Moreover, Vallès-Penedès faunas also show a few similarities with the central European ones. Biostratigraphical results are combined with novel magnetostratigraphic data allow constraining the age of several major regional to continental bioevents that characterize the early Miocene, including dispersal events from other continents into Western Europe.

Finally, small mammal faunas are used to reconstruct regional paleoclimate between ca. 19 and 15 Ma and to compare it with other Western Europe records. Rainfall patterns are inferred from small-mammal community structure and indicate regional aridification coinciding with the height of the mid-Miocene Climatic Optimum between 16.5 and 15 Ma. The Vallès-Penedès is further recognized as a transitional area between the forested and humid central European bioprovince and the more arid and rainfall seasonal inner Iberian bioprovince. Such situation, which had previously been recognized for the middle and early late Miocene already existed at the beginning of this epoch.

Resum

El registre de rosegadors del Miocè inferior i principis del Miocè mitjà (des de finals del Ramblià fins a l'Aragonià mitjà; ca. 19-15 Ma) del Vallès-Penedès (Catalunya, Nord-Est d'Espanya) és molt més ric i continu del que es pensava. Aquesta tesi està centrada en la descripció de la fauna de cricètids durant aquesta *època* i en les seves implicacions biostratigràfiques, paleobiogeografiques i paleoambientals.

El cos principal d'aquesta tesi es centra en l'estudi sistemàtic dels cricètids de totes les localitats de la conca del Vallès-Penedès durant el Miocè inferior i principis del Miocè mitjà. El material estudiat consta de prop d'unes 1000 dents aïllades, així com fragments de mandíbules i maxil·les i també un crani parcial. Al registre de rosegadors de la conca del Vallès-Penedès hi trobem quatre gèneres diferents durant el Miocè inferior i principis del Miocè mitjà (final del Ramblià – Aragonià mitjà, MN3-MN5). El cricètid arcaic *Melissiodon dominans* és comú durant la zona A del Ramblià (ca. 19.3-17.2 Ma), abans de la dispersió dels anomenats 'cricètids moderns'dels gèneres *Democricetodon* i *Megacricetodon*. Aquests cricètids moderns són components dominants de l'Aragonià (ca. 16,5-15 Ma) i inclouen quatre espècies del gènere *Democricetodon* (*D. hispanicus, D. cf. decipiens, D. gracilis, D.* sp. 4) i un del gènere *Megacricetodon (M. primitivus*). El paracricetodontí *Eumyarion weinfurteri* i els últims *Melissiodon dominans* completen l'associació de cricètids, però ambdues espècies són generalment rares. En general, la successió de cricetids del Miocè inferior mostra diverses afinitats amb la de la zona de tipus de l'Aragonià, la conca de Calatayud-Montalbán (Aragó, centre-est d'Espanya), permetent l'ús de la mateixa biostratigrafia local d'alta resolució, amb només petites diferències. A més, les faunes del Vallès-Penedès també presenten algunes semblances amb les d'Europa central. Els resultats biostratigràfics es combinen amb noves dades magnetostratigràfiques que permeten precisar l'edat de alguns esdeveniments biòtics importants que caracteritzen el Miocè inferior, incloent esdeveniments de dispersió d'altres continents vers a Europa occidental.

Finalment, es reconstrueixen les condicions paleoclimàtiques regionals entre ca. 19 i 15 Ma en base a la fauna de petits mamífers i es comparen amb altres registres d'Europa occidental. Els patrons de paleoprecipitació inferits a partir de l'estructura de la comunitat de petits mamífers indiquen una aridificació regional coincidint amb l'Òptim Climàtic del Miocè mitjà entre fa 16,5 i 15 Ma. A més, el Vallès-Penedès és reconegut a més com a àrea de transició entre la bioprovincia de centreeuropa més boscosa i humida, i la bioprovincia centreibèrica més àrida i amb estacionalitat en el règim de precipitacions. Aquesta situació, que ja havia estat reconeguda anteriorment per al Miocè mitjà i inicis del Miocè tardà, ja existia al començament d'aquesta època.

Acknowledgements

This thesis was conducted thanks to an AGAUR (Agència de Gestió d'Ajuts Universitaris i de Recerca) FI pre-doctoral grant by the Generalitat de Catalunya (2017 FI B_ 00054) with the support of the "Secreteriat d'Universitats i de Recerca from the Generalitat de Catalunya" and the European Social Fund. This research was also funded by the Agencia Estatal de Investigación from the Spanish Ministerio de Economía, Industria y Competitividad and the Agencia Estatal de Investigación (AEI) from Spain/European Regional Development Fund of the European Union (projects CGL2017-82654-P and CGL2016-76431- and by the CERCA Programme of the Generalitat de Catalunya (project 2014 SGR 416 research group). Fieldwork was supported by the Departament de Cultura of the Generalitat de Catalunya (project 2014/100584 and CLT009/18/00068) and the National Geographic Society (grant number 9640-15). Erasmus stay at the University of Utrecht was funded by the Erasmus pràctiques program of the Universitat Autònoma de Barcelona.

First, I would like to express my sincere gratitude to my supervisor Dr. Isaac Casanovas Vilar for the continuous support, his patience, motivation and immense knowledge. When I first entered to his office as a volunteer I would never have imagined that I would end up turning one of my passions into my job. Isaac accepted me, first as a volunteer, then as a bachelor and master student, and finally as a Ph.D. student. He taught me all I know about paleontology and especially about the fantastic world of 'rodentology'. His guidance helped me with all the research and writing of this thesis. Thank you!

Besides my supervisor, I would like to thank the tutor of this thesis Prof. Jacint Ventura Queija and the coordinator of the Biodiversity Doctorate Program Dr. Asumpció Malgosa from the Universitat Autònoma de Barcelona for their technical support and guidance. In addition I extend my most sincere greetings to Dr. Anna Soler Membrives, Dr. Anselm Rodrigo Domínguez and Dr. Maite Carrason López de Letona as part of the "seguiment de doctorat" committee.

I would also like to thank Dr. Lars van den Hoek Ostende from Naturalis Biodiversity Center from Leiden and Dr. Wilma Wessels from Utrecht University, for their support and guidance during my stay in Utrecht University and Naturalis Biodiversity Center , in Leinden, as an Erasmus student was very important to me. Without them it would not be possible to conduct this research.

My sincere gratitude to all Intitut Català de Paleontologia (ICP) members and other institution collaborators that helped with the writing of this thesis, Dr. Joan Madurell-Malaperia (for his conversations and to letting me participate in his "underground" expeditions), Dr. Juan Abella, Dr. Marc Furió, Dr. Josep Mª Robles, Dr. Angel Luján, Dr. Israel García-Paredes, Dr- Israel Sánchez, Prof. Salvador Moya-Solà. Thanks to Dr. Daniel DeMiguel, Prof. Lluís Cabrera, Dr. Miquel Garcés and the ICP director Dr. David M. Alba for their comments and advice especially on the discussion chapters of this thesis. To Jordi Galindo, Manel Llenas, Manel Méndez, Pere Figuerola, Xènia Aymerich and Marina Rull for their technical support in the field, managing the collections and preparing the material.

I would also like to thank to my more experienced colleagues Dr. Pablo Peláez-Campomanes, Dr. M. Ángeles Álvares-Sierra, Dr. Ariana Oliver, Dr. Ana Rosa Gómez, Prof. Hans de Bruijn, Dr. Jêrome Prieto, Prof. Lawrence Flynn and Dr. Yuri Kimura for their support during all these years of hard work.

I would like to thank ICP colleagues and friends, Alessandro Urciuoli, Florian Bouchet, Guillem Pons, Guillem Orlandi, Teresa Calderón, Sharrah Mckenzie, Víctor Vinuesa, Rafel Matamalas, Saverio Bartolini and Melike Bilgin for always being there in the good moments and also in the bad ones, and especially to my room mates Maria Prat and Leonardo Sorbelli for always being there, for night movie sessions (even when I fall asleep halfway of the movie) and all the easy-going conversations. Especial thanks to Leonardo for the incredible design of the cover of this thesis.

To my friends and especially to Jordi, Paola, Guillem, Mariona, Rosa, Angel for being there and for believing in me, even when I did not believe in myself. For all the laughs and role-playing games that helped me to maintain my mental health within a reasonable level especially during the writing process of this thesis. Also I want to thank the Aikido family. They taught me more than a few aikido techniques; they showed me a new way to see the world around me.

Last but not least I would like to thank my family, my parents Marta and J. Damià and my sister Anna for supporting me spiritually and mentally throughout writing this thesis and for life in general.

FOREWORD. AIM AND STRUCTURE OF THIS WORK

The Vallès-Penedès Basin in Catalonia (Spain) is a classical area for the study of the Miocene terrestrial vertebrate faunas in Western Europe. First vertebrate finds from this highly fossiliferous area date back to the late 19th century and are amongst the earliest ones reported from Catalonia. From then on, generations of paleontologists have studied the Miocene record of the basin, with special attention to large mammals. With the introduction of systematic screen-washing techniques by the early 1970s vast quantities of small mammal fossils were also recovered, so overnight largely overlooked groups such as rodents and insectivores turned out to be amongst the better represented and studied. Now, the Vallès-Penedès Basin is regarded as one of the best Miocene terrestrial records in the Old World, with hundreds of accurately dated sites that have delivered tens of thousands of specimens in total. Not surprisingly, it is even the type area for a European land mammal age, the Vallesian. The stratigraphic record of the basin ranges from the early Miocene to the late Miocene, thus including the Ramblian, Aragonian, Vallesian and Turolian European land mammal ages. However, our knowledge of this record is unbalanced, as the earlier claims of quality and quantity can only be made for the late Aragonian and the Vallesian. Other parts of the record have received fewer attention, particularly the early Miocene interval, including the Ramblian and early Aragonian ages.

Traditionally the early Miocene of the Vallès-Penedès has been reputedly regarded as poor in fossil content if not completely barren in some places. There is some true in this claim, yet the early Miocene includes some major sites, such as els Casots, which match the best Vallesian sites (such as Can Llobateres) in the number of recovered remains. Indeed, the early Miocene had not been systematically sampled for decades and, as far as small mammals are concerned, many sites were never sampled using modern screen-washing methods.

I got involved into this project while I was a Biology degree student and volunteer at Institut Català de Paleontologia Miquel Crusafont (ICP). As most paleontological projects it started with fieldwork, actually almost a decade of fieldwork. Starting in 2011 a team of the ICP led by my thesis supervisor had been exploring the early Miocene outcrops all over the basin. The aim was increasing the number of early Miocene sites known to date and increase sample size for this interval, particularly for small mammals. Biostratigraphical and paleoecological studies would follow so that the early Miocene part of the record would not faint as compared to the better studied time periods in the Vallès-Penedès. As systematic paleontology and taxonomy is the basis of all paleontological research, I was assigned a major task which would eventually develop into this thesis: the description of the cricetid rodent fauna. Cricetids are the most abundant group in most early Miocene sites of the area, and they further are a key element in Miocene European biostratigraphy and biochronology. If we wanted to produce a detailed biostratigraphy cricetids had to be studied in detail first. My first field campaign as ICP volunteer was in 2013 and after that, I dug up fossils, screen-washed sediment and even sorted up great part of the material that would be studied as part of my thesis. In 2015 I finished my degree and started working with the cricetids as part of my master project. After the master I decided to continue with this project with the Ph.D. It has taken me five years to complete this work. I know is just part of a larger project, but compared to the point where we started I can proudly say that we now know many more things about the early Miocene of the Vallès-Penedès, at the very least about the cricetids!

This thesis is devoted to the study of the cricetid faunas of the early Miocene of the Vallès-Penedès Basin as well as their biostratigraphical, paleobiogeographical and paleoecological implications. To do so, this thesis has been organized in separate chapters, most of them already published separately as scientific papers. Published papers define the most important part of this work and correspond to the systematic description of the early Miocene cricetid fauna recovered in different sites of the Vallès-Penedès which includes four species belonging to the genus *Democricetodon*, one species of *Megacricetodon*, and the rare genera *Eumyarion* and *Melissiodon*, each one represented by a single species in the region. In addition, an early Miocene representative small mammal fauna of this basin (les Cases de la Valenciana site) is described in its entirety (i.e., marsupials, insectivorans, lagomorphs and rodents). Each chapter includes a section on biostratigraphical implications, plus occasionally some very preliminary paleoenvironmental inferences. Yet, in the last chapter (Discussion) I have summarized all the biostratigraphical information, further including additional data derived from magnetostratigraphy and the review of the large mammal fauna, to provide the first high-resolution chronology of the early Miocene record of the Vallès-Penedès Basin. More refined paleoclimatological and paleoenvironmental inferences based on the study of the small mammal faunas are also provided in that chapter together with a discussion of the effects of the mid-Miocene global climatic changes on the Vallès-Penedès faunas. This discussion section is meant to be expanded and published separately as a scientific paper in the near future.

The work ends with a conclusions chapter that briefly summarizes all the previous ones. In addition, I have included three appendices for reference purposes: the small mammal faunal lists of all the early Miocene sites of the Vallès-Penedès (as well as other details such as situation and age of the sites); the museum catalogue numbers and measurements taken for each studied specimen; the morphotype frequency tables for the studied specimens of the genera *Democricetodon* and *Megacricetodon*.

Below I provide the list of scientific papers included in this thesis. Although I have been the main author of all of them there are obvious topics in which I am not a specialist, such as lagomorphs and insectivores, so that corresponding part of the works was written by my colleagues:

•Jovells-Vaqué, S. and Casanovas-Vilar, I. 2018. A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallès-Penedès Basin (Catalonia). Journal of Vertebrate Paleontology, 38(5): e1520714. doi:10.1080/

02724634.2018.1520714.

- Jovells-Vaqué, S., García-Paredes, I., Furió, M., Angelone, Chiara., Van den Hoek Ostende, L.W., Berrocal Barberà, M., DeMiguel, D., Madurell-Malapeira, J. & Casanovas-Vilar, I. 2018. Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). Historical Biology, (30:3): 404-421. doi:10.1080/08912963.2017.1317768.

- Jovells-Vaqué, S., Ginestí, M., Casanovas-Vilar, I. 2017. Cricetidae (Rodentia, Mammalia) from the early Miocene site of els Casots (Vallès-Penedès Basin, Catalonia). Fossil Imprint, 73(1-2): 141–154, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line). doi:DOI 10.1515/if-2017-0007.

- Jovells-Vaqué, S., Ginestí, M. & Casanovas-Vilar, I. First cranial of *Democricetodon hispanicus* Freudenthal, 1967 (Rodentia, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). Preliminary results.2017. In: Barrios de Pedro,S.; Blanco Moreno, C; de Celis, A; Colmenar,J.; Cuesta, E.; García-Martínez, D.; Gascó, F.; Jacinto, A; Malafaia, E; Marín Jimenez, M.; de Miguel Chaves, C.; Mocho, P.; Pais, V.; Parámo Blázquez, A.; Pereira, S.; Serrano Martínez, A.; Vidal, D. (Eds.), A Glimpse of the Past. Book of abstracts XV meeting of Young researchers in Paleontology. pp. 223-226. Pombal (Portugal).

- Jovells-Vaqué, S. and Casanovas-Vilar, I. in press. Dispersal and early evolution of the first modern cricetid rodents in Western Europe: new data from the Vallès-Penedès Basin (Catalonia). – Comptes Rendus Palevol. (submitted 8/12/2019; accepted 04/2020)

ABBREVIATIONS

ELMA: European Land Mammal Ages

FCO: First common occurrence

FO: First occurrence

HMP: Precipitation in the wettest month

ICP: Institut Català de Paleontologia

IPS: Institut de Paleontologia de Sabadell (acronym used for the collection numbers of the ICP)

L: Anteroposterior length

LCO: Last common occurrence

LMP: Precipitation in the driest month

LO: Last occurrence

Ma: Megaannum (one million years)

MAP: Mean annual precipitation

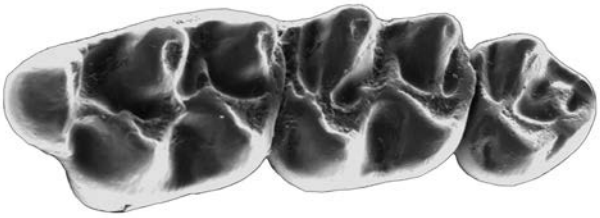
MCO: Miocene Climatic Optimum

MGB: Museu de Geologia de Barcelona (now Museu de Ciències Naturals de Barcelona), Barcelona, Spain.

MN: European Mammal Neogene zones

W: Labiolingual width

For the Vallès-Penedès Basin locality acronyms see Chapter 2.3 and Appendix 1.



Chapter 1: Introduction

CHAPTER 1: INTRODUCTION

1.1: THE STUDY OF EARLY MIOCENE FOSSIL RODENTS OF THE VALLÈS-PENEDÈS BASIN, A HISTORICAL PERSPECTIVE

1.1.1. EARLY STUDIES (1898-1940)

The first discoveries of fossil vertebrates from the early Miocene of the Vallès-Penedès Basin date back from the XIX^th^ century, when Father Jaume Almera, founder of the Museum of Geology of the Barcelona Seminar, was given several vertebrate remains found in the coal mines of La Fontsanta (Subirats, l'Alt Penedès) and Molí Calopa site (Rubí, el Vallès Occidental). Being a geologist mostly interested in stratigraphy, Almera entrusted their identification to some of the most renowned European paleontologists of his time, including Marcellin Boule, Charles Depéret and Albert Gaudry among others (Almera, 1898, 1899). The recovered fossils comprised scarce remains that were assigned to rhinocerotids and ruminants, but also included two rodents: *Sciurus feignouxi* and *Cricetodon gerandium* (Almera, 1899). Later on, during the first half of the XX^th^ century, Father Ramon Bataller, from the same museum, surveyed important parts of the Vallès-Penedès Basin and discovered many new sites (Bataller, 1918, 1924, 1928). As far as rodents are concerned, Bataller published the first monograph on this group in Spain, which was written in Catalan and appeared in the midst of Spanish Civil War (Bataller, 1938). Bataller wrongly included lagomorphs as part of the rodents ("ratadors" in his words) and described the material he had collected at different sites, mostly dating from the early Oligocene and the latest middle Miocene. Furthermore, he proposed a chronological succession of the sites based on their stratigraphic position and after a comparison of the rodent fauna with that recovered at other European localities. He also compared the recovered fauna with other European sites. As far as the early Miocene is concerned, Bataller (1938) studied material from the sites already reported by Almera (1898, 1899) from the Vallès-Penedès Basin. On the basis of the recovered fauna Almera (1891, 1898, 1899) had attributed these continental outcrops to the Aquitanian age (which by that time was situated within the late Oligocene rather than the early Miocene). Nevertheless, the appearance of the formations, characteristically red in color and with predominance of clays and silts (and known as the 'red layers'), resembled that of the Oligocene deposits in the nearby Ebro Basin, which belong to the early Oligocene. Therefore, later authors such as Sierra et al. (1930), assigned the same age to the Vallès-Penedès red layers. Yet, Bataller (1938) considered correct their correlation to the Aquitanian (then still considered to be late Oligocene).

1.1.2. CRUSAFONT, VILLALTA, TRUYOLS AND "*EL BURDIGALIENSE CONTINENTAL DEL VALLÉS-PENEDÉS*", A MASTERPIECE IN MAMMALIAN PALEONTOLOGY (1940-1970)

The systematic survey and study of the Miocene successions of the Vallès-Penedès Basin did not start until the 1940s. Miquel Crusafont, a pharmacist of Sabadell with a keen interest in paleontology started collecting remains all around his town and assembling an important collection. Crusafont would eventually leave his job to become a professional paleontologist. He was soon joined by his colleagues Josep Fernández de Villalta and, somewhat later, Jaume Truyols, who was mostly interested in geology rather than paleontology. The trio envisioned a work on the early Miocene outcrops of the Vallès-Penedès Basin, the so-called 'red layers', which by then were considered poor in fossil content. They performed intensive fieldwork, contacted the main quarries that were active at the time and by the end of the decade had already discovered tens of new sites and assembled a notable collection of vertebrate fossils. The 'red layers' did not have as much fossils as later deposits but were not poor at all. This vast amount of work would be published first as a short paper (Crusafont and Truyols, 1954) followed by a longer monograph entitled *El Burdigaliense continental del Vallés-Penedés* [The continental Burdigalian of the Vallès-Penedès] (Crusafont et al., 1955; figure 1.1). This is generally regarded as one of the finest and most comprehensive works in Spanish paleontology and stratigraphy of that period. It is divided into two parts, a first one on geology and stratigraphy (by Truyols and Crusafont) and a second one on systematic paleontology (by Crusafont and Villalta). The first one includes detailed maps and several geological cross sections of the 'red layers'. In addition, the authors paid special attention to the cartography and stratigraphy of the Miocene marine deposits in the Vallès-Penedès Basin, which were attributed to the early middle Miocene (Langhian) based on their fossil mollusk content. Crusafont et al. (1955) showed that the 'red layers' were always placed stratigraphically below the Langhian deposits, so they had to belong to the early Miocene (Burdigalian). In the paleontological part of the work Crusafont and Villalta reported up to 46 different mammal species from 23 new fossil sites, most of them previously unknown. Many of these sites were very poor but some of them yielded a remarkable collection of fossils such as Can Julià (Gelida, l'Alt Penedès), la Costablanca (Castellbisbal, el Baix Llobregat) or el Molí de Can Calopa (Rubí, el Vallès Occidental). The recovered fauna, which included proboscideans as well as the equid *Anchitherium* clearly confirmed the early Miocene age of the 'red layers'.

All the recovered material was thoroughly described and some new species (and even new genera) were erected. Even though both Crusafont and Villalta devoted most of their careers to the study of larger mammals, in this monograph they also described the insectivorans, rodents and lagomorphs and erected several new species. As far as rodents are concerned the new species erected in this work are the cricetid *Melissiodon arambourgi* (see chapter 5) and the sciurid *Heteroxerus rubricati*. In the concluding chapters of the monograph the authors included a discussion on the age and the paleoenvironment of the sites, even featuring an early analysis of paleobiodiversity dynamics and changes in community structure that was ahead of their time (Crusafont et al., 1955: 224-235). The work concludes with several appendices describing the remains of birds, herpetofauna, continental mollusks and plants. Even a brief final appendix re-evaluates the significance of the fossils reported by Almera (1898, 1899), although unfortunately most of them had been destroyed or lost in the early days of Spanish Civil War when anarchist militias sacked the

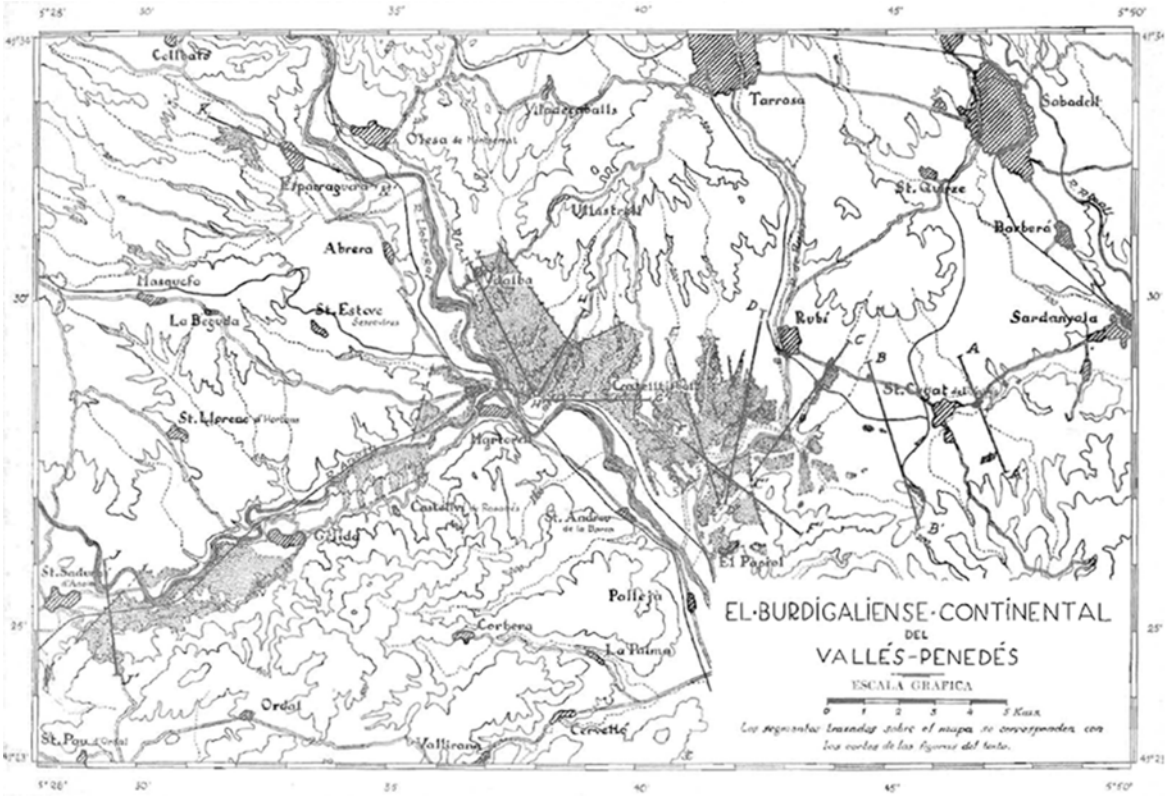


Figure 1.1: Geological map of part of the Vallès-Penedès Basin taken from Crusafont et al. (1955). The shadowed areas indicate where early Miocene sediments crop out.

Museum of Geology of Barcelona Seminar (Reguant i Serra, 2004).

After this seminal contribution few other works were devoted to the early Miocene successions, partly because the attention of Crusafont and co-workers focused in the late Miocene (Vallesian) sites near the towns of Sabadell and Terrassa (el Vallès Occidental), which yielded huge collections. Yet Crusafont et al. (1968) reported a new fossiliferous site in la Costablanca sector (la Costablanca II), which mostly delivered lagomorph and small-sized artiodactyl remains as well as fragmentary dental and postcranial material of the equid *Anchitherium aurelianense* (described in Rotgers and Alba, 2011). Later on, Golpe-Posse (1974) provided updated faunal lists for the main sites, sometimes citing taxa that had not been previously reported.

1.1.3. Jordi Agustí: The first thesis on Miocene rodents and the success of rodent-based biostratigraphy (1979-1989)

In the late 1970s, geologist Lluís Cabrera, from the University of Barcelona, conducted a detailed stratigraphical and sedimentological study of the early Miocene successions for his degree thesis (Cabrera, 1979). Cabrera also discovered new localities such as el Turó de les Forques (Castellbisbal, el Baix Llobregat) or Can Martí Vell (Gelida, l'Alt Penedès) that mostly delivered small mammals. The samples were handled to Jordi Agustí, from the Institute of Paleontology of Sabadell (IPS; precursor of the actual ICP), who at the time was writing a doctoral thesis on Neogene myomorph rodents of Catalonia under the supervision of Miquel Crusafont (Agustí, 1981). Agustí and Cabrera screen-washed those samples as well as a few additional ones from other early Miocene sites and assembled a small but representative collection. These authors published a brief report on the sites of Can Julià and Can Martí Vell in Gelida (Agustí and Cabrera, 1980) but the systematic descriptions of part of the rodents would have to wait until the completion of Agustí's doctoral thesis (Agustí, 1981). There he described some rodent remains that were part of the personal collection of Josep F. de Villalta (now the collection is in the Museum of Natural Sciences of Barcelona) and the IPS collection recovered at the following sites: Sant Andreu de la Barca (including two levels), el Molí de Can Calopa, el Fallol, el Canyet and Sant Mamet. In addition, thanks to the collaboration with Cabrera, material from the following sites was also included: la Costablanca II (named 'les Forques' in Agustí, 1981), Can Julià 6 and Can Martí Vell (levels 1 and 2). Agustí (1981) described numerous rodent species from these sites and proposed a local biostratigraphy for the whole Vallès-Penedès record exclusively based on rodents (Agustí, 1981; also published separately as Agustí, 1982). For the early Miocene this author distinguished two distinct local biozones: *Pseudodryomys ibericus* zone and *Megacricetodon minor primitivus* [= *Megacricetodon primitivus*] zone. These were correlated to other regional zonations from Iberian Peninsula and France as well as to the then recently established Mammal Neogene (MN) zones of Mein (1975). Indeed, the *P. ibericus* zone is basically equivalent to MN3b while the *M. primitivus* zone would equal to MN4a (Agustí, 1981, 1982). The *P. ibericus* zone would include the following localities: Sant Andreu de la Barca, el Molí de Can Calopa and la Costablanca II. These sites delivered very scarce remains, mostly comprising glirids (*Pseudodryomys ibericus*, *Peridyromys murinus*), the cricetid *Melissiodon dominans* and the eomyid *Ligerimys ellipticus*. The latter species was represented by just two lower molars recovered at Sant Andreu de la Barca. The scarce material recovered was inadequate to confidently identify this species. Indeed, *L. ellipticus* is exclusively known from MN4 (see for example Álvarez Sierra, 1987), so the Sant Andreu de la Barca material certainly belongs to another species (see also new faunal data from this locality in chapter 10). Regarding the *M. minor primitivus* zone, it would include and richer sites than the *P. ibericus* zone. The faunas would be characterized by the presence of the cricetids *M. minor primitivus* [= *M. primitivus*] and *Democricetodon* aff. *hispanicus* [= *D. hispanicus*] plus the glirids *Microdyromys* cf. *koenigswaldi*, *Pseudodryomys simplicidens* [= *Simplomys simplicidens*] and *Glirudinus modestus*. The eomyid *Ligerimys florancei* would first appear during this zone while *L. ellipticus* and the cricetid *M. dominans* would persist from the previous one. This biozone includes the sites of el Fallol, el Canyet, Sant Mamet, Can Julià 6 and Can Martí Vell, which was erected as its type locality. The latter locality includes two levels that delivered the richest early Miocene rodent fauna of the Vallès-Penedès known to date, comprising over one hundred specimens in total. The description of this rodent fauna was also published as a separate paper (Agustí, 1983).

Besides a systematic and biostratigraphic part, Agustí (1981) also included a brief paleobiogeographical discussion in his thesis. As far as the early Miocene is concerned, this author already noted that the MN3 sites of the Vallès-Penedès Basin were similar to those of inner Iberian basins (such as the Calatayud-Montalbán Basin), being characterized by the lack of cricetids other than *Melissiodon* (a period which would later be called 'cricetid vacuum'; Daams and Freudenthal, 1989). Agustí (1981: 217) remarked the absence of *Armantomys*, a glirid characterized by robust high-crowned cheek teeth endemic to inner Iberian basins. The sites of the *M. minor primitivus* zone, correlated to MN4a, were far more diverse than older sites (although this was almost certainly an artifact of sample size) and were dominated by a few species of cricetids (*D. hispanicus*, *M. primitivus*) and eomyids (*L. florancei*, *L. ellipticus*). Glirids were common and more diverse than in the Spanish inland. The MN4a Vallès-Penedès sites showed the highest similarity with other localities of the Spanish levant (Bunyol, Rubielos de Mora), although they also showed remarkable affinity with southern France (Pellecahus, Soucaret). In contrast, the Vallès-Penedès sites only showed a 22% of similarity with the localities from the Calatayud-Montalbán Basin (Valtorres) and even lower similarity values with Central Europe (11% with Erketshofen). Later on Agustí (1989) would expand these paleobiogeographical results and distinguish an Ibero-Levant biogeographical province during most of the Miocene, thus showing that only very rarely the Iberian Peninsula would have functioned as a homogenous biogeographic unit.

During the mid and late 1980s Agustí and co-workers from the IPS (usually Salvador Moyà-Solà and Josep Gibert) published a series of synthetic accounts on the Vallès-Penedès record (Agustí et al., 1984, 1985; Agustí and Moyà-Solà, 1990). The most notable of these contributions is perhaps Agustí et al. (1985) in which the authors provided updated faunal lists of many early Miocene sites including el Molí de Can Calopa, Sant Andreu de la Barca, Can Martí Vell, Sant Mamet and Vilobí del Penedès. The latter locality, situated below a gypsum unit corresponding to a Burdigalian sabkha, had been reported a few years earlier by Aguilar (1981). In addition, the authors situated most sites in generalized stratigraphic series (by L. Cabrera) and refined their correlation with MN zones.

1.1.4. The discovery of els Casots and the turn of the century (1989-2011)

Later studies on early Miocene rodents include the doctoral thesis of Elis Aldana Carrasco (1991) supervised by Jordi Agustí and devoted to Neogene sciuromorph rodents of Catalonia (Sciuridae and Castoridae). Aldana Carrasco (1991) reviewed the sciurids of all the early Miocene sites of the Vallès-Penedès (results were published separately in Aldana Carrasco, 1992). The beavers (Castoridae), so common in the late Miocene sites of this basin (Sant Quirze, Castell de Barberà, Can Llobateres) do not occur during the early Miocene.

More or less at the same time, in 1989, the discovery of els Casots site in Subirats (l'Alt Penedès) reinvigorated research in early Miocene deposits of the Vallès-Penedès (figure 1.2). The site was discovered by an amateur paleontologist who already

Figure 1.2: Panoramic view of els Casots site in 2011. Photo: I. Casanovas-Vilar.

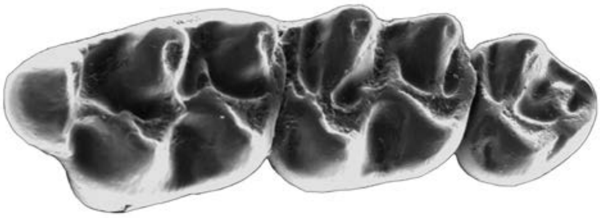
found tens of nicely-preserved macromammal fossils on surface and reported the findings to Salvador Moyà-Solà, from the IPS. Systematic excavations at the site started the same year and lasted until 1994 (Moyà-Solà and Rius Font, 1993; Casanovas-Vilar et al., 2011a), with some minor campaigns in the later 1990s (figure 1.3). They allowed for the recovery of more than 3,000 large vertebrate remains, comprising reptiles, birds, and mammals including remarkably complete and even semi-articulated specimens (Moyà-Solà and Rius Font, 1993; Casanovas-Vilar et al., 2011a; see also chapters 7 - 8). As far as small mammals are concerned, several levels of els Casots were screen-washed and more than 400 specimens were recovered. Els Casots mammal fauna was the subject of several systematic studies, mostly dealing with the artiodactyls (Pickford and Moyà-Solà, 1994, 1995; Duranthon et al., 1995). On the other hand, rodents were only preliminarly described in a brief publication for a national congress (Agustí and Llenas, 1993), except for the sciurids which had already been described in detail in Aldana Carrasco (1991, 1992). Apart from els Casots site, during the 1990s other early Miocene sites were resurveyed and sampled for microvertebrates. These include the upper levels of Vilobí del Penedès (the so-called 'oyster levels'; see Agustí et al., 1990), les Escletxes del Papiol, Sant Andreu de la Barca (Agustí and Galobart, 1997) or Sant Mamet (chapter 9; Appendix 1). However, by the mid 1990s the attention was driven to Vallesian (earliest late Miocene) sites, specially primate-bearing ones (such as Can Llobateres). The detailed magnetostratigraphic study of the Miocene successions of the Vallès-Penedès was the subject of the doctoral thesis of Miguel Garcés (University of Barcelona), but it almost exclusively considered the Vallesian part of the record (Garcés Crespo, 1995; Garcés et al., 1996, 1997; Agustí et al., 1997). Garcés Crespo (1995) however featured the long magnetostratigraphic section of Can Santjoan (Sant Cugat del Vallès), which ranged from the latest early Miocene to the marine middle Miocene (Langhian) and also included Sant Mamet site. This author correlated Sant Mamet to the reverse magnetic polarity chron C5Br, yielding an approximate age of about 16 Ma, which is in agreement with its MN4 fauna. Garcés conducted additional magnetostratigraphical surveys of the early Miocene outcrops of the basin during the late 1990s and early 2000s but the results (as well as those of the Can Santjoan section) were never published. In the early 2000s, the construction of a landfill led to the discovery of the extremely rich fossiliferous series of the Abocador de Can Mata (els Hostalets de Pierola, l'Anoia). This series covers the late Aragonian (late middle Miocene) and has delivered about 200 accurately-dated fossil sites and more than 60,000 remains (see Casanovas-Vilar et al., 2016a,b; Alba et al., 2017). Furthermore, remarkably complete hominoid and pliopithecoid primate fossils have been recovered thanks to the paleontological survey at Abocador de Can Mata (Moyà-Solà et al., 2004, 2009a,b; Alba et al., 2010, 2015, 2017). In accordance, most of the latest research on Miocene Vallès-Penedès faunas has focused in the study of this exceptional set of sites, including recent major bio- and magnetostratigraphical studies (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011b, 2016a, b; Alba et al., 2017). Hence, the already long-forgotten early Miocene sites remained unstudied and unsampled for decades.

1.1.5. A NEW LOOK AT THE EARLY MIOCENE

This situation of abandonment would finally come to an end in 2011, when a team of the Institut Català de Paleontologia Miquel Crusafont (ICP) led by Isaac Casanovas-Vilar reprised the survey of the

Figure 1.3: Systematic excavation at els Casots site during the 1990s. Photo: Salvador Moyà-Solà.

early Miocene outcrops. Unfortunately, some important sites, such as those of Sant Andreu de la Barca, had been destroyed as a result of public and private construction works. Yet, it was possible to sample some classical sites (e.g., la Costablanca II, el Molí de Can Calopa, les Cases de la Valenciana, Sant Mamet) and screen-wash large amounts of sediment to recover a significant number of microvertebrate specimens. In addition, new fossiliferous localities were discovered and sampled, including some of the oldest sites in the basin, such as el Turó de les Forques. Some preliminary data were published in synthetic works by Casanovas-Vilar et al. (2011c, d, 2016a), mostly updating biostratigraphical data. At the same time major systematic excavations were conducted, such as that of les Cases de la Valenciana between 2012 and 2015 (see chapter 6) and more recently (starting in 2019) els Casots. Field campaigns between 2016 and 2017 focused on continental and transitional deposits associated to the beginning of the Miocene marine transgressive episodes in the Vallès-Penedès yielding the first middle Aragonian (MN5, middle Miocene) sites in the basin (see chapter 2 and 9). These intensive field campaigns have resulted in the recovery of hundreds of large mammal remains and thousands of microvertebrate specimens. Concerning rodents, more than 2,000 specimens have been recovered (over 3,500 considering the MN5 sites), thus multiplying by a factor of ten the previous sample. At the same, magnetostratigraphical surveys and stratigraphical studies carried out during the late 1990s and early 2000s were completed and most of the early Miocene sites can now be situated in detailed series (see chapter 9). For the first time the early Miocene succession of the Vallès-Penedès Basin can be adequately characterized and the chronology of the main bioevents can be firmly established. The present work will only focus on the cricetid faunas, yet a broader discussion on the chronology of faunal and climatic changes in the early Miocene of this region is provided in chapter 9.



Chapter 2: CHRONOLOGICAL AND GEOLOGICAL SETTING

CHAPTER 2: CHRONOLOGICAL AND GEOLOGICAL SETTING

2.1: EUROPE IN THE EARLY MIOCENE: PALEOGEOGRAPHY, CLIMATE AND MAMMAL FAUNAS

The Miocene epoch is the first and longest epoch of the Neogene period and spans from the end of the Oligocene, 23.03 Ma to the beginning of the Pliocene, 5.33 Ma (Hilgen et al., 2012). During this long period, there were major geographic, climatic and environmental changes, which would give the world its modern appearance (Prothero, 2006). Some of the major extant ecosystems, such as grasslands and savannahs (Cerling et al., 1997; Strömberg, 2011), expanded during the Miocene and by the end of the epoch most of the living families of animals and plants where on scene.

The Miocene is divided in three parts (see Hilgen et al., 2012 for updated boundary ages): early (23.03-15.97 Ma), middle (15.97-11.61) and late (11.61-5.33 Ma). The early Miocene in turn includes two stages, the Aquitanian (23.03-20.44 Ma) and the Burdigalian (20.44-15.97 Ma) and multiple land mammal ages which differ in each continent (see Hilgen et al., 2012). In Europe these include the Agenian and Orlenian European Land Mammal Ages (ELMA; Steininger, 1999), although in the Iberian Peninsula regional stages are more frequently used. These include the Ramblian (Daams et al., 1987) and Aragonian (Daams, 1977), although most of the latter corresponds to the middle rather than the early Miocene. Throughout this work, which focusses in the Iberian record, the regional stages will be mostly used.

On a global scale, Miocene paleogeographical changes determined oceanic circulation and climate. The Isthmus of Panama (the land bridge that unites North and South America) had not formed yet, thus allowing water circulation between the Pacific and Atlantic oceans. Similarly, during the early Miocene Africa was separated from Eurasia by the Tethyan Seaway, a relic of the ancient western Tethys ocean that corresponds to the actual Mediterranean (figure 2.1). The Tethyan Seaway connected the Atlantic with the Indo-Pacific, thus ensuring a circum-global oceanic circulation at low latitudes with major implications for heat and nutrient transfer (Hotinski and Toggweiler, 2003). However, by the early Miocene the Tethyan Seaway started to be restricted and fragmented because of tectonic events (Rögl, 1999; Popov et al., 2006). Indeed, the Miocene was a time of intense tectonic activity and mountain uplift, in the Americas the Rocky Mountains and the Andes formed due to the subduction of the Pacific tectonic plate below the American continent. At the same time, the Indian plate continued its collision with Asia, resulting in further uplift of the Himalayan mountains and the Tibetan Plateau. The circum-Mediterranean regions also experienced intense tectonic activity and mountain uplift related to the collision of Eurasia with the African plate. As result a landbridge was stablished between both continents through Arabia and Anatolia (the so-called *Gomphotherium* Landbridge; Rögl, 1999) but at the same time this severed the connections between the Mediterranean and the Indo-Pacific. The northern pull of the African plate against southern Europe also triggered the uplift of mountain ranges such as the Alps, Carpathians,

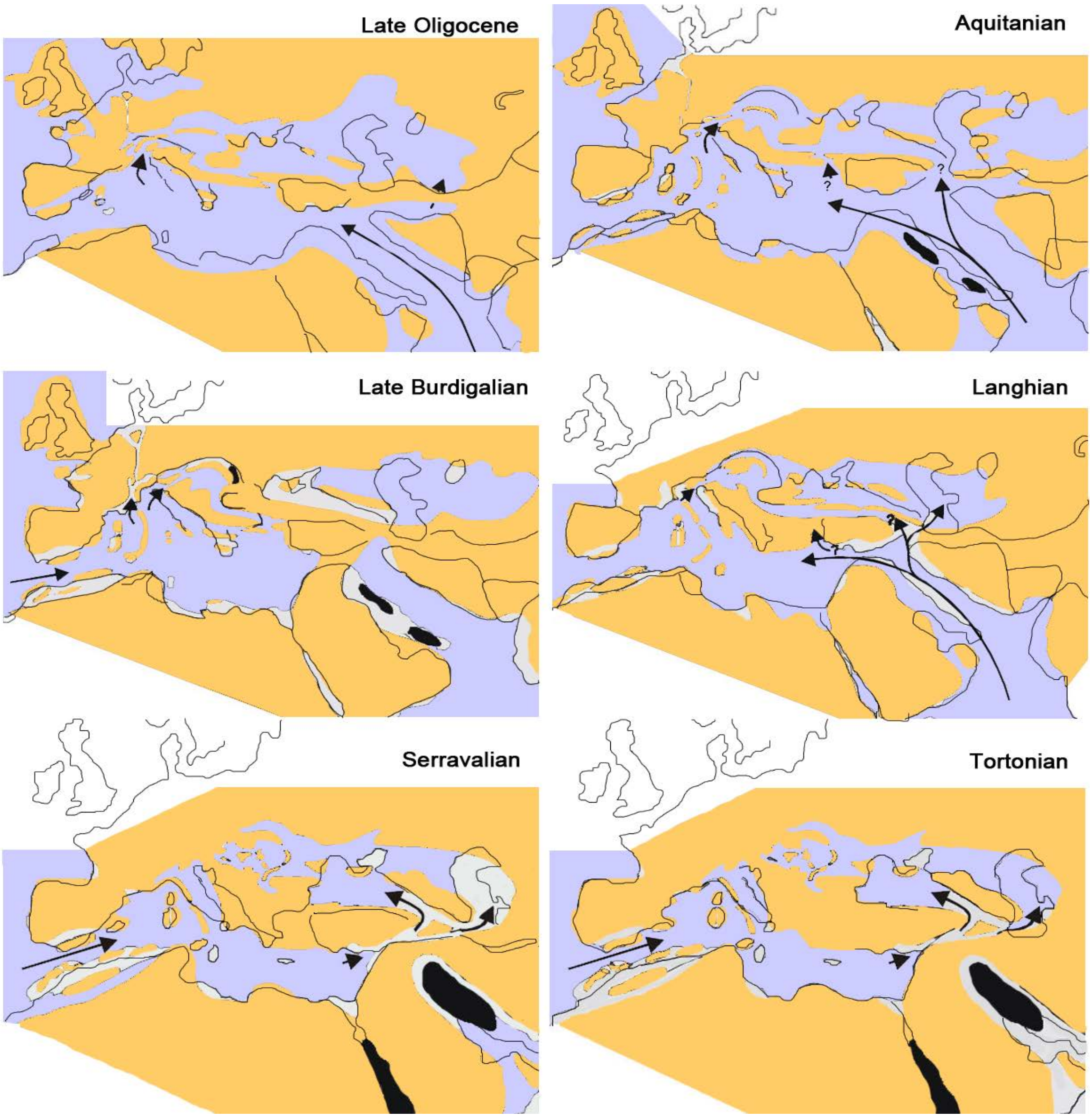


Figure 2.1: Paleogeographical evolution of the Mediterranean regions from the late Oligocene to the early late Miocene (Tortonian), that is from about 30 to 7 Ma. Orange indicates emerged areas, blue indicates sea and light grey flooded continental platform. Arrows indicate connections between major seas. Major evaportic deposits are marked in black. Modified from Rögl, 1999.

Dinarides, Taurus and the Zagros which subdivided the Tethys Seaway in two parts (Rögl, 1999; Popov et al., 2006). North of the mountain ranges there was a shallow inland sea, the Paratethys, which extended from central Europe (Austria) to central Asia (Kazahstan). It was subdivided into a western Central Paratethys (also called Pannonian or Carpathian Basin) and a much larger Eastern Paratethys (Rögl, 1999; Popov et al., 2006; Harzhauser and Piller, 2007; figure 2.1). All that remains of this large inland sea are the Black, Caspian and Aral seas, amongst other smaller saline lakes. During its long existence the Paratethys was at times reconnected with the western Tethys or its successors, the Mediterranean and the Indian Ocean. By the early Oligocene (27.5 Ma), the continuous tectonic movements caused a closure of the main open seaways of the Paratethys, thus resulting in its isolation for the first time. The only marine connection of the Paratethys with the open sea was through the far west with the Mediterranean and via the Rhine Graben with the North Sea (Martini, 1990; Harzhauser and Piller, 2007). During the early Miocene (23 Ma) the Paratethys returned to open marine conditions with the temporary re-opening of its Indo-Pacific connection. It is in the early Burdigalian (around 20 Ma) with the formation of the *Gomphotherium* Landbridge that the Indo-Pacific seaway was effectively severed thus connecting Africa and Eurasia for the first time in millions of years (Rögl, 1999). At the same time, the eastern Paratethys was reduced to the isolated Kotsakhurian Sea with strong endemism and reduced salinity (Rögl, 1999). As for the Western and Central Paratethys it remained connected with the Mediterranean Sea and with the North Sea by the Rhine Graben connection (figure 2.1).

The *Gomphotherium* Landbridge was a key event that allowed faunal exchange between Africa and Eurasia. Since the late Eocene African faunas had evolved in isolation and included a plethora of endemic mammal groups such as tubulidentates, hyracoids or proboscideans. In addition, it was the last refuge of other mammals that had vanished elsewhere, such as primates or creodont carnivorans (Agustí and Antón, 2002). At the same time, the global increase in temperature from the early to mid Miocene (Zachos et al., 2001) may have favored the expansion of the African faunas to the north thanks to the expansion of the tropical and subtropical climate belts to higher latitudes (Pickford and Morales, 1994). Proboscideans are first recorded outside Africa in Pakistan, already by the late Oligocene (ca. 28 Ma; Antoine et al., 2003), that is, long before the *Gomphotherium* Landbridge formed. In Europe, gomphotheres are not recorded until much later, around 20-19 Ma (Sen, 2013; see also chapter 10) and later on by about 16 Ma (if not somewhat earlier), they managed to cross the Bering Strait and disperse into North America (Woodburne, 2004). Another group to successfully disperse into Eurasia were primates, particularly hominoids, which underwent a remarkable evolutionary radiation that will last until the end of the Miocene (Andrews and Kelley, 2007; Ward, 2007; Casanovas-Vilar et al., 2011b, Andrews, 2015). However, dispersal was in both ways and the wave of Eurasian mammals to immigrate into Africa was far greater. These included rhinocerotids, bovids, giraffids, felids, hyaenids and other animals that today are associate with the African savannah as well as numerous groups of rodents, such as sciurids, cricetids and ctenodactylids (Van der Made, 1999; Sen, 2013).

At the other side of the world, low sea levels established a connection between Eurasia and North America via the Bering Landbridge, which not only allowed the dispersal of proboscideans into the New World but also that of many other groups (see Woodburne, 2004). These dispersed in several waves, the first one already in the earliest Miocene (early Arikarean North American Land Mammal Age [NALMA], ca. 23 Ma) and involving certain rhinocerotids, chalicotheres as well as mustelid and amphicyonid carnivorans. In the late Arikarean (ca. 19 Ma) blastomerycid and dromomerycid ruminants joined the assemblage. However, major dispersals took place during the Hemingfordian NALMA (18.8-16 Ma) and included several different groups of carnivorans (mustelids, procyonids, amphicyonids, ursids, felids); teleoceratine and aceratherine rhinocerotids; antilocaprid ruminants; insectivorans (soricids, plesiosoricids); lagomorphs; and several rodents (eomyids, the cricetid *Copemys* and the sciurid *Petauristodon*). Proboscideans, first represented by the mammutid *Zygolophodon*, would not disperse until the Hemingfordian/Barstovian boundary, around 16 Ma. Quite surprisingly, only one taxon dispersed against this flow of immigrants, the three-toed browsing equid *Anchitherium*, which would be present in Eurasia not earlier than 20 Ma (Woodburne, 2004; see also chapter 10). The reasons for such unbalanced exchange are poorly understood.

Nevertheless, the early Miocene western Eurasian mammal faunas would not only be enriched by the entry of a few African and American taxa but by a true flood of eastern immigrants. Most of them would disperse during the early Orlenian ELMA (early Aragonian in the Iberian Peninsula), that is between 17 and 16 Ma, thus coinciding with the major dispersals into North America (Van der Made, 1999). The eastern immigrants included the chalicotheres, teleoceratine and aceratherine rhinocerotids, listriodontine suids, and primitive ruminants such as the tragulids (Van der Made, 1999; Agustí and Antón, 2002; see also chapter 10). At the same time there was a true 'revolution' in the herbivore community with the appearance of multiple groups of horned ruminants such as the earliest cervids, bovids and giraffids (*Teruelia, Lorancameryx*) as well as the strange-looking extinct paleomerycids. On the other hand, the carnivore mammal fauna was enriched with early felids (*Pseudaelurus*) and ursids that confronted more archaic groups such as amphicyonids. As far as small mammals are concerned, the dispersal of the first 'modern' cricetids of the genera *Democricetodon* and *Megacricetodon* was the most remarkable event as these genera would diversify and dominate European rodent assemblages well until the late Miocene (see chapter 9-10).

However, the early Miocene was not only characterized by a shifting paleogeography and faunal interchanges between the northern continents and, for the first time, between those continents and Africa. It was also a time of global warming after the Oligocene icehouse (Zachos et al., 2001). Starting by the latter part of the Oligocene (around 27 to 26 Ma) a warming trend started to reduce the extent of the Antarctic ice sheet. From this point until the middle Miocene global ice volume remained low and mean global temperatures increased until peaking between 17 and 15 Ma, a period known as the Mid-Miocene Climatic Optimum (MCO, Zachos et al., 2001). This represented the last truly warm period of the Cenozoic, as mean global temperatures followed a stepwise decrease starting at 14 Ma until the present, only briefly punctuated by short-lasting warm intervals (Zachos et al., 2001). During the early Miocene broadleaved evergreen forests characterized by laurel trees and evergreen oaks extended over Central Europe (Kovar-Eder, 2003; Pound et al., 2012). Today subtropical forests of similar composition thrive in areas of China and Taiwan as well as in the Canary Islands (laurisilva). In the Mediterranean regions the environment was apparently more arid and seasonal (Kovar-Eder, 2003). In the Iberian Peninsula, including Catalonia, the early Miocene plant assemblages are dominated by microphyllous leguminous trees or shrubs (*Acacia, Cassia, Caesalpinia*) that also include some megathermic taxa and would be indicative of subtropical woodlands with seasonal rainfall (Sanz de Síria Catalán, 1996; Barrón et al., 2010; Jiménez-Moreno et al., 2010; see chapter 10). Laurel forests similar to those occurring in central Europe would be restricted to humid environments such as riparian zones and mid altitudes (Sanz de Síria Catalán, 1996; Barrón et al., 2010). In the southern peninsula the environment was even more arid, as indicated by the predominance of herbs in the pollen spectra and the presence of some subdesertic taxa (Jiménez-Moreno et al., 2010).

The MCO took global temperatures to their maximum values during the Neogene, implying further melting of the Antarctic ice sheets and a consequent global sea-level increase (Zachos et al., 2001). Therefore, during the Langhian (ca. 16 Ma), the Indo-Pacific connection between the entire Mediterranean and the Paratethys re-opened for a brief period, thus restoring the circum-global warm-water circulation. Coastal basins, such as the Vallès-Penedès, the Aquitanian (southern France) and Tagus (Portugal) basins were partially flooded during the Langhian marine transgression (Rögl, 1999). Nearly every paleoclimatic indicator points towards warmer temperatures (see Prothero, 2006). For example, coral reefs expanded their range being recorded at high latitudes (such as New Zealand Northern Island). Fringing coral reefs also developed in the Vallès-Penedès Basin, which was partially covered by a shallow warm sea swarming with subtropical mollusks (see chapter 2.2). At the same time, mangroves attained a maximum development occurring at mid and relatively high latitudes (including the Vallès-Penedès Basin, see chapter 2.2). During the MCO subtropical vegetation extended as far north as the Canadian Arctic, Alaska and eastern Siberia, further illustrating the extent of this last warm period (Agustí and Antón, 2002; Prothero, 2006).

This climatic optimum would come to an abrupt end by 14 Ma when mean global temperatures cooled down as a result of the restablishment of a major ice sheet in eastern Antarctica (Zachos et al., 2001). This implied worldwide marine regression and important effects in the marine biota (Miller et al., 2005). The diversity of many groups, such as mollusks, declined in mid and high latitudes as subtropical taxa either contracted their ranges to the tropics or became extinct (Prothero, 2006). Ectothermic vertebrates were also affected. Crocodilians, which were widespread in mid latitudes during the early Miocene and the beginning of the middle Miocene, disappeared from Central Europe at about 14 Ma (Böhme, 2003). At the same time, Central European evergreen forests progressively incorporated an increasing number of temperate (largely deciduous) trees (the so-called Arcto-Tertiary geoflora including *Alnus, Acer, Populus, Salix, Ulmus, Zelkova*) while the number of tropical and subtropical taxa disappeared (Kovar-Eder, 2003; Pound et al., 2012). In the Iberian Peninsula, inland areas became more arid and dominated by shrubs and herbs, whereas Arcto-tertiary elements invaded the montainous and riparian environments, coexisting with evergreen species and some tropical relicts (Barrón et al., 2010). On the eastern side of the Mediterranean, south of the Paratethys, the environment appears to have become more arid and seasonal. This is consistent with the development of a characteristic open woodland fauna in this region (often referred to as 'Greek-Iranian Province') that includes hyaenids, bovids and giraffids amongst others (Agustí and Antón, 2002). Relatively high-crowned herbivores are recorded there for the first time (Fortelius et al., 2002; Eronen et al., 2010) and a mosaic of grass-dominated (with C3 grasses) and more forested areas seem to have characterized the landscape (Strömberg, 2011). During the later Miocene, this open-country fauna extended into vast areas of the Old World, and, to a certain point, the modern African savannah fauna could be considered its surviving branch (Kaya et al., 2018).

The causes behind this global mid-Miocene cooling are debated and probably involve multiple factors. First, we have a number of tectonic events that affected oceanic and atmospheric circulation. The connection between the Mediterranean and the Indian Ocean was definitively severed by the early Serravalian (Rögl, 1999; see figure 2.1). Tectonic activity in the circum-Mediterranean realm also implied the isolation of the Eastern and Central Paratethys, basins, with thick evaporite sedimentation in certain areas of the Central Paratethys (Rögl, 1999; see figure 2.1). Simultaneously, the uplift of the Himalayas and the Tibetan Plateau, which had started 50 million years ago, accelerated during the middle and late Miocene (Harrison et al., 1992; Kutzbach et al., 1993; Zhisheng et al., 2001). The height of these reliefs significantly affected global atmospheric circulation and climates, implying cooling and aridification of the Asian interior as well as the onset of Indian and east Asian monsoons by the late Miocene (Kutzbach et al., 1993). Finally, falling concentrations of atmospheric carbon dioxide have been related to the massive burial of organic carbon in deep-marine sediments along the Pacific Rim, such as in the Monterey Formation of California (Vincent and Berger, 1985). The so-called Monterey Hypothesis postulates that continued drawdown of organic carbon between 17 and 13.5 Ma would have promoted icehouse conditions.

The topics discussed in this work must be viewed in this context of changing climate and paleogeography, faunal dispersals and extinctions. Even if the focus is placed on a very specific group (cricetids) in a very specific area (the Vallès-Penedès Basin), the major faunal events described are ultimately related to these continental to global changes.

2.2: THE VALLÈS-PENEDÈS BASIN

The Vallès-Penedès Basin is a small Neogene basin situated in the North-East of the Iberian Peninsula. As we have seen in the previous chapter (Chapter 1) the highly fossiliferous Miocene outcrops of this basin have been studied ever since the XIXth century. As result the Vallès-Penedès is now regarded as a classical area for the

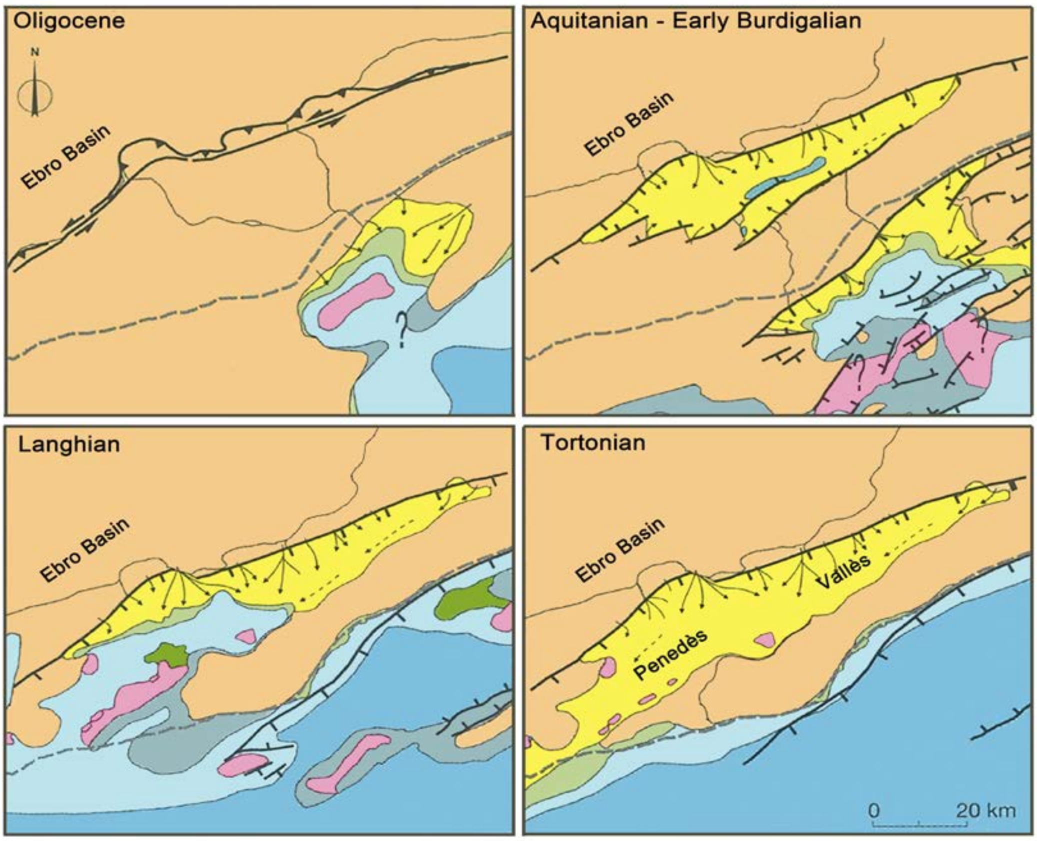


Figure 2.2: Paleogeographic evolution of the Vallès-Penedès Basin during the Miocene. Yellow indicates alluvial fan sediments, green and purple indicate carbonate platform and evaporites. Modified from Cabrera et al. 2004, 2010.

study of the Miocene terrestrial faunas in Europe and comprises a rich, continuous and well-dated fossil record (for an updated overview see Casanovas-Vilar, 2016a). In addition, the structure and stratigraphic arrangement of the sedimentary infill has been the subject of multiple studies, so that a clear picture of the origin and evolution of this basin is now available (for updated reviews see Roca et al., 1999; Cabrera et al., 2004, 2010).

The formation of the Vallès-Penedès Basin (figure 2.2) started during the late Oligocene as the collision between the African and Eurasian plates affected the western Mediterranean. The subduction of the Tethys oceanic crust under the Eurasian plate resulted in the formation of a system of basins and reliefs (horsts and grabens) limited by normal faults of NE-SW and NNE-SSW orientation (Roca and Guimerà, 1992; Roca et al. 1999; Cabrera et al. 2004). These included the Valencia Trough and the Gulf of Lion, which separated Iberia from an uplifted block defined by Corisca, Sardinia and the Balearic Islands during the late Oligocene (Roca and Guimerà, 1992; Roca et al., 1999). During the latest Oligocene and the early Miocene, the Iberian margin of the Valencia Trough experienced a process of rifting resulting in the development of several basins parallel to the coastline including the Camp de Tarragona, Vallès-Penedès, Baix Llobregat and Pla de Barcelona basins, among others (Roca and Gimerà, 1992; Roca et al., 1999; Cabrera et al., 2004). Sedimentation in some of these new basins (Campins, Pla de Barcelona) already began by the Oligocene (latest Rupelian – Chattian, ca. 28 Ma; Anadón and deVillalta, 1975; Cabrera et al., 2004; Parcerisa et al., 2007; figure 2.2). In other basins such as the Baix Llobregat and Vallès-Penedès Basin, the sedimentation infill started somewhat later by the early Miocene (Cabrera et al., 2004, 2010).

The Vallès-Penedès Basin is a half-graben that measures about 100 km length by about 12–14 Km breadth depending on the area. It is bounded by the horsts defined by two parallel mountain ranges, the Prelittoral and Littoral Ranges, also known as the Catalan Coastal Ranges (Cabrera et al. 2004, 2010; figure 2.2). The half-graben basement and surrounding reliefs consist of Paleozoic metasediments deformed during the Hercynian Orogeny (Devonian-early Permian) and intruded by plutonic rocks (mostly granitoids), that extensively crop out at the Collserola, Montnegre and Montseny reliefs (figure 2.3). These rocks are unconformably overlaid by terrigenous and carbonate Mesozoic rocks, which in turn are discordantly covered by Paleogene sediments (mostly terrigenous). These younger lithologies of the basemen make up most of the Montserrat, Montmell, Garraf and Ordal mountains (Figure 2.3).

The half-graben is bounded at the northwest by the Vallès-Penedès master fault (Bartrina et al., 1992; Roca et al., 1999).

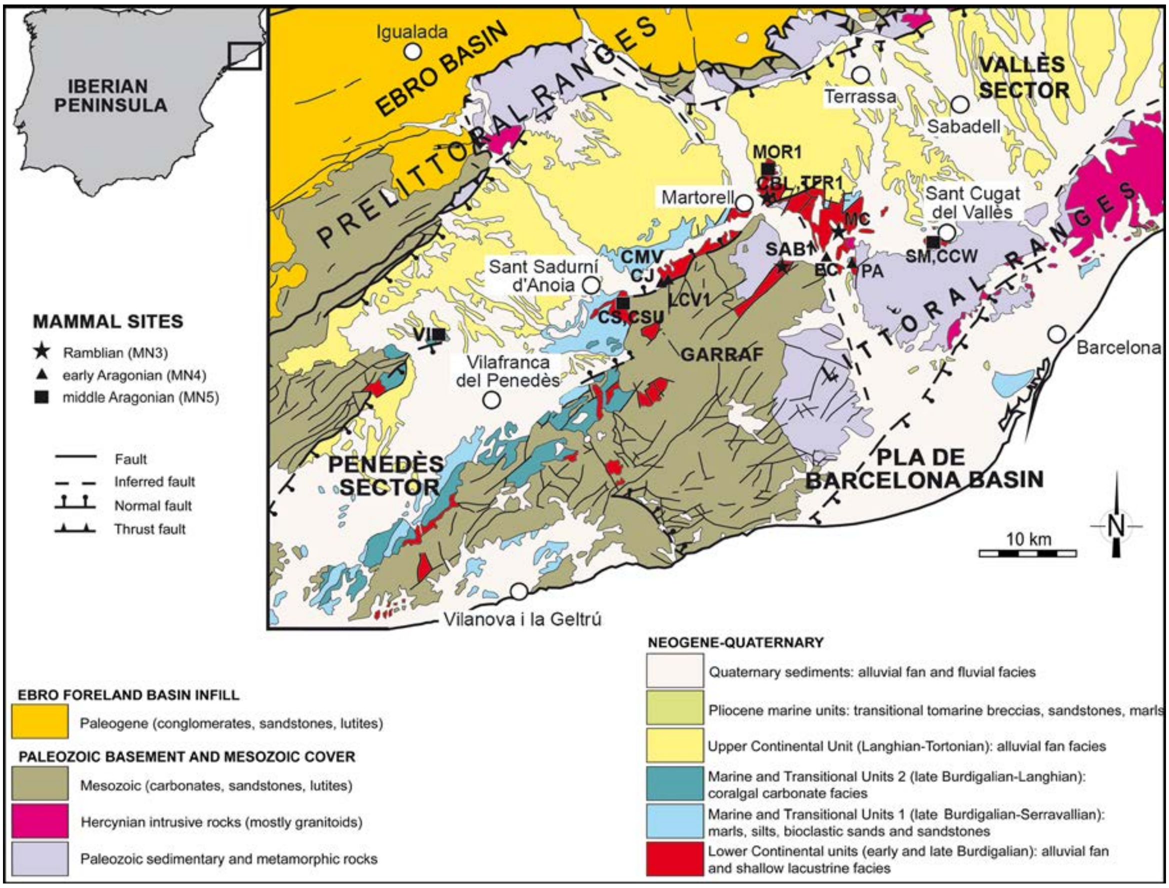


Figure 2.3: Geographical location and simplified geological map of the Vallès-Penedès Basin indicating the main mammal localities ranging from MN3 to MN5 (modified from Casanovas-Vilar et al., 2016). For locality acronyms see Appendix 1.

Major features of the stratigraphic record in the Vallès-Penedès half-graben were controlled by tectonic activity of its main bounding faults and sea level changes in the western Mediterranean (Cabrera, 1981; Bartrina et al., 1992; Cabrera and Calvet, 1996; Roca et al., 1999; Cabrera et al., 2004). The Vallès-Penedès master fault was tectonically active throughout the Miocene, and even when the rifting phase concluded by the middle Miocene (late Burdigalian-Langhian), thermal subsidence was concentrated on the northwestern margin, allowing for the accumulation of an important sediment thickness (up to 4000 m; Bartrina et al., 1992; Cabrera and Calvet, 1996; Roca et al., 1999; Cabrera et al., 2004). In the less tectonically active southeastern margin of the basin (limited by the Littoral Ranges) sediment thickness is notoriously lower. Until the middle Miocene the Vallès-Penedès presented the typical graben profile, with tectonic activity in all the bounding faults. However, by the middle Miocene activity ceased in the southeastern faults and subsidence was concentrated into the northwestern margin effectively turning the basin into a half-graben. Early Miocene deposits crop out in the southeastern part of the basin (Crusafont et al., 1955; Cabrera, 1979; Agustí et al., 1985; Casanovas-Vilar et al., 2011c, d, 2016a; see chapter 2.2.1). Major and minor faults at this margin margin were overlapped by the sedimentary infill during the Burdigalian and Langhian, which were affected by later major fault reactivations (Cabrera, 1981; Cabrera and Calvet, 1996).

The Miocene record of the Vallès-Penedès Basin has been informally divided into three main lithostratigraphic units: Lower Continental Complexes (LCC); Marine and Transitional Complexes (MTC) and Upper Continental Complexes (UCC) (Cabrera, 1979, 1981; Cabrera and Calvet, 1996; Cabrera et al., 2004, de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a; figure 2.4). The LCC formed during the early Miocene and consist of alluvial fan red-bed deposits with minor shallow lacustrine sequences (see chapter 2.2.1. below). During the latest early Miocene and the beginning of the middle Miocene (Langhian) several sea-level changes took place in the context of the MCO (Zachos et al., 2001; see chapter 2.1). The Littoral Ranges defined an important relief isolating the Vallès-Penedès from the Mediterranean, but the basin was still open to the sea by its southwestern extreme, so that part of the basin was flooded during sea-level highstands (Figure 2.2). At least three different episodes of marine transgression and regression affected the Vallès-Penedès: late Burdigalian, Langhian and early Serravallian (Cabrera and Calvet, 1996; Cabrera et al., 1991; de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a; see chapter 10). These resulted in the deposition of the MTC, which are better developed in the southwestern half of the basin (Penedès sector) because it was more directly connected to the sea. Carbonate coralgal platform deposits, marine bay and transitional fan-delta siliciclastic systems persistently occupied that area. Marine environments attained their maximum development during the Langhian, when they extended into the Vallès sector of the basin reaching Sant Cugat del Vallès and Cerdanyola del Vallès. Poorly developed shallow marine and transitional deposits can be found in these areas. The early Serravallian transgression was restricted to the southwestern margin of the basin.

From the Serravallian onwards sedimentation was again dominated by alluvial fans which define the UCC. These were sourced from the northwestern reliefs and some systems (e.g., the Olesa-Les Fonts alluvial fan system) were huge, attaining a radius of 10 to 15 km (Agustí et al., 1985, 1997; Cabrera and Calvet, 1996; Garcés et al., 1996; Roca et al., 1999; Casanovas-Vilar et al., 2008, 2016a,b; de Gibert and Casanovas-Vilar, 2011). The proximal coarse-grained facies were deposited near the northwestern margin of the basin, whereas the mudstone-dominated medial to distal facies spread towards the south and southeast. The latter facies include most of the vertebrate-bearing sites of the Vallès-Penedès and have been intensively sampled during decades. To date more than 300 fossiliferous sites ranging from the late Aragonian to the middle Turolian ELMAs (approximately from the early Serravallian to the latest Tortonian, i.e. from about 14 to 7 Ma) are known and have delivered tens of thousands of remains (see Casanovas-Vilar et al. 2016a,b). Most of the sites are located in the Abocador de Can Mata area (els Hostalets de Pierola, Penedès sector [southwest half of the basin]) and around the cities of Sabadell and Terrassa (Vallès sector [northeast half of the basin]). Detailed bio- and magnetostratigraphical studies have been carried out focusing on this part of the record (Garcés, 1995; Garcés et al., 1996; Agustí et al., 1997; Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011b, 2016a,b; Alba et al., 2017), which stands out as one of the most complete Miocene successions in the Old World. Not surprisingly, Crusafont (1950) already defined an ELMA based on the rich early late Miocene Vallès-Penedès successions, the Vallesian (currently known to range from 11.2 to 8.9 Ma; see Hilgen et al., 2012). After its definition the Vallesian was quickly accepted and used in other regions of the Old World for the late Miocene fossil faunas characterized by the entry of the first hipparionine horses. At the end of the Miocene (between 5.96 and 5.33 Ma), the Messinian Event implied the tectonic closure of the Gibraltar Strait. Without receiving the colder waters of the Atlantic the Mediterranean was unable to cope with the high evaporation rates and soon was entirely desiccated leading to the deposition of huge salt deposits (Hsü et al., 1973, 1977). In coastal basins such as the Vallès-Penedès and particularly the Baix Llobregat basins the Messinian Event resulted in an interruption of sedimentation and the development of deeply entrenched erosive surfaces affecting both the basement and earlier Miocene sequences (Cabrera and Calvet, 1996). The early Pliocene (Zanclean) is scarcely represented at the Vallès-Penedès by alluvial-fluvial deposits near Piera (Gallart, 1981). During the Zanclean, an important marine transgression also flooded the coastal basins, such as el Baix Llobregat (Martinell, 1988), but did not extend into the Vallès-Penedès. These early Pliocene deposits lay discordantly over Miocene and basement sediments and have delivered a rich fauna of marine invertebrates (Martinell, 1988) as well as plant remains (Sanz de Síria Catalán, 1996). Finally, Pleistocene and Holocene alluvial and colluvial sediments were deposited unconformably over the Neogene series.

2.2.1 EARLY MIOCENE STRATIGRAPHY OF THE VALLÈS-PENEDÈS

The early Miocene outcrops of the Vallès-Penedès Basin define the Lower Continental Complexes (LCC), which are mostly defined by characteristically red-colored alluvial sediments intercalated with minor lacustrine units ranging from the Ramblian to the Langhian (from ca. 20–16 Ma).

This unit crops out in a narrow fringe close to the southern boundary of the basin, attached to the Littoral Ranges, from the Garraf to Collserola mountains (figure 2.3). The alluvial sediments were deposited by alluvial fans sourced from the reliefs that limit the basin. Fans with catchment areas in the northwestern reliefs covered a larger radius than those sourced from the southeastern border, especially in the upper units of the LCC (Cabrera, 1979, 1981; Agustí, 1985; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). During the early Burdigalian, the LCC were deposited in a context of extensional tectonics, with transverse faults and main faults in the southeastern margin being active and limiting a series of small basins and highlands (Cabrera, 1979, 1981; Cabrera et al., 1991, 2004; Cabrera and Calvet, 1996). Three main sedimentary domains can be distinguished: Baix Penedès, Alt Penedès and Vallès Occidental (Cabrera, 1981). In addition, some minor associated sub-basins, such as the Sant Andreu de la Barca one (figure 2.5), formed at this time. Sediment thickness of the LCC varies as a consequence of fault activity that greatly influenced their sedimentation. Seismic profile and geological core drilling data indicate that it may range from tens or hundreds of meters to more than 1,000 m (Martorell-1 well; Bartrina et al., 1992). During their deposition, the LCC overlapped major faults in the southeastern margin of the basin, which became inactive during the latest Burdigalian (Cabrera, 1981; Cabrera and Calvet, 1996). From then on only the Vallès-Penedès master fault (at the northwestern margin) was functioning so the entire sedimentary regime was modified during the middle Miocene. As explained in the previous chapter, the Vallès-Penedès developed into a half-graben, which explains the restricted outcrop area of the LCC near the southeastern margin of the basin. In the northwestern part, Serravallian and Tortonian alluvial fan sediments sourced from the Pre-littoral Ranges (defining the UCC, see previous chapter) buried most of these early Miocene deposits below kilometers of sediments (Bartrina et al., 1992; Cabrera and Calvet, 1996; Roca et al., 1999; Cabrera et al., 2004. The inverse reactivation (compressive rather than extensive) of the faults of the southeastern margin by the latest Miocene further affected the LCC, fragmenting them in disconnected blocks that complicate their correlation (Cabrera, 1981; Cabrera and Calvet, 1996).

The LCC define an informal stratigraphic unit (on the scale of a formation) and can be further subdivided into three subunits (which would equal to members). These are very useful in lithostratigraphical correlation and were first recognized by Cabrera (1979) being only slightly modified in subsequent works (Cabrera, 1981; Agustí, 1985; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). Below the different subunits are briefly described,

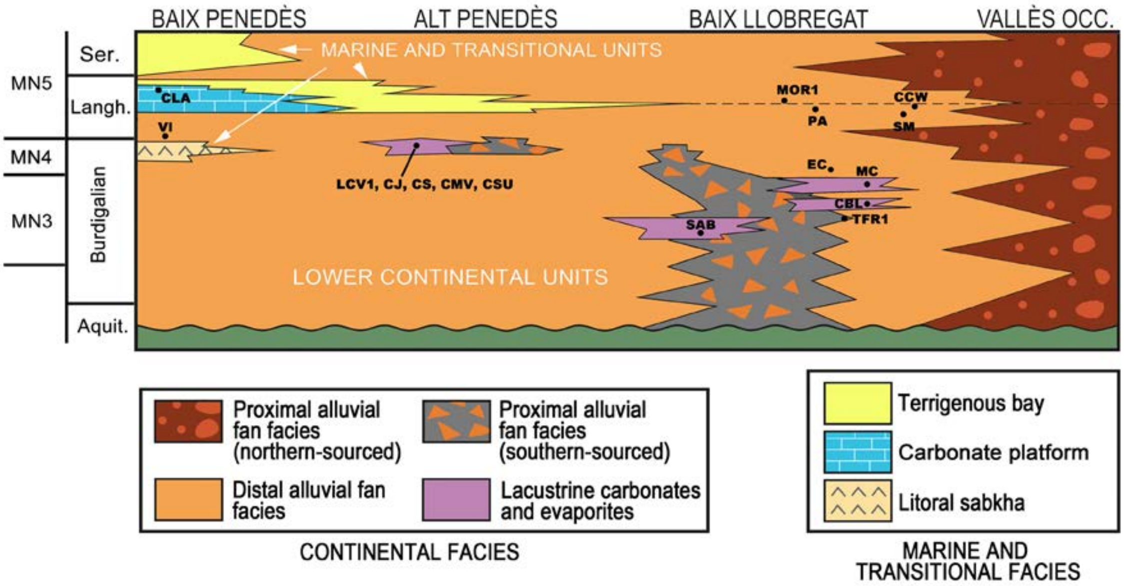


Figure 2.4: Generalized stratigraphic scheme of the early to early middle Miocene sedimentary record of the Vallès-Penedès Basin showing the main lithostratigraphic units and their relationships (modified after Cabrera et al., 1991 and De Gibert and Casanovas-Vilar, 2011). Note the different early Miocene lacustrine systems (including most localities) as well as the marine deposits associated with the Langhian transgression. For locality acronyms see Appendix 1.

further providing an interpretation of the sedimentary environment and briefly mentioning their main fossiliferous localities.

Lower Detrital Unit (LDU)

The LDU unit lays over Mesozoic rocks in the Penedès sector and over Paleozoic rocks in the Vallès sector. This unit is of highly variable thickness, ranging from 5 to almost 70 m depending on the sector. Its first 5 to 10m are defined by coarse-grained, clast-supported breccias that erode materials of the basement. They present an intense red color, except at el Turó de les Forques (Castellbisbal, el Baix Llobregat; figure 2.6) where they show grey decolorations. This basal breccia unit is overlaid by similarly colored conglomerates and breccias with markedly erosive channeled bases. The clasts are only slightly rounded, thus evidencing a close source area. They crop out in restricted areas such as in Puig Pedrós (Rubí, el Vallès Occidental) and Sant Andreu de la Barca (el Baix Llobregat; figure 2.5), but are entirely missing at el Turó de les Forques and la Costablanca (Martorell), likely because this area represented a marginal paleorelief during the Burdigalian (Cabrera, 1979). In certain areas of the basin, such as in el Molí de Can Calopa (Rubí), they alternate with thinner layers of red sandstones and lutites. Cabrera (1979) interprets the basal breccias as colluvial material deposited at the base of the hillslopes defined by the margins of the basin. The upper breccias, conglomerates and occasional sandstones and lutites would have been deposited in the context of alluvial fans sourced from the southeastern reliefs. The more massive conglomerate and breccia layers would correspond to the proximal alluvial fan facies, while those alternating with sandstones and lutites would correspond to medial facies (Cabrera, 1979). Regrettably, the depositional environment did not favor bone preservation so that this unit includes just a single fossil site, el Turó de les Forques (Castellbisbal), located in the basal breccia strata and having mostly delivered small mammal remains.

Detrital-Carbonated Unit (DCU)

This unit is highly discontinuous and crops out at different points of the basin, such as el Turó de Can Calopa (Rubí), la Costablanca (figure 2.7), Sant Andreu de la Barca and Subirats (l'Alt Penedès). Its thickness is also variable, ranging from about 30 m in els Casots (Subirats; see figure 2.12 and chapter 10) to 65 m in la Costablanca and over 150 m in el Turó de Can Calopa (Cabrera, 1979; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). It was deposited in a context of distal alluvial fan facies coexisting with floodplains and shallow lake systems (Cabrera, 1979). The morphology and structure of the DCU differs in the various areas, showing particularities in each case. Even the age of this unit differs in the Vallès and Penedès sector (see below and chapter 10).

The DCU in the Vallès sector deposited during the Ramblian (middle to late Burdigalian) and is best represented at la Costablanca and el Turó de Can Calopa. The lowermost strata in these areas comprise intensely red lutite layers which present greyish to blueish decolorations towards the top (Cabrera, 1979; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). Thin sandstone and conglomerate layers of a few decimeters thick often occur within these deposits. At la Costablanca this unit is 15 m thick, whereas it may reach as much as 75 m in el Turó de Can Calopa. On top of these layers follows a succession of ocher carbonates interbedded with grey lutites. Carbonate layers can be between 0.5 and 2 m thick and may include fossils of ostracods, charophytes and freshwater gastropods, specially at la Costablanca (Cabrera, 1979; Cabrera et al., 1991). Occasionally, the carbonate and grey lutite layers have also delivered fossil leaves at la Costablanca (Sanz de Síria Catalán, 1981, 1993). These units show a cyclical alternation of lutite and carbonate sequences. Lenticular gypsum aggregates are developed on the upper part of the sequences, indicating high evaporation. Sometimes, particularly at el Turó de Can Calopa, diagenetic processes have removed the primary gypsum leaving just casts of gypsum crystals in the carbonates. The secondary (fibrous) gypsum formed in this way can be found infilling fissures that affect this unit (Parcerisa i Duocastella, 2002). This cyclical alternation of lutites, carbonates and evaporites evidences the existence of shallow ephemeral lakes which would repeatedly dry out. On the other hand, the grey colored lutites indicate the existence of hydromorphic soil sand often include iron nodules (Cabrera, 1979; Cabrera et al., 1991; Parcerisa i Duocastella, 2002). At Sant Andreu de la Barca the DCU succession is remarkably different, the lacustrine carbonate and marl layers alternating with calcareous breccias and evaporites (Cabrera et al., 1991).

Finally, the DCU is well represented at the Alt Penedès, cropping out at the towns of Gelida and Subirats, and often being referred to as the Subirats Detrital-Carbonate Unit (Cabrera, 1979, 1981; Agustí and Cabrera, 1980). Its estimated thickness is around 40 m (Cabrera, 1979, 1981; see also chapter 10) and predominantly consists of lutites interbedded with much thinner carbonate and lignite layers. The base of the unit (which crops out at Cal Sutxet and els Casots, Subirats) consists of poorly sorted breccias developed on top of the Mesozoic basement (figure 2.4, chapter 10). These deposits are just a few meters thick and are followed by predominantly grey lutites that show a few 'floating' Mesozoic clasts towards the bottom of the unit. Interbedded carbonate layers usually measure between a few decimeters to one meter, whereas lignite layers (which had been mined in Subirats during the late XIXth century, see chapter 1.1.1.) are apparently rare and just a few decimeters thick. A notable difference with other detrital-lacustrine units is the total absence of evaporites. The Subirats DCU is interpreted as the distal tor marginal facies of small alluvial fan systems where occasionally small lake systems developed (Cabrera, 1979, 1981). The DCU include the richer early Miocene sites in the basin (Casanovas-Vilar et al. 2011c,d, 2016a). These comprise el Molí de Can Calopa (figure 2.8) and la Costablanca II in the Vallès sector of the Basin and Sant Andreu de la Barca in the Baix Llobregat, all of them corresponding to the Ramblian (MN3). The Subirats DCU is by far the richest and includes the remarkable sites of les Cases de la Valenciana (figure 2.10), Can Martí Vell (figure 2.11), Can Julià and els Casots (figure 2.12) besides some minor localities. All the sites from the Subirats DCU have been correlated to the early Aragonian (MN4; see chapter 10).

Upper Detrital Unit (UDU)

It is the most important early Miocene unit, and it is thicker in the Vallès sector than in the Penedès. Its total thickness is difficult to assess because it is affected by several faults, yet it may be as much as 580 m in some areas of the Vallès sector (Rubí; Parcerisa i Duocastella, 2002). It is defined by red-orange conglomerates, sandstones, and lutites. It can be divided into two parts, the lower one consisting of channel deposits with a high lateral continuity interbedded with lutitic layers of 1 to 3 m thickness. The conglomerates and sandstones that define the channel deposits are arranged in layers of 0.5 to 1.5 m thick. The upper subunit shows a clear predominance of conglomerates and sandstones, which can be arranged in massive layers of up to 15 m thick (cropping out for example in Can Flavià de les Illes at Castellbisbal; Cabrera et al., 1991). These coarse litologies define channel deposits with a markedly erosive base and fewer lateral continuity as compared to those of the lower subunit (Parcerisa i Duocastella, 2002). Several sedimentary structures allow measuring the direction of paleocurrents: imbricated clasts in the conglomerates as well as ripples and flute casts in the sandstones. These all indicate that, in sharp contrast with older units, the materials of the UDU were sourced from the northwestern reliefs (Cabrera, 1979, 1981; Cabrea et al., 1991; Parcerisa i Duocastella, 2002). The UDU is interpreted as medial to distal facies of large alluvial fans with catchment areas in those reliefs, particularly during the upper subunit. Petrological analyses of the conglomerates have revealed the presence of clasts made of Paleogene rocks (carbonates and conglomerates) that only crop out in the Ebro Basin (Parcerisa i Duocastella, 2002), thus indicating that the alluvial fans even eroded Cenozoic materials adjacent to the septentrional reliefs. Towards the top of the UDU the layers progressively lose their characteristic red color and become yellowish and greyish. The uppermost conglomeratic layers even occasionally show some fragments of mollusk shells between the clasts, thus being indicative of transition towards marine environments (for example at Santa Maria de Vilalba, Abrera, el Baix Llobregat; Cabrera, 1979). Indeed, just on top of the UDU Langhian calcarenites rich in marine mollusk fragments crop out in the Vallès sector (Cabrera, 1979, 1981; Cabrera et al., 1991). Langhian marine and transitional sediments of the MTC follow, but these are far better represented in the Penedès sector. The UDU includes relatively few early Miocene sites, but notable examples include les Escletxes del Papiol (el Papiol, el Baix Llobregat, figure 2.18) and Sant Mamet (Sant Cugat del Vallès, el Vallès Occidental, figure 2.15), both situated just a few meters below marine and transitional Langhian deposits (Crusafont et al., 1955; Agustí et al., 1985; Casanovas-Vilar et al., 2011c,d, 2016a). The classical sites around el Papiol (Can Canals, Can Cerdà), which have now disappeared, were also within this unit, also few meters below the marine sediments (Crusafont et al., 1955; Alba et al., 2018). Finally, two sites which have only delivered small vertebrates have been recently located in the transitional facies belonging to the uppermost part of the UDU or the lowermost part of the MTC (see following chapter 2.3): la Riera del Morral 1 (Abrera, figure 2.17) and Can Cabanes W (Sant Cugat del Vallès, figure 2.16). All the sites within the UDU are correlated to the early Aragonian (MN4; see chapter 10).

Vilobí Gypsum Unit (VGU)

The early Miocene record of the Vallès-Penedès Basin not only comprises alluvial fan and shallow lacustrine sediments belonging to the LCC, but also marine and transitional sediments that were deposited during the late Burdigalian (Cabrera, 1979, 1981; Cabrera and Calvet, 1996; Agustí et al., 1990; Cabrera et al., 1991; de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a). These notably include the Vilobí Gypsum Unit which is a remarkably thick (up to 60 m; Ortí and Pueyo, 1976; Cabrera, 1979, 1981; Agustí et al., 1990) and was mined from roman times until the 1990s. This unit has been interpreted as a coastal sabkha, that is a saline shallow lake over the tidal zone where evaporites accumulated in an arid to semiarid climate. Occasionally tidal-flood deposits intercalate with evaporites at sabkhas. Early Miocene sediments lay directly over the basement of Mesozoic carbonates which define an elevated block in this part of the basin. Indeed, this elevated block is just the northwestern continuation of the horst defined by the Bonastre relief, which was partly overlapped by continental and transitional sediments when tectonic activity ceased in this sector of the basin during the late Burdigalian (Cabera, 1981). The early Miocene sequence at Vilobí del Penedès begins with basal breccias made of carbonate clasts followed by a few meters of ocher and grey lutites interbedded with thin layers of carbonates (figure, 2.14). These are soon overlaid by the gypsum unit (Ortí and Pueyo, 1976; Agustí et al., 1990). The first half of the gypsum unit includes finely stratified gypsum layers with occasional thin carbonate and lutite intercalations in its lowermost part. These stratified gypsum layers are followed by almost 40 m of massive gypsum crystals defining radial aggregates and megacrystals. The last few meters of the gypsum unit are made of gypsarenites, that is, sandstone deposits entirely made of grains eroded from the gypsum. The gypsum unit is followed by ocher to reddish lutite layers and gray marls (10 m; see Ortí and Pueyo, 1976; Agustí et al., 1990) capped by a bed of biocalcarenites including countless oyster fossils. The gray marls over the VGU have delivered planktonic foraminifera that clearly indicate the late Burdigalian age of these sediments (Magné, 1978). In addition, they have also provided fossil pollen that indicates the presence of *Avicennia* mangroves bordering the coastline at this area (Bessedik and Cabrera, 1985; see chapter 10). As far as mammal fossils are concerned, the oyster layers have delivered small mammals that indicate an early Aragonian (MN4) age (Aguilar, 1981; Agustí et al., 1985, 1990).

2.3: EARLY MIOCENE SITES OF THE VALLÈS-PENEDÈS

In this chapter an updated overview of the early Miocene sites of the basin is provided, briefly describing their situation, stratigraphic context and age. Brief remarks on the recovered fauna are provided, but these topics, particularly their age, are more thoroughly discussed in chapter 10. For the situation of the sites see figure 2.3, for a graphical summary of their lithostratigraphic correlation to the Vallès-Penedès units see figure 2.4.

2.3.1. RAMBLIAN SITES

As detailed in chapter 2.2, the sedimentary infill of the Vallès-Penedès Basin started during the early Miocene, but the lowermost part of this epoch (Aquitanian) appears to be missing. The oldest sites date back to the Ramblian (early Burdigalian), biozone MN3 (19.3-17.2 Ma). These sites are mostly located in sediments associated to the shallow lacustrine facies of the DCU (figure 2.4), except for el Turó de les Forques, corresponding to the LDU (see chapter 2.2.1). They exclusively occur in the Vallès sector of the basin. Ramblian sites are characterized by the absence of cricetids other than the rare *Melissiodon dominans* (Agustí, 1981, 1985; Casanovas-Vilar et al. 2011c,d, 2016a; see chapter 5 and 10), as characteristic of the so-called 'cricetid vacuum' corresponding to the late Ramblian (local zone A; Daams and Freudenthal, 1989). Glirids are diverse and common, the genera *Vasseuromys* and *Pseudodryomys* being dominant. The eomyids are relatively common and are represented by the genera *Ligerimys (L. antiquus, L. fahlbuschi)* and *Pseudotheridomys (P. fejfari,* see chapter 10) As for large mammals, the equid *Anchitherium* and the gomphoterid *Gomphotherium* are present at certain sites and confirm their correlation to MN3 (see Agustí et al., 2001).

Sant Andreu de la Barca (SAB)

Sant Andreu de la Barca site (figure 2.5) was in the municipality that bears the same name and comprised different fossiliferous levels that delivered both micro- and macrovertebrates. The site was destroyed because of the construction of a landfill, but an emergency excavation could be carried before, resulting in the recovery of a rich vertebrate collection (Agustí and Galobart, 1997). From a geological point of view, Sant Andreu de la

Figure 2.5: Lacustrine carbonate layers near the Sant Andreu de la Barca site (SAB). The fossiliferous levels reported in Agustí and Galobart (1997) have now been destroyed. Photo: I. Casanovas-Vilar.

Barca is not exactly situated in the Vallès-Penedès, but in a small associated graben (the Sant Andreu de la Barca graben) that formed during the early rifting phase. The fossiliferous levels were part of a shallow lacustrine unit, the Sant Andreu de la Barca DCU (see chapter 2.2.1) that dates back to the early Burdigalian. Sant Andreu de la Barca has delivered a rich small mammal collection including bout 140 specimens mostly belonging to glirids (*Vasseuromys rambliensis* vel *cristinae, Pseudodryomys ibericus*) and eomyids (*Ligerimys antiquus*; see chapter 10). The large mammal fauna remarkably includes both *Anchitherium* and *Gomphotherium*, likely representing one of the oldest sites to record these immigrants in the basin (see chapter 10).

El Turó de les Forques (TFR)

El Turó de les Forques (Castellbisbal) is also known with other names, such as 'Turó del Telègraf', 'Les Forques' or (erroneously, see below) 'Costablanca II' (figure 2.6). It is a small outcrop of grayish breccias directly deposited over Paleozoic rocks of the basin basement. The site was reported by Cabrera (1979) who interpreted the sediments as a colluvium defining the base of the LDU in the Costablanca sector. The Costablanca DCU (see below) follows this basal layer. Intensive screen-washing in 2011 delivered a few poorly-preserved large mammal remains (*Cainotherium*, crocodile osteoderms, turtle shell fragments) plus a rich sample of microvertebrates comprising about 300 specimens (Casanovas-Vilar and De Miguel, 2013). The small mammal fauna is similar to that recovered at Sant Andreu de la Barca including some genera that had not been reported from he Vallès-Penedès before, such as the eomyid *Pseudotheridomys*

Figure 2.6: Sampling for microvertebrates at el Turó de les Forques site level 1 (TFR1). Note the grey lutites with abundant clasts of metamorphic rocks. Photo: I. Casanovas-Vilar

and the dimylid insectivore *Cainodus* (Van den Hoek Ostende et al. 2020; see chapter 10). In 2011 a second fossiliferous level defined by grayish lutites, was located a few meters apart from the breccias and only delivered turtle shell fragments. Hence the breccias are often referred to as el Turó de les Forques 1, while this new outcrop is termed el Turó de les Forques 2.

La Costablanca (CBL)

The name of this site is sometimes written 'la Costa Blanca', which is indeed the correct toponym. The Costablanca DCU unit is one of the best examples of the early Miocene shallow lacustrine-palustrine environments of the Vallès-Penedès and has delivered vertebrate fossils (large and small), freshwater and continental mollusks, ostracods, macroflora and algae (figure 2.7). It is a 200-m-thick cyclical succession alternating lutites, carbonates and primary gypsum (for a more detailed description see chapter 2.2.1 and references therein). Crusafont et al. (1955) already found some vertebrate fossils in the lutites and later on Crusafont et al. (1968) discovered a richer level near the base of the succession which was named la Costablanca II. It corresponds to intensely red lutites that include numerous ferruginous nodules, root casts, continental gastropod molds and isolated vertebrate remains, mostly of small size. The site has delivered scarce remains of the equid *Anchitherium* (Crusafont et al., 1968, Rotgers and Alba, 2011) as well as a diverse artiodactyl fauna that includes two species of the suid *Aureliachoerus* (see chapter 10). In 2011 and 2014 Costablanca II was surveyed for microvertebrates (Casanovas Vilar et al., 2016c).

Two distinct fossiliferous levels were detected, but these only produced a small collection of no more than 50 specimens, most of the glirids (*Pseudodryomys ibericus, Peridyromys murinus* and others; see chapter 10). On the other hand, plant remains have been described by Sanz de Siria (1981, 1993), who recognized up to 30 different taxa and inferred that during the Ramblian climate at the Vallès-Penedès was tropical to subtropical and presented a marked rainfall seasonality.

El Molí de Can Calopa (MC)

This site is also known 'Molí Calopa' and is located near the ruins of the Can Calopa farmhouse in the town of Rubí (figure 2.8). It is one of the first vertebrate fossil sites discovered in Catalonia and is already mentioned by Almera (1891, 1898, 1899). It was later intensively studied by Crusafont et al. (1955) who reported several vertebrate remains including carnivores, artiodactyls, perissodactyls, lagomorphs, reptiles and a few rodents Indeed, el Molí de Can Calopa is the type locality for the xerine sciurid, *Heteroxerus rubricati* (Crusafont et al. 1955). These authors also reported other sites in the vicinity of the locality (Torrent de Vilaroc, Torrent de Can Serrafussà, Ca n'Esteper, l'Infern, el Fallol) which only delivered scarce remains and have now disappeared due to the construction of a huge industrial area.

El Molí de Can Calopa is yet another of the shallow lacustrine units developed during the early Burdigalian. The lowermost part of the Molí de Can Calopa

Figure 2.7: Intense red lutite layers at the lowermost part of la Costablanca (CBL) detrital-carbonate unit. Red lutites may be intercalated with thinner sandstone layers (clearly visible at the middle of the image). The greyish layers at the top of the hill correspond to lacustrine lutites and carbonates. Vertebrate fossils have been recovered from the red layers only. Photo: I. Casanovas-Vilar.

Figure 2.8: Lowermost part of el Molí de Can Calopa (MC) series showing alternating layers of intensely red conglomerates, sandstones and lutites. In this part of the succession conglomerate and sandstone layers (such as the one shown in the image) can be various meters thick. Photo: I. Casanovas-Vilar.

series includes and alternation of intensely red lutites, sandstones, and conglomerates which are interpreted as medial to distal alluvial fan facies belonging to the LDU (see chapter 2.2.1 and references therein). Lacustrine sediments are almost 75 m thick (Cabrera, 1979, 1981; Parcerisa Duocastella, 2002), and consist of an alternation of grey lutites, carbonates and gypsum that define a small hill, el Turó de Can Calopa. Vertebrate fossils were recovered in the uppermost lutitic layers, just below the lacustrine series (Crusafont et al., 1955). Test samples were collected and screen-washed in 2011, but only produced scarce dental remains belonging to the ochotonid lagomorph *Lagopsis* (Casanovas-Vilar and DeMiguel, 2013).

2.3.2. EARLY ARAGONIAN SITES

Early Aragonian (MN4) sites are located both in the Vallès and Penedès sector of the basin but are better represented in the latter. They occur in varied stratigraphic contexts. In the Vallès sector are mostly located in red lutites corresponding to alluvial fan facies of the UDU (see chapter 2.2.1), sometimes near (or associated to) transitional Langhian deposits (Sant Mamet, les Escletxes del Papiol). In the Penedès sector they mostly occur within the Subirats DCU, which includes the best sites of this age in the basin (els Casots, les Cases de la Valenciana, Can Martí Vell and Can Julià). All the early Aragonian sites are located close to the Litoral Ranges, except for Vilobí del Penedès and la Vinya Vella. The former occurs in transitional facies overlaying a thick unit of evaporites corresponding to a coastal sabkha (see chapter 2.2.1). In its turn, la Vinya Vella is located in Esparraguera (el Baix Llobregat), near the northwestern margin of the basin (see below). This set of sites is correlated to the early Aragonian (MN4) because of the presence of the 'modern' cricetid genera *Democricetodon* and *Megacricetodon* (Agustí et al., 2001; Hilgen et al., 2012; see also chapters 9 and 10). However, depending on the criteria used to define the MN4/MN5 boundary certain sites such as els Casots or Vilobí del Penedès should be better correlated to the beginning of MN5, that is to the earliest middle Aragonian (see discussion in chapter 10).

In the Calatayud-Montalbán Basin, the type area for the Aragonian ELMA, the early part of this age includes two distinct local biozones: B and C (see Daams et al., 1999; Van der Meulen et al., 2012). In local zone B, *Democricetodon hispanicus* is the only cricetid species present, whereas in zone C *Megacricetodon primitivus* as well as additional *Democricetodon* species are recorded (allowing for the subdivision of zone C into subzones Ca and Cb according to the *Democricetodon* species present; see Van der Meulen et al., 2012). In all the Vallès-Penedès sites both the genera *Democricetodon* and *Megacricetodon* are recorded, thus indicating their correlation to zone C, which would imply an age of 16.5 to 16 Ma (see chapter 9 and 10). Zone B, corresponding to the earliest Aragonian (ca. 17-16.5 Ma; Daams et al., 1999, Van der Meulen et al., 2012) would be entirely missing in the Vallès-Penedès record (see chapters 9 and 10). The absence of zone B does not reflect a sedimentary hiatus, at least in the Vallès sector, but the lack of fossiliferous sediments. Zone C rodent faunas of the Vallès-Penedès are well known and not only include abundant remains of the cricetids *Democricetodon* and *Megacricetodon*, but also of the eomyid *Ligerimys* (represented by *L. florancei* and *L. ellipticus*) and a diverse glirid fauna including the genera *Glirudinus, Microdyromys, Peridyromys, Pseudodryomys, Simplomys* and *Bransatoglis*. A similar subdivision of zone C into two subzones as in Calatayud-Montlabán (see Van der Meulen et al., 2012) may be applied to the Vallès-Penedès, with the upper zone being characterized by the appearance of several *Democricetodon* species (*D. decipiens, D. gracilis*) replacing *D. hispanicus* and *L. ellipticus* as the only eomyid species present (see chapters 9 and 10). On the other hand, the large mammal fauna is also well known, mostly thanks to the exceptional site of Els Casots. The artiodactyls show several first local appearances, including suids (*Listriodon*), tragulids (*Dorcatherium*) and bovids (*Eotragus*). Other first appearances include the earliest deinotheres, belonging to the genus *Prodeinotherium*.

EL CANYET (EC)

This site was first reported by Crusafont et al. (1955) and was located next to the road leading from Molins de Rei to Castellbisbal. By that time, it corresponded to an active red lutite quarry that were exploited for a brickyard (figure 2.9). It delivered a few large mammals (amphicyonids, cervids, suids; Crusafont et al., 1955; Golpe-Posse, 1974) as well as some micromammals, which mostly include ochotonid lagomorphs. The scarce small mammal material is part of the Villalta collection, curated at the Museum

Figure 2.9: Miocene sandstone and lutite layers near el Canyet (EC) site. The site was affected by the construction of a highway and was probably destroyed. Photo: I. Casanovas-Vilar.

of Natural Sciences of Barcelona, and part (sciurids, some lagomorphs) at the ICP. Agustí (1981) described the glirids and cricetids, whereas Aldana Carrasco (1991, 1992) described the sciurids.

The cricetids include some remains of *Democricetodon hispanicus*, thus confirming its MN4 age (Agustí, 1981; see chapter 9). The glirids are represented by *Pseudodryomys ibericus*, while the sciurids include well-preserved mandibles of the large-sized squirrel *Dehmisciurus obtusidens* (Aldana Carrasco, 1991, 1992). Agustí (1981) already noted that the construction of a highway had affected this site. Its current situation is unknown, but the fossiliferous outcrops were likely destroyed during the construction of the highway as well as result of the expansion of nearby industrial areas.

LES CASES DE LA VALENCIANA (LCV)

This site is part of the Subirats Detrital-Carbonatic Unit (Subirats DCU, see chapter 2.2.1) which is interpreted as a group of seasonal shallow lakes that existed during the early Miocene in this area (Cabrera, 1979, 1981; Agustí and Cabrera, 1980). The main sedimentation of this unit corresponds to grayish lutites rich in vertebrate fossils. The main sites of the Subirats DCU are les Cases de la Valenciana, Can Martí Vell and Can Julià, situated in Gelida (l'Alt Penedès) municipality near the road C-243b; and els Casots and Cal Sutxet located in Subirats (l'Alt Penedès) municipality. These are the richest early Miocene sites in the Vallès-Penedès Basin.

Les Cases de la Valenciana (see chapter 6) was discovered in the 1950s and yielded some macrovertebrate remains including carnivores, amphicyonids,

Figure 2.10: Les Cases de la Valenciana (LCV) site. A: Systematic excavation of level 1 during 2015.; B: Rhinocerotid humerus and rib remains. Photos: I. Casanovas-Vilar and D. DeMiguel.

artiodactyls, tortoises and small crocodiles (Crusafont et al., 1955). This site is situated next to the road between Gelida and Sant Sadurní d'Anoia (C-243b) and consists of greyish lutites (figure 2.10). In 2011, some minor works in the road exposed some fossils that were soon detected by a team of the ICP that would later conduct several systematic excavation campaigns (in 2012, 2014 and 2015; Casanovas-Vilar et al., 2014, Casanovas-vilar and DeMiguel, 2017; see chapter 6). These new campaigns yielded 450 macrovertebrate remains and about the same number of identifiable microvertebrate remains after screen-washing all the excavated sediment. Of all this, two disarticulated partial skeletons stand out, one belonging to the giant tortoise *Titanochelon* cf. *bolivari* (Lujan et al. 2017) and the other one to the rhinocerotid

Dromoceratherium mirallesi (Sanisidro et al. 2018). In addition, a second fossiliferous level, named les Cases de la Valenciana 2, was discovered a few meters above the classical one. It is a massive layer of lacustrine carbonates which included several rib fragments of a megaherbivore which were extracted in block (Llenas Avellaneda, 2015). Because of the discovery of these new fossiliferous level the classical locality is also often referred to as les Cases de la Valenciana 1.

The small mammal fauna is thoroughly descrived in chapter 6 and includes marsupials (*Amphiperatherium*), insectivores, lagomorphs and a remarkable diversity of rodents (11 different species comprising sciurids, glirids, eomyids and cricetids). The presence of the cricetids *D. hispanicus* and *M. primitivus* coupled with that of the eomyids *L. florancei* and *L. ellipticus* favors a correlation with local subzone Ca from the type Aragonian (16.5-16.3 Ma; see chapter 6).

CAN MARTÍ VELL (CMV)

Can Martí Vell (Gelida) also belongs to the Subirats DCU. It is situated next to the same road as les Cases de la Valenciana (C-243b), just one kilometer south of that site. It consists of a 20-m-thick series of alternating red and grey lutites cropping out east of the Can Martí Vell farmhouse (Cabrera, 1979; Agustí and Cabrera, 1980; figure 2.11). This site was first reported by Cabrera (1979) and a preliminary faunal list was given in Agustí and Cabrera (1980) These authors published a short stratigraphic series that only included two vertebrate bearing levels, which they named Can Martí Vell I and II. When a team of the ICP visited the site in 2014, recent agricultural works had completely exposed the Can Martí Vell series.

Figure 2.11: Surface survey at the Can Martí Vell (CMV) site. Grey lutite layers correspond to fossiliferous levels CMV1 and CMV2. Photo: I. Casanovas-Vilar.

Three fossiliferous beds, each one corresponding to a level of grey lutites, were detected and numbered from top to bottom Can Martí Vell 1, 2 and 3 (CMV1-CMV3; Casanovas-Vilar et al., 2016c; Llenas Avellaneda et al., 2016). Equivalence with the levels studied by Agustí and Cabrera (1980) is uncertain, but CMV3 certainly corresponds to Can Martí Vell II, whereas Can Martí Vell 1 may either correspond to CMV1 or CMV2. Anyway, given their close stratigraphic position all the levels are generally considered as a single site in most works (e.g., Agustí et al., 1985). Systematic screen-washing in 2015 allowed for the recovery of almost 800 identifiable micromammal specimens, most of them from CMV3 (Llenas Avellaneda et al., 2016). The rodent fauna had been described by Agustí (1983) and comprises cricetids, eomyids and diverse glirids (*Peridyromys, Simplomys, Microdyromys, Glirudinus, Bransatoglis*).

The 2015 field campaign allowed adding a few rodent taxa to the list (the sciurids *Heteroxerus* and *Atlantoxerus*), diverse insectivores (see Van den Hoek Ostende et al., 2020) as well as the marsupial *Amphiperatherium*. The rodent fauna is very similar to that of les Cases de la Valenciana (see chapter 6) including two species of the eomyid *Ligerimys* (*L. florancei* and *L. ellipticus*) and the cricetids *D. hispanicus* and *M. primitivus,* thus evidencing a correlation to subzone Ca (see chapters 6, 9 and 10).

CAN JULIÀ (CJ)

Following the road C-243b from Gelida to Sant Sadurní, just about 500 m south of Can Martí Vell there is another site, Can Julià, also part of the Gelida municipality. It also belongs to the Subirats DCU, corresponding to grey lutites. It was first reported by Crusafont and Villalta (1952), while the recovered fauna was described in greater detail in Crusafont et al. (1955), who remarked that it was one of the richest early Miocene sites in the area. The site delivered mostly macrovertebrates, including felids, gomphotheres, rhinocerotids, suids, cervids and paleomerycids. Later on, Agustí and Cabrera (1980) reported a few rodent remains. These were described in Agustí (1981), and only comprise the eomyid *L. ellipticus* and the cricetid *M. primitivus.* These allow a correlation to zone Aragonian zone C, but subzone cannot be specified (see chapters 6, 9 and 10). However, it is worth noting that the micromammal collection was in all probability found in different layers than larger mammals, because by the arly 1970s the site surveyed by Crusafont and co-workers had already been destroyed (Golpe-Posse, 1974).

ELS CASOTS (CS), CAL SUTXET (CSU) AND THE LA FONTSANTA COAL MINES

All these sites are also part of the Subirats DCU and are located next to els Casots neighborhood, in the municipality of Subirats. Hence they are just a few kilometers south of other sites from the same lacustrine unit, such as les Cases de la Valenciana and Can Martí Vell. In this area the Subirats DCU alternates greyish and ocher lutite layers with carbonates and occasionally thin lignite deposits (Cabrera, 1979, 1981; Moyà-Solà and Rius Font, 1993; Casanovas-Vilar et al.,

Figure 2.12: Els Casots (CS) site. For a general view fo the site see Figure 1.3 A: Excavation campaign in 2019; B: Juvenile gomphoterid remains being excavated. Photos: I. Casanovas-Vilar.

2011a; figure 2.12). As explained in chapter 1.1.1, the lignite layers were mined during the late XIXth century leading to the discovery of some of the first vertebrate fossils in Catalonia. Once the mines closed, no new discoveries are reported from this area, even though Crusafont and co-workers visited the area and the abandoned mines they only found a few fossilized palm leaves (Crusafont et al., 1955). Later on, in 1989 the impressive els Casots site was discovered and systematically excavated in the following years under the lead of Salvador Moya Solà (see chapter 1.1.4 and chapters 7-8). Excavations allowed for the recovery of more than 3,000 large vertebrate remains, including remarkably complete and even semi-articulated specimens. These come from multiple fossiliferous levels, mostly defined by greyish to black lutites. The most spectacular fossils include partial skeletons of the early bovid *Eotragus noyei*, the large-sized amphicyonid carnivore *Euroamphicyon olisiponensis*, the suid *Eurolistriodon adelli* and the paleomerycid ruminant *Ampelomerx ginsburgi*. The latter two species were indeed erected based on material recovered at the site (Duranthon et al., 1995; Pickford and Moyà-Solà, 1995). As far as small mammals are concerned, several levels of els Casots were screen-washed and more than 400 specimens recovered. Els Casots mammal fauna has been the subject of several systematic studies, the most important ones dealing with the artiodactyls (Pickford and Moyà-Solà, 1994, 1995; Duranthon et al., 1995; Alba et al., 2014), equids (Rotgers and Alba, 2011), crocodilians (Díaz-Aráez et al., 2017) and mustelids (Valenciano et al., 2020). As far as rodents are concerned, only the sciurids have been described in detail in (Aldana Carrasco, 1991, 1992). Agustí and Llenas (1993) presented a brief account of the recovered rodent fauna, further providing a preliminary correlation. The presence of the cricetids *D. hispanicus* and *M. primitivus* as well as that of the eomyid *L. ellipticus* allows for a correlation to

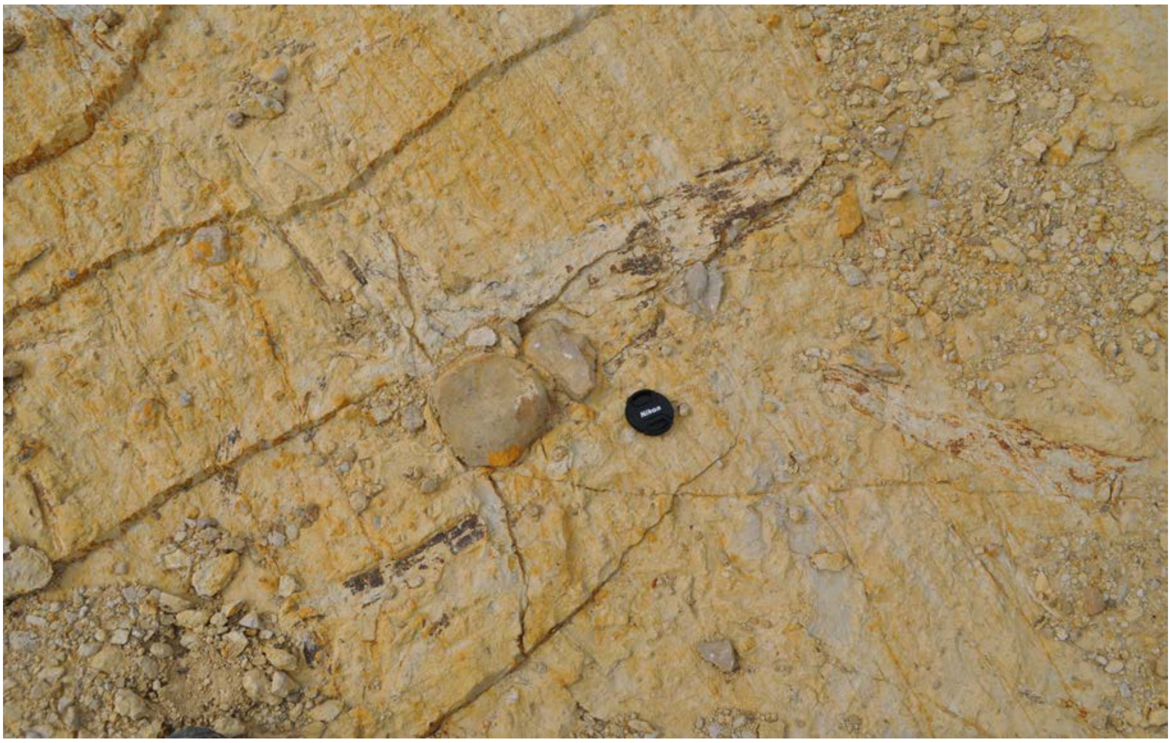


Figure 2.13: Detail of Cal Sutxet (CSU) site. Note the ‘floating’ clasts of grey Mesozoic carbonates at the center of the image and the carbonaceous impressions of aquatic plant twigs below and to the right of them. Photo: I. Casanovas-Vilar.

Figure 2.14: The abandoned Vilobí (VI) gypsum quarry. The grey layers are the thick gypsum deposits. Ocher sediments on top correspond to the transitional lutites, including oyster coquinas, that have also delivered small mammal fossils. Photo: I. Casanovas-Vilar.

Aragonian subzone Cb, yielding an approximate age of 16.3-16 Ma (see chapters 7-10). The absence of *L. florancei*, coupled with the occurrence of a second, larger sized, *Democricetodon* species indicates that els Casots is somewhat younger than other sites of the Subirats DCU, such as les Cases de la Valenciana or Can Martí Vell, which are correlated to subzone Ca. New magnetostratigraphic data (see chapter 10) have confirmed this younger age. After being abandoned for decades the ICP resumed systematic excavations, coupled with geological surveys and other studies in 2018.

Regarding Cal Sutxet, it corresponds to a small outcrop next to els Casots which was discovered in 2011. It is a bed of ocher siltstones with some floating clasts made of basement rocks (Mesozoic carbonates) (figure 2.13). Impressions of plant twigs also occur near the base of the layer. These sediments represent the lowermost deposits of the Subirats DCU in this area, directly deposited over the Mesozoic carbonate basement. A test sample was collected in 2011 allowing for the recovery of some rodent remains. These include the cricetids *D. hispanicus* and *M. primitivus*, thus indicating a similar age to that of els Casots (Casanovas-Vilar et al., 2011c).

VILOBÍ DEL PENEDÈS (VI)

Vilobí (Vilobí del Penedès, l'Alt Penedès) is located in an old (now abandoned) gypsum quarry (figure 2.14). The thick (60 m) gypsum deposits defined the Vilobí Gypsum Unit and are interpreted as coastal sebkhas developed by the end of late Burdigalian (see chapter 2.2.1 and references therein). These gypsum layers are overlaid by ocher to reddish lutite layers and grey marls (10 m; see Ortí and Pueyo, 1976; Agustí et al., 1990) capped by an oyster coquina. The gray marls have delivered planktonic foraminifera that clearly indicate a late Burdigalian age (Magné, 1978), as well as fossil pollen showing the presence of coastal mangroves (Bessedik and Cabrera, 1985).

As far as mammal fossils are concerned, the oyster coquina beds have delivered small mammals only. Magné (1978) first reported a *Megacricetodon* molar from these beds, while later authors listed the glirid *Peridyromys* as well and attributed the materials to biozone MN4 (Aguilar, 1981; Agustí et al., 1985, 1990). Later on, the oyster beds were intensely surveyed and screen-washed during the 1990s allowing for the recovery of about 300 isolated small mammal teeth belonging to cricetids, eomyids, glirids, sciurids, lagomorphs, and insectivores that have yet to be studied. The site is labelled as 'Vilobí Ostrea' (including two different levels) in the ICP collections. The cricetids (including *Megacricetodon primitivus* and two species of *Democricetodon*) are described in chapter 9 and some remarks on the rest of the rodent fauna are provided in chapter 10. The occurrence, although very scarce, of the eomyid *Ligerimys ellipticus* favors a correlation with Aragonian subzone Cb yielding an approximate age of 16 Ma (see chapter 10). The insectivores are described in Van den Hoek Ostende et al. (2020). In addition 'Vilobí Ostrea', the lowermost levels in the Vilobí gypsum quarry (those preceding the gypsum unit; see chapter 2.2.1) were sampled in 2016 but did not yield any identifiable remains.

LA VINYA VELLA (VV)

This is the only early Miocene site located near the northwestern margin of the basin. It was discovered by Rafael Subirana, who reported the finding to Crusafont and co-workers. It is a small outcrop of red lutites north of the town of Esparraguera (el Baix Llobregat) that delivered a scarce macromammal fauna including felids, artiodactyls and lagomorphs (Crusafont et al., 1955). Crusafont et al. (1955) note that this site is placed below paler lutite and conglomerate layers that they assign to the middle Miocene, noting lithological similarities with the levels cropping out at els Hostalets de Pierola. Therefore, marine environments would not have extended to this part of the basin. The exact location and age of this site is currently uncertain.

2.3.3. SITES ASSOCIATED TO THE MARINE AND TRANSITIONAL COMPLEXES

The following sites are placed a few meters below or interbedded with Langhian marine and transitional sediments. Their age is controversial as they may either belong to the latest early Miocene or the very beginning of the middle Miocene. New bio- and magnetostratigraphical data are provided in chapter 10 and allow solving these uncertainties. Below a brief description of the sites and their stratigraphical context is provided, without discussing in detail the recovered fauna and age.

SANT MAMET (SM)

Sant Mamet (Sant Cugat del Vallès, el Vallès Occidental) is a classical site discovered in the 1950s which delivered mostly small-sized vertebrate remains,

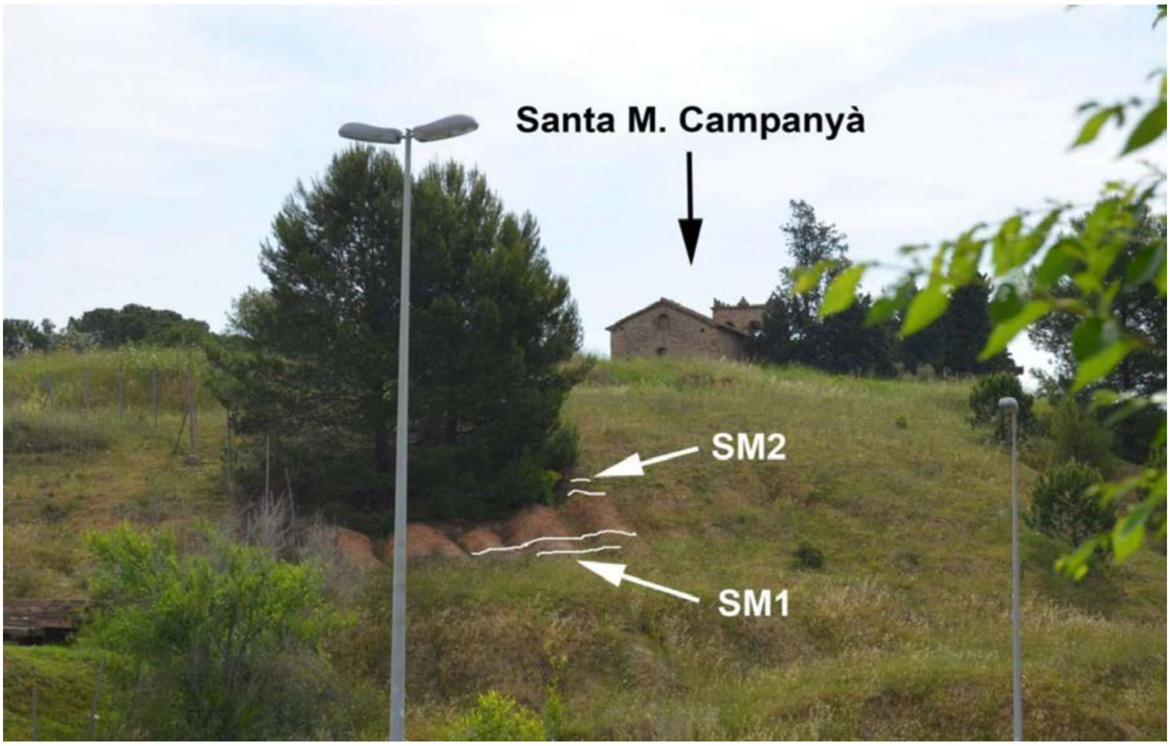


Figure 2.15: Sant Mamet (SM) site in 2016. SM1 and SM2 indicate two fossiliferous levels, although only SM1 has delivered a rich small mammal collection. On the top of the hill there is the small old church (XIth century) of Santa Maria de Campanyà also called of Sant Mamet. The church is built over a Langhian oyster coquina. Photo: I. Casanovas-Vilar.

especially from artiodactyls, carnivores, and rodents (Crusafont et al., 1955; Agustí et al., 1985; figure 2.15). Sant Mamet is the type locality for the small artiodactyl *Cainotherium miocaenicum*, one of the most common taxa in the early Miocene of the Vallès-Penedès. The classical site was located in an ancient brickyard and likely included several different fossiliferous lutite levels which were affected by the construction of an industrial area in the 1990s.Before the classical levels disappeared some test samples were taken for the recovery of small vertebrates and magnetostratigraphic studies were carried out (Garcés Crespo, 1995). The test samples delivered scarce rodent and lagomorph remains, while the magnetostratigraphic results indicated a correlation to chron C5Br, thus yielding an age between 16-15Ma (Garcés Crespo, 1995). This is consistent with faunal data, which indicate an MN4 age (Agustí, 1981; Agustí et al., 1985) and further supported by their stratigraphic position, as it is just a few meters below an oyster coquina corresponding to the Langhian transgression maximum (Crusafont et al., 1955; Agustí et al., 1985). Even though the classical levels were destroyed, in 2016 new fossiliferous layers were discovered and in 2017 they were intensively sampled. This allowed for the recovery of a small collection fo about 50 specimens including several cricetids (*Megacricetodon primitivus, Democricetodon* cf. *decipiens, Democricetodon gracilis*) and the eomyid *Ligerimys ellipticus*, previously unknown from the site. The rodent fauna allows refining its biostratigraphical correlation to Aragonian subzone Cb.

Can Cabanes West (CCW)

Can Cabanes West (Sant Cugat del Vallès) is situated really close to Sant Mamet further corresponding to a similar stratigraphic context. The locality corresponds to grayish lutites corresponding to transitional deposits interbedded with littoral sandstones rich in decapod trace fossils (*Ophiomorpha, Spongeliphorma*; De Gibert and Robles, 2005). These are placed about 15 m below bioclastic sandstones full of turritellid sea snails (figure 2.16). All these sediments are also related to the Langhian transgressive maximum and represent one of the marine outcrops located further inland. De Gibert and Robles (2005) reported scarce rodent remains (*Democricetodon, Glirudinus, Spermophilinus*) from this site, which was sampled again in 2015 and yielded a few additional rodent material. The recovered rodent fauna is very similar to that of Sant Mamet, thus indicating a similar age.

La Riera del Morral (MOR)

La Riera del Morral (Abrera, el Baix Llobregat) is a recently discovered site. Same as Can Cabanes Oest (see above) it is located in transitional facies of Langhian age (Casanovas-Vilar and Jovells-Vaqué, 2017; figure 2.17). The fossiliferous layer of Riera del Morral consists of grayish marls with some yellow decorations that present some burrows produced by marine organisms and have also delivered some mollusks and foraminifera. The only identifiable micromammal remains recovered at this site are two molars belonging to a large-sized *Democricetodon* species (see chapter 9).

Figure 2.16: Detail of the fossiliferous greyish lutites at the Can Cabanes W (CCW) site. Photo: I. Casanovas-Vilar.

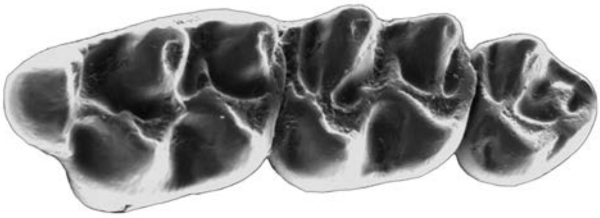
Figure 2.17: Riera del Morral (MOR1) site. The fossiliferous level is a thin marl layer placed below thicker conglomerate deposits. Photo: I. Casanovas-Vilar

Les Excletxes del Papiol (PA)

Crusafont et al. (1955) reported a series of sites from el Papiol (el Baix Llobregat): Can Canals, Can Cerdà and Can Mas. These corresponded to ancient clay quarries and occasionally delivered vertebrate remains (figure 2.18), including insectivorans, lagomorphs, suids, cainotherids, cervids, rhinocerotids and proboscideans amongst others (Crusafont et al. 1955). Can Mas notably delivered a well-preserved mandible of Gomphotherium (Crusafont et al., 1955), while a pangolin femur (*Necromanis* cf. *franconica*) was recovered at Can Cerdà and only recently described, representing the first record of this group from the Iberian Peninsula (Alba et al., 2018). Unfortunately, these sites were destroyed by intensive quarrying and the quarries were later filled with rubble. However, Crusafont et al. (1955) also mention the finding of a few molar

Figure 2.18: Les Escletxes del Papiol (PA) site. Geologist Miguel Garcés (Universitat de Barcelona) is standing on the fossiliferous red lutites which delivered small mammals. The thick grey deposits on the background are coralgal reef carbonates corresponding to the Langhian. Photo: I. Casanovas-Vilar.

fragments of a deinothere in the red clay outcrops placed below the area known as les Excletxes del Papiol. Les Escletxes del Papiol is a classical Langhian locality corresponding to a small-sized coralgal reef known since the XIXth century (see Permanyer, 1990). The intensely red clays are placed between the marine carbonates that made out the reef and a coquina layer (see chapter 10). Therefore, they most likely belong to the middle (Langhian) rather than the early Miocene. These deposits were surveyed again in the 1990s and delivered a rich small-mammal collection that includes 130 identifiable rodent specimens, mostly belonging to the cricetid *Megacricetodon primitivus.* The site is labeled in the ICP collections as les Escletxes del Papiol. The absence of the eomyid *Ligerimys* is consistent with a MN5 (see chapter 10).



Chapter 3: INTRODUCTION TO RODENTS

CHAPTER 3: INTRODUCTION TO RODENTS

Rodents represent more than 40% of mammalian biodiversity, usually being the most diverse and abundant order in many ecosystems. Rodents are commonly characterized as small and diversified terrestrial mammals, specialized for gnawing and with a high reproduction rate. The number of species and families of rodents differs according to the opinion of the authors, but it is close to 2,600 (Pardiñas et al., 2017; D'Elía et al. 2019). There are about 30 extant families besides a similar number of fossil ones (Hartenberger, 1998; Pardiñas et al., 2017). Their radiation includes subterranean species, gliding squirrels, a large array of semiaquatic lineages, as well as the more common arboreal, scansorial and cursorial forms. The rodent size range is very variable from some species of small mice weighing 5 g to capybaras which can weigh over 70 kg. Some extinct species of South American rodents were even larger, with *Josephoartigasia monesi*, a plio-pleistocene relative of the extant pakarana, reaching an estimated body mass of nearly 1,000 kg (Rindercknetch and Blanco, 2008). However, most of them weigh less than 1 kg (D'Elía et al. 2019). Regarding the reproduction rates, only some families such as the Muridae and Arvicolidae are characterized by high reproduction rates and short longevities, while in other families these rates are much moderate. Owing to their small to medium size, short breeding cycle and high adaptability, rodents have repeatedly occupied similar niches and colonized similar environments at different times during their long evolutionary history (Pardiñas et al., 2017).

3.1 MAIN ANATOMICAL CHARACTERISTICS

Rodents have several autapomorphic features that allow them to be distinguished from any other mammal, most of them in the skull, mandible, and dentition. In this chapter, a general overview of the main anatomical traits of rodents is presented.

3.1.1 CRANIUM AND MANDIBLE

The skull in rodents can be highly variable, but some traits are common to all of them (figure 3.1). Rodent skulls have a distinctly elongated rostrum because of the enlargement of the premaxillary bones. The incisive foramina are also elongated, same as the nasals which are also flared anteriorly. Elongation of the rostrum is explained by the presence of a long diastema between the incisors and the cheek teeth, which is often longer than the cheek tooth row. The diastema on the cranium is always longer than that on the mandible. Another notable feature of rodents is the elongated, through-like glenoid fossa and anteroposteriorly elongated mandibular condyle. These confers rodents the ability to disengage the mandible from molar to molar occlusion and bring it forward so that incisor tips occlude. This is very important for cropping food and necessary for sharpening the incisors, because of they are ever-growing. Typically, rodent mandibles are smaller than the cranium. All these anatomical features are functionally related to gnawing (incisor bite), and also occur (but are not so pronounced) in lagomorphs (Hartenberger, 1985; Korth, 1994; and Hautier and Cox, 2015).

Other features of the rodent skull comprise the orbital cavity which is located

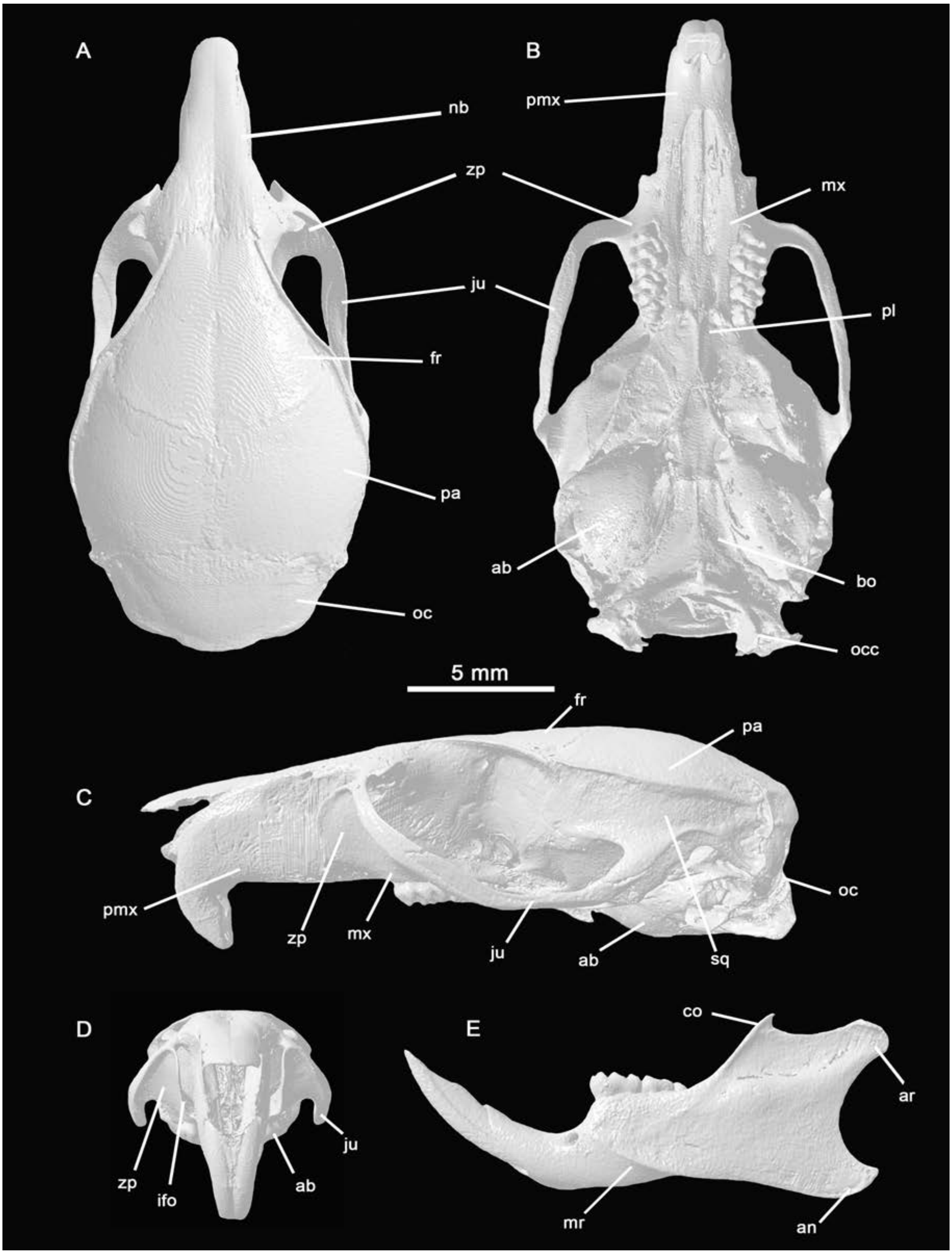


Figure 3.1: Rodent cranium and mandible. A, dorsal view of the cranium; B, ventral view; C, lateral view; D, frontal view of the cranium; E, left mandible. Cranium and mandible of *Acomys cahirrinus* (Muridae, Deomyinae) from the University Museum of Zoology Cambridge Morphosourse collection (DOI: 10.17602/M2/M48255). ab, auditory bulla; an, angular process; ar, articular process; bo, basioccipital; co, coronoid process; fr, frontal; ju, jugal; ifo, infraorbital foramen; mr, masseteric ridge; mx, maxillary; nb, nasal bones; oc, occipital; occ, occipital condyle; pa, parietal; pl, palatine; pmx, premaxillary; sq, squamosal; zp, zygomatic plate.

dorsally to the cheek teeth; the robust anterior ramus of the zygoma lying anterior to the first cheek teeth. Most rodents possess an auditory bulla which is entirely made by a lateral and medial expansion of the ectotympanic bone (Novacek, 1985; Mason, 2015). This condition is only known for a few other groups of mammals, such as lagomorphs, and is used as a character for determining supraordinal relationships (Novacek, 1985). In addition, middle ear structure is highly variable in rodents, sometimes being incredibly complex, and diagnostic of the main groups (see Lavocat and Parent, 1985; Mason, 2015).

The rodent mandible is unique in many regards. In most rodents, the two hemimandibles are only loosely attached and can move relatively one another. As already said, the mandible presents a conspicuous diastema separating the incisor from the cheek tooth row. The articular condyle (or process) rises above the tooth row. Two additional processes are observed in the mandibular ramus: coronoid (on the dorsal side) and angular (on the ventral side) (Druzinsky et al. 2015). The coronoid process is generally small and pointed, frequently hook-shaped. It serves for insertion area of the temporal muscle, which is used mostly in vertical movements of the jaw. The reduction of this muscle implies a reduction of the coronoid process. In contrast, the angular process, which serves as insertion area for the masseter muscle (see chapter 3.1.3), is well developed and may project posteriorly beyond the level of the articular process. The masseter is used in propalinal movements of the mandible, that is, to pull the mandible in a forward and backward motion. The attachment of the masseter to the lateral side of the mandible has been modified in association to changes in the zygoma (see chapter 3.1.3). The masseter inserts in the so-called masseteric fossa, a depression bordered by well-defined ridges (the masseteric ridges) in rodents. In primitive eutherian mammals the masseteric fossa does not reach the level of the most posterior molars, but in rodents it is placed much more anteriorly (Korth, 1994). In those rodents in which the masseter extends onto the rostrum, the masseteric fossa may even extend to a point anterior to the cheek tooth row. Again, all these modifications are related to an increased emphasis in propalinal jaw movements (Druzinsky et al. 2015).

On the other hand, traditionally rodents had divided into two suborders, Sciurognathi ('squirrel-mandible') and Hystricognathi ('porcupine mandible'), owing to mandible morphology. Tullberg (1899) was the first to propose this subdivision, which was used during most of the 20th century (Hautier et al. 2011). This division is based on the relative position of the angular process relative to the plane of the incisors. Sciurognathous jaws are characterized by an angular process originating in the same plane that includes the incisors. On the contrary, the hystricognathous jaws show the origin of the angular process distinctly lateral to the plane of the incisors. Recent phylogenetic studies have confirmed the hystricognaths as a strongly supported monophyletic clade (currently an infraorder; see D'Elía et al., 2019). On the other hand, sciurognaths placed together unrelated rodent groups, so this term is now only used to describe mandible anatomy. Subordinal division on the basis of mandible shape is now abandoned (see Fabre et al., 2012; D'Elía et al., 2019).

3.1.2 DENTITION

Rodent dentition is highly specialized for gnawing. Although rodents are a large and morphologically diverse group, they share universal characteristics among the dentition, such as one upper and one lower ever-growing incisor on each quadrant of the skull and mandible, always separated by a diastema (longer in the maxilla than in the mandible) from the check teeth. The latter include a maximum of two upper premolars and one lower premolar and three upper and lower molars. There are no canines. The upper premolars are the third (P3) and fourth (P4) ones, whereas lower one is the fourth (p4). Summarizing, rodents have a maximum of 22 elements and their dental formula is 1023/1013. However, many rodent families have this pattern reduced showing 1003/1003 as a dental formula (Korth, 1994). Lagomorphs, which are closely related to rodents and are included together with them in the larger clade Glires (see chapter 3.2), are easily distinguished from rodents because they present a second pair of upper incisors (the so-called peg teeth).

Rodent and lagomorph incisors are ever-growing with enamel restricted to the anterior surface and slightly to the lateral and medial sides. Such kind of incisors are called gliriform incisors. However, these are not restricted to Glires and have evolved in other mammals such as multituberculates, tillodonts, taeniodonts, some marsupials and artiodactyls among others (Korth, 1994). In rodents gliriforms incisors are known to be the second deciduous incisors (dI2/di2; Lucket, 1985) but are often referred to as I1/i1 (e.g., Korth, 1994). The base of the incisors extends backward to the posterior part of the mandible (ramus) or into the maxilla (Korth, 1994). Moreover, the incisors may have ridge and groove ornamentation on their surface, which can be diagnostic of particular species or groups (Martin, 1980; Flynn, 1985). Finally, rodent incisor enamel consists of two layers. The outer layer (portio externa) consists of enamel prisms which are radially oriented in all rodents, whereas the inner layer (portio interna) which can show different patterns (pauciserial, uniserial, multiserial). The simplest pattern, pauciserial, is found in most primitive rodents, whereas other patterns are found in later groups. Complex enamel microstructure patterns contribute to resistance against dental wear and cracking, yet their function is not fully understood (Gomes Rodrigues, 2015). Furthermore, enamel microstructure can also be of interest from a systematic and phylogenetic point of view (see Sahni, 1985; Von Koenigswald, 1985).

Rodent cheek teeth are primitively brachydont and bunodont. The premolars are generally smaller and simpler than the molars, particularly the P3, which is a single-rooted tooth with a conical crown. In primitive rodents, the molars are transversely elongate and show the basic tribosphenic pattern (Korth, 1994), but derived rodents have diverged considerably from it making cusp homology difficult to determine. The lower molars are longitudinally elongated in primitive rodents and lack the paraconid, maintaining only the metaconid and protoconid in the trigonid (Korth, 1994). However, in many rodents, such as cricetids, a new cusp, the anteroconid, has evolved *de novo* to occupy the position of the paraconid. In most rodents the cheek teeth pattern is complicated with additional transverse ridges and cusps which has led to a different terminology than in other mammals. Indeed, even different anatomical terminologies are used for the different rodent families (e.g., see chapter 3.3.2).

3.1.3 Zygomasseteric structure

Specialization for gnawing in rodents is also reflected in the chewing muscles on the skull and mandible that show different insertion patterns associated with the different usage given by rodents. The rodent masticatory muscles are much more differentiated than in other mammal orders, especially the masseter, which is divided into the superficial, lateral and medial masseter (Wood, 1965). Importance of these respective parts, positions of origin and insertion on the skull and the mandible varies widely between rodents. Since the mid-19th century the pattern of masseter arrangement has been used for the classification of rodents into major groups (see also chapter 3.2). Initially, Waterhouse (1839) distinguished three different groups: Leporina (rabbits and hares), Hystricina (porcupines and allies) and Murina (all other rodents). Later on, Brandt (1855) proposed a similar arrangement into Lagomorpha (= Leporina), Hystricomorpha

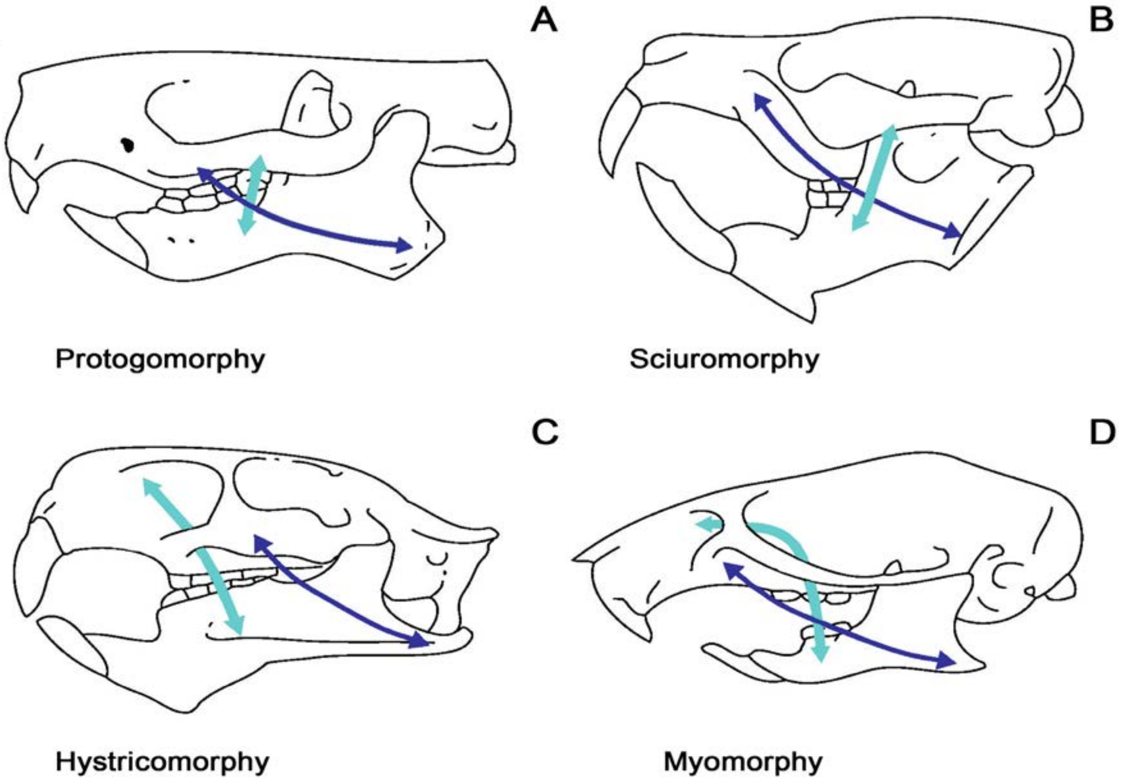


Figure 3.2: Zygomasseteric structure types. Light blue line indicates the medial masseter while dark blue line indicates the lateral masseter. A: Protogomorphy; B: Sciuromorphy; C: Hystricomorphy; D: Myomorphy. Modiefied from Hautier et al. 2008.

(= Hystricina), Sciuromorpha (squirrels and relatives) and Myomorpha (mouse-like rodents and relatives). Lagomorphs would be latter placed into their own order, but the three rodent groups introduced by Brandt (1855) were retained during the 20th century and ranked as suborders (as in the highly influential Simpson, 1945). Finally, Wood (1965) followed the Waterhouse-Brandt subdivision but concluded that these could not be used for subordinal classification of rodents and preferred distinguishing the variations in zygomasseteric structure as 'evolutionary grades'. He further introduced a fourth grade for the most primitive rodents, the protrogomorphous zygomasseteric structure. Later studies have confirmed Wood's conclusions and zygomasseteric structure is no longer used for subordinal classification of rodents (see chapter 3.2) as it is now known that some morphologies have evolved convergently in different lineages (see Swanson et al., 2019). Yet, zygomasseteric structure is basic to describe rodent cranial anatomy and as such is briefly introduced here.

PROTROGOMORPHY

Protrogomorphy (figure 2.3A) was first introduced by Wood (1965) and represents the ancestral morphological condition in rodents in which no part of the masseter originates from the rostrum and the infraorbital foramen is small. The superficial masseter originates from the lateral surface of the maxilla and inserts on the angular process of the mandible. The lateral masseter (also known as anterior deep masseter) originates from the zygomatic arch and inserts on the ventral side of the angular process of the mandible. The medial masseter (also known as posterior deep masseter or zygomaticomandibularis) is small and originates from the medial surface of the zygomatic arch. It inserts along the dorsal portion of the masseteric ridge of the mandible. The protrogomorphous condition is observed in many primitive rodents (ischyromyds, sciuravids, mylagaulids), in the oldest representatives of more derived families (sciurids, glirids) and in the aplodontids, which today are solely represented by the mountain beaver (*Aplodontia rufa*). African mole-rats (Bathyergidae) are considered secondarily protrogomorphous because their muscular arrangement is clearly derived from a hystricomorphous condition (Cox et al., 2020). Bathyergids are unique in combining a hystricognathous mandible and a protrogomorphous zygomasseteric arrangement.

SCIUROMORPHY

The sciuromorphous condition is present in squirrels, beavers and pocket gophers among others. In these rodents, the superficial masseter originates from the masseteric tubercle, which is located just ventral and lateral to the infraorbital foramen. The insertion area for the superficial masseter is situated on the angular process, at the posterior border of the mandible. The anterior and ventral part of the zygomatic arch is tilted and broadened forming the zygomatic plate. The lateral masseter originates from the zygomatic plate and the area of the rostrum immediately anterior to it. This muscle inserts on the lateral surface of the mandible. The medial masseter originates only from the ventral margin of the zygomatic arch and also inserts on the lateral side of the mandible (figure 3.2B).

HYSTRICOMORPHY

The hystricomorphous condition is present in the guinea pigs, agoutis, capybaras, jerboas and jumping mice among others. In addition, this muscular arrangement is also present in some old members of myomorph lineages, such as muroids (see below). In this group the medial masseter originates from the rostrum and runs through a hypertrophied infraorbital foramen and finally inserts on the lateral surface of the mandible. The infraorbital foramen is usually large an oval, very conspicuous in anterior view of the cranium. The superficial and lateral masseters originate from the ventrolateral border of the zygomatic arch and insert on the lateral surface of the mandible. The origin area for the superficial masseter is situated more anteriorly respect to the lateral masseter (figure 3.2C). In hystricognathous and hystricomorph rodents these two portions of the masseter (superficial and lateral) insert on the well-developed and laterally deflected angular process.

MYOMORPHY

Myomorphy characterizes muroids (mouse-like rodents) as well as all glirids but the genus *Graphiurus* (Afican dormouse), which is hystricomorphous (Hautier et al., 2008). The myomorphous zygomasseteric structure combines features of the hystricomorphous and sciuromorphous ones. The medial and the superficial masseter portions are mesially directed. The medial masseter originates from the side of the rostrum, usually from a shallow depression (figure 3.2D). As in hystricomorphs it then passes through a moderately enlarged, keyhole-shaped, infraorbital foramen until finally inserts on the lateral surface of the mandible. Same as in sciuromorphs, the superficial masseter originates from the masseteric tubercle and inserts on the angular process, while the lateral masseter originates from the zygomatic plate and also inserts on the lateral surface of the mandible. Myomorphy is thought to have evolved independently in muroids and glirids. Older muroids, such as *Pappocricetodon*, *Cricetops*, *Eucricetodon*, *Pseudocricetodon* or *Leidimys*, showed an hystricomorphous structure (Vianey-Liaud, 1985; Flynn, 1985). Myomorphy evolved from this condition as the lateral masseter expanded further anteriorly coinciding with the expansion of the zygomatic plate (Flynn, 1985). In advanced muroids the zygomatic plate is vertically tilted because the lateral masseter expands dorsally lateral to the infraorbital foramen. These further results in the constriction of the lower part of this foramen, which then takes the characteristic key-hole shape (Flynn, 1985). In glirids myomorphy apparently evolved directly from the protrogomorphous condition, without a hystricomorphous phase (Vianey-Liaud, 1985; Hautier et al., 2008).

The evolution of the different zygomasseteric arrangements from a primitive protrogomorphous condition reflects increased emphasis in propalinal jaw movements in rodents. The masseter muscles pull the jaw anteriorly and enable gnawing. Anterior expansion of the masseters increases exerted forces during incisor biting as well as during mastication (Turnbull, 1970; Druzinsky, 2010, Swanson et al., 2019). Recent work using computer-modelling techniques (Cox et al., 2012; Cox and Jeffery, 2015) has shown that the different zygomasseteric structures may enable rodents to be more efficient at different types of feeding. Few taxa have been analyzed, but preliminary conclusions show that sciuromorphy would generate efficient incisor biting; hystricomorphy efficient molar chewing and myomorphy will be well adapted to all feeding modes (Cox et al., 2012).

3.2 ORIGIN AND CLASSIFICATION OF RODENTS

3.2.1 THE GLIRES CONCEPT AND THE RELATIONSHIPS OF RODENTS WITH OTHER MAMMALIAN ORDERS

As we saw on chapter 3.1, rodents show several autapomorphic traits, particularly referred to dentition and the zygomasseteric structure. These allow recognizing rodents as a cohesive group. However, their position within the mammalian family tree has historically been discussed (for an extended review see Hautier and Cox, 2015). Lucket and Hartenberger (1985) identified the relationship of rodents to other eutherian mammals as a bone of contention. Thankfully, thanks to molecular phylogenetic studies, a consensus has now been achieved.

Rodents and lagomorphs have been recognized to be closely allied since the times of Linnaeus. Indeed, the Swedish naturalist already introduced the order Glires in the first edition of *Systema Naturae* (Linnaeus, 1735) to include rodents (*Sciurus*, *Castor*, *Hystrix*, *Mus*), lagomorphs (*Lepus*) and shrews (*Sorex*). The defining character of Glires would be "Dentes primores 2" [two main teeth] (Linnaeus, 1735). In later editions shrews were taken out of the Glires but eventually rhinoceroses were included (see Linnaeus, 1758). Later classifications removed rhinoceroses but made no distinctions between rodents and lagomorphs placing altogether in the Glires (Blumenbach, 1779) or 'Rongeurs' (Cuvier, 1798, 1800).

An important modification was introduced by Illiger (1811) who erected eight rodent groups, one of them being the "rabbit-like" group, that he named Duplicidentata because of the two pairs of incisors in the upper jaw. Much later the term Simplicidentata was introduced for all rodents with only one pair of upper incisors (i.e., true rodents; Lilljeborg, 1866). The name Rodentia was first used by the British traveler and naturalist Thomas Edward Bowdich, although this author also included lagomorphs and the primate aye-aye (*Daubentonia madagascarensis*) within rodents (Bowdich, 1821). On the other hand, studies of the zygomasseteric structure by Waterhouse (1839) complemented by Brandt (1855) (see chapter 3.1.3) proposed an arrangement of the Glires into four major groups: Lagomorpha (rabbits, hares and pikas), Hystricomorpha (porcupines and relatives), Sciuromorpha (squirrels and relatives) and Myomorpha (mouse-like rodents and relatives). Later on, Tullberg (1899) subdivided the rodents into two great groups according to mandible morphology (see chapter 3.1.1): Sciurognathi ('squirrel-mandible') and Hystricognathi ('porcupine mandible'). The Waterhouse-Brandt rodent subgroups would define lower-ranked divisions within these two large groups, the Sciurognathi including the Sciuromorpha and Myomorpha and the Hystricognathi including the Hystricomorpha as well as the newly-introduced Bathyergomorpha (comprising African mole-rats). Tullberg (1899) referred to rodents as Simplicidentata (following Lilljeborg, 1866) and considered them a suborder of the Glires, together with a second suborder, the Duplicidentata (lagomorphs). However, this author noted that duplicidentates showed enough distinct features to warrant the creation of a separate order. This was formally proposed by Gidley (1912) who erected the order Lagomorpha following the terminology of Brandt (1855). The remaining Glires would define the order Rodentia and the three groups introduced by Brandt (1855) were retained during the 20th century and generally ranked as suborders (e.g., Simpson, 1945). However, some classification systems combined the groups of Tullberg (1899) based on mandible shape with those of Brandt (1855). These generally regarded Sciurognatha and Hystricognatha as suborders, and divisions based on zygomasseteric structure (Sciuromorpha, Myomorpha, Hystricomorpha) as infraorders (e.g., Ellerman, 1940). Wood (1965) recognized protrogomorphy, an additional, more primitive zygomasseteric arrangement (see chapter 3.1.3), characteristic of many of the first rodents and today only present in the mountain beaver (*Aplodontia rufa*). Protrogomorphs were considered a suborder by Wood (1965) and variously as a suborder or infraorder within the Sciurognatha in later works (e.g., Chaline and Mein, 1979). Nevertheless, during the second half of the 20th century, most reviews of the classification of rodents noted that not all rodent families fitted well within the defined groups. For example, Simpson (1945) did not place the ctenodactyloids (which are sciurognathous and hystricomorphous) in any group, and Wood (1965) left several clades (Castoroidea, Theridomyoidea, Thryonomyoidea) out of the defined suborders. This difficulty of fitting all rodent families (extant and extinct) into the recognized sub- and infraorders let to some authors to further subdivide the group. To this regard Thaler (1966) proposed up to ten different suborders and Chaline and Mein (1979) eight. McKenna (1975) choose not to subdivide the order. Furthermore, McKenna (1975) denied the concept of Glires and found lagomorphs to be more related to macroscelids (African elephant shrews) than rodents. This was contested by following morphological studies based on skull, dentition and fetal membranes that concluded that Glires define a monophyletic group (Lucket, 1985; Novacek, 1985, 1986). Yet, in their monumental *Classification of Mammals Above the Species Level* McKenna and Bell (1997) did not use the term Glires and grouped rodents and lagomorphs together with macroscelids and a few primitive placentals (the extinct zalambdalestids, anagalids and pseudictopids) in the grandorder Anagalida. This hierarchical classification provided occurrences and ranges for all known genera, fossil and extant, and introduced a myriad of fine divisions which fall within classes and orders. For example, the order Rodentia was included within the mirorder Simplicidentata together with their closest extinct relatives, the Eurymylidae (see chapter 3.2.2). Similarly, the order Lagomorpha was part of the mirorder Duplicidentata with the Mimotonids.

By the late 20th century and particularly during the early years of the new millennium the advent of molecular phylogenetic methods triggered a radical reorganization of the mammalian (and rodent) family tree. Early application of these methods produced awkward results and found guinea pigs (*Cavia porcellus*) to be closer to primates than to other rodents (*Mus*, *Rattus*; Graur et al., 1991; D'Erchia et al., 1996). This questioned not only rodent monophyly but also the Glires concept. However, these results are now known to be derived from methodological issues, namely: very poor taxonomic sampling (just three rodents: *Cavia*, *Mus* and *Rattus*), the use of few molecular loci, and oversimplified phylogenetic models (Fabre et al., 2015). Later studies considering more representative samples of both taxa and genes confirmed both the monophyletic status of rodents and their close relationship with lagomorphs into the Glires clade (Huchon et al., 1999, 2002; Adkins et al., 2001; Montgelard et al., 2008; Blanga-Kanfi et al., 2009; Fabre et al., 2012, 2015). In addition, broader molecular studies comprising all mammal orders, have repeatedly placed Glires within the Euarchontoglires clade (generally ranked as superorder), which also include Scandentia (tree shrews), Primates and Dermoptera (colugos) (see Murphy et al., 2001; Springer et al., 2003).

3.2.2 ORIGIN OF RODENTS

Molecular studies have placed the divergence of Euarchontoglires from other placental mammals during the late Cretaceous (ca. 100-90 Ma; Murphy et al., 2001; Springer et al., 2003). According to some current estimates (e.g., Springer et al., 2003) glires themselves, would have diverged also during the Late Cretaceous as did somewhat later lagomorphs and even the major rodent suborders (see chapter 3.2.3). Other molecular-based estimates (e.g., Huchon et al., 2002) have pushed these estimates to younger ages, but still within the latest Cretaceous or close to the Cretaceous/Paleogene boundary. A similarly old divergence date is inferred for other placental mammal orders when considering molecular data, yet taxa that can be unambiguously attributed to these orders do not appear in the fossil record until much later, during the latest Paleocene (60-55 Ma), implying ghost lineages spanning almost 40 million years (for a review see Rose and Archibald, 2005). This marked and consistent lack of agreement has three potential different explanations (see Rose and Archibald, 2005): 1) the fossil record is incomplete; 2) the molecular clock is incorrect; 3) the Long Fuse hypothesis. The latter hypothesis is perhaps the more interesting because it considers that molecular estimates are correct and that the fossil record is complete enough to address this question. Therefore it agrees in placing the divergence of most placental orders within the Late Cretaceous and that fossils belonging to these orders actually exist, but these remain unrecognized because they lack the diagnostic traits of modern forms (Archibald and Deutschman, 2001). As far as Glires are concerned, zalambdalestids, a group of Asian eutherians that first appeared at 90-85 Ma, have been related to this group mostly because they present a gliriform lower incisor resembling those of rodents and lagomorphs (Archibald et al., 2001). However, this has been strongly contested by other authors who relate Glires to other archaic Paleocene placental groups (Meng, 2004; Meng and Wyss, 2005; Asher et al., 2005).

Basal Glires are known from the Paleocene of Asia and include several taxa of small herbivores characterized by their gliriform incisors and well-developed diastemata. Two main groups, generally ranked as orders (e.g., McKenna and Bell, 1997), can be distinguished: Mimotonida and Mixodontia. The former have been considered ancestral to lagomorphs because they show minute peg-like incisors (I3) behind the upper gliriform pair and similar cheek tooth morphology (Li and Ting, 1985; Meng, 2004; Asher et al., 2005). On the other hand, mixodonts appear to be closer (or ancestral to) rodents. These include the family Eurymylidae, that comprises the genera *Eurymylus*, *Rhombomylus* and *Heomys*, which are all known from nicely-preserved cranial and in some cases postcranial remains (Meng et al., 2003; Meng, 2004; Meng and Wyss, 2005). The eurymylid skull resembles that of rodents in: 1) showing a much larger upper than lower diastema; 2) having lost the I3; 3) lacking the second upper premolar (P2), which is retained in lagomorphs. Yet, eurymylids still show two lower premolars on the jaw (p3 and p4), that is one more than is primitive for rodents, and the upper third premolar (P3) is still relatively large and bicuspid, rather than reduced and conical as in rodents (Meng et al., 2003; Meng, 2004; Meng and Wyss, 2005). Furthermore, the postcranial skeleton of eurymylids is that of a generalized terrestrial mammal (Meng et al., 2003) whereas that of mimotonids already shows adaptations for running and leaping, as in extant lagomorphs (Asher et al., 2005).

The oldest known rodent is the ischyromyid (see chapter 3.2.3) *Acritoparamys atavus* from the latest Paleocene (early Clarkforkian, ca. 56 Ma) of Montana (USA; Korth, 1994; Janis et al., 2008). Some authors (e.g., Flynn, 2008) consider the family Anagalidae (including the genera *Alagomys* and *Tribosphenomys*) from the late Paleocene of Asia and North America to be the most primitive rodents, whereas others regard them as a sister group to all other rodents (Meng and Wyss, 2001; Meng et al., 2004; Dawson, 2015). Be that as it may, rodents subsequently radiated during the latest Paleocene and early Eocene in both North America and Asia, where several distinct families are recorded (Dawson, 2003). In Europe rodents are not recorded until somewhat later, by the earliest Eocene (MP7) in Portugal and southern France, being represented by several species of ischyromyids (Escarguel, 1999). European rodents may have dispersed from North America, since the Turgai Strait, a narrow epicontinental sea between Europe and Asia, represented an effective barrier during the Eocene (Escarguel, 1999; Dawson, 2003).

3.2.3 CLASSIFICATION OF RODENTS

Molecular phylogenies, based on mitochondrial and nuclear DNA sequences for extant rodents, have contributed to converge to a new rodent classification and led to the abandonment of the previous ones (figure 3.3). These studies propose subdivide the order Rodentia into three main monophyletic clades (for updated reviews see Fabre et al., 2015; D'Elía et al., 2019; Flynn et al. 2019 and references therein):

SQUIRREL-RELATED CLADE

This group includes the families Sciuridae (squirrels), Gliridae (dormice)

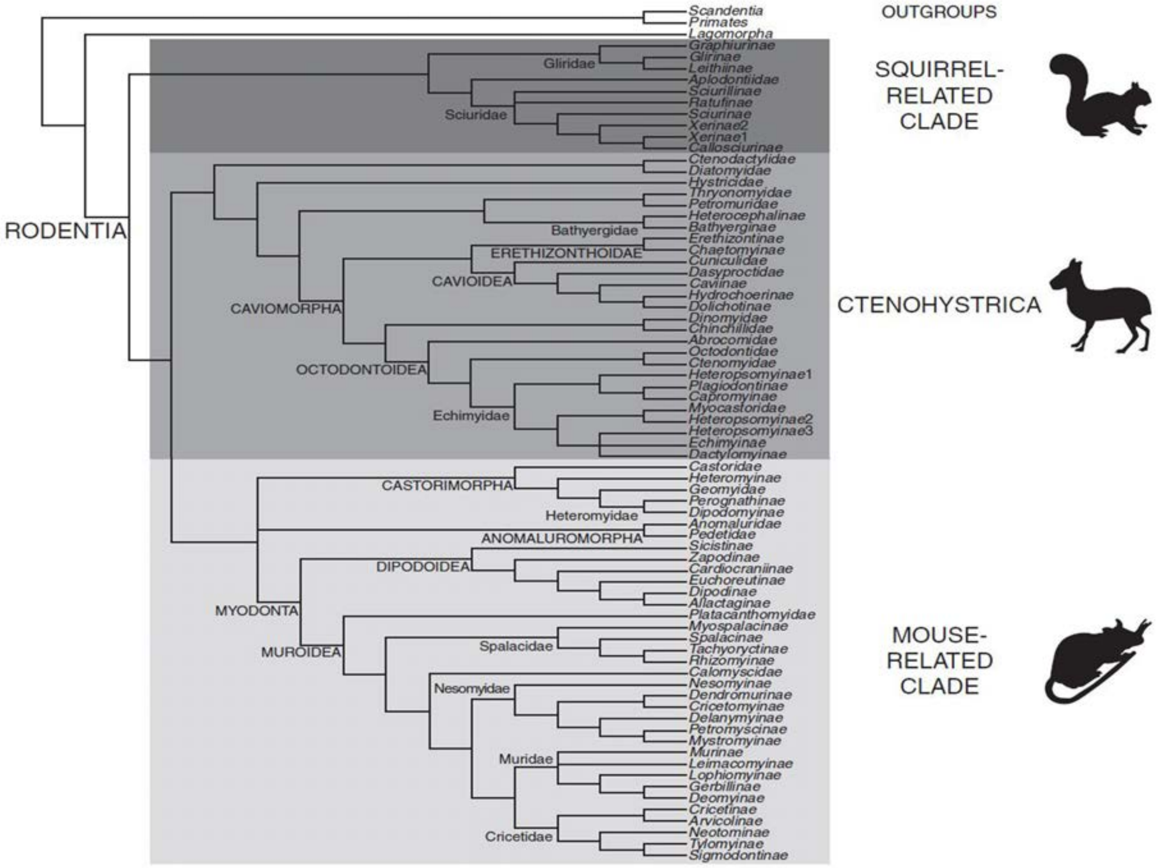


Figure 3.3: Current molecular phylogeny of rodents to the subfamily level after Fabre et al. 2015.

and Aplodontidae (mountain beaver) and is the first great clade to have diverged. They are in many ways the most primitive and conservative rodents. The oldest representatives of the extant families date back to the middle (the aplodontid *Spurimus* and the glirid *Eogliravus*) and late Eocene (the sciurids *Douglassciurus* and *Hesperopetes*). Extinct archaic groups such as the Ischyromyidae and Mylagaulidae and Theridomyidae are often regarded as members of this clade (Janis et al., 2008; Asher et al., 2019). Recent analyses have concluded that the Ischyromyidae, which include the oldest rodents dating back to the late Paleocene (see chapter 3.2.2), would be closely related to aplodontids + sciurids (Asher et al., 2019). All these archaic groups, the aplodontids and the earliest representatives of sciurids (Emry & Thorington, 1982) and glirids (Vianey-Liaud, 1985) are protrogomorphous. Later and extant sciurids are sciuromorphous while glirids are either hystricomorphous (*Graphiurus*) or myomorphous. As far as mandible morphology is concerned, all the members of this clade are sciurognathous. Molecular studies have found a close relationship between sciurids and aplodontids (Mercer and Roth, 2003; Steppan et al., 2004a; Montgelard et al., 2008; Blanga-Kanfi et al., 2009; Fabre et al., 2012). Furthermore, molecular systematics of sciurids (Mercer and Roth, 2003; Steppan et al., 2004a) and glirids (Montgelard et al., 2003) have contributed to clarify intra-familial relationships. Time-calibrated phylogenetic analyses have shown that the dispersal and radiation of the different squirrel subfamilies and tribes coincided with major tectonic, sea-level or paleoclimatic events (Mercer and Roth, 2003). The squirrel-related clade is generally regarded as a suborder that retains the old name Sciuromorpha (Wilson and Reeder, 2005; D'Elía et al., 2019). However, Flynn et al., (2019), suggested a new name for this clade, the suborder Eusciurida, which is a crown group including all living Sciuridae, Aplodontiidae, and Gliridae.

Guinea-pig-related clade

This is a very diverse clade comprising up to 17 distinct families characterized by their hystricomorphous zygomasseteric structure. The guinea-pig-related clade is considered a suborder, generally retaining the old name Hystricomorpha (Wilson and Reeder, 2005; Fabre et al., 2015; D'Elía et al., 2019) although the term Ctenohystrica has also been used to reflect inclusion of Ctenodactyloidea in this suborder (see Huchon et al., 2002). Molecular phylogenetic results allow recognizing two main groups which are often regarded as infraorders (Wilson and Reeder, 2005; Fabre et al., 2015; D'Elía et al., 2019): Ctenodactylopmorphi and Hystricognathi. The ctenodactylomorphs would solely include the extant Ctenodactylidae (gundis) and Diatomyidae (Laotian rock rat plus several extinct forms). These are sciurognathous and hystricomorph rodents of Asian origin. Ctenodactyloids are one of the oldest rodent groups, first appearing in the earliest Eocene and quickly becoming the dominant rodents in the Paleogene faunas of Asia (Dawson, 2003). Basal forms, such as *Cocomys*, are protrogomorphous (Li et al., 1989). The Hystricognathi are all hystricognathous and hystricomorphous (except for the extant African mole-rats which are secondarily protrogomorphous; see Cox et al., 2020). This group has representatives both in the Old and New World. Old world forms include Hystricidae (porcupines), Bathyergidae (African mole-rats), Phyomyidae (cane-rats) and Petromuridae (dassie-rats) which are now mostly restricted to Africa, while the New World forms comprise the diverse radiation (10 extant families) of caviomorph rodents. Some authors (e.g., Wilson and Reeder, 2005; Fabre et al., 2015) include the New World groups in the parvorder Caviomorpha, while others (e.g., Blanga-Kanfi et al., 2009) regard the Old World ones to the Phiomorpha. The origin of caviomorphs had been a hotly debated topic with authors advocating for an evolution from North American reithroparamyines (Wood, 1974) and others showing affinities with African hystricognaths and favoring a scenario of arrival by rafting across the Atlantic (Hoffstetter, 1972). Molecular phylogenetics have effectively solved this long-standing controversy clearly grouping together caviomorphs with African histricognaths Huchon et al., 2002; Adkins et al., 2001; Montgelard et al., 2008; Blanga-Kanfi et al., 2009; Fabre et al., 2012, 2015). The oldest caviomorphs (*Cachiyacuy*, *Canaanimys*) date from the middle Eocene from Peruvian Amazonia (Antoine et al., 2012), therefore being slightly older, although clearly more derived, than the oldest phiomorphs which come from the late Eocene of northern Africa (*Protophiomys*, *Gaudeamus*). Caviomorphs would have diverged from phiomorphs during the early to middle Eocene (Poux et al., 2006).

MOUSE-RELATED CLADE

Mouse-related rodents include more than one thousand extant species, thus comprising one quarter of all mammal diversity. These are all sciurognathous rodents and may include sciuromorph, hystricomorph and myomorph forms. This clade is divided into three groups alternatively designated as suborders or infraorders (Wilson and Reeder, 2005; Fabre et al., 2015; D'Elía et al., 2019). The first one, the Castorimorpha, includes three families of American origin, Castoridae (beavers), Geomyidae (pocket gophers) and Heteromyidae (jumping mice), which are all sciuromorphous. The extinct families Eomyidae and Eutypomyidae would also be part of this suborder, the latter being the sister group of the Castoridae (Janis et al., 2008). On the other hand, several studies have shown that the extinct Eomyidae are close relatives of Geomyidae and Heteromyidae (Wahlert, 1978; Fahlbusch, 1985). The Anomaluromorpha includes two exclusively African families: Anomaluridae (scaly-tailed flying squirrels) and Pedetidae (springhares). The second group, the Anomaluromorpha, includes less than 10 species of saltatorial (pedetids) and arboreal or gliding (anomalurids) rodents that share a hystricomorphous zygomasseteric structure. The last suborder is the Myomorpha (sometimes referred to as Myodonta) and comprises two superfamilies: Dipodoidea and Muroidea. The dipodoids include just a single family, the Dipodidae (jerboas and jumping mice), while muroids include up to six extant families plus several extinct ones (see chapter 3.3.1). Muroids are the most diverse mammals and consist of the Platacanthomyidae (spyny dormice), Spalacidae (blind mole-rats and bamboo rats), Nesomyidae (Malgasy rats and mice and African climbing mice), Calomyscidae (mouse-like hamster), Cricetidae (hamsters, New World rats and mice, voles) and Muridae (Old World rats and mice plus gerbils). Dipodoidea are hystricomorphous and extant Muroidea are myomorphous, but older forms are known to have been hystricomorphous (Vianey-Liaud, 1985; Flynn, 1985).

D'Elía et al. (2019) noted that no formal name had been proposed for the mouse-related clade, and introduced the suborder Supramyomorpha, regarding Castorimorpha, Anomaluromorpha and Myomorpha as infraorders. However, other classifications upgrade the latter to subordinal status (Wilson and Reeder, 2005), which would imply that the order Rodentia would include five suborders. The relationships between the three main clades of the mouse related-clade group remain unsolved (Fabre et al. 2012, 2015).

The oldest Myomorpha is *Erlianomys combinatus* from the earliest Eocene of China (Li and Meng, 2010), which is not referable to any of the two superfamilies of this group (Dipodoidea or Muroidea). Castorimorphs are first recorded by the end of the early Eocene in North America, being represented by the extinct eutypomyids (Korth, 1994; Flynn and Jacobs, 2008). Other families within the Castorimorpha are first recorded throughout the Eocene. Finally, the oldest Anomaluromorpha are surprisingly not recorded from Africa but Asia, from the latest middle Eocene of Myanmar (*Pondaungimys*; Dawson et al., 2003). This rodent group dispersed into Africa during the later Eocene, its first record there coinciding with that of anthropoid primates (Coster et al., 2015). Phylogenetic relationships within these major clades have been particularly studied for the Myomorpha, mostly focusing on the Muroidea, the most speciose mammals (e.g., Michaux et al., 2001; Jansa and Weksler, 2004; Steppan et al., 2004b; Schenk et al., 2013; Steppan and Schenk, 2017). These analyses consistently recognize dipodoids as an outgroup to muroids. Within muroids, platacanthomyids and spalacids are found to be basal to other muroids, which Steppan et al. (2004b) grouped in the unranked clade Eumuroida. This far larger clade includes the nesomyids, cricetids, murids and calomyscids, which solely include the mouse-like hamster. Most analysis find murids and cricetids to be more closely related to each other than they are to nesomyids. The relationships of extinct muroid groups are unclear and need to be reviewed in detail, however older groups are usually placed within the family Cricetidae, which then becomes clearly paraphyletic (see chapter 3.3.1).

3.3 THE CRICETIDAE

3.3.1 ORIGIN AND EARLY RADIATION OF THE CRICETIDAE

Oldest myomorphs (*Erlianomys*; see chapter 3.2.3) date back to the early Eocene of Asia and are not referable to any of the extant superfamilies (Dipodoidea or Muroidea). Dipodoids differ from extant muroids in showing an hystricomorphous zygomasseteric structure coupled with the presence of an upper fourth premolar (P4) and even a third one (P3) in the oldest forms (Korth, 1994). The presence of a P4 implies that the first upper molar (M1) has a square outline and lacks an anterocone (see chapter 3.3.3). Muroids have lost the P4 and present elongated first molars (both upper and lower) with distinct anterocones/ids. However, the oldest muroids, dating back to the middle Eocene of Asia still retain some of these plesiomorphic features. These basal muroids are known from isolated cheek teeth and mandible and maxillary fragments from southern China and Kazakhstan belonging to the genera *Palasiomys* and the better-known *Pappocricetodon*. Their molars are longer than wide and the M1 presents a clear anterocone and a well-defined anterior lobe. Maxillary fragments of early species of *Pappocricetodon* from China reveal that it retained a hystricomorphous zygomasseteric structure as well as a minute, peg-like P4 (or dP4), and M1 and M2 of subequal size (Wang and Dawson, 1994). These features resemble the condition of dipodoids, however the morfology of the infraorbital foramen is clearly distinct in *Pappocricetodon*. In dipodoids there is a neurovascular canal ventromedial to the infraorbital foramen clearly separated from it by means of a bony septum. In contrast, such bony septum isolating the neurovascular canal is absent in all muroids, even if they show a primitive hystricomorphous structure such as *Pappocricetodon* (Wang and Dawson, 1994).

A remarkable radiation of early muroids occurred in Asia during the late Eocene and early Oligocene (Wang and Dawson, 1994; Lindsay, 1994; Dawson, 2003; Maridet and Ni, 2013), comprising many different genera: *Aralocricetodon*, *Cricetops*, *Edirnella*, *Eocricetodon*, *Eucricetodon*, *Meteamys*, *Pappocricetodon*, *Paracricetops*, *Raricricetodon*, *Selenomys*, *Witenia* etc. These are primitive muroids characterized by a hystricomorphous zygomasseteric structure, but already showing elongated first molars with a well defined anterocone/id region (Flynn, 1985; Wang and Dawson, 2004). Muroids expanded their range during the late Eocene, when they are first recorded in eastern Europe and North America. Oldest European muroids date back to the late Eocene of Serbia (Zvonce, Bustranje) and include *Witenia*, a genus of Asian affinities, and the closely-related endemic *Bustrania* (De Bruijn et al., 2019). Both taxa represent very primitive muroid groups, related to the earliest muroids, such as *Pappocricetodon* (De Bruijn et al., 2019). *Edirnella*, a taxon also known from Turkey and the Caucasus and probably related to *Melissiodon* (Ünay-Bayraktar, 1989), and the closely-related endemic *Mogilia* are also present in late Eocene Serbian assemblages (Wessels et al., 2018). Later on, post '*Grande Coupure*' Oligocene European faunas already include several muroid genera, such as *Eucricetodon*, *Pseudocricetodon*, *Heterocricetodon*, *Paracricetodon* and *Melissiodon* (see Dawson, 2003). All these genera share the plesiomorphic hystricomorphous zygomasseteric structure, although incomplete myomorphy has been documented in *Eucricetodon* and *Pseudocricetodon*, and one lineage of *Eucricetodon* (*E. atavus* to *E. collatum*) evolved towards a fully myomorphous condition (Vianey-Liaud, 1974, 1985). On the contrary, the earliest North American muroids are represented by the well-known late Eocene (Chadronian) genus *Eumys*, which already presented a myomorphous zygomasseteric structure (Wood, 1937; Flynn, 1985; Korth, 1994; Lindsay, 2008). *Eumys* is the oldest-known myomorph muroid, predating earliest myomorph *Eucricetodon* by more than 10 million years. This clearly indicates that myomorphy evolved at least two times in parallel in muroids (Vianey-Liaud, 1974, 1985; Flynn, 1985).

While most paleontologists tend to refer to ancient muroids as 'cricetids' (and therefore place the origin of the family in the middle Eocene), current molecular phylogenies restrict the content of the family to encompass just hamsters (Cricetinae), voles (Arvicolinae) and New World rats and mice (Sigmodontinae, Neotominae, Tylominae; see chapter 3.3.2). These extant groups all share an advanced myomorphous zygomasseteric configuration coupled with a cricetid molar pattern (see chapter 3.3.3). Additional features include unornamented incisor enamel and medium- to small-sized third molars, which distinguish them from some extinct genera such as *Eumys* (Lindsay, 2008). If such restricted definition of the Cricetidae is to be adopted, the earliest members that can be ascribed to this group are the late Oligocene Asian genera *Spanocricetodon* and *Primus*, which are closely related to later, early Miocene, genera such as *Democricetodon* (Theocharopoulos, 2000). These late Oligocene and Miocene taxa are known from both Eurasia and North America (*Copemys*) and currently included within the subfamily Copemyinae (referred to as Democricetodontinae by some authors; see chapters 3.3.2 and 3.3.4). However, here the broader view of the Cricetidae favored by most paleontologists is used (see discussion in chapter 3.3.2) which allows for the inclusion of other extinct groups such as melissiodontines or megacricetodontines.

3.3.2 CLASSIFICATION OF THE CRICETIDAE

With more than 600 species (Pardiñas et al. 2017) the Cricetidae is one of the more diverse rodent families and one of the major groups within the superfamily Muroidea (Michaux et al., 2001; Steppan et al., 2004b; Jansa and Weksler, 2004; Schenk et al., 2013; Steppan and Schenk, 2017). The position of cricetids within muroid rodents has been profusely debated, even though they have been generally viewed as ancestral to murids. Miller and Gidley (1918) were the first to attempt a classification of muroids by sorting them into various distinct families, based on the morphology of the infraorbital foramen and cheek teeth pattern. These authors distinguished the Muridae from the Cricetidae based on the presence of an additional row of cusps on the upper molars (see chapter 3.3.3) The Cricetidae of Miller and Gidley (1918) included several subfamilies: Cricetinae (including sigmodontines and nesomyids), Microtinae, Gerbillinae and Lophiomyinae (the latter two currently included within the Muridae, see below). However, this classification of the muroids was basically a cricetid/murid dichotomy to the exclusion of fossorial forms (Spalacidae, Rhizomyidae) and spiny dormice (Plathacantomyidae). Such divisions were featured with little modifications in the influential classification of mammals by Simpson (1945). The groundbreaking attempt by Chaline et al. (1977) incorporated a paleontological perspective and included most fossil groups (such as cricetodontines, melissiodontines or anomalomyines) as subfamilies within the Cricetidae. Although many of their ancestor-descendant relationships are now disputed, this is the first strong case that deviates from the traditional widely adopted cricetid/murid dichotomy by placing African mice and rats (Nesomyidae), voles (Arvicolidae) or giant poached rats (Cricetomyidae) into families of their own. Most paleontologists have favored this classification or muroids and generally distinguished cricetids from murids (e.g., Flynn, 1985; Hartenberger 1998; Casanovas-Vilar, 2007). However, McKenna and Bell's (1997) classification of mammals divided the Muroidea into just two families: Simimyidae and Muridae. The former just include the genera *Simimys* and *Nonomys* from the late Eocene (Chadronian) of North America, which might be ancestral to all other muroids or should be better regarded an aberrant side branch to dipodoids (Emry, 1981; Korth, 1994). The Muridae would include all the families recognized by previous authors but downgraded to the subfamily rank. The subfamily Cricetinae was meant to include just hamsters, leaving New World rats and mice, voles and others (including many extinct groups) into separate subfamilies. This avoided making the Cricetidae a paraphyletic group, at the cost of including one third of all mammals within just one family. However, this classification attempt was generally not followed and the family name Cricetidae continued to be used, although sometimes noting that it was almost certainly a paraphyletic group (e.g., Casanovas-Vilar, 2007: 54).

Soon, molecular studies shook the muroid family tree. These recognized different groups within the Muroidea that debunked the old cricetid notion (Michaux et al., 2001; Steppan et al., 2004b; Schenk et al., 2013; Fabre et al. 2012, 2015; Steppan and Schenk, 2017). The Cricetidae would just include the following extant subfamilies: the Holarctic Arvicolinae (voles and lemmings); the Palearctic Cricetinae (hamsters); the North American Neotominae (woodrats and harvest mice); the central South American Sigmodontinae (rice rats) and the Tylomyinae (climbing rats) from North and Central America. Voles and hamsters would be closely related and sister group to the three New World subfamilies (Neotominae, Sigmodontinae, Tylomyinae). Groups traditionally included within the Cricetidae, such as the Nesomyinae, Lophiomyinae or Myospalacinae, were removed. Within muroids, platacanthomyids and spalacids are found to be basal to other muroids, which Steppan et al. (2004b) grouped in the unranked clade Eumuroida. This far larger clade comprises the nesomyids, cricetids, murids and calomyscids, which solely include the mouse-like hamster. Most analyses conclude that murids (which would include the Gerbillinae and Murinae) are more closely related to cricetids than to the African Nesomyids, while the Calomyscidae would be basal to all other eumuroids (Michaux et al., 2001; Steppan et al., 2004b; Schenk et al., 2013; Fabre et al. 2012, 2015; Steppan and Schenk, 2017). The cricetid molar pattern (see chapter 3.3.3) was found to be the primitive condition in muroid rodents and has been retained in various extant families which are only distantly related (Jansa and Weksler, 2004). The advanced muroids, or Eumuroida, are characterized by their V-shaped infraorbital foramen which extends to the roof of the palate and well-developed zygomatic plate (Norris et al., 2004). In more basal muroids, such as spalacids and platacanthomyids, the infraorbital foramen is more rounded and the zygomatic plate narrower and more horizontal (Miller and Gidley, 1918; Norris et al., 2004). On the other hand, *Calomyscus*, the most basal eumuroid, presents a V-shaped infraorbital foramen coupled with a relatively narrow zygomatic plate (Ellerman, 1940: 404). The cricetid molar pattern would be the plesiomorphic condition for eumuroids.

Regarding the extinct groups, many paleontologists still refer the ancient forms to the Cricetidae, but their phylogenetic relationships are unclear and some may be as closely related to cricetids as they are to other muroid families. Therefore, including certain fossil forms, especially ancient groups such as the eucricetodontines or cricetopines, automatically results in a paraphyletic Cricetidae. Within this broad concept of cricetids Oligocene and Miocene forms are frequently ranked as subfamilies (Paracricetodontinae, Cricetodontinae, etc.). However, it seems clear that the older Oligocene forms, such as Eucricetodontinae (*Eucricetodon*, *Leidimys*) or Cricetopinae (*Cricetops*, *Melissiodon*), which show a hystricomorphous or transitional myomorphous zygomasseteric structure (Flynn, 1985; Korth, 1994; Lindsay, 2008) are almost certainly better regarded as basal muroids, as they share this primitive zygomasseteric structure with dipodoids. These ancient groups do not appear to be closer to cricetids (sensu stricto) as they are to other muroid groups such as spalacids or platacanthomyids, for example. The more derived Miocene forms are often included within the subfamily Cricetodontinae, the various groups ranked as tribes (Eumyini, Cricetodontini, Megacricetodontini; e.g., Mein and Freudenthal, 1971a; Chaline et al., 1977; McKenna and Bell, 1997;

Lindsay, 2008). These are more advanced muroids with a myomorphous zygoma and brachyodont to mesodont dentition (Flynn, 1985; Korth, 1994; Lindsay, 2008). However, these are not a uniform group and have been variously related to extant groups of muroids. For example, some specialists trace the origin of American cricetids (Sigmodontinae, Neotominae, Tylomyinae) back to the genus *Copemys* (Jacobs and Lindsay, 1984; Korth, 1994; Linday, 2008), which is first recorded by the early Miocene (about 19 Ma, see Lindsay 2008). Most authors include this genus within the tribe Copemyini together with other extinct forms, such as *Democricetodon* from Eurasia (see chapter 3.3.4), as well as some extant forms such as *Peromyscus* (which molecular phylogenies include within the Neotominae, e.g., Steppan and Schenk, 2017). Indeed, some authors exclude the Copemyini from Cricetodontinae and rank them as a subfamily closely related to extant Cricetidae (sensu stricto) (i.e., as recognized in molecular phylogenies), particularly allied to American forms. On the other hand, the genus *Megacricetodon* (see chapter 3.3.4), which has been customarily included within the Cricetodontinae (e.g., Mein and Freudenthal, 1971a; Chaline et al., 1977; McKenna and Bell, 1997), is generally considered to be closer to the Muridae (Jacobs, 1977; Flynn, 1985; Lindsay, 1988; Jacobs and Downs, 1994). This would make the Cricetodontinae a paraphyletic group as well. The relationships of other widespread cricetodotines, such as *Cricetodon*, are even less clear. Finally, it is worth remarking that molecular phylogenies consistently recover the mouse-tailed hamster, *Calomyscus*, as an outgroup to all other eumuroids (Michaux et al., 2001; Steppan et al., 2004b; Schenk et al., 2013; Fabre et al. 2012, 2015; Steppan and Schenk, 2017), so Michaux et al. (2004) suggested that this might be closely related to cricetodontines, if not their last surviving member. As had been exposed earlier, some primitive characters of the skull may justify this conclusion. Whatsoever it may be, all these questions will remain unsolved until an ambitious phylogenetic study of muroids combining morphological and molecular data and including fossil species is undertaken.

In this work, the broader concept of the family Cricetidae favored by most paleontologists rather than the restricted definition revealed by molecular studies will be followed. The extinct groups will be regarded as subfamilies and tribes within the Cricetidae.

3.3.3 Dentition: The cricetid plan

Most cricetid fossil remains are isolated cheek teeth and some maxillary and mandibular fragments with teeth still attached. The cricetid postcranial material is scarce and consequently relatively unknown. Therefore, generic and species determination is mainly based on cheek tooth morphology.

Cricetids, same as all muroids, are characterized by the following dental formula 1003/1003. However, some primitive muroids (i.e. cricetids sensu lato) presented a P4 (see chapter 3.3.1) while a few have lost their last molars, such as the Australian water rat (*Hydromys chrysogaster*, family Muridae). The primitive cricetid tooth morphology is also known as “the cricetid plan” (Schaub, 1925) and can be defined as consisting of four main cusps,

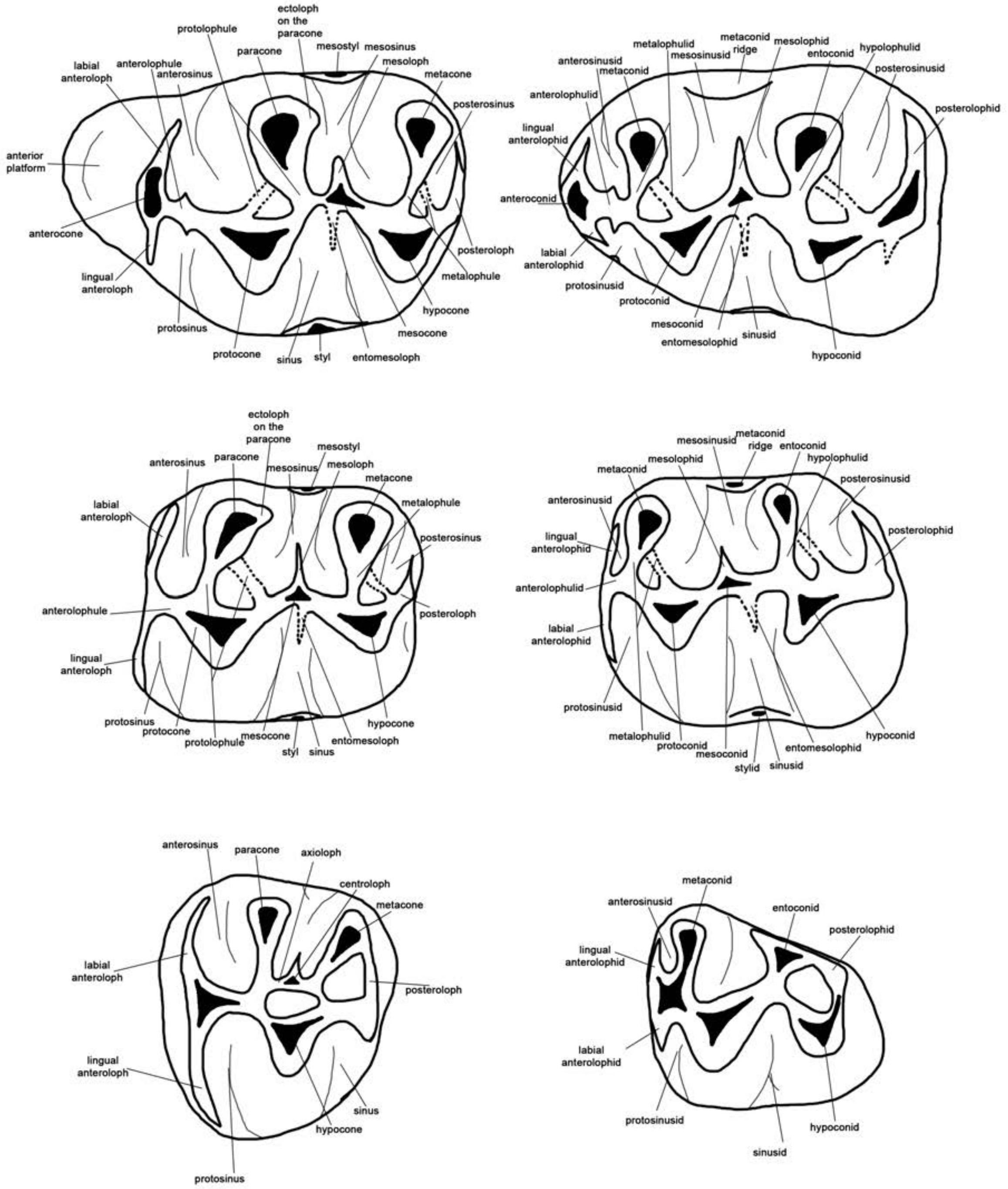


Figure 3.4: Anatomical terminology for cricetid molars. Modified from Freudenthal and Daams, 1988; Daams and Freudenthal, 1988 and Maridet, 2003.

two labial and two lingual, joined by narrow transverse lophs (-ids). The main cusps are the paracone, protocone, hypocone and metacone in the upper molars and the protoconid, metaconid, hypoconid and entoconid in the lower ones. In addition the protocone (-id) is connected to the hypocone (-id) by means of a longitudinal ridge (figure 3.4). The first upper molar (M1) is elongated because of the presence of an additional anterior cusp, the anterocone, which is placed labially. Similarly, the lower first molar (m1) is also elongated because of the presence of an additional cusp, the anteroconid, which is placed more or less centrally. The anterior part of the m1 is narrower than the anterior part of the M1. There might be additional transverse ridges with variable development, such as the anteroloph (-id), mesoloph (-id) and posteroloph (-id), although some primitive cricetids show even more transverse ridges. Finally, the connections between labial and lingual cusps may either consist of a single loph (-id) or be double. As already said first molars (M1/m1) are elongated and are also the largest cheek teeth. Second molars (M2/m2) have a square shape, and third molars (M3/m3) are the smallest showing an important reduction of their posterior margin. The M3 is generally button shaped, whereas the m3 is less reduced and has a triangular outline (figure 3.4).

Primitively, upper molars present three roots: a flattened lingual root and two cylindrical labial ones. The lower molars just present two roots, mesial and distal, which might be cylindrical or mesiodistally flattened. Later forms may present additional roots or on the contrary lose them entirely, as in derived arvicolines (voles and lemmings) which show unrooted ever-growing molars.

The cricetid plan appears in all muroid groups and it represents the plesiomorphic condition for Eumuroidea (Jansa and Weksler, 2004; Lazzari et al., 2008) as already suggested by previous studies (Miller and Gidley, 1918; Simpson, 1945; Petter, 1966; Flynn, 1985). The dental variation and evolution of the basic cricetid plan concerns the relative size of the molars, the shape of the cusps and the addition or reduction of ridges. Some families among the muroids have evolved highly modified variations of the cricetid plan as a response to food requirements and the environment. However, the groups studied in the present work, as well as most Miocene muroids, show a clear cricetid plan with only little variations.

3.3.4 EARLY MIOCENE CRICETIDS OF WESTERN EUROPE

Cricetids were major components of the European rodent faunas since the early Oligocene (see chapter 3.3.1), the genera *Eucricetodon*, *Pseudocricetodon* and *Melissiodon* being widespread and common. Most European rodent families and lineages, except for the diverse theridomyids, made it through the Oligocene/Miocene transition without important losses (for an overview see Dawson, 2003 or Maridet et al., 2013). The earliest Miocene rodent faunas were dominated by a diverse assemblage of glirids (*Bransatoglis*, *Glirudinus*, *Microdyromys*, *Miodyromys*, *Peridyromys*, *Pseudodryomys*, *Vasseuromys*; see Daams, 1999) and eomyids (*Apeomys*, *Eomyodon*, *Pseudotheridomys*, *Rhodanomys*, *Ritteneria*; see Engesser, 1999). Semiaquatic castorids (*Steneofiber*) persist from late Oligocene times as well as terrestrial (*Heteroxerus*, *Palaeosciurus*) and arboreal/gliding (*Blackia*) sciurids. Cricetids are still represented in the earliest Miocene (Agenian, MN1-MN2) faunas by the genera *Eucricetodon*, *Pseudocricetodon* and *Melissiodon*. These are all primitive cricetids which showed complex molar patterns, ornamented incisor enamel and primitive hystricomorphous zygomasseteric structure (except for some *Eucricetodon* species, see chapter 3.3.1). However, both *Eucricetodon* and *Pseudocricetodon* disappeared around 20 Ma (see Larrasoaña et al., 2006), well before the first appearance of more derived cricetid genera (*Democricetodon*) in Western Europe by the latest Ramblian (late MN3; Van der Meulen et al., 2003, 2012). This time lapse without cricetids is known as the "Cricetid vacuum" (Daams and Freudenthal, 1989). Just the genus *Melissiodon* is scarcely recorded during this time. Derived cricetid groups, initially represented by the genera *Democricetodon* and *Megacricetodon* dispersed into Europe between 17 and 16 Ma and from then on characterized the latest early Miocene and middle Miocene rodent faunas. These were joined by the genus *Eumyarion*, related to Oligocene cricetids such as *Eucricetodon* (see below), and by *Melissiodon*, which would still persist until the early/middle Miocene boundary.

As we will see in later parts of this work, the early Miocene cricetid faunas of the Vallès-Penedès Basin are much more diverse than previously thought. At the genus level these include taxa related to Oligocene forms, *Melissiodon* and *Eumyarion*, as well as the more derived Miocene cricetids *Megacricetodon* and *Democricetodon*, which have traditionally been placed within the subfamily Cricetodontinae (see chapter 3.3.1). A classification of these genera is provided below (see chapters 3.3.1 and 3.3.2).

Family Cricetidae Fischer [de Waldheim],
1817
Subfamily Cricetopinae Matthew and
Granger, 1923
Tribe Melissiodontini Schaub, 1925
Genus *Melissiodon* Schaub, 1920

Melissiodon is one of the most peculiar cricetid genera. This genus is restricted to Europe and its long stratigraphic range expands from early Oligocene (MP23; Dawson, 2003) to the very end of the early Miocene (MN4; Mödden, 1999). Because of its unique morphology, *Melissiodon* was initially included in a monotypic family or subfamily, the Melissiodontinae (Shaub, 1925; Mein and Freudenthal, 1971a; Mödden, 1999). *Melissiodon* presents several plesiomorphic characters, such as a hystricomorphous zygomasseteric structure with a broadly open infraorbital foramen and almost horizontal anterior root of the zygoma (Schaub, 1933; Vianey-Liaud, 1974). The third molars, especially the lower ones are relatively elongated as in primitive cricetids such as *Pseudocricetodon* and *Eucricetodon*.

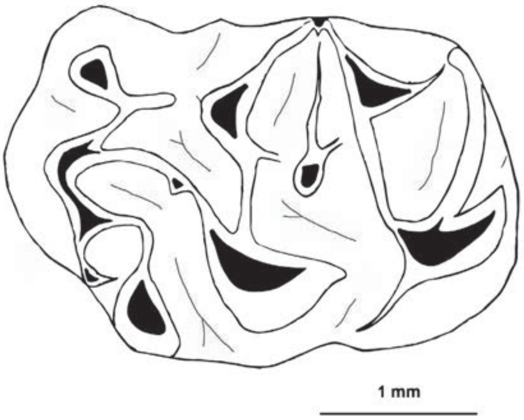


Figure 3.5: Schematic drawing of an M1 of the genus *Melissiodon*.

Melissiodon owes its name to the strange check teeth morphology that resembles a honeycomb with many pits surrounded by thin and high ridges (figure 3.5). Its mandible is also unusual for a cricetid in being particularly elongated and with a low corpus plus a long and laterally deviated diastema and incisor. Furthermore, the masseteric scar does not form the usual triangular ridges on the labial side of the mandible and is posteriorly situated (Schaub, 1933; Vianey-Liaud, 1974). The lower incisors are relatively small and show an unornamented incisor enamel. The unique dental morphology together with a peculiar mandible shape suggests a different diet and lifestyle from that of contemporaneous cricetids. Some authors have suggested that it may have been frugivorous (Mein and Freudenthal, 1981) while others regard it as insectivorous (Van Dam, 2006; Hordijk et al., 2015; Van Dam and Utescher, 2016).

For a long time *Melissiodon* was the only member of the subfamily Melissidontinae Schaub, 1925, but more recent findings and phylogenetic studies have greatly changed this picture. First, Ünay-Bayraktar (1989) added a second genus to the subfamily, *Edirnella* from the mid Oligocene (MP25) of the Turkish Thrace. *Edirnella* is characterized by its large size and is assigned to the Melissiodontinae because of the presence of a well-developed antero-lingual cusp on the M1, which she referred to as *Melissiodon* cusp (Ünay-Bayraktar, 1989: 33-34; “cingulumhügel” [cingulum hill] in Hrubesch, 1957) although in this work is called protostyl in agreement with the general terminology for cricetid molars by Mein and Freudenthal (1971b) and Freudenthal et al. (1994). Other features in common with *Melissiodon* are the relatively slender pointed pyramidal cusps, but *Edirnella* differs in showing a far less complex molar pattern with better defined cusps resembling that of *Paracricetodon* (Ünay-Bayraktar, 1989). More recently *Edirnella* has been recovered from the late Eocene of the Lesser Caucasus in the Turkish northeast (De Bruijn et al., 2003) and Serbia (Wessels et al., 2018). Late Eocene to early Oligocene deposits in Serbia record the oldest European muroids (see chapter 3.3.1) and include several archaic families (De Bruijn et al., 2019) plus a remarkable diversity of melissidontines that includes various species belonging to a new genus, *Mogilia*, as well as cf. *Edirnella* (Wessels et al., 2018). The molar morphology, consisting of multiple ridges, is more complex in *Mogilia* than in *Edirnella*, thus approaching the condition of *Melissiodon*. However, in *Mogilia* the ridges are lower and the morphology of the anterior region of the first molars is clearly different than in *Melissiodon* (Wessels et al., 2018). A recent phylogenetic analysis by Maridet and Ni (2013) has questioned this phylogenetic hypothesis and proposed that *Melissiodon* is related to Oligocene and early Miocene cricetids from Asia and Anatolia and should be included in the family Cricetopinae (which would then become a senior synonym of Melissiodontinae) together with genera such as *Cricetops*, *Selenomys*, *Meteamys* or *Aralocricetodon*. *Edirnella*, which was also included in the analysis, would be closer to *Pseudocricetodon*, *Heterocricetodon*, *Adelomyarion* and *Raricricetodon*, being grouped with these taxa in an entirely different subfamily, the Pseudocricetodontinae (Maridet and Ni, 2013). While this agrees with the less derived morphology of *Edirnella,* this analysis did not consider important characters such as incisor enamel microstructure (see Wessels et al., 2018; chapter 5). Whatever the case, 'melissiodontines' clearly split very early in muroid evolution and are amongst the first muroids to be recorded outside Asia. In the Vallès-Penedès Basin, *Melissiodon* is scarce although generally present in many early Miocene sites, particularly older ones. Crusafont et al. (1955) erected the species *Melissiodon arambourgi* on the basis of the Vallès-Penedès material, but this species has not been reported from other areas. A review of the genus *Melissiodon* in the Vallès-Penedès is provided in chapter 5.

Family Cricetidae Fischer [de Waldheim], 1817

Subfamily Eucricetodontinae Mein and Freudenthal, 1971

Genus *Eumyarion* Thaler, 1966

Eumyarion is a genus of small to medium-sized cricetids that are characterized for an archaic cheek tooth morphology resembling that of older Oligocene cricetids such as *Eucricetodon* (figure 3.6). As in *Eucricetodon* the M1 shows a well-developed and relatively isolated anterior region (prelobe), the third molars (particularly the m3) are relatively long, and the molars present multiple transverse ridges, with the cusps often subordinated to the main lophs. In addition, the zygomasseteric structure of *Eumyarion* is archaic, subhystricomorphous to only incipiently myomorphous as in *Eucricetodon* (Lindsay, 1977; Flynn, 1985). The incisors are ornamented, showing two longitudinal ridges same as in some primitive cricetids such as *Eucricetodon* but these are also observed in more derived forms including *Cricetodon* and even some *Democricetodon* species (Flynn, 1985). The mandible of known species (e.g., *Eumyarion leemanni* see Casanovas-Vilar, 2007; *Eumyarion* sp. see Prieto et al., 2014) is short and robust, with a relatively verticalized corpus as in the Oligocene cricetids *Eucricetodon*, *Pseudocricetodon* and *Heterocricetodon* (see Vianey-Liaud, 1974).

For some time between the 1960s and 1980s European species of *Eumyarion* were referred to the American genus *Cotimus* Black, 1961, which in turn was later synonymized with *Leidimys* Wood, 1936 (see Martin, 1980). Thaler (1966) erected *Eumyarion* as a subgenus of *Cotimus*, which was later upgraded to the genus level by Mein and Freudenthal (1971a). However, this was not always followed and European species were still sometimes referred to *Cotimus* until Engesser (1979) outlined several differences in molar morphology that would indicate that *Leidimys* (=*Cotimus*) is less derived than *Eumyarion* relative to Oligocene cricetids such as *Eucricetodon.*

Leidimys is known from late Oligocene and early Miocene deposits

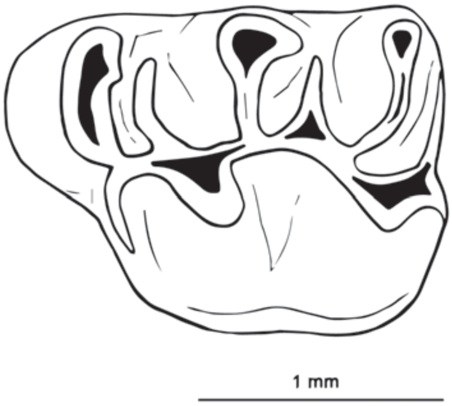


Figure 3.6: Schematic drawing of an M1 of the genus *Eumyarion*

(Korth, 1994; Lindsay, 2008), thus well before the oldest record of *Eumyarion* (see below), but relationships between both genera are unresolved.

Eumyarion has been generally allied to Oligocene cricetids, but its exact phylogenetic position and classification is discussed. In their classification of European Cenozoic cricetids Mein and Freudenthal (1971a) introduced the subfamily Eucricetodontinae for the Oligocene genera *Eucricetodon*, *Pseudocricetodon* and probably *Heterocricetodon*, while placing *Paracricetodon* in a separate subfamily (Paracricetodontinae). Regarding *Eumyarion*, these authors recognized affinities with eucricetodontines but preferred to leave this genus as 'Cricetidae incertae sedis' partly because it was separated from eucricetodontines by a considerable temporal gap (Mein and Freudenthal, 1971a: 30-31). Ünay-Bayraktar (1989) followed this taxonomical opinion but upgraded the Eucricetodontinae to the family level, further recognizing two subfamilies: Eucricetodontinae and Eumyarioninae. The latter would include the genera *Mirrabella* and *Deperetomys* besides *Eumyarion*, which are also first recorded by the early Miocene. Freudenthal et al. (1992) also follow this classification but regarding the eucricetodontines to the subfamily level and without further subdiving this group. Later classifications, such as McKenna and Bell (1997) follow this work and place *Eumyarion* together with *Eucricetodon* in the tribe Eucricetodontini, which in turn is included in the subfamily Paracricetodontidae. However, there is a mistake in this classification scheme. Mein and Freudenthal (1971a) erected the subfamilies Paracricetodontinae and Eucricetodontinae in the same work, and later on Vianey-Liaud (1974: 124) regarded them as synonyms. Although Paracricetodontinae is cited slightly earlier than Eucricetodontinae in Mein and Freudenthal (1971a) this does not establish precedence in zoological nomenclature. In this particular case, the principle of the first reviser determines the priority (ICZN, 1999: art. 24.2). Vianey-Liaud explicitly did so in her description of the cranial anatomy of European Oligocene cricetids (Vianey-Liaud 1974: 124) and selected the name Eucricetodontinae, which is to be considered the valid name for the subfamily.

Eumyarion is first recorded in Pakistan at 23.5 Ma, near the Oligocene/ Miocene boundary (Antoine et al., 2013; Flynn et al., 2013) and posteriorly expands into Anatolia by the early Miocene (MN2-MN3; De Bruijn and Saraç, 1991; Joniak et al., 2017). In Central and Western Europe this genus is not recorded until the later part of the early Miocene (MN4), apparently being associated with the dispersal of the advanced cricetids *Democricetodon* and *Megacricetodon* (Kalïn, 1999; Kälin and Kempf, 2009; Van der Meulen et al., 2012). *Eumyarion* was a common element in Western European faunas during the middle Miocene and the beginning of the late Miocene, except in the inner Iberian Basins (see Van der Meulen et al., 2005; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008).The last occurrence of the genus *Eumyarion* is during the late Vallesian (MN10) at Suchomasty (Czech Republic; Kälin, 1999) and the Vallès-Penedès Basin (Casanovas-Vilar, 2016b). *Eumyarion* is a long-ranging genus and it has been suggested that it may have given rise to the Anomalomyinae, a subfamily of burrowing or fossorial cricetids that was widespread during the Miocene in Europe (Mein and Freudenthal, 1971a; De Bruijn and Saraç, 1991; Bolliger, 1999).

The genus *Eumyarion* is very common in late Aragonian and early Vallesian sites of the Vallès-Penedès Basin (see Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008, 2010, 2016a), but much rarer in older deposits. However, the species *Eumyarion weinfurteri* has been reported from some early Aragonian sites such as Can Martí Vell and Sant Mamet, although only a few isolated teeth have been recovered (Agustí, 1981, 1983). In this work a few additional remains from Les Cases de la Valenciana (chapter 6) and Les Escletxes del Papiol (chapter 10) are reported. It is worth noting that this species had been previously reported from Central Europe (Germany, Switzerland, Czech Republic; see chapter 10).

Family Cricetidae Fischer [de Waldheim], 1817
Subfamily Copemyinae Jacobs and Lindsay, 1984
Genus *Democricetodon* Fahlbusch, 1964

Democricetodon is a small to medium-sized muroid and represents the first genus of 'modern cricetid' to be recorded in Western Europe, making its first appearance in the region by the end of the early Miocene (figure 3.7). The term 'modern cricetid' is informally used to refer to Miocene genera such as *Democricetodon*, *Copemys* or *Megacricetodon* to distinguish them from older Oligocene muroid taxa such as *Eucricetodon* or *Melissiodon*. 'Modern' characters include the derived myomorphous zygomasseteric structure. *Democricetodon* shows a fully myomorphous zygoma, with a V-shaped infraorbital foramen, clearly pinched on its ventral margin, and a broad and verticalized zygomatic plate (Schaub, 1925; Vianey-Liaud, 1974; Lindsay, 1977; Flynn, 1985). Other derived features include usually unornamented incisor enamel and greatly reduced third molars, specially the M3, the anterocone of the M1 is large and the anteroconid of the m1 wide, undivided and generally asymmetrical (see Lindsay, 2008). These cranial and dental features resemble those of extant genera of Cricetidae sensu stricto such as *Peromyscus* and *Cricetulus*.

Fahlbusch (1964) divided the genus *Cricetodon* Lartet, 1851 and united the species *brevis*, *affine* and *gaillardi* in his newly erected genus *Democricetodon*. Later on, the same author pointed out the dental similarity between *Democricetodon* and the North American genus *Copemys* Wood, 1936 further suggesting that both forms should be better distinguished as subgenera within *Copemys* (Fahlbusch, 1967). This was not followed by Mein and Freudenthal (1971a),

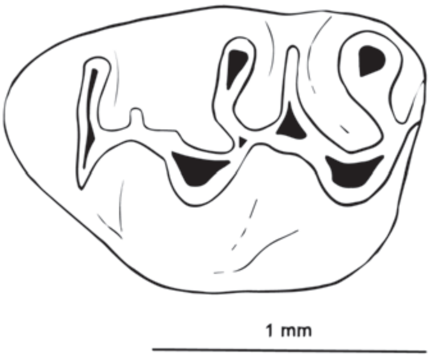


Figure 3.7: Schematic drawing of an M1 of the genus *Democricetodon*.

who argued for a generic separation based on the morphology and position of the incisive foramina. However, as Engesser (1979) noted, this character shows considerable intraspecific variability so its systematic value is doubtful. *Democricetodon* and *Copemys* share a similar skull with a well-developed rostrum and a similarly slender mandible with a lingually inclined cheek tooth range and the pronounced coronoid process higher than the articular one (Engesser, 1979). In addition, both genera present and entepicondylar foramen perforating the distal end of the humerus above the medial epicondyle (Mein and Freudenthal, 1971a; Engesser, 1979), which Mein and Freudenthal (1971) considered to be diagnostic of the Cricetinae (=Cricetidae sensu stricto). Indeed, this character is present in many cricetid (senso stricto) groups, including most cricetines and neotomines as well as all tylomines, but it is absent in the sigmodontines and arvicolines (Weksler, 2006). It also occurs in other Miocene genera such as *Megacricetodon* (see below), so it likely represents the plesiomorphic condition for Cricetidae. Anyway, despite the dental, cranial and postcranial similarities between *Copemys* and *Democricetodon*, there are a few subtle differences, such as the generally more reduced M3 in *Copemys* (Engesser, 1979) and the absence of incisor enamel ornamentation in the North American genus (Lindsay, 2008). Some European and Asian species of *Democricetodon* present incisor ornamentation in the form of two longitudinal ridges (Flynn, 1985; Lindsay, 2008). Most specialists regard these two genera as distinct, an opinion followed here, but acknowledge that they are closely related, sharing a common Asian ancestor, or that *Democricetodon* might have given rise to *Copemys*. Both genera are first recorded at the same time in Asia and North America, at around 20 Ma. *Copemys*, is a clear immigrant into North America as it cannot be related to any of the older cricetid genera present in the continent (Lindsay, 1972, 2008).

Democricetodon had been traditionally included within the subfamily Cricetodontinae Schaub, 1925, which for a long time comprised all Miocene cricetids. Mein and Freudenthal (1971a) were the first to distinguish *Democricetodon* from other Miocene cricetids (*Cricetodon*, *Megacricetodon*) and place it closer to the extant Cricetinae, an opinion followed by later authors (e.g., Chaline et al., 1977, Hartenberger and Crusafont, 1979). Owing to affinities with North American *Copemys*, later authors included this genus together with *Democricetodon* within the same subfamily, the Copemyinae Jacobs and Lindsay, 1984, placing the origin of Miocene North American forms in the Old World (Jacobs and Lindsay, 1984; Korth, 1994; Lindsay, 2008). Lindsay (1987) introduced the tribe Democricetodontini, which was later synonymized (at least in part) with the Copemyini in McKenna and Bell (1997), who included this subtribe within the Cricetodontinae. Later authors, such as Theoracharopoulos (2000) and Lindsay (2008) used the term Democricetodontinae/ Democricetodontini, but Copemyinae/ Copemyini should have preference. In this work, *Democricetodon* is included within the subfamily Copemyinae together with other genera (*Copemys*, *Primus*, *Spanocricetodon*, *Karydomys*).

The oldest Eurasian copemyines, represented by the genera *Primus*, *Karydomys* and *Spanocricetodon*, first appear more or less simultaneously in China (Maridet et al., 2011a), Pakistan (Lindsay et al., 2005), Turkey and Greece (Theoracharopoulos, 2000). The oldest *Democricetodon* are recorded slightly later, by the earliest Miocene (ca. 22 Ma) from the same regions (Flynn et al., 2013; Flynn and Wessels, 2013; 70 Maridet et al., 2011b; Meng et al., 2003). *Democricetodon* is the first cricetid to appear in Western Europe after the 'cricetid vacuum' (ca. 19.5 to 17 Ma; Daams and Freudenthal, 1989), being already present in low numbers during the late MN3 (17 Ma) in the Calatayud-Montalbán Basin of east-central Spain (Van der Meulen et al., 2003, 2012) and slightly before (17.2 Ma) in the Ebro Basin (Agustí et al. 2011). The first common occurrence of this genus is used to define the lower boundary of biozone MN4 and consequently the lower boundary of the Aragonian land mammal age (Agustí et al., 2001; Hilgen et al., 2012). *Democricetodon* was slightly later joined by *Megacricetodon* (see below) and these two genera soon radiated in multiple species and became major components of the early and middle Miocene rodent faunas of Eurasia. The first appearance and evolution of different *Democricetodon* and *Megacricetodon* species is a diagnostic criterion for local biozonation in several European basins (e.g., Abdul Aziz et al., 2008, 2010; 55 Casanovas-Vilar et al., 2016a; Daams et al., 1999; Kälin and Kempf, 2009; Prieto and Rummel, 2016; Van der Meulen et al., 2012). Finally, *Democricetodon* is regarded as a likely ancestor for many Miocene Eurasian cricetid genera, including *Cricetulodon* and *Neocricetodon*, for example (see Kälin, 1999).

Quite recently the taxonomy of the genus *Democricetodon* was subject to profound changes after the synonymization of the genera *Fahlbuschia* Mein and Freudenthal, 1971, *Pseudofahlbuschia* Freudenthal and Daams, 1988 and *Renzimys* Lacomba, 1983 by Van der Meulen et al. (2003). Freudenthal and Daams (1988) considered these genera, which are restricted to Western Europe (Iberian Peninsula and France), to be derived from *Democricetodon*. Older species, which date back to the early Aragonian (MN4), are indeed very similar to *Democricetodon*, but later ones differ by their considerably larger size and more reduced mesolophs/ids (see Freudenthal and Daams, 1988; Van der Meulen et al., 2003). Since these differences appear to be subtle, Van der Meulen et al. (2003) considered all these genera to be junior subjective synonyms of *Democricetodon* Fahlbusch, 1964. This has been strongly contested by Freudenthal (2006), but most researchers have accepted the synonymy of these genera at least until a detailed comparison can be undertaken considering material other than dentition (e.g., cranial material; see Casanovas-Vilar, 2007).

Democricetodon is a common element of the early Miocene (early Aragonian, MN4) Vallès-Penedès rodent faunas. To date, all the recovered material (mostly coming from Can Martí Vell and Els Casots) has been ascribed to *Democricetodon* aff. *hispanicus* (Agustí, 1981, 1983; Agustí et al., 1985; Agustí and Llenas, 1993). In chapters 6-9 all the early Miocene material belonging to this genus (including some cranial remains; see chapter 8) is reviewed leading to a reinterpretation of this attribution as well as to the identification of additional

Democricetodon species in this basin. The biostratigraphic implications of these new taxonomic data are discussed mostly in chapters 9 and 10.

Family Cricetidae Fischer [de Waldheim], 1817
Subfamily Megacricetodontinae Mein and Freudenthal, 1971
Genus *Megacricetodon* Fahlbusch, 1964

Megacricetodon is also a small to medium-sized cricetid genus which, along with *Democricetodon*, was very widespread and abundant in Eurasia between the early Miocene and the beginning of the late Miocene (i.e., between about 17 and 9.5 Ma). Same as *Democricetodon*, species within this genus were long included within *Cricetodon* Lartet, 1851, until Fahlbusch (1964) subdivided it and erected the genus *Megacricetodon*. This genus also represents a 'modern cricetid', clearly derived as compared to older Oligocene muroids. Derived features include the completely myomorphous zygomasseteric structure, with a V-shaped infraorbital foramen, although with a less constricted ventral margin as compared to *Democricetodon* (Schaub, 1925; Hartenberger, 1967; Vianey-Liaud, 1974; Lindsay, 1977; Flynn, 1985). The zygomatic plate is broad, but slightly less vertical than in *Democricetodon* and other cricetids (Lindsay, 1977; Flynn, 1985). Other cranial differences between both genera include the presence of a well-defined masseteric tubercle antero-ventral to the zygomatic plate for the insertion of the superficial masseter, a feature also observed in *Cricetodon* (and/or *Hispanomys*, pers. obs.) (Hartenberger, 1967; Bi et al., 2008) but absent in *Democricetodon* (see Schaub, 1925; Vianey-Liaud, 1974). In *Megacricetodon* the incisive foramina are long, extending posteriorly beyond the anterior margin of the M1 (Hartenberger, 1967; Vianey-Liaud, 1974) as characteristic for the Cricetodontinae (Mein and Freudenthal, 1971a). On the other hand, the mandible is more similar to that of *Democricetodon*, showing a better developed coronoid process than *Cricetodon* (Bi et al., 2008). In general, cranial characters are less derived than in *Democricetodon* and *Copemys*, more closely resembling the condition in *Cricetodon* (Hartenberger, 1967; Mein and Freudenthal, 1971a). Therefore, *Megacricetodon* has been traditionally included within the subfamily Cricetodontinae, together with *Cricetodon*, *Deperetomys*, *Hispanomys*, *Ruscinomys* and other genera (e.g., Mein and Freudenthal, 1971a; Chaline et al., 1977). This had been also the case of *Democricetodon*, however most authors considered it more closely related to extant cricetines and sigmodontines and soon was placed within the Cricetinae/Cricetidae (see above). Nevertheless, *Megacricetodon* presents a series of diagnostic dental features that in the opinion of some authors warrant its placement in a separate subfamily (e.g., Jacobs and Lindsay, 1984; Lindsay,

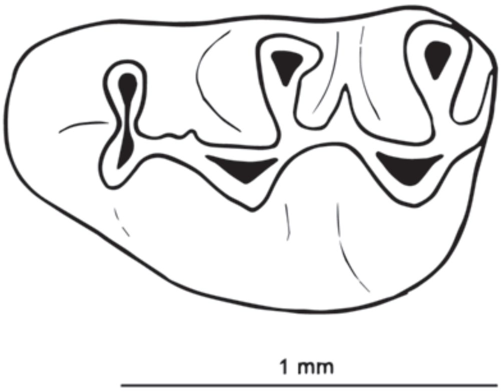


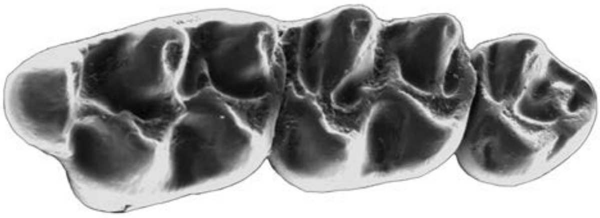
Figure 3.8: Schematic drawing of an M1 of the genus *Megacricetodon*.

1988, 2008; Wessels et al., 2001, Wessels, 2009). Contrary to most cricetodontines, incisor enamel in *Megacricetodon* shows no ornamentation (Flynn, 1985). The M1 show a well-developed anterocone which is always clearly divided into two cusps, while the m1 is greatly elongated with a prominent anteroconid that can be subdivided into two cusps in some species (Mein and Freudenthal, 1971a; Lindsay, 1988; figure 3.8). Some lineages show a tendency towards the arrangement of the main cusps in opposite pairs and reduction of the transverse ridges, thus emphasizing cusps which become more prominent (Lindsay, 1988). This dental morphology resembles that of early murids such as *Potwarmus* and *Antemus* (Jacobs, 1977; Jacobs and Downs, 1994; Flynn, 1985; Lindsay, 1988) so that *Megacricetodon* is generally considered to be closer to the Muridae (including murines and gerbillines; see chapters 3.2.2 and 3.3.2) than to the Cricetidae sensu stricto. Indeed, the Megacricetodontinae may form a monophyletic clade with the Muridae. However, most paleontologists include this genus within the cricetids in a broad sense.

Postcranials of *Megacricetodon* are known and offer some interesting insights into its phylogenetic relationships and lifestyle. Bi et al. (2018) described a partial skeleton of *Megacricetodon yei* from the middle Miocene of the Junggar Basin of China. Overall, the postcranial anatomy shows that *M. yei* was a generalized terrestrial quadruped also capable of climbing. The humerus shows a clear entepicondylar foramen, same as *Democricetodon* and many extant cricetids (see above). This foramen is apparently absent in *Cricetodon* (Mein, 1967; Mein and Freudenthal, 1971a) as well as in at least many extant Muridae. However, Mein (1967) described several humera attributed to *Megacricetodon gregarius* from La Grive (France) which lack the entepicondylar foramen. Therefore, this might be a variable character that provides little systematic information.

First representatives of *Megacricetodon* representatives have been approximately simultaneously recorded from China (Maridet et al., 2011), Pakistan (Lindsay et al., 2005) and Anatolia (Wessels et al. 2001) at around 19-18 Ma. In Europe, this genus is first recorded somewhat later than *Democricetodon*, already within the MN4. Its oldest occurrence is at Hüenerbach (Switzerland), with an estimated age of 17.1 Ma. In the Iberian Peninsula, *Megacricetodon primitivus* is the first species to appear, its oldest record being at the Calatayud-Montalbán Basin (Aragón, Spain) at about 16.5 Ma (Van der Meulen et al. 2012; Oliver and Peláez-Campomanes, 2016). Same as *Democricetodon*, *Megacricetodon* will become a dominant component of the early and middle Miocene faunas of Eurasia, further radiating in numerous species (up to 40 have been described!). It has been profusely used in biostratigraphy and biochronology, the different lineages and species allowing to characterize local to regional biozones (e.g., Abdul Aziz et al., 2008, 2010; Casanovas-Vilar et al., 2016a; Daams et al., 1999; Kälin and Kempf, 2009; Prieto and Rummel, 2016; Van der Meulen et al., 2012).

In the early Miocene sites of the Vallès-Penedès Basin, only the species *Megacricetodon primitivus* has been reported (Agustí, 1981, 1983; Agustí et al., 1985; Agustí and Llenas, 1993). In chapters 6-9 all the early Miocene material belonging to this genus is reviewed, while its role in local biostratigraphy is discussed mostly in chapters 9 and 10.



Chapter 4: Methodology

CHAPTER 4: METHODOLOGY

Even though rodents are amongst the most diverse and abundant mammals in fossil sites, their small size makes it hard to find them during systematic excavations. Only when notably complete remains are preserved, such as skulls or partial skeletons, these minute animals can be recovered during the excavations. This happens in very few localities, but for instance during the excavation of the early Miocene els Casots site at the Vallès-Penedès Basin a few cranial remains even with associated postcranials of *Democricetodon* cf. *hispanicus* were found (Jovells-Vaqué et al. 2017, see chapter 8). However, this is not the rule and as a consequence, specific field techniques involving screen-washing to recover small vertebrate remains have been developed. These methods allow for the recovery of isolated teeth, mandible fragments and postcranials belonging to small mammals, birds and herpetofauna. In the case of small mammals isolated cheek teeth are readily identifiable, whereas incisors and especially postcranial material, not being associated to the rest of the skeleton, is of difficult attribution and is often left unstudied. Therefore, it is not surprising that the diagnoses of most extinct rodent genera and species rely on cheek teeth dental characters.

This chapter introduces the field techniques used to recover most of the small mammal material from the studied sites. Since this work is centered in the cricetids, the terms and abbreviations used in the descriptions will be briefly exposed (see also chapter 3.3.3), measurement methods, statistics and plotting techniques used in the systematic part of the work (chapters 5 to 9). Other small mammal groups (other rodent families, lagomorphs, eulipotyphlans and marsupials) are described in chapter 6. However, since they occupy only a small part of this work these are not treated here. For this specific case see references on dental terminology and measurement methods in chapter 6.

The final part of this chapter introduces the bio- and magnetostratigraphic concepts and methods used in the final part of this work (chapter 9 and specially chapter 10). The very last section 4.6 introduces the use of small mammals as paleoenvironmental proxies and details the methods used to infer paleoclimatic parameters such as precipitation. These methods are used in chapter 10 to study early Miocene paleoclimatic trends in the Vallès-Penedès Basin.

4.1 FIELD TECHNIQUES

As already said, recovering small mammal remains can be challenging because of its size. The first studies of micromammal faunas generally could only consider a few specimens because of the difficulty of finding them in the field. The only exception were karstic sites, which often included bone breccias made of thousands of small vertebrate fossils, but these were rare. Around the 1950s specific methods to recover small fossils were slowly introduced. Initially these included dry or wet screening of the sediments removed in systematic excavations, which in many cases provided good (though not optimal) results. The 1960s represented a turning point. At that time Dutch paleontologists Hans de Bruijn and Matthijs Freudenthal working at the Calatayud-Montalbán and

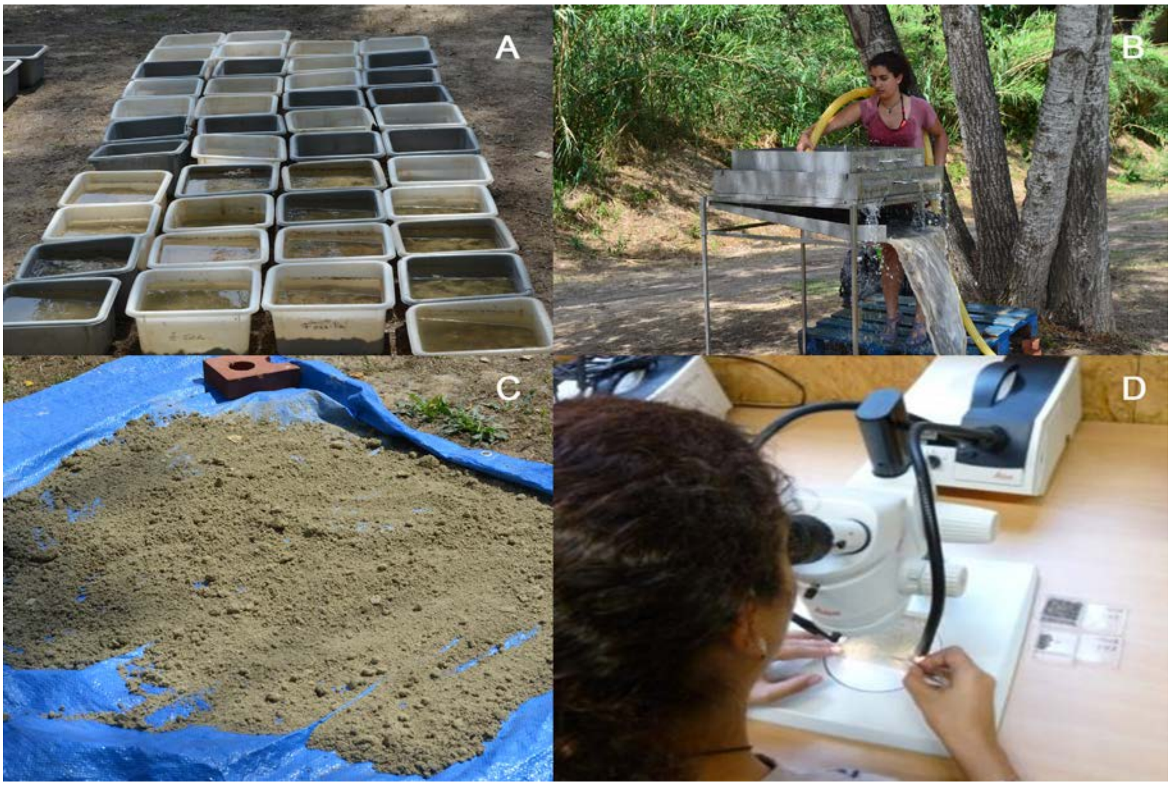


Figure 4.1: Screen-washing and sediment sorting procedure. A: Dried sediment is immersed in water to be disintegrated; B: Screen-washing with a modified 'Freudenthal washing table'. A special sieve is used for this procedure with different mesh sizes depending on the sediment. C: The washed residue is dried in the sun; D: Sediment sorting process under the steromicroscope. The small teeth, bone fragments, shells, and other identifiable fossil remains are separated manually from the sediment, which is discarded.

Teruel Basins (Aragón, Spain) devised a new method to process large sediment samples and recover rich collections of microvertebrate fossils. Freudenthal assembled a series of sieves with different mesh sizes in a foldable table for wet screen-washing using hoses (see a sketch and description in Daams and Freudenthal, 1988). Although never patented, the sieving equipment became popularly known as the 'Freudenthal washing table' and has been used (with slight modifications) ever since. In the 1970s this technique was first used to sample Vallès-Penedès sites.

The method consists of several phases:

Select an area to be sampled. The area will be prospected in search for suitable facies for the preservation of microvertebrates. Normally these are lutites and marl layers that correspond to lacustrine and palustrine areas or the distal alluvial fan facies. Other lithologies, such as sandstones and conglomerates, represent higher-energy sedimentary environments and are usually less favorable for the preservation of small vertebrate remains, though these can also be found. Finally, microvertebrates can be present in other lithologies such as lignites. Close inspection of the appropriate layers usually results in finding small fragmentary fossils at bare eyes. The presence of other small fossils, such as freshwater mollusks, is often correlated with the presence of microvertebrates.

Once the layer is selected, its coordinates and stratigraphic position are accurately recorded, and pictures of the layer and surroundings are taken so it will be easy to locate it in the future. A concise description of the lithology is also written down. Then, a test sample of approximately 100-150 kg of sediment is taken, in order to evaluate the presence and richness in fossil microvertebrates. This phase is omitted if the layer to be sampled corresponds to a systematic excavation or if it is already known to have delivered microfossils.

The sample collected at the field is screen-washed, either at the lab using small sieves or at the field using a 'Freudenthal washing table'. This process consists of several phases. First, the collected sample needs to be completely dried. To do so, the sediment is extended over plastics and dried in the air. Normally it takes about one day to get the sediment completely dehydrated. Once it is dry, the sediment is distributed in buckets which are later filled with water (figure 4.1A). The dried sediment immersed in water quickly disintegrates as water penetrates between clay layers. The washing table (in this case a larger and slightly modified version of Freudenthal's original designed by Dr. Hans de Bruijn) consists of 3 to 4 washing trays that are situated at different levels following a decreasing mesh size from the coarser one (10 mm) to the thinner one (0.5 mm). The sediment is dropped in the 10 mm mesh and washed using water pipes with moderate water pressure (figure 4.1B). The finer sediment passes through a ramp to the 2.5 mm mesh, then to the 0.7 mm and finally to the 0.5 mm mesh. All sediment below 0.5 mm grain size is discarded. The process results in the extraction of the mud and the separation of the sediment in several fractions. The trays must be emptied regularly because a large amount of sediment can obtrude the mesh holes. To improve efficiency several hoses can be used (one at each tray), thus allowing to quickly process large samples of up to several tons of sediment (see below) relatively fast. Once the screen-washing is complete wet sediment needs to be dried again (figure 4.1C). Before processing a new sample all the sieving equipment must be thoroughly washed with brushes and high-pressure water to avoid sample contamination.

Once dry, the different sieved fractions can be dry-sieved again to separate the samples into fractions of more homogenous granulometry. The sediment finally is stored in plastic bags carefully labeled with the site acronym, date of collecting and fraction granulometry. This material will be stored at the museum to be processed in the laboratory.

In the lab the different sediment fractions are inspected under a stereomicroscope in the search for small fossils (figure 4.1D). These fossils are separated into different categories: micromammal cheek teeth; rodent and lagomorph incisors; micromammal postcranial bones; macromammal bone and tooth fragments; and mollusk shells and shell fragments. The sediment is then discarded. A test sample is considered positive it if just delivers one identifiable small mammal cheek tooth, however it is preferable that 5 to 10 cheek teeth are found, which would indicate that the site is rich. If fewer teeth are recovered but the site is especially relevant (because its stratigraphical position for example) a larger sample is collected.

Next, a larger final sample is collected. The size of this final sample is estimated on the basis of the number of recovered cheek teeth in the test sample. The goal is obtaining a representative collection of more than 100 identifiable cheek teeth, but sometimes larger samples are collected. For example, the test sample of Can Martí Vell 3 (see Llenas Avellaneda et al., 2016) comprised 75 kg of sediment and delivered 23 identifiable cheek teeth belonging to rodents, lagomorphs and insectivores. The final sample was adjusted to 1,000 kg because the site appeared to be extremely rich, resulting in the recovery of 470 additional identifiable cheek teeth. On the other hand, at les Cases de la Valenciana 1 (see Casanovas-Vilar et al., 2017 and chapter 6) all the sediment removed during the systematic excavation (18,000 kg) was screen-washed. The sample has not been fully processed, but around 800 identifiable cheek teeth were recovered (only half of these are considered in chapter 6). The processing of the final sample follows the same steps described previously: screen-washing, dry-screening and sediment sorting under the stereomicroscope. The latter phase can demand a lot of time in the case of large samples.

Finally, when fossils have been separated from the sediment they are given a collection number preceded by an acronym referring to the museum or institution that curates the specimens. For the Institut Català de Paleontologia Miquel Crusafont, the acronym used is 'IPS' corresponding to the old name of the institution 'Instituto de Paleontología de Sabadell'. This labeling method allows the museum to get a full record of every fossil and registering them in a database. Postcranial bones, isolated incisors, and most of the mandibles and skull fragments are stored in small plastic boxes labelled with a single collection number. Small mammal cheek teeth are prepared differently. These are fixed using a non-greasy, pliable and removable adhesive (blue-tac, pliable art eraser or similar) on construction game pieces (small bricks of Lego®). The tooth is placed at one side of the piece and the empty space next to it is used to write down or stick the label with the collection number. Different pieces containing the specimens of the same site are assembled and placed inside plastic boxes for storage. This is a clean, clear and easy way of storing the small mammal collection although it requires more space than other methods (such as fixing the specimens on a microscope slide). Labels used in most of the collections described in this thesis include a microchip which can be scanned with a barcode scanner. This chip is linked to a database file that immediately shows all the basic information related to this specimen (collection number, site and collection date).

These are the basic procedures used to obtain and curate micromammal fossils at the ICP. However, there may be some modifications. Acid attack is the most frequent, and different acids are used to dissolve certain kinds of sediment and sometimes to reduce the amount of residue to be sorted. For example, if the sediment is rich in carbonates and/or carbonate cement, this can be dissolved using a solution of acetic acid (CH_3COOH). Usually low concentrations are used (5 to 10 %) to avoid damaging the fossil material. Anyway, when a sample has been treated with acid this is accurately recorded. In the case of el Turó de les Forques 1 and les Cases de la Valenciana 1, a solution of 4 % formic acid ($HCOOH$) with a tricalcium phosphate ($Ca_3(PO_4)_2$) buffer (to protect fossil material) was used to dissolve well-cemented clays (see Casanovas-Vilar and DeMiguel, 2013).

4.2 Anatomical terminology and measurement methods for cricetid cheek teeth

Like in many other extinct small mammals, most cricetid fossil remains are isolated cheek teeth and occasionally some maxillary and mandibular fragments. Therefore, generic and species determination is mainly based on cheek tooth morphology. The primitive cricetid tooth morphology is also known as "the cricetid plan" (Schaub, 1925) and is described in chapter 3.3.3. Dental terminology is not standard and there are slight variations, especially regarding the name of minor transverse ridges. Dental terminology used throughout this work (see figure 3.4 in chapter 3.3.3) is based on Mein and Freudenthal, 1971b, Freudenthal et al. 1994 and Oliver and Peláez-Campomanes (2013). In the case of the complex morphology of *Melissiodon* cheek teeth interpretative drawings accompany the description and pictures (see chapter 5). For *Democricetodon* and *Megacricetodon*, which are usually well represented by samples of hundreds of specimens, several authors have defined morphotypes for different dental characters

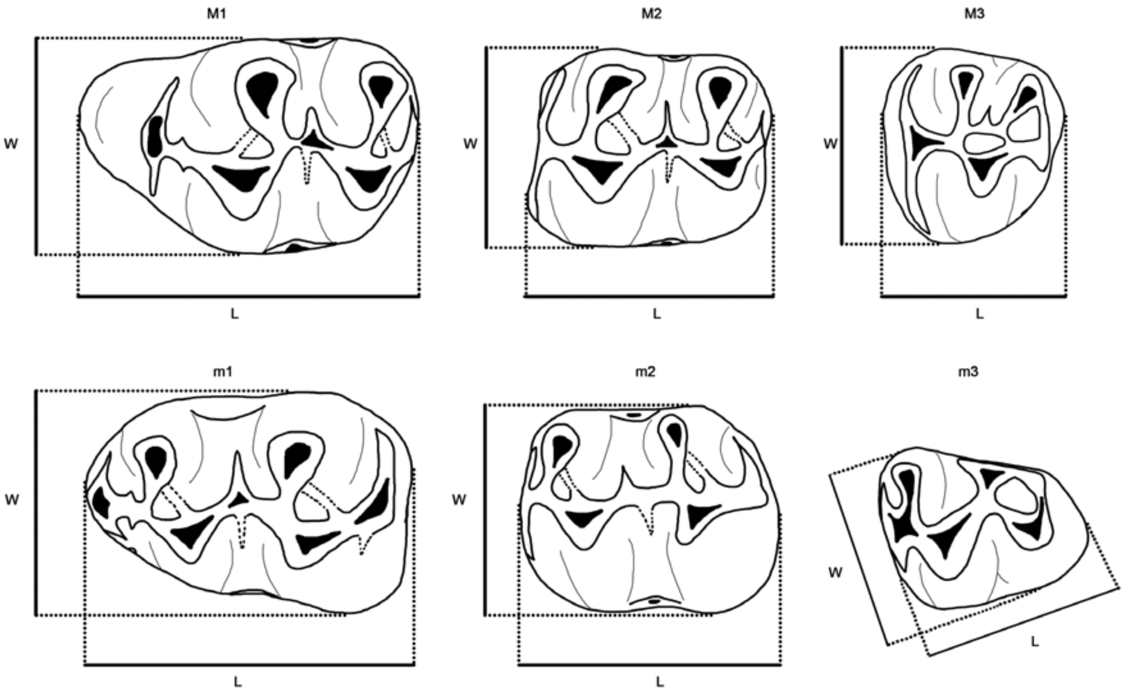


Figure 4.2: Measurement method for cricetid cheek teeth. L: mesiodistal length; W: buccolingual width. Modified from Freudenthal and Daams, 1988; Daams and Freudenthal, 1988

that enable rapid description and tabulation of character frequencies. Morphotype coding in chapter 9 (see also Appendix 3) for *Megacricetodon* is modified from Daams and Freudenthal (1988) and Oliver and Pelaez-Campomanes (2016). For *Democricetodon* it follows Van der Meulen et al. (2003) and Maridet (2003) with slight modifications. Cheek teeth measurement method follows Daams and Freudenthal, 1988 (see Appendix 2). Two measurements are taken for each complete tooth; the mesiodistal length (L) and buccolingual width (W) (figure 4.2), using an optical micrometer. Measurements are given in millimeters to the nearest 0.01 mm. Possible inaccuracies of the measuring method were taken into account so that each measurement was replicated three times and the average calculated. Estimated measurements (because of minor damage or distortion) are given between brackets, whereas ">" indicates that the measurement cannot be confidently taken but certainly exceeded the reported value.

The specimens were photographed using an Environmental Scanning Electron Microscope (ESEM) at the University of Barcelona (UB) Scientific Services. No coating of the specimens was required.

In the descriptions dental morphological features are not abbreviated, although abbreviations appear in some figures and are explained in the caption (for example see chapter 5). Throughout the text, uppercase letters are used for upper dental elements and lowercase letters for lower ones. Besides cricetids, other small mammal groups (other rodent families, lagomorphs, eulipotyphlans and marsupials) are briefly described in chapter 6. References on dental terminology and measurement methods for these taxa are provided in chapter 6.

4.3 STATISTICS AND PLOTTING TECHNIQUES

Summary statistics were calculated for length and width measurements of the cheek teeth using the R software (R Core Team, 2017). The calculated summary statistics comprise minimum, maximum, mean and standard deviation for upper and lower molars and are reported in tables (see chapters 5-9 and appendix 3). R package ggplot2 was used to perform length-by-width scatter plots. These plots are a quick way to visualize two variables (in this case length and width see chapter 4.2) for multiple data points (specimens). Shape and color coding are used to identify the points so that additional categorical variables, such as taxonomic identification or locality, are also displayed for comparative purposes.

4.4 BIOSTRATIGRAPHY AND BIOCHRONOLOGY

4.4.1. PRINCIPLES, PROCEDURES AND STATE OF ART

Mammals are crucial to date and correlate Cenozoic continental sediments. However, the mammal record is less continuous (both geographically and stratigraphically) than that of marine organisms. In general, mammal fossils are not continuously vertically distributed along stratigraphical sections, but occur in isolated sites, correlative sites within an area sometimes being separated by hundreds of meters or even located in sections nearby. Some types of sites even lack a stratigraphic context entirely, such as fissure fillings but may provide a rich fauna useful for biochronological correlation.

European mammal paleontologists and stratigraphers have tried to define formal continental stratigraphic/chronologic systems for the Neogene during the last fifty years. Even though some of these systems, such as the MN zonation (see below), are broadly used there are diverging opinions on how mammal-based systems should be defined. In the case of the European Neogene this has resulted in different chronologic/stratigraphic systems, based on different philosophies, being simultaneously used (for historical reviews see Lindsay and Tedford, 1989; Van Dam, 2003; Hilgen et al., 2012). These diverging philosophies (or 'schools of thought') have developed side by side and are often referred to as the 'faunal school' and the 'stratigraphic school'. The stratigraphic approach is grounded on strict biostratigraphic principles as stated in stratigraphic guides (Salvador, 1994; see also Woodburne, 2004). Biostratigraphy refers to the characterization of a body of rock strata based on the fossils it contains, thus resulting in biostratigraphic units. Biostratigraphic units can be characterized by the first occurrence of a taxon, its last occurrence, its maximum abundance or by the presence of a characteristic association of taxa, amongst others. These result in different kinds of biostratigraphic units (e.g., range zone, concurrent range zone, abundance zone, etc.) which are often named after their characteristic taxa (Salvador, 1994). This approach is particularly popular in the regions where well-exposed, long and relatively continuous stratigraphic sections occur, such as in the Iberian Peninsula (see chapter 4.4.3).

The faunal approach considers whole faunas as the means of dividing time and typically implies the construction of a system of time-ordered (reference) localities. This approach has been championed by French paleontologists, not surprisingly because France lacks well-exposed and continues sections but includes many rich isolated fossil sites, often corresponding to fissure fillings. The earliest attempts date back to Thaler (1965) who arranged chronologically a sections of European localities corresponding to certain stages of faunal evolution ("niveaux repères d'évolution"). Later on, Mein (1975) developed the MN system, which although not adhering strictly to the stratigraphic or faunal school should be considered closer to the latter (see chapter 4.4.2). The faunal approach is closer to biochronology, as little to no attention is paid to the stratigraphy of the localities and rather identifies an exact point in time (the localities). However, it has been criticized because it poses several problems. The most important one is that a large amount of faunal information has to be considered and somehow (often subjectively) properly averaged and weighted (see Van Dam, 2003). In contrast, the strict stratigraphic procedures of the 'stratigraphic school' are straightforward in the definition of biozones.

Ideally, biostratigraphy should

precede biochronology and not vice versa (see Woodburne, 2004). In other words, first a local biostratigraphy should be proposed showing the occurrence of particular bioevents within stratigraphic sections. Later on, these sections should be correlated to a global standard, for example using magnetostratigraphy, so that an age can be assigned to each one of these local bioevents. After comparison with other local biostratigraphies the chronology of selected bioevents can be specified and used to define biochronologic units with a well-defined geographical extent. However, the patchiness (both temporally and spatially) of the mammal record makes following this procedure extremely difficult. For example, in the case of the Iberian record several land mammal ages, such as the Aragonian, have been defined and an accurate chronology for the main bioevents is available (see chapter 4.4.3). Unfortunately, the geographical applicability of these 'mammal ages' is unknown. They certainly can be applied to the Iberian Peninsula, but it is unclear if they could be extended, at least as originally defined, to other European areas. Therefore, many of these ages are often regarded as regional and not included in biochronological synthesys considering Europe as a whole (e.g., Steininger, 1999).

As far as the ages of the European faunas, localities and units are concerned, calibrations have traditionally depended on magnetostratigraphy. Nevertheless, radiometric dates of volcanic layers in association with mammal occurrences and direct calibrations of sites intercalated with marine records have also been used. Finally, quantitative estimates for ages of non-calibrated sites have been produced by multivariate analysis of faunal list information (for a review see Hilgen et al., 2012 and references therein).

In this work, a strict biostratigraphic procedure is followed, starting with the recognition of local biozones (figure 4.3). Longer distance correlations, as well as the chronology of particular bioevents within a broader context, are also discussed.

4.4.2 MAMMAL NEOGENE (MN) UNITS

The most widely used biochronological scale in the European Neogene is that of the MN (acronym for Mammal Neogene) units or zones. MN zones were introduced by French paleontologist Pierre Mein in a congress held at Bratislava (Slovakia) in 1975. Mein's proposal was an informal chart comprising up to 17 MN units numbered from oldest to youngest and covering the Miocene and Pliocene (Mein, 1975). In this initial scheme each MN is characterized by a sections of criteria: first and last appearance of selected taxa occurrence characteristic taxa and lineages of a given zone (although not necessarily restricted to that zone). Mein himself did not adhere to a strict faunal or stratigraphic approach (see chapter 4.4.1); neither did he define the zones after taxon names, nor did he follow Thaler (1965) in using reference localities to define zones. Mein's apparent intention was introducing an efficient and easy biochronologic tool rather than a strictly defined formal system. This explains why the MN system was later modified and used in different ways by advocates of the faunal and stratigraphic schools of thought. The first major modification would arrive just one year after their introduction, when Fahlbusch (1976) associated a reference locality to each one of the MNs and further included the MNs as subdivisions of broader European Land Mammal Ages (ELMAs; such as the Orleanian, Astaracian, Vallesian, Turolian and Ruscinian). Mein regarded these reference localities as an illustration rather than a definition of the MN units (Mein, 1989, 1999). However, De Bruijn et al. (1992) formalized the status of the reference localities. These authors adopted an extreme faunal approach and decided to define the MN zones as the reference localities themselves. Therefore, MNs represented just a sequence of time-ordered reference faunas, with no boundaries between them. However, this ordinal system complicates correlations and, unless multivariate methods are used, introduces a significant amount of subjectivity (Van Dam, 2003).

Other developments included the proposals (e.g., Mein, 1989, 1999) for a subdivision of certain units into parts 'a' and 'b', although these are often difficult to recognize and may have a regional meaning instead. Finally, some authors have adopted a stratigraphic approach to define the MN zones. Notable examples are Steininger (1999) and Agustí et al. (2001), who redefined MN zones as formal biostratigraphical units with clear boundaries and linked to land mammal ages. Agustí et al. (2001) defined MN boundaries based on the first appearance of selected large and small mammal taxa (species or genera). The age of the events was constrained using magnetostratigraphical data from long and continuous sections in Spain and Switzerland. The MNs as defined by Agustí et al. (2001) are indeed formal biostratigraphical units, with clear diagnoses and well-defined boundaries. However, they are based mostly on the Spanish record, so that they may indeed represent regional biostratigraphical units and should not be equaled to MNs, which are intended for application across all Europe (see discussion in Van Dam, 2003). Later reviews of the MN system have considered both approaches (faunal and stratigraphical) and defined MNs either by a sections of bioevents or as a sequence of precisely dated reference localities (see Hilgen et al., 2012: table 29.2). This introduces some problems, as some reference localities for particular MNs may be placed outside this MN as stratigraphically defined. One example is Can Llobateres 1 in the Vallès-Penedès Basin, the reference locality for MN9 with an estimated age of about 9.8 Ma (see Casanovas-Vilar et al., 2016b). If MN10 is defined by the first occurrence in Europe of the murine *Progonomys* at around 10 Ma (see Van Dam et al., 2014), then Can Llobateres 1 should be placed within the MN10! Another problem with reference localities is that in some cases reference localities corresponding to different units might be really close

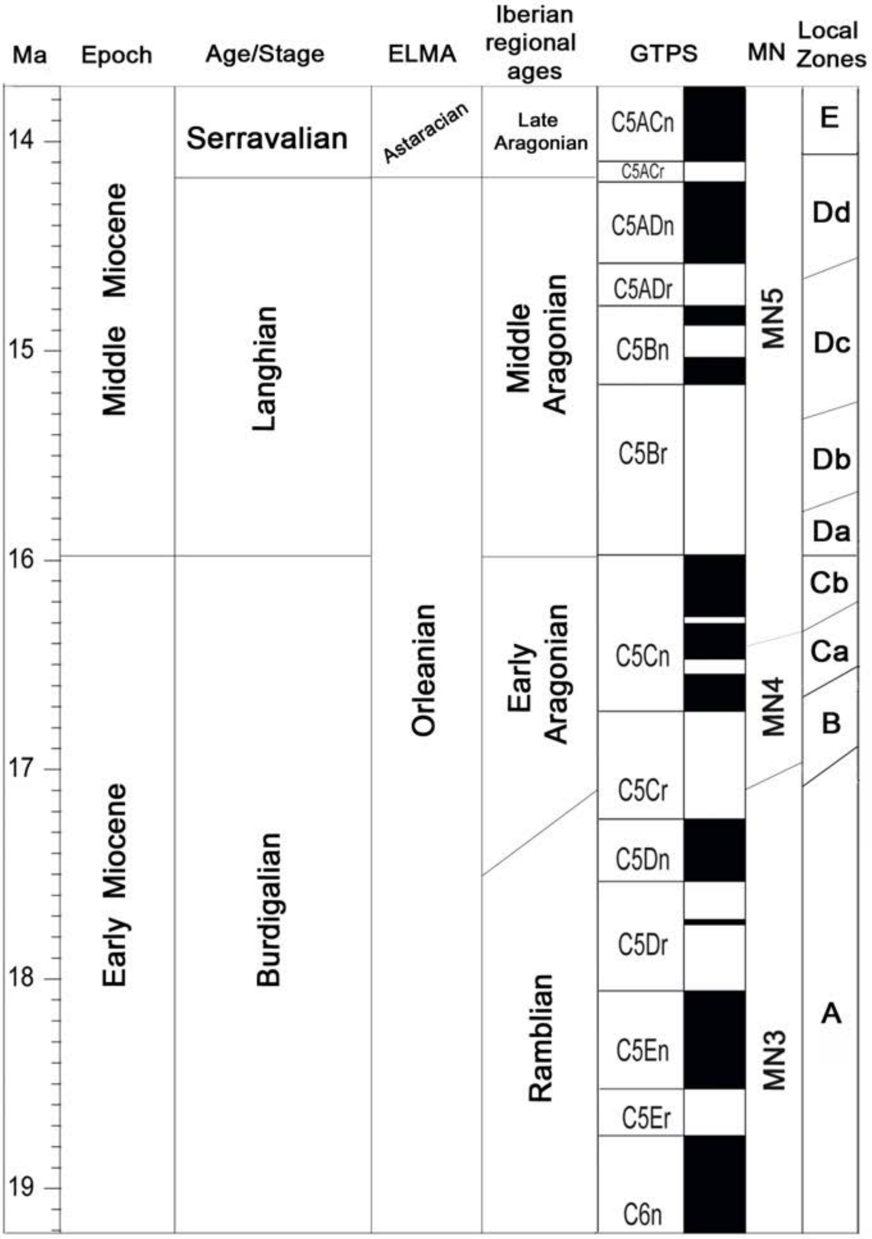


Figure 4.3: Magnetostratigraphic and biochronologic scheme used in this thesis. ELMA, European Land Mammal Ages; MN European Mammal Neogene zones. Based on: Ogg et al. 2012 for the Geomagnetic Polarity Time Scale (GTPS); Hilgen et al. 2012, for Miocene ages, ELMA, and MN; Van der Meulen et al. 2012 for the Iberian regional zones.

in age, such as Can Llobateres 1 (MN9, 9.8 Ma) and Masía del Barbo (MN10, 9.6 Ma), which may be undesirable.

Other serious difficulties of MN zones and other biochronologic/ biostratigraphic units are provinciality and diachrony (Van Dam, 2003). It has been known for a long time that distinct bioprovinces can be recognized in the European Miocene (see Casanovas-Vilar et al., 2010 and references therein), which implies that at times of high provinciality localities from distinct regions may share very few taxa at the specific and generic level. Furthermore, certain mammal bioevents are known to be diachronic. For example, the first common occurrence of the cricetid *Democricetodon* is used to define the lower boundary of MN4 and also marks the beginning of the Aragonian land mammal age (see Hilgen et al., 2012). This event occured between 17.6 and 17.2 Ma in Central Europe (Switzerland, Bavaria; see Abdul Aziz et al., 2010; Kälin and Kempf, 2009), somewhat earlier than in the Iberian Peninsula, were *Democricetodon* is not recorded until 17 Ma and does not become a common component of the faunas until about 16.8 Ma (Agustí et al., 2011; Van der Meulen et al., 2011, 2012).

This work focusses in part of the early and middle Miocene, comprising units MN3 to MN5 (figure 4.3). A stratigraphic approach taking MN boundaries as defined by Agustí et al. (2001) and Hilgen et al. (2012) was favoured. The lower boundary of MN3 is defined by the first occurrence of the eomyid *Ligerimys* (see Hilgen et al., 2012) and placed at about 19.5 Ma. Other significant mammalian events occur within MN3, including the 'cricetid vacuum' and the dispersal of gomphotheres and anchitheriine horses into Western Europe (Agustí et al., 2001). The MN3 reference locality is Winteshof-West (Germany) a karstic fissure with an estimated age of 18.5-17.5 Ma (Hilgen et al., 2012). The lower boundary of MN4 is marked by the first common occurrence of the cricetid *Democricetodon* at about 17.2 Ma (Hilgen et al., 2012). The first record of additional cricetid genera (*Megacricetodon, Eumyarion*) occurs later within the MN4 (e.g., see Van der Meulen et al., 2011, 2012). La Romieu (France) is the reference locality for MN4 and has an estimated age of 17.1-16.7 Ma (Hilgen et al., 2012). Criteria for defining the lower boundary of MN5 vary. While Hilgen et al. (2012) consider the last occurrence of the eomyid *Ligerimys florancei* and place this boundary at 16.4 Ma, Agustí et al. (2001) consider the first occurrence of the cricetid *Megacricetodon collongensis*, which following Daams et al. (1999b) they place at 16 Ma in the Calatayud-Montalbán Basin. However, this material has been recently assigned to different *Megacricetodon* species (*Megacricetodon vandermeuleni, Megacricetodon alvarezae;* see Oliver Pérez, 2015), so this definition should be reviewed. Additional small mammal occurrences within MN5 include the minute eomyid *Keramidomys* and later on the cricetid Cricetodon (Abdul Aziz et al., 2009; Kälin and Kempf, 2009). The first record of *Cricetodon* is strongly diachronic, occurring at about 14 Ma in the Iberian Peninsula, almost one million years later than in Central Europe (see Van der Meulen et al., 2011, 2012). The reference locality for the MN5 is the Faluns de Pontlevoy-Thenay (France), representing shallow marine to transitional sands rich in fossil mammals and invertebrates. The age of this site is estimated around 15 Ma (Hilgen et al., 2012).

4.4.3 REGIONAL AGES AND LOCAL BIOZONES

As already mentioned in chapter 4.4.1 some researchers followed a strict stratigraphic approach for the definition of mammal-based chronological divisions of the European Neogene. This can be traced back to the late 19th century, when Italian paleontologist Lorenzo Pareto (Pareto, 1865) introduced the Villafranchian for terrestrial sediments now considered to be equivalent to part of the Pliocene and the earliest Pleistocene. In the 1950s Catalan paleontologist Miquel Crusafont would introduce the Vallesian age for the early late Miocene (Crusafont, 1950), which is characterized by the first appearance in Europe of hipparionine horses and has its stratotype in the Vallès-Penedès Basin. The same author would also introduce the Turolian (Crusafont, 1965), the mammal age following the Vallesian and with a stratotype in the Teruel Basin, also in Spain. Indeed, the rich, continuous and well exposed Miocene continental sequences of east and central Spain have logically implied a preference for a stratigraphic approach rather than a faunal one. During the second half of the 20th century Dutch paleontologists Remmert Daams and Matthijs Freudenthal working in the east-central basins strongly championed this approach and defined two land mammal ages: the Ramblian and the Aragonian. The Aragonian had been first proposed by Fahlbusch (1976) but was formally defined by Daams et al. (1977) as the time interval between the first occurrence of the equid *Anchitherium* and *Hipparion*, which defined the lower boundary of the Vallesian. The stratotype for this new stage is the area near Villafeliche (Aragon, Spain), in the Calatayud-Montalbán Basin. This area includes an astonishing number of fossil sites, but these have delivered mostly small mammals. Daams et al. (1977) already proposed a tripartite division of the Aragonian into lower, middle and upper and provided a correlation with MN zones. As continued research in the Aragonian type area increased the amount of available material and improved resolution Daams and Freudenthal (1981) proposed a finer division of this age into seven local biozones identified by a letter, from A (the oldest biozone) to G. In addition, these authors included two biozones for the early Vallesian in the Calatayud-Daroca Basin (H and I). Some of these biozones would be further subdivided into subzones (particularly zones D and G) in later works (Daams and Freudenthal, 1988a, b; Daams et al., 1999a, b; Van der Meulen et al., 2012; García-Paredes et al., 2016). On the other hand, the age of zone boundaries has been established with great accuracy thanks to a combination of bio- and magnetostratigraphic methods (Krijgsman et al., 1996, Daams et al., 1999a, b; Van der Meulen et al., 2012; García-Paredes et al., 2016).

The Ramblian age is particularly controversial, starting with its definition. *Anchitherium*, which according to the original definition of the Aragonian age (see Daams et al., 1977) marks its lower boundary turned out to be extremely rare in the type area. Indeed, this taxon was of little use as biostratigraphic marker in an area which mostly included localities that had only delivered small mammals. Therefore, Daams et al. (1987) redefined the lower boundary of the Aragonian and introduced the term Ramblian. The base of the Aragonian was characterized by the first common occurrence of cricetids of the genus *Democricetodon* and despite strong criticism (e.g., De Bruijn et al., 1992) this criterion has remained unchanged to date. The Ramblian age correlates approximately to the MN3 and area is this stage is Navarrete del Rio in Calamocha, Teruel (Aragon, Spain). The former Aragonian zone A was included within the Ramblian, and an older zone Z was also introduced. The lower boundary of the Ramblian has been loosely defined by the first occurrence of the eomyid *Ligerimys*. Older Miocene biozones have been defined (X and Y; see Daams and Van der Meulen, 1983) but these are generally not included in the Ramblian (rather they are considered Agenian) and only seldom used. Magnetostratigraphic data have helped constrain the age of some Ramblian sites in the type area (Daams et al., 1999b) as well as in the Ebro Basin (Larrasoaña et al., 2006; Agustí et al., 2011), but the age of the lowermost boundary has not been refined and is currently estimated between about 20.5 and 19.3 Ma, thus being coincident with the MN2/MN3 boundary (Agustí et al., 2001; Larrasoaña et al., 2006; Hilgen et al., 2012).

The Aragonian and particularly the Ramblian are often regarded as regional stages restricted to the Iberian Peninsula even if the criteria used to define their boundaries could easily be extended to other areas of Europe. However, the fine local biozonations established in the type areas are unlikely to match other equivalent European records. For the early and middle Aragonian this has been tested by Van der Meulen et al. (2011, 2012) comparing the Calatayud-Montalbán record to that of the North Alpine Foreland Basin of Switzerland. These authors not only showed that the Iberian local biozones cannot be extended to the Swiss record, but also that certain bioevents used to define local zone (and MN) boundaries are certainly diachronic. Yet, as will be discussed particularly in chapters 9 and 10 this local zonation can be broadly applied to the Vallès-Penedès early Miocene record.

The time interval covered in this thesis comprises part of the late Ramblian (zone A) and the early Aragonian (zones B and C), including the early/middle Aragonian boundary (between zones C and D). Ramblian zone A ranges from about 19.3 to 17 Ma (lower boundary after Larrasoaña et al., 2006; upper boundary after Agustí et al., 2011). Its lower boundary is defined by the last common occurrence of the cricetid *Eucricetodon*, so this time interval corresponds to the ‘cricetid vacuum’. Therefore, rodent faunas are characteristically dominated by the eomyids *Ligerimys*, and *Pseudotheridomys* and devoid of cricetids other than *Melissiodon*, which is generally rare and not even recorded in the type area (Van der Meulen et al., 2012). Regarding the glirids, the same genera present in the older zone Z persist and are abundant during zone A. In the Calatayud-Montalbán Basin *Democricetodon* is present in the uppermost part of this zone, but it is rare (Van der Meulen et al., 2012). Zone B is the first biozone of the early

Aragonian and is defined as the interval between the first common occurrence of *Democricetodon* hispanicus and the first occurrence of *Megacricetodon primitivus*. This is a short-lasting biozone which in the type area it ranges from about 16.8 to 16.5 Ma (Van der Meulen et al., 2012). The eomyid *Ligerimys florancei* is also recorded within this zone. Zone C is divided in the type area into subzones Ca and Cb. Subzone Ca ranges from 16.5 to 16.3 Ma and is defined by the concurrent range of the cricetids *Megacricetodon primitivus* and *Democricetodon moralesi* (Van der Meulen et al., 2012). *Democricetodon decipiens* replaces *D. hispanicus*. Within this zone two *Ligerimys* species, *L. florancei* and *L. ellipticus*, are recorded. However, *L. ellipticus* replaces *L. florancei* in the youngest localities and persists as the only eomyid species before the appearance of *Keramidomys*. The cricetid *Eumyarion* is present at Teruel and Valencia but is not reported from the Aragonian type area until the following subzone. Subzone Cb ranges from about 16.3 to 15.9 Ma in the type area and is characterized by the concurrent range of *Democricetodon moralesi* and *L. ellipticus* (Van der Meulen et al., 2012). In addition, a second *Democricetodon* species, *D. franconicus*, is first recorded within this zone. The assemblages are dominated by *L. ellipticus* and cricetids and the glirid *Microdyromys koenigswaldi* is common. The last common occurrence of the eomyid *L. ellipticus* at 15.9 Ma marks the boundary between zones C and D, as well as the boundary between the early and middle Aragonian. Subzone Da comprises the interval between this bioevent and the first record of *Megacricetodon vandermeuleni* at about 15.8 Ma (referred to as *Megacricetodon* n. sp. 1 in Van der Meulen et al., 2012; see also García-Paredes et al., 2016). The successive subzones within zone D (Db, Dc and Dd) are characterized by the first appearance of cricetid species of the genera *Megacricetodon* and *Democricetodon*. Faunas in zone D are entirely dominated by cricetids of these genera.

It is worth noting that the local subdivision of the Aragonian in the type area into multiple subzones is subject to the interpretation of the evolution of the genus *Democricetodon* and has been strongly contested by Freudenthal (2006), to the point that a different ordering and chronology of the sites has been proposed. However the proposals by Van der Meulen et al. (2012) and García-Paredes et al. (2016) were followed regarding biozone definition and chronology. The correlation of the Vallès-Penedès early Miocene sites to the Ramblian and Aragonian local zones is a recurrent subject in this work and is thoroughly discussed in chapters 9 and 10.

4.5 MAGNETOSTRATIGRAPHIC METHODS

Earth's magnetic field most interesting characteristic is that it reverses polarity at irregular intervals, creating a 'bar code' of alternating normal (north oriented) and reverse (south oriented) polarity chrons with characteristic uneven durations. Magnetostratigraphy refers to the application of the principles of stratigraphy to the pattern of polarity reversals registered in the rock succession through natural magnetic acquisition. Different kinds of ferromagnetic minerals in rocks align with Earth magnetic field at the time of rock formation, either from magma solidification or when magnetic grains of detrital origin are deposited. The latter is the most common situation in sedimentary successions and is called detrital remanent magnetization. However, the natural magnetization originated at time of rock formation may be overprinted by magnetic components acquired later in geological history, for example through weathering of the rocks or after thermochemical reactions associated to tectonics or burial processes. When using paleomagnetic and rock magnetic techniques at the laboratory and the field one must verify that the sample faithfully records magnetic polarity at the time of formation (Langereis et al., 2010; Garcés and Beamud, 2016).

The Gemagnetic Polarity Time Scale (GPTS) is the reference 'bar code' showing the pattern of magnetic polarity reversals through geological time and their duration (figure 4.3). The template of magnetic anomaly patterns recorded from the ocean floor was (and still is) the central tool for the construction of the GPTS from the Early Cretaceous (ca. 124 Ma) onward. Combined magnetostratigraphic, biostratigraphic and radioisotopic results of deep-sea sediments and land-based sections have improved the accuracy of the GPTS (Langereis et al., 2010; Garcés and Beamud, 2016). Correlating the polarity reversal pattern retrieved from a rock succession to the reference GPTS is a standard method for relative dating applicable to a wide array of sedimentary (and also volcanic) rock types formed in different environmental contexts (continental, marine). The latest version of the GPTS is that of Ogg (2012) and is the one used throughout this work.

The samples for magnetostratigraphic analysis consist of a series of small rock cylinders extracted using a hand core drill with a diamond drill bit. Occasionally hand samples (chunks broken of the rock face) may also be taken. Orientation of the samples must be carefully recorded, as well as geographical coordinates and stratigraphic position. The number of samples to be taken is variable, but generally several samples are retrieved from each site to average sampling errors. Spacing of the sampling sites within a stratigraphic sections is also variable, depending on the length and lithology of the sections or sedimentary rates amongst other factors, but must be done in approximately regular intervals (Garcés and Beamud, 2016). Once the samples are at the laboratory will be processed to obtain their natural remanent magnetization (NRM). After these analyses, all the samples from the same site are averaged to obtain the magnetic polarity of the site. Then each of the sampling sites, together with its polarity results, is position in the stratigraphic sections of interest in order to identify stretches of the chapter with the same magnetic polarity. Each one of these stretches with the same polarity is called local magnetozone. Magnetozones are labelled, such as N1, N2, N3...to refer to local magnetozones of normal polarity, and a local magnetostratigraphy is obtained. This local magnetostratigraphic profile is a 'bar code' to be compared with the reference, the GPTS. Magentozones are then identified as polarity chrons (or subchrons) and matched with the GPTS, thus providing a relative age for the different sampling sites (Langereis et al. 2010; Garcés and Beamud, 2016). Sufficiently long local magnetostratigraphical profiles (usually in the range of hundreds of meters) produce a characteristical patern of polarity reversals that can be directly linked to the GPTS. In the case of shorter sections, or for those sections affected by faulting, magnetostratigraphy has to be combined with other dating techniques, such as biostratigraphy or radioisotopic dating (if possible), to provide 'anchor' points that can help resolving the correlation of local magnetostratigraphic profiles.

Magnetostratigraphic studies of the Vallès-Penedès Basin have been aimed at the Vallesian (early late Miocene) and late Aragonian (late middle Miocene) part of the record (Garcés, 1995; Garcés et al., 1996; Agustí et al., 1997; Moyà-Solà et al., 2009; Casanovas-Vilar et al., 2011, 2016b; Alba et al., 2017). Early Miocene sequences of this are had not been previously studied, except for the Sant Mamet (=Rubí in figure 2.15 chapter 10) chapter (Garcés, 1995). Seven different sections were sampled for magnetostratigraphy: la Costablanca, Molí de Can Calopa, Martorell – Santa Maria de Vilalba, Gelida, els Casots, Rubí and El Papiol (see chapter 2.3 and chapter 10). Despite the variety of lithologies and grain sizes all sections include abundant mudstone beds, which were sampled with a density of 1-2 m/site or higher. This ensures sufficient temporal resolution to rely on the completeness of the magnetostratigraphic record at the level of chrons and subcrhons of the GPTS. Biostratigraphic data as well as intercalations with shallow marine sediments, particularly by the beginning of the middle Miocene, contribute to refine the chronology of the most important sites and bioevents (see chapter 10). Most sections were sampled by the early 2000s by Miguel Garcés, except for Sant Mamet, which was sampled by the mid 1990s, and els Casots, which was not sampled until 2019. Sampling of els Casots was challenging because the fossil locality occurs at the surface and there are almost no sections nearby exposing the lower part of the Miocene sections. Therefore, in spring 2019 exploratory core drilling at els Casots was undertaken and a 30-m-thick core was retrieved to be sampled for magnetostratigraphy. Samples were drilled from the oriented core, taking into account direction and dip of the bedding plane to ensure accuracy (see Casanovas-Vilar et al., 2019). A preliminary magnetostratigraphy for the early to middle Miocene of the Vallès-Penedès record is presented and discussed in chapter 10.

4.6 SMALL MAMMALS AS PALEOENVIRONMENTAL PROXIES

4.6.1 METHODS IN PALEOECOLOGY

Paleoecology is the study of the lifestyle of fossil organisms together with their relationships to each other and the environment they lived in (Brenchely and Harper, 1998). Paleoecology may be concerned about the ecology of a single organism (paleoautoecology) or have a broader scope, looking at entire assemblages or communities of organisms and their link to surrounding environment. In most studies, only part of the community is studied, such as the small mammal community or the freshwater mollusk community to cite two examples, and ecological functions of fossil taxa are established through analogies or homologies with living organisms. However, a fossil assemblage is by no means equivalent to a living community, as taphonomical biases have affected it, which puts severe constraints that have to be considered in paleoecological studies.

For example, transport can mix material from species inhabiting different habitats into a single accumulation site; relative abundances of the different species may not reflect actual species abundances in the living assemblage, etc. In the case of small mammals there is yet another important bias: predators as accumulation agents. It is thought that most of the small mammal accumulations, particularly in cave environments, derive from owl (or other raptors) pellets (see Andrews, 1990). Therefore, if these predators are selective, they may completely alter species composition and relative abundances in fossil sites as compared to living communities. All these potential taphonomical biases are to be considered, especially when quantitative rather than presence/absence data are used in paleoecological analyses. In addition, paleoecological studies should compare sites with similar taxonomic compositions and corresponding to similar sedimentary environments (i.e., there is no point in comparing a rodent assemblage recovered from a karstic site to a fossil macroflora recovered in lacustrine facies).

Attempts to reconstruct terrestrial paleoenvironments and paleoclimates are almost as old as paleontology itself. For example, in the 19th century the finding of mammals inhabiting tropical environments, such as hippopotamuses, as far north as England was interpreted by paleontologists such as W. Boyd Dawkins and Edouard Lartet as an evidence for different climatic regimes (for a review see Faith and Lyman, 2019: chapter 5). By the beginning of the 20th century, paleobotanists started using plant remains as paleoclimatic proxies (for a review see Peppe et al., 2018). On the one hand, following the ideas of Alexander von Humbolt that climatic tolerance strongly influences the distribution of plants, macrofloral and pollen assemblages consisting of multiple plant species (some of them belonging to living genera) were used to infer climatic parameters considering the geographical range and climatic tolerance of extant relatives. This method requires accurate taxonomical identifications, so at the same time an alternative approach based on leaf physiognomy was developed. This different method recognized that leaf size and shape correlates strongly with climate an represent the earliest example of taxon-free analyses. These methods would be later applied to vertebrates, particularly mammals. To this regard, researchers have considered the presence or relative abundance of one single or multiple indicator taxa presenting a narrow range of ecological tolerance, particularly for Pleistocene sites, which often include several species which are still extant (for a review see Faith and Lyman, 2019: chapter 5). However, as we go further back in time such inferences become difficult because most of the species and genera are extinct and some even lack extant, closely related relatives. This is an important difference between the paleomastological and paleobotanical record, as most modern plant genera are already known by the Neogene (or even earlier; see review in Peppe et al., 2018). Therefore, mammal paleontologists have considered taxon-free methods or ecomorphology, that is linking morphological form with a particular ecological context (Damuth, 1992). A notable, and broadly used example, is cheek tooth height (hypsodonty) in ungulates, which has been shown to correlate with precipitation and has been used to track precipitation patterns over time and space (Fortelius et al., 2002). Ecomorphology may consider a single taxon or whole communities. In the latter approach, ecological characteristics of each member of the paleocommunity, such as body size, diet and locomotion are considered. Counts of species in each one of these ecological categories (or ecovariables see Kovarovic et al., 2018) are then computed and used to characterize and compare extant and fossil communities (Andrews et al., 1979). These allows for broad environmental characterizations, for example, tropical forests include a higher proportion of frugivore and arboreal species than savannahs. However, this method does not allow for quantitative paleoeoenvironmental reconstructions, rather it is intended for assigning fossil faunal assemblages to a particular habitat type or making qualitative assessments (ordinal-scale) on given environmental variables such as temperature or rainfall. Yet, functions relating biological data and environmental variables can be derived to provide high-resolution quantitative estimates (see chapter 4.6.3).

Finally, there is a whole set of paleoecological methods that will not be discussed in here but that are increasingly popular and have only been occasionally applied to fossil rodents. These include the use of dental meso- and microwear or stable isotope analyses of dental enamel for paleodietary inferences (for an updated review of these methods see Croft et al., 2018).

4.6.2 PALEOENVIRONMENTAL INFERENCES USING SMALL MAMMALS

The introduction of systematic screen-washing methods by the 1960s (see chapter 4.1) allowed assembling huge small mammal collections from many different sites. Although cheek teeth were usually the only material identified to the genus or species level, these already provided a significant sample suitable for quantitative analyses. An early example of such kind of analyses focusing on Iberian Neogene rodents is the seminal work by Dutch paleontologists Anne Van de Weerd and Remmert Daams (1978). Heavily influenced by pollen analysis, these authors classified fossil rodents according to their humidity preferences (Van de Weerd and Daams, 1978: 460) and considering the relative abundances of 'wet' rodents constructed a humidity curve for the Iberian Neogene record. The curve is basically a 'pollen diagram' were pollen grains are rodent teeth (Van de Weerd and Daams, 1978: 465). The basic method used to assign humidity preferences to extinct rodents is actualism, although broad ecomorphological inferences based on cheek teeth morphology are also considered in a few instances. This method was later refined and used to build more detailed relative humidity and temperature curves (e.g., Daams and Van der Meulen, 1984; Daams et al., 1988).

Jordi Agustí also applied the technique to the Miocene rodent faunas of the Vallès-Penedès Basin (Agustí, 1981), although preferred considering rodent families rather than ecological groups. These methods would be latter complemented with and compared to large-mammal-based estimates (Agustí et al., 1984). Until the 1990s, these analyses relied on the use of rodent teeth as the 'pollen grains' of mammal paleontology to construct diagrams of relative abundances, no statistics were used. Van der Meulen and Daams (1992) were the first to use multivariate statistics (principal components analysis [PCA], cluster analysis) to study the rodent record in relation to long-term paleoenvironmental changes. These methods were applied to 59 Miocene rodent assemblages from the Calatayud and Teruel Basins to identify which species tended to co-occur more frequently as well as to identify the main components of the faunal assemblage at each moment. The distribution of the different clusters, and the main principal components of the rodent faunas was then represented as function of time. Finally, the results were interpreted after the ecological characterization of the main rodent taxa using the usual actualistic approach (as in Van de Weerd and Daams, 1978; Daams and Van der Meulen, 1984; Daams et al., 1989). However, for the first time the authors considered the predominant life-history traits (r or K strategy) in extant representatives of the rodent families. The final result was the usual relative humidity and temperature curves, but this time derived from multivariate analyses rather than simple relative abundance of rodent groups.

Later works included even more sophisticated methods. For example, Van Dam and Weltje (1999) used end-member modelling (a kind of linear mixing model) and more detailed rodent ecological groups to provide qualitative estimates for several climatic parameters (humidity, temperature, seasonality) for the late Miocene of the Teruel Basin. Other authors have used multivariate statistics or other complex computation methods but have mostly focused in paleobiogeographical questions rather than paleoclimatic reconstruction (e.g., Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008; Furió et al., 2011).

On the other hand, Hernández Fernández (2006) provided one of the first quantitative estimates based on the bioclimatic analysis of the European late Pleistocene rodent faunas. This method considers the distribution of extant mammalian species in ten extant terrestrial biomes (following Walter, 1970 biome classification) and assigns a score to each locality (recent or fossil) on the basis of the percent of the fauna found at that locality that is characteristic of each biome (Hernández Fernández, 2001; Hernández Fernández and Peláez-Campomanes, 2003, 2005). Then, transfer functions (see chapter 4.6.3) are derived from extant data using multiple linear regressions and can be used to provide quantitative estimates of up to eleven climatic factors (temperature and precipitation, plus seasonality in these two variables). These methods have also been applied to the Miocene rodent record of the Ibero-Occitan region by Gómez Cano (2013). However, since most rodent genera and species are extinct, extant related species had to be used instead , which might be controversial (see section 4.6.3).

4.6.3. Paleoprecipitation estimates

As explained in chapter 4.6.2, rodents, as well as other small mammals, have been profusely used in paleoenvironmental and paleoclimatic reconstruction employing increasingly sophisticated methods over the past decades. However, until relatively recently these were only used to provide qualitative estimates of environmental variables, even if complex statistic methods were used (e.g., Van der Meulen and Daams, 1992; Van Dam and Weltje, 1999). Hernández-Frenández (2006) and Van Dam (2006) were the first to provide quantitative small-mammal-based estimates for several climatic parameters. Besides promising more detail in paleoenvironmental reconstruction, quantitative estimates potentially avoid the subjectivity inherent to other analytical approaches. The general premise (see review in Faith and Lyman, 2019) is the existence of a relationship between environmental variables (e.g., precipitation values) and biological data (e.g., species diversity of arboreal mammals). Then a training set of modern biotic communities from various sites is compiled together with their associated environmental parameters. The relationship between the modern biotic communities and the environmental variables is tested and used to derive a function (usually but not always a simple or multiple regression), known as the transfer function. The transfer function is applied to the fossil data (fossil sites) and provides quantitative estimates of the paleoenvironmental variables based on present-day relationships.These methods have several important assumptions, most notably:

I. The target environmental variable is an important determinant of the taxonomic composition.

II. Environmental variables other than the target one have negligible effects on the taxonomic composition.

III. Taxonomic uniformitarianism. The taxa included in the modern training set are the same as in the fossil assemblages and their responses to the environment through time and space are also the same. This assumption can be relaxed using taxon-free approaches (see chapter 4.6.1).

Additionally, these methods require of a robust extant dataset, with an adequate geographical coverage and encompassing enough variation in environmental variables. Furthermore, the transfer function must be accurate and unbiassed, allowing for accurate predictions.

Some of the methods that have been devised for quantitative paleo-environmental reconstruction based on small mammal faunas cannot be applied to the Miocene because they violate the assumption of taxonomic uniformitarianism. For example, the bioclimatic analysis of Hernández-Fernández (Hernández Fernández, 2001; Hernández Fernández and Peláez-Campomanes, 2003, 2005; see chapter 4.6.2) is based on the occurrence of extant species in different terrestrial biomes. As many of these species (or related species within the same genus) are recorded in the Pleistocene, the method works well for recent ages, but presents many problems when going further back in time (see chapter 4.6.2). A solution to this problem may be using higher taxonomic categories (subfamily, family), but then the method will lose resolution. Legendre et al. (2005) faced a similar analytical problem. These authors found a strong correlation between the number of extant sigmodontine species (including not only sigmodontines but also neotomines and tylomines in the original work) and mean annual dayly temperature. Then applied their transfer function to the

French Miocene record considering Miocene cricetids (sensu lato) as likely equivalents of sigmodontines. This method results in unrealistically low predictions when only a few species are recorded, yielding an estimate of just 11.8 ºC for the late Vallesian site of Soblay, which is lower than present mean annual temperature for the same region. Quite obviously, the method cannot be applied to early Miocene sites, which may include just one cricetid species and sometimes none (especially during the 'cricetid vacuum' see chapter 3.3.4).

Taxon-free methods are better suited for the Miocene record, and have been used to estimate paleoprecipitation (Van Dam, 2006; Van Dam and Utescher, 2016). Overall, this method relates the amount of precipitation to the number of arboreal and invertivorous species of small mammals. Previous studies have shown the relationship between the amount of precipitation and mammal diversity, such as the positive correlation between the number of primate species and mean annual rainfall (Reed and Fleagle, 1995). Kay and Madden (1997) already found a strong positive correlation between the number of arboreal and frugivore species in extant tropical South American mammal communities. Van Dam (2006) builds on this earlier research and considers about 20 extant localities from Europe, Asia Minor and North Africa. Counts of the number of invertivore and arboreal species of eulipotyphlans, lagomorphs and rodents are compiled. Chiropterans are excluded, as well as semi-aquatic species (beavers, desmans) because their presence is ultimately linked to the local occurrence of water bodies rather than to rainfall. Then invertivory and arboreality indices are computed dividing the number of species within a given category by the total number of species in the locality as follows:

Invertivore index (PI)

$PI=100 \times NI/N$

NI=number of invertivore species

N=total number of species

Arboreality Index (PA)

$PA=100 \times NA/N$

NA=number of arboreal species

N=total number of species

Both measures are taxon-free because they rely on the relative diversity of species belonging to specific dietary and locomotion categories, rather to the presence of indicator taxa. The presence of primary consumers with a arboreal feeding habitat and/or locomotion is dependent on the productivity and complexity of the vegetation which are, in turn, largely dependent on precipitation (Kay and Madden, 1997). Gliding mammals, such as flying squirrels, are also included within this category. On the other hand, as secondary consumers, insectivorous species profit from the abundance of insects and other small invertebrates (earthworms, snails) in moist environments such as forests and humid soils, and hence are dependent on precipitation as well. In addition, small-sized insectivores such as shrews display high metabolic rates, resulting in high water loss and overheating in warm and dry areas (Reumer, 1995). Invertivory and arboreality index are found to show significant correlations with precipitation values and the following transfer functions can be derived (see Van Dam, 2006; correlation coefficient R2 is indicated in each case):

Mean annual precipitation (*MAP*):

$MAP=11.080+47.178\ln^{2}(PA+1)+12.492PI$
$(R^{2}=0.82)$

Precipitation of the driest month (*LMP*):

$LMP=1.525+11.250\ \ln(PA+1)$
$(R^{2}=0.80)$

Precipitation of the wettest month (*HMP*):

$HMP=8.108+1.674\ln^{3}(PA+1)+1.896PI$
$(R^{2}=0.74)$

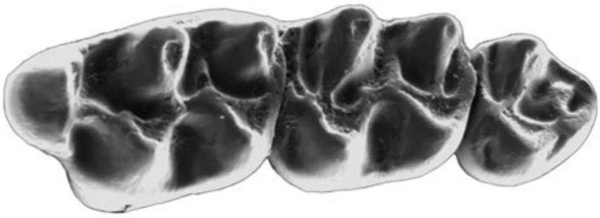
The caracterization of fossil taxa as invertivores is relatively straightforward as invertivore species are characterized by sharp-pointed cusps and deep valleys. Eulipotyphlans are the typical representatives, but some rodents such as the muroid *Melissiodon* are also regarded as insectivores because of the presence of certain unique dental features and a particular mandible shape (Van Dam, 2006; Van Dam and Utescher, 2016; see also chapter 3.3.4 and chapter 5). Inference of arboreal/scansorial adaptations is more controversial because cheek teeth are the only elements known of most extinct micromammals. Yet, some exceptional fossils have shown that some eomyids (*Eomys quercyi*; Storch et al., 1996), the dormouse *Glirulus lissiensis* (Mein and Romaggi, 1991) and obviously flying squirrels (although there is only strong evidence for *Miopetaurista*, see Casanovas-Vilar et al., 2018) were gliders. Van Dam (2006) and Van Dam and Utescher (2016) relied on actualism to consider the spiny dormouse *Neocometes* (family Platacanthomyidae) and some extinct squirrels (*Sciurus*, *Dehmisciurus* and all the alleged flying squirrels) as arboreal.

Semi-aquatic	Invertivorous	Arboreal
Desmaninae	Eulipotyphla	Pteromyini
Asoriculus	*Melissiodon*	Ratufini
Neomys		*"Sciurus" giganteus*
Macroneomys		*Sciurus*
Castoridae		Glirinae
Mimomys hassiacus-savini		Bransantoglirinae
Arvicola		*Glirulus*
Dolomys nehringi-milleri		*Paraglirulus*
Kislangia		*Microdyromys complicatus*
		Microdyromys koenigswaldi
		Microdyromys praemurinus
		Microdyromys remmerti
		Vasseuromys
		Ramys
		Pseudotheridomys
		Eomyodon
		Keramidomys
		Neocometes

Table 4.1: Neogene fossil taxa with semi-aquatic locomotion, arboreal feeding habitat and invertivorous diet. Modified from Van Dam, 2006; Van Dam and Utescher, 2016.

Concerning the glirids, the authors relied on earlier work (Van der Meulen and De Bruijn, 1982; De Bruijn, 1998) that had recognized that arboreal species generally show a more complex molar morphology than terrestrial ones, and considered arboreal those species with seven or more transverse ridges on the M1/2. Dental complexity is used in the case of eomyids, and species with five of more transverse ridges (pentalopohodont) are regarded as arboreal, and those with four (tetralophodont) or less as terrestrial. This follows the work of Hershkovitz (1967) on New World cricetids, who found that pentalophodont species tend to live in forests whereas those with a simpler molar morphology generally inhabit open country. These criteria could also be applied to Miocene muroids, but this group was not considered in the ecological classification of Van Dam (2006) and Van Dam and Utescher (2016). The classification of the considered fossil taxa as arboreal, invertivore or semi-aquatic (excluded) is shown in table 4.1.

In chapter 10 we use the transfer functions of Van Dam (2006) and Van Dam and Utescher (2016) to provide precipitation estimates for selected early Miocene sites of the Vallès-Penedès Basin. Only those localities including more than 100 identified small mammal cheek teeth are considered. We also excluded the localities in which one of the orders (rodents, lagomorphs or eulipotyphlans) has not been fully studied or is absent. This has forced the exclusion of els Casots site, which did not deliver eulipotyphlan remains (or they were lost). Small mammals are not used to estimate past temperatures because available transfer functions seem inadequate (see earlier discussion on Legendre et al., 2005). Therefore, estimates based on other proxy data including pollen and macroflora and ectothermic vertebrates from the Vallès-Penedès Basin are incorporated (see chapter 10 and references therein). Finally, considering paleoprecipitation and paleotemperature estimates, the most likely environments or habitats associated to each site are discussed. Moreover, small-mammal-based paleoprecipitation estimates were calculated for several European regions besides the Vallès-Penedès Basin: Calatayud-Montalbán Basin, Rubielos de Mora Basin, Ribesalbes-Alcora Basin, Foia de Bunyol, Southern France, Swiss North Alpine Foreland Basin and Southern Germany. Data were primarily taken from Van der Meulen et al. (2012) for Calatayud-Montalbán, from Crespo Roures (2017) for the Ribesalbes-Alcora and Foia de Bunyol basins (Valencia), from Van den Hoek Ostende et al. (2017) for Rubielos de Mora Basin (Teruel) and from Kälin and Kempf (2009) for Switzerland. Data from selected French and German sites were downloaded from the NOW database of fossil mammals (The NOW Community, 2020). In chapter 10, the results of these comparisions between European regions will be discussed.



Chapter 5: "A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallès-Penedès Basin (Catalonia)"

Journal of Vertebrate Paleontology

Published: November 2018

Journal of Vertebrate Paleontology e1520714 (9 pages)

DOI: 10.1080/02724634.2018.1520714

ARTICLE

A REVIEW OF THE GENUS *MELISSIODON* (CRICETIDAE, RODENTIA) IN THE VALLÈS-PENEDÈS BASIN (CATALONIA)

SÍLVIA JOVELLS-VAQUÉ and ISAAC CASANOVAS-VILAR*
Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP,
C/de les Columnes, s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain
silvia.jovells@icp.cat; isaac.casanovas@icp.cat

ABSTRACT—*Melissiodon* is a plesiomorphic cricetid genus characterized by its unique molar morphology, defined by many pits surrounded by thin and high ridges. This genus is endemic to Europe and ranges from the early Oligocene to the early Miocene. However, it is generally rare in rodent assemblages, particularly during the Miocene, rich samples only being available from a few German sites. Here we review all the *Melissiodon* material from the Vallès-Penedès Basin (Catalonia, Spain). This genus is present in several early Miocene sites ranging from biozone MN3 to MN4, but the scarcity of the material has precluded confident taxonomic assignments. Furthermore, the validity of *Melissiodon arambourgi*, a species based on a single specimen from the Vallès-Penedès site of el Fallol, has been questioned. After recent field campaigns, the available material has increased significantly, which allows for more robust taxonomic conclusions. All the Vallès-Penedès specimens are here referred to *Melissiodon dominans*, a widely dispersed species in the European early Miocene. After a revision of the holotype of *M. arambourgi*, we confirm that the original description and figures do not agree with it and conclude that it is a junior subjective synonym of *M. dominans.* The last occurrence of *Melissiodon* in the area is in the Sant Mamet site, located just a few meters below middle Miocene marine deposits, and represents one of the youngest records of this long-ranging genus.

Citation for this article: Jovells-Vaqué, S., and I. Casanovas-Vilar. 2018. A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallès-Penedès Basin (Catalonia). Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2018.1520714.

INTRODUCTION

Melissiodon is one of the more peculiar cricetid genera and owes its name, meaning 'honeycomb tooth,' to its unique molar morphology characterized by many pits surrounded by thin and high ridges. The genus is exclusively known from Europe and has a long stratigraphic range spanning from the early Oligocene (MP23; Dawson, 2003) to the latest early Miocene (MN4; Mödden, 1999). Given its peculiar dental morphology, *Melissiodon* has been often regarded as a monotypic subfamily (Schaub, 1925; Mein and Freudenthal, 1971a) or family (Freudenthal et al., 1992; Mödden, 1999). However, Ünay-Bayraktar (1989) allocated her genus *Edirnella*, from the middle Oligocene of the Turkish Thrace Basin, to the subfamily Melissiodontinae. More recently, Wessels et al. (2018) have described a diverse array of melissiodontines from the late Eocene and early Oligocene of southeastern Serbia. Yet the phylogenetic position of *Melissiodon* and the validity of the Melissiodontidae/nae is highly controversial. A recent phylogenetic analysis by Maridet and Ni (2013) indicated that *Melissiodon* is related to Oligocene–early Miocene Asian and Anatolian cricetid taxa and should be included within the subfamily Cricetopinae (which would be a senior synonym of Melissiodontinae). It would further define a monophyletic group, the tribe Melissiodontini, with the genera *Selenomys* and *Mirabella*. Although they share a number of synapomorphies (Maridet and Ni, 2013), the overall molar morphology of these genera is strikingly different. As the genus name indicates, the molars are selenodont in *Selenomys*, whereas *Mirabella* presents semihypsodont molars with a pattern more similar to the basic cricetid morphology (Schaub, 1925; Mein and Freudenthal, 1971b). However, all these genera share several plesiomorphic characters, such as relatively long third molars with no reduction of the posterior cusps or the presence of numerous transverse ridges. In addition, the skulls of *Melissiodon* and *Selenomys* shows a hystricomorphous zygomasseteric structure (no cranial material is known for *Mirabella*). This latter character argues for a basal position of melissiodontins in cricetid phylogeny, because derived taxa are all myomorphous (Flynn, 1985; Vianey-Liaud, 1985). Regarding *Edirnella*, the other alleged 'melissiodontine' known at that time, Maridet and Ni (2013) assigned it to the subfamily Pseudocricetodontinae, which agrees with the less derived dental morphology of this genus. However, this phylogenetic analysis did not consider enamel microstructure (schmelzmuster) of the lower incisor, which is known to be an important systematic character (Koenigswald, 2004; Kalthoff, 2006). *Melissiodon*, *Edirnella*, and the newly erected Serbian genus *Mogilia* all share the primitive type 1 schmelzmuster in their lower incisors, which, in the opinion of some authors (Wessels et al., 2018), would justify including them in a single Melissiodontinae subfamily.

Little is known about the paleobiology of *Melissiodon*, but its unique dental morphology and peculiar mandible shape suggest a diet and lifestyle different from that of contemporaneous cricetids. Even though the postcranial skeleton is not known, Mein and Freudenthal (1981) suggested that its cheek teeth may reflect a frugivorous diet and even ventured that this

---

*Corresponding author.

cricetid may have been arboreal. As first noted by Schaub (1920), the mandible of *Melissiodon* is indeed peculiar, because it is low, with an elongated diastema and posteriorly situated masseteric scar. Furthermore, its lower incisors are relatively reduced. This aberrant mandibular shape has been likened to that of Sulawesi and Phillippines shrew rats (*Echiotrix*, *Crunomys*), murids that forage on invertebrates, mostly earthworms (Hordijk et al., 2015). Therefore, these authors inferred an insectivorous diet for *Melissiodon*. In either of these two scenarios (frugivorous or insectivorous), *Melissiodon* would have preferred humid forested environments where its food resources would be more abundant. Although these interpretations should be tested with additional data, they are supported by the fact that rich collections of this genus come from localities where forest-dwelling rodents (such as dormice and tree squirrels) are diverse and abundant (e.g., Wintershof-West, Germany, MN3; Dehm, 1950).

Melissiodon is generally a rare find. The only samples with abundant specimens have been recovered in a few German sites (Wintershof-West, Schnaitheim, Gaimersheim, Bernloch; Hrubesch, 1957), and some species are only known from a single or a few specimens (*M. schlosseri*, *M. arambourgi*; Mödden, 1999). In the Iberian Miocene, the genus has only been reported from some sites of the Calatayud-Montalbán and Teruel basins (Aragon) ranging in age from MN2 to MN4 (Daams et al., 1987; Sesé, 1987; Van der Meulen et al., 2012); from a few MN4 sites of the Bunyol and Ribesalbes-Alcora basins (Valencia; Adrover et al., 1987; Crespo et al., 2014); and from a few MN3 sites of the Vallès-Penedès Basin (Catalonia; Crusafont et al., 1955; Agustí, 1981). In most of these sites, just a few specimens have been recovered and are generally ascribed either to *Melissiodon* cf. *dominans* or to *Melissiodon* sp. In contrast, a new species, *Melissiodon arambourgi*, was erected on the basis of the single specimen recovered at el Fallol, in the Vallès-Penedès Basin (Crusafont et al., 1955). This species would be related to *M. dominans*, present at contemporaneous sites from central Europe, but differs from all other *Melissiodon* species mainly by the morphology of the protoconid hind arm. Therefore, Hrubesch (1957) proposed an independent origin of this species in his detailed review of the genus. Agustí (1981) described new *Melissiodon* material from the Vallès-Penedès (Molí de Can Calopa, Sant Andreu de la Barca) and reviewed the holotype of *M. arambourgi*, concluding that the published figures and description did not agree with it. This author concluded that the Vallès-Penedès material was not significantly different from *M. dominans* and synonymized *M. arambourgi* with it, an opinion that has been generally followed (Mein and Freudenthal, 1981; Sesé, 1987; but see Mödden, 1999). Recently, field campaigns in the early Miocene deposits of this area have been resumed and have provided rich micromammal samples that occasionally include new *Melissiodon* remains. Here we describe this new material and further review all other specimens recovered in the Vallès-Penedès Basin.

GEOLOGICAL SETTING AND AGE

The Vallès-Penedès Basin (Barcelona, Catalonia; Fig. 1) is an elongated half-graben parallel to the coastline and limited by the Catalan Coastal Ranges that has provided a rich record of continental vertebrates spanning most of the Miocene (Casanovas-Vilar et al., 2016). The studied material was recovered from early Miocene localities that have been dated by means of litho- and biostratigraphy (Agustí, 1982; Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016), although their age could be further refined after ongoing magnetostratigraphic studies. Turó de les Forques 1 is the oldest site and is placed in a small outcrop of the Basal Breccia Unit, a lithostratigraphic formation that comprises the oldest sediments in the basin (Cabrera, 1981; Agustí et al., 1985; Cabrera et al., 1991; de Gibert and Casanovas-Vilar, 2011). The remaining sites belong to the overlying Lower Continental Units, corresponding to the early Miocene and cropping out only near the southern margin of the basin. These units consist of intensely red alluvial fan facies with local carbonate and evaporite deposits corresponding to shallow lake systems. Sant Andreu de la Barca 1 and Molí de Can Calopa sites are located in two different ephemeral lake systems. All these localities are correlated to biozone MN3 (Ramblian, ca. 19.5–17.2 Ma), mainly because of the absence of cricetids other than *Melissiodon* and by the presence of certain large mammal taxa that dispersed into western Europe during this zone, such as the proboscidean *Gomphotherium* and the equid *Anchitherium* (Casanovas-Vilar et al., 2011, 2016). The site of Sant Mamet is clearly younger, being located just a few meters below Langhian (beginning of middle Miocene) marine deposits (Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016). In addition, the fauna of Sant Mamet includes the cricetids *Eumyarion weinfurteri*, *Democricetodon hispanicus* (Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016; Jovells-Vaqué et al., 2017, 2018), and *Megacricetodon primitivus* (which was found after the 2017 field campaign). The presence of the latter species, together with the common occurrence of *Democricetodon*, unambiguously indicates that this locality correlates to MN4 (early Aragonian, 17.2–16.4 Ma).

MATERIALS AND METHODS

The holotype of *Melissiodon arambourgi* from el Fallol (Crusafont et al., 1955) as well as the specimens from Molí de Can Calopa (Agustí, 1981) were collected after systematic surface surveying of the sites in successive campaigns between the 1950s and 1970s. The remaining specimens were recovered after screen-washing campaigns mostly during the early 1990s (Sant Andreu de la Barca 1, Sant Mamet; see Agustí and Galobart, 1997) and in 2011 (Turó de les Forques 1). Some specimens, particularly those of Turó de les Forques 1 and Sant Andreu de la Barca 1, presented a hard carbonate crust covering most of the crown. It was possible to mechanically remove this crust from most specimens except a few from Turó de les Forques 1. Dental terminology is modified after Freudenthal et al. (1994) and Maridet and Ni (2013) (Fig. 2). Classification of *Melissiodon* follows Maridet and Ni (2013). All measurements are given in millimeters and were taken with an optical micrometer to the nearest 0.01 mm. Estimated measurements (because of minor damage or distortion) are between brackets, whereas ">" indicates that the measurement cannot be reliably taken but certainly exceeded the reported value. The MN zone definitions for western Europe follow Agustí et al. (2001), whereas boundaries are as defined in Hilgen et al. (2012).

Abbreviations

Institutional Abbreviations—**IPS**, Institut de Paleontologia de Sabadell (now **ICP**, Institut Català de Paleontologia Miquel Crusafont), Sabadell, Spain; **MGB**, Museu de Geologia de Barcelona (now Museu de Ciències Naturals de Barcelona), Barcelona, Spain, 'V' preceding collection number indicates that the specimen belongs to the Villalta Collection, donated to the museum in the 1980s.

Anatomical Abbreviations—**L**, anteroposterior length; **W**, labiolingual width.

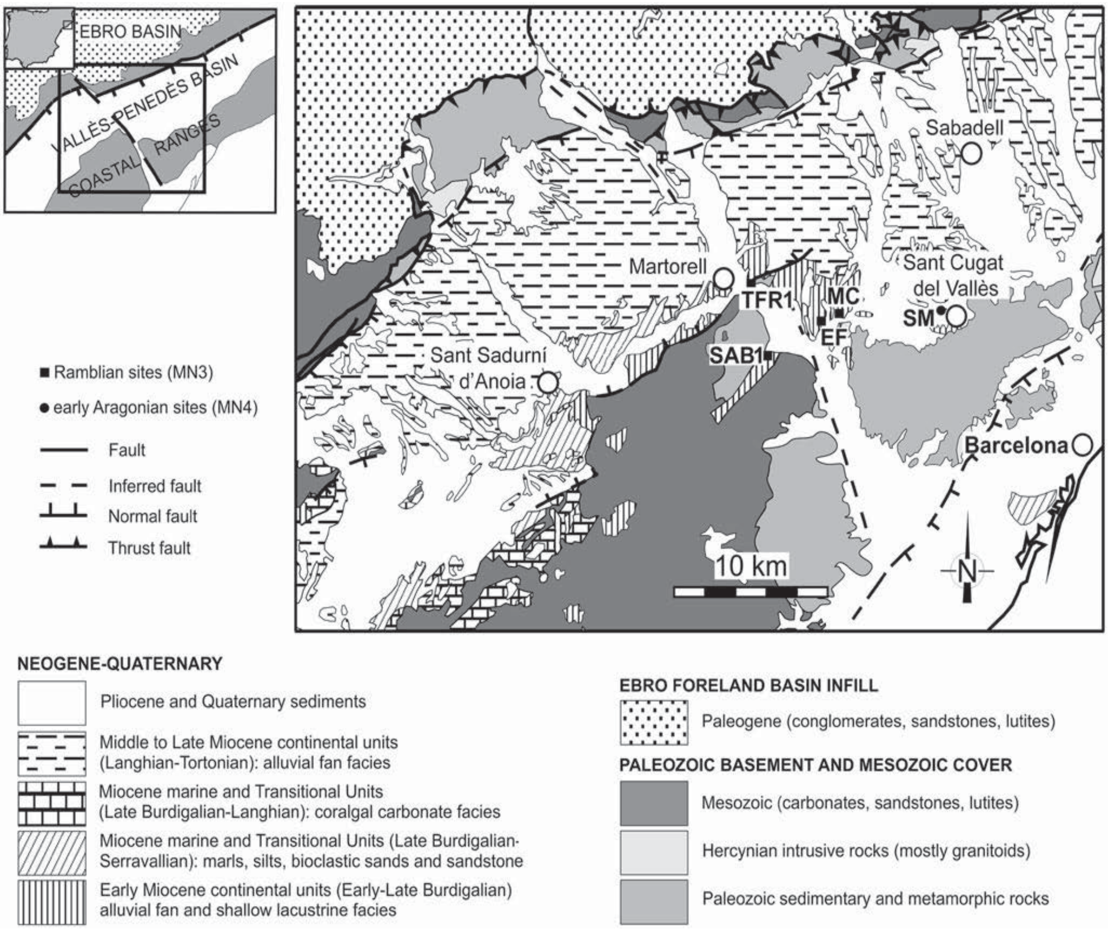


FIGURE 1. Geographic location and simplified geological map of the Vallès-Penedès Basin indicating the early Miocene sites that have delivered *Melissiodon* remains (modified from Casanovas-Vilar et al., 2016). **Locality abbreviations**: **EF**, El Fallol; **MC**, Molí de Can Calopa; **SAB1**, Sant Andreu de la Barca 1; **SM**, Sant Mamet; **TFR1**, Turó de les Forques 1.

Other Abbreviations—**MN**, European Mammal Neogene zones; **MP**, European Mammal Paleogene zones.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer von Waldheim, 1817
Subfamily CRICETOPINAE Matthew1923
Granger, 1923

Tribe MELISSIODONTINI Schaub, 1925

MELISSIODON Schaub, 1920
MELISSIODON DOMINANS Dehm, 1950
(Fig. 2)

Melissiodon nova sp.: Crusafont et al., 1954:65.
Melissiodon arambourgi: Crusafont and Villalta in Crusafont et al., 1955:131, fig. 26 (original diagnosis).
Melissiodon dominans: Agustí, 1981:152.
Melissiodon cf. *dominans*: Agustí et al., 1985:62.

Occurrence, Material, and Measurements—The studied material comprises a total of 12 specimens from five different sites (measurements in millimeters; approximate measurements of slightly broken or damaged specimens are within brackets). El Fallol: right mandibular fragment (IPS18269) with m2–m3 (m2: L = [2.60], W = [2.03]; m3: L = [2.64], W = [2.12]). This specimen is the holotype of *Melissiodon arambourgi*. Molí de Can Calopa: maxillary fragment with associated fragment of M1 (IPS20721), fragment of left mandible (IPS22935) with damaged m2–m3 (m2: L = [2.43], W = [1.97]; m3: L = [2.58], W = [1.90]). Sant Andreu de la Barca 1: one right m1 (IPS19219: L = 2.94, W = 2.05), one left m3 (IPS86077: L = 2.82, W = 1.88), one fragment of left m1 (MGB V7859: L —, W >1.72). Sant Mamet: one left M1 (IPS85757: L = 2.96, W = 1.99). Turó de les Forques 1: two right M1s (IPS85463: L = 3.48, W = 2.46; IPS85464: L = 3.37, W = 2.15), one left M2 (IPS85465: L = 2.53, W = [2.13]), one fragment of M2 (IPS85466: L >2.11, W = [2.32]), one fragment of m2 (IPS85467: L —, W = [1.87]).

Remarks on the Holotype of *Melissiodon arambourgi* and Other Described Material—The holotype of *M. arambourgi* is a right mandibular fragment with m2–m3 from el Fallol (IPS18269), which is the only material considered in the original description of the species (Crusafont et al., 1955). Currently, the m2 of the holotype is badly damaged, with only the labial cusps preserved, although it was complete according to the original description and figures (Crusafont et al., 1955:131, fig. 26). Agustí (1981) argued that the original figures and description do not agree with the material and considered *M. arambourgi* a junior subjective synonym of *M. dominans*. After a reexamination of the holotype, we have confirmed these assessments (see below). Agustí (1981) reported another *Melissiodon* specimen from San Andreu de la Barca 1 and two more from Molí de Can Calopa. The San Andreu de la Barca 1 specimen is an anterior fragment of a left m1, part of the Villalta Collection and kept at the Museu de Ciències Naturals de Barcelona (MGB V7859), that was misidentified by Agustí (1981) as an m2. Regarding the specimens from Molí de Can Calopa, these included a maxillary fragment with M1–M2 (IPS20721) that has been damaged so that only part of the M1 is now preserved (see below). A micrograph of the M1 of this specimen is reproduced in Agustí (1981:pl. 2, fig. 19). The second specimen recovered at this site is a mandibular fragment with m2–m3 (Fig. 2D).

Validity of *Melissiodon arambourgi*

After a reexamination of the holotype of *M. arambourgi*, we concur with Agustí (1981) that the original description and figures do not correspond with it. Crusafont et al. (1955) argued that *M. arambourgi* was close to *M. dominans*, but the protoconid hind arm in the m3 of the former species is long and oblique, merging with the entoconid and thus differs from all other known species of *Melissiodon*. Additional diagnostic traits of *M. arambourgi* would include the m2 markedly narrower in its anterior margin than in the posterior one, and the position of the protoconid, which is located slightly more anterior than the metaconid. This peculiar morphology led Hrubesch (1957) to propose an independent origin for this species. However, none of these diagnostic characters can be seen in the holotype. The protoconid hind arm does not connect with the entoconid but with the cingulid that closes the mesosinusid, the protoconid is placed opposite the metaconid, and the anterior and posterior margins of the m2 are of similar dimensions. Therefore, we agree with previous authors in considering *M. arambourgi* a junior subjective synonym of *M. dominans* (Agustí, 1981; Mein and Freudenthal, 1981; Sesé, 1987).

Description

The molars are relatively wide. The lower molars are somewhat more elongated and slender than the upper ones. The basic cricetid molar morphology can be recognized but is complicated by the presence of numerous ridges and well-developed accessory cusps. The main cusps are triangular, pointed, and integrated into the narrow connecting lophs so that they become crescent-shaped after moderate wear. Longitudinal and transverse ridges are generally formed by opposite spurs departing from the main cusps. These spurs become lower at the point where they meet, and small cuspules may develop in this position.

M1—Two M1s have been recovered from Turó de les Forques 1, but one of them (IPS85464) is covered by a hard carbonate crust that hides many morphological details. The single specimen from Sant Mamet (Fig. 2B) is somewhat smaller and is the only one that preserves the roots. Regarding the fragment recovered at Molí de Can Calopa (IPS20721), only the hypocone, entoloph, and part of the protocone are preserved. There are four cylindrical roots situated below the main cusps, the one below the protocone being conspicuously larger than the others. The anterocone complex is large and protrudes from the labial margin of the tooth. The anterocone presents two cusps, the larger one being placed in a centrolingual position. The two cusps are separated by a deep and wide anterior furrow. The protostyle is as large as or slightly larger than the anterocone cusps. The protostyle shows two well-defined spurs, one anterior and one labial, that connect with the lingual anteroloph. In its turn, the anteroloph shows a thickening at this point, which is particularly evident in worn specimens. An anterior cingulum departs from the base of the protocone, almost closing the protosinus in IPS85463 from Turó de les Forques 1 (Fig. 2A), whereas in the remaining ones it is open. Similarly, the anterosinus is partially closed by a well-defined cingulum departing from the anterior wall of the paracone. Slightly lingual to the labial cusp of the anterocone, there is a posteriorly directed low spur that joins an even lower anterior spur of the metacone. A cuspule may develop at the point where both spurs meet (as in Fig. 2B). The anterolophule is oblique and defined by an anterior spur of the protocone and a posterior spur originating from the lingual cusp of the anterocone. A minute cuspule is also formed at the point where both spurs meet. The paracone presents a spur or short ridge on each of its sides so that with moderate wear it shows a star-shaped outline (Fig. 2B). The protolophule is simple and defined by a lingual spur of the paracone and a labial one of the protocone. The anterior arm of the entoloph is formed at the point where both spurs meet and is very short. In IPS85757 (Fig. 2B), the anterior arm of the entoloph is vestigial, being interrupted before reaching the mesocone. The mesocone is as large as the main cusps and only slightly lower. The mesoloph is placed slightly distally and departs from the posterior arm of the entoloph rather than from the mesocone. This ridge is slightly arched and posteriorly directed in its labial end. In IPS85463 (Fig. 2A), it merges with the robust mesostyle, whereas in IPS85757 (Fig. 2B) it is interrupted before reaching the mesostyle. In IPS85463, a short and very low anterolingual spur departs from the mesoloph. The mesosinus is closed by a continuous cingulum formed by a posterior spur from the paracone, the mesostyle, and an anterior spur from the metacone. The sinus is transverse and partially closed by a cingulum departing from the anterior wall of the hypocone and a short posterior spur from the protocone. The metalophule is simple and merges with the opposite anterolingual spur of the metacone. In IPS85463, this spur directly joins the posterior arm of the entoloph and is separated by a shallow groove from the metalophule (Fig. 2A). In its turn, the anterior arm of the metalophule in IPS85757 shows two short anterior spurs directed toward the mesoloph (Fig. 2B). The posteroloph is well developed and joins the posterior spur of the metacone, thus closing the posterosinus. A low cingulum is formed at the point where both ridges meet, bordering the labial wall of the metacone. In addition, the hypocone shows a rather developed spur that originates from the lingual wall of the hypocone and then curves posteriorly and labially, delimiting a posterolingual valley. We refer to this spur as the labial posteroloph.

M2—Two specimens have been recovered from Turó de les Forques 1; however, only the distal half is preserved in one of them (IPS85466) and the other one was damaged while removing the carbonate crust that covered the crown (IPS85465). Roots are not preserved in any of the recovered specimens. The labial anteroloph is high and merges with the paracone, thus closing the anterosinus. The paracone shows an anteriorly directed spur (likely homologous with the protolophule) that merges with the labial anteroloph, so that a triangular anterolabial fossette is defined. The lingual anteroloph departs from a cusp-like anterior thickening (likely homologous with the anterocone) and is markedly lower than the labial one. This ridge is cingulum-like and closes the protosinus. The area between the protocone and the paracone is not well preserved, but apparently there are no additional ridges connecting both

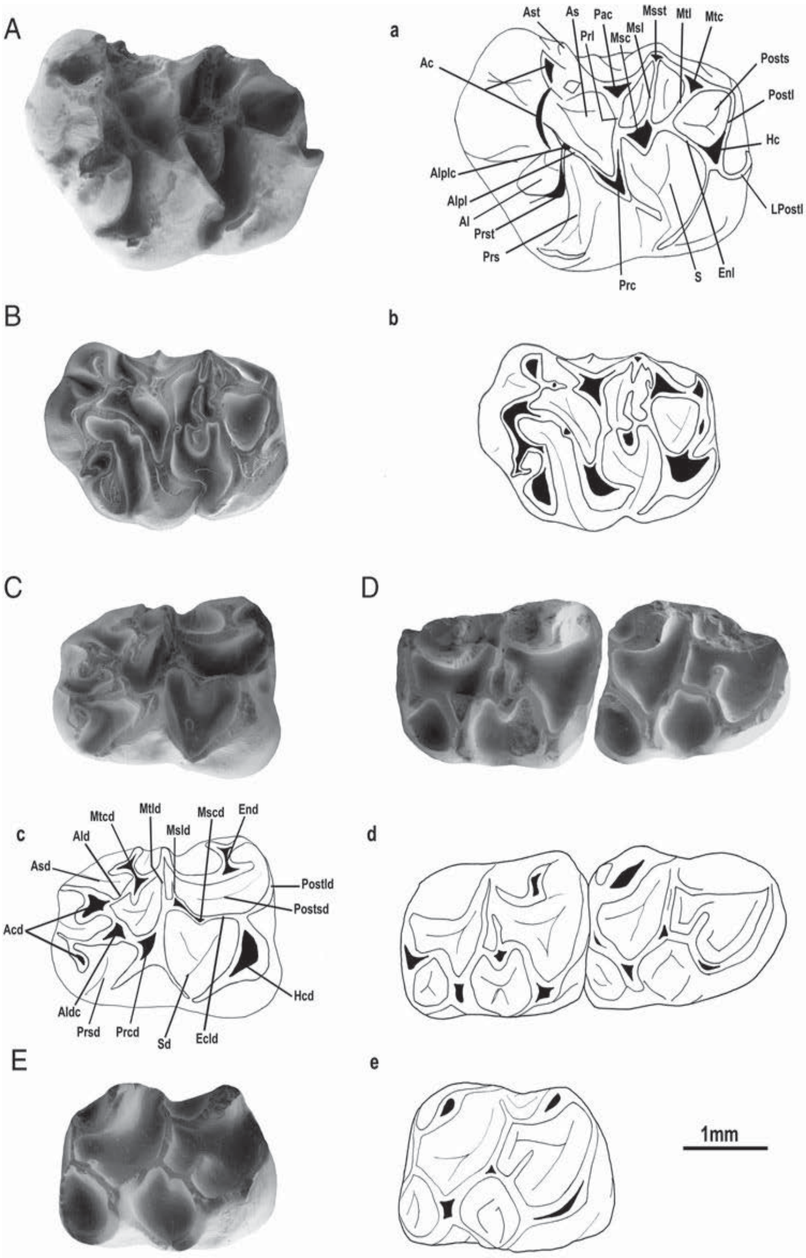


FIGURE 2. Scanning electron microscope (SEM) micrographs (**A**–**E**) and interpretative drawings (**a**–**e**) of *Melissiodon* molars from the Vallès-Penedès sites. **A**, **a**, right M1 (reversed) from Turó de les Forques 1, IPS85463; **B**, **b**, left M1 from Sant Mamet, IPS85757; **C**, **c**, right m1 (reversed) from Sant Andreu de la Barca 1, IPS19219; **D**, **d**, left m2–m3 from Molí de Can Calopa, IPS22935; **E**, **e**, left m3 from Sant Andreu de la Barca 1, IPS86077. **Abbreviations**: **ac**, anterocone; **acd**, anteroconid; **al**, anteroloph; **alpl**, anterolophule; **alplc**, anterolophule cusp; **alpld**, anterolophulid; **alpldc**, anterolophulid cusp; **as**, anterosinus; **asd**, anterosinusid; **ast**, anterostyle; **ecld**, ectolophid; **end**, entoconid; **enl**, entoloph; **hc**, hypocone; **hcd**, hypoconid; **lpostl**, labial posteroloph; **msc**, mesocone; **mscd**, mesoconid; **msl**, mesoloph; **msld**, mesolophid; **msst**, mesostyl; **mtc**, metacone; **mtcd**, metaconid; **mtl**, metalophule; **pac**, paracone; **postl**, posteroloph; **postld**, posterolophid; **posts**, posterosinus; **prc**, protocone; **prcd**, protoconid; **prl**, protolophule; **prs**, protosinus; **prsd**, protosinusid; **prst**, protostyle; **s**, sinus; **sd**, sinusid.

cusps. Similarly, the area of the mesosinus is not well preserved in IPS85465 and is covered by a crust in IPS85466. The entoloph is short and defines an 'M'-shaped structure connecting the protocone, mesocone, and hypocone. In its turn, the mesocone is well developed. The morphology of the mesoloph is complex, this ridge being defined by an anterior arm and a posterior one that meet in the middle of the mesosinus. From then on, they continue as a single ridge until they merge with the irregular ridge that closes the mesosinus. The sinus is transverse and closed by cingula departing from the hypocone and the protocone. The metalophule is simple and anterior to the hypocone. In both specimens, the metalophule shows an anterior spur directed toward the mesoloph, and even contacts it in IPS85465. The posterior part of the M2 is analogous to that of the M1.

m1—A complete m1 (Fig. 2C) and an anterior fragment of m1 (MGB V7859) have been recovered from Sant Andreu de la Barca 1. The m1 shows two broad roots, anterior and posterior. The anterior part of the molar is narrower than the posterior one and shows two main cusps separated by a deep anterior groove that we interpret as a double anteroconid (a different option would be interpreting the labial cusp as a protostylid instead). The lingual anteroconid shows two short anterior and two short posterior spurs. One of the posterior spurs merges with an opposite spur of the metaconid, which may correspond to the metalophulid. The second posterior spur is labially directed and merges with the anterolophulid, which is thick and long. The labial anteroconid is rounded and integrated into a short anterolabial cingulid that connects with the anterolophulid at its lingual end. The protosinusid and anterosinusid are open. There is no transverse connection joining the protoconid with the metaconid. The metaconid shows two posterior spurs. The lingualmost one is longer, arched and cingulid-like, curving toward the lingual margin of the molar to fuse with the mesostylid. The entoconid shows a similarly developed anterior spur that also curves to join the mesostylid so that the mesosinus is closed. In its turn, the sinus is closed by two cingulids descending from the posterior wall of the protoconid and the anterior one of the hypoconid, respectively. The ectolophid is relatively long and the mesoconid relatively small compared with the mesocone in the upper molars. Anterior to the mesoconid, there are two lingually directed transverse ridges. The first one departs from the distal wall of the protoconid and may correspond to the protoconid hind arm and joins the cingulid that closes the mesosinusid. The second one corresponds to the mesolophid and is shorter, not reaching the lingual cingulid. The hypolophulid is absent, implying that the entoconid and hypoconid are not connected. The posterolophid is long but becomes progressively lower. This ridge shows an hypoconulid-like thickening near the hypoconid. The entoconid presents two short posterior spurs.

m2—The best-preserved specimen is IPS22935 from Molí de Can Calopa (Fig. 2D), already described by Agustí (1981), which is only missing part of the metaconid. There is a clear anteroconid that is lower and slightly smaller than the main cusps. The lingual anterolophid is markedly higher than the labial one and closes the anterosinusid. The metaconid shows an anterior spur that merges with the anterolophid, although this feature can only be distinguished clearly in IPS85467 from Turó de les Forques 1. The protosinusid is reduced and closed by the labial anterolophid and a low cingulid departing from the protoconid. There is no connection between the protoconid and the metaconid. In other morphological features, the m2 is very similar to the m1. The mesolophid is slightly longer than in the m1. In IPS22935, this ridge departs from the mesoconid and curves anteriorly toward the protoconid hind arm. The posterolophid is slightly higher than in the m1 and does not show the hypoconulid-like thickening.

m3—The dimensions of the three m3s are quite variable, but the m3 is always longer than the m2 and somewhat narrower. The posterior margin of the m3 is as wide as the anterior one, but it has a more rounded outline. Root morphology can only be observed in IPS86077 from Sant Andreu de la Barca 1, which shows two broad roots, anterior and posterior. Contrary to most cricetids, the distal half of the m3 is not reduced. Accordingly, its occlusal morphology resembles that of m2. There are four main cusps of similar size: protoconid, metaconid, hypoconid, and entoconid. The anteroconid and mesoconid are not conspicuous as in the other lower molars. All the main valleys are closed by ridges or cingulids as in the m2, although, except for the posterolophid, these are somewhat lower. The ectolophid is long and presents two labially directed ridges. The anterior one is longer and points slightly backward, merging with the cingulid that closes the mesosinusid as in the m2. We interpret this ridge as the protoconid hind arm and not as the mesolophid (contrary to Agustí, 1981) because it is placed more anteriorly than this ridge. The second ridge is parallel to the first one, being directed toward the entoconid but without merging with it in any of the studied specimens, including the holotype of *M. arambourgi* (IPS18269). We agree with Agustí (1981) in interpreting this ridge as an incomplete hypolophulid. Therefore, the m3 would lack the mesolophid.

DISCUSSION

The Vallès-Penedès specimens agree in size (Table 1) with *M. dominans* and further show several of its diagnostic features (see Hrubesch, 1957). In the M1, these include the large anterocone complex that protrudes on the labial margin of the tooth resulting in a sinuous labial outline rather than more straight as in *M. schaubi*, for example. In the same molar, the anterocone consists of two well-developed cusps separated by a deep furrow. The M1 also shows a robust protostyle that connects with the lingual cusp of the anterocone by means of two ridges. The lower molars show a reduced mesolophid, this transverse ridge being completely absent in the m3. The mesolophid is always missing in the m3 of Wintershof-West, the type locality of *M. dominans*, and may also be absent in some m1 and m2 (Dehm, 1950; Hrubesch, 1957). The m1 shows two robust anterior cusps, but the labial one is not as large as the protoconid, the latter being a diagnostic character of *M. schlosseri*, a species known by only two specimens (an m1 and an m3) from the MN2 site of Haslach in Germany (Hrubesch, 1957).

The M1 recovered at Sant Mamet is remarkable not only because it is the youngest (MN4) occurrence of the genus in the basin but also because of its significantly smaller dimensions as compared with *M. dominans* from the type locality (Table 1; Dehm, 1950; Hrubesch, 1957; Ziegler and Fahlbusch, 1986). The same occurs with the scarce *Melissiodon* material from French and German MN4 localities (Mein and Freudenthal, 1981; Ziegler and Fahlbusch, 1986; Bulot et al., 2009). Mein and Freudenthal (1981:5–6) assigned the Vieux-Collonges specimen (one m1) to *M.* aff. *dominans*, remarking on its smaller size (Table 1) and a single minor morphological difference in the entoconid. Bulot et al. (2009) assigned their MN4 material to *Melissiodon* sp., further noting its reduced dimensions (Table 1). However, Ziegler and Fahlbusch (1986) showed that the MN4 German specimens fit within the lower size range of *M. dominans* from Wintershof-West and ascribed them to this species. Similarly, the French MN4 material fits within this range. Therefore, we do not find justification for assigning these younger specimens to a different species. In conclusion, in the Vallès-Penedès Basin, *Melissiodon* is solely represented by the species *M. dominans*, which would range from MN3 to MN4. Its last record is at the site of Sant Mamet, located just a few meters below middle Miocene (Langhian) marine deposits, likely being one of the youngest occurrences of this long-ranging genus (Crusafont et al., 1955; Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016).

In the Iberian Peninsula, *Melissiodon* has been reported from a handful of sites from Aragon and Valencia. These include many of the sites of the Ramblian mammal age type area near Calamocha (Teruel, Aragon) such as Navarrete del Río, Ramblar 1, 3B, and 7, or Valhondo 3A (Sesé, 1987). All these sites are correlated to Ramblian local zone Z, which correlates to latest MN2 and earliest MN3 (Larrasoaña et al., 2006). *Melissiodon* also has been reported from Ramblian sites from the nearby Calatayud-Montalbán Basin (San Roque 4A and 4B), correlated to local zone A (equivalent to most of MN3; Van der Meulen et al., 2012). A few kilometers south, the genus has been recently described from the Montalvos 2 site in the Teruel Basin, correlated to local subzone Ca (equivalent to part of MN4; Hordijk et al., 2015). In Valencia, the genus is restricted to MN4 and has been reported from Cerro de la Cruz (= Bunyol classic site) and Barranco del Candel in the Bunyol-Xiva Basin (Daams, 1976; Adrover et al., 1987), as well as from Mas d'Antolino B3 and Barranc de Campisano 1 in the Ribesalbes-Alcora Basin (Crespo et al., 2014). In all the Iberian sites, *Melissiodon* is very rare, being represented by just a few molars and molar fragments, which contrasts with its somewhat greater abundance in central Europe. It is also worth noting that in the Vallès-Penedès Basin, the genus is

TABLE 1. Length and width (L × W) measurements for different samples of *Melissiodon dominans* and *Melissiodon schlosseri* from selected sites in Spain, France, and Germany. All measurements are in millimeters, approximate measurements of slightly broken or damaged specimens are within brackets. See main text for abbreviations used and catalog numbers of the Vallès-Penedès specimens. Data for the Spanish sites are taken from Sesé (1987) and Hordijk et al. (2015); from French ones from Mein and Freudenthal (1981) and Bulot et al. (2009); and from German sites from Hrubesch (1957) and Bulot et al. (2009).

	Element					
Site	M1	M2	M3	m1	m2	m3
Sant Mamet	2.96 × 1.99	–	–	–	–	–
Turó de les forques	3.47 × 2.46	2.53 × [2.13]	–	–	–	–
	3.37 × 2.15	>2.11 × [2.32]	–	–	–	–
		– × [1.87]	–	–	–	–
Sant Andreu de la Barca 1	–	–	–	2.94 × 2.05	–	2.82 × 1.88
Molí Calopa	–	–	–	–	[2.43] × [1.97]	[2.58] × [1.90]
El Fallol	–	–	–	–	[2.60] × [2.03]	[2.64] × [2.12]
Bañon 11A	–	– × 1.83	–	–	–	–
Ramblar 1A	–	2.23 × 2.13	1.89 × 2.08	–	–	2.55 × –
Montalvos 2	3.40 × 2.32	2.35 × 1.99	1.78 × 2.11	2.68 × 1.94	2.5 × 2.09	2.37 × 1.67
	3.49 × 2.27	–	–	–	–	–
Saint-Vicent de la Lamonjoie	3.20 × 2.24	2.32 × 2.01	–	2.68 × 1.96	–	2.55 × 1.80
	3.16 × 2.27	2.50 × 2.00	–	–	–	2.61 × 1.74
Jauquet	3.40 × 2.37	2.34 × 1.88	1.72 × 2.01	2.72 × 2.06	–	–
	3.48 × 2.42	–	–	2.40 × 1.78	–	–
	–	–	–	2.56 × 1.93	–	–
Vieux-Collonges	–	–	–	2.32 × 1.78	–	–
Béon 2	–	2.14 × 1.75	–	2.30 × 1.78	–	–
Wintershof-West (mean values)	3.35 × 2.53	2.31 × 2.07	1.75 × 2.1	2.60 × 2.10	2.38 × 2.09	2.61 × 1.88
Haslach (*M. schlosseri*)	–	–	–	2.42 × 1.78	–	2.54 × 1.79

more common than in Aragon and Valencia, where a sample of hundreds of rodent specimens is required to recover just one or two molars of *Melissiodon*. In the Vallès-Penedès sites, a sample size of just 50 molars usually includes a few specimens of this genus. The greater abundance of *Melissiodon* could be related to its preference for humid and forested habitats, because throughout the Miocene the environment was more humid and forested in the Catalan coastal basins as compared with the interior of Spain (Agustí, 1990; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2016).

From the beginning of the middle Miocene (Langhian), *Melissiodon* is no longer recorded in the Vallès-Penedès Basin. This period coincided with higher mean global temperatures and a marked sea level increase associated to the mid-Miocene Climatic Optimum (Zachos et al., 2001). The southwestern half of the Vallès-Penedès Basin was covered by a shallow tropical sea (see Cabrera et al., 1991; Casanovas-Vilar et al., 2016), and paleobotanical evidence from a few sites in the area points toward a relatively more arid and seasonal climate as compared with the early Miocene, particularly during the late Langhian (Sanz de Síria Catalán, 1993, 2001). The climate was probably tropical/subtropical, with a long dry season (Sanz de Síria Catalán, 1993, 2001), and this would certainly have affected *Melissiodon*, which purportedly preferred more humid and forested habitats. Testing this hypothesis is beyond the scope of this work. However, we must note that although this may explain the extinction of this genus in the Vallès-Penedès (or even in the Iberian Peninsula), other factors must be considered in other European regions, such as Germany, which had a completely different climate during the middle Miocene.

CONCLUSIONS

The *Melissiodon* material from the early Miocene of the Vallès-Penedès Basin had been previously ascribed to the species *Melissiodon arambourgi*. This species is here recognized as a junior subjective synonym of *Melissiodon dominans* so that all the material is transferred to the latter species. This genus is present in the area between the MN3 and MN4 biozones (early Miocene), being last recorded in a site just a few meters below Langhian (middle Miocene) marine deposits. *Melissiodon* appears to have been more common in the Vallès-Penedès Basin than in other areas of the Iberian Peninsula. This might be related to the preference of this genus for humid and forested environments, which characterized the Catalan coastal basin, in contrast to particularly the interior Iberian basins, which had drier climates. The extinction of *Melissiodon* in the Vallès-Penedès Basin could be related to a shift toward drier and more seasonal conditions during the early–middle Miocene transition.

ACKNOWLEDGMENTS

This research has been funded by the Agencia Estatal de Investigación from the Spanish Ministerio de Economía, Industria y Competitividad and the Agencia Estatal de Investigación (AEI) from Spain/European Regional Development Fund of the European Union (projects CGL2017-82654-P and CGL2016-76431-P and RYC-2013-12470 research contract to I.C.V.), by the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya (2014 SGR 416 research group, 2018FI B1 00201 predoctoral grant to S.J.V.), and by the CERCA Programme of the Generalitat de Catalunya. Field work was supported by the Departament de Cultura of the Generalitat de Catalunya (project 2014/100584) and the National Geographic Society (grant number 9640-15). We are indebted to J. Prieto (Ludwig Maximilian University of Munich) for providing invaluable German literature and translations. We thank V. Vicedo and L. Troya (Museu de Ciències Naturals de Barcelona) for their assistance when consulting the specimens of the Villalta Collection. We also thank the preparation staff of the Institut

Català de Paleontologia Miquel Crusafont for their excellent work with the fragile specimens. We acknowledge the constructive comments by the two reviewers (W. Wessels, G. Daxner-Höck) and the editor (F. Bibi) on the manuscript, which improved the final result.

ORCID

Sílvia Jovells-Vaqué http://orcid.org/0000-0003-0358-0840
Isaac Casanovas-Vilar http://orcid.org/0000-0001-7092-9622

LITERATURE CITED

Adrover, R., P. Mein, and M. Belinchón. 1987. La fauna de roedores en el Aragoniense medio del Barranco del Candel, Buñol (provincia de Valencia, España). Paleontologia i Evolució 21:43–61.

Agustí, J. 1981. Roedores miomorfos del Neógeno de Cataluña. Ph.D. dissertation, Universitat de Barecelona, Barcelona, Spain, 288 pp., 3 pls.

Agustí, J. 1982. Biozonación del neogeno continental de Cataluña mediante roedores (Mammalia). Acta Geológica Hispánica 17: 21–26.

Agustí, J. 1990. The Miocene rodent succession in eastern Spain: a zoogeographical appraisal; pp. 375–404 in E. H. Lindsay, V. Fahlbusch, and P. Mein (eds.), European Neogene Mammal Chronology. NATO ASI Series. Series A: Life Sciences, Volume 180. Plenum Press, New York.

Agustí, J., and A. Galobart. 1997. Noves localitats amb mamífers fòssils en el Miocè de la Conca del Vallès-Penedès. Tribuna d'Arqueologia 1996–1997:9–22.

Agustí, J., Cabrera, L., and S. Moyà-Solà. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. Paleontologia i Evolució 18:57–81.

Agustí, J., L. Cabrera, M. Garcés, W. Krijgsman, O. Oms, and J. M. Parés. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth-Science Reviews 52: 247–260.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, 115 pp.

Bulot, C., P.-O. Antoine, and F. Duranthon. 2009. Rongeurs et lagomorphes du Miocène inférieur de Béon 2 (MN4, Montréal-du-Gers, SW France). Annales de Paléontologie 95:197–215.

Cabrera, L. 1981. Influencia de la tectónica en la sedimentación continental de la cuenca del Vallès-Penedès (provincia de Barcelona, España) durante el Mioceno inferior. Acta Geológica Hispánica 16:163–169.

Cabrera, L., F. Calvet, J. Guimerà, and A. Permanyer. 1991. El registro sedimentario miocenico en los semigrabens del Vallès-Penedès y de el Camp: organización secuencial y relaciones tectonica sedimentación; in F. Colombo (ed.), I Congreso del Grupo Español del Terciario, Libro-Guía Excursion n. 4. Universitat de Barcelona, Barcelona, Spain, 132 pp.

Casanovas-Vilar, I., and J. Agustí. 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 248: 169–189.

Casanovas-Vilar, I., D. DeMiguel, J. Galindo, J. M. Robles, M. Garcés, and L. Cabrera. 2011. The continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain); pp. 93–100 in A. Pérez García, F. Gascó, J. M. Gasulla, and F. Escaso (eds.), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella, Spain.

Casanovas-Vilar, I., A. Madern, D. M. Alba, L. Cabrera, I. García-Paredes, L. W. van den Hoek Ostende, D. DeMiguel, J. M. Robles, M. Furió, J. van Dam, M. Garcés, C. Angelone, and S. Moyà-Solà. 2016. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). Comptes Rendus Palevol 15:791–812.

Crespo, V. D., F. J. Ruiz Sánchez, M. Freudenthal, and P. Montoya. 2014. Primer registro del género *Melissiodon* (Mammalia, Cricetidae) en la cuenca de Ribesalbes-Alcora (Castelló, España); pp. 53–55 in R. Royo Torres, F. Javier Verdú, and L. Alcalá (eds.), XXX Jornadas de Paleontología de la Sociedad Española de Paleontolgía !Fundamental! Fundación Conjunto Paleontológico de Teruel, Dinópolis, Teruel, Spain.

Crusafont, M., J. F. de Villalta, and J. Truyols. 1954. Sobre la caracterización del Burdigaliense continental en la cuenca del Vallés-Pendés. Memorias y Comunicaciones del Instituto Geológico Provincial 11:63–73.

Crusafont, M., J. F. de Villalta, and J. Truyols. 1955. El Burdigaliense continental de la cuenca del Vallés-Penedés. Memorias y Comunicaciones del Instituto Geológico 12:3–272.

Daams, R. 1976. Miocene rodents (Mammalia) from Cetina de Aragón (Prov. Zaragoza) and Buñol (Prov. Valencia), Spain. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B 79: 152–182.

Daams, R., M. Freudenthal, and M. A. Álvarez Sierra. 1987. Ramblian; A new stage for continental deposits of early miocene age. Geologie en Mijnbouw 65:297–308.

Dawson, M. R. 2003. Paleogene rodents of Eurasia. DEINSEA 10: 97–126.

de Gibert, J. M., and I. Casanovas-Vilar. 2011. Contexto geológico del Mioceno de la Cuenca del Vallès-Penedès. Paleontologia i Evolució Memòria especial 6:39–45.

Dehm, R. 1950. Die Nagetiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 91:321–428.

Fischer von Waldheim, G. 1817. Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou 5:357–471.

Flynn, L. J. 1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups; pp. 589–616 in W. P. Luckett and J.-L. Hartenberger (eds.), Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. NATO ASI Series. Series A: Life Sciences, Volume 92. Plenum Press, New York.

Freudenthal, M., M. Hugueney, and E. Moissenet. 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). Scripta Geologica 104:57–114.

Freudenthal, M., J. I. Lacomba, and M. A. Sacristán. 1992. Classification of European Oligocene cricetids. Revista Española de Paleontología número extraordinario 1992:49–57.

Hilgen, F. J., L. J. Lourens, and J. A. Van Dam. 2012. The Neogene Period; pp. 923–978 in F. M. Gradstein, J. G. Ogg, M. Schmitz, and G. Ogg (eds.), The Geologic Time Scale 2012. Elsevier, Amsterdam, The Netherlands.

Hordijk, K., A. Bosma, H. de Bruijn, J. van Dam, C. Geraedts, L. van den Hoek Ostende, J. Reumer, and W. Wessels. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos2, Teruel Basin, Spain. Palaeobiodiversity and Palaeoenvironments 95:321–346.

Hrubesch, K. 1957. Zahnstudien an tertiären Rodentia als Beitrag zu deren Stammesgeschichte. Über die Evolution der Melissiodontidae, eine Revision der Gattung *Melissiodon*. Bayerische Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Klasse 83:1–101.

Jovells-Vaqué, S., I. García-Paredes, D. DeMiguel, J. Madurell-Malapeira, and I. Casanovas-Vilar. 2017. The early Miocene rodent succession of the Vallès-Penedès Basin (Catalonia, Spain): preliminary results after the 2011–2016 field campaigns. Zitteliana 91:48.

Jovells-Vaqué, S., I. García-Paredes, M. Furió, C. Angelone, L. W. van den Hoek Ostende, M. B. Barberà, D. DeMiguel, J. Madurell-Malapeira, and I. Casanovas-Vilar. 2018. Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). Historical Biology 30: 404–421.

Kalthoff, D. C. 2006. Incisor enamel microstructure and its implications to higher-level systematics of Eurasian Oligocene and Early Miocene hamsters (Rodentia) by. Palaeontographica Abteilung A 277:67–80.

Koenigswald, W. von. 2004. The three basic types of schmelzmuster in fossil and extant rodent molars and their distribution among rodent clades. Palaeontographica Abteilung A 270:95–132.

Larrasoaña, J. C., X. Murelaga, and M. Garcés. 2006. Magnetobiochronology of Lower Miocene (Ramblian) continental sediments from the Tudela Formation (western Ebro basin, Spain). Earth and Planetary Science Letters 243:409–423.

Maridet, O., and X. Ni. 2013. A new cricetid rodent from the early Oligocene of Yunnan, China, and its evolutionary implications for early Eurasian cricetids. Journal of Vertebrate Paleontology 33: 185–194.

Matthew, W. D., and W. Granger. 1923. Nine new rodents from the Oligocene of Mongolia. American Museum Novitates 102:1–10.

Mein, P., and M. Freudenthal. 1971a. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. Scripta Geologica 2:1–37.

Mein, P., and M. Freudenthal. 1971b. Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. Partie 1: Le genre *Cricetodon* Lartet, 1851. Scripta Geologica 5:1–51.

Mein, P., and M. Freudenthal. 1981. Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. Partie 2: Cricetodontinae incertae sedis, Melissiodontinae, Platacanthomyinae, et Anomalomyinae. Scripta Geologica 60:1–11.

Mödden, C. 1999. Family Melissiodontidae; pp. 343–346 in G. E. Rössner and K. Heissig (eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Sanz de Síria Catalán, A. 1993. Datos sobre la paleoclimatología y paleoecología del Neógeno del Vallès-Penedès según las macrofloras halladas en la cuenca y zonas próximas. Paleontologia i Evolució 26–27:281–289.

Sanz de Síria Catalán, A. 2001. Flora y vegetación del Mioceno medio de la depresión del Vallès-Penedès. Paleontologia i Evolució 32–33:79–92.

Schaub, S. 1920. *Melissiodon* nov. gen., ein bisher übersehener oligocäner Muride. Senckenbergiana 2:43–47.

Schaub, S. 1925. Die hamsterartigen nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft 45:1–112.

Sesé, C. 1987. *Eucricetodon* and *Melissiodon* (Cricetidae, Rodentia) from the Ramblian and Lower Aragonian of the Calamocha area (Calatayud-Teruel Basin, Spain). Scripta Geologica 83:1–17.

Ünay-Bayraktar, E. 1989. Rodents from the middle Oligocene of Turkish Thrace. Utrecht Micropaleontological Bulletins. Special Publication 5. Utrecht, The Netherlands.

Van der Meulen, A. J., I. García-Paredes, M. Á. Álvarez Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Pélaez-Campomanes. 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geologica Acta 10:159–179.

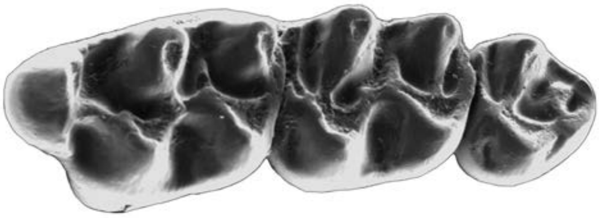
Vianey-Liaud, M. 1985. Possible evolutionary relationships among Eocene and lower Oligocene rodents of Asia, Europe and North America; pp. 277–309 in W. P. Luckett and J.-L. Hartenberger (eds.), Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. NATO ASI Series. Series A: Life Sciences, Volume 92. Plenum Press, New York.

Wessels, W., A. A. Van de Weerd, H. de Bruijn, and Z. Markovic. 2018. New Melissiodontinae (Mammalia, Rodentia) from the Paleogene of south-east Serbia. Palaeobiodiversity and Palaeoenvironments 98:471–487.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K. 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Ziegler, R., and V. Fahlbusch. 1986. Kleinsäuger-Faunen aus der basalen Oberen Süßwasser-Molasse Niederbayerns. Zitteliana 14:3–58.

Submitted March 14, 2018; revisions received July 24, 20187; accepted August 3, 2018.
Handling editor: Faysal Bibi.



Chapter 6: "Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain)"

Historical Biology

Published: April 2017

HISTORICAL BIOLOGY, 2018
VOL. 30, NO. 3, 404–421
https://doi.org/10.1080/08912963.2017.1317768

Taylor & Francis
Taylor & Francis Group

Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain)

Sílvia Jovells-Vaqué[a], Israel García-Paredes[b], Marc Furió[a], Chiara Angelone[c,a], Lars W. Van den Hoek Ostende[d], Mariona Berrocal Barberà[a], Daniel DeMiguel[a], Joan Madurell-Malapeira[a] and Isaac Casanovas-Vilar[a]

[a]Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain; [b]Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Madrid, Spain; [c]Dipartimento di Scienze, Università Roma Tre, Roma, Italy; [d]Naturalis Biodiversity Center, Leiden, The Netherlands

ABSTRACT
The Valles-Penedes Basin (Catalonia, Spain) is classical area for the study of Miocene land mammal faunas. Nevertheless, the early Miocene part of the record has deserved little attention as compared to younger intervals. Most notably, the small mammals of this age have not been described in detail, consequently hampering the correlation of the Valles-Penedes record with other chronological schemes. In this work we describe the rich and diverse small mammal fauna from Les Cases de la Valenciana site (Gelida, Alt Penedès) which includes marsupials, eulipotyphlans, lagomorphs and rodents. On the basis of the presence of the cricetids *Megacricetodon* and *Democricetodon* this site is correlated with European Neogene zone MN4, yielding an age of 17–16 Ma. However, the rodent assemblage is comparable to that of chronologically close localities of the Calatayud-Montalbán Basin (Aragon, Spain), indicating that the same biochronological scheme can be applied to both areas. In this way, the coexistence of the eomyids *Ligerimys ellipticus* and *Ligerimys florancei* coupled with the presence of *Megacricetodon primitivus* indicates a correlation with local biozone Ca of the Calatayud-Montalban Basin, ranging from 16.3 to 16 Ma. Finally, the correlation of other early Miocene sites of the Valles-Penedes Basin is discussed and refined.

ARTICLE HISTORY
Received 19 October 2016
Accepted 6 April 2017

KEYWORDS
Early Miocene; eulipotyphla; Lagomorpha; Rodentia; Iberian Peninsula; biostratigraphy

Introduction

The Vallès-Penedès Basin, located in Catalonia (Spain), is a classical area for the study of the Miocene land mammal faunas. The earliest discoveries date back to the end of the nineteenth century with the discovery of a few remains at the now abandoned coal mines of la Fontsanta in the town of Subirats as well as in the brickyard of Molí de Can Calopa in Rubí (Almera 1898). In the following decades a handful of new mammal sites were discovered, including now well-known localities such as Piera, Sant Quirze or Els Hostalets de Pierola (see for example Bataller Calatayud 1938). However, major surveying campaigns were undertaken during the 1940s and 1950s by Miquel Crusafont, Josep F. de Villalta and Jaume Truyols and led to the discovery of tens of new sites, particularly near the towns of Sabadell and Terrassa, most of them dating from the late middle Miocene and the early late Miocene. As a result, the Vallès-Penedès Basin became a reference area for the study of European Miocene faunas, and eventually the Vallesian mammal age, corresponding to the earliest part of the late Miocene, was defined on the basis of its faunal record (Crusafont Pairó 1950). The early Miocene is also represented in the basin, but the known sites at the time were comparatively poorer than younger ones. Almost all of these sites are located in an easily-recognizable stratigraphical unit defined by red clays that crops out near the reliefs in the southern margin of the basin. This unit had been either attributed to the early Oligocene (Rupelian; Sierra et al. 1930) or the early Miocene (Bataller Calatayud 1938) because the few fossil remains did not allow reaching firm stratigraphical conclusions. Crusafont and his co-workers intensively sampled the red clay unit and discovered more than 20 mammal-bearing localities that provided a fauna of about 40 species (Crusafont et al. 1955). The authors provided compelling evidence for the early Miocene age of the unit on the basis of its faunal content and its stratigraphical position below marine facies corresponding to the Langhian (middle Miocene; see below). During the following years these researchers turned their attention to the middle and late Miocene sites, so no new campaigns were performed for decades. Only Can Martí Vell, a new early Miocene locality discovered in the late 1970s was sampled for small mammals (Agustí & Cabrera 1981; Agustí 1983) and, later on during the early 1990s, the exceptionally rich site of Els Casots was discovered and excavated. This site is located next to the old coal mines of la Fontsanta in Subirats and provides a rich fauna including both micro- and macrovertebrates (Casanovas-Vilar et al. 2011a). However, after the excavations at Els Casots concluded, field activity in the early Miocene deposits was interrupted until 2011, when our team surveyed the classical sites and discovered a number of new localities.

CONTACT Isaac Casanovas-Vilar isaac.casanovas@icp.cat

Les Cases de la Valenciana is a classical site discovered by Crusafont and co-workers, who reported the finding of scarce artiodactyls and carnivore remains (Crusafont et al. 1955). However, after this initial survey the site was abandoned and partially covered by crops, although it was regularly visited by amateur palaeontologists who eventually found some rhinocerotid teeth (Vicente Castells 1987). In 2005 the main fossiliferous layer was exposed again as the result of minor works in an adjacent road that also unearthed some bones that were found by our team in 2011. Field campaigns resumed between 2012 and 2015 restulting in the discovery of hundreds of macrovertebrate remains, including a partial skeleton of the rhinoceros *Plesiaceratherium mirallesi*. In addition, the sediment removed during the excavation was screen-washed and sorted providing the first small vertebrate remains from this site. Although not all the sediment has been processed, the recovered sample comprises about 170 identifiable remains that include mostly small mammals: rodents, lagomorphs, insectivores and scarce didelphid marsupials. Other small vertebrates, such as snakes, lizards and small crocodiles have also been found. In this work we describe the small mammal remains recovered at Les Cases de la Valenciana site and further discuss their implications for the age and paleoenvironment of this locality.

Geological setting

The Vallès-Penedès Basin is an elongated half-graben parallel to the Catalan coastline (NE Spain) bounded by the Catalan Coastal Ranges (Figure 1). The sedimentary infill covers almost the entire Miocene (Ramblian–Turolian) and is mostly defined by continental sediments deposited in the context of alluvial fans sourced from the bounding reliefs (Cabrera et al. 1991, 2004; De Gibert & Casanovas-Vilar 2011; Casanovas-Vilar et al. 2016a). The early Miocene deposits of the Vallès-Penedès crop out in a relatively small fringe close to the southwestern margin of the basin (Figure 1) and generally consist in small-ranging alluvial fan deposits made of red mudstones, sandstones and conglomerates (Cabrera 1981; Cabrera et al. 1991, 2004; De Gibert & Casanovas-Vilar 2011; Casanovas-Vilar et al. 2016a). Mammal sites are commonly located in the distal, mudstone-dominated facies of these fan systems. In certain areas of the basin shallow carbonate and evaporitic lake systems were developed, such as near the towns of Gelida and Subirats, where the sediments define the so-called Subirats lacustrine unit. This unit has provided the few rich early Miocene mammal sites of the basin: els Casots in Subirats, and Can Julià, Can Martí Vell and Les Cases de la Valenciana

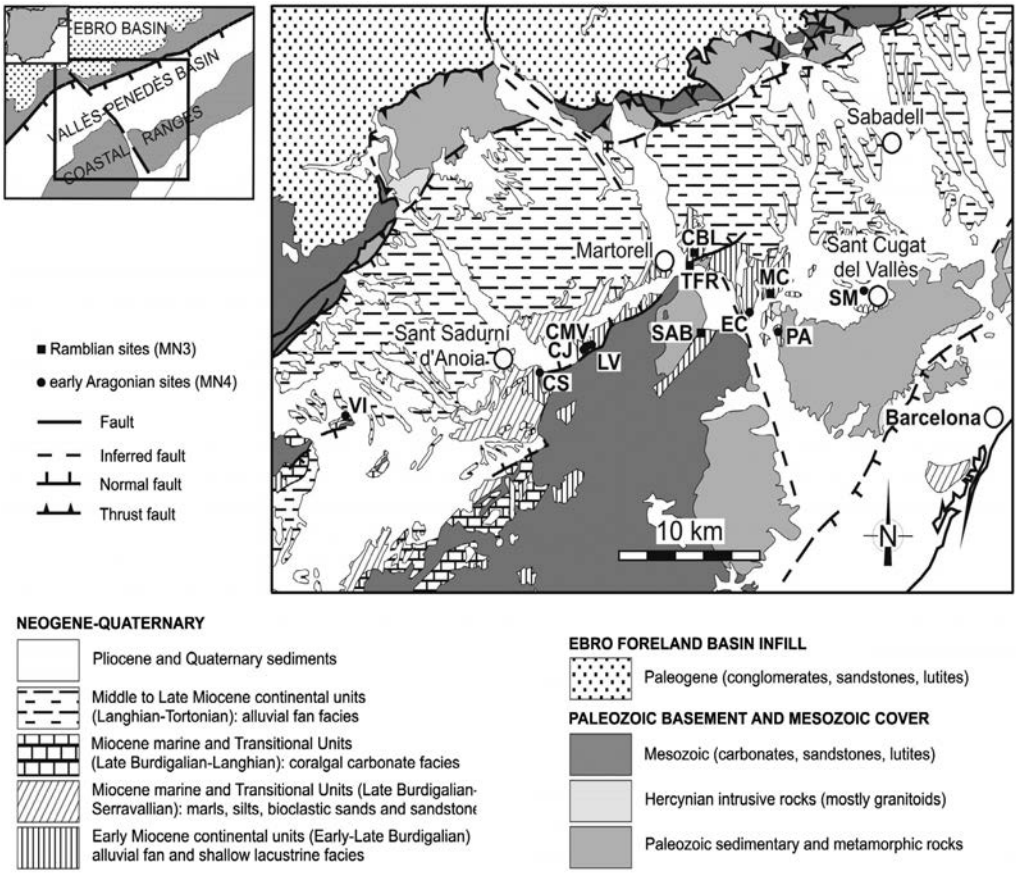


Figure 1. Geographical location and simplified geological map of the Vallès-Penedès Basin indicating the main early Miocene mammal localities (modified from Casanovas-Vilar et al. 2016a).

Notes: Locality acronyms are as follows: CBL = La Costablanca; CJ = Can Julià; CMV = Can Martí Vell; CS = Els Casots; EC = El Canyet; LV = Les Cases de la Valenciana; MC = Molí de Can Calopa; PA = Escletxes del Papiol; SAB = Sant Andreu de la Barca; SM = Sant Mamet; TFR = Turó de les Forques; VI = Vilobí del Penedès.

in Gelida (Crusafont et al. 1955; Agustí & Cabrera 1981; Agustí et al. 1985; Casanovas-Vilar et al. 2016a; Figure 1).

Crusafont et al. (1955) were the first to sample the sites of Can Julià, which provided a representative macromammal assemblage, and Les Cases de la Valenciana, which only delivered scarce remains. After the main fossiliferous layers of Les Cases de la Valenciana were exposed again field campaigns started in 2012 and continued until 2015. The campaigns included systematic excavation and screen-washing coupled with the recording of stratigraphical information. Les Cases de la Valenciana resulted in the discovery of two fossiliferous levels: Les Cases de la Valenciana 1 (LV1) and 2 (LV2). LV2 corresponds to a small layer of lacustrine carbonates that delivered several rib fragments of an unidentified large mammal. LV1 is placed four meters below LV2 in the stratigraphic series and corresponds to the marl layer excavated by Crusafont et al. (1955). This marl is interpreted as having formed in a swampy environment as is also evidenced by the occurrence of small crocodilians (cf. *Diplocynodon*). LV1 has delivered more than 400 macrovertebrate fossils, including one partial skeleton of the giant tortoise *Titanochelon* sp. and another one from the poorly-known rhinocerotid *Plesiaceratherium mirallesi* which are currently being described. The rest of the macrofauna includes artiodactyls (*Cainotherium*, *Procervulus* and small suoids) and carnivores. The small mammal material described in this work was recovered after screen-washing the sediment removed during the systematic excavation of LV1.

Material, methods and abbreviations

The described material is housed at the Institut Català de Paleontologia Miquel Crusafont at Sabadell (Barcelona, Spain). Collection numbers are given in the main text and Tables 1–7. The nomenclature of the teeth and the orientation for measuring follow Klietmann et al. (2014a) for *Amphiperatherium* and *Galerix*, and Furió et al. (2015) for *Heterosorex*. Concerning the rodents, dental terminology follows Black (1963), Cuenca (1988) and Van de Weerd (1976) for the Sciuridae; De Bruijn (1965–1966) and Daams (1981), modified after García-Paredes et al. (2009) for the Gliridae; Fahlbusch (1970) for the Eomyidae; Mein and Freudenthal (1971) and Freudenthal et al. (1994) for the Cricetidae. Measurement methods follow Cuenca (1988) and Van de Weerd (1976) for the Sciuridae; García-Paredes et al. (2009) for the Gliridae; Álvarez Sierra (1987) for the Eomyidae; and Daams and Freudenthal (1988) for the Cricetidae. Finally, concerning the ochotonid lagomorphs, nomenclature follows Angelone and Sesé (2009). All measurements are in millimeters.

Abbreviations. **P**, premolars; **M**, molars; **d**, deciduous dentition. Uppercase letters are used for upper elements and lowercase letters for lower ones. **L**, length; **W**, width; **LV1**, Les Cases de la Valenciana 1; **MN**, Mammal Neogene Zones (after Mein 1975, 1999; age boundaries are according to Hilgen et al. 2012); **IPS**, Institut Català de Paleontologia Miquel Crusafont (used as an acronym preceding the collection number).

Table 1. Collection numbers and measurements (in millimeters) for the cheek teeth of *Lagopsis penai* from Les Cases de la Valenciana 1.

Element	Collection number	Length
p3	IPS-86606	1.70
	IPS-86607	1.43
	IPS-93666	1.67
Lower molariform	IPS-86601	
	IPS-86604	
	IPS-86605	
	IPS-86608	
P3	IPS-93669	1.31
	IPS-93670	1.27
Upper molariform	IPS-86603	1.32
	IPS-86661	1.24
	IPS-93665	1.32
	IPS-93667	1.34
	IPS-93668	1.49

Table 2. Collection numbers and measurements (in millimeters) for the cheek teeth of *Microdyromys koenigswaldi* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
M1	IPS-86514	0.82	0.97
	IPS-86515	0.83	0.93
p4	IPS-86517	0.63	0.61
m1	IPS-86509	–	–
	IPS-86518	0.90	0.86
m2	IPS-86519	–	–
	IPS-86520	0.97	0.92

Table 3. Collection numbers and measurements (in millimeters) for the cheek teeth of *Simplomys simplicidens* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
P4	IPS-86500	0.74	0.91
	IPS-86501	0.72	–
	IPS-86502	0.73	0.92
M2	IPS-86503	1.14	1.43
	IPS-86504	1.19	1.53
p4	IPS-86505	0.60	0.68
m2	IPS-86525	–	–
	IPS-86526	–	–
	IPS-86527	–	–
m3	IPS-86513	–	–

Table 4. Collection numbers and measurements (in millimeters) for the cheek teeth of *Ligerimys florancei* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
dP4	IPS-86464	1.24	1.02
	IPS-88887	–	1.01
P4	IPS-86465	1.27	1.23
	IPS-86466	1.27	1.27
M1	IPS-86467	1.29	1.47
	IPS-86468	1.27	1.35
	IPS-86469	1.29	1.34
M2	IPS-88886	1.15	1.25
M1/M2	IPS-86470	–	–
M3	IPS-86471	0.88	1.06
m1/m2	IPS-86481	1.23	1.12
	IPS-86492	1.34	1.07
	IPS-86494	–	1.22
	IPS-88888	1.34	1.17
	IPS-88889	1.24	1.20
m3	IPS-86483	0.99	0.95

Table 5. Collection numbers and measurements (in millimeters) for the cheek teeth of *Ligerimys ellipticus* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
M1	IPS-86486	1.02	1.21
	IPS-86487	0.98	1.07
M2	IPS-86485	0.92	1.13
	IPS-86496	0.96	1.18
M1/M2	IPS-86497	–	1.19
	IPS-86498	–	–
	IPS-86499	–	1.14
dp4	IPS-86488	1.09	0.83
p4	IPS-86472	1.07	0.94
	IPS-86473	0.97	0.91
	IPS-86474	1.07	0.90
m1/m2	IPS-86475	1.13	1.03
	IPS-86476	1.14	1.04
	IPS-86477	1.05	0.99
	IPS-86478	1.17	1.08
	IPS-86479	1.05	0.97
	IPS-86480	1.14	1.03
	IPS-86489	1.16	1.07
	IPS-86490	1.17	0.98
	IPS-86491	–	1.03
	IPS-86493	1.14	–
	IPS-86495	0.94	0.83
	IPS-88890	–	–
	IPS-88891	1.14	1.11
	IPS-88892	1.06	1.09
m3	IPS-86482	0.86	0.88
	IPS-86484	0.97	0.84
	IPS-88893	0.85	0.81
	IPS-88894	0.86	0.91

Table 7. Collection numbers and measurements (in millimeters) for the cheek teeth of *Megacricetodon primitivus* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
M1	IPS-86432	1.36	0.85
	IPS-86433	1.38	0.83
	IPS-86434	1.46	1.03
	IPS-88874	1.30	0.89
	IPS-88875	1.19	0.80
M2	IPS-86435	1.05	0.85
	IPS-86436	1.03	0.81
	IPS-86437	–	0.96
	IPS-88876	0.93	0.77
	IPS-88877	0.93	0.86
M3	IPS-86438	0.66	0.62
	IPS-86439	0.67	0.65
m1	IPS-86440	1.29	0.71
	IPS-86441	1.29	0.82
	IPS-86442	1.34	0.88
	IPS-86443	1.22	0.75
	IPS-88878	1.20	0.81
	IPS-88879	1.19	0.79
m2	IPS-86444	1.07	0.85
	IPS-86445	0.99	0.85
	IPS-86446	1.09	0.87
	IPS-86447	–	–
	IPS-86448	0.85	0.72
	IPS-88880	1.06	0.82
	IPS-88881	1.12	0.85
m3	IPS-86449	0.79	0.70
	IPS-86450	0.89	0.68
	IPS-86451	0.79	0.69
	IPS-88882	0.85	0.66

Table 6. Collection numbers and measurements (in millimeters) for the cheek teeth of *Democricetodon hispanicus* from Les Cases de la Valenciana 1.

Element	Collection number	Length	Width
M1	IPS-88883	1.61	1.09
M2	IPS-86452	1.31	1.05
	IPS-86453	1.25	1.09
M3	IPS-86454	0.88	0.81
m1	IPS-86455	–	0.90
m2	IPS-86456	1.25	1.06
	IPS-88884	1.31	0.96
m3	IPS-86457	1.11	0.94

Systematic palaeontology

Infraclass Metatheria Huxley, 1880

Family Herpetotheriidae Trouessart, 1879

Genus *Amphiperatherium* Filhol, 1879
Amphiperatherium frequens (Von Meyer, 1846) (Figure 2(A))
Material and measurements IPS-86622, M3; 2 fragmented upper molars (IPS-86615, IPS-86623). As the necessary points to fix the reference line indicated in Klietmann et al. (2014b) are missing in the M3, its width (2.67) has been measured parallel to the posterior side.

Description

Only upper cheek teeth have been recovered at LV1 and these are limited to three fragmented molars. The M3 shows a tiny antimetaconus, a double-cusped metaconulus, a rather curved than pointed metastyle and a smooth concave curvature of the labial margin posterior to the ectoflexus. The main cusps (paraconus, metaconus and protoconus) do not display any diagnostical trait in the M3. The other two elements are too fragmented to provide further information.

Discussion

The triangular morphology of the upper fragmented molars in occlusal view is similar to that of some talpids. However, the rather narrow shape of the lingual part, the reduction of the stylar cusps and cingula, and the wear pattern creating a double-crested ectoloph are characteristic of the herpetotheriid metatherian mammals. The absence of complete tooth-rows (specially the lower molar series) makes the species identification difficult. However, it is highly likely that the molars belong to *Amphiperatherium frequens*, as this is the only marsupial species documented in the Miocene of Europe (Ziegler 1999). Although the strictly diagnostic character located in M3 (often small anticonus) is missing, the overall morphology of the preserved parts in this tooth is not in disagreement with such specific ascription. *Amphiperatherium* has been reported in other localities from Spain, though its occurrences are scattered in both space and time. Hitherto, its presence has been mentioned in Montalvos 2 (Hordijk et al. 2015) and Buñol (Robles et al. 1991). However, the only material adequately figured and described comes from Mas d'Antolino and Barranc de Campisano (Furió et al. 2012), where unfortunately most of the teeth found were deciduous upper premolars (dP3).

Infraclass Eutheria Huxley, 1880

Order Eulipotyphla Waddell, Okada, Hasegawa, 1999

Family Erinaceidae Fischer, 1814

Genus *Galerix* Pomel, 1848

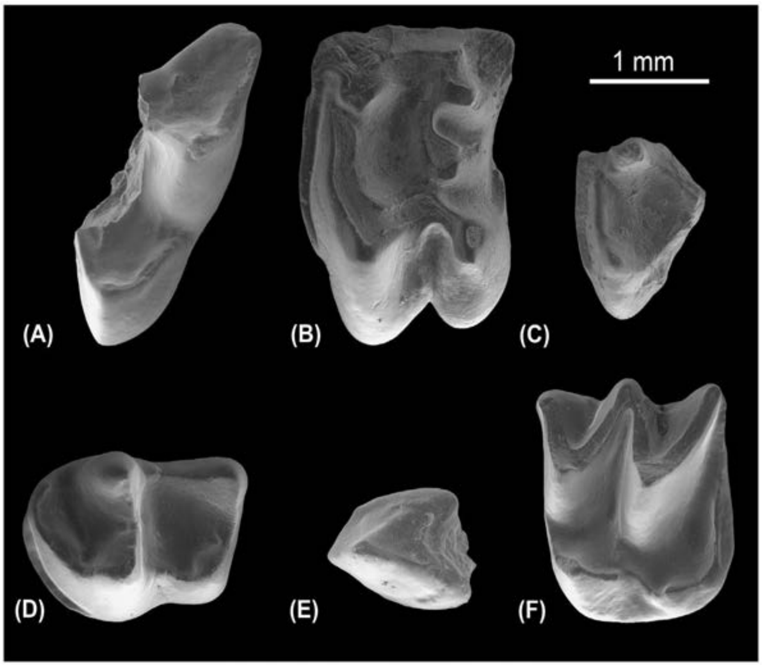


Figure 2. Marsupials and eulipotyphlans from Les Cases de la Valenciana 1.
Notes: (A) *Amphiperatherium frequens*, right M3 (reversed), IPS-86622. (B-D) *Galerix* cf. *symeonidisi*, (B), left M2, IPS-86824. (C), left M3, IPS-85596. (D), left m3, IPS-86825. (E-F) *Heterosorex neumayrianus*, (E), right lower antemolar (reversed), IPS-86600. (F), right M1 (reversed), IPS-86826. Scale: 1 mm.

Galerix* cf. *symeonidisi Doukas 1986 (Figure 2(B)–(D))

Material and measurements IPS-86824, M2 (LD: 1.90, WD: 2.47, LdJ: 1.86, WdJ: 2.47); IPS-86596, M3 (L: 1.11, W: -); IPS-86598, p1 (L: 1.11, W: 0.60); IPS-86597, p2 (L: 1.14, W: 0.56); IPS-86825, m3 (L: 1.90, W: 1.21).

Description

Upper cheek teeth

The M2 has a strong protocone-hypocone connection, but the metaconule does not show a clear connection with them. The metaconule is crescent shaped, but its posterior arm does not reach the posterolabial corner. The anterior cingulum is interrupted at the anterior part of the protocone. The M3 is triangular in occlusal view, in spite of the broken anterolabial part. The central basin is closed, but there is a small notch down the paracone, thus partially interrupting the anterior crest.

Lower cheek teeth

The p1 is single-rooted. It has an oval aspect in occlusal view, and it bears an advanced main cusp and a small elevation at its posterior margin. The p2 has also an oval aspect in occlusal view, but it is instead double-rooted. Moreover, its tip lies more posteriorly than in the p1, and there is no posterior elevation. The m3 has a subrectangular occlusal outline. The talonid is only somewhat shorter and narrower than the trigonid. The paralophid is curved and the paracone is not discernible as a clear-cut cuspid. The hypoconid and entoconid can still be identified as small elevations at each side of the posterior margin of the talonid basin.

Discussion

The morphology of the M2, which is clearly wider than long and has a crescent shaped metaconule, is indicative of a Galericini species, a tribe that is very common in the Miocene of Europe. Furthermore, the posterior arm of the metaconule not reaching the posterolabial corner of the M2 is diagnostic for the genus *Galerix*. The measurements of the M2 and m3 fit within the lower part of the range known for *G. remmerti* from the Ramblian of the Daroca-Calamocha area (see Van den Hoek Ostende 2003). The M3 is even below the known range for this species. Furthermore, the absence of protocone-metaconule connection in M2 is not in agreement with the ascription to this species. The metaconule not connected to the protocone is more frequently found in *G. exilis* and *G. symeonidisi*. In fact, the length of the only recovered M2 fits quite well within the range of *Galerix* when the two species co-occur in other Spanish localities, but not when only *G. exilis* is present (Van den Hoek Ostende & Doukas 2003: figure 4). Therefore, the material from LV1 is tentatively attributed to *G. symeonidisi*.

Family Heterosoricidae Viret and Zapfe, 1952

Genus *Heterosorex* Gaillard, 1915
Heterosorex neumayrianus (Schlosser, 1887) (Figure 2(E), (F))

Material and measurements IPS-86600, a (L: 1.22, W: 1.00); IPS-86826, M1 (L: 1.67, W: 1.93).

Description

Upper cheek teeth

Only one M1 of *Heterosorex* has been found in LV1. Its occlusal outline is square, and its ectoloph is asymmetric, with an anterior part shorter than the posterior one, and a mesostyle only faintly divided. There is no posterior emargination because a straight continuous cingulum covers this side. The hypocone is only visible as a small elevation of the continuous ridge connecting the posterior cingulum and the endoloph. The metaloph is divided into two branches, a short and faint one directed towards the base of the metacone, and another one longer, almost parallel to the lingual border, connecting with the hypocone.

Lower cheek teeth

Only a lower antemolar of *Heterosorex* has been found. It has a heart-shaped occlusal outline, with a slight asymmetry, the labial side being a bit longer than the lingual one. The labial and the lingual margins are convex, whereas the posterior one is concave. The main cusp occupies an anterior position. An anterior crest descends abruptly from the main cusp to the anterior tip of the tooth. This morphology is very characteristic within lower antemolars of the Heterosoricidae. Unfortunately, diagnostic characters have yet to be proposed for these dental elements.

Discussion

The Heterosoricidae are represented in the European Miocene by two genera: *Heterosorex* and *Dinosorex*. In the upper molars, these genera differ in the development of the lingual cusps. The poorly distinguished hypocone in the endoloph identifies the M1 of Les Cases de Valenciana 1 as belonging to *Heterosorex*. During the Early Miocene, *H. neumayrianus* is apparently the only species present in Europe, yet some authors discriminate different subspecies within it. The measurements of the M1 fit quite well within the ranges of *H. neumayrianus* provided by Ziegler (1989) for Ulm-Westtangente and Klietmann et al. (2014b) for Petersbuch 28, but the material is too scarce to identify the subspecies, even tentatively. Whereas *Heterosorex* has a rather continuous presence in the early Miocene of central Europe (e.g. Ziegler 1989; Klietmann et al. 2014b), its record in the Iberian Peninsula is limited to a few episodes. Van den Hoek Ostende (2003) noted its presence in latest MN 2 localities. Other than that, it is mainly known from Zone C (MN4) localities, such as Buñol (Robles et al. 1991), Montalvos 2 (Hordijk et al. 2015), from several localities in the Calatayud-Montalbán Basin (Van der Meulen et al. 2012) and in the locality of O'Donell in the Madrid Basin (Van den Hoek Ostende & Furió 2005).

Order Lagomorpha Brandt, 1855

Family Ochotonidae Thomas, 1897

Genus *Lagopsis* Schlosser, 1884
Lagopsis penai (Royo, 1928) (Figure 3(A), (B))
Material: 2 P3, 5 upper molariforms, 3 p3, 4 broken lower molariforms (see Table 1 for collection numbers).
Measurements see Table 1.

Description

Upper cheek teeth

The teeth are relatively small. The P3 presents a mesial hipercone covering the lagicone. In the same teeth, the mesoflexus is variable, quickly disappearing with wear and leaving a shallow concavity. The hypoflexus is deep. The mesial and distal hypercones of the P3 show variable proportions. The upper molariforms (P4-M2) present a long hypoflexus and do not have fossettes.

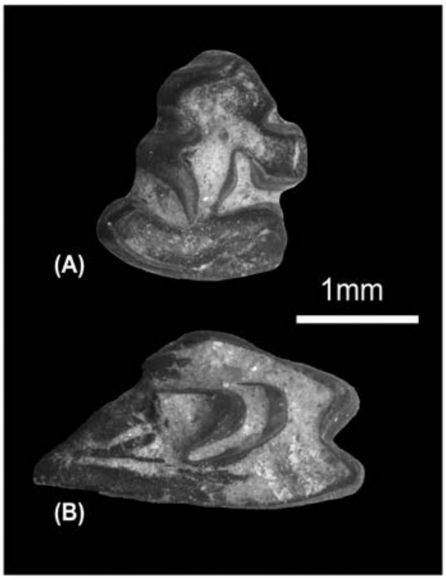


Figure 3. Lagomorphs from Les Cases de la Valenciana 1.
Notes: (A, B) *Lagopsis penai*, (A), left p3, IPS-93666. (B), right P3, IPS-93669. Scale: 1 mm.

Lower cheek teeth

The teeth are also of small size. The anteroconid in the p3 is roughly trianglular and not indented. However, this cusp presents a concavity in the labial side wich is not filled with cement. The metaconid in the p3 is smaller than the anteroconid and quadrangular. The protoconid is also small. The mesoflexid is bifurcated. An entoconid enamel hiatus was probably present in the p3, but it is difficult to observe because of the poor preservation of the specimens. The remaining lower molariforms are so broken that no measurements could be taken and most of the details of the occlusal morphology cannot be observed.

Discussion

The morphological characters of the dental occlusal surface and the size of dental remains allow assigning the ochotonid remains from LV1 to *Lagopsis penai*. In Spain this species characterizes the MN3b-MN4a (López Martínez 1989; Angelone 2009). In the Vallès-Penedès Basin *L. penai* is known from all collections from 'Rubí-Papiol' (see López Martínez 1989 and references therein). These specimens were probably surface collected during the 1950s from the early Miocene deposits that crop out at the towns of Rubí and Papiol and are not assigned to a given site. Nevertheless, some remains can be attributed to specific sites, such as the specimens from Molí de Can Calopa (a site located in Rubí) and one from San Mamet (in Sant Cugat del Vallès; López Martínez 1989). Compared to the assemblage of *L. penai* from Molí de Can Calopa, the size of the p3 in the sample of LV1 is approximately the same, although the occlusal morphology of the p3 is more advanced. Actually in LV1 the p3 shows a more marked anteroconid labial undulation. This agrees with a younger age for LV1 as compared to Molí de Can Calopa.

The genus *Prolagus* is absent in LV1. This is a remarkably uncommon situation, since usually *Lagopsis* coexists with *Prolagus*, and indeed their relative abundances have been used to infer palaeoenvironmental conditions. A higher percentage of *Lagopsis* would indicate relatively warmer temperatures and more arid conditions (López Martínez 1984, 2001).

Order Rodentia Bowdich, 1821

Family Sciuridae Fischer de Waldheim, 1817

Genus *Heteroxerus* Schaub, in Stehlin and Schaub, 1951

Heteroxerus rubricati Crusafont, Villalata, Truyols, 1955 (Figure 5(M))
Material and measurements IPS-86528, broken M1/2 (L:–, W: 1.34); IPS-88907, broken M1/M2 (L: 1.36, W: –); IPS-88908, dp4 (L: 1.17, W: 1.16); IPS-88909, m3 (L: 1.55, W: 1.21).

Description

Upper cheek teeth

The two recovered specimens are broken. The crown is relatively high and the main cusps are massive. The metaloph is interrupted before reaching the hypocone, ending in a prominent metaconule as large as the metacone. The metaconule contacts the posteroloph in one specimen (IPS-86528). The valleys are shallow, the central one presenting a mesostyl in its labial end.

Lower cheek teeth

The tooth crown is relatively high. The dp4 is much narrower in its anterior part than in the posterior one. It shows four prominent cusps: metaconid, protoconid, hypoconid and a somewhat lower entoconid. In addition there is a well defined anteroconulid. The ectolophid is low and the central valley shallow. The metaconid and protoconid are separated by a deep groove. The entolophid is complete and high. In the m3 the entoconid cannot be distinguished. This molar shows massive cusps and a shallow valley delimited by a thick continuous ridge. There is a vestigial anterior cingulid at the base of the protoconid. The entolophid is absent in the m3.

Discussion

Heteroxerus rubricati was erected by Crusafont et al. (1955) on the basis of a mandible with the complete permanent dentition from the Vallès-Penedès site Molí de Can Calopa, which dates back to the late Ramblian (MN3) and is thus older than Les Cases de la Valenciana. This species is recorded from other early Aragonian (MN4) sites from the Vallès-Penedès Basin such as Sant Mamet, el Canyet and Els Casots (Aldana Carrasco 1991, 1992). At Els Casots it is recorded together with the much larger xerine *Atlantoxerus idubedensis* (Aldana Carrasco 1991, 1992). *Heteroxerus rubricati* persisted in the area until the early Vallesian (MN9), being abundantly represented at sites such as Can Poncic, where it co-occurs with *Heteroxerus* cf. *grivensis* (Aldana Carrasco 1991, 1992). However, *H. rubricati* is easily distinguished from the latter species by its smaller size and reduced anterior cingulid in the lower molars (Cuenca 1988).

Family Gliridae Muirhead, 1819

Genus *Glirudinus* De Bruijn 1965–1966
Glirudinus modestus (Dehm 1950) (Figure 4(A))
Material and measurements IPS-86522, broken M1; IPS-86516, p4 (L: 0.55, W: 0.57); IPS-86523, m2 (L: 0.89, W: 0.82).

Description

Upper cheek teeth

The only recovered specimen is a broken M1 (IPS-86522) without labial and posterolabial margin. The preserved part of the crown is flat and low. There are eight oblique ridges which are relatively low. The anterolingual border is rounded and the anteroloph ends lingually free. Metaloph and protoloph are connected forming an oblique V-shaped trigon pattern, with two centrolophs and one extra ridge between the protoloph and the anterior centroloph. The anterior centroloph is longer than the posterior one. The posteroloph is lingually connected to the trigon and there is an extra ridge in the posterior valley. The lingual end of the two extra ridges and the posterior centroloph do not reach the medial part of the occlusal surface and are aligned parallel to it.

Lower cheek teeth

The p4 (IPS-86516) is very small and the occlusal surface is slightly concave. The four main ridges are well developed. Anterolophid and metalophid are connected lingually and there is a small centrolophid that does not reach the lingual border. Mesolophid and posterolophid are connected lingually and there is a small extra ridge in the posterior valley. The m2 (IPS-86523; Figure 4(A)) has a rectangular outline with a low crow and a slightly concave occlusal surface. It has nine oblique ridges which are thin and low. Anterolophid, metalophid and centrolophid are connected lingually, and the lingual end of the metalophid and centrolophid is far backwards. The labial connection between anterolophid and metalophid is narrow. There are two extra ridges in the anterior valley; the anterior one is long and reaches the lingual border, and the posterior one is almost connected to the medial part of the anterior extra ridge. The centrolophid is long. Mesolophid and posterolophid are connected lingually and there is a long extra ridge in the posterior valley that reaches the lingual border.

Discussion

The described specimens from LV1, although scarce, fit well within the size and dental pattern ranges of the type material of *Glirudinus modestus* from Wintershoft-West (Germany, MN3) described by Dehm (1950), Mayr (1979) and Wu (1993). In the Vallès-Penedès Basin, the genus *Glirudinus* is represented by three species: *G. modestus*, *G. gracilis*, and *G. undosus*. *Glirudinus modestus* has been reported from the early Aragonian site of Els Casots (MN4; Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a), although it already occurs together with *G. gracilis* at the Ramblian locality of Sant Andreu de la Barca (Agustí & Galobart 1997), and with *G. undosus* at the early Aragonian (MN4) localities of Can Martí Vell 1 and 2 (Agustí 1983; Agustí et al. 1985). *Glirudinus*

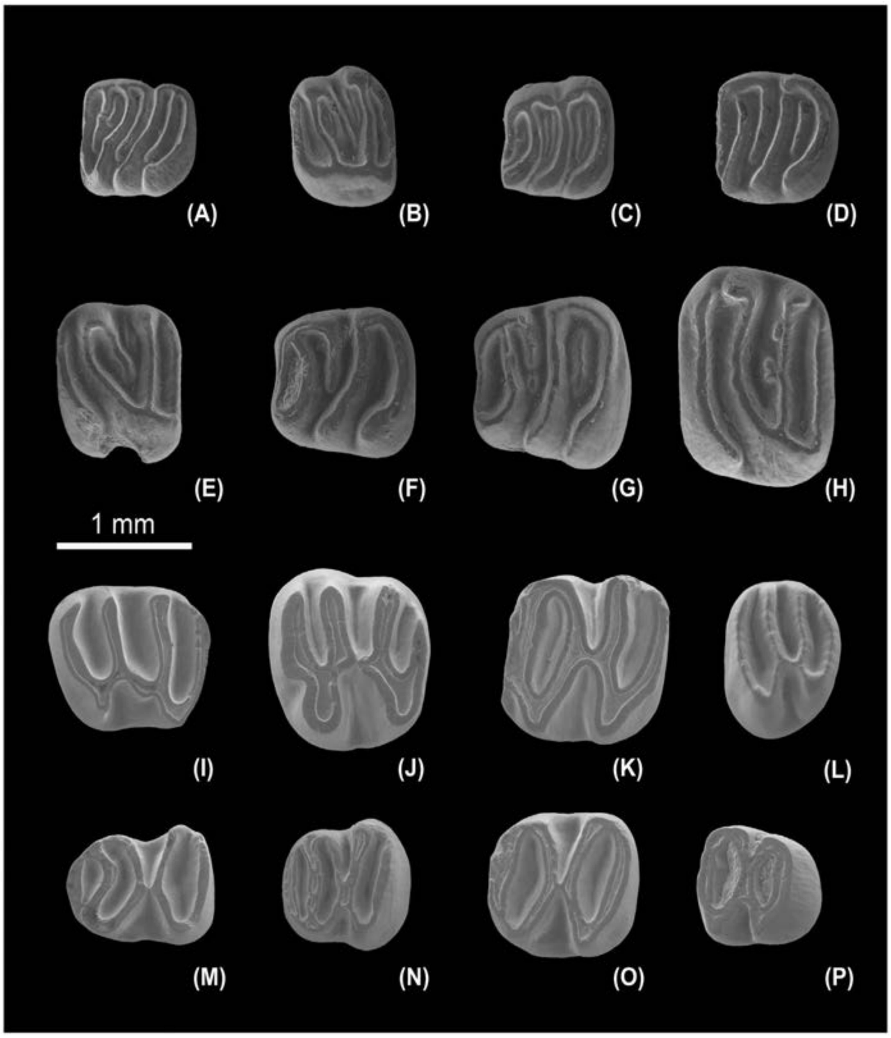


Figure 4. Glirids and eomyids from Les Cases de la Valenciana 1.

Notes: Notes: (A) *Glirudinus modestus*, right m2 (reversed), IPS-86523. (B–D) *Microdyromys koenigswaldi*, (B) right M1 (reversed), IPS-86514; (C) right m1 (reversed), IPS-86518; (D) right m2 (reversed), IPS-86520. (E, F) *Peridyromys murinus*, (E) left M1/M2, IPS-86506; (F) right m1 (reversed), IPS-86510. (G) *Pseudodryomys ibericus*, left m1, IPS-86508. (H) *Simplomys simplicidens*, right M2 (reversed), IPS-86504. (I–K) *Ligerimys florancei*, (I), right dP4 (reversed), IPS-86464. (J), left P4, IPS-86466. (K), left m1/m2, IPS-86888. (L–P) *Ligerimys ellipticus*, (L), right M2 (reversed), IPS-86485. (M), left dp4, IPS-86488. (N), right p4 (reversed), IPS-86473. (O), right m1/m2 (reversed), IPS-86480. (P) right m3 (reversed), IPS-86484. Scale: 1 mm.

modestus differs from *G. gracilis* and *G. undosus* by its simpler dental pattern, whereas its size is intermediate between both species, *G. undosus* being larger. Although this genus is not very common in the Spanish record, *G. modestus* is a representative taxa of the Ramblian and early Aragonian rodent faunas from the Calatayud-Montalbán Basin (Daams 1985; García-Paredes 2006; Van der Meulen et al. 2012; García-Paredes et al. 2016). Furthermore, it has been reported from several Ramblian localities of the Loranca Basin (Province of Cuenca; Morales et al. 1999); and the Aragonian of Bunyol (Valencia; Daams 1976) and the Barranco de Morteral section (Valencia; Ruiz-Sánchez et al. 2003).

Genus *Microdyromys* De Bruijn 1965–1966
Microdyromys koenigswaldi De Bruijn 1965–1966 (Figure 4(B)–(D))
Material 2 M1, 1 p4, 2 m1, 1 m2 and 1fragment of m2 (see Table 2 for collection numbers).
Measurements Table 2.

Description

Upper cheek teeth

The M1 has a sub-square outline and a markedly concave occlusal surface. The lingual side of the crown is ornamented. The number of ridges is seven, and the four main ridges are connected lingually forming a continuous endoloph. Anteroloph and posteoloph end free at the labial margin. The trigone has a U-shaped pattern with two centrolophs and one extra ridge between the protoloph and the anterior centroloph. The anterior centroloph is long and connected labially to the protoloph. Posterior centroloph is shorter than anterior one and it is labially connected to the metaloph in one specimen (IPS-86515) but in the other one is separated by a groove (IPS-86514; Figure 4(B)).

Lower cheek teeth

The p4 is relatively worn. Anterolophid and metalophid are connected labially and lingually. There is a small extra ridge in the

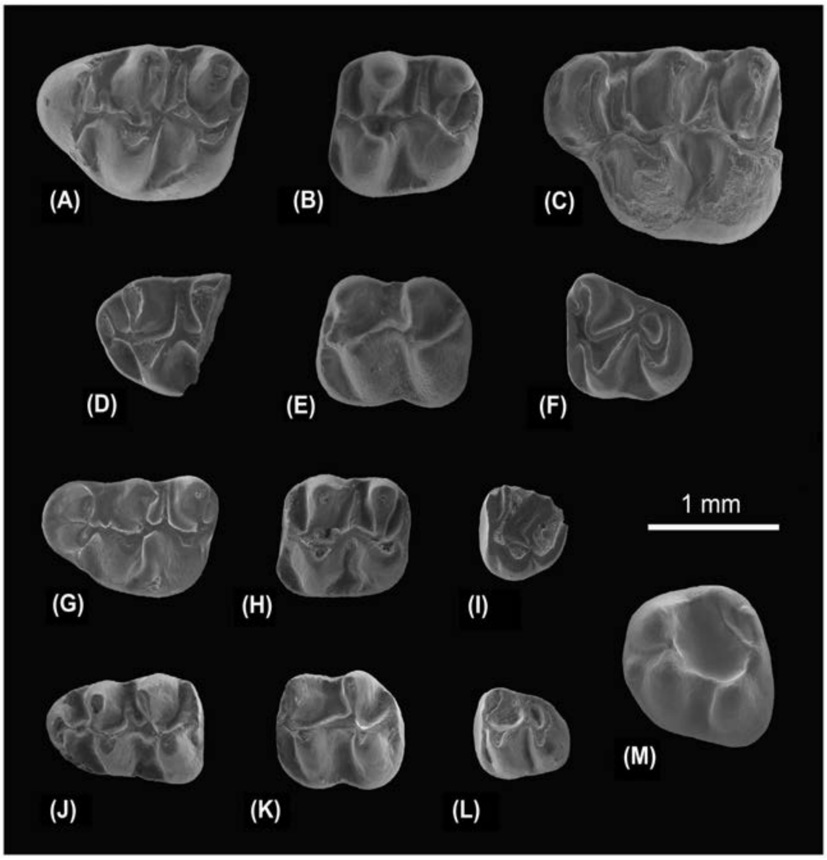


Figure 5. Sciurids and cricetids from Les Cases de la Valenciana 1.

Notes: (A, B, D–F) *Democricetodon hispanicus*, (A), right M1 (reversed), IPS-88883. (B), left M2, IPS-86452. (D), right m1 (broken, reversed), IPS-86455. (E), right m2 (reversed), IPS-88884. (F), right m3 (reversed), IPS-86457. (C) *Eumyarion* sp., left M1, IPS-88885. (G-M) *Megacricetodon primitivus*, (G), right M1 (reversed), IPS-86432. (H), left M2, IPS-86435. (I), right M3 (reversed), IPS-86439. (J), left m1, IPS-86440. (K), left m2, IPS-86444. (L), right m3 (reversed), IPS-86451. (M) *Heteroxerus rubricati*, right dp4 (reversed), IPS-88908. Scale 1 mm.

anterior valley which is connected medially to the anterolophid because of wear. The centrolophid is small and does not reach the lingual border; its anterior side is almost in contact with the metalophid. Mesolophid and posterolophid are connected lingually and there is a well-developed extra ridge in the posterior valley. The m1 has a trapezoidal outline. The occlusal surface is concave and the labial border is prominent. The number of ridges is seven, including one extra ridge in the anterior and posterior valley. Anterolophid and metalophid are connected lingually as also occurs for the mesolophid and posterolophid. One m1 (IPS-86518; Figure 4(C)) has a very small extra ridge of the anterior valley, a continuous endolophid in the lingual border and the centrolophid does not reach the lingual border. The remaining m1 (IPS-86509) is larger and has a long centrolophid that extends to the labial border and connects the mesolophid; it is broken and partially corroded and, therefore, it is attributed to *M.* cf. *koenigswaldi*. The m2 is represented by a posterior fragment (IPS-86519) and one complete specimen (IPS-86520; Figure 4(D)). It has an almost rectangular outline with a rounded posterior border. The extra ridge of the anterior valley is absent, and the centrolophid and the extra ridge of the posterior valley are long and well developed.

Discussion

The genus *Microdyromys* is abundant and widely distributed along Europe and Asia. It was described by De Bruijn (1965–1966) who designated *M. koenigswaldi* from the middle Aragonian locality Valdemoros 3B (local zone Dc, MN5, Calatayud-Montalbán Basin) as the type species of the genus. Daams (1981) provided a detailed description of several assemblages of *Microdyromys* from Germany, Switzerland, France, and Spain, emphasizing that the great overlap in size and occlusal pattern makes the distinction between species difficult. Additionally, this author (op. cit.) erected the species *M. legidensis* based on material from the early Aragonian locality Villafeliche 2A (zone B, MN4, Calatayud-Montalbán Basin), which differs from *M. koenigswaldi* only by its smaller size. The dental pattern of the material from LV1 agrees well with that of *M. koenigswaldi* and, therefore, *M. legidensis*. The size of the described specimens from LV1 partially overlaps with the ranges of *M. koenigswaldi* and *M. legidensis* from their type localities, fitting better with the assemblages of localities intermediate in age between them (with the exception of the larger specimen IPS-86509 that seems more similar to *M. koenigswaldi*). García-Paredes (2006) described a trend in size increase between *M. legidensis* from the early Aragonian and *M. koenigswaldi* from the middle Aragonian, and suggested synonymizing *M. legidensis* with *M. koenigswaldi*, having priority the latter name. Therefore, the *Microdyromys* material from LV1 is ascribed to *M. koenigswaldi*.

In the Vallès-Penedès Basin *Microdyromys* sp. ('*legidensis-koenigswaldi* group' according to Agustí 1983) is reported from the early Aragonian localities Can Martí Vell 1 and 2 (MN4; Agustí 1983, 1990) and referred to as *M.* cf. *koenigswaldi* by

Agustí et al. (1985), and Els Casots (MN4; Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a). More recently, the presence of *M.* cf. *koenigswaldi* has been reported from the late Aragonian of the basin (Casanovas-Vilar et al. 2016a). Although *M. koenigswaldi* is only occasionally found in the Vallès-Penedès Basin, it has been extensively recorded in other Spanish basins, being especially abundant in the early and middle Aragonian of the Calatayud-Montalbán Basin (García-Paredes 2006; García-Paredes et al. 2010; Van der Meulen et al. 2012; García-Paredes et al. 2016) and ranging until the late Vallesian in the Duero Basin (Álvarez Sierra et al. 1990).

Genus *Peridyromys* Stehlin and Schaub 1951
Peridyromys murinus (Pomel 1893) (Figure 4(E), (F))
Material and measurements IPS-86506, M1/2 (L: 0.96, W: –); IPS-86507, broken M1/2; IPS-86510, m1 (L: 1.10, W: 1.01); IPS-86512, corroded m3; IPS-86521, m3 (L: 0.90, W: 0.90).

Description

Upper cheek teeth

The M1 and M2 of *Peridyromys murinus* are difficult to distinguish from one another and traditionally they have been studied together as M1/2, like in other species of Gliridae (e.g. Daams 1981; García-Paredes 2006). The occlusal surface is concave and has a square outline with rounded corners. The M1/2 has the basic occlusal pattern of the Gliridae, consisting of four main ridges, the metaloph and protoloph connected forming an asymmetrical Y-shaped pattern directed backwards, with one or two centrolophs. One specimen (IPS-86507) only presents the anterior centroloph, and its lingual border is almost completely broken. In the remaining specimen (IPS-86506; Figure 4(E)) the labial border is also slightly broken. It has two centrolophs, the anterior one is of medium length and well developed, whereas the posterior one is short and lower than the main ridges.

Lower cheek teeth

The m1 has a subrectangular outline and concave occlusal surface. As the M1/2, it shows the basic occlusal pattern of the Gliridae, consisting in four main ridges and a medium-length centrolophid (IPS-86510; Figure 4(F)). Anterolophid and metalophid are connected lingually, and the centrolophid is connected to the lingual border at a right angle. Mesolophid and posterolophid are also connected lingually. The m3 has the same basic pattern as the m1, with the posterior part rounded and narrower than the anterior one. The posterior valley is open at the lingual and labial side in one specimen (IPS-86521); the remaining specimen (IPS-86512) is too worn and partly corroded at the lingual half of the occlusal surface to be described.

Discussion

Peridyromys murinus is a widely known species ranging from the late Oligocene to the middle Miocene of Europe (Daams 1999). The size and dental pattern of the specimens from LV1 fit perfectly within the ranges of the assemblages of *Peridyromys murinus* from Western Germany, France and Spain (Daams 1981; García-Paredes 2006). In the Vallès-Penedès Basin the species is known from late Ramblian (Sant Andreu de la Barca, La Costablanca; Agustí & Galobart 1997; Casanovas-Vilar et al. 2011b) and early Aragonian sites (Can Martí Vell 1 and 2, Els Casots, Vilobí; Agustí 1981, 1983; Agustí et al. 1985; Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a).

Genus *Pseudodryomys* De Bruijn 1965–1966
Pseudodryomys ibericus De Bruijn 1965–1966 (Figure 4(G))
Material and measurements IPS-86524, fragment of M3; IPS-86508, m1 (L: 1.20, W: 1.17); IPS-86511, m1 (L: 1.17, W: 1.12).

Description

Upper cheek teeth

The only available specimen is a fragment of M3 in which the anteroloph, the posteroloph and the lingual margin are missing. It has two centrolophs, the anterior one is longer than the posterior one and it is lingually connected to the protoloph. The lingual half of the protoloph is directed backwards and there is one extra ridge between the protoloph and the anterior centroloph.

Lower cheek teeth

The two m1 have a subrectangular outline with the posterior part wider than the anterior one. The occlusal surface is concave and there are six ridges. The anterolophid, metalophid and centrolophid are connected lingually. In one specimen (IPS-86511), the anterior valley is open labially, whereas in the remaining specimen (IPS-86508; Fig. 4(G)) there is a narrow connection between anterolophid and metalophid. The centrolophid is relatively short in one specimen (IPS-86511). In the remaining one (IPS-86508; Figure 4(G)) it is longer, discontinuous at the labial end, and reaches the medial part of the occlusal surface. Mesolophid and posterolophid are connected lingually and there is a well-developed extra ridge in the posterior valley.

Discussion

Despite the scarcity of the material from LV1, the size and morphology fit well within the ranges of *Pseudodryomys ibericus* from the Calatayud-Montalbán Basin (García-Paredes 2006). *Pseudodryomys ibericus* is mainly distributed in the early and middle Miocene of central and southwestern Europe, being particularly common and relatively abundant in the Spanish record. In the Vallès-Penedès Basin, this species is a dominant component of the late Ramblian rodent faunas (Casanovas-Vilar et al. 2016a), being reported from the oldest Miocene locality of the area, Turó de les Forques (Casanovas-Vilar et al. 2016a) as well as from La Costablanca (Agustí et al. 1985), Molí de Can Calopa (Agustí 1981; Agustí et al. 1985; Casanovas-Vilar et al. 2011b) and Sant Andreu de la Barca (Agustí 1981; Agustí et al. 1985; Casanovas-Vilar et al. 2011b). *Pseudodryomys ibericus* is common as well in the early Aragonian rodent faunas of this basin, such as Vilobí (Casanovas-Vilar et al. 2011b) and Els Casots (Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a). In the Calatayud-Montalbán Basin, this species ranges until the zone E (middle Aragonian, MN5; García-Paredes 2006; Van der Meulen et al. 2012; García-Paredes et al. 2016).

Genus *Simplomys* García-Paredes, in García-Paredes et al. 2009
Simplomys simplicidens De Bruijn 1965–1966 (Figure 4(H))

Material 3 P4, 2 M2, 1 p4, 3 fragments of m2, 1 broken m3 (See Table 3 for collection numbers).
Measurements Table 3.

Description

Upper cheek teeth

The P4 has an oval or subtriangular outline. The dental pattern is very simple. The anteroloph is short and isolated and it is situated in the middle part of the anterior border. Protoloph and metaloph are connected forming a relatively symmetrical Y-shaped pattern. The posteroloph is isolated and relatively short but longer than the anteroloph; it is divided in one specimen (IPS-86501). The M2 has a concave occlusal surface and a nearly rectangular outline, being wider than long. The dental pattern is simple consisting in four main ridges. The anteroloph ends free at the lingual and labial border. Protoloph and metaloph are connected forming an asymmetrical Y-shaped pattern directed backwards, and connected lingually to the posteroloph. The posteroloph is straight and ends free at the labial border. In one specimen (IPS-86504; Figure 4(H)) there are two small and low cusp-like structures inside the central valley next to the metaloph.

Lower cheek teeth

The only available p4 (IPS-86505) has an extremely reduced dental pattern, being difficult to homologize the observed structures with the main ridges and to use the traditional nomenclature. The anterior part is very small, formed by a C-shaped structure open to the anterior margin which is assumed to be formed by the union of the anterolophid and metalophid. The mesolophid is the longest ridge; it has a central position and is connected to a posterolingual cusp (interpreted as the entoconid). In the middle of the posterior margin there is one isolated cusp (interpreted as the hypoconid). The m2 is represented by three fragments; two of them (IPS-86525, IPS-86526) have a short centrolophid connected lingually to the metalophid and anterolophid, and there is no extra ridge in the posterior valley. The only available m3 (IPS-86513) is broken at the lingual border but it shows part of a short centrolophid. The posterior part is rounded and has some degree of reduction; the mesolophid and the posterior valley do not reach the labial border and the valley is open in a medial position.

Discussion

The material from LV1 fits perfectly with the size range and morphology of *Simplomys simplicidens* from the type area of the Aragonian (Calatayud-Montalbán Basin). It has been extensively studied and discussed by García-Paredes (2006) and García-Paredes et al. (2009), showing trends towards size increase of the molars, simplification of the premolars and simplification of the posterior part in the m3. The morphology and size of the specimens from LV1 is similar to that of the material from the early Aragonian sites of the Calatayud-Montalbán Basin.

Simplomys simplicidens is recorded in most of the fossil faunas from the early and middle Miocene of the Iberian Peninsula and it also occurs in other European countries such as France, Germany, and Switzerland (García-Paredes et al. 2009). In the Calatayud-Montalbán Basin, this species ranges until local zone E (middle Aragonian, MN5; García-Paredes 2006; García-Paredes et al. 2009; Van der Meulen et al. 2012; García-Paredes et al. 2016). In the Vallès-Penedès Basin, *S. simplicidens* is an important part of the late Ramblian and early Aragonian rodent faunas (Casanovas-Vilar et al. 2016a), being recorded so far at Turó de les Forques (MN3; Casanovas-Vilar et al. 2011b), Can Marti Vell 1 and 2 (MN4; Agustí 1981, 1983), El Canyet (MN4; Agustí 1981; Casanovas-Vilar et al. 2011b), Vilobí (Casanovas-Vilar et al. 2011b) and Els Casots (Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a).

Family Eomyidae Winge, 1887

Genus *Ligerimys* Schaub, in Stehlin and Schaub, 1951
Ligerimys florancei Schaub, in Stehlin and Schaub, 1951 (Figure 4(I)–(K))
Material 2 dP4, 2 P4, 2 M1, 1 M2 and 1 fragment of M1/M2, 1 M3, 4 m1/m2 and 1 fragment of m1/m2, 1 m3 (see Table 4 for collection numbers).
Measurements Table 4.

Description

Upper cheek teeth

The wear surface is flat. The mesoloph is absent and the central syncline is conspicuously wider than the anterior and the posterior ones. All labial valleys are open, even though the posterior syncline may be closed in highly worn M1/M2. The longitudinal ridge is oblique, resulting in a proverse sinus. In one of the P4 (IPS-86466, Figure 4(J)) the longitudinal ridge is constricted at its mid point. The P4 and one out of three M1/M2 (IPS-86467) show a highly reduced anterolingual valley in front of the protocone. In their turn, there is a weak longitudinal connection between the metaloph and the posteroloph in two M1/M2 (IPS-86468, IPS-86470). The M3 is rounded and highly reduced, with a vestigial sinus in its posterolingual corner. The main ridges curve backwards in their lingual end and show multiple constrictions.

Lower cheek teeth

The wear surface is flat. The metalophid and the mesolophid merge labially and lingually, and the same occurs with the hypolophid and the posterolophid in almost all molars. This results in an 8-shapped occlusal pattern defined by two rhomboids connected by a short longitudinal ridge located at the middle width of the molar. The lingual end of both rhomboids is directed obliquely forwards, resulting in a retroverse sinusid. In one specimen (IPS-86888, Figure 4(K)) the distal rhomboid is not closed lingually. Some specimens, such as IPS-86888 (Figure 4(K)), show a vestigial anterolophid and anterior valleys. The lingual arm of the anterolophid is better developed than the labial one.

Discussion

Ligerimys florancei shows a broad geographical range, being recorded from Spain to Switzerland and Germany. In some Spanish sites this species co-occurs with the endemic *Ligerimys ellipticus*, such as in Bunyol (Valencia; Daams 1976) or Can Martí Vell 1 and 2 (Vallès-Penedès Basin; Agustí 1983), although it is generally rarer. Even though both species are very similar, *L. florancei* shows a number of morphological features that allow them to distinguish it from *L. ellipticus* (Daams 1976; Álvarez Sierra 1987). *Ligerimys florancei* is larger, and the main ridges in the lower cheek teeth define two rhomboids rather than two ellipses as in *L. ellipticus*. The sinusid is retroverse in *L. florancei* and transverse in *L. ellipticus*, and the anterolophid is more frequently absent in the latter species. All these features allow recognizing this species in LV1. As it happens in Can Martí Vell 1 and 2, *L. florancei* is rarer than *L. ellipticus*, being represented by just 17 specimens, whereas there are 29 specimens of the second species.

Ligerimys ellipticus Daams 1976 (Figure 4(L)–(P))
Material 2 M1, 2 M2 and 3 fragments of M1/M2, 1 dp4, 3 p4, 11 m1/m2 and 3 fragments of m1/m2, 4 m3 (see Table 5 for collection numbers).
Measurements Table 5.

Description

Upper cheek teeth

The wear surface is flat. The M1 and M2 are very similar, but can be distinguished because the first molars are longer and show a more rectangular outline. The main ridges define two transverse ellipses. The metaloph and the posteroloph close the posterior ellipse at a low crown high whereas the anterior ellipse, defined by the anteroloph and the protoloph is labially open. The longitudinal ridge is very short and oblique, being displaced quite lingually. The sinus is slightly proverse in the M1 and transverse in the M2. One M1 (IPS-86487) shows a peculiar morphology with a longer longitudinal ridge and a short and isolated transverse ridge (presumably a vestigial mesoloph) at the edge of the central syncline.

Lower cheek teeth

The wear surface is flat. The lower cheek teeth are distinguished by the presence of two transverse ellipses defined by the main ridges (metalophid, mesolophid, hypolophid, posterolophid) and joined by an extremely short longitudinal ridge in central position. This short longitudinal ridge can be constricted or very low. The sinusid is transverse. The ellipses are closed both labially and lingually in the molars whereas in the p4 and dp4 the posterior ellipse, defined by the hypolophid and the metalophid, may be open lingually. The dp4 is elongated and shows a well defined anterolophid that contacts the metaconid lingually but does not reach the protoconid with its labial end. The anterolophid delimits a well-defined synclinid. The p4 is also quite elongated and narrower in its anterior half. It shows a well-defined anterolophid that merges with the metaconid and the protoconid, thus delimiting a very narrow anterior synclinid. The mesolophid and the hypolophid are very close to one another and contact widely. All the recovered m1/m2 but one (IPS-86477) present a vestigial anterolophid normally consisting just in a low labial arm. An extremely short and higher lingual anterolophid is present in IPS-86480 (Figure 4(O)), while in IPS-86489 and IPS-86490 a vestige of both arms of the anterolophid is present. This ridge is more frequently absent in the m3, with only one specimen (IPS-86482) out of three showing a vestigial labial anterolophid.

Discussion

Ligerimys ellipticus is clearly distinguished from *L. florancei* by the characteristic morphology of the molars, particularly the lower ones, as well as by its smaller dimensions (see above). The material from LCV1 differs from that of Bunyol, the type locality of the species, by the consistent occurrence of a vestigial anterolophid in almost all the recovered m1/m2. Agustí (1983) already noted the same difference in the material of this species from Can Martí Vell 1 and 2 and argued that this may indicate that the Vallès-Penedès sites are slightly older. Interestingly, the anterolophid is absent in the few lower molars of *L. ellipticus* recovered at Els Casots (Agustí & Llenas 1993). This, coupled with the absence of *L. florancei* from the site, may indicate that this site is slightly younger since in the Aragonian type area *L. ellipticus* replaces *L. florancei* in the upper part of zone Ca, with both species co-occurring in a few sites (Van der Meulen et al. 2012). The extinction of the genus *Ligerimys* marks the upper boundary of the biozone MN4 (Kälin & Kempf 2009; Van der Meulen et al. 2012). However, the last representatives of this genus in Central Europe and the Iberian Peninsula are different. In Central Europe *L. florancei* is the last species of the genus present and disappears at about 16.7 Ma (Kälin & Kempf 2009). In the Aragonian type area in Spain, this species is replaced by the endemic *L. ellipticus* at 16.4 Ma, and the genus ultimately disappears at 15.93 Ma (Van der Meulen et al. 2012).

Family Cricetidae Fischer, 1817
Genus *Democricetodon* Fahlbusch, 1964
Democricetodon hispanicus Freudenthal 1967 (Figure 5(A), (B), (D)–(F))
Material: 1 M1, 2 M2, 1 M3, 1 fragment of m1, 1 m2 and 1 fragment of m2, 1 m3 (see Table 6 for collection numbers).
Measurements Table 6.

Description

Upper cheek teeth

The M1 and M2 present long mesolophs, almost reaching the labial margin of the molar. The anterocone of the M1 is slightly subdivided into two cusps, with a simple anterolophule connected to the lingual cusp. There is a medium-sized labial spur in the anterolophule and the anterior valleys are closed by the arms of the anteroloph. The protolophule is double in the upper molars, but the two arms are complete in only one M2 (IPS-86452, Figure 5(B)). In the only recovered M1 (IPS-88883, Figure 5(A)) the anterior arm is incomplete, and in the remaining M2 (IPS-86453) the posterior arm just touches the metacone. The metalophule is simple and anterior to the hypocone in the M2. In the M1, it is posterior to this cusp and results in a quite reduced posterosinus. The sinus is wide and transverse in all the upper molars. The main valleys are closed by well-developed cingula, particularly the lingual ones. The only M3 recovered is too worn and does not preserve details of its occlusal morphology.

Lower cheek teeth

The mesolophid in the lower molars is variable, being of medium length in the only recovered m1 and in one m2 (IPS-86456), while it is absent in the other (IPS-88884, Figure 5(E)) and in the recovered m3. The anteroconid of the m1 is simple and bean shaped. The anterior valleys of the m1 are closed by the arms of the anterolphulid, which are quite low. In the m2 and m3 the anterior valleys are quite reduced, particularly the anterosinusid. The sinusid is wide and points slightly forwards in the m1 and m2, whereas it is slightly retroverse in the m3. This valley is closed by a low cingulid.

Discussion

The described specimens are very similar to *Democricetodon hispanicus* from Villafeliche 2A, the type locality of this species (Freudenthal 1967). This species is distinguished from its supposed descendant, *D. decipiens*, by its smaller size and longer mesolophs/ids (Van der Meulen et al. 2003). It also differs from the somewhat younger *D. franconicus* by the smaller dimensions of most molars (except the first ones) and the more frequently posterior protolophule in the M1, amongst other features (Van der Meulen et al. 2003). Finally, *D. koenigswaldi*, which occurs in younger sites, differs from *D. hispanicus* by its larger size, and predominantly double metalophule in the M2. Some of these and other species of the genus *Democricetodon* were initially included within the genus *Fahlbuschia*, but we follow Van der Meulen et al. (2003) in considering it a junior synonym of *Democricetodon* (for a different opinion see Freudenthal 2006). Even though the recovered material is scarce it allows for a confident attribution to *D. hispanicus*, since it fits the size range of this species, clearly smaller than other Iberian species of the same genus. In addition, the mesolophs/ids are mostly well developed and the protolophule is double in the M2 and posterior in the M1 (albeit there is a vestigial anterior arm). Finally, the metalophule is simple in the M1 and M2. All these features fit with the emended diagnosis for the species provided by Van der Meulen et al. (2003). However, there are some singularities. *D. hispanicus* normally shows a simple undivided anterocone in the M1 instead of slightly split as in the LV1 specimen. The protolophule of the M1 shows a vestigial anterior arm, a feature that can also occur in a significant percent of specimens *D. hispanicus* (see Van der Meulen et al. 2003: 418). Agustí (1983) reported the presence of *Democricetodon* aff. *hispanicus* at Can Martí Vell 1 and 2 and Agustí and Llenas (1993) also cited it from Els Casots. This species would be distinguished from *D. hispanicus* by its slightly larger size and would also be present at the site of Bunyol (Valencia; Daams & Freudenthal 1974). Daams and Freudenthal (1988) later erected the species *Fahlbuschia* (= *Democricetodon*) *decipiens* for the Bunyol specimens. This species would coexist at the Valencian site with a few *D. hispanicus* specimens which can be easily recognized by their smaller size (Daams & Freudenthal 1988; Van der Meulen et al. 2003). However, the material from the Vallès-Penedès sites is fully comparable in size and morphology with *D. hispanicus* from the type locality Villafeliche 2A and with that of other sites of the Calatayud-Montalbán Basin, so we prefer ascribing it to this species. Only a single specimen from Els Casots (IPS-45052) stands outs because of its larger size and a longer mesolophid. This specimen may well belong to a second *Democricetodon* species.

Megacricetodon primitivus (Freudenthal 1963) (Figure 5(G)–(M))
Material: 5 M1, 4 M2 and 1 fragment of M2, 2 M3, 6 m1, 6 m2 and 1 fragment of m2, 4 m3 (see Table 7 for collection numbers).
Measurements Table 7.

Description

Upper cheek teeth

The M1 show a deeply split anterocone with a well defined and platform-like anterior cingulum at its base. The anterior part of the molar is reduced in the M2, but all the specimens retain a protosinus closed by a low lingual anteroloph. The labial anteroloph and the anterosinus are better developed in the M2. The protolophule is mostly simple in the M1 and M2, being posterior to the protocone in the M1 and anterior to it in the M2. However, one M1 (IPS-86432, Figure 5(G)) shows a vestigial anterior protolophule and one M2 (IPS-86435, Figure 5(H)) presents a posterior arm that does not reach the metacone. The mesoloph varies from long to medium-sized in the M1 and M2 presents a vestigial anterior protolophule that does not reach the metacone. The metacone in the M2 usually shows a short ectoloph directed towards the mesoloph but that does not merge with it. The metalophule is transverse or slightly anterior in the M2 and slightly posterior in the M1, so that the posterosinus is not reduced. The sinus is wide and transverse in the M1 and M2. All the main valleys in the upper molars are closed by low cingula, which tend to be more pronounced in the lingual side. The M3 are highly reduced and the occlusal morphology can only be described for one specimen which is quite worn (IPS-86439, Figure 5(I)). The protosinus is missing in the M3, although there is a vestige of lingual anteroloph. The anterosinus is closed by the labial anteroloph. The sinus is reduced and very narrow, so that the protocone directly contacts the hypocone. There is no trace of mesoloph in this molar.

Lower cheek teeth

The mesolophid is absent in the m3 and in one m2 (IPS-86444, Figure 5(K)) while in the remaining lower molars it varies from medium to short. The metalophulid and hypolophulid are simple. The anteroconid in the m1 consists in a single rounded cusp. In the same molar the anterior valleys are wide and are closed by the arms of the anterolophid, which are quite low. On the contrary, the anterior valleys, and particularly the anterosinusid, are reduced in the m2 and m3. Indeed, this valley is vestigial in one m2 (IPS-86445) and has almost disappeared in all the m3. The sinusid is clearly proverse in the m1, mostly transverse in the m2 and retroverse in the m3. The lingual valleys are closed by low cingulids.

Discussion

The material from LV1 belongs to a small-sized *Megacricetodon* species, such as *M. primitivus*, *M. collongensis* or *M. minor*, which are abundant components of the Aragonian faunas of the Iberian Peninsula (Daams & Freudenthal 1988). All these species show a similar morphology being characterized by their predominantly long to medium-sized mesoloph/ids and the frequent double protolophules and metalophules in the M1 and M2. However, a number of morphological features allow ascribing the material of LV1 to *M. primitivus*. The anterocone in the M1 is deeply split as in *M. primitivus* and not predominantly simple to slightly split as in *M. minor* (Oliver & Peláez-Campomanes 2014). On the other hand, *M. collongensis* from Vieux-Collonges (France) differs from *M. primitivus* by its slightly larger size as well as by the presence of a subdivided anteroconid in some m1 and the higher percentage of double protolophules in the M1 and M2. The anteroconid is always simple and rounded in the m1 from LV1 and the protolophule consists of just a single arm in the M1 and M2, even though an incomplete second arm exists in just two specimens. In addition, the material perfectly agrees in size with the specimens from Valtorres, the type locality of *M. primitivus* (Freudenthal 1963; Daams & Freudenthal 1988; Oliver et al. 2008; Oliver & Peláez-Campomanes 2014). *Megacricetodon primitivus* is restricted to southwestern Europe, where it is the first species of this genus to be recorded (Daams & Freudenthal 1988; Oliver et al. 2008; Van der Meulen et al. 2012; Oliver & Peláez-Campomanes 2014). The first occurrence of this species at 16.49 Ma is diagnostic of zone Ca in the Aragonian type area (Van der Meulen et al. 2012; see below), which overlaps with part of the MN4. In the Vallès-Penedès Basin *M. primitivus* is recorded at Can Martí Vell 1 and 2 (Agustí & Cabrera 1981; Agustí 1981, 1983) and Els Casots (Agustí & Llenas 1993; Casanovas-Vilar et al. 2011a). The specimens from LV1 are somewhat smaller than the ones from Can Martí Vell 1 and 2 and Els Casots but agree in other morphological aspects. They are also generally smaller than those of the type locality for the species, Valtorres (see Oliver & Peláez-Campomanes 2014) but fit within its size range. Another remarkable difference is the lower abundance of double protolophules in the M1 and M2 from LV1. This also occurs in the material from Can Martí Vell 1 and 2 (Agustí 1983) as already noted by Oliver and Peláez-Campomanes (2014).

Genus *Eumyarion* Thaler, 1966
Eumyarion sp. (Figure 5(C))
Material and measurements IPS-88885, M1 with the enamel partly corroded and damaged in its distal part (L: 1.91, W: 1.41).

Description

This molar is outstanding because its large size and unique morphology, which clearly indicate the presence of a third cricetid genus in LV1. The specimen is damaged in its posterior part and the enamel is corroded, particularly on the lingual cusps. The anterocone region (prelobe) is well developed and individualized from the rest of the teeth. It is bean shaped, defining an anterior mure. The labial spur of the anteroloph is well-developed and almost reaches the labial margin of the teeth. This spur is weakly connected to the short anterior arm of the protolophule. The anterosinus is closed by a low ridge and the protosinus is highly reduced. The mesoloph is thick and long and ends in a mesostylid. There is a vestigial ectomesoloph which gives the sinus a heart shape. The metalophule is simple and slightly anterior to the hypocone.

Discussion

The plesiomorphic morphological features of this molar, such as its individualized anterocone region and complex morphology with well-developed transverse ridges (labial spur of the anteroloph, thick mesoloph) allow ascribing it to the genus *Eumyarion*. This genus is the last representative of the Paracricetodontinae, a primitive cricetid subfamily that includes mostly Palaeogene forms (Freudenthal et al. 1992; Hugueney 1999). *Eumyarion* is first recorded in the MN4 (Mein 1999) and it has been reported from two close sites of the Vallès-Penedès Basin: Can Martí Vell 1 and Sant Mamet. In both localities, it is represented by just a few specimens that have been attributed to *Eumyarion weinfurteri* (Agustí 1981, 1983). The M1 from LV1 agrees in size with this species and is also morphologically similar (see de Bruijn 2009). However, in *E. weinfurteri* the anterocone is slightly subdivided into two cusps and the labial spur of the anteroloph is better developed, reaching a posterior spur of the paracone (de Bruijn 2009). *Eumyarion valencianum,* which was erected on the basis of material from Bunyol (Daams & Freudenthal 1974) occurs in chronologically close sites from the Calatayud-Montalbán Basin (Olmo Redondo 5, 8 and 9, Vargas 1A; see Van der Meulen et al. 2012). The material from LV1 also agrees in size and morphology with this species, sharing a simple, bean-shaped anterocone with it and the better developed posterior protolophule. However, there is a vestigial ectomesoloph in the described specimen, while this feature is missing in *E. valencianum* (Daams & Freudenthal 1974). Intra- and interspecific variation in the genus *Eumyarion* can be considerably high (e.g. de Bruijn 2009; Casanovas-Vilar et al. 2010; Maridet & Sen 2012) and only a single specimen has been recovered at LV1, therefore, we refrain ascribing it to a given species.

Biostratigraphy

The Miocene mammal record of the Vallès-Penedès Basin has been the subject of multiple revisions but most of the attention has been driven to the late Aragonian and Vallesian mammal ages, which comprise the latest middle Miocene and the earliest late Miocene. This part of the record is covered by numerous rich sites and the combination of bio- and magnetostratigraphic data has resulted in a high-resolution chronology (see Agustí et al. 1997; Casanovas-Vilar et al. 2011c, 2016a, 2016b). The number of sites is conspicuously lower for the early Miocene part of the record and, with some exceptions, these are much poorer. Furthermore, a magnetostratigraphical sampling is now on course (M. Garcés, unpublished data), so for the moment the chronological arrangement of the main sites and bioevents is entirely based on litho- and biostratigraphical correlations.

In their pioneering study, Crusafont et al. (1955) already divided the early Miocene into two parts, noting that some taxa which are more characteristic of the middle Miocene (i.e. *Bunolistriodon*, *Dorcatherium*) are present in only some sites. Many of the taxa that define this subdivision are the same used to distinguish between the MN3 and MN4 biozones (after Mein 1999 and Agustí et al. 2001). Later on, the study of the rodent fauna by Agustí (see Agustí 1981, 1982) allowed a significant refinement of the chronology of the sites and introduced the first local biostratigraphy for the early Miocene. Although the local zones were not used in following works, these subdivisions were generally kept and Agustí et al. (1985) further subdivided the MN4 record of the Vallès-Penedès into two subzones. The first one would include solely the site of Sant Mamet (Sant Cugat del Vallès) and would be characterized by the presence of *Democricetodon hispanicus* and the absence of *Megacricetodon*. The second one would include all other sites (e.g. Can Martí Vell, Can Julià, Vilobí del Penedès) and would be characterized by the presence of *Democricetodon* aff. *hispanicus* and *Megacricetodon minor primitivus*.

After those works significant efforts have been devoted to the early and middle Miocene continental chronology in several European regions, but most notably in the Calatayud-Montalbán Basin in Aragon (east-central Spain). This basin holds the type area for the Ramblian (Daams et al. 1987) and Aragonian (Daams et al. 1977) mammal stages and has an excellent small-mammal record ranging from the early to the beginning of the late Miocene (late Ramblian to early Vallesian, i.e. from approximately

18 to 10 Ma; see Daams et al. 1999; Van der Meulen et al. 2012; García-Paredes et al. 2016). In addition, the detailed study of the rodent fauna has allowed the establishment of a high-resolution biostratigraphic framework consisting of multiple local zones which have also been calibrated by the means of magnetostratigraphy (for an updated review see Van der Meulen et al. 2012). However, these zones appear to have a limited regional application, so that even the order of the main bioevents (used not only to define the boundaries of these zones but also those of the broader MN zones) differs from that of other European areas such as the Swiss Alpine Foreland Basin (see Kälin & Kempf 2009; Van der Meulen et al. 2012). Their application to other Iberian records is a matter of debate. Recent studies (Casanovas-Vilar et al. 2016a, 2016b) have shown that for the late Aragonian and early Vallesian different biostratgraphic schemes must be used for the relatively close Vallès-Penedès, to the point that the most characteristic taxa for some of the Vallesian zones are absent in the Calatayud-Montalbán and Teruel basins. As far as the early Miocene is concerned, the similarities between both records appear to have been higher (Casanovas-Vilar et al. 2011b, 2016a).

Agustí and Cabrera (1981) and Agustí et al. (1985) already correlated the mammal-bearing sites of Gelida to the late part of the MN4, mostly based on the presence of the cricetid *Megacricetodon primitivus* in both Can Julià and Can Martí Vell. Current definitions of the MN4 are based either in the first common occurrence of the genus *Democricetodon* (Hilgen et al. 2012) or the first occurrence of *Megacricetodon primitivus* (Agustí et al. 2001). *Democricetodon* is already recorded in the late MN3, although it is very rare (Daams et al. 1999; Agustí et al. 2001; Hilgen et al. 2012; Van der Meulen et al. 2012). In LV1 the cricetid fauna includes *Democricetodon hispanicus* and *Megacricetodon primitivus*, thus indicating a straightforward correlation to the MN4, yielding an age of 17.2–16.4 Ma (age boundaries after Hilgen et al. 2012). However, if we take into account the rodent succession and local biostratigraphy of the Calatayud-Montalbán Basin we can achieve a higher resolution. In that area the MN4 comprises two distinct biozones, B and C, the latter being distinguished by the first appearance of *Megacricetodon* (Daams et al. 1999; Van der Meulen et al. 2012). In addition, zone C is further subdivided into subzones Ca and Cb (Van der Meulen et al. 2012). In subzone Ca two different species of the eomyid *Ligerimys* coexist, namely *L. florancei* and *L. ellipticus*, its putative descendant (Álvarez Sierra 1987), that replaces the former before the end of zone Ca (Van der Meulen et al. 2012). In subzone Cb *L. ellipticus* is the only eomyid present and the cricetid fauna is enriched with the appearance of other species of the genus *Democricetodon* (*D. franconicus*, *D. moralesi*) as well as by the genus *Eumyarion* (although it is recorded earlier in localities of the Teruel and Valencia areas, see Van der Meulen et al. 2012). In LV1 we record both *L. florancei* and *L. ellipticus*, with the second one being more abundant than the former. This would indicate a correlation to subzone Ca, but there are some discrepancies. For example, *D. hispanicus* is not recorded in subzone Ca in Calatayud-Montalbán, being replaced by its descendant *D. decipiens*. However, the presence of the glirids *Glirudinus modestus*, *Microdyromys koenigswaldi*, *Peridyromys murinus*, *Pseudodryomys ibericus* and *Simplomys simplicidens* perfectly agrees with this correlation, so we tentatively correlate this locality with zone Ca. This would yield an age of about 16.5–16.3 Ma for Les Cases de la Valenciana, although it should be further constrained with the aid of magnetostratigraphical data. The marsupial, eulipotyphlan and lagomorph fauna recovered at Les Cases de la Valenciana also supports this correlation. The combination of the eulipotyphlans *Galerix symeonidisi* and *Heterosorex neumayrianus* with the marsupial *Amphiperatherium* in Spain is known from various localities in zone C.

All the remaining sites within the Subirats lacustrine unit (Can Martí Vell 1 and 2, Els Casots, Can Julià) show similar rodent faunas and are also tentatively correlated to subzone Ca. The classical site of Sant Mamet in Sant Cugat del Vallès (Crusafont et al. 1955) would also be close in age. This site is characterized by a peculiar cricetid fauna that includes *Melissiodon dominans*, *Eumyarion weinfurteri* and *Democricetodon hispanicus* (Agustí et al. 1985). No eomyids or *Megacricetodon* have been recovered from Sant Mamet, but its stratigraphical position immediately below the marine Langhian deposits, argues against an older age (contra Agustí et al. 1985).

Other early Miocene sites of the basin such as Molí de Can Calopa or La Costablanca are clearly older, and are characterized by the absence of cricetids other than the unique genus *Melissiodon* (Casanovas-Vilar et al. 2011b, 2016a) as diagnostic for the late Ramblian zone A (Van der Meulen et al. 2012). In Sant Andreu de la Barca, this *Melissiodon* coexists with a diverse glirid fauna including *Peridyromys murinus*, *Pseudodryomys* aff. *ibericus*, *Glirudinus modestus*, *Glirudinus gracilis* and *Bransatoglis astaracensis* (Agustí & Galobart 1997). In the remaining Ramblian sites of the area the glirid fauna is generally poorer. The earliest Aragonian, that is zone B, which is characterized by the first common occurrence of *Democricetodon* coupled with the absence of *Megacricetodon* (Daams et al. 1999; Van der Meulen et al. 2012), would not be represented in the Vallès-Penedès, as in all the known sites both cricetid genera co-occur.

Conclusions

The early Miocene record of the Vallès-Penedès Basin has been little studied in comparison to the middle and late Miocene one. However, it includes a good number of rich localities that have delivered both large and small mammals. Les Cases de la Valenciana is one of such localities and has provided a representative sample of small mammals that includes marsupials (*Amphiperatherium frequens*), eulipotyphlans (*Galerix* cf. *symeonidisi*, *Heterosorex neumayrianus*), lagomorphs (*Lagopsis penai*) and rodents. Amongst the rodents eomyids (*Ligerimys florancei*, *Ligerimys ellipticus*) are particularly abundant and the cricetids (*Democricetodon hispanicus*, *Megacricetodon primitivus*, *Eumyarion* sp.) are well represented. Glirids (*Glirudinus modestus*, *Microdyromys koenigswaldi*, *Peridyromys murinus*, *Pseudodryomys ibericus*, *Simplomys simplicidens*) are diverse and relatively common, whereas sciurids, solely represented by *Heteroxerus rubricati*, are very rare. The cricetid fauna indicates an unambiguous correlation to MN4. However, the site can also be tentatively correlated to the local zones of the Calatayud-Montalbán Basin. The occurrence of *M. primitivus*, *L. florancei* and *L. ellipticus* would favor a correlation to subzone Ca (about 16.5–16.3 Ma). Other nearby localities, such as Can Martí Vell and Els Casots, would also be correlated to this subzone. Some classical sites of the Vallès-Penedès, such as Molí de Can Calopa and La Costablanca, would be older, being correlated to the late Ramblian (MN3). On the other hand, our recent field campaigns have resulted in the discovery of several new mammal sites which are located in transitional deposits of the Langhian units of the Vallès-Penedès, so that they would cover the earliest middle Miocene in the area. Although the material has yet to be prepared, these preliminary results show that the Vallès-Penedès Miocene record may be more continuous than customarily assumed.

Acknowledgements

We thank Josep M. Robles (ICP), who was the first to report and show us the exposed fossiliferous levels at Les Cases de la Valenciana. In addition, we would like to thank all the colleagues, students and friends who enthusiastically joined the palaeontological excavations at the site between 2012 and 2015. The town council of Gelida, and specially its culture councilor Josep Anfruns, kindly supported our campaigns providing a place for safe storage of fossil material and tools and allowing us to screen-wash the excavated sediments in municipal facilities. And finally, we would like to express our gratitude to the neighbors of La Valenciana district (Gelida) who kindly helped during the field campaigns and frequently visited the site to see the progress of the excavations.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work has been supported by the Spanish Ministerio de Economía y Competitividad (project CGL2014-54373-P and RYC-2013-12470 research contract to ICV), the Agencia Estatal de Investigación (AEI) from Spain and the European Regional Development Fund of the European Union (CGL2016-76431-P), as well as the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya (CERCA Programme) 2014 SGR 416 research group and FI_B 00054 pre-doctoral grant to SJV.The 2015 field campaign at Les Cases de la Valenciana was partly financed by the National Geographic Society under grant number 9640-15.

ORCID

Sílvia Jovells-Vaqué http://orcid.org/0000-0003-0358-0840
Marc Furió http://orcid.org/0000-0002-4582-3268
Chiara Angelone http://orcid.org/0000-0002-7140-9431
Lars W. Van den Hoek Ostende http://orcid.org/0000-0003-3114-0121
Daniel DeMiguel http://orcid.org/0000-0001-6138-7227
Joan Madurell-Malapeira http://orcid.org/0000-0003-4639-9451
Isaac Casanovas-Vilar http://orcid.org/0000-0001-7092-9622

References

Agustí J. 1981. Roedores Miomorfos del Neógeno de Cataluña [Myomorph rodents from the Neogene of Catalonia] [dissertation]. Barcelona: Universitat de Barcelona.

Agustí J. 1982. Biozonación del neógeno continental de Cataluña mediante roedores (Mammalia) [Biozonation of the continental Neogene of Catalonia by the means of rodents (Mammalia)]. Acta Geol Hisp. 17:21–26.

Agustí J. 1983. Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallès-Penedès, Cataluña, España) [Early Miocene rodents (Mammalia) from Can Martí Vell (Vallès-Penedès, Catalonia, Spain)]. Estudios Geol. 39:417–430.

Agustí J. 1990. The Miocene rodent succession in Eastern Spain: a zoogeographical appraisal. In: Lindsay EH, Fahlbusch V, Mein P, editors. European neogene mammal chronology. New York (NY): Plenum Press; p. 375–404.

Agustí J, Cabrera L. 1981. Nuevos datos sobre la biozonación del Burdigaliense continental de la cuenca del Vallès-Penedès [New data about the biozonation of the continental Burdigalian of the Vallès-Penedès basin]. Acta Geol Hisp. 15:81–84.

Agustí J, Galobart À. 1997. Noves localitats amb mamífers fòssils en el Miocè de la Conca del Vallès-Penedès [New localities with fossil mammals in the Miocene of the Vallès-Penedès Basin]. Trib Arqueol. 1996–1997:9–22.

Agustí J., Llenas M. 1993. Los roedores del Mioceno inferior de Els Casots (Vallès-Penedès). Nota preliminar [Early Miocene rodents from Els Casots (Vallès-Penedès). Preliminary report]. Comunicaciones de las IX Jornadas de Paleontología; 1993 Oct 28–30; Málaga: Universidad de Málaga.

Agustí J, Cabrera L, Moyà-Solà S. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès [Stratigraphical synopsis of the Neogene of the Vallès-Penedès graben]. Paleontol Evol. 18:57–81.

Agustí J, Cabrera L, Garcés M, Parés JM. 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. Palaeogeogr Palaeoclimatol Palaeoecol. 133:149–180.

Agustí J, Cabrera L, Garcés M, Krijgsman W, Oms O, Parés JM. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth Sci Rev. 52:247–260.

Aldana Carrasco EJ. 1991. Roedores Esciuromorfos del Neógeno de Cataluña [Sciuromorph rodents from the Neogene of Catalonia] [dissertation]. Cerdanyola del Vallès: Universitat Autònoma de Barcelona.

Aldana Carrasco EJ. 1992. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España) [Sciurinae (Rodentia, Mammalia) from the Miocene of the Vallès-Penedès Basin]. Treb Mus Geol Barcelona. 2:69–97.

Almera J. 1898. Sobre la serie de mamíferos fósiles descubiertos en Cataluña [On the several fossil mammals discovered in Catalonia]. Mem Real Acad Cien Art Barcelona. 2:351–357.

Álvarez Sierra MA. 1987. Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior español [Systematic and biostratigraphic study of the Eomyidae (Rodentia) of the Spanish upper Oligocene and early Miocene]. Scripta Geol. 86:1–207.

Álvarez Sierra MÁ, Civis J, Corrochano A, Daams R, Dabrio CJ, García E, González A, López Martínez N, Mediavilla R, Rivas Carballo R, Valle MF. 1990. Un estratotipo del límite Aragoniense-Vallesiense (Mioceno medio-Mioceno superior) en la sección de Torremormojón (Cuenca del Duero, Provincia de Palencia) [A stratotype for the Aragonian-Vallesian boundary (middle Miocene-upper Miocene) from the Torremormojón section (Duero Basin, province of Palencia)]. Stud Geol Salmant Act Pal. 68:57–64.

Angelone C. 2009. Lagomorphs from the Miocene of Sandelzhausen. Pal Z. 83:67–75.

Angelone C, Sesé C. 2009. New characters for species discrimination within the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). J Palaeontol. 83:80–88.

Bataller Calatayud JR. 1938. Els Ratadors fòssils de Catalunya [Fossil Rodents of Catalonia]. Barcelona: Impremta de la Casa d'Assistència President Macià.

Black CC. 1963. A review of the North American Tertiary Sciuridae. Bull Mus Comp Zool. 130:109–248.

Cabrera L, Calvet F, Guimerà J, Permanyer A. 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: Organización secuencial y relaciones tectónica sedimentación [The Miocene sedimentary record of the Vallès-Penedès and El Camp half grabens: sequential arrangement and tectonic-sedimentation relationships]. Barcelona: Universitat de Barcelona.

Cabrera L, Roca E, Garcés M, de Porta J. 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana) [Late Oligocene-Neogene stratigraphy and tectonosedimentary evolution of the central part of the Catalan margin (Catalan Coastal Range)]. In: Vera JA, editor. Geología de España [Geology of Spain]. Madrid: Sociedad Geológica Española-Instituto Geológico y Minero de España; p. 569–573.

Casanovas-Vilar I, Angelone C, Alba DM, Moyà-Solà S, Köhler M, Galindo J. 2010. Rodents and lagomorphs from the Middle Miocene hominoid-bearing site of Barranc de Can Vila 1 (els Hostalets de Pierola, Catalonia, Spain). N Jb Geol Paläont Abh. 257:297–315.

Casanovas-Vilar I, Alba DM, Moyà-Solà S. 2011a. Parada 1: Panorámica general de la cuenca y yacimiento de els Casots (Subirats): una fauna de vertebrados del Mioceno Inferior [Stop 1: Panoramic view of the basin and els Casots site (Subirats): an Early Miocene vertébrate fauna]. Paleontol Evol Mem Esp. 6:81–88.

Casanovas-Vilar I, DeMiguel D, Galindo J, Robles JM, Garcés M, Cabrera L. 2011c. The continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). In: Pérez-García A, Gascó F, Gasulla JM, Escaso F, editors. Viajando a mundos pretéritos. Ayuntamiento de Morella: Morella; p. 93–100.

Casanovas-Vilar I, Alba DM, Garcés M, Robles JM, Moyà-Solà S. 2011c. Updated chronology of the Miocene hominoid radiation in Western Eurasia. Proc Natl Acad Sci USA. 108:5554–5559.

Casanovas-Vilar I, Madern A, Alba DM, Cabrera L, García-Paredes I, Van den Hoek Ostende LW, DeMiguel D, Robles JM, Furió M, van Dam JA, et al. 2016a. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). C R Palevol. 15:791–812.

Casanovas-Vilar I, Garcés M, Van Dam J, García-Paredes I, Robles JM, Alba DM. 2016b. An updated biostratigraphy for the late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). Geol Acta. 14:195–217.

Crusafont Pairó M. 1950. La cuestión del llamado Meótico español. Arrahona. 1950:41–48.

Crusafont M, de Villalta JF, Truyols J. 1955. El Burdigaliense continental de la Cuenca del Vallès-Penedès [The continental Burdigalian of the Vallès-Penedès Basin]. Mem Com Inst Geol. 12:1–272.

Cuenca Bescós G. 1988. Revisión de los Sciuridae del Aragoniense y del Rambliense en la fosa de Calatayud-Montalbán [Review of the Aragonian and Ramblian Sciuridae in the Calatayud-Montalbán basin]. Scripta Geol. 87:1–116.

Daams R. 1976. Miocene rodents (Mammalia) from Cetina de Aragón (prov. Zaragoza) and Buñol (prov. Valencia), Spain. Proc Kon Ned Akad Wetensch B. 79:152–182.

Daams R. 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. Utrecht Micropal Bull Spec Publ. 3:1–115.

Daams R. 1985. Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain). Scripta Geol. 77:1–20.

Daams R. 1999. Gliridae. In: Rössner G, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfeil; p. 301–318.

Daams R, Freudenthal M. 1974. Early Miocene Cricetidae (Rodentia, Mammalia) from Buñol (Prov. Valencia, Spain). Scripta Geol. 24:1–19.

Daams R, Freudenthal M. 1988. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*. Scripta Geol. 1:39–132 (spec. issue).

Daams R, Freudenthal M, Van de Weerd A. 1977. Aragonian, a new stage for continental deposits of Miocene age. Newsl Stratigr. 6:42–55.

Daams R, Freudenthal M, Álvarez-Sierra MA. 1987. Ramblian: a new stage for continental deposits of Early Miocene age. Geol Mijnb. 65:297–308.

Daams R, Van der Meulen AJ, Álvarez Sierra MA, Peláez-Campomanes P, Calvo JP, Alonso Zarza MA, Krijgsman W. 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsl Stratigr. 37:103–139.

De Bruijn H. 1965-1966. Some new Miocene Gliridae (Rodentia Mammalia) from the Calatayud area (prov. Zaragoza, Spain). Proc Kon Ned Akad Wet. 69:58–71.

de Bruijn H. 2009. The *Eumyarion* (Mammalia, Rodentia) assemblage from Sandelzhausen (Miocene, Southern Germany): a test on homogeneity. Paläontol Z. 83:77–83.

De Gibert JM, Casanovas-Vilar I. 2011. Contexto geológico del Mioceno de la Cuenca del Vallès-Penedès [Geological background of the Miocene of the Vallès-Penedès Basin]. Paleontol Evol Mem Esp. 6:39–45.

Dehm R. 1950. Die Nagetiere aus dem Mittel-Miozän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern [The mammals from the Middle Miocene (Burdigalian) of Wintershoft-West near Eichstätt in Bavaria]. N Jb Min Geol Paläont. 91:321–428.

Doukas CS. 1986. The mammals from the Lower Miocene of Aliveri (Island of Evia. Greece). Part 5. The insectivores. Proc Kon Ned Akad Wet. 89:15–38.

Fahlbusch V. 1970. Populationsverchiebungen bei tertiären Nagetieren; eine Studie an oligozänen und miozänen Eomyidae Europas [Population changes in Tertiary rodents; a study of Oligocene and Miocene European Eomyidae]. Abh. Bayer. Akad. Wiss. Math Naturw Kl Abh N F. 145:1–136.

Freudenthal M. 1963. Entwicklungsstufen der miozänen Cricetodontinae (Mammlia, Rodentia) Mittlespaniens und ihre stratigraphische Bedeutung [Succession of Miocene Cridetodontinae (Mammalia, Rodentia) in central Spain and their stratigraphic significance]. Beaufortia. 10:51–157.

Freudenthal M. 1967. Betrachtungen über die gattung *Cricetodon* [Reflections on the genus *Cricetodon*]. Proc Kon Ned Akad Wet. 68:239–305.

Freudenthal M. 2006. The status of Democricetodon, Fahlbuschia, Pseudofahlbuschia and Renzimys (Cricetidae, Mammalia). A reply to Van der Meulen et al. (2004). Geobios. 39:43–55.

Freudenthal M, Lacomba J, Sacristán M. 1992. Classification of European Oligocene cricetids. Rev Esp Paleontol. 1992:49–57 (num. extra).

Freudenthal M, Hugueney M, Moissenet E. 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). Scripta Geol. 104:57–114.

Furió M, Ruiz-Sánchez FJ, Crespo VD, Freudenthal M, Montoya P. 2012. The southernmost Miocene occurrence of the last European herpetotheriid *Amphiperatherium frequens* (Metatheria, Mammalia). C R Palevol. 11:371–377.

Furió M, Prieto J, Van den Hoek Ostende LW. 2015. Three million years of "Terror-Shrew" (*Dinosorex*, Eulipotyphla, Mammalia) in the Miocene of the Vallès-Penedès Basin (Barcelona, Spain). C R Palevol. 14:111–124.

García-Paredes I. 2006. Patrones evolutivos de los Gliridae (Rodentia, Mammalia) del Mioceno inferior y medio del área tipo del Aragoniense (Cuenca de Calatayud-Montalbán) [Evolutionary patterns of the Gliridae (Rodentia, Mammalia) from the lower and middle Miocene of the Aragonian type area (Calatayud-Montalbán Basin)] [dissertation]. Madrid: Universidad Complutense de Madrid.

García-Paredes I, Peláez-Campomanes P, Álvarez-Sierra MA. 2009. Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene. Zool J Linnean Soc. 157:622–652.

García-Paredes I, Peláez-Campomanes P, Álvarez-Sierra MA. 2010. Microdyromys remmerti, sp. nov., a new Gliridae (Rodentia, Mammalia) from the Aragonian type area (Miocene, Calatayud-Montalbán basin, Spain). J Vert Paleontol. 30:1594–1609.

García-Paredes I, Álvarez-Sierra MA, Van den Hoek Ostende LW, Hernández-Ballarín V, Hordijk K, López-Guerrero P, Oliver P, Peláez-Campomanes P. 2016. The Aragonian and Vallesian high-resolution micromammal succession from the Calatayud-Montalbán Basina (Aragón, Spain). C R Palevol. 15:781–789.

Hilgen FJ, Lourens LJ, Van Dam JA. 2012. The neogene period. In: Gradstein FM, Ogg JG, Schmitz M, Ogg G, editors. The geologic time scale. Amsterdam: Elsevier; p. 923–978.

Hordijk K, Bosma A, De Bruijn H, Van Dam J, Geraedts C, Van den Hoek Ostende LW, Reumer JWF, Wessels W. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos 2, Teruel Basin. Spain Palaeobio Palaeoenv. 95:321–346.

Hugueney M. 1999. Genera *Eucricetodon* and *Pseudocricetodon*. In: Rössner G, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfeil; p. 347–358.

Kälin D, Kempf O. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. N Jb Geol Paläont Abh. 254:177–235.

Klietmann J, Nagel D, Rummel M, Van den Hoek Ostende LW. 2014a. *Amphiperatherium* and Erinaceidae of Petersbuch 28. Bull Geosci. 89:1–20.

Klietmann J, Nagel D, Rummel M, Van den Hoek Ostende LW. 2014b. *Heterosorex* and Soricidae (Eulipotyphla, Mammalia) of the fissure Petersbuch 28; micro-evolution as indicator of temporal mixing? C R Palevol. 13:157–181.

López Martínez N. 1984. Los Lagomorfos (Mammalia) de la sucesión del Mioceno inferior de Calamocha (prov. de Teruel) [The lagomorphs (Mammalia) from the early Miocene series of Calamocha (prov. of Teruel)]. Col Pal. 39:27–44.

López Martínez N. 1989. Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España [Systematic and biostratigraphic review of the Lagomorpha (Mammalia) of the Tertiary and Quaternary of Spain]. Mem Mus Pal U Zaragoza. 3:1–342.

López Martínez N. 2001. Palaeobiogeographical history of *Prolagus*, an European ochotonid (Lagomorpha). Lynx. 32:215–231.

Maridet O, Sen S. 2012. Les Cricetidae (Rodentia) de Sansan [The Cricetidae (Rodentia) from Sansan]. Mém Mus Natl Hist Nat. 203:29–65.

Mayr H. 1979. Gebissmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands [Studies on dental morphology of the Miocene Gliridae (Mammalia, Rodentia) from Southern Germany] [dissertation]. Munich: Ludwig-Maximilians Universität.

Mein P. 1975. Résultats du Groupe de Travail des Vertébrés [Results of the vertebrate working group]. In: Senes J, editor. Report on activity of RCMNS working groups – 6 Congress of the Regional Comittee of Mediterranean Neogene Stratigraphy, Proceedings. Bratislava: SAV; p. 78–81.

Mein P. 1999. European Miocene mammal biochronology. In: Rössner G, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfeil; p. 25–38.

Mein P, Freudenthal M. 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe [A new classification of the Cricetidae (Mammalia, Rodentia) of tertiary of Europe]. Scripta Geol. 2:1–37.

Morales J, Nieto M, Peláez-Campomanes P, Soria D, Álvarez-Sierra MA, Alcalá L, Amezua L, Azanza B, Cerdeño E, Daams R, et al. 1999. Vertebrados continentales del Terciario de la cuenca de Loranca (Provincia de Cuenca) [Continental vertebrates from the tertiary of the Loranca Basin (Province of Cuenca)]. In: Aguirre E, Rábano I, editors. La huella del pasado: Fósiles de Castilla-La Mancha. Toledo: Junta de Comunidades de Castilla-La Mancha; p. 237–260.

Oliver A, Peláez-Campomanes P. 2014. Evolutionary patterns of early and middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia) from Spain. Palaeontogr Abt A. 303:85–135.

Oliver Pérez A, Guerrero L, Peláez-Campomanes P. 2008. Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España) [First representative of the genus *Megacricetodon* from the Calatayud-Daroca Basin (Zaragoza, Spain)]. SEPAZ. 8:317–329.

Robles F, Belinchón M, García-Flor J, Morales J. 1991. El Neógeno continental de Buñol y del Valle del Río Cabriel [The continental Neogene of Buñol and the Cabriel River Valley]. Rev Esp Paleontol num extra. 1991:205–215.

Ruiz-Sánchez FJ, de Santiesteban Bové C, Lacomba Andueza JI. 2003. Nuevas faunas de roedores fósiles (Mammalia, Rodentia) de edad Aragoniense inferior y medio en la serie del Barranco Morteral (cuenca del Río Magro, prov. de Valencia, España) [New fossil rodent faunas (Mammalia, Rodentia) of early and middle Aragonian age from the Barranco de Morteral serie (Magro River Basin, province of Valencia, Spain)]. Col Pal vol ext. 1:579–594.

Sierra A., San Miguel M., Marcet J., Cerezo R. 1930. Memória Explicativa de la Hoja núm. 420 (San Baudilio de Llobregat) del Mapa Geológico de España [Explanatory memory of foil num. 420 (Sant Boi de Llobregat) of the Geologic Map of Spain]. Madrid: Instituto Geológico y Minero de España.

Van de Weerd A. 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region. Spain Utrecht Micropal Bull Spec Publ. 2:1–185.

Van den Hoek Ostende LW. 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area. Col Pal vol ext. 1:281–310.

Van den Hoek Ostende LW, Doukas CS. 2003. Distribution and evolutionary history of the Early Miocene erinaceid *Galerix symeonidisi* Doukas, 1986. DEINSEA. 10:287–303.

Van den Hoek Ostende LW, Furió M. 2005. Spain. Scripta Geol. 5:149–284 (spec. issue).

Van der Meulen AJ, Peláez-Campomanes P, Daams R. 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain). Col Pal vol ext. 1:385–441.

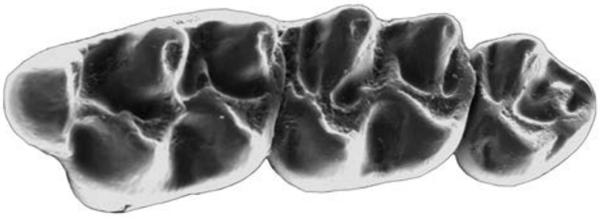
Van der Meulen AJ, García-Paredes I, Álvarez-Sierra MA, Van den Hoek Ostende LW, Hordijk K, Oliver A, Peláez-Campomanes P. 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geol Acta. 10:159–179.

Vicente Castells J. 1987. Noves troballes al jaciment de mamífers de Cases de la Valenciana (Gelida, Alt Penedès) [New discoveries at the Cases de la Valenciana mammal site (Gelida, Alt Penedès)]. But C Est Nat Barcel Nord. 3:130–131.

Wu W. 1993. Neue Gliridae (Rodentia, Mammalia) aus untermiozänen (orleanischen) Spaltenfüllungen Süddeutschlands [New Gliridae (Rodentia, Mammalia) from the lower Miocene (Orleanian) fissure fillings of Southern Germany]. Documenta Naturae. 81:1–149.

Ziegler R. 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands [Heterosoricidae and Soricidae (Insectivora, Mammalia) from the upper Oligocene and lower Miocene of Southern Germany]. Stutt Beitr Naturkd B. 154:1–73.

Ziegler R. 1999. Order Marsupialia. *Amphiperatherium*, the last European Opossum. In: Rössner G, Heissig K, editors. The Miocene land mammals of Europe. Munich: Verlag Dr. Friedrich Pfeil; p. 53–74.



Chapter 7: “Cricetidae (Rodentia, Mammalia) from the early Miocene site of els Casots (Vallès-Penedès Basin, Catalonia)”

Fossil Imprint

Published: August 2017

FOSSIL IMPRINT • vol. 73 • 2017 • no. 1–2 • pp. 141–154
(formerly ACTA MUSEI NATIONALIS PRAGAE, Series B – Historia Naturalis)

NATIONAL MUSEUM

CRICETIDAE (RODENTIA, MAMMALIA) FROM THE EARLY MIOCENE SITE OF ELS CASOTS (VALLÈS-PENEDÈS BASIN, CATALONIA)

SÍLVIA JOVELLS-VAQUÉ[1], MONTSERRRAT GINESTÍ[1], ISAAC CASANOVAS-VILAR[1,*]

[1] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA–ICP, Carrer de les Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; e–mail: isaac.casanovas@icp.cat, silvia.jovells@icp.cat, montserratginesti@gmail.com.
*corresponding author

Jovells-Vaqué, S., Ginestí, M., Casanovas-Vilar, I. (2017): Cricetidae (Rodentia, Mammalia) from the early Miocene site of els Casots (Vallès-Penedès Basin, Catalonia). – Fossil Imprint, 73(1-2): 141–154, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Els Casots is an extremely rich early Miocene site located in the Vallès-Penedès Basin (Catalonia, Spain) that has provided both micro- and macrovertebrates. However, the small mammals have been poorly studied. In this work we describe the cricetid fauna from els Casots and provide further insights into the chronology of the site. The cricetids are very common and include the species *Megacricetodon primitivus* and *Democricetodon hispanicus*. A second, larger-sized *Democricetodon* species is also represented by just one molar. The presence of *M. primitivus* together with the eomyid *Ligerimys ellipticus* indicates a correlation to zone MN 4 and to the local zone C of the Calatayud-Montalbán Basin (Aragón, east-central Spain), the type area of the Aragonian mammal age. This is further supported by the presence of two different *Democricetodon* species. A correlation to the local subzones of that area is attempted, but unfortunately the cricetid succession is not the same in both basins. However, the fact that *L. ellipticus* is the only eomyid species present at els Casots would indicate that this site is somewhat younger than other MN 4 localities from the Vallès-Penedès, where this species coexists with its ancestor *Ligerimys florancei*.

Key words: Cricetidae, Rodentia, *Megacricetodon*, *Democricetodon*, biostratigraphy, early Miocene, Catalonia, Iberian Peninsula

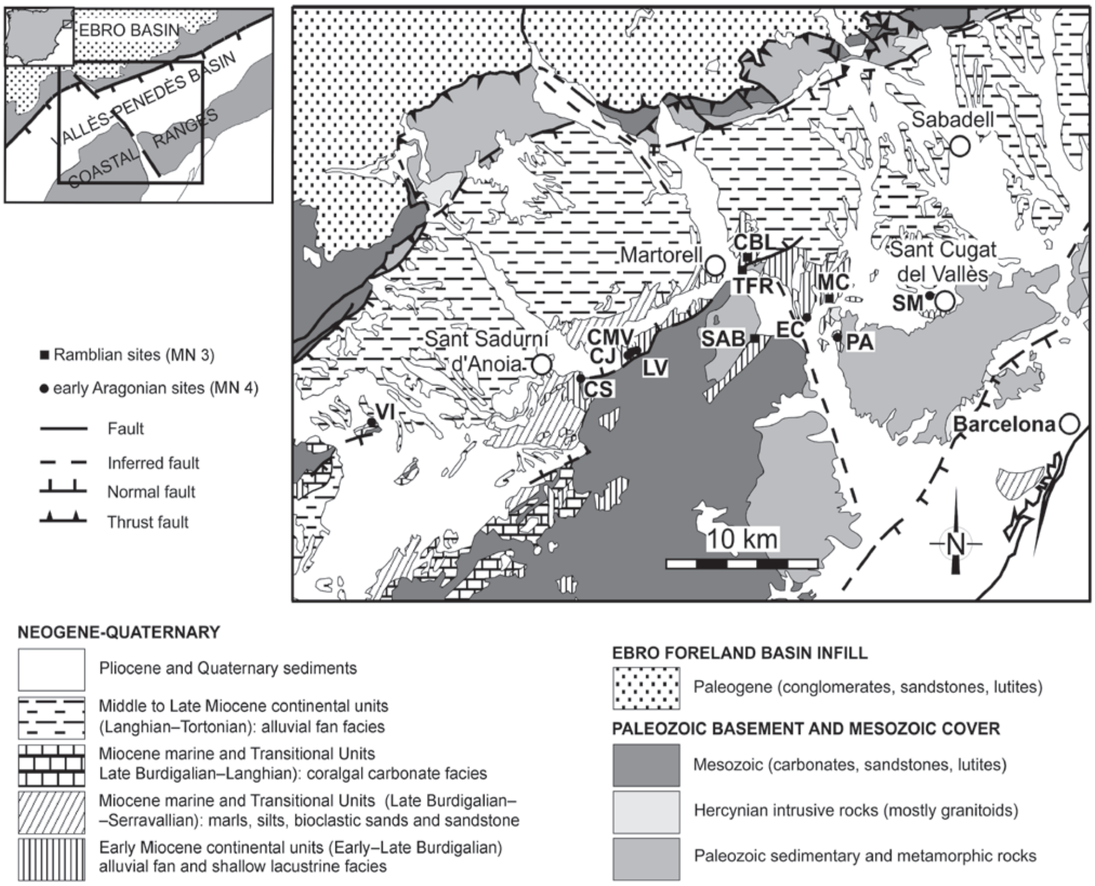
Received: February 28, 2017 | Accepted: April 24, 2017 | Issued: August 15, 2017

Introduction

The Vallès-Penedès Basin (Catalonia, Spain) is a reference area for the study of the Miocene terrestrial vertebrate faunas of Western Europe. Earliest findings date back to the late 19th century, starting with the discovery of a few mammal remains in the lignite mines of la Fontsanta, in the town of Subirats (Almera 1898, Crusafont et al. 1955). In the following century, especially after the 1940s, the Miocene outcrops of this basin were systematically surveyed, resulting in the discovery of hundreds of new sites and the collection of tens of thousands of specimens (for a historical review see Casanovas-Vilar et al. 2016a). Eventually, even a land mammal age, the Vallesian, was defined on the basis of the late Miocene record of the Vallès-Penedès Basin and was successfully applied to other areas of the Old World (Crusafont Pairó 1950). Recently, the middle and late Miocene records of the basin have been intensively studied and most of the major sites have been correlated to detailed local magnetostratigraphical sections that allow for a high-resolution chronology (Casanovas-Vilar et al. 2016a, b). In comparison, the early Miocene part of the record has been studied very little. In the Vallès-Penedès Basin the early Miocene is represented by about 20 sites that comprise the Ramblian (MN 3) and early Aragonian ages (MN 4; Casanovas-Vilar et al. 2011a, 2016a). Many of these sites were already reported by Crusafont et al. (1955) in a lengthy monograph on the early Miocene successions of the area and their mammal fauna. The early Miocene sites, particularly the older ones, are very poor in comparison with the younger ones from the same basin. In addition, their correlation is based entirely on biostratigraphy (Agustí et al. 1985, Casanovas-Vilar et al. 2011a, 2016a).

In the recent years there has been a renewed interest in this part of the record, with the sampling of some of the classical sites and ongoing magnetostratigraphical studies. However, these new field campaigns have confirmed that early Miocene sites of the Vallès-Penedès are indeed poor. Els Casots site, discovered in 1989, is an exception to this pattern. It is located in the town of Subirats (Alt Penedès, Barcelona), just a few hundred meters away from the now abandoned lignite mines that provided the first vertebrate findings in the late 19th century. After five field campaigns during the 1990s more than a thousand remains were

DE GRUYTER OPEN DOI 10.1515/if-2017-0007



Text-fig. 1. Geographical location and simplified geological map of the Vallès-Penedès Basin indicating the main early Miocene mammal localities (modified from Casanovas-Vilar et al. 2016a). Locality acronyms are as follows: CBL = La Costablanca; CJ = Can Julià; CMV = Can Martí Vell; CS = els Casots; EC = El Canyet; LV = Les Cases de la Valenciana; MC = Molí de Can Calopa; PA = Escletxes del Papiol; SAB = Sant Andreu de la Barca; SM = Sant Mamet; TFR = Turó de les Forques; VI = Vilobí del Penedès.

collected, thus this site is comparable to other "classical" sites of the basin, such as Can Llobateres (Moyà-Solà and Rius Font 1993). The recovered material includes fishes, reptiles, birds and micro- and macromammals (Moyà-Solà and Rius Font 1993, Casanovas-Vilar et al. 2011b). To date, only a small part of the fossils has been prepared and studied in detail, particularly the artiodactyls (Pickford and Moyà-Solà 1994, 1995, Duranthon et al. 1995, Van der Made 1997, Orliac 2006, Alba et al. 2014), but resulting in the description of two new species, the suid *Eurolistriodon adelli* Pickford et Moyà-Solà, 1995 and the palaeomerycid *Ampelomeryx ginsburgi* Duranthon, Moyà-Solà et Köhler, 1995. More recently, the equid *Anchitherium* von Meyer, 1844 was first reported from the site (Rotgers and Alba 2011) and the cranial remains of the small crocodilian *Diplocynodon ratelii* Pomel, 1847, which is particularly abundant, were described (Díaz Aráez et al. 2017). The rest of the large mammal fauna, which amongst others includes several carnivores (amphycionids, felids, hyaenids), and at least two species of rhinocerotids and proboscideans (gomphotheres and deinotheres) has been the subject of only preliminary reports (Moyà-Solà and Rius Font 1993, Casanovas-Vilar et al. 2011a). As far as small mammals are concerned, Aldana Carrasco (1992) described the sciurid rodents and Agustí and Llenas (1993) provided a brief account of the remaining rodent fauna with succinct descriptions but no figures. The updated faunal list (Casanovas-Vilar et al. 2011b) shows a very diverse rodent fauna that includes two species of sciurids (*Atlantoxerus idubedensis* Cuenca Bescós, 1988, *Heteroxerus rubricati* Crusafont, Villalta et Truyols, 1955); eight glirids (*Glirudinus modestus* (Dehm, 1950), *Microdyromys* sp., *Muscardinus* sp., *Peridyromys murinus* (Pomel, 1853), *Pseudodryomys ibericus* De Bruijn, 1966, *Simplomys julii* (Daams, 1989), *Simplomys simplicidens* (De Bruijn, 1966), *Bransatoglis* sp.); the eomyid *Ligerimys ellipticus* Daams, 1976; and three cricetids (*Democricetodon hispanicus* Freudenthal, 1967, *Democricetodon* sp. 2, *Megacricetodon primitivus* (Freudenthal, 1963)). Els Casots has been correlated to the MN 4 (early Aragonian; Agustí and Llenas 1993, Casanovas-Vilar et al. 2011a, b, 2016a) because of the presence of the cricetids *Megacricetodon* and *Democricetodon*. The occurrence of the tragulid

Dorcatherium Kaup, 1833 and the bovid *Eotragus* Pilgrim, 1939, which were first recorded within this zone in Western Europe (Agustí et al. 2001), further supports this correlation. In addition, the coexistence of *Megacricetodon primitivus*, *Democricetodon hispanicus* and *Ligerimys ellipticus* (although very rare) is characteristic of local biozone C of the Calatayud-Montalbán Basin (see Daams et al. 1999, Van der Meulen et al. 2012), thus els Casots has been also tentatively correlated to this zone (Casanovas-Vilar et al. 2011a, b, 2016a, Jovells-Vaqué et al. in press).

Cricetid rodents are of the uttermost importance for the correlation of Miocene sites, being the basis for regional and local biostratigraphical scales. In this work, we describe the dental material of the cricetids from els Casots and further provide some new insights into its age. In addition, two partial skulls of the cricetid *Democricetodon hispanicus* and associated postcranial material have been recovered in this site. This material has been preliminarily described in Jovells-Vaqué et al. (2017) and will not be discussed here.

Geological setting

The Vallès-Penedès Basin is an elongated half-graben parallel to the coastline and extending between the Catalan Littoral Ranges (Text-fig. 1). It originated during the latest Oligocene and the Miocene as a result of the opening of the northwestern Mediterranean (Cabrera and Calvet 1996, Roca et al. 1999, Cabrera et al. 2004). The basin is limited by normal faults with a vertical slip greater than 1000 m. Most of the record consists of continental alluvial fan sediments sourced from the limiting reliefs except for at least three episodes of marine transgression during the late Burdigalian, Langhian and early Serravallian which mostly affected the southwestern half of the basin (Cabrera et al. 1991, 2004, Cabrera and Calvet 1996, Roca et al. 1999, De Gibert and Casanovas-Vilar 2011, Casanovas-Vilar et al. 2016a). The early Miocene sediments correspond to the Ramblian and early Aragonian (MN 3–MN 4) and generally crop out near the southeastern margin of the basin (Text-fig. 1). They mostly consist of small-ranging alluvial fan deposits made of intense red mudstones, sandstones and conglomerates (Cabrera 1981, Cabrera et al. 1991, 2004, De Gibert and Casanovas-Vilar 2011, Casanovas-Vilar et al. 2016a). The main vertebrate sites are located in the mudstone-dominated distal areas of the fan systems. In certain areas small lacustrine systems developed, such as in la Costablanca (Castellbisbal), el Molí de Can Calopa (Rubí) or Subirats. Els Casots is placed in the Subirats lacustrine unit, which also includes other remarkable mammal sites such as Can Julià (Crusafont et al. 1955), Les Cases de la Valenciana (Crusafont et al. 1955, Jovells-Vaqué et al. in press) and Can Martí Vell (Agustí 1981, 1983). This unit is predominantly made of grayish to yellowish lutites interbedded with relatively thin layers of carbonates and lignites. The latter were extracted from the long-abandoned coal mines of la Fontsanta, next to the site of els Casots. The site itself corresponds to a small lake of about 5 km^2 surrounded by small reliefs made of Mesozoic carbonates. The two-meter-thick stratigraphic series of the site includes massive limestones corresponding to the center of the lake and mudstone deposits corresponding to more marginal shallow areas (Moyà-Solà and Rius Font 1993, Casanovas-Vilar et al. 2011b). Mudstone deposits vary from gray to yellow and black and are particularly rich in gastropod and plant remains. Vertebrate remains have been recovered throughout the series, including the carbonates, but are more abundant in the black mudstones which have even produced partial skeletons (Moyà-Solà and Rius Font 1993, Casanovas-Vilar et al. 2011b). In addition, three of these black layers, termed els Casots 72, 73 and 74, were screen-washed and provided a rich collection of microvertebrate remains, including the material described in this work.

Materials and methods

The described material is housed in the Institut Català de Paleontologia Miquel Crusafont at Sabadell (Barcelona, Spain). Collection numbers are given in the main text and for the figured specimens. Dental terminology and measurement methods for cricetid cheek teeth follow Oliver and Peláez-Campomanes (2013) and Freudenthal and Daams (1988). All measurements are in millimeters. Summary statistics are presented for our largest sample (els Casots 74) rather than reporting all the measurements. The material from the three fossiliferous levels (els Casots 72, 73, 74) is described together in the systematic section.

Abbreviations

IPS – Institut Català de Paleontologia Miquel Crusafont collection number;

L – mesio-distal length; M/m – molars, upper case letters indicate upper molars and lower case lower ones; Max. – maximum; Min. – minimum; MN – Neogene Mammal Zones (after Mein 1975, 1999; age boundaries follow Hilgen et al. 2012); S.D. – standard deviation; W – bucco-lingual width.

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer [de Waldheim], 1817

Genus *Democricetodon* Fahlbusch, 1964

Democricetodon hispanicus Freudenthal, 1967

Pl. 1, Figs 1–5

1993 *Democricetodon* aff. *hispanicus*; Agustí and Llenas, p. 70.

1993 *Fahlbuschia* sp.; Agustí and Llenas, p. 70 (? partim).

Material from els Casots level 72. 3 M3 (IPS 45092, IPS 45093, IPS 94650); 1 m1 (IPS 19522).

Material from els Casots level 73. 1 M3 (IPS 19503); 8 m1 (IPS 19517, IPS 45051, IPS 45053 – IPS 45058); 7 m3 (IPS 19519, IPS 94653, IPS 94698, IPS 94700, IPS 94701, IPS 94637, IPS 94638).

Material from els Casots level 74. 10 M1 (IPS 19491, IPS 45000 – IPS 45008); 15 M2 (IPS 19491, IPS 45006 – IPS 45008, IPS 19475, IPS 45019 – IPS 45027, IPS 19490); 5 M3 (IPS 45006, IPS 45008, IPS 45027, IPS

94602, IPS 94652); 12 m1 (IPS19481, IPS 45040 – IPS 45050); 15 m2 (IPS 19474, IPS 45059 – IPS 45071, IPS 94609); 8 m3 (IPS 45069, IPS 19473, IPS 45082 – IPS 45087).

Measurements. See Tables 1–3.

Description. M1. The M1 have three roots. The most mesial of them is cylindrical and located below the anterocone, a second one is positioned at the postero-labial corner of the molar and the last one is flattened and occupies the lingual part of the tooth. All studied specimens have a simple anterocone, except one in which this cusp is slightly subdivided (IPS 45001). The arms of the anteroph are well developed, and enclose the anterior valleys. The anterophule is simple and placed somewhat lingually. The protosinus is relatively reduced. The protolophule consists of a single posterior arm that joins the entoloph behind the protocone. IPS 45000 exhibits a double protolophule with a very low anterior arm. A vestigial anterior arm is also present in IPS 45008 (Pl. 1, Fig. 1), but it is interrupted before reaching the paracone. In some specimens, there is a short ectoloph on the paracone. The mesoloph is of medium length in six out of nine specimens; in the remaining ones it is short. The metalophule consists of a posterior arm only that connects the metacone with the posteroloph just behind the hypocone. The sinus is always wide and transverse. The posterosinus is highly reduced and closed by the posteroloph. The sinus is closed by well-developed cingulum.

M2. The M2 have two roots (mesial and distal) which are flattened. The anteroloph shows a long and high labial arm that encloses the narrow anterosinus. The protosinus is vestigial and is also closed by a much lower lingual arm of the anteroloph. In six out of 13 specimens, the protolophule consists of an anterior arm and a posterior one, which is connected to the entoloph posteriorly to the protocone. In the other nine specimens, the posterior arm of the protolophule is incomplete (for example in IPS 45008; Pl. 1, Fig. 1), being interrupted before merging with the paracone. In nine out of 15 specimens, the mesoloph is long, while it is of medium length in five, and short in only one. When long, the labial end of the mesoloph may end in a small mesostyle at the edge of the mesosinus or it may curve distally to contact the anterior wall of the metacone. The sinus is transverse and closed by a cingulum. The metalophule is short and simple, being transverse in half of the specimens and anterior to the hypocone in the remaining ones. The posteroloph closes the posterosinus, while the mesosinus is closed by a low cingulum.

M3. The M3 have two cylindrical roots. These molars show a characteristic button shape and a reduced distal half. The anterosinus is almost closed by the well-developed labial arm of the anteroloph. As in the M2, the protosinus is highly reduced and is closed by a low lingual arm of the anteroloph. The hypocone is rotated antero-labially and connects with the protocone by means of a neo-entoloph. The protolophule consists of a single anterior arm in all specimens. The metacone cannot be clearly distinguished and it connects with the hypocone through a short metalophule. The mesosinus is closed by a cingulum which is continuous with the posteroloph. The posterosinus is reduced to a tiny circular valley.

Table 1. Measurements (in mm) of *Democricetodon hispanicus* from els Casots level 72. Only complete specimens were measured.

Element	Collection number	L	W
M3	IPS 45092	0.69	0.75
M3	IPS 45093	0.94	0.97
M3	IPS 94650	0.93	0.95
m1	IPS 19522	1.41	1.11

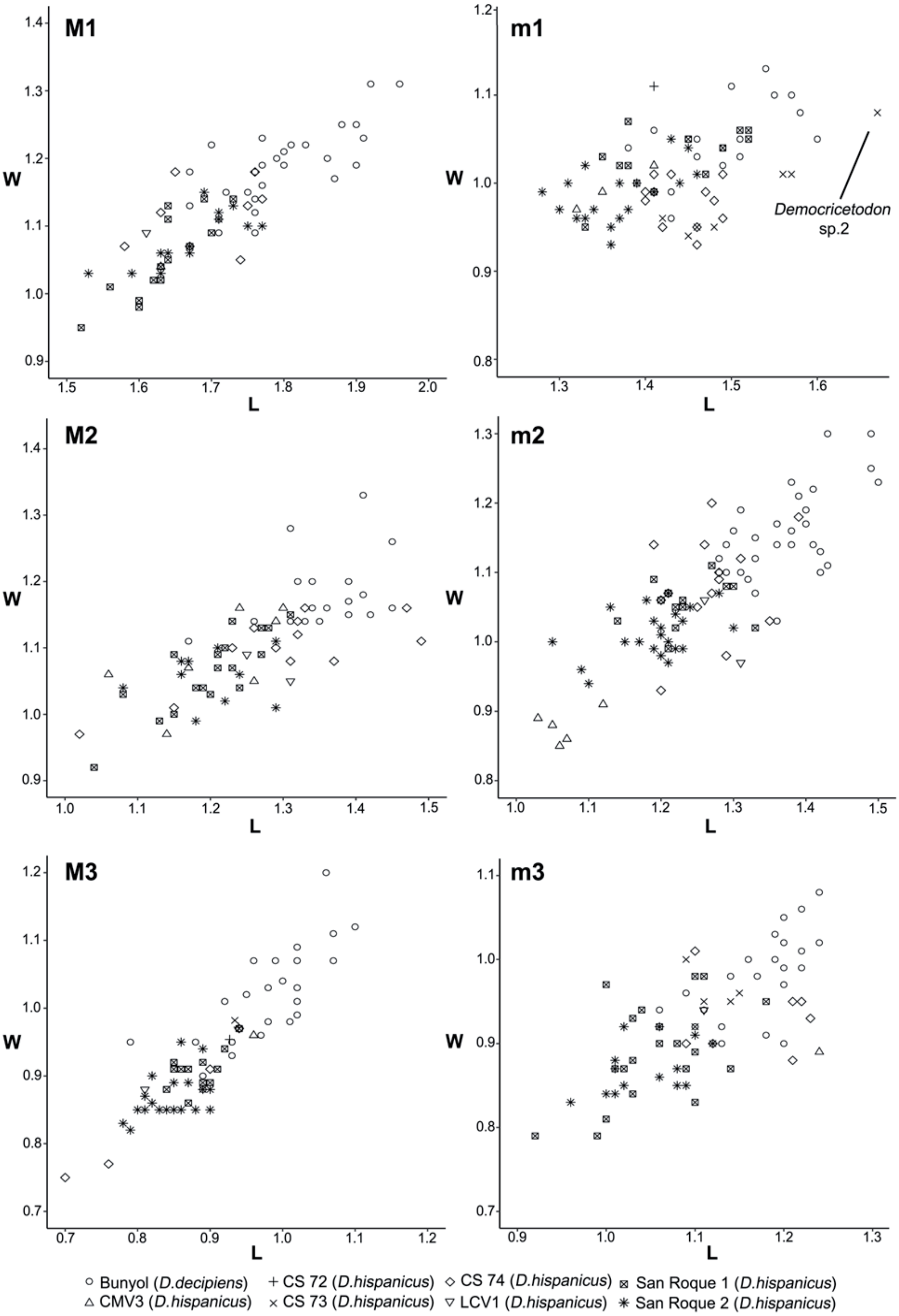
Table 2. Measurements (in mm) of *Democricetodon hispanicus* from els Casots level 73. Only complete specimens were measured.

Element	Collection number	L	W
M3	IPS 19503	0.93	0.98
m1	IPS 19517	1.56	1.01
m1	IPS 45051	1.42	0.96
m1	IPS 45054	1.45	0.94
m1	IPS 45055	1.48	0.95
m1	IPS 45056	1.46	0.95
m1	IPS 45057	1.57	1.01
m1	IPS 45058	1.45	0.94
m3	IPS 19519	1.12	0.90
m3	IPS 94653	1.14	0.94
m3	IPS 94698	1.09	0.92
m3	IPS 94700	1.09	0.99
m3	IPS 94637	1.11	0.95

m1. They have two cylindrical roots, one located below the anteroconid and the other one below the posterior part of the teeth. The anteroconid is simple and rounded. The mesolophid is variable in length, being short in six out of 21 specimens, of medium length in 12 and long in the remaining ones. The anterior valleys are closed by the arms of the anterolophid, which are quite low. The sinusid is wide and mostly points forwards, although it may be transverse in a few specimens. This valley and the mesosinusid are closed by a low cingulid. The hypolophulid is very short and merges with the entolophid anteriorly to the hypoconid. The metalophulid, is absent in IPS 19481 (Pl. 1, Fig. 2) and in IPS 45055 it is interrupted before reaching the protoconid. In the other specimens, the metalophulid is very short and anterior to the protoconid. The posterolophid closes the posterosinusid, reaching the posterior wall of the entoconid.

m2. These teeth have two cylindrical roots (mesial and distal). The lingual anterolophid and the anterosinusid are reduced. The protosinusid is closed by the labial arm of the anterolophid. The mesolophid is short in nine out of 15 specimens and absent in two, while in the remaining four it is of medium length. The remaining morphological features replicate those of the m1.

m3. The specimens present two cylindrical roots (mesial and distal). The anterior valleys are relatively reduced and they appear to be closed by the arms of the anterolophid which are quite low. The metaconid is prominent and connects with the anterolophid by means of an extremely



Text-fig. 2. Length/width scatter plot for the molars of *Democricetodon hispanicus* and *D. decipiens* from different Spanish sites. Locality acronyms are as follows: BU = Bunyol; CMV3 = Can Martí Vell 3; CS72 = els Casots level 72; CS73 = els Casots level 73; CS74 = els Casots level 74; LCV1 = Les Cases de la Valenciana 1; SR1 = San Roque 1; SR2 = San Roque 2. Data for SR1 and SR2 taken from Freudenthal and Daams (1988), data for BU taken from Daams and Freudenthal (1974).

Table 3. Summary measurements (in mm) for *Democricetodon hispanicus* from els Casots level 74. Only complete specimens were measured.

Element	L				W				N
	Min.	Mean	Max.	S. D.	Min.	Mean	Max.	S. D.	
M1	1.58	1.69	1.77	0.07	1.05	1.12	1.19	0.05	8
M2	0.93	1.25	1.49	0.16	0.84	1.07	1.16	0.09	14
M3	0.73	0.91	1.33	0.23	0.77	0.83	0.96	0.09	5
m1	1.40	1.44	1.49	0.03	0.93	0.98	1.01	0.03	12
m2	1.19	1.26	1.39	0.06	0.93	1.08	1.20	0.07	15
m3	1.09	1.17	1.23	0.06	0.88	0.94	1.01	0.04	8

short metalophulid. The mesolophid is absent in all the specimens. The entoconid is greatly reduced and is integrated into the hypolophulid, which is well developed and wide. The sinusid is generally open and points backwards. The posterosinusid is reduced and completely closed by the posterolophid which is very high. The mesosinusid is also closed by a high ridge that departs from the posterior wall of the metaconid.

Discussion. The specimens from els Casots fit within the size range of *Democricetodon hispanicus* (Text-fig. 2; see also Van der Meulen et al. 2003). However, a few somewhat larger dental elements (M2, and some m1, m2 and m3) previously led Agustí and Llenas (1993) to ascribe the material to *D.* aff. *hispanicus*. Nevertheless, the described material perfectly corresponds in morphology with *D. hispanicus* and only very few specimens are slightly above the upper size range of the species. *Democricetodon hispanicus* is distinguished from chronologically and geographically close species such as *D. decipiens* FREUDENTHAL et DAAMS, 1988, *D. franconicus* FAHLBUSCH, 1966 and *D. koenigswaldi* (FREUDENTHAL, 1963) by its smaller size (Van der Meulen et al. 2003). It further differs from *D. decipiens* by its longer mesolophids and from *D. koenigswaldi* by the predominance of transverse or anterior metalophules in the M2 (Van der Meulen et al. 2003). In els Casots material, the mesolophs are predominantly of medium length or long in the M1 and M2. In the lower molars, the mesolophid is predominantly long in the m1 and short in the m2. The protolophule is predominantly posterior in the M1 and double in the M2, with a generally better-developed anterior arm. The metalophule is always posterior to the hypocone in the M1 and anterior to the hypocone or transverse in the M2. All these characters fit with *D. hispanicus*, although long mesolophs/ids are somewhat more frequent in the material from other localities (see Freudenthal and Daams 1988, Van der Meulen et al. 2003). *Democricetodon decipiens* is distinguished from the material of els Casots by the presence of predominantly short mesolophids in the lower molars, a situation that in the described material only occurs in the m2. *Democricetodon hispanicus* occurs in other sites of the Vallès-Penedès Basin such as Les Cases de la Valenciana (Jovells-Vaqué et al. in press) and Can Martí Vell 1 and 2 (Agustí 1981, 1983), which are also included in the Subirats lacustrine unit. The material of all these sites is very similar in size and morphology, which could presumably be due to their similar age.

Democricetodon sp. 2

Pl. 1, Fig. 6

1993 *Fahlbuschia* sp.; Agustí and Llenas, p. 70 (partim).

Material. 1 m1 (IPS 45052) (Pl. 1, Fig. 6) from els Casots level 73.

Measurements. L = 1.67, W = 1.08.

Description. m1. This specimen has two roots: a cylindrical one located under the anteroconid and distal one which is flattened. The anteroconid is simple and rounded. The anterior valleys are narrow, specially the anterosinusid, and closed by the well-developed arms of the anterolophulid. The metalophulid is short and reaches the longitudinal ridge anteriorly to the protoconid. The mesolophid is long and reaches the lingual margin of the teeth. The mesosinusid is closed by a low cingulid. The sinusid points markedly forwards and is closed by a low cingulid which emerges from the base of the protoconid and reaches the hypoconid. The hypolophulid is simple and merges with the hypoconid anteriorly. Finally, the posterolophid is thick and reaches the base of the entoconid, thus enclosing the posterosinusid.

Discussion. Agustí and Llenas (1993: 70) reported a few larger-sized lower molars from els Casots 73 that they tentatively attributed to a "primitive form of *Fahlbuschia* of small dimensions". Amongst the studied specimens, only the described m1 appears to be above the size range of *Democricetodon hispanicus* (Text-fig. 2), being slightly larger than the type material of *Fahlbuschia decipiens* from Bunyol (Valencia; Daams and Freudenthal 1974, Freudenthal and Daams 1988). Van der Meulen et al. (2003) consider *Fahlbuschia* MEIN et FREUDENTHAL, 1971 a junior synonym of *Democricetodon* (but see Freudenthal (2006) for a different taxonomic opinion) and propose emended diagnoses for several species of this genus. Their emended diagnosis for *D. decipiens* stresses its larger size as compared to *D. hispanicus* and predominantly short mesolophs and mesolophids (Van der Meulen et al. 2003: 429). The described m1 shows a long mesolophid comparable to that of *D. hispanicus* specimens from the same site and is slightly larger than *D. decipiens*, being closer in size to *D. moralesi* VAN DER MEULEN, PELÁEZ-CAMPOMANES et DAAMS, 2003 or *D. koenigswaldi* (Van der Meulen et al. 2003). However, in these species the mesolophid is generally even more reduced than in *D. decipiens*. Unfortunately, the diagnosis of *Democricetodon* species requires of sufficient material in order to evaluate the variation in features such as the length of the mesoloph/id or the morphology of the protolophule/metalophule in the upper molars (see Maridet 2003, Van der Meulen et al. 2003). Clearly the material from els Casots 73 does not allow for such assessment, so it is therefore ascribed to a second, larger-sized *Democricetodon* species. Further material could clarify its taxonomical attribution and provide valuable biostratigraphic information.

Genus *Megacricetodon* Fahlbusch, 1964

Megacricetodon primitivus (Freudenthal, 1963)

Pl. 1, Figs 7–11

1993 *Megacricetodon minor primitivus*; Agustí and Llenas, p. 70.

Material from els Casots level 72. 2 M1 (IPS 45094, IPS 94649); 2 M2 (IPS 45094, IPS 45089); 2 M3 (IPS 45094, IPS 45089); 3 m1 (IPS 44995, IPS 44996, IPS 19514); 3 m2 (IPS 19515, IPS 44997, IPS 19523).

Material from els Casots level 73. 7 M1 (IPS 44963 – IPS 44968, IPS 94641); 1 M3 (IPS 94639); 6 m1 (IPS 44969 – IPS 44974); 1 m3 (IPS 94640).

Material from els Casots level 74. 6 M1 (IPS 44936 – IPS 44941); 2 M2 (IPS 44961, IPS 44984); 1 M3 (IPS 19479); 17 m1 (IPS 44942 – IPS 44958); 15 m2 (IPS44948 – IPS 44951, IPS 44959, IPS 44960, IPS 44962, IPS 44981 – IPS 44983, IPS 44985, IPS 94255, IPS 94256, IPS 94587, IPS 94588); 5 m3 (IPS 44949, IPS 44991 – IPS 44994).

Measurements. See Tables 4–6.

Description. M1. All the specimens have three roots. The most mesial root is cylindrical and located under the anterocone; there is a flattened root at the lingual half side and a cylindrical one at the postero-labial corner of the molar. The anterocone is deeply split with the labial cusp conspicuously larger than the lingual one. A few specimens show a faint anterior cingulum at the base of the anterocone, but in most specimens the anterior wall of the anterocone is smooth. The anterolophule connects the protocone with the lingual cusp of the anterocone. There is no labial spur on the anterophule. The protolophule consists of a posterior arm that connects the paracone with the entoloph posteriorly to the protocone. However, four out of 15 M1 show a vestigial extremely short anterior arm of the protolophule that does not reach the paracone. There is a short posterior ectoloph in the paracone spur in three specimens, while this character is absent in the remaining ones. The mesoloph varies from long to absent. It is long in three out of 15 specimens, of medium length in six (for example in IPS 44939; Pl. 1, Fig. 7), short in four and absent in the remaining two. The metalophule consists of a single arm that curves distally and joins the metacone with the posteroloph in a somewhat labial position. This implies that the posterosinus is highly reduced. The posteroloph is thin and partially closes this valley. The sinus is transverse. All the main valleys are closed by cingula, which are more pronounced on the lingual side. However, there is no lingual mesocingulum.

Table 4. Measurements (in mm) of *Megacricetodon primitivus* from els Casots level 72. Only complete specimens were measured.

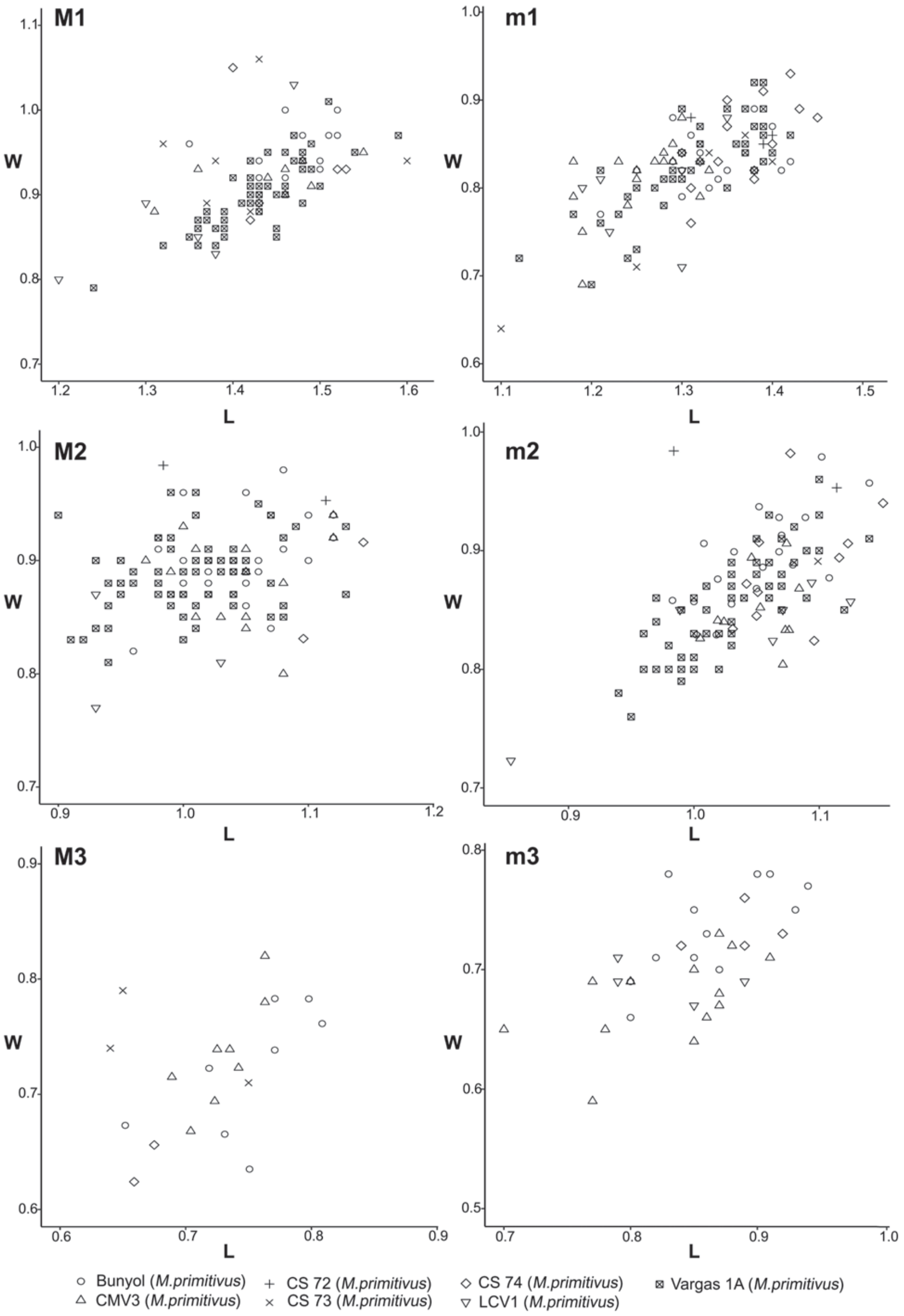
Element	Collection number	L	W
M2	IPS 45094	0.98	0.98
M2	IPS 45089	1.11	0.95
M3	IPS 45094	0.64	0.74
M3	IPS 45089	0.65	0.79
m1	IPS 44995	1.39	0.85
m1	IPS 44996	1.31	0.87
m1	IPS 19514	1.36	0.85
m2	IPS 19515	1.01	0.83
m2	IPS 44997	1.03	0.80
m2	IPS 19523	1.13	0.87

Table 5. Measurements (in mm) of *Megacricetodon primitivus* from els Casots level 73. Only complete specimens were measured.

Element	Collection number	L	W
M1	IPS 44963	1.42	0.88
M1	IPS 44964	1.37	0.89
M1	IPS 44965	1.38	0.94
M1	IPS 44966	1.32	0.96
M1	IPS 44967	1.60	0.94
M1	IPS 44968	1.43	1.06
M1	IPS 94641	1.64	1.16
m1	IPS 44969	1.25	0.71
m1	IPS 44970	1.33	0.84
m1	IPS 44971	1.40	0.83
m1	IPS 44972	1.10	0.64
m1	IPS 44973	1.32	0.83
m1	IPS 44974	–	0.83
M3	IPS 94639	0.84	0.72
m3	IPS 94640	0.89	0.70

Table 6. Summary measurements (in mm) for *Megacricetodon primitivus* from els Casots level 74. Only complete specimens were measured.

Element	L				W				N
	Min.	Mean	Max.	S. D.	Min.	Mean	Max.	S. D.	
M1	1.40	1.46	1.53	0.06	0.87	0.93	1.05	0.07	5
M2	1.10	–	1.14	–	0.83	–	0.93	–	2
m1	1.30	1.37	1.45	0.05	0.76	0.85	0.93	0.04	15
m2	1.03	1.09	1.20	0.05	0.82	0.89	0.98	0.05	12
m3	0.84	0.92	1.08	0.09	0.72	0.73	0.76	0.02	5



Text-fig. 3. Length/width scatter plot for the molars of *Megacricetodon primitivus* from different Spanish sites. Locality acronyms are as follows: BU = Bunyol; CMV3 = Can Martí Vell 3; CS72 = els Casots level 72; CS73 = els Casots level 73; CS74 = els Casots level 74; LCV1 = Les Cases de la Valenciana 1; VR1 = Vargas 1. Data for VR1 taken from Daams and Freudenthal (1988), data for BU taken from Daams and Freudenthal (1974).

M2. The M2 have two flattened roots, mesial and distal. The anterior valleys are closed by the well-developed arms of the anterolophule. The labial arm is noticeably higher than the lingual one. The protosinus is very reduced, being vestigial in some specimens (for example in IPS 44961; Pl. 1, Fig. 8). The protolophule and the metalophule are simple, consisting in an anterior arm only. Two specimens (including IPS 44961; Pl. 1, Fig. 8) show a vestige of the posterior arm of the protolophule that can be recognized as a small protuberance posterior to the protocone. The mesoloph is always long, reaching the labial border of the molar although it becomes very low towards its end. In three specimens (for example IPS 44961; Pl. 1, Fig. 8), there is a short to medium-sized posterior ectoloph on the paracone, while it is absent in the remaining one. When present, the ectoloph approaches the mesoloph without contacting with it. The sinus is transverse. The posteroloph is well developed and reaches the base of the metacone, thus resulting in a closed posterosinus. The sinus and mesosinus are closed by relatively well-developed cingula.

M3. The M3 show a rounded outline and two cylindrical roots (labial and lingual). There is no trace of the protosinus and the lingual anteroloph. The anterosinus is narrow and partially closed by the well-developed labial arm of the anteroloph. The protolophule is simple and connects the paracone with the anteroloph in front of the protocone. The mesoloph and metalophule are highly variable. In one specimen, the mesoloph is long, ending in a prominent mesostyle and the metalophule is parallel to it and ends in a small metacone (IPS 45094). In a second one (IPS 19479; Pl. 1, Fig. 9), this ridge is shorter and isolated from the entoloph and the mesostyle but it shows a weak contact with the metalophule. A third specimen (IPS 45089) shows a peculiar morphology with an arched axioloph and a long, slightly posteriorly-directed mesoloph. The metacone is indistinguishable at the end of the metalophule, and the posterior and labial valleys are closed by a high ridge. The posteroloph is well developed and partially closes the very narrow posterosinus. The sinus is transverse and narrow, being closed by a low cingulum.

m1. The molars have two cylindrical roots, anterior and posterior. In slightly worn specimens, the anteroconid is simple and rounded. The anterior valleys are wide and closed by the arms of the anterolophid, which are low. The anterolophulid is very low and situated in a more or less central position. The anterolophulid shows a labial spur in six out of 26 specimens, it is generally short and low, but in a few instances, it reaches the labial anterolophid. The metalophulid and the hypolophulid are both simple, being defined by a very short anterior arm. The mesolophid is always present, being short in most specimens (20/26; see for example IPS 44950; Pl. 1, Fig. 10) and somewhat longer in a few others (6/26). The sinusid is wide and proverse. It is closed by a pronounced cingulid while the mesosinusid is open. The posterolophid is high and thick and closes a rather wide posterosinusid.

m2. The m2 have two cylindrical roots, mesial and distal. The anterior valleys are closed by the arms of the anterolophid. Unworn molars show a highly reduced to vestigial anterosinusid which quickly disappears because of wear (IPS 44950; Pl. 1, Fig. 10). The mesolophid is always present. Most specimens show a short mesolophid (15/18; see for example IPS 44950; Pl. 1, Fig. 10), although medium-length ones also occur (3/18) and one specimen (IPS 19515) shows a long mesolophid which is extremely low at its lingual end. The sinusid is wide and transverse to slightly proverse. This valley is closed by a cingulid in most specimens, although it is not as well developed as in m1. The remaining morphological features resemble those of the m1.

m3. The m3 are elongated and show two cylindrical roots. The anterior valleys are reduced, specially the anterosinusid, which is vestigial in some specimens. These valleys are closed by the arms of the anterolophid, which are low. The metalophulid is thick and short, joining the metaconid with the anterolophid in front of the protoconid. The mesolophid is absent in all the molars but one, (IPS 44994), which exhibits a vestige of this ridge just behind the protoconid. The sinusid is relatively wide and mostly retroverse. This valley is closed by a low cingulid as described for the m2. The hypolophulid is very thick and anterior to the hypoconid. The entoconid is reduced. The posterolophid is thick and short, but it closes the posterosinusid. The mesosinusid is closed by a high cingulid.

Discussion. The specimens from els Casots are similar in size to small *Megacricetodon* species such as *M. primitivus*, *M. minor* Lartet, 1851 and *M. collongensis* Mein, 1958 (Text-fig. 3; see also Daams and Freudenthal 1988, Oliver and Peláez-Campomanes 2014). However, a number of morphological features allow us to confidently ascribe the material from els Casots to *Megacricetodon primitivus.* The anterocone in the M1 is clearly divided and not predominantly simple or slightly split as in *M. minor. Megacricetodon collongensis* (Mein 1958) is similar in size, but shows a symmetrically split anterocone. In contrast, in *M. primitivus* and the specimens from els Casots, the labial cusp of the anterocone is generally larger than the lingual one (Oliver and Peláez-Campomanes 2014). The mesoloph in the M1 is variable, but is mostly of medium length, while in the M2 it is always long and low. Mesoloph development is similar in the type material from Valtorres (Freudenthal 1963) and in *M. primitivus* from other Spanish sites (Daams and Freudenthal 1988, Oliver Pérez et al. 2008, Oliver and Peláez-Campomanes 2014) but the mesoloph in the M2 is most commonly of medium length. The M2 protolophule is simple with only one anterior arm and in a few cases a vestigial posterior arm. Similarly, the protolophule is simple and posterior in the M1 with a vestige of the anterior protolophule occurring in a few specimens. Double protolophules are more common in other Spanish samples from the Calatayud-Montalbán Basin (Oliver Pérez et al. 2008, Oliver and Peláez-Campomanes 2014) as well as from Bunyol (Daams and Freudenthal 1974, Adrover et al. 1987) but not in other samples from the Vallès-Penedès Basin such as Can Martí Vell 1 and 2 (Agustí 1981, 1983) or Les Cases de la Valenciana 1 (Jovells-Vaqué et al. in press). Els Casots specimens perfectly agree in size and morphology with *M. primitivus* from these Vallès-Penedès sites although a few dental elements (particularly the lower molars) are slightly larger.

Biostratigraphic implications and conclusions

The cricetid fauna from els Casots comprises three different species: *Democricetodon hispanicus*, *Democricetodon* sp. 2 and *Megacricetodon primitivus*. The presence of *Megacricetodon primitivus* together with *Democricetodon* and *Ligerimys* SCHAUB, 1951 is indicative of an early Aragonian MN 4 age (Mein 1999, Agustí et al. 2001, Hilgen et al. 2012) as already proposed in previous publications (Agustí and Llenas 1993, Casanovas-Vilar et al. 2011a, b, 2016b). *Democricetodon* has already been recorded in the latest MN 3, although it is very rare (Daams et al. 1999, Hilgen et al. 2012, Van der Meulen et al. 2012), whereas the last occurrence of the eomyid *Ligerimys* marks the lower boundary of zone MN 5 (Daams et al. 1999, Agustí et al. 2001, Kälin and Kempf 2009, Hilgen et al. 2012, Van der Meulen et al. 2012). Zone MN 4 corresponds to local biozones B and C in the Calatayud-Montalbán Basin (east-central Spain), the type area of the Aragonian (see Daams et al. 1999, Van der Meulen et al. 2012). The first occurrence of *M. primitivus* marks the beginning of zone C, although this species persists in the area until zone Db (late MN 5; Van der Meulen et al. 2012, Oliver and Peláez-Campomanes 2014, García-Paredes et al. 2016). Zone C is further subdivided into subzones Ca and Cb on the basis of the species of *Democricetodon* present. While *D. decipiens* is restricted to zone Ca, its descendant *D. moralesi* characterizes zone Cb (Van der Meulen et al. 2003, 2012). *Democricetodon hispanicus*, which is the species co-occurring with *M. primitivus* at els Casots and all other Vallès-Penedès sites, is restricted to zones A and B (late Ramblian and earliest Aragonian) in the Calatayud-Montalbán Basin (Van der Meulen et al. 2012), thus arguing against a correlation of these sites with zone C. On the other hand, zone Ca also includes the replacement of the eomyid *Ligerimys florancei* STEHLIN et SCHAUB, 1951 by its descendant *L. ellipticus* (Álvarez Sierra 1987), with the two species coexisting in a few sites (Van der Meulen et al. 2012). The latter species, the last member of the genus *Ligerimys*, disappears at the end of zone Cb. Both *Ligerimys* species are recorded in other sites of the Subirats lacustrine unit, such as Can Martí Vell 1 and 2 (Agustí 1981, 1983) and Les Cases de la Valenciana 1 (Jovells-Vaqué et al. in press), but only *L. ellipticus* is present at els Casots, being represented by just seven specimens out of more than 200 rodent teeth. This fact, together with the presence of a second, larger-sized *Democricetodon* species has been considered to indicate a younger age for els Casots when compared to the remaining sites (Agustí and Llenas 1993). Such an assumption seems reasonable, yet els Casots could either be correlated to the upper part of subzone Ca or to subzone Cb. The correlation attempt is further complicated by the presence of the cricetid *Eumyarion* THALER, 1966 in Les Cases de la Valenciana 1, Can Martí Vell 1 and 2 and Sant Mamet but not in els Casots (Agustí 1981, 1983, Agustí et al. 1985, Jovells-Vaqué et al. 2017). This genus is not recorded in the Calatayud-Montalbán Basin until zone Cb, but has been recorded in Ca sites in the Teruel and Valencia area (Van der Meulen et al. 2012).

To sum up, we conclude that the presence of *Megacricetodon primitivus* and *Ligerimys ellipticus* at els Casots favors a correlation with zone C of the Calatayud-Montalbán Basin. This is further supported by the common occurrence of *Democricetodon* which is represented by two different species. *Democricetodon* serves as the basis for the subdivision of zone C into subzones Ca and Cb in that area, but unfortunately is represented by different species (*D. decipiens* and *D. moralesi*). The fact that *L. ellipticus* is the only eomyid present would favor a correlation to late zone Ca or to zone Cb, thus implying an age of about 16.4–15.9 Ma (ages after Van der Meulen et al. 2012), so that els Casots would indeed be slightly younger than other sites of the Subirats lacustrine unit (see Jovells-Vaqué et al. in press). The local zonation for the Aragonian in the type area could be roughly applied to the Vallès-Penedès Basin (as suggested by Casanovas-Vilar et al. 2011a, 2016a) but the cricetid succession shows some remarkable differences which hampers the use of detailed subzones. Concerning the genus *Democricetodon*, some characteristic species are not recorded in the Vallès-Penedès Basin, and apparently *D. hispanicus* persists for a longer time, thus coexisting with *M. primitivus* and *Eumyarion*. Hopefully, ongoing magneto- and biostratigraphical studies in the long-neglected early Miocene successions of this basin will shed new light on this issue.

Acknowledgements

This work was supported by the Spanish Ministerio de Economía y Competitividad (project CGL2014-54373-P and RYC-2013-12470 research contract to ICV), the Agencia Estatal de Investigación (AEI) from Spain and the European Regional Development Fund of the European Union (CGL2016-76431-P), as well as the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya (CERCA Programme and 2014 SGR 416 research group and FI_B 00054 pre-doctoral grant to SJV). We thank Mariona Berrocal (ICP research volunteer) for her support in preparing and labeling the studied collections. We thank the reviewers of this manuscript (A. Oliver and J. Prieto) who made constructive comments and suggestions that certainly improved the final result. Finally, we would like to thank professors R. Musil and O. Fejfar for their inspiring work in paleontology as well as to the editors of this special volume for inviting us to contribute to it.

References

Adrover, R., Mein, P., Belinchón, M. (1987): La fauna de roedores en el Aragoniense medio del Barranco del Candel, Buñol (província de Valencia, España) [The middle Aragonian rodent fauna from Barranco del Candel, Buñol (province of Valencia, Spain)]. – Paleontologia i Evolució, 21: 43–61. (in Spanish)

Agustí, J. (1981): Roedores Miomorfos del Neógeno de Cataluña [Myomorph rodents from the Neogene of Catalonia]; Ph. D. Dissertation. – MS, Universitat de Barcelona, Barcelona, Spain, 288 pp. (in Spanish) (copy in library of Biology Faculty of Universitat de Barcelona)

Agustí, J. (1983): Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallès-Penedès, Cataluña, España) [Rodents (Mammalia) from the early Miocene of Can Matí Vell (Vallès-Penedès, Catalonia, Spain]. – Estudios Geológicos, 39(5-6): 417–430. (in Spanish)

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J. M. (2001): A calibrated mammal scale for the Neogene of Western Europe. State of the art. – Earth-Science Reviews, 52(4): 247–260. https://doi.org/10.1016/S0012-8252(00)00025-8

Agustí, J., Cabrera, L., Moyà-Solà, S. (1985): Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès [Stratigraphic synopsis of the Neogene from the Vallès-Penedès Basin]. – Paleontologia i Evolució, 18: 57–81. (in Spanish)

Agustí, J., Llenas, M. (1993): Los roedores del Mioceno inferior de Els Casots (Vallès-Penedès). Nota preliminar [Rodents from the early Miocene of Els Casots (Vallès-Penedès). Preliminary report]. – In: Comunicaciones de las IX Jornadas de Paleontología, 28–30 de octubre de 1993. Universidad de Málaga, Málaga, pp. 70–72. (in Spanish)

Alba, D. M., DeMiguel, D., Morales, J., Sánchez, I. M., Moyà-Solà, S. (2014): New Remains of *Dorcatherium crassum* (Artiodactyla: Tragulidae) from the Early Miocene (MN4) of Els Casots (Subirats, Vallès-Penedès Basin). – Comptes Rendus Palevol, 13(2): 73–86. https://doi.org/10.1016/j.crpv.2013.09.003

Aldana Carrasco, E. J. (1992): Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España) [The Sciurinae (Rodentia, Mammalia) from the Miocene of the Vallès-Penedès Basin (Catalonia, Spain)]. – Treballs del Museu de Geologia de Barcelona, 2: 69–97. (in Spanish)

Almera, J. (1898): Sobre la serie de mamíferos fósiles descubiertos en Cataluña [On the series of fossil mammals discovered in Catalonia]. – Memorias de la Real Academia de las Ciencias y las Artes de Barcelona, 3ª época, 2: 351–357. (in Spanish)

Álvarez Sierra, M. A. (1987): Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior Español [Taxonomical and biostratigraphical studies of Eomyidae (Rodentia) from Late Oligocene and Early Miocene of Spain]. – Scripta Geologica, 86: 1–207. (in Spanish)

Cabrera, L. (1981): Estratigrafía y características sedimentológicas generales de las formaciones continentales de la cuenca del Vallès-Penedès (Barcelona, España) [Stratigraphy and sedimentological characteristics of the continental formations from the Vallès-Penedès Basin (Barcelona, Spain)]. – Estudios Geológicos, 37(1-2): 35–43. (in Spanish)

Cabrera, L., Calvet, F. (1996): Onshore Neogene record in NE Spain: Vallès-Penedès and El Camp half grabens (NW Mediterranean). – In: Friend, P. F., Dabrio, C. J. (eds), Tertiary Basins of Spain the Stratigraphic Record of Crustal Kinematics. Cambridge University Press, Cambridge, UK, pp. 97–105. https://doi.org/10.1017/cbo9780511524851.017

Cabrera, L., Calvet, F., Guimerà, J., Permanyer, A. (1991): El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: Organización secuencial y relaciones tectónica sedimentación [The Miocene sedimentary record in the Vallès-Penedès and El Camp half grabens: sequential organziation and tectonic-sedimentation relationships]. – In: Colombo, F. (ed.), Libro Guía no. 4 del I Congreso Grupo Español del Terciario. Vic, pp. 1–132. (in Spanish)

Cabrera, L., Roca, E., Garcés, M., de Porta, J. (2004): Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana) [Late Oligocene to Neogene stratigraphy and tectonosedimentary evolution of the central sector of the Catalan margin (Catallan Littoral Range)]. – In: Vera, J. A. (ed.), Geología de España. SGE–IGME, Madrid, pp. 569–573. (in Spanish)

Casanovas-Vilar, I., Alba, D. M, Robles, J. M., Moyà-Solà, S. (2011b): Parada 1. Panorámica general de la cuenca y yacimiento de Els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior [Stop 1. Overview of the basin and Els Casots site (Subirats): an early Aragonian vertebrate fauna]. – Paleontologia i Evolució, Mem. Esp. 6: 81–88. (in Spanish)

Casanovas-Vilar, I., DeMiguel, D., Galindo, J., Robles, J. M., Garcés, M., Cabrera, L. (2011a): The Continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). – In: Pérez García, A., Gascó, F., Gasulla, J. M., Escaso, F. (eds), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella, Castellón, pp. 93–100.

Casanovas-Vilar, I., Garcés, M., Van Dam, J., García-Paredes, I., Robles, J. M., Alba, D. M. (2016b): An Updated Biostratigraphy for the Late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). – Geologica Acta, 14(3): 195–217. http://dx.doi.org/10.1344/GeologicaActa2016.14.3.1

Casanovas-Vilar, I., Madern A., Alba, D. M., Cabrera, L., García-Paredes, I., Van den Hoek Ostende, L. W., DeMiguel, D., Robles, J. M., Furió, M., Van Dam, J., Garcés, M., Angelone, C., Moyà-Solà, S. (2016a): The Miocene Mammal Record of the Vallès-Penedès Basin (Catalonia). – Comptes Rendus Palevol, 15(7): 791–812. https://doi.org/10.1016/j.crpv.2015.07.004

Crusafont, M., de Villalta, J. F., Truyols, J. (1955): El Burdigaliense continental de la Cuenca del Vallés-Penedés [The continental Burdigalian of the Vallès-Penedès Basin]. – Memorias y Comunicaciones del Instituto Geológico Diputación Provincial de Barcelona, 12: 1–272. (in Spanish)

Crusafont Pairó, M. (1950): La cuestión del llamado Meótico Español [The issue of the so-called Spanish Maeotian]. – Arraona, 1950: 41–48. (in Spanish)

Daams, R., Freudenthal, M. (1974): Early Miocene Cricetidae (Rodentia, Mammalia) from Buñol (Prov. Valencia, Spain). – Scripta Geologica, 24: 1–19.

Daams, R., Freudenthal, M. (1988): Cricetidae (Rodentia) from the Type-Aragonian; the Genus *Megacricetodon*. – Scripta Geologica, Special Issue 1: 39–132.

Daams, R., Van der Meulen, A. J., Álvarez Sierra, M. A., Peláez-Campomanes, P., Pedro Calvo, J., Alonso Zarza, M. A., Krijgsman, W. (1999): Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). – Newsletters on Stratigraphy, 37(3): 103–139. https://doi.org/10.1127/nos/37/1999/103

De Gibert, J. M., Casanovas-Vilar, I. (2011): Contexto geológico del Mioceno de la Cuenca del Vallès-Penedès [Geological context of the Miocene of the Vallès-Penedès Basin]. – Paleontologia i Evolució, Mem. Esp. 6: 39–45. (in Spanish)

Díaz Aráez, J. L., Delfino, M., Luján, A. H., Fortuny, J., Bernardini, F., Alba, D. M. (2017): New Remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the Early Miocene of the Iberian Peninsula. – Comptes Rendus Palevol, 16(1): 12–26. https://doi.org/10.1016/j.crpv.2015.11.003

Duranthon, F., Moyà-Solà, S., Köhler, M. (1995): *Ampelomeryx ginsburgi* nov. gen., nov. sp. (Artiodactyla, Cervoidea) et la famille des Palaeomerycidae. – Comptes Rendus de l’Académie des Sciences, Série II, Fascicule a, 321(4): 339–346.

Freudenthal, M. (1963): Entwicklungsstufen der miozänen Cricetodontinae (Mammalia, Rodentia) Mittelspaniens und ihre Stratigraphische bedeutung. – Beaufortia, 10: 51–157.

Freudenthal, M. (2006): The status of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* (Cricetidae, Mammalia). A reply to Van Der Meulen et al. (2004). – Geobios, 39(1): 43–55. https://doi.org/10.1016/j.geobios.2004.08.005

Freudenthal, M., Daams, R. (1988): Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen., and *Renzimys*. – Scripta Geologica, Special Issue 1: 133–252.

García-Paredes, I., Álvarez-Sierra, M. Á., Van den Hoek Ostende, L. W., Hernández-Ballarín, V., Hordijk, K., López-Guerrero, P., Oliver, A., Peláez-Campomanes, P. (2016): The Aragonian and Vallesian high-resolution micromammal succession from the Calatayud-Montalbán Basin (Aragón, Spain). – Comptes Rendus Palevol, 15: 781–789. https://doi.org/10.1016/j.crpv.2015.09.014

Hilgen, F. J., Lourens, L. J., Van Dam, J. A. (2012): The Neogene period. – In: Gradstein, F. M., Ogg, J. G., Schmitz, M., Ogg, G. (eds), The Geologic Time Scale 2012. Elsevier, Amsterdam, pp. 923–978. https://doi.org/10.1016/b978-0-444-59425-9.00029-9

Jovells-Vaqué, S., García-Paredes, I., Furió, M., Angelone, C., Van den Hoek Ostende L.W., Berrocal Barberà, M., DeMiguel, D., Madurell-Malapeira, J., Casanovas-Vilar I. (in press): Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). – Historical Biology, [published online: 19 April 2017]. https://doi.org/10.1080/08912963.2017.1317768

Jovells-Vaqué, S., Ginestí, M., Casanovas-Vilar, I. (2017): First cranial material of *Democricetodon hispanicus* Freudenthal, 1967 (Rodentia, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). – In: Barrios de Pedro, S., Blanco Moreno, C., de Celis, A., Colmenar, J., Cuesta, E., García-Martínez, D., Gascó, F., Jacinto, A., Malafaia, E., Martín Jiménez, M., de Miguel Chaves, C., Mocho, P., Pais, V., Parámo Blázquez, A., Pereira, S., Serrano Martínez, A., Vidal, D. (eds), A Glimpse in the Past. Abstract book of the XV Encuentro de Jóvenes Investigadores en Paleontología/XV Encontro de Joven Investigadore em Paleontologia, pp. 223–226.

Kälin, D., Kempf, O. (2009): High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. − Neues Jahbuch für Geologie und Paläontologie, Abhandlungen, 254 (1-2): 177−235. https://doi.org/10.1127/0077-7749/2009/0010

Maridet, O. (2003): Révision du genre *Democricetodon* (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d’Europe occidentale: évolution, paléobiodiversité et paléobiogéographie; Ph. D. dissertation. – MS, Université Claude Bernard – Lyon 1, Lyon, France, 252 pp. (copy in library of Université Claude Bernard – Lyon 1)

Mein, P. (1958): Les mammifères de la faune sidérolithique de Vieux-Collonges. – Nouvelles Archives du muséum d’Histoire Naturelle de Lyon, 5: 1–122.

Mein, P. (1975): Résultats du Groupe de Travail des Vertébrés. – In: Seneš, J. (ed.), Report on the Activity of the RCMNS Working Groups – 6 Congress of the Regional Committee of Mediterranean Neogene Stratigraphy. SAV, Bratislava, pp. 78–81.

Mein, P. (1999): European Miocene Mammal Biochronology. – In: Rössner, G. E., Heissig, K. (eds), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 25–38.

Moyà-Solà, S., Rius Font, L. (1993): El jaciment paleontològic dels Casots (Subirats, Alt Penedès) [Els Casots paleontological site (Subirats, Alt Penedès)]. – Tribuna d’Arqueologia, 1991(2): 7–12. (in Catalan)

Oliver A., Peláez-Campomanes, P. (2013): *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon*. – Journal of Vertebrate Paleontology, 33(4): 943–955. https://doi.org/10.1080/02724634.2013.743896

Oliver, A., Peláez-Campomanes, P. (2014): Evolutionary patterns of early and middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia). – Palaeontographica, Abt. A, 303(4-6): 85–135. https://doi.org/10.1127/pala/303/2014/85

Oliver Pérez, A., López Guerrero, P., Peláez-Campomanes, P. (2008): Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España) [First representative of the genus *Megacricetodon* fom the Calatayud-Daroca Basin (Zaragoza, Spain)]. – Palaeontologica Nova, Publicaciones del Seminario de Paleontología de Zaragoza, 8: 317–329. (in Spanish with English abstract)

Orliac, M. J. (2006): *Eurolistriodon tenarezensis*, sp. nov., from Montréal-du-Gers (France): implications for the systematics of the European Listriodontinae (Suidae, Mammalia). – Journal of Vertebrate Paleontology, 26(4): 967–980. https://doi.org/10.1671/0272-4634(2006)26[967:ETSNFM]2.0.CO;2

Pickford, M., Moyà-Solà, S. (1994): *Taucanamo* (Suoidea, Tayassuidae) from the Middle Miocene (MN04a) of Els Casots, Barcelona, Spain. – Comptes Rendus de l’Académie des Sciences, Série II, Fascicule 2, 319(12): 1569–1575.

Pickford, M., Moyà-Solà, S. (1995): *Eurolistriodon* gen. nov., (Suoidea, Mammalia) from Els Casots, early middle Miocene, Spain. – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Biological, chemical, geological and medical sciences, 98(4): 343–360.

Roca, E., Sans, M., Cabrera, L., Marzo, M. (1999): Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). – Tectonophysics, 315(1-4): 209–229. https://doi.org/10.1016/S0040-1951(99)00289-9

Rotgers, C., Alba, D. M. (2011): The genus *Anchitherium* (Equidae: Anchitheriinae) in the Vallès-Penedès Basin (Catalonia, Spain). – In: Pérez-García, A., Gascó, F., Gasulla, J. M., Escaso, F. (eds), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella, pp. 347–354.

Van der Made, J. (1997): Systematics and stratigraphy of the genera *Taucanamo* and *Schizochoerus* and a classification of the Palaeochoeridae (Suoidea, Mammalia). – Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Biological, chemical, geological, physical, and medical sciences, 100(1-2): 127–139.

Van der Meulen, A. J., García-Paredes, I., Álvarez- Sierra, M. A., Van den Hoek Ostende, L. W., Hordijk, K., Oliver, A., Pélaez-Campomanes, P. (2012): Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. – Geologica Acta, 10(2):159–179. http://dx.doi.org/10.1344/105.000001710

Van der Meulen, A. J., Pélaez-Campomanes, P., Daams, R. (2003): Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain). – Coloquios de Paleontologia, Vol. Ext. 1: 385–441.

Explanations of the plate

PLATE 1

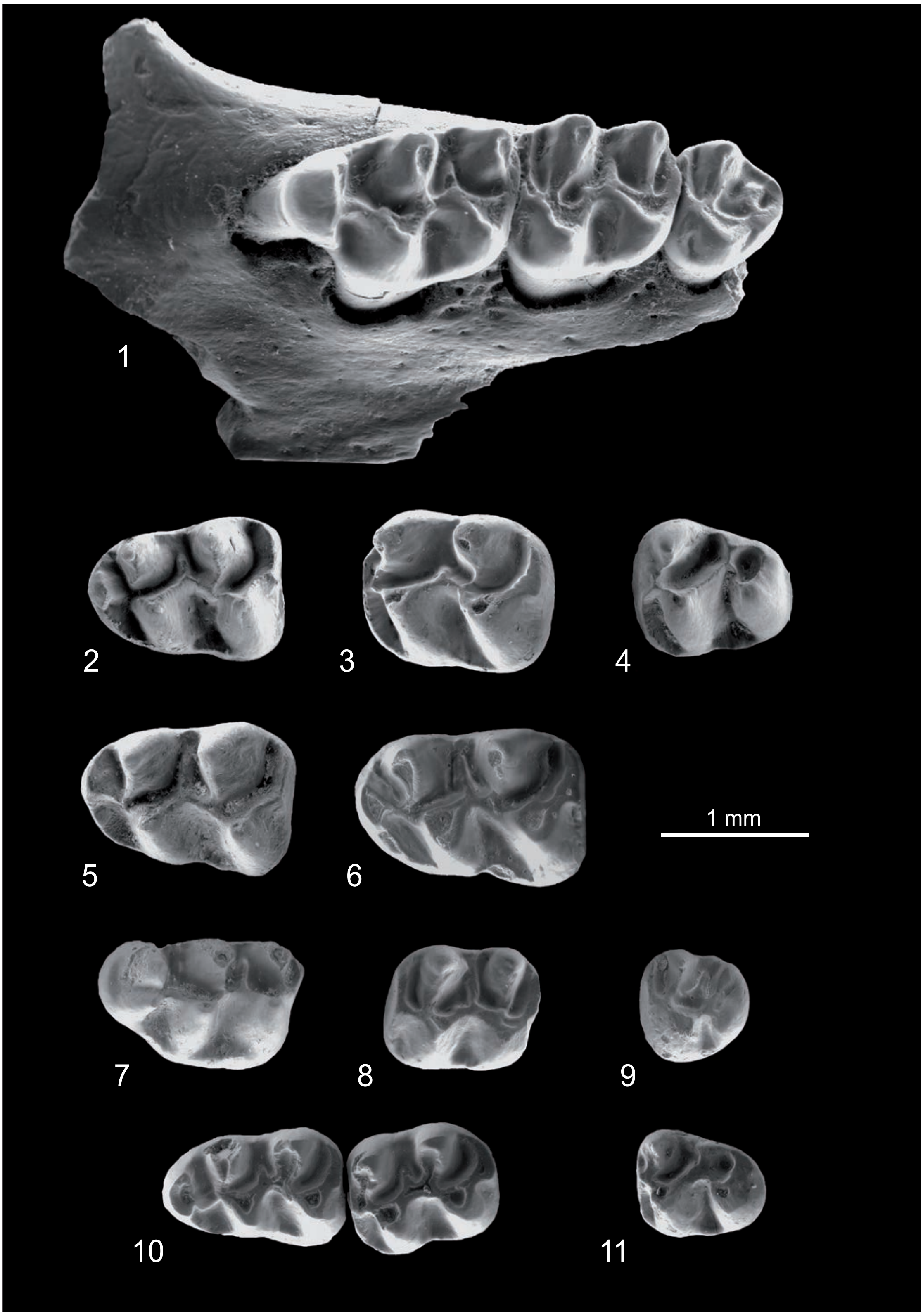
Scanning electron microscope (SEM) micrographs of the Cricetidae from els Casots.

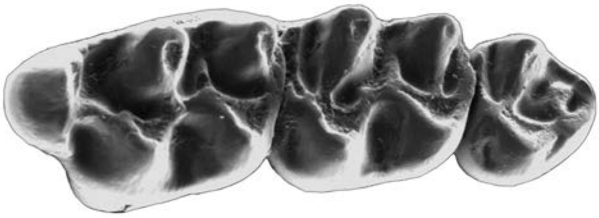
Democricetodon hispanicus from els Casots 74
1. Right maxillary fragment with M1–M3 (reversed); IPS 45008.
2. Left m1; IPS 19481.
3. Right m2 (reversed); IPS 45059.
4. Left m3; IPS 19473.
5. Right m1 (reversed); IPS 45049.

Democricetodon sp. 2 from els Casots 73
6. Left m1; IPS 45052.

Megacricetodon primitivus from els Casots 74
7. Right M1 (reversed); IPS 44939.
8. Left M2; IPS 44961.
9. Left M3; IPS 19479.
10. Right m1 – m2 (reversed); IPS 44950.
11. Right m3 (reversed); IPS 44992.

PLATE 1





Chapter 8: "First cranial material of *Democricetodon hispanicus* Freudenthal, 1967 (Rodentia, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). Preliminary results".

A Glimpse of the Past. Book of abstracts XV meeting of young researchers in paleontology.
XVEJIP - Pombal, Portugal

Published: April 2017

First cranial material of *Democricetodon hispanicus* Freudenthal, 1967 (Rodentia, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). Preliminary results

Sílvia Jovells-Vaqué[1*], Montserrat Ginestí[1], Isaac Casanovas-Vilar[1]

[1]*Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain.
*corresponding author, e-mail: sjovellsv@gmail.com

Keywords: rodents, early Miocene, MN4, Iberian Peninsula

INTRODUCTION

The Vallès-Penedès Basin (Catalonia, Spain) is a classical area for the study of Miocene terrestrial faunas of Western Europe. However, its early Miocene record has been little studied in comparison to the middle and late Miocene ones. The early Miocene record of the basin comprises part of the Ramblian (MN3) and the early Aragonian (MN4) mammal ages which are represented by relatively poor sites, with the notable exception of els Casots (Casanovas-Vilar et al., 2016). This site was discovered in the late 1980s, it is located in the town of Subirats and corresponds to a small lacustrine system of early Miocene age (Casanovas-Vilar et al., 2011). After successive field campaigns between 1989 and 1994 an exceptionally rich vertebrate fauna was recovered, with some notably complete specimens corresponding to partial skeletons of several taxa (Casanovas-Vilar et al., 2011). While part of the large mammal fauna has been already described, the small mammals were only briefly presented by Agustí & Llenas (1993) and just the sciurid rodents have been formally described (Aldana, 1992). The rodent fauna allows for a tentative correlation to the Calatayud-Montalbán Basin (Aragón) zone C (Agustí & Llenas, 1993; Casanovas-Vilar et al., 2011, 2016; Jovells-Vaqué, 2016; Jovells-Vaqué et al., in prep.), corresponding to the upper part of the mammal zone MN4 (Van der Meulen et al., 2012). In this work, we provide a description of the recovered cranial material of the cricetid rodent *Democricetodon hispanicus*, which has been previously identified at the site on the basis of isolated cheek teeth (Agustí & Llenas, 1993; Jovells-Vaqué et al., in prep.). All the studied material is housed in the Institut Català de Paleontologia Miquel Crusafont at Sabadell (Barcelona, Spain).

Jovells-Vaqué et al., 2017

DESCRIPTION

Material and measurements: a dorsal half of the cranium and part of the rostrum (IPS 30527), a block of sediment containing a partial cranium, mandibles and postcranial material in close spatial proximity and therefore attributed to the same individual (IPS 100123). Cheek teeth measurements for IPS 100123 are provided in Table 1. The specimens are crushed due to diagenesis but are not deformed.

	M1e	M2e	M3e	M1d	M2d	M3d	m1d	m2d	m1e	m2e	m3e
Length	1.74	1.11	0.73	1.70	1.21	0.77	1.41	1.12	1.34	1.12	1.07
Width	1.10	1.14	0.92	1.07	1.11	0.86	-	-	-	-	-

Table 1. Cheek teeth measurements for IPS 100123. All measurements are in millimeters.

Cranial and postcranial material: IPS 100123 (Fig.1A) includes a partial cranium, seen in ventral view, with the rostrum and complete palate and cheek teeth that allow for a confident attribution to *D. hispanicus*. The upper incisors are ophistodont and not ornamented. The palate does not extend posteriorly from the M3. In addition, there are other cranial fragments corresponding to the crushed auditory bulla and probably to the palatines and pterygoid. The same block includes the two mandibles, which are slender and elongated. The articular process is directed backwards and projects more posteriorly than the angular one. The coronoid process is apparently lower than the articular one. The postcranial material included in the same block comprises two articulated proximal caudal vertebrae (and another isolated one); a partial radius; and a left calcaneus. In IPS 30527 (Fig.1B) only the dorsal half of the cranium and part of the rostrum can be observed. The rostrum is short and the zygomatic plate extends relatively dorsally. The plate is bounded by well-defined ridges and the infraorbital foramen is keyhole shaped. The origin of the medial masseter muscle extends into the side of the rostrum. The zygomatic plate of *Democricetodon* characteristically extends far dorsally than in other contemporary cricetid genera, such as *Eumyarion* or *Megacricetodon* (see Flynn et al., 1985). The parietal does not present marked temporal ridges. The left zygomatic arch is complete and relatively slender. IPS 30527 is attributed to *D. hispanicus* on the basis of skull size and the derived morphology of the zygomatic plate, which can also be observed in IPS 100123. *Megacricetodon primitivus*, the other cricetid species present at the site, is smaller. Furthermore, the morphology of the zygomatic plate is different in the few skulls available of other *Megacricetodon* species (see Flynn et al., 1985 and references therein).

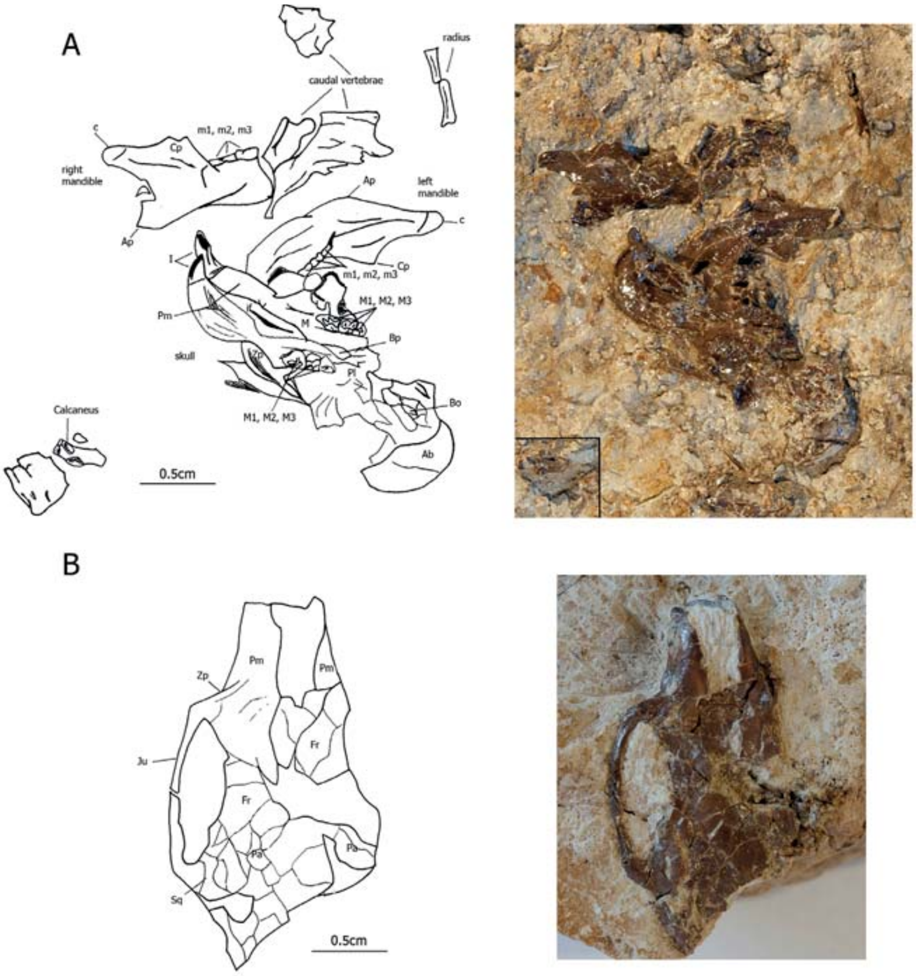


Figure 1. *Democricetodon hispanicus*. 1A: Plate with several bones attributed to the same individual (IPS 100123). An interpretative drawing is included left of the picture. Ab: auditory bulla; Ap: articular process; Bp: basisphenoid; Bo: basioccipital; C: articular condyle; Cp: coronoid process; I: incisive; if: incisive foramina; M: maxilla, M1, M2, M3: upper molars; m1, m2, m3: lower molars; Pm: premaxilla; Pl: palatine; Zp: zygomatic plate. 1B: Crushed cranium of (IPS 30527) and interpretative drawing at its left. Fr: frontal; Ju: jugal; Pa: parietal; Pm: premaxilla; Sq: squamosal; Zp: zygomatic plate.

DISCUSSION AND CONCLUSSIONS

Most fossil cricetids are only known from their isolated cheek teeth. Therefore, the materials recovered at els Casots offers a unique possibility of studying the cranial morphology of *Democricetodon hispanicus* and infer the relationships of this taxon with other genera. Our preliminary studies indicate that *Democricetodon* presents more advanced zygomasseteric morphology than contemporaneous cricetids, such as *Eumyarion, Megacricetodon* or *Cricetodon.* To this regard, it is more like cricetines, which show zygomatic plates that extend more dorsally and with narrower infraorbital foramina. Ongoing studies of the cranial morphology will help to clarify the phylogenetic position of this taxon.

ACKNOWLEDGEMENTS

This work was funded by the Spanish Ministerio de Economía y Competititvidad (CGL2014-54373-P, CGL2016-76431-P, RYC-2013-12470 to ICV), FI DGR–2017 pre-doctoral grant to SJV and CERCA Programme and 2014 SGR 416 GRC of the Generalitat de Catalunya. We also thank Ana Rosa Gómez Cano and Paloma López Guerrero for the comprehensive review of this article.

REFERENCES

Aldana, E.J. 1992. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España). *Treballs del Museu de Geologia de Barcelona,* 2:69-97.

Agustí, J. & Llenas, M. 1993. Los roedores del Mioceno inferior de els Casots (Vallès-Penedès). Nota preliminar. *Comunicaciones de las IX Jornadas de Paleontología,* 70-72.

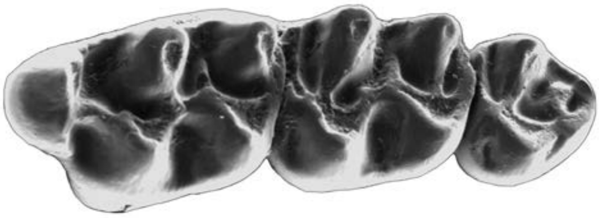
Casanovas-Vilar, I.; Alba, DM.; Moyà-Solà, S. 2011. Parada1. Panorámica general de la Cuenca y Yaciemiento de Casots (Subirats): Una fauna de Vertebrados del Aragoniense inferior. *Paleontologia i Evolució, Memòria Especial,* 6: 81-88.

Casanovas-Vilar, I.; Madern, A.; Alba, DM.; Cabrera, L.; Garcia-Paredes, I.; Van den Hoek Ostende, LW.; DeMiguel, D.; Robles, JM.; Furió, M.; Van Dam, JA.; Garces, M.; Angelone, C.; Moya-Sola, S. 2016. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). *Comtes Rendus Palevol,* 15: 791-812.

Flynn, L.J.; Jacobs, L.L.; Lindsay, E.H. 1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In: Luckett WP. & Hartenberger JL. (Eds.), Evolutionary Relationships Among Rodents: A Multidiciplinary Analysis. Plenum Press, New York, 589-616.

Jovells-Vaqué, S. 2016. Early Miocene cricetids (Rodentia) from les Cases de la Valenciana (Vallès-Penedès Basin, Catalonia). Universitat de Barcelona, Barcelona, 60 pp.

Van der Meulen, A.J.; García-Paredes, I.; Álvarez-Sierra, M.A.; Van den Hoek Ostende, L.W.; Hordijk, K.; Oliver, A.; Peláez-Campomanes, P. 2012. Updated Aragonian biostratigraphy: Small Mammal Distribution and its implications for the Miocene European Chronology. *Geologica Acta,* 10: 159-179.



Chapter 9: “Dispersal and early evoultion of the first modern cricetid rodents in Western Europe: new data from the Vallès-Penedès Basin (Catalonia).”

Compte Rendus Palevol

Acepted: April 2020

Dispersal and early evolution of the first modern cricetid rodents in Western Europe: new data from the Vallès-Penedès Basin (Catalonia)

Dispersion et évolution initiale des premiers rongeurs cricétidés modernes en Europe occidentale: nouvelles données du Bassin du Vallès-Penedès (Catalogne)

Sílvia Jovells-Vaqué[1] & Isaac Casanovas-Vilar[1*]

[1]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, C/de les Columnes, s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain, silvia.jovells@icp.cat; isaac.casanovas@icp.cat.

Abstract

Modern cricetids originated in Asia and dispersed into Western Europe by the end of the early Miocene, where they quickly became major components of the rodent faunas. Here we review the early Miocene rodent record of the genera *Democricetodon* and *Megacricetodon* in the Vallès-Penedès Basin (Catalonia, Spain). *Democricetodon* is represented by four species in the studied sites (*D. hispanicus*, *D.* cf. *decipiens*, *D. gracilis* and a large-sized undetermined species) and *Megacricetodon* by one (*M. primitivus*).The cricetid succession bears several similarities with that of the nearby Calatayud-Montalbán Basin (east-central Spain) to the point that the same detailed local biostratigraphy could be extended to the Catalan basin. The rare presence of certain *Democricetodon* species (*D. gracilis*) and other small mammal taxa also reveal affinities with regions beyond the Iberian Peninsula and indicate that the Vallès-Penedès Basin was more humid and forested than inland Iberian basins during the early Miocene.

Résumé

Les cricétidés modernes sont originaires d'Asie et se sont dispersés en l'Europe occidentale à la fin du Miocène inférieur. Nous passons ici en revue les enregistrements du Miocène inférieur des genres *Democricetodon* et *Megacricetodon* du bassin du Vallès-Penedès (Catalogne, Espagne). *Démocricétodon* est représenté par quatre espèces (*D. hispanicus, D. cf. decipiens, D. gracilis* et une espèce indéterminée de grande taille) et *Megacricetodon* par une (*M. primitivus*). La succession de cricétides présente plusieurs similarités avec celle du bassin voisin de Calatayud-Montalbán (centre-est de l'Espagne) à tel point que la même biostratigraphie locale détaillée pourrait être étendue au bassin catalan. La rare présence de certaines espèces de *Democricetodon* (*D. gracilis*) ainsi que celle d'autres taxons de petits mammifères montrent également des affinités avec régions au-delà de la Péninsule Ibérique et indique que le bassin du Vallès-Penedès était plus humide et boisé que les bassins ibériques intérieurs au Miocène inférieur.

Keywords: *Democricetodon, Megacricetodon,* early Miocene, Iberian Peninsula, Biostratigraphy, Western Europe

Mots clés: *Democricetodon, Megacricetodon,* Miocène inférieur, Péninsule Ibérique, Biostratigraphie, Europe occidentale

1. Introduction

The cricetids *Democricetodon* (Fahlbusch, 1964) and *Megacricetodon* (Fahlbusch, 1964) are major components of the early and middle Miocene rodent faunas of Eurasia, to the point that one or two species of these cricetids may account for more than 90% of the recovered rodent remains in some sites (e.g. Daams and Freudenthal, 1988). Both are incredibly diverse, each one comprising more than 30 recognized species with a relatively limited stratigraphic and geographic range. In turn, these species define multiple independent lineages characterized by marked temporal changes in size and morphology. Therefore, it is not surprising that these cricetids have been widely used in biostratigraphy and biochronology. Indeed, the first appearance and evolution of different *Democricetodon* and *Megacricetodon* species in combination with other rodent taxa is used to define most of the local biozones for the early and middle Miocene in several European regions (Abdul Aziz et al., 2008, 2010; Casanovas-Vilar et al., 2016a; Daams et al., 1999; Kälin and Kempf, 2009; Prieto and Rummel, 2016; Van der Meulen et al., 2012). On the other hand, they also play an important role in continental biochronology, the first appearance of these genera (as well as that of certain widely dispersed species) marking the boundaries between higher-ranking biochronological units, such as mammal ages in China (Qiu et al., 2013) and MN (Mammal Neogene) zones in Europe (Agustí et al., 2001; Hilgen et al., 2012; Mein, 1999).

Democricetodon and *Megacricetodon* are two of the first genera commonly referred to as 'modern cricetids' (see comments on classification in section 3.1.) to distinguish them from older muroid taxa that had characterized the Oligocene faunas of Eurasia (e.g., the genera *Eucricetodon*, *Pseudocricetodon* and *Melissiodon*). Modern cricetids, namely the genera *Spanocricetodon* and *Primus*, first appear simultaneously in Anatolia and Pakistan, respectively, by the latest Oligocene (Theocharopoulos, 2000).

The oldest *Democricetodon* are recorded slightly later, by the earliest Miocene (ca. 22 Ma) from Anatolia, Pakistan and China (Flynn et al., 2013; Flynn and Wessels, 2013; Maridet et al., 2011; Meng et al., 2003). On the other hand, *Megacricetodon* is also first recorded from the early Miocene (ca. 19-17 Ma) of Anatolia (Wessels et al., 2001). In Western Europe, part of the early Miocene (MN3, from about 19.5 to 17 Ma) is devoid of cricetids because of the extinction of all the Oligocene taxa, except for the rare occurrence of *Melissiodon*. This interval, called the 'cricetid vacuum', comes to an abrupt end with de dispersal of the modern cricetids *Democricetodon* and *Megacricetodon* (Daams and Freudenthal, 1989). *Democricetodon* is already recorded during the late MN3 (17 Ma) in the Calatayud-Montalbán Basin of east-central Spain, where it occurs in low numbers (Van der Meulen et al., 2003, 2012). The first common occurrence of this genus is used to define the lower boundary of biozone MN4 (Agustí et al., 2001; Hilgen et al., 2012). In its turn, *Megacricetodon* is recorded slightly later in Western Europe, its first occurrences corresponding to MN4 sites from Greece, the Czech Republic, Switzerland, France and Spain (for an updated review see Oliver and Pélaez Campomanes, 2016). From then on, both genera diversify in the different geographic regions and become characteristic of the middle Miocene faunas.

Early modern cricetid faunas have been particularly well studied in the Calatayud-Montalbán Basin of Spain, where they are very well represented (Daams and Freudenthal, 1988; Freudenthal and Daams, 1988; Oliver Pérez, 2015; Oliver and Peláez-Campomanes, 2014, 2016; Van der Meulen et al., 2003). These genera are also common in other Iberian basins, including the Foia de Bunyol (Adrover et al., 1987; Daams and Freudenthal, 1974) or the Riu Magre Basin (Ruiz-Sánchez et al., 2003), both in Valencia, or the Ebro Basin (Ruiz-Sánchez et al., 2003; Suárez-Hernando, 2017). However, these include relatively few fossil sites and the recovered material of the earliest modern cricetids is generally scarce. The coastal Vallès-Penedès Basin, located in Catalonia, northeast Spain comprises a rich record covering most of the Miocene (Casanovas-Vilar et al., 2016b). Until recently, the early Miocene successions of this area had been little studied in comparison to middle and late Miocene ones, yet these included a handful of remarkable sites. However, recent survey and sampling campaigns have focused on the early Miocene part of the record, resulting in the recovery of rich fossil microvertebrate samples from 'classical' and newly-discovered localities. About 30 sites are known to date, and these have delivered more than 2,000 identifiable rodent cheek teeth. Only a small part of this material has been described and biostratigraphical studies are now in course. Cricetids are common in almost all sites and deserve special attention because of their biostratigraphical implications. Detailed descriptions of the cricetid fauna of Can Martí

Vell (Agustí, 1983), Les Cases de la Valenciana (Jovells-Vaqué et al., 2018) and els Casots (Jovells-Vaqué et al., 2017) sites have been published, as well as a review of the genus *Melissiodon* (Jovells-Vaqué and Casanovas-Vilar, 2018). However, most of the cricetid material had not been studied yet. Here we identify and describe all the early Miocene material belonging to the genera *Democricetodon* and *Megacricetodon*. This allows for a refined biostratigraphical correlation of the studied localities based on high-resolution local zonations defined for other Iberian basins. Finally, the occurrence of certain species with Central European affinities and their paleobiogeographical implications are also discussed.

2. Geological setting and age

The record of the Vallès-Penedès Basin (Barcelona, Catalonia) covers most of the Miocene, ranging from the Ramblian (ca. 20 Ma) to the middle Turolian (ca. 7 Ma) European land mammal ages (Casanovas-Vilar et al., 2016b). This basin is an elongated half-graben parallel to the coastline bounded by the Catalan Littoral Ranges (Fig. 1) that was formed in the context of the opening of the northwestern Mediterranean during the late Oligocene (Cabrera and Calvet, 1996; Roca et al., 1999; Cabrera et al., 2004). Major features of the stratigraphic record of the Vallès-Penedès were controlled by tectonic activity of the main limiting faults and sea level changes in the western Mediterranean. The sediment infill of the basin is mostly continental, except for brief episodes of marine transgression that occurred during the latest early Miocene and the beginning of the middle Miocene. The studied material was recovered from early and early middle Miocene localities that have been dated by means of litho- and biostratigraphy (Agustí, 1982; Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016b).

The early Miocene record of the Vallès-Penedès starts at the Ramblian, biozone MN3 (ca. 19.5-17.2 Ma). Ramblian sites correspond to the so-called ‘cricetid vacuum’ (Daams and Freudenthal, 1989) and do not include cricetids other than *Melissiodon* (Casanovas-Vilar et al., 2011, 2016b; Jovells-Vaqué and Casanovas-Vilar, 2018). The oldest sites recording the modern cricetids *Democricetodon* and *Megacricetodon* are correlated to the early Aragonian, biozone MN4 (Casanovas-Vilar et al., 2011, 2016b; Jovells-Vaqué et al., 2017, 2018). These belong to the Lower Continental Units, a lithostratigraphical formation that crops out near the southern margin of the basin (Fig. 1). These units consist of intensely red alluvial fan facies sourced from the surrounding reliefs as well as occasional shallow lake deposits consisting of carbonates, evaporites, carbons and mostly greyish to greenish lutites (Cabrera, 1979, 1981, Cabrera et al., 1991; Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016b; de Gibert and Casanovas-Vilar, 2011). Lake deposits include the richest early Miocene fossil sites in the basin (Fig. 2). The Subirats lacustrine unit, extending a few kilometers between the towns of Subirats and Gelida (Agustí and Cabrera, 1980; Cabrera 1979, 1981; Cabrera et al., 1991; Casanovas-Vilar et al., 2011; Jovells-Vaqué et al., 2017, 2018) includes the localities of Les Cases de la Valenciana, Can Martí Vell (levels 1 to 3) and Els Casots (levels 72, 73 and 74). Each one of these levels has delivered more than 150 identifiable rodent teeth, about half of them cricetids. At Els Casots area the Subirats lacustrine unit lies directly on top of the pre-Miocene basement of the basin, there consisting of Cretaceous carbonates (Fig. 1). The nearby site of Cal Sutxet corresponds to a yellowish lutite layer which occasionally includes sharp boulders eroded from the basement. Other sites belonging to the Lower Continental Complexes include, el Canyet, Sant Mamet and Les Escletxes del Papiol, which are all located in the distal, mudstone-dominated facies of alluvial fan systems sourced from the southern reliefs (Fig. 2).

Between 17 and 15 Ma several sea level changes took place in the context of the Mid-Miocene Climatic Optimum (Zachos et al., 2001) and, since the southwestern basin end was open to the sea, the Vallès-Penedès was flooded repeatedly. At least three episodes of marine transgression and regression are recorded: late Burdigalian, Langhian and early Serravallian (Cabrera et al., 1991; Cabrera and Calvet, 1996; Casanovas-Vilar et al., 2016b; de Gibert and Casanovas-Vilar, 2011). The sequences deposited at this time define the Marine and Transitional Units (Fig. 2). Sediments corresponding to the oldest late Burdigalian (latest early Miocene) transgression only crop out in the Penedès sector of the basin, where they define the Vilobí evaporitic unit (Fig. 2). This consists of gypsum which was deposited in coastal playa lakes (sabkha) as well as littoral sandstones and lutites (Agustí et al., 1990; Magné, 1978; Ortí and Pueyo, 1976). The Vilobí del Penedès fossil site is particularly rich, having delivered more than 300 identifiable rodent specimens, and is located in a terrigenous coquina full of large-sized ostreids (*Crassostrea gryphoides*) which presumably indicate bay deposits (Casanovas-Vilar et al., 2019). The Langhian (beginning of the middle Miocene) transgression is the best represented marine episode. At that time, marine environments extended up to the Vallès sector, with the development of shallow marine and transitional deposits (Figs. 1–2). On the other hand, carbonate coralgal shelf deposits (including minor fringing reefs), marine bay and transitional fan-delta siliciclastic systems persistently occupied the Penedès sector, directly connected to the sea (Cabrera et al., 1991; Cabrera and Calvet, 1996; Casanovas-Vilar et al., 2016b; de Gibert and Casanovas-Vilar, 2011). In the Vallès sector, the sites of Riera del Morral and Can Cabanes W are both located in transitional Langhian deposits associated with marine invertebrates and ichnofauna (Fig. 2; de Gibert and Robles, 2005; Casanovas-Vilar and Jovells-Vaqué, 2017). Finally, Les Escletxes del Papiol and Sant Mamet sites, also in the Vallès sector, are located just a few meters below Langhian marine deposits, but still placed in distal alluvial fan facies belonging to the Lower Continental Units (Fig. 2; Agustí et al., 1985; Casanovas-Vilar et al., 2011, 2016b). Detailed lithostratigraphical data, as well as associated faunal data, allow for a confident stratigraphical succession of the studied localities which is further reinforced by biostratigraphical results (Fig. 2; see also section 5.1.). However, the age of these sites will be surely refined after ongoing magnetostratigraphical studies.

3. Material, methods and abbreviations

The described material is housed at the Institut Català de Paleontologia Miquel Crusafont in Sabadell (Barcelona, Spain) and the Museu de Ciències Naturals de Barcelona (MGB). Collection numbers are given in the main text as well as for figured specimens. Almost all the material was recovered after systematic screen-washing campaigns during the early 1990s (Els Casots, Vilobí del Penedès, Les Escletxes del Papiol) and between 2011 and 2017 (Les Cases de la Valenciana, Can Martí Vell, Cal Sutxet, Sant Mamet, Can Cabanes W, Riera del Morral 1). Agustí (1983) collected a remarkably rich sample from Can Martí Vell, but this material could not be found within the MGB collections. The rich sample recovered during the 2015 field campaign at this site is described instead. Similarly, Agustí (1981) described a few *Megacricetodon primitivus* specimens from Can Julià 6, a nearby classical site already reported in Crusafont et al. (1955), which we could not find within the ICP collections. The material from old collections, including the specimens from El Canyet as well as some from Sant Mamet, probably derives from surface surveys. Dental terminology follows Oliver and Peláez-Campomanes (2013), whereas measurement method is after Daams and Freudenthal (1988: 42, Fig. 1). Morphotype coding follows Van der Meulen et al. (2003) and Maridet (2003) for *Democricetodon* and Oliver and Peláez-Campomanes (2013) for *Megacricetodon* with slight modifications. All measurements are given in millimeters and were taken with an optical micrometer to the nearest 0.01 mm. Estimated measurements (because of minor damage or distortion) are between brackets, whereas “>” indicates that the measurement cannot be confidently taken but certainly exceeded the reported value. Summary statistics and scatterplots were performed using the R software (R Core Team, 2017). MN zone definitions for Western Europe follow Agustí et al. (2001), whereas age boundaries are as defined in Hilgen et al. (2012).

3.1. Classification of the cricetids

The contents and definition of the cricetid family are a matter of debate. McKenna and Bell (1997) ranked cricetids as a mere subfamily within the huge Muridae family, but most classifications upgrade the Cricetidae to the family rank (e.g., D'Elía et al., 2019; Fabre et al., 2012, 2015; Hartenberger, 1998; Steppan et al., 2004; Steppan and Schenk, 2017; Wilson and Reeder, 2005). Recent molecular phylogenetic analyses recognize the Cricetidae as a distinct family from the Muridae, both being part of the larger Muroidea superfamily (Fabre et al., 2012, 2015; Steppan et al., 2004; Steppan and Schenk, 2017). The Cricetidae include the extant hamsters (Cricetinae), voles and lemmings (Arvicolinae) as well as the three subfamilies of New World rats and mice (Neotominae, Sigmodontinae and Tylominae; Fabre et al., 2012, 2015; Steppan et al., 2004; Steppan and Schenk, 2017). Other muroid groups (e.g., Nesomyidae, Spalacidae, Platacanthomyidae) that had been included within the cricetids are now considered separate families. The phylogenetic relationships of most extinct genera are uncertain, and even their ascription to the Cricetidae is questionable, specially for older forms which might be as closely related to extant cricetids as they are to other muroid families. As far as the genera *Democricetodon* and *Megacricetodon* are concerned, these are generally considered to be closer to extant cricetids (Flynn, 1985; Kälin, 1999; Lindsay, 2008). *Democricetodon* in particular has been related to extant cricetines and is generally placed in a subfamily within the cricetids (the Democricetinae) together with the closely-related North American genus (or subgenus) *Copemys* (Lindsay, 2008). On the other hand, *Megacricetodon* is generally considered to be closer to the Muridae (including murines, gerbillines and other minor extant subfamilies) since its dental morphology resembles that of early murids such as *Potwarmus* and *Antemus* (Jacobs, 1977; Jacobs and Downs, 1994; Flynn, 1985; Lindsay, 1988). *Megacricetodon* is sometimes included within a separate subfamily (Megacricetodontinae; e.g., Lindsay, 1988, 2008; Wessels et al., 2001; Wessels, 2009) that may form a monophyletic clade with the Muridae (Flynn, 1985). In any case, most authors agree in including both generea within the cricetids in a broad sense. This is the classification scheme followed here, although we acknowledge that *Megacricetodon* may be closer to murids.

3.2. Abbreviations

Institutional Abbreviations. IPS, Institut de Paleontologia de Sabadell (now ICP, Institut Català de Paleontologia Miquel Crusafont), Sabadell, Spain; MGB, Museu de Geologia de Barcelona (now Museu de Ciències Naturals de Barcelona), Barcelona, Spain, 'V' preceding collection number indicates that the specimen belongs to the Villalta Collection, donated to the museum in the 1980s.

Measurement Abbreviations. L, anteroposterior length; W, labiolingual width.

Locality Abbreviations. CB, Costablanca; CCW, Can Cabanes W; CJ, Can Julià; CMV1, Can Martí Vell – level 1; CMV2, Can Martí Vell – level 2; CMV3, Can Martí Vell – level 3; CS72, els Casots – level 72; CS73, els Casots – level 73; CS74, els Casots – level 74; CSU, Cal Sutxet; EC, El Canyet; LCV, Les Cases de la Valenciana – level 1 (classical site); MC, Molí de Can Calopa; MOR1, Riera del Morral – level 1; PA, Les Escletxes del Papiol; SAB1, Sant Andreu de la Barca – level 1; SM, Sant Mamet – level 1; TFR1, Turó de les Forques – level 1; VI, Vilobí del Penedès.

Other Abbreviations. MN, European Mammal Neogene zones.

4. Systematic paleontology

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer von Waldheim, 1817

Genus *Democricetodon* Fahlbusch, 1964

Democricetodon hispanicus Freudenthal, 1967

A catalog of the studied material and measurements is given in Appendix A. See Tables 1-6 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix B.

Description:

M1 (Fig. 4A, B): All studied specimens have a simple anterocone, except one from CS74 in which this cusp is slightly subdivided (IPS45001 from CS74). The arms of the anteroloph are well developed and close the anterior valleys. The anterolophule is simple and placed somewhat lingually. However, IPS45002 from CS74 shows a forked anterolophule with both arms reaching the anterocone. The protosinus is relatively reduced. The protolophule normally consists of a single posterior arm that joins the entoloph behind the protocone, but it may also be double with a better-developed anterior arm (Appendix B, Table 3). In IPS45008 from CS74 (Fig. 4A), the anterior arm is interrupted before reaching the paracone. In some specimens, there is a short ectoloph on the paracone. The mesoloph varies from short to long in all the studied specimens (Appendix B, Table 5), however this ridge is most commonly long (LCV1, CMV3) or of medium length (CS74). The metalophule consists of a posterior arm only that connects the metacone with the posteroloph just behind the hypocone. In one specimen, V7846 from el Canyet, the metalophule is double with an anterior arm merging the entoloph anteriorly to the hypocone. In IPS19491 from CS74 the metalophule is completely absent. The posterosinus is highly reduced and closed by the posteroloph. The sinus is closed by a well-developed cingulum originating from the hypocone in all studied specimens.

M2 (Fig. 4A, B): The anteroloph shows a long and high labial arm that closes the narrow anterosinus. The protosinus is vestigial and is also closed by a much lower lingual arm of the anteroloph. The protolophule generally consists of an anterior arm and a posterior one (Appendix B, Table 7). The latter merges the entoloph posteriorly to the protocone in most cases, however, in a few specimens the posterior arm of the protolophule is incomplete (for example in IPS45008 and IPS19491 from CS74, Fig. 4A, B), being interrupted before merging with the paracone.The ectoloph on the paracone is variable being present or absent (Appendix B, Table 8). When present, the ectoloph does not merge with the mesoloph. The length of the mesoloph ranges from long to short but is more commonly long (Appendix B, Table 9). The sinus is transverse and closed by a cingulum originating from the hypocone. The metalophule is short and simple, joining the entoloph anteriorly to the hypocone. However, in V7846 from EC the metalophule is simple and transverse to the hypocone, and in IPS19475 from CS74 it is double with similarly well-developed anterior and posterior arms. The posteroloph closes the posterosinus, while the mesosinus is closed by a low cingulum.

M3 (Fig. 4A): The anterosinus is almost closed by the well developed labial arm of the anteroloph in all the studied specimens. There is no trace of the protosinus and the lingual anteroloph is reduced to just a tiny lingual cingulum. The protolophule is simple and connects with the anterior part of the paracone. There is no mesoloph and the metalophule is simple and short. The posteroloph is well developed and closes the very narrow posterosinus. The metacone is reduced and can be slightly displaced to the lingual side (e.g., IPS45008, Fig. 4A). The mesosinus is closed by a thin low ridge continuous with the posteroloph. The sinus is highly reduced, transverse and narrow, being closed by a low cingulum descending from the hypocone.

m1 (Fig. 4C): The anteroconid is simple and rounded. The anterior valleys are closed in some specimens from CS72 and CS74 (e.g., IPS19481, Fig. 4C) by the arms of the anterolophid, which are quite low. The mesolophid is variable in length, ranging from short to long, although a medium-length mesolophid is most common. The sinusid is wide and generally points forwards, although it may be transverse in a few specimens. The sinusid is closed by a low cingulum. The mesosinusid is more often open except in one specimen from CMV1 (IPS96841) in which it is closed by the metaconid ridge (Appendix B. Table 13). The hypolophulid is short and merges with the entolophid anteriorly to the hypoconid. The metalophulid, is absent in IPS19481 from CS74 (Fig.4C). In the other specimens, the metalophulid is very short and may be either transverse or slightly anterior to the protoconid. The posterolophid closes the posterosinusid, reaching the posterior wall of the entoconid.

m2 (Fig. 4D): The lingual anterolophid and the anterosinusid are reduced so that they completely disappear with moderate dental wear, as in IPS86281 from CSU. The protosinusid is closed by the labial arm of the anterolophid. The mesolophid is highly variable, ranging from short to long but also being frequently absent (Appendix B, Table 17). In all the remaining morphological features the m2 resemble the m1.

m3 (Fig. 4E): The anterior valleys are very reduced to the point that in some specimens the lingual arm of the anterolophid is vestigial, the anterosinusid thus being absent. The metaconid connects with the anterolophid by means of an extremely short metalophulid. The mesolophid is absent in all the specimens. The entoconid is highly reduced being integrated into the hypolophulid. The sinusid is posteriorly directed. This valley is generally open in the CS74 specimens as well as in IPS85740 from CCW while in those from LCV and CMV3 it is closed by a low cingulid. The posterosinusid is reduced and completely closed by the posterolophid which is very high. The mesosinusid is also closed by a high ridge departing from the posterior wall of the metaconid.

Comparisons and remarks:

The Vallès-Penedès specimens fit within the size and morphological range of *Democricetodon hispanicus* (see Van Der Meulen et al., 2003) being remarkably similar to the material from the type locality, Villafeliche 2A (Calatayud-Montalbán Basin, Aragon, Spain; Freudenthal,1967). This species is distinguished from the chronologically and geographically close species *Democricetodon decipiens* (Freudenthal and Daams, 1988), *Democricetodon franconicus* Fahlbusch, 1966 and *Democricetodon koenigswaldi* (Freudenthal, 1963) by its smaller size (Van der Meulen et al., 2003). The Vallès-Penedès samples (particularly the youngest ones such as CS73 and CS74) overlap with upper size range of *D. hispanicus*, with a few specimens, generally M2 and m2 being larger, well within the size range of *D. decipiens* (Fig.3, Appendix A). However, these specimens can be distinguished from *D. decipiens* by the development of mesolophs and mesolophids, which are always longer in *D. hispanicus* (Van der Meulen et al., 2003). Besides its smaller size, *D. hispanicus* further differs from *D. koenigswaldi* by its less developed metalophule on the M2 (Van der Meulen et al., 2003). In *D. koenigswaldi* the metalophule is frenquently double or merges the entoloph posterior to the hypocone, whereas in the studied specimens this ridge is generally simple and merges the entoloph anterior to the hypocone. Similarly, the protolophule is predominantly double in *D. koenigswaldi*, and although double protolophules occur in *D. hispanicus*, simple ones are almost equally common (Van der Meulen et al., 2003; see also Appendix B, Tables 3 and 7). The described specimens show all these diagnostic features that unambiguously indicate an ascription to *D. hispanicus*, which would be the first *Democricetodon* species to be recorded in the basin.

Several of the morphological trends that have been described for the Calatayud-Montalbán material (Van der Meulen et al., 2003) can also be recognized in the Vallès-Penedès. In the upper molars simple protolophules become more common in younger samples, such as CS74 (see Appendix B, Tables 3 and 7). Similarly, the spur on the paracone is more frequent in these sites. The mesoloph is predominantly long in the older sites, whereas in younger ones we may also find medium-sized and short mesolophs (Appendix B, Tables 5 and 9). Compared to the upper molars the mesolophids are always more reduced than the mesolophs, particularly for the m2. In the younger sites (CS74, CCW, SM) the mesolophid is predominantly short or absent on the m2 and short to medium-length on the m1. The only remarkable differences with the Calatayud-Montalbán samples include the slightly larger size of some Vallès-Penedès specimens and the higher occurrence of double protolophules on the M2. In the Calatayud-Montalbán basin, double protolophules occur in a maximum of 25 % of the specimens (Villafeliche 2A; see Freudenthal and Daams, 1988; Van der Meulen et al., 2003), whereas in the Vallès-Penedès material they predominate (Appendix B, Tables 3 and 7). Another morphological feature that only occurs in the Vallès-Penedès is the presence of forked anterolophules, which occur in one specimen from LV1 and another one from CS74. Agustí (1981, 1983) already noted some of these features regardigng the CMV and EC specimens, particularly stressing the larger size and shorter mesolophids, and he ascribed the material to *D.* aff. *hispanicus.* Similarly, Agustí and Llenas (1993) also ascribed the material of CS73 and CS74 to *D.* aff.

hispanicus. These authors only compared the described specimens to those of Villafeliche 2A (Calatayud-Montalbán Basin), the type locality of this species (Freudenthal, 1967). Villafeliche 2A is correlated to local subzone B (estimated age 16.63 Ma; Van der Meulen et al., 2012), thus being somewhat older than the Vallès-Penedès sites. Considering the evolutionary trends towards size increase and reduction of mesolophs/ids within the *D. hispanicus*–*D. lacombai* lineage, these differences could well be explained by the younger age of the Vallès-Penedès specimens. Indeed, when the whole intraspecific variation is taken into account (and not that existing in just one site), the described material perfectly agrees with size variation in *D. hispanicus*, although being close to the upper boundary. As far as the development of the mesolophid is concerned, medium length and short mesolophids generally predominate in most *D. hispanicus* from the Calatayud-Montalbán sites (see Van der Meulen et al., 2003).

Democricetodon gracilis Fahlbusch, 1964

A catalog of the studied material and measurements is given in Appendix A. See Table 1-6 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix B.

Description:

M1 (Fig. 4F): The anterocone is simple in the two specimens from SM (IPS10342 and IPS103751). The protolophule is always double. Both arms of the protolophule reach the paracone, but the anterior arm is equally developed or is thinner than the posterior and weakly reaches the paracone (Fig. 4F, Appendix B, Table 3). The anterosinusid is closed by the labial anteroloph. On the contrary, the low lingual anteroloph does not reach the protocone, resulting in an open protosinus. The anterolophule is simple. The paracone shows a very short posterior ectoloph in the two specimens. The mesoloph is long, but it does not reach the labial margin of the teeth (Appendix B, Table 5). The mesosinus is closed by a low cingulum. The metalophule is simple and merges the entoloph posterior to the hypocone. The sinus is transverse and closed by a low and arched cingulum originating from the hypocone.

M2 (Fig. 4G): Two specimens have been recovered from SM (IPS103752 and IPS103753). The labial anteroloph is well developed whereas the lingual one is vestigial. The protosinus is also vestigial. In one specimen the protolophule is double (IPS103753, Fig. 4G), whereas in the other one it is simple and transverse (IPS103752, Appendix B, Table 7). Both molars show a very short ectoloph on the paracone. The mesoloph is long but not reaching the labial margin of the teeth in any of the studied specimens. The metalophule is simple and anterior to the hypocone in the specimen IPS103752, and it is not observable in IPS103753, Fig.4G), likely because it was very low and this area is covered with encrusted sediment.

m1 (Fig. 4H): The anteroconid and the anterior region of the molar is reduced. The anteroconid is simple and round. The arms of the anterolophid are thin and long, closing the anterior valleys. The metalophulid is simple and very short, merging with the anterolophulid anterior to the protoconid. The anterolophulid is generally low where it joins the metalophulid and the protoconid. The mesolophid is very long and reaches the lingual margin of the tooth, sometimes merging with a very low cingulid (Appendix B, Table 14). The sinusid points slightly forward and is closed by a low cingulid descending from the protoconid. The mesosinusid is enclosed by a cingulid in the SM specimen IPS103754 (Fig. 4H) whereas for CS73 and VI it is open. The hypolophulid is simple and merges with the entolophid just anterior to the hypoconid. The posterolophid is thin and long, it reaches the base of the entoconid and closes the posterosinusid.

m2 (Fig. 4I): The anterior valleys of the teeth are very narrow and closed by the arms of the anterolophid (Appendix B, Table 15). The sinusid, which points slightly forward, and the mesosinusid are closed by low cingulids. In the CCW specimen (IPS85738) the mesolophid is of medium length and merges with the entoconid. In the other specimen this ridge is also medium length, but it does not merge with the entoconid (Appendix B, Table 17). All the remaining morphological features are analogous to those described for the m1.

m3(Fig. 4J): The mesolophid is absent. The sinusid is transverse and closed by a low cingulid. The posterosinus is closed by a very high posterolophid that merges with the reduced entoconid. The mesosinusid is closed by a low cingulid (e.g. IPS105145 from SM, Fig. 4J). All other morphological features are analogous to those described for the m1 and m2.

Comparisons and remarks:

A few specimens of small size evidence the presence of a second *Democricetodon* species in SM and VI, where it coexists with *D.* cf. *decipiens* (see below and Fig. 3). Similarly, a single m1 from CS73 stands out for its small size, clearly smaller than *D. hispanicus* and much smaller than *Democricetodon* sp. from the same site (see Fig. 3). Finally, the *Democricetodon* specimens recovered at CCW, geographically and chronologically very close to SM, are of small-size, particularly the m2 and the m3. The recovered upper molars are further characterized by long mesolophs, the predominantly double protolophule on M1 and M2, and posterior metalophule on M1. The mesolophid is long in lower molars except m3, in which it is absent. The anteroconid region of the m1 is very short, particularly in the specimen from SM (IPS103754). The described specimens are smaller than all other *Democricetodon* species present at Western Europe at the time but *D. gracilis* (see Fahlbusch, 1964; Maridet, 2003; Wessels and Reumer, 2009). Furthermore, their morphology fits within the variation range of this species, which shows long mesolophs on M1 and medium length ones on the M2; a predominantly double protolophule on M2; a posterior metalophule on M1 and an anterior or transverse one on most M2; and a short anterior region of the m1 (Maridet, 2003; Wessels and Reumer, 2009). Nevertheless, there are a few differences. In the material of the type locality (Sandelzhausen, Germany, MN5) the mesolophids are predominantly of medium length or short on m1 and m2 and the protolophule is generally posterior on the M1, not partially double as in the specimens from SM (IPS103753). Agustí (1981) already ascribed a few specimens from SM to *D.* cf. *gracilis* and a few more to *D.* aff. *hispanicus*, further remarking that they certainly belonged to a smaller and more primitive species than the one present at EC and CMV (that he identified as *D.* aff. *hispanicus*, see above). Here we confirm the ascription of the small-sized specimens to *D. gracilis* further including those previously identified as *D.* aff. *hispanicus* and ascribe to this species material from the chronologically close sites (CS73, VI, CCW).

Democricetodon gracilis is known from Central Europe (Germany, Switzerland, Austria, Czech Republic; Maridet, 2003; Wessels and Reumer, 2009), France (Maridet, 2003) and Turkey (Theocharopoulos, 2000), but it is very rare in Spain. Indeed, this species had only been previously reported from two localities from the Bardenas Reales de Navarra (Ebro Basin): Loma Negra 64 and Pico del Fraile 2 (Suárez-Hernando, 2017). These two sites belong to the middle Aragonian (zone D) while magnetostratigraphical data indicate a correlation to chron C5Br, yielding an estimated age of 15.7–15.9 Ma (Suárez-Hernando, 2017). The Vallès-Penedès sites that have delivered *D. gracilis* are slightly older, belonging to the latest early Aragonian (subzone Cb; see below).

Democricetodon gracilis is distinguished from the similarly-aged *Democricetodon franconicus* by its smaller size and more reduced m1, amongst other morphological features (Maridet, 2003). In the Calatayud-Montalbán Basin *D. franconicus* is first recorded in sites from subzone Cb (late early Aragonian, MN4), which are about the same age as CS73, VI and SM (Van der Meulen et al., 2003, 2012). In that area, *D. franconicus* would give rise to an anagenetic lineage including (in chronological order)

D. koenigswaldi, *D. larteti* and *D. crusafonti* (Van der Meulen et al., 2003). *Democricetodon larteti* and *D. crusafonti* are common components of the late Aragonian (MN6, MN7+8) Vallès-Penedès faunas being index fossils for local biostratigraphy (Casanovas-Vilar et al. 2016a, b). While *D. koenigswaldi* might be present in some Vallès-Penedès sites (see section 4.4.), *D. franconicus*, the oldest member of this lineage, appears to be absent.

Democricetodon cf. *decipiens* (Freudenthal and Daams, 1988)

A catalog of the studied material and measurements is given in Appendix A. See Table 1-6 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix B.

Description:

M1 (Fig. 4K): The anterocone is simple in all studied specimens. The anterolophule is simple IPS19548 from VI (Fig. 4K) and forked in IPS19368 from SM, with both arms reaching the anterocone separately (Appendix B, Table 2). The protolophule is simple and merges with the entoloph posterior to the protocone. The ectoloph on the paracone is present in the SM specimen and absent in the VI one. The mesoloph is short, almost vestigial, and the metalophule is simple and posterior to the hypocone. All valleys are closed by low cingula.

M2 (Fig. 4L): The anterior valleys are narrow and closed by the well-developed arms of the anteroloph. The protolophule is double (Appendix B, Table 7). Nevertheless, in the VI specimens (Fig. 4L) the posterior arm is incomplete, being interrupted before reaching the paracone. In the same specimens the anterior arm is transverse and constricted at the point it merges with the paracone. The ectoloph on the paracone is absent. The mesoloph ranges from short to long, but it is more commonly of medium length. This ridge may be arched posteriorly as in IPS87106 from VI (Fig. 4L). The metalophule is posterior to the hypocone in all specimens but in IPS86386 from PA, which shows a transverse metalophule. The sinus is closed by a low cingulum.

M3 (Fig. 4M): Only two specimens have been recovered: IPS86941 and IPS87108 from VI. Both molars show well-developed anterolophs closing the anterior valleys. The protolophule is double with a better developed posterior arm. The mesoloph is either absent or fused with the posterior arm of the protolophule. The sinus is vestigial and closed by a low cingulum. Similarly, the posterosinus is also reduced to a tiny fossete and closed by the thick posteroloph. The metacone is undistinguishable and the mesosinus is closed by a high and thick ridge.

m1 (Fig. 4N): Only two complete specimens have been recovered: IPS87109 and IPS87110, both from VI. The anteroconid is simple and bean shaped. The labial anterolophid is well developed, thus closing the protosinusid (Appendix B, Table 11), while the anterosinusid is open because the lingual anterolophid does not reach the base of the metaconid. The mesolophid is of medium length in all studied specimens. The metalophulid and the hypolophulid are anterior to the protoconid and hypoconid, respectively. A cingulid descending from the metaconid partially closes the mesosinusid, but this valley remains open. The sinusid is proverse and closed by a low cingulid.

m2 (Fig. 4O): The molars are squared, being relatively wide. The lingual anterolophid is highly reduced in most of the studied specimens, thus resulting in very narrow anterosinusid. The mesolophid is either short (IPS86387 from PA, Fig. 4O) or absent (IPS87116 from VI). The metalophulid is simple and anterior as well as the hypolophulid. The remaining morphological features resemble those described for the m1 (see Appendix B Tables 11 – 14).

m3: Just IPS86388 from PA has been recovered. The anterosinusid is absent and the anterolophid presents only a labial arm, which is well developed and closes the protosinusid. The mesolophid is completely absent and the mesosinusid is closed by a ridge. The entoconid is barely distinguishable. The sinusid is transverse and closed by a low cingulid that originates from the protoconid and reaches the hypoconid.

Comparisons and remarks:

In the sites VI, PA and SM a *Democricetodon* species larger than *D. hispanicus* is present. However, the material in all these sites is very scarce, so species attribution is tentative. These specimens are distinguished not only by their larger dimensions but also by the more reduced mesoloph/ids as compared to *D. hispanicus* (Appendix B). In the studied specimens the mesoloph/ids are predominantly of medium length or short, whereas in *D. hispanicus* these ridges are more frequently long (Appendix B, Tables 14 and 17). Van der Meulen et al. (2003) reviewed the genus *Democricetodon* in the Calatayud-Montalbán Basin and recognized two different anagenetic lineages (but see Freudenthal, 2006 for a completely opposed view). *Democricetodon hispanicus* and *D. decipiens* are recognized as successive members of the same lineage. Later species in the same lineage are (in chronological order): *Democricetodon moralesi*, *Democricetodon jordensi* and *Democricetodon lacombai*. This lineage shows a set of anagenetic trends including: size increase, reduction of mesoloph/ids, loss of the anterior protolophule on upper molars, and presence of a forked anterolophule on the M1 (Van der Meulen et al., 2003). Many of these morphological features are observed in the studied specimens, particularly the M1. As far as size is concerned, the specimens fit within the size range of *D. decipiens*, being larger than *D. hispanicus* and at the same time smaller than *D. moralesi* or the similarly-aged *Democricetodon koenigswaldi*, which belongs to the second lineage (Van der Meulen et al., 2003) (Fig.3). However, the material is too scarce for a confident attribution to this species, so it is assigned to *D.* cf. *decipiens* until further specimens are recovered.

Democricetodon sp. 4

A catalog of the studied material and measurements is given in Appendix A. See Table 1-6 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix B.

Description:

M2 (Fig. 4P): Only a single M2 has been recovered, IPS88868 from MOR1 which is highly worn and slightly damaged on its labial margin. Both arms of the anteroloph are high and long and close the anterior valleys. The protolophule is double with both arms similarly well developed. The paracone is damaged, but apparently it did present a short ectoloph. The mesoloph is of medium length and the mesosinus is wide and closed by a cingulum. The sinus is transverse and closed by a merging the protocone with the hypocone. The metalophule is simple and transverse. The posteroloph is long and reaches the metacone, thus resulting in a closed posterosinus.

m1 (Fig. 4Q): Only one m1 has been recovered: IPS45052 from CS73. The anteroconid is asymmetric. The anterior valleys of the teeth are narrow, especially the anterosinusid, and closed by the arms of the anterolophid. The metalophulid is short and merges with the anterolophulid just anterior to the protoconid. The mesolophid is long, almost reaching the lingual margin of the molar and pointing anteriorly. The mesosinusid is closed by a low cingulid which presents a thickening resembling a mesostylid. The sinusid points markedly forward and is closed by a low cingulid merging the protoconid with the hypoconid. The hypolophulid is simple and merges with the entolophid anterior to the hypoconid. Finally, the posterolophid is thick and reaches the base of the entoconid, thus closing the posterosinusid.

m2 (Fig. 4R): IPS105188 from MOR1 is the only m2 recovered. The molar is relatively wide. It shows a highly reduced lingual anterolophid and a vestigial anterosinusid. On the contrary, the labial arm of the anterolophid is well developed and closes the protosinusid. The mesolophid is vestigial. The sinusid is narrow and transverse. The remaining morphological features resemble those described for the m1.

Comparisons and remarks:

These three specimens stand out among all other early Miocene *Democricetodon* specimens found in the Vallès-Penedès Basin because of their larger size (Fig. 3). They are larger than *D. hispanicus* and *D. decipiens*, the few recovered specimens fitting within the range size of *D. moralesi*, *D. koenigswaldi* and *Democricetodon mutilus (*Fig. 3). Some characters of the M2 of MOR1 fit better with *D. moralesi* (Van der Meulen et al., 2003) or *D. mutilus* (Wessels and Reumer, 2009) such as the symmetrically double protolophule and simple transverse metalophule. While these characters may also occur in *D. koenigswaldi*, double and posterior metalophules predominate on the M2 instead of transverse ones. Furthermore, the anteroconid of the m1 recovered at CS73 is characteristically asymmetric as in *D. moralesi*. However, this specimen presents a long mesolophid, which is a rare feature in both *D. moralesi* and *D. koenigswaldi* but very common in *D. mutilus* from Sandelzhausen (Southern Germany; Wessels and Reumer, 2009). Interestingly, the CS73 m1 had been previously ascribed to the genus *Fahlbuschia* (Agustí and Llenas, 1993) which was later synomymized with *Democricetodon* (Van der Meulen et al., 2003; but see Freudenthal, 2006). Jovells-Vaqué et al. (2017:146) ascribed this specimen to a second, larger-sized *Democricetodon* species that would have coexisted with *D. hispanicus*. These authors already noted some affinities with *D. moralesi* and *D. koenigswaldi.* Concerning the specimens from MOR1, the single M2 and m2 are the only identifiable rodent material found at the site. Clearly the material is too scarce to confidently ascribe it to the species level. Furthermore, it may well be possible that the specimen from CS73 and those from MOR1 belong to different *Democricetodon* species of similar size. In the Calatayud-Montalbán Basin *D. moralesi*, ranges from local subzone Cb (late early Aragonian, MN4) to Db (middle Aragonian, MN5; Van der Meulen et al., 2003, 2012). On the contrary, *D. koenigswaldi* is not recorded until much later, its first occurrence defining the lower boundary of subzone Dd (late middle Aragonian, MN5; Van der Meulen et al., 2003, 2012). Since CS73 is correlated to zone C (Jovells-Vaqué et al., 2017; see section 5.1.) *D. moralesi* would be a more likely candidate than *D. koenigswaldi*. MOR1 is younger, coinciding with the Langhian transgression at the Vallès-Penedès Basin, but probably not as late as subzone Dd, so an attribution to *D. moralesi* is also more probable in this case. It is worth remarking that the morphology and size of the few recovered specimens also fits with *D. mutilus*, a species known from Serbia, Hungary, Austria, Germany, Switzerland and France, but not recorded in the Iberian Peninsula. This species co-occurs with *D. gracilis* in certain Swiss (Kälin and Kempf, 2009) and German sites (Wessels and Reumer, 2009), which is also present at CS73. While *D. mutilus* is also a likely candidate for the ascription of the limited Vallès-Penedès sample, only the recovery of further material will allow clarifying the identity of this larger-sized *Democricetodon* species in CS73 and MOR1.

Genus *Megacricetodon* Fahlbusch, 1964
Megacricetodon primitivus Freudenthal, 1963

A catalog of the studied material and measurements is given in Appendix C. See Tables 7-12 for summary statistics and comparisons. See also Figure 5 for measurements and comparisons. Morphotype frequency tables are given in Appendix D.

Description:

M1 (Fig. 4S, T): The anterocone is deeply split with the labial cusp larger than the lingual one in most molars, but in the material from younger sites (PA, VI) both cusps are more frequently of similar size (Appendix D, Table 1). Most of the specimens, such as IPS44939 from CS74 or IPS86432 from LCV (Fig.4T), show a well-developed cingulum or anterior platform at the base of the anterocone. The presence of a labial spur on the anterolophule is variable, but it is more frequently absent. When present, it is very short, almost vestigial, see IPS86997 from VI (Fig. 4S) and IPS86432 from LCV1 (Fig. 4T; Appendix D, Table 3). The protolophule is always simple and merges with the anterolophule posteriorly to the protocone. The mesoloph is always present, most frequently being long, short in just a few specimens. The ectoloph on the paracone is also variable. In the specimens from LV1 and PA it is more frequently absent, whereas in the other sites a short ectoloph is frequently present but it never merges with the mesoloph. In all the specimens from the VI the ectoloph is relatively longer, almost touching the long mesoloph, such as in IPS86997 (Fig. 4S). The metalophule consists of a single arm posterior to the hypocone that may be placed quite lingually, particularly in younger samples such as VI and PA, thus resulting in a highly reduced posterosinus. The sinus is transverse in all studied specimens.

M2 (Fig. 4U, V): The anterior valleys of the teeth are closed by the well-developed arms of the anterolophule. The labial arm is notably higher than the lingual one. The protosinus is reduced. The protolophule is simple and slightly anterior to the protocone in most cases (Appendix D, Table 10), except in a few specimens from VI (e.g., IPS87022, Fig.4V) and PA (e.g., IPS86335) that present a double protolophule with a stronger anterior arm. In a few other specimens, such as IPS86435 from LCV (Fig. 4U), the protolophule shows a vestigial posterior arm. The ectoloph is variable and in some specimens such as IPS86328 from PA, IPS87022 from VI (Fig. 4V) and IPS 86888 from VI the ectoloph is well developed and weakly connects the paracone and the mesoloph. The mesoloph is present in all specimens but IPS86444 from LV1. This ridge is generally of medium length or long. The metalophule is simple in all the studied specimens and generally transverse or slightly anterior (Appendix D, Table 15). The sinus normally is transverse in the younger localities such as VI and PA but in most specimens from LCV and CMV3 it points forwards (Appendix D, Table 14).

M3 (Fig. 4W): The teeth are extremely reduced and button shaped. The labial anteroloph is well developed and delimits the narrow anterosinus (IPS19479 from CS74, Fig.4W). The lingual anteroloph and protosinus are generally vestigial as in IPS86439 from LCV1. The protolophule is simple and merges with a very short anterolophule anterior to the protocone. The mesoloph is highly variable, in some cases such as IPS19479 from CS74 (Fig.4W) the mesoloph is long and has a small mesostyle at the end. The metacone is recuded, being barely distinguishable in many specimens such in IPS45094 from CS72. The metalophule is anterior to the hypocone. The posteroloph is well developed and closes the posterior valley of the tooth. The transverse and narrow sinus is closed by a low cingulum. Some specimens present a reduced sinus and the protocone and hypocone show a weak direct connection (IPS86439 from LCV1).

m1 (Fig. 4X, Y): The anteroconid is simple and round in all the studied specimens but in a few teeth from PA and CS74 which show a sligh subdivision of this cusp (Appendix D, Table 16). In these cases, the two cusps of the anteroconid are of similar size. A few specimens from CS74 (6 out of 17), such as IPS44950 (Fig. 4X), show a vestigial and low labial spur on the anterolophulid (Appendix D, Table 17). Such spur is absent in all the remaining material. The mesolophid is variable, being more frequently short or of medium length, and only rarely long or absent. The mesosinusid is open (e.g. IPS86440 from LCV1, Fig.4Y). The metalophulid and the hypolophulid are both simple, anterior and quite short in all specimens. The sinusid is generally wide and transverse, although in some specimens this valley points forward (e.g., IPS44950 from CS74, Fig.

4X). The posterolophid is well developed and reaches the entoconid thus closing the posterosinusid.

m2 (Fig. 4X, Z): The anterior valleys of the teeth are closed by the arms of the anterolophid. The lingual arm of the anterolophid is highly reduced (e.g, IPS86444 from LCV) and sometimes absent (e.g., IPS44950 from CS74, Fig.4X). As in the case of the m1, the mesolophid is variable, but it is more frequently short or of medium length, only very rarely long or absent (e.g. IPS86444 from LCV1, Fig.4Z). The remaining morphological features resemble those of the m1.

m3 (Fig. 4A'): All the valleys of the m3 are reduced, including the sinusid and the mesosinusid, as compared to those of the m1 and m2. The protosinusid is particularly narrow and it is closed by the labial anterolophid, which is quite low. The anterosinusid and lingual anterolophid are vestigial or have completely disappeared in some molars (e.g., IPS86451 from LCV1, Fig.4A'). The sinusid and mesosinusid are closed by low cingulids. The mesolophid is absent in all the studied specimens. The entoconid is highly reduced, being barely recognizable in most teeth. The posterolophid is well developed and closes the posterosinusid.

Comparisons and remarks:

The described specimens are similar in size to those of small *Megacricetodo*n species (Fig. 5) such as *Megacricetodon primitivus* (Freudenthal, 1963)*,* *Megacricetodon collongensis* (Mein, 1958) and *Megacricetodon minor* (Lartet, 1851), which are abundant in the Iberian Peninsula during the Aragonian (Daams and Freudenthal, 1988; Oliver Pérez, 2015; Oliver and Peláez-Campomanes, 2016). However, several morphological features allow for the ascription of the material to *M. primitivus*. The size of the specimens overlaps with that of *M. primitivus* and *M. minor*, but in the studied material the anterocone in the M1 is deeply split as in *M. primitivus* and not simple to slightly split as in *M. minor. Megacricetodon collongensis* is of similar size, although slightly larger than *M.primitivus* (Oliver and Peláez-Campomanes, 2014; Fig.5). This species further differs from *M. primitivus* by the much more frequent occurrence of subdivided anteroconids on the m1 and the higher proportion of double protolophules and metalophules on M1 and M2 (Oliver and Peláez-Campomanes, 2014). Except for a few specimens from PA and CS74, in the studied material the anterocone is predominately simple and rounded, while and the protolophule and metalophule are predominantly simple in the M1. However, in a few M2 from LV1, PA and VI the protolophule shows an incomplete posterior arm and in a few others from PA and VI the protolophule is double. The metalophule is simple in all M2. The mesolophs/ids are generally long or of medium length in all molars but in the m3, which has no mesolophid. This contrasts with the type material from Valtorres (Calatayud-Montalbán Basin, Spain), in which this ridge is less developed, more frequently being short to medium length in all molars but the m3, where it is generally absent (Freudenthal, 1963; Daams and Freudenthal, 1988; Oliver and Peláez-Campomanes, 2014). Other differences with the type material include the larger size of some of the specimens from the younger sites (VI, PA), which is however within the size range for the species (see Daams and Freudenthal, 1988; Oliver and Peláez-Campomanes, 2014). Agustí (1981, 1982) recognized a second larger-sized species of *Megacricetodon* in CMV represented by a single m1. This specimen measures 1.38 by 0.78 (length by width) and therefore fits perfectly within the range of *M. primitivus* (see Oliver and Peláez-Campomanes, 2014), not being even especially large. Therefore, we ascribe it to the latter species, which would be the only *Megacricetodon* species present at the Vallès-Penedès during the early Miocene.

Megacricetodon primitivus is the first *Megacricetodon* species to be recorded in the Iberian Peninsula, its oldest record being at the site of Artesilla in the Calatayud-Montalbán Basin (Oliver Pérez, 2008; Oliver and Peláez Campomanes, 2014). This site is correlated to local subzone Ca and its age is estimated as 16.49 Ma (Van der Meulen et al., 2012). This species persists in the Calatayud-Montalbán Basin for almost one million years, its last record being at Valdemoros 8A correlated to local subzone Db, with an estimated age of 15.68 Ma (Oliver and Peláez-Campomanes, 2014). Its disappearance coincides with the first record of additional, larger-sized *Megacricetodon* species in the region, such as *Megacricetodon vandermeuleni* (Oliver and Peláez-Campomanes, 2013, 2016). *Megacricetodon primitivus* does not show directional changes in size or morphology throughout its range, despite showing a high inter- and intra-populational variability (Olivar and Peláez-Campomanes, 2014). This contrasts with the situation in most *Megacricetodon* lineages and other coeval cricetids, such as *Democricetodon*, which do show clear anagenetic trends during the same time span. The Vallès-Penedès material also reflects this situation. Size of the molars remains stable, with only a minor increase in the length of m1 (see Table 2). As far as morphology is concerned, the only temporal trends are the rare occurrence of split anteroconids on the m1 in the specimens from younger sites as well as an apparent trend towards the reduction of the posterosinus on M1. In the younger localities, such as VI and PA, the metalophule is connected to the posteroloph more obliquely, thus delimiting a more reduced posterosinus. While this is also observed in a significant number of specimens from older sites, such as in those from CMV3, it is by far more common in younger ones. Such pattern is not observed in the Calatayud-Montalbán material, the posterosinus of the M1 being generally more reduced, comparable to the specimens from VI and PA, even in the oldest sites (see Oliver and Peláez Campomanes, 2014: table 10).

5. Discussion

5.1. Biostratigraphy and correlations

Overall the early Miocene cricetid succession in the Vallès-Penedès Basin is similar to that of other regions, such as the Calatayud-Montalbán Basin (Van der Meulen et al., 2012) or the Swiss Molasse Basin (Kälin and Kempf, 2009) (Fig.6). The order of events in all these regions is as follows: 1) after the last occurrence of *Eucricetodon*, there is a 'cricetid vacuum' (Daams and Freudenthal, 1989) with only the genus *Melissiodon* present; 2) the first modern cricetid to be recorded is *Democricetodon*; 3) *Megacricetodon*, a second genus of modern cricetid, appears slightly later, together with the paracricetodontine *Eumyarion*; 4) by the end of the early Miocene additional *Democricetodon* species are recorded in all the regions. Even though *Democricetodon* and *Megacricetodon* are represented by distinct species in Central Europe and Iberia well since their first occurrence, and there is a clear diachrony in the timing of the events (Van der Meulen et al., 2012) their order is the same in both regions (Fig.6). The first modern cricetid recorded in the Swiss Molasse is *D. franconicus*, which first occurs at 17.6 Ma. On the other hand, in Calatayud-Montalbán *D. hispanicus* is present in low numbers at 17 Ma (Van der Meulen et al., 2003, 2012). The genus *Megacricetodon*, represented by *M. collongensis*, first occurs at 17.2 Ma in Switzerland, whereas in Spain it first appears at 16.6 Ma and is represented by *M. primitivus*. Finally, *Eumyarion*, an archaic 'cricetid' genus related to Oligocene forms such as *Eucricetodon* (Freudenthal et al., 1992), first appears simultaneously with *Megacricetodon* in Switzerland (Kälin and Kempf, 2009) and perhaps slightly later in Spain (Van der Meulen et al., 2012).

Previous works have remarked that the early Miocene rodent succession of the Vallès-Penedès shows several coincidences with that of Calatayud-Montalbán, thus indicating that the same detailed local zonation could be used in both areas (Casanovas-Vilar et al., 2011, 2016b; Jovells-Vaqué et al., 2017, 2018). Our results support these earlier conclusions albeit they also show some significant differences. In the Calatayud-Montalbán Basin the Ramblian sites corresponding to the 'cricetid vacuum' are correlated to local zone A (ca. 19.5–16.77 Ma; Daams and Freudenthal, 1988; Daams et al., 1999; Van der Meulen et al., 2012). In the Vallès-Penedès Basin Ramblian sites include Sant Andreu de la Barca, Turó de les Forques, La Costablanca, and Molí de Can Calopa (Casanovas-Vilar et al., 2011, 2016b). These have delivered a glirid-dominated fauna that also includes the cricetid *Melissiodon* (Jovells-Vaqué and Casanovas-Vilar, 2018) but no modern cricetids. Besides the absence of cricetids other than *Melissiodon*, these sites are also characterized by a high abundance of glirids and eomyids, represented by the genera *Ligerimys* and (more infrequently) *Pseudotheridomys*.

Local zone B of the Calatayud-Montalbán Basin (16.77–16.49 Ma) marks the beginning of the Aragonian and is characterized by *Democricetodon hispanicus* as the only modern cricetid present (Daams and Freudenthal, 1988; Daams et al., 1999; Van der Meulen et al., 2012). This interval, corresponding to the earliest part of the MN4, would be entirely missing in the Vallès-Penedès. Casanovas-Vilar et al. (2016b: 802) mentioned scarce remains of *Democricetodon* from Turó de les Forques (indeed just a single m1). However, this was later found to be an unfortunate contamination from LCV, which was being sorted at the same time. The specimen was distinguished because of its different color and aspect of the sediment still trapped in the main valleys, both matching LCV.

The presence and abundance of the eomyid *Ligerimys ellipticus* characterizes zone C (16.49–15.93 Ma) together with the first appearance of *Megacricetodon* (*M. primitivus*) and *Eumyarion* (Daams and Freudenthal, 1988; Daams et al., 1999; Van der Meulen et al., 2012). The sites of the Subirats lacustrine unit (LCV, CMV and CS) are the oldest MN4 sites in the basin and they already record both *Megacricetodon* and *Eumyarion* (Agustí, 1981, 1983; Jovells-Vaqué et al., 2017, 2018). *Ligerimys ellipticus* is present in most of the studied sites (see Fig. 6). Its absence in EC, CSU and CCW can certainly be attributed to the scarce sample recovered at these sites. However, these localities can be correlated to zone C because of the presence of *M. primitivus* in CSU and *Eumyarion* in EC. Regarding CCW, it is lithostratigraphically correlated to SM, which, in turn, unambiguously belongs to zone C. Van der Meulen et al. (2012) subdivided zone C into subzones Ca (16.49–16.30 Ma) and Cb (16.3–15.93 Ma) according to the *Democricetodon* species present and the replacement of *Ligerimys florancei* by its descendant *Ligerimys ellipticus*. The replacement occurred within subzone Ca, but in a couple of Vallès-Penedès sites, LCV and CMV, both *Ligerimys* species co-occur, even though *L. ellipticus* is by far more abundant. In all the remaining sites only *L. ellipticus* is present and it is rare. While this would apparently support a distinction of subzones Ca and Cb in the Vallès-Penedès Basin as well, it is contradicted by the different cricetid succession. In LCV and CMV *D. hispanicus* is present, while in the Calatayud-

Montalbán Basin its descendant *D. decipiens* is the only *Democricetodon* that occurs in subzone Ca (Van der Meulen et al., 2003, 2012). In CS, which would be correlated to subzone Cb, two additional *Democricetodon* species are recorded (*D. gracilis* and the larger-sized *D.* sp. 4), but *D. hispanicus* is most abundant. *Democricetodon* cf. *decipiens* is recorded in VI, SM and PA, coexisting with *D. gracilis* in VI. In MOR1 *D.* cf. *moralesi* is represented by scarce remains. In Calatayud-Montalbán, the replacement of *D. decipiens* by its descendant *D. moralesi* defines the lower boundary of subzone Cb (Van der Meulen et al., 2012). A second *Democricetodon* lineage first occurs in that basin during subzone Cb (*D. franconicus*, Van der Meulen et al., 2003, 2012), which is not present in the Vallès-Penedès. On the contrary, *D. gracilis* is not recorded in Calatayud-Montalbán, but is first recorded in the Swiss Molasse during the late MN4 (Kälin and Kempf, 2009), more or less at the same time it is first recorded in the Vallès-Penedès Basin. The Ebro Basin sites that have delivered this species are slightly younger, being correlated to the earliest MN5 (Suárez-Hernando, 2017). Clearly, the Vallès-Penedès sites can be correlated to zone C of the Calatayud-Montalbán Basin, but the distinction of subzones in the Catalan basin is questionable. Yet, it seems clear that LCV and CMV, which still record the eomyid *L. florancei* together with *L. ellipticus*, are older than the remaining sites. At CS, VI and SM additional *Democricetodon* species are recorded, which would argue for a younger age of these sites, even if the *Democricetodon* species differ.

For PA and MOR1, two of the younger sites (see Fig.2), the correlation is not clear. The rodent fauna of PA includes three cricetids (*M. primitivus*, *D.* cf. *decipiens* and *Eumyarion* cf. *weinfunteri*) but no eomyids. *Megacricetodon primitivus* is by far the most abundant cricetid in the sample, *D.* cf. *decipiens* being represented by just four molars (one broken) and *Eumyarion* by one. Total sample size includes more than 100 identifiable rodent specimens so that the absence of *Ligerimys* is intriguing. If confirmed, the presence of *D. decipiens* would suggest a correlation to zone C. The PA site is located just tens of meters below Langhian marine limestones (Casanovas-Vilar et al., 2011; 2016b), so it may be middle Miocene rather early Miocene. The absence of *Ligerimys*, which disappears at the beginning of the middle Aragonian (MN5), zone D (Van der Meulen et al., 2012), would support this tentative correlation. Regarding MOR1, this locality is located in transitional facies associated to the Langhian marine transgression and it has only delivered two molars which are attributed to an undetermined, large-sized *Democricetodon* species. Considering its stratigraphical position we correlate it to the beginning of the middle Miocene. Recently, a series of karstic fissure fillings have been located within Langhian limestones in Clariana

(Castellet i La Gornal, Penedès sector). Several fissures have delivered a rich sample comprising thousands of small mammals including insectivorans, chiropterans, lagomorphs and rodents. The rodent fauna has yet to be prepared and studied, but it includes *Cricetodon* and a medium-sized *Megacricetodon* species, probably *M. collongensis*. *Cricetodon* first occurs during the late MN5 (zone E) in Calatayud-Montalbán, where it coexists with *M. collongensis*. Clariana sites may well be of similar age and, together with PA and MOR1, fill the gap between the early (MN4) and late Aragonian (MN6–MN7+8) sites in the Vallès-Penedès Basin. Ongoing magnetostratigraphical studies in the early and middle Miocene successions of this basin will surely refine these correlations.

5.2. Paleobiogeographic and paleoenvironmental implications

Several studies have stressed the differences in faunal composition between the Vallès-Penedès Basin and other, more inland, areas of the Iberian Peninsula during the Miocene (Agustí, 1990; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2005, 2008; Maridet et al., 2007, 2013). As far as rodents are concerned, differences with the central Iberian basins are particularly clear during the latest Aragonian (middle Miocene, MN7+8) and the Vallesian (late Miocene, MN9–MN10), with more diverse faunas including a greater number of purported forest-dwelling taxa in the Vallès-Penedès (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008). This pattern is also recognized for the larger mammals, for example hominoid primates, chalicotheres and tapirs are present at the Vallès-Penedès and other Catalan Basins (Cerdanya and Seu d'Urgell basins, in the Pyrennees) but unknown from elsewhere in Spain at that time. Catalonia is consistently recognized as a transitional area between the humid and forested environments of west and central Europe and the drier landscapes of inner Iberia (Casanovas-Vilar et al., 2005, 2008).

This situation probably already existed during the early Miocene, although available data are still scarce. Nevertheless, Costeur and Legendre (2008a, b) showed that the early Miocene (MN3–MN4) large mammal faunas from the Vallès-Penedès are distinct from those of other Iberian basins, and include a slightly higher diversity of herbivores, particularly suiforms. In this regard, they are closer to contemporary faunas from southern France and Germany. The insectivorans (Eulipotyphla) show a clear latitudinal diversity gradient throughout the Miocene in Western Europe, with decreasing generic diversity at lower latitudes, mostly because of the absence of many genera and even entire families in the inner basins of the Iberian Peninsula at particular time intervals (Furió et al., 2011; Madern and Van den Hoek Ostende, 2015). During the early Miocene central Europe presented a remarkable diversity of talpids and soricids, but only a few species are recorded in inner Spain. Indeed, the early Miocene (MN3–MN4) insectivore faunas of the Calatayud-Montalbán Basin generally include the erinaceid *Galerix* and the talpid *Desmanodon* besides a few more genera (such as *Heterosorex* and *Miosorex*) (Van der Meulen et al., 2012; Furió et al., 2017). The early Miocene insectivore faunas of the Vallès-Penedès have been recently described (Van den Hoek Ostende et al., in press). Overall, the insectivores confirm the intermediate position of the Vallès-Penedès, but show that differences with the inland were less pronounced than during the middle and late Miocene (Van den Hoek Ostende et al., in press). The presence of dimylids (*Plesiodimylus*, *Chainodus*), particularly in Ramblian sites would suggest somewhat more humid conditions in Catalonia. Dimylids were specialized insectivores, presumably malacophagous, which would have favored moist forested environments (Ziegler, 1999). Finally, this latitudinal pattern from more humid and forested environments in central Europe to drier landscapes in the Iberian Peninsula is also confirmed by paleobotanical data from the earliest middle Miocene (Bruch et al., 2004; Fauquette et al., 2007; Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2010).

As far as rodents are concerned, Agustí (1990) and Maridet et al. (2007, 2013) recognized the unique character of the early Miocene Vallès-Penedès faunas, particularly during the early Aragonian (MN4). In the Calatayud-Montalbán Basin, the rodent faunas at the time include a diverse assemblage of ground-dwelling glirids, the cricetids *Democricetodon* and *Megacricetodon* as well as the eomyid *Ligerimys* and occasional terrestrial sciurids (see Van der Meulen et al., 2012; García-Paredes et al., 2016). On the other hand, rodent faunas from France, Switzerland and Germany are enriched with a higher diversity of both species and families, including arboreal sciurids (*Dehmisciurus*, *Miopetaurista*), semiaquatic castorids (*Steneofiber*), and several other 'cricetids' including *Anomalomys*, *Eumyarion* and *Melissiodon* (Maridet et al., 2007, 2011). Some of these taxa are shared with the Vallès-Penedès, including the arboreal squirrel *Dehmisciurus* (present at EC, CS and SM; Aldana Carrasco, 1991, 1992) or the cricetids *Eumyarion* (Agustí, 1981, 1983; Jovells-Vaqué et al., 2018) and *Melissiodon* (Jovells-Vaqué and Casanovas-Vilar, 2018). In addition, presumably arboreal glirids (characterized by molars with many transverse ridges, e.g., *Muscardinus*, *Glis*, *Glirudinus*; see Van der Meulen and de Bruijn, 1982) are more common in Central Europe and the Vallès-Penedès than in the Iberian inland. Yet, in the Catalan basin, taxa of Iberian affinities generally predominate over those originating from Central Europe. Iberian taxa include certain ground-dwelling glirids, such as the hypsodont *Armantomys*, only recorded at Turó de les Forques – level 1 and Costablanca (Ramblian, MN3), and *Simplomys simplicidens*, which is more widespread and abundant. These are characterized by a simpler molar pattern, with fewer transverse ridges as in extant ground-dwelling mouse dormice (*Myomimus*; see Van der Meulen and de Bruijn, 1982).

The early Miocene cricetids of the Vallès-Penedès show an interesting mixture of elements belonging to the two different biogeographical provinces. *Democricetodon hispanicus* and *D. decipiens* are restricted to Iberia while *M. primitivus* also occurs in southern France (Oliver and Peláez-Campomanes, 2016). On the other hand, *Democricetodon gracilis* is a common component of central European faunas (Abdul Aziz, 2008; 2010; Daxner-Höck et al., 1998; Kälin and Kempf, 2009; Maridet, 2003; Wessels and Reumer, 2009). Other 'cricetids' shared with central Europe include *Eumyarion weinfurteri* and *Melissiodon dominans*. The former is very rare in the inner Spanish basins (Van der Meulen et al., 2012), and when present it is represented by the species *Eumyarion valencianum*, which also occurs in Valencia (Daams and Freudenthal, 1974; Ruiz-Sánchez et al., 2003). On the other hand, *Melissiodon* is even rarer and generally disappears much earlier than in the Vallès-Penedès, where it last occurs at SM, just a few meters below the marine sediments of the Langhian transgression (Jovells-Vaqué and Casanovas-Vilar, 2018).

Numerous works have provided ecological assigments of fossil rodent taxa which allow for paleoenvironmental inferences based on dental morphology or consider the ecological preferences and distribution of extant relatives (e.g., Daams et al., 1988; Van der Meulen and Daams, 1992; Van Dam and Weltje, 1999; Van Dam, 2006; Casanovas-Vilar and Agustí, 2007). The genera *Democricetodon* and *Megacricetodon* are medium to small-sized cricetids with brachyodont and bunodont molars often assumed to have been generalists (e.g., Van Dam and Weltje, 1999, Casanovas-Vilar and Agustí, 2007). However, Daams et al. (1988: 291) assigned different ecological preferences to the Iberian species of those genera, with small-sized forms with long mesolphs/ids (e.g., *Democricetodon gaillardi*, *Megacricetodon minor*) presumably favoring more humid environments. Heshkovitz (1967) noted than in extant sigmodontine cricetids, the forms with a well-developed mesoloph/id (pentalophodont) are usually forest-dwellers while those in which these ridges are reduced or absent (tetralophodont) tend to prefer open country. All the *Democricetodon* and *Megacricetodon* species present at the Vallès-Penedès during the early Miocene present mesolophs/ids of variable length, but long ridges are only particularly common in *Megacricetodon primitivus* and *Democricetodon gracilis*. Other cricetid genera, such as *Eumyarion*, show additional transverse ridges, such as an ectomesolophid in the lower molars or a long labial spur on the anterolophule of the M1. *Eumyarion* is generally considered to have preferred humid and forested environments (Daams et al., 1988; Casanovas-Vilar and Agustí, 2007; Van Dam, 2006). As already said, *Eumyarion weinfurteri*, a Central European form, is recorded at the Vallès-Penedès during the early Aragonian (LCV, CMV, SM), although it is not common. In contrast, this genus is completely absent from the Iberian inland at that time, which is taken as an evidence for the exitence of more arid environments. Regarding *Melissiodon*, the fourth cricetid genus recorded at the early Miocene Vallès-Penedès site, its unique molar pattern and aberrant mandible shape, resembling that of shrew rats, have been related to an insectivorous diet (Hordijk et al., 2015). *Melissiodon* would have preferred humid forested environments where its food resources would be more abundant. Indeed, both *Eumyarion* and *Melissiodon* are generally more common in faunas which include a high number of forest-dwelling elements. *Melissiodon* is far more common and persists for a longer time in the Vallès-Penedès Basin as compared to the inner Iberian basins (Jovells-Vaqué and Casanovas-Vilar, 2018). The presence of these two cricetid genera during the early Miocene in the Vallès-Penedès indicates affinities with Central Europe and would be indicative of forested environments. *Democricetodon gracilis* which is also a Central European element, may have also favored such kind of environments since it is abundant in faunas including a large proportion of forest-dwellers, such as Oberdof (MN4, Austria; Daxner-Höck et al., 1998) or Sandelzhausen (MN5, Germany; Wessels and Reumer, 2009). Therefore, the cricetid faunas support the general impression that during the early Miocene the Vallès-Penedès already represented a transition zone between the forested regions of west and central Europe and the more arid inner Iberian Peninsula. However, this is a preliminary conclusion that should be further explored and tested using more refined, quantitative, paleoecological analyses.

6. Conclusions

The early Miocene rodent record of the Vallès-Penedès Basin ranges from the Ramblian (MN3) to the end of the early Aragonian (MN4) and is richer and more continuous than previously thought. Modern cricetids are a common component of MN4 faunas and include four species of the genus *Democricetodon* (*D. hispanicus, D. cf. decipiens*, *D. gracilis*, *D. sp.* 4) and one of the genus *Megacricetodon* (*M. primitivus*). In turn, these modern forms co-occur with two archaic ‘cricetids’: *Melissiodon dominans* and *Eumyarion weinfurteri.* The rich and detailed rodent succession of the Calatayud-Montalbán Basin (Spain) and the Swiss Molasse Basin has shown that *Democricetodon* is the first genus of modern cricetids to disperse in Western Europe, *Megacricetodon* occurring slightly later (Kälin and Kempf, 2009; Van der Meulen et al., 2012). However, in the Vallès-Penedès both genera appear simultaneously at LCV, the oldest MN4 site, where they are represented by *D. hispanicus* and *M. primitivus*. This may evidence a brief hiatus in the record, corresponding to the earliest MN4 (equivalent to local zone B of Calatayud-Montalbán). In the older sites (LCV, CMV) only *D. hispanicus* and *M. primitivus* are present, but later localities (CS) record additional *Democricetodon* species *(D. gracilis, D.* sp. 4). In even younger sites, close to middle Miocene marine deposits, *D. hispanicus* is replaced by its descendent *D.* cf. *decipiens* (VI, SM, PA). The cricetid and eomyid succession indicates close affinities with the nearby Calatayud-Montalbán Basin, to the point that the same local zonation could be used in the Vallès-Penedès (see Daams et al., 1999; Van der Meulen et al., 2012). The oldest Vallès-Penedès sites, which are devoid of cricetids other than *Melissiodon*, would correlate to local zone A (Ramblian). All other sites would correlate to local zone C, zone B being entirely missing in the Vallès-Penedès. Van der Meulen et al. (2012) subdivided zone C into subzones Ca and Cb owing to the species of *Ligerimys* and *Democricetodon* present. However, the extension of such fine subdivision to the Vallès-Penedès record is controversial because not all diagnostic criteria are met. The eomyid succession is analogous in both basins, with *L. ellipticus* coexisting with its ancestor *L. florancei* in subzone Ca and replacing it in subzone Cb. However, the *Democricetodon* species succession in both areas differ, since *D. hispanicus*, which is restricted to zone B in Calatayud-Montalbán persists for a longer time in the Vallès-Penedès, well into zone C. On the other hand, *D. decipiens*, a species wich characterizes subzone Ca would be scarcely represented in the Vallès-Penedès, further occurring in younger sites than in Calatayud-Montalbán (Fig.6). *D. gracilis*, a species mostly recorded from central Europe, is present in some sites (CS73, VI, SM, CCW), thus indicating also affinities with northern faunas (Fig.6). The fourth, for the moment undetermined, *Democricetodon* species is represented by just a few molars that fit within the morphological and size range of *D. moralesi* and *D. mutilus*. While an attribution to the former species would indicate affinities with Calatayud-Montalbán, the latter would show greater influence of central European faunas and, if confirmed, would be the first record of this species in the Iberian Peninsula. *Eumyarion weinfurteri,* another central European form, is sporadically recorded. The occurrence of these cricetids may indicate the occurrence of more humid and forested environments as compared to more inland Iberian basins. Evidence provided by large mammals, insectivores, other rodents and paleobotanical data supports this interpretation.

Funding

This research has been funded by the Agencia Estatal de Investigación from the Spanish Ministerio de Economía, Industria y Competitividad and the Agencia Estatal de Investigación (AEI) from Spain/European Regional Development Fund of the European Union [projects CGL2017-82654-P and CGL2016-76431-P and RYC-2013-12470 research contract to I.C.V.], by the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya [2014 SGR 416 research group, 2018FI B1 00201 predoctoral grant to S.J.V.], and by the CERCA Programme of the Generalitat de Catalunya. Fieldwork was supported by the Departament de Cultura of the Generalitat de Catalunya [project 2014/100584] and the National Geographic Society [grant number 9640-15].

Acknowledgements

We thank V. Vicedo and L. Troya (Museu de Ciències Naturals de Barcelona) for their assistance when consulting the specimens of the Villalta Collection. We are indebted to Pablo Pélaez-Campomanes (Museo Nacional de Ciencias Naturales, Madrid) who provided valuable data for graphs and comparisons. We thank the constructive comments by the editor and reviewers of this manuscript which surely improved the final result.

References

Abdul Aziz, H., Böhme, M., Rocholl, A., Zwing, A., Prieto, J., Wijbrans, J. R., Heissig, K., Bactadse, V., 2008. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). Int. J. Earth Sci. 97, 115–134. http://doi.org/10.1007/s00531-006-0166-7.

Abdul Aziz, H., Böhme, M., Rocholl, A., Prieto, J., Wijbrans, J. R., Bachtadse, V., Ulbig, A., 2010. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of the early to middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). Int. J. Earth Sci. 99, 1859–1886. https://doi.org/10.1007/s00531-009-0475-8.

Adrover, R., Mein, P., Belinchón, M., 1987. La fauna de roedores en el Aragoniense medio del Barranco del Candel, Buñol (provincia de Valencia, España). Paleontol. Evol. 21, 43–61.

Aldana Carrasco, E.J., 1991. Roedores Esciuromorfos del Neógeno de Cataluña Sciuromorph rodents from the Neogene of Catalonia. Cerdanyola del Vallès (Doctoral dissertation). Universitat Autònoma de Barcelona, Barcelona, 179 p., 59, tb., 25 pl.

Aldana Carrasco, E.J., 1992. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España). Treb. Mus. Geol. Barcelona. 2,69–97.

Agustí, J., 1981. Roedores miomorfos del Neògeno de Cataluña (Doctoral dissertation). Universitat de Barcelona, Barcelona, 288 p., 3 pl.

Agustí, J., 1982. Biozonación del neogeno continental de Cataluña mediante roedores (Mammalia). Acta Geol. Hisp. 17, 21–26.

Agustí, J., 1983. Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallès-Penedès, Cataluña, España). Estu. Geol. 39, 417-430.

Agustí, J., 1990. The Miocene rodent succession in eastern Spain: a zoogeographical Appraisal, in: Lindsay E. H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. NATO ASI Series. Series A: Life Sciences, Volume 180. Plenum Press, New York, pp. 375–404.

Agustí, J., Cabrera, L., Moyà-Solà, S., 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. Paleontol. Evol.18, 57-81.

Agustí, J. i Cabrera, L., 1980. Nuevos datos sobre la biozonación del Burdigaliense continental de la cuenca del Vallés-Penedés. Acta Geol. Hisp. 15, 81-84.

Agustí, J., L. Cabrera, M. Garcés, W. Krijgsman, O. Oms, J. M. Parés., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth-Sci. Rev. 52, 247-260. https://doi.org/10.1016/S0012-8252(00)00025-8

Agustí, J., Llenas, M., 1993. Los Roedores del Mioceno inferior de Els Casots (Vallès-Penedès). Nota preliminar. Comunicaciones de Las IX Jornadas de Palontología, 70–72.

Bowdich, T. E., 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, pp. 115.

Bruch, A.A., Utescher, T., Alcalde, Olivares C., Dolakova, N., Ivanov, D., Mosbrugger, V., 2004. Middle and Late Miocene spatial temperature patterns and gradients in Europe - preliminary results based on palaeobotanical climate reconstructions. Cour. Forsch.-Inst. Senckenberg 249, 15–27.

Cabrera, L., 1979. Estudio Estratigráfico i Sedimentológico de los Depósitos Basales del Mioceno de la Depresión del Vallés-Penedés (Doctoral dissertation). Universitat de Barcelona, Barcelona, 361 p.

Cabrera, L., 1981. Estratigrafía y características sedimentológicas generales de las formaciones continentales de la cuenca del Vallès-Penedès (Barcelona, España). Estu. Geol. 37, 35-43. http://revistes.ub.edu/index.php/ActaGeologica/article/view/4239

Cabrera, L., Calvet, F., 1996. Onshore Neogene record in NE Spain: Vallès-Penedès and El Camp half grabens (NW Mediterranean), in: Friend, P. F., Dabrio, C. J.(Eds.), Tertiary Basins of Spain the Stratigraphic Record of Crustal Kinematics. Cambridge University Press, Cambridge, UK, pp. 97–105.

Cabrera, L., Calvet, F., Guimerà, J. i Permanyer, A., 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: organización secuencial y relaciones tectónica sedimentación, in: Colombo, F. (Ed.), Libro-guía excursión no. 4, I Congreso del Grupo Español del Terciario. Universitat de Barcelona. Barcelona, pp. 1-132.

Cabrera, L., Roca, E., Garcés, M., de Porta, J., 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana), in: Vera, J. A. (Ed.), Geología de España. SGE–IGME, Madrid, pp. 569–573.

Casanovas-Vilar, I., Moyá-Solá, S., Agustí, J., Köhler, M., 2005. The geography of a faunal turnover: tracking the vallesian crisis, in: Elewa D. A. M. T. (Ed.), Migration of Organisms. Springer Berlin Heidelberg, pp. 247–300. http://doi.org/10.1007/3-540-26604-6_9

Casanovas-Vilar, I., Alba, D. M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Angelone, C., 2008. Biochronological, taphonomical, and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). J. Hum. Evol. 55, 589–603. http://doi.org/10.1016/j.jhevol.2008.05.004

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Moyà-Solà, S. 2011. Registro paleontológico continental del Mioceno de la Cuenca del Vallès-Penedès. Paleontol. Evol., mem. esp. 6, 55-80.

Casanovas-Vilar, I., Garcés, M., Van Dam, J., García-Paredes, I., Robles, J.M., Alba, D.M. 2016a. An updated biostratigraphy for the late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). Geol. Acta 14, 195–217. http://doi.org/ 10.1344/GeologicaActa2016.14.3.1.

Casanovas-Vilar, I., Madern A., Alba, D. M., Cabrera, L., García-Paredes, I., Van den Hoek Ostende, L. W., DeMiguel, D., Robles, J. M., Furió, M., Van Dam, J., Garcés, M., Angelone, C., Moyà-Solà, S., 2016b. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). CR Palevol. 15, 791–812. http://doi.org/10.1016/j.crpv.2015.07.004.

Casanovas-Vilar, I., Jovells-Vaqué, S., Cabrera, L., Gómez, M., Albalat, D., Llenas, M., and Moyà-Solà, S., 2019. Memòria sobre la intervenció paleontològica als dipòsits del Miocè dels termes de Sant Cugat del Vallès, Cabrera d'Anoia, Vilobí del Penedès, Castellet i la Gornal i Sant Jaume dels Domenys. Campanya 2016. Memòria intervenció paleontològica (Unpublished field report). Institut Català de Paleontologia Miquel Crusafont, Bellaterra, 88 p.

Casanovas-Vilar, I., Agustí, J., 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. Palaeogeogr., Palaeoclimatol., Palaeoecol. 248, 169–189. http://doi.org/10.1016/j.palaeo.2006.12.002.

Casanovas-Vilar, I., and Jovells-Vaqué, S., 2017. Memòria de la intervenció paleontològica de mostreig a Riera del Morral 1 (Abrera, el Baix Llobregat). Campanya 2016. Memòria intervenció paleontològica. (Unpublished field report). Institut Català de Paleontologia Miquel Crusafont, Bellaterra, 39 p.

Costeur, L., and S. Legendre., 2008a. Spatial and Temporal Variation in European Neogene Large Mammals Diversity. Palaeogeogr., Palaeoclimatol., Palaeoecol. 261, 127–44. https://doi.org/10.1016/j.palaeo.2008.01.011

Costeur, L., Legendre, L., 2008b. Mammalian communities document a latitudinal environmental gradient in the Middle Miocene Climatic Optimum. Palaios. http://doi.org/10.2110/palo.2006.p06-092r

Crusafont, M., de Villalta, J. F., Truyols, J., 1955. El Burdigaliense continental de la Cuenca del Vallés- Penedés. Mem. y Comun. Ins. Geol. Diput. Prov. Barcelona. 12, 1–272.

D'Elía, G., Fabre, P-H., Lessa, E.P., 2019. Rodent systematics in an age of discovery: recent advances and prospects. J. Mammal. 100, 852–71. http://doi.org/10.1093/jmammal/gyy179.

Daams, R., Freudenthal, M., 1974. Early Miocene Cricetidae (Rodentia, Mammalia) from Buñol (Valencia, Spain). Scr. Geol. 24, 1–19.

Daams, R., Freudenthal, M., 1988. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*. Scr. Geol. Spec. Issue. 1, 39–132.

Daams, R., Freudenthal, M., 1989. The Ramblian and Aragonian: limits, subdivision, geographical and temporal extension, in: Lindsay E. H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. Springer US, New York, pp. 51–59.

Daams, R., Freudenthal, M., Van der Meulen, A.J. 1988. Ecostratigraphy of micromammal faunas from the Neogene of Spain. Scr. Geol. Spec. Issue 1, 287–302.

Daams, R., Van der Meulen, A.J., Álvarez Sierra, M.A., Peláez-Campomanes, P., Calvo, J.P., Alonso Zarza, M.A., Krijgsman, W., 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsl. Strati. 37, 102–139. http://doi.org/10.1127/nos/37/1999/103

Daxner-Höck, G., Haas, M., Meller, B., Steininger, F.F. 1998. Wirbeltiere aus dem Unter-Miozän des Lignit-Tagebaues Oberdorf (Weststeirisches Becken, Österreich). 7. Palökologie, Sedimentologie und Stratigraphie. Ann. Naturhist. Mus. Wien A 99, 195–224.

De Gibert, J. M., Casanovas-Vilar, I., 2011. Contexto geológico del Mioceno de la Cuenca del Vallès-Penedès. Paleontol. Evol. Mem. Esp. 6, 39–45.

DeGibert, J., Robles, J.M., 2005. Firmground ichnofacies recording high-frequency marine flooding events (Langhian Transgression, Vallès-Penedès Basin, Spain). Geol. Acta. 3, 295–305.

Fabre, Pierre-Henri, Lionel Hautier, Dimitar Dimitrov, and Emmanuel J. P Douzery. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. BMC Evol. Biol.12, 88. http://doi.org/10.1186/1471-2148-12-88

Fabre, P.H., Hautier L., Douzery E. J. P., 2015. A synopsis of rodent molecular phylogenetics systematics and biogeography, in: Cox, P. G., Hautier, L. (Eds.) Evolution of the Rodents: Advances in Phylogeny, Functional Morphology and Development, Cambridge University Press, UK, pp. 19-69.

Fahlbusch, V., 1964. Die Cricetiden (Mamm.) Der Oberen Sübwasser-Molasse Bayerns. Bayer. Akad. Wiss. Math.-Natur Wiss. K. Abh. 118, 4–136.

Fahlbusch, V., 1966. Cricetidae (Rodentia, Mamm.) aus der mittelmiozänen Spaltenfüllung Erkertshofen bei Eichstätt. Mitt. Bayer. Staatssamml.Paläont. Hist. Geol. 6, 109–131.

Fauquette, S., Suc, J.-P., Jiménez-Moreno, G., Micheels, A., Jost, A., Favre, E., Bachiri-Taoufiq, N., Bertini, A., Clet-Pellerin, M., Diniz, F., Farjanel, G., Feddi, N., and Zheng, Z., 2007. Latitudinal climatic gradients in the Western European and Mediterranean regions from the mid-Miocene (c. 15 Ma) to the mid-Pliocene (c. 3.5 Ma) as quantified from pollen data, in: Williams, M., Haywood, A.M., Gregory, F.M., and Schmidt, D.N. (Eds.), Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies, The Micropalaeontological Society, Special Publications, The Geological Society, London, pp. 481–502. http://doi.org/10.1144/TMS002.22

Fischer von Waldheim, G., 1817. Adversaria zoologica. Mém. Soc. Nat. Moscou. 5, 357–471.

Flynn, L. J., 1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups, in: W. P. Luckett and J.-L. Hartenberger (Eds.), Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. NATO ASI Series. Series A: Life Sciences, Volume 92. Plenum Press, New York, pp. 589–616.

Flynn, L.J., Lindsay, E.H., Pilbeam, D., Mahmood Raza, S., Morgan, M.E., Barry, J.C., Badgley, C.E., Behrensmeyer, A.K., Cheema, I.U., Rahim Rajpar, A., Opdyke, N.D., 2013. The Siwaliks and Neogene evolutionary biology in South Asia, in: Wang, X., Flynn, L.J., Fortelius, M. (Eds.), Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 353–372.

Flynn, L.J., Wessels, W., 2013. Paleobiogeography and South Asian small mammals: Neogene latitudinal and faunal variation, in: Wang, X., Flynn, L.J., Fortelius, M. (Eds.), Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 445–460.

Freudenthal, M., 1963. Entwicklungsstufen der miozänen Cricetodontinae (Mammlia, Rodentia) Mittlespaniens und ihre stratigraphische. Beaufortia 10, 51–157.

Freudenthal, M., 1967. On the Mammalian Fauna of the Hipparion-Beds in the Calatayud-Teruel Basin (Prov. Zaragoza, Spain). Part III. *Democricetodon* and *Rotundomys* (Rodentia). Proc. Kon. Akad. Wetensch. 70, 298–315.

Freudenthal, M., 2006. The Status of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* (Cricetidae, Mammalia). A Reply to Van Der Meulen et al. (2004). Geobios 39, 43–55. http://doi.org/10.1016/j.geobios.2004.08.005

Freudenthal, M., Daams, R., 1988. Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen., and *Renzimys* Scr. Geol., Spe. Issue. 1, 133–252.

Furió, M., Casanovas-Vilar, I., Van den Hoek Ostende, L. W., 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. Palaeogeogr., Palaeoclimatol., Palaeoecol. 304 , 219–29. http://doi.org/10.1016/j.palaeo.2010.01.039

Furió, M., van den Hoek Ostende, L.W, Agustí, J., Minwer-Barakat, R., 2017. Evolución de las asociaciones de insectívoros (Eulipotyphla, Mammalia) en España y su relación con los cambios climáticos del Neógeno y el Cuaternario. Ecosist. 27, 38–51. http://doi.org/10.7818/re.2014.27-1.00

Hartenberger, J. L., 1998. Description de la des Rodentia (Mammalia) du Paléocène supérieur au Miocène; incidences phylogénétiques. C. R. Acad. Sci. Paris Sciences de la Terre et des Planètes 326, 439–444.

Herskovitz, P. 1967. Dynamics of rodent molar evolution: a study based on New World cricetinae, family Muridae. J. Dent. Res. 46 suppl. to num. 5, 829–842.

Hilgen, F. J., Lourens L. J., Van Dam, J. A., 2012. The Neogene period, in: Gradstein, F. M., Ogg, J. G., Schmitz, M., Ogg, G. (Eds.), The Geologic Time Scale 2012. Elsevier, Amsterdam, pp. 923–978. http://doi.org/10.UI I6/B978-0-444-5942S-9.00029-9

Hordijk, K., Bosma, A., De Bruijn, H., Van Dam, J., Geraedts, C., Van den Hoek Ostende, L.W., Reumer, J., Wessels, W. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos 2, Teruel Basin, Spain. Palaeobio. Palaeoenv. 95, 321–346. http://doi.org/10.1007/s12549-015-0203-2

Jacobs, L. L., 1977. A new genus of Murid Rodent from the Miocene of Pakistan and comments on the origin of the Muridae. PaleoBios 25, 1–11.

Jacobs, L. L., Downs, W. R., 1994. The evolution of murine rodents in Asia, in: Y. Tomida, Y., Li, C., Setoguchi, T. (Eds.), Rodent and Lagomorph Families of Asian Origins and Diversification. Nat. Sci. Mus. Monogr. 8, 149–56.

Jiménez-Moreno, G., Suc, J-P., 2007. Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen records. Palaeogeogr., Palaeoclimatol., Palaeoecol. 253, 208–25. http://doi.org/10.1016/j.palaeo.2007.03.040

Jiménez-Moreno, G., Fauquette,S., Suc J-P., 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Rev. Palaeobot. Palynol. 162, 403–415. http://doi.org/10.1016/j.revpalbo.2009.08.001

Jovells-Vaqué, S., Ginestí, M., Casanovas-Vilar, I., 2017. Cricetidae (Rodentia, Mammalia) from the early Miocene site of els Casots (Vallès-Penedès Basin, Catalonia). Foss. Impr. 73, 141–154. http://doi.org/10.1515/if-2017-0007

Jovells-Vaqué, S., García-Paredes, I., Furió, M., Angelone, C., Van den Hoek Ostende, L. W., Barberà, M. B., DeMiguel, D., Madurell-Malapeira, J., Casanovas-Vilar, J., 2018. Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). Hist. Biol. 30, 404–421. http://doi.org/10.1080/08912963.2017.1317768

Jovells-Vaqué, S., Casanovas-Vilar, I. 2018. A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallès-Penedès Basin (Catalonia). J. Vertebr. Paleontol. 38,5. https://doi.org/10.1080/02724634.2018.1520714

Kälin, D., 1999. Tribe Cricetini, in: Rössner,G., Heissig, K. (Eds.), The Miocene Land Mammals of Europe, Munich, pp. 373–387.

Kälin, D., Kempf, O., 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrb. Geol. Paläontol.-Abh. 254, 177–235. http://doi.org/10.1127/0077-7749/2009/0010

Lartet, E., 1851. Notice sur la colline de Sansan, suivie d'une récapitulation des diverses espèces d'animaux vertébrés fossiles trouvés soit à Sansan, soit dans d'autres gisements du terrain Miocène dans le bassin sous-pyrénéen. J.A. Portes, Auch, 45 p.

Lindsay, E. H., 1988. Cricetid rodents from Siwalik deposits near Chinji Village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae. Palaeovertebrata 18, 95–154.

Lindsay, E., 2008. Cricetidae, in: Janis, C.M., Gunnell, G.F., Uhen, M.D. (Eds.), Evolution of Tertiary Mammals of North America, Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, New York, pp. 456-479.

Madern, P.A., Van den Hoek Ostende, L. W., 2015. Going south: latitudinal change in mammalian biodiversity in Miocene Eurasia. Palaeogeogr., Palaeoclimatol., Palaeoecol. 424, 123–31. http:// doi.org/10.1016/j.palaeo.2015.02.011

Magné, J., 1978. Études microstratigraphiques sur le Néogène de la Méditerrané Nord-Occidentale. Vol. I: les bassins néogènes catalans (Doctoral dissertation). Université Paul Sabatier, CNRS, Toulouse, 259 p.

Maridet, O., 2003. Révision du genre Democricetodon (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occientale: évolution, paléobiodiverstié et paléobiogéographie (Doctoral dissertation). Université Claude Bernard-Lyon, Lyon, 252 p.

Maridet, O., 2011. Earliest occurrence of Democricetodon In China , in the Early Miocene of the Junggar Basin (Xinjiang), and comparison with the genus Spanocricetodon, (October 2015). Vertebr. PalAsiat. 49, 393–405. http://doi.org/1000-3118(2011)04-0393-13

Maridet, O., Escarguel, G., Costeur, L., Mein, P., Hugueney, M., Legendre, S., 2007. Small mammal (rodents and lagomorphs) European biogeography from the Late Oligocene to the mid Pliocene. Global Ecol. Biogeogr. 16, 529–544. https://doi.org/10.1111/j.1466-8238.2006.00306.x

Maridet, O., Costeur, L., Legendre, S., 2013. European Neogene rodent communities: explaining family-level replacement through a spatiotemporal approach. Hist. Biol. 25, 655–677. https://doi.org/10.1080/08912963.2012.739170

McKenna, M.C., Bell, S.K., 1997. Classification of mammals above the species level. Columbia University Press, New York, xii + 631 p.

Mein, P., 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges. – Nouv. Arch. Mus. Hist. Nat. Lyon 5, 1–122.

Mein, P., 1999. European Miocene Mammal Biochronology., in: Rössner, G. E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, pp. 25–38.

Meng, J., Yaoming, H., Chuankui, L., 2003. The Osteology of Rhombomylus (Mammalia, Glires): Implications for phylogeny and evolution of Glires. Bull. Am. Mus. Nat. Hist. 275, 1–247. http://doi.org/10.1206/0003090(2003)275<0001:TOORMG>2.0.CO;2

Oliver, A., Peláez-Campomanes, P., 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon*. J. Vertebr. Paleontol. 33, 943–955. http://doi.org/10.1080/02724634.2013.743896

Oliver, A., Peláez-Campomanes, P., 2014. Evolutionary patterns of early and middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia) from Spain. Palaeontogr. Abt. A 303, 85–135. http://doi.org/10.1127/pala/303/2014/85

Oliver, A., Pelaez-Campomanes, P., 2016 Early Miocene evolution of the rodent *Megacricetodon* in Europe and its paleobiogeographical implications. Act. Palaeontol. Pol. 61, 211–219. http://doi.org/10.4202/app.00099.2014

Oliver Pérez, A., 2015. Evolution of *Megacricetodon* from the Aragonian and Vallesian (Miocene) of the Iberian Peninsula (Doctoral dissertation). Universidad Complutense de Madrid, Madrid, 326 p.

Ortí, F., Pueyo, J. J., 1976. Yeso primario y secundario del depósito de Vilobí (Provincia de Barcelona, España). Rev. Inst. Invest. Geol. Diput. Barcelona 31, 5–34.

Prieto, J., Rummel, M., 2016. Some considerations about the small-mammal evolution in South Germany, with emphasis on late Burdigalian-earliest Tortonian (Miocene) cricetid rodents. C. R. Palevol. 15, 837–854. https://doi.org/10.1016/j.crpv.2016.08.002

Qiu, Z., Qiu, Z., Deng, T., Li, C., Zhang, Z., Wang, B-Y., Wang, X., 2013. Neogene land mammal stages/ages of China: toward the goal to establish an Asian land mammal stage/age scheme, in: Wang, X., Flynn, L., Fortelius, M., (Eds.), Fossil Mammals of Asia. Neogene Biostratigraphy and Chrnology. Columbia University Press, New York, pp. 91–123.

R Core Team. 2017. R: A language and environment for statistical computing. R Found ation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roca, E., Sans, M., Cabrera, L., Marzo, M., 1999. Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). Tectonophys. 315, 209–229. https://doi.org/10.1016/S0040-1951(99)00289-9

Ruiz-Sánchez, F. J., Santisteban Bové, C., Lacomba, J. I., 2003. Nuevas faunas de roedores fósiles (Mammalia, Rodentia) de edad Aragoniense inferior y medio en la serie del Barranco de Morteral (Cuenca Del Río Magro, Prov. de Valencia, España). Col. Paleontol., 579–594.

Steppan, S., Adkins, R., Anderson, J., 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biol. 53, 533–553. http://doi.org/10.1080/10635150490468701

Steppan, S. J., Schenk, J. J., 2017. Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. PLoS One 12, e0183070. http://doi.org/10.1371/journal.pone.0183070

Suárez-Hernando, O., 2017. Magnetobiocronología y paleoecología del Mioceno inferior-medio en las Bardenas Reales de Navarra (cuenca del Ebro) (Doctoral dissertation). Euskal Herriko Unibertsitatea, Leioa, 315 p.

Theocharopoulos, K. D., 2000. Late Oligocene-Middle Miocene *Democricetodon, Spanocricetodon* and *Karydomys* nov. gen. from the eastern Mediterranean area. Gaia 8, 1–92.

Van Dam, J. A., 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe. The use of small mammals as paleoprecipitation proxies.

Palaeogeogr. Palaeoclimatol. Paleoecol. 238, 190–218. http/doi.org/10.1016/j.palaeo.2006.03.025

Van Dam, J.A., Weltje, G.J. 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity succession: an application of end-member modelling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 151, 267–305. https://doi.org/10.1016/S0031-0182(99)00015-2

Van den Hoek Ostende, L. W., Casanovas-Vilar, Furió, M. In press. Stuck in the middle. A geographical appraisal of the oldest insectivores – and a marsupial – from the Vallès-Penedès (early Miocene, Catalonia, Spain). C. R. Palevol.

Van der Meulen, A.J., de Bruijn, H. 1982. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece). Part II, The Gliridae. Proc. K. Ned. Akad. Wetensc. B 85, 485–524.

Van der Meulen, A.J., Daams, R. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 93, 227–253. https://doi.org/10.1016/0031-0182(92)90099-Q

Van der Meulen, A. J., Pélaez-Campomanes, P., Daams, R., 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel Basin (Zaragoza, Spain). Col. Paleontol. 1, 385–441.

Van der Meulen, A. J., García-Paredes, J. I., Alvarez Sierra, M.A., van den Hoek Ostende L.W., Hordijk, K., Oliver, A., Pélaez-Campomanes, P., 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geol. Acta. 10,159–179. http://doi.org/ 10.1344/105.000001710

Wessels, W., Theocharopoulos, K. D., Bruijn, H., Ünay, E., 2001. Myocricetodontinae and Megacricetodontini (Rodentia) from the lower Miocene of NW Anatolia. Lynx 32, 321–388.

Wessels, W. 2009. Miocene Rodent Evolution and Migration. Muroidea from Pakistan, Turkey and Northern Africa. Geologica Ultraiectina 307, 11-297.

Wessels, W., Reumer, B. M., 2009. *Democricetodon* and *Megacricetodon* (Mammalia, Cricetidae) from the Miocene of Sandelzhausen, Southern Germany. Paläontol. Z. 83, 187–205. http://doi.org/10.1007/s12542-009-0006-8

Wilson, D. E., Reeder, D. M. (Eds.), 2005. Mammal Species of the World. A Taxonomic and Geographic Reference. Volume 2. Johns Hopkins University Press, Baltimore, Maryland, pp. 1–2142.

Zachos, J. C., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693. http://doi.org/10.1123/science.1059412.

Ziegler, R., 1999. Order Insectivora, in: Rössner, G. E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, pp. 53-74.

Table 1–6: Summary measurements (in mm) of Democricetodon hispanicus, D. gracilis, D. cf. decipiens and Democricetodon sp. 4 from different early Miocene sites of the Vallès-Penedès Basin. Only complete specimens were measured. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and 1659 Freudenthal (1988: 42, Fig. 1).

Tableau 1–6: Mesures résumées (en mm) de Democricetodon hispanicus, D. gracilis, D. cf. decipiens et Democricetodon sp. 4 de différentes localités du Miocène inférieur du Bassin du Vallès-Penedès. Seuls les spécimens complets ont été mesurés. Les 1663 acronymes des localités et les abréviations des mesures sont expliqués dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1).

Table 7–12: Summary measurements (in mm) of Megacricetodon primitivus from different early Miocene sites of the Vallès-Penedès Basin. Only complete specimens were measured. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and Freudenthal (1988: 42, Fig. 1).

Tableau 7–12. Mesures résumés (en mm) de Megacricetodon primitivus de différentes localités du Miocène inférieur du Bassin du Vallès-Penedès. Seuls les spécimens complets ont été mesurés. Les acronymes des localités et les abréviations des mesures sont expliqués dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1).

Table 1. Summary statistics for *Democricetodon* M1.

M1	**L**					**W**					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**Mean**	**max.**	**s.d.**	**N**	**species**
SM	-	1.87	-	-	1	-	1.20	-	-	1	*D.* cf. *decipiens*
VI	-	1.91	-	-	1	-	1.25	-	-	1	*D.* cf. *decipiens*
SM	1.54	-	1.58	-	2	0.99	-	1.03	-	2	*D.gracilis*
CS74	1.58	1.69	1.77	0.07	8	1.05	1.12	1.19	0.05	10	*D.hispanicus*
CMV3	1.47	1.52	1.63	-	3	1.04	1.05	1.08	-	3	*D.hispanicus*
LCV1	1.61	1.64	1.66	-	3	0.93	1.03	1.09	-	3	*D.hispanicus*
EC	-	1.63	-	-	1	-	1.17	-	-	1	*D.hispanicus*

Table 2. Summary statistics for *Democricetodon* M2.

M2	**L**					**W**					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**	**species**
MOR1	-	1.6	-	-	1	-	1.2	-	-	1	*D.* sp. 4
SM	-	1.34	-	-	1	-	1.17	-	-	1	*D.* cf. *decipiens*
PA	-	1.39	-	-	1	-	-	-	-	-	*D.* cf. *decipiens*
VI	1.29	-	1.45	-	2	1.18	-	1.23	-	2	*D.* cf. *decipiens*
SM	1.18	-	1.2	-	2	1.01	-	1.07	-	2	*D.gracilis*
CS74	0.93	1.25	1.49	0.16	13	0.84	1.07	1.16	0.09	14	*D.hispanicus*
CMV3	1.06	1.22	1.35	0.10	8	0.97	1.09	1.16	0.07	8	*D.hispanicus*
LCV1	1.06	1.25	1.33	0.09	8	0.93	1.06	1.14	0.06	8	*D.hispanicus*
EC	1.29	-	1.30	-	2	1.06	-	1.13	-	2	*D.hispanicus*

Table 3. Summary statistics for *Democricetodon* M3.

M3	**L**					**W**					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**	**species**
VI	-	0.93	-	-	1	-	1.01	-	-	1	*D.* cf. *decipiens*
CS74	0.73	0.84	0.91	-	3	0.77	0.88	0.96	-	3	*D.hispanicus*
CS73	-	0.93	-	-	1	-	0.98	-	-	1	*D.hispanicus*
CS72	0.7	-	0.94	-	2	0.75	-	0.97	-	2	*D.hispanicus*
CMV3	0.91	-	0.96	-	2	0.95	-	0.96	-	2	*D.hispanicus*
LCV1	0.81	0.88	0.93	-	3	0.88	0.91	0.95	-	3	*D.hispanicus*

Table 4. summary statistics for *Democricetodon* m1.

m1	L					W					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**	**species**
CS73	-	1.67	-	-	1	-	1.08	-	-	1	*D.* sp. 4
VI	1.48	-	1.56	-	-	0.80	0.98	1.09	-	3	*D.* cf. *decipiens*
VI	1.21	-	1.35	-	2	0.86	-	0.89	-	2	*D.gracilis*
SM	-	1.28	-	-	1	-	0.91	-	-	1	*D.gracilis*
CS73	-	1.28	-	-	1	-	0.92	-	-	1	*D.gracilis*
CCW	-	1.37	-	-	1	-	0.90	-	-	1	*D.gracilis*
CS74	1.4	1.44	1.49	0.03	12	0.93	0.97	1.01	0.02	12	*D.hispanicus*
CS73	1.42	1.48	1.57	0.05	8	0.94	0.98	1.11	0.05	8	*D.hispanicus*
CSU	-	1.31	-	-	1	-	0.86	-	-	1	*D.hispanicus*
CMV3	1.32	1.39	1.48	-	5	0.96	1.01	1.06	-	5	*D.hispanicus*
LCV1	1.38	1.45	1.50	-	3	0.96	0.98	1.00	-	3	*D.hispanicus*

Table 5. Summary statistics for *Democricetodon* m2.

m2	L					W					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**	**species**
MOR1	-	1.51	-	-	1	-	1.31	-	-	1	*D.* sp. 4
PA	-	1.31	-	-	1	-	1.21	-	-	1	*D.* cf. *decipiens*
VI	1.26	-	1.33	-	2	1.01	1.12	1.17	-	3	*D.* cf. *decipiens*
SM	-	1.13	-	-	1	-	0.96	-	-	1	*D.gracilis*
CCW	-	1.17	-	-	1	-	0.99	-	-	1	*D.gracilis*
CS74	1.19	1.26	1.39	0.06	15	0.93	1.07	1.20	0.07	15	*D.hispanicus*
CSU	1.15	1.22	1.29	-	3	1.03	1.05	1.07	-	3	*D.hispanicus*
CMV3	-	1.12	-	-	1	-	0.91	-	-	1	*D.hispanicus*
LCV1	1.06	1.21	1.31	0.1	10	0.88	0.97	1.05	0.07	10	*D.hispanicus*

Table 6. summary statistics for *Democricetodon* m3.

m3	L					W					
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**	**species**
PA	-	1.21	-	-	1	-	1.04	-	-	1	*D.* cf. *decipiens*
VI	-	1.11	-	-	1	-	0.81	-	-	1	*D.gracilis*
SM	0.97	-	1.02	-	2	-	0.85	-	-	2	*D.gracilis*
CCW	-	0.99	-	-	1	-	0.77	-	-	1	*D.gracilis*
CS74	1.09	1.17	1.23	0.05	7	0.88	0.92	0.95	0.02	6	*D.hispanicus*
CS73	1.09	1.11	1.14	0.02	5	0.9	0.94	1	0.03	5	*D.hispanicus*
CMV3	-	1.24	-	-	1	-	0.89	-	-	1	*D.hispanicus*
CMV2	-	1.12	-	-	1	-	0.94	-	-	1	*D.hispanicus*
LCV1	1.11	1.14	1.19	-	3	0.899	0.92	0.94	-	3	*D.hispanicus*

Table 7. Summary statistics for *Megacricetodon primitivus* M1

M1	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	1.41	1.50	1.64	0.07	12	0.94	0.99	1.07	0.03	11
VI	1.37	1.45	1.58	0.06	23	0.89	0.95	1.07	0.05	24
CSU	-	1.51	-	-	1	1.00	-	1.02	-	2
CS73	1.32	1.45	1.64	0.12	7	0.88	0.97	1.16	0.10	7
CS74	1.40	1.46	1.53	0.06	5	0.87	0.93	1.05	0.07	5
CMV3	1.31	1.44	1.55	0.07	10	0.77	0.91	0.97	0.04	18
LCV1	1.34	1.43	1.91	0.17	11	0.83	0.90	1.03	0.06	12

Table 8. Summary statistics for *Megacricetodon primitivus* M2.

M2	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	0.99	1.09	1.17	0.04	14	0.86	0.94	1.02	0.04	14
VI	1.01	1.08	1.22	0.05	40	0.81	0.90	0.97	0.04	41
CSU	-	-	-	-	-	-	0.98	-	-	1
CS72	0.98	-	1.11	-	2	0.95	-	0.98	-	2
CS74	1.10	-	1.14	-	2	0.83	-	0.92	-	2
CMV3	0.97	1.05	1.12	0.04	18	0.80	0.88	0.94	0.03	18
CMV1	-	1.05	-	-	1	-	0.96	-	-	1
LCV1	0.96	1.05	1.11	0.03	15	0.77	0.87	0.96	0.04	16

Table 9. Summary statistics for *Megacricetodon primitivus* M3

M3	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	0.71	0.77	0.86	-	4	0.75	0.79	0.86	-	4
VI	0.77	0.92	0.92	-	2	0.76	0.93	0.96	-	2
CS72	0.64	-	0.65	-	2	0.74	-	0.75	-	2
CS73	-	0.84	-	-	1	-	0.72	-	-	1
CS74	-	0.75	-	-	1	-	0.71	-	-	1
CMV3	0.64	0.73	0.82	0.04	13	0.67	0.74	0.83	0.05	13
CMV1	0.66	0.70	0.73	-	3	0.68	0.75	0.81	-	3
LCV1	0.68	0.76	0.78	0.10	3	0.66	0.70	0.79	0.10	3

Table 10. Summary statistics for *Megacricetodon primitivus* m1.

m1	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	1.48	1.38	1.48	0.07	7	0.78	0.84	0.94	0.05	7
VI	1.21	1.33	1.47	0.06	19	0.75	0.81	0.89	0.03	22
SM	-	[1.37]	-	-	1	-	[0.92]	-	-	1
CSU	-	1.34	-	-	1	-	0.82	-	-	1
CS72	1.31	1.36	1.39	-	3	0.85	1.36	1.39	-	3
CS73	1.10	1.27	1.40	0.11	5	0.64	0.77	0.84	0.09	6
CS74	1.08	1.35	1.45	0.09	17	0.76	0.85	0.93	0.04	18
CMV3	1.18	1.25	1.33	0.05	18	0.69	0.81	0.90	0.04	18
CMV1	1.14	1.18	1.27	-	3	0.73	-	0.83	-	2
LCV1	1.13	1.23	1.35	0.05	16	0.71	0.79	0.88	0.04	17

Table 11. Summary statistics for *Megacricetodon primitivus* m2.

m2	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	0.95	1.12	1.20	0.06	18	0.70	0.91	0.97	0.05	19
VI	0.99	1.09	1.15	0.04	30	0.78	0.90	0.99	0.04	32
CSU	-	1.10	-	-	1	-	0.91	-	-	1
CS72	1.01	1.06	1.13	-	3	0.81	0.84	0.87	-	3
CS74	1.03	1.09	1.09	0.05	12	0.82	0.89	0.98	0.05	12
CMV3	0.98	1.05	1.10	0.03	17	0.80	0.85	0.91	0.02	17
CMV2	-	1.10	-	-	1	-	0.89	-	-	1
LCV1	0.85	1.02	0.85	0.06	15	0.72	0.84	0.95	0.04	15

Table 12. Summary statistics for *Megacricetodon primitivus* m3.

m3	**L**					**W**				
locality	**min.**	**mean**	**max.**	**s.d.**	**N**	**min.**	**mean**	**max.**	**s.d.**	**N**
PA	0.87	0.93	1.00	-	4	0.70	0.76	0.84	-	4
VI	0.87	0.92	1.00	0.04	13	0.66	0.73	0.92	0.07	13
CS73	-	1.00	-	-	1	-	0.81	-	-	1
CS74	0.84	0.92	1.08	0.09	5	0.72	0.74	0.77	0.02	5
CMV3	0.70	0.84	0.92	0.05	17	0.57	0.68	0.74	0.04	18
LCV1	0.79	0.83	0.89	-	4	0.68	0.69	0.71	-	4

The Annexes A to D of this article are localted in the appendices 2 and 3 of the present tesis. The more detailed information of its content is provided below.

Appendix A: Catalogue number and length and width measurements (in mm) of Democricetodon hispanicus, D. gracilis, D. cf. decipiens and Democricetodon sp. 4 from different early Miocene sites of the Vallès-Penedès Basin. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and Freudenthal (1988: 42, Fig. 1).

Annexe A: Numéro de catalogue et dimensions (en mm) de Democricetodon hispanicus, D. gracilis, D. cf. decipiens et Democricetodon sp. 4 de différentes localités du Miocène inférieur du Bassin du Vallès-Penedès. Les acronymes des localités et les abréviations des mesures sont expliqués dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1).

Appendix B: Morphotype frequency tables for the Democricetodon species. For locality acronyms see section 3.2. of the main text. For details on morphotype coding see section 3 and references therein.

Annexe B: Tableaux de fréquence de morphotypes pour les espèces de Democricetodon. Pour les acronymes des localités, voir section 3.2. dans le texte principal. Pour détails sur la définition des morphotyes, voir la section 3 et références qi y sont citées.
Appendix C: Catalogue number and length and width measurements (in mm) of Megacricetodon primitivus from different early Miocene sites of the Vallès-Penedès Basin. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and Freudenthal (1988: 42, Fig. 1).

Annexe C: Numéro de catalogue et dimensions (en mm) de Megacricetodon primitivus de différentes localités du Miocène inférieur du Bassin du Vallès-Penedès. Les acronymes des localités et les abréviations des mesures sont expliqués dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1).

Appendix D: Morphotype frequency tables for Megacricetodon primitivus. For locality acronyms see section 3.2. of the main text. For details on morphotype coding see section 3 and references therein.
Annexe D: Tableaux de fréquence de morphotypes pour Megacricetodon primitivus. Pour les acronymes des localités, voir section 3.2. dans le texte principal. Pour détails sur la définition des morphotyes, voir la section 3 et références qi y sont citées.

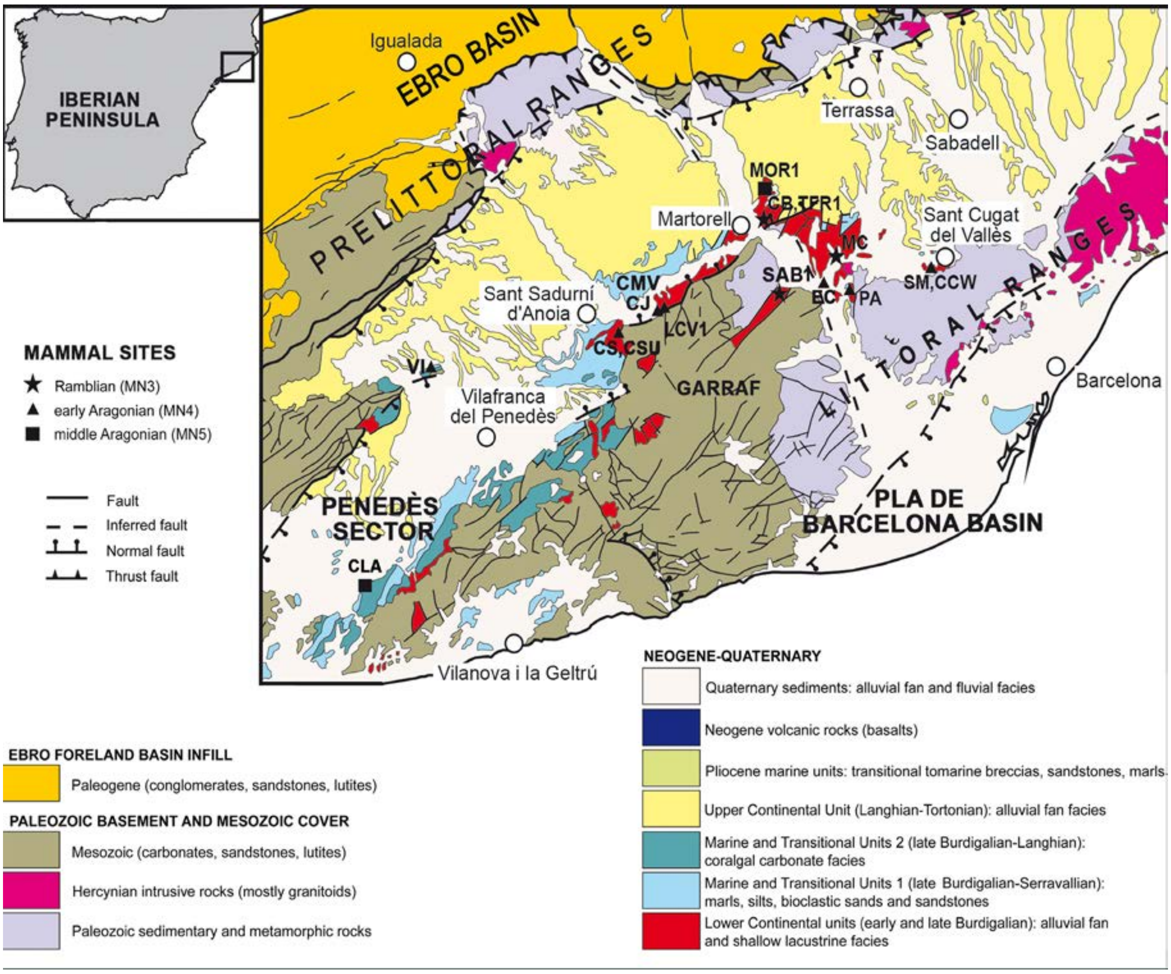


Figure 1: Geographical location and simplified geological map of the Vallès-Penedès Basin indicating the main mammal localities ranging from MN3 to MN5 (modified from Casanovas-Vilar et al., 2016). For locality acronyms see section 3.2. of the main text.

Figure 1: Situation géographique et carte géologique simplifiée du Bassin de Vallès-Penedès montrant les principales localités de mammifères de MN3 à MN5 (modifiées de Casanovas-Vilar et al., 2016). Pour les acronymes des localités, voir la section 3.2. dans le texte principal.

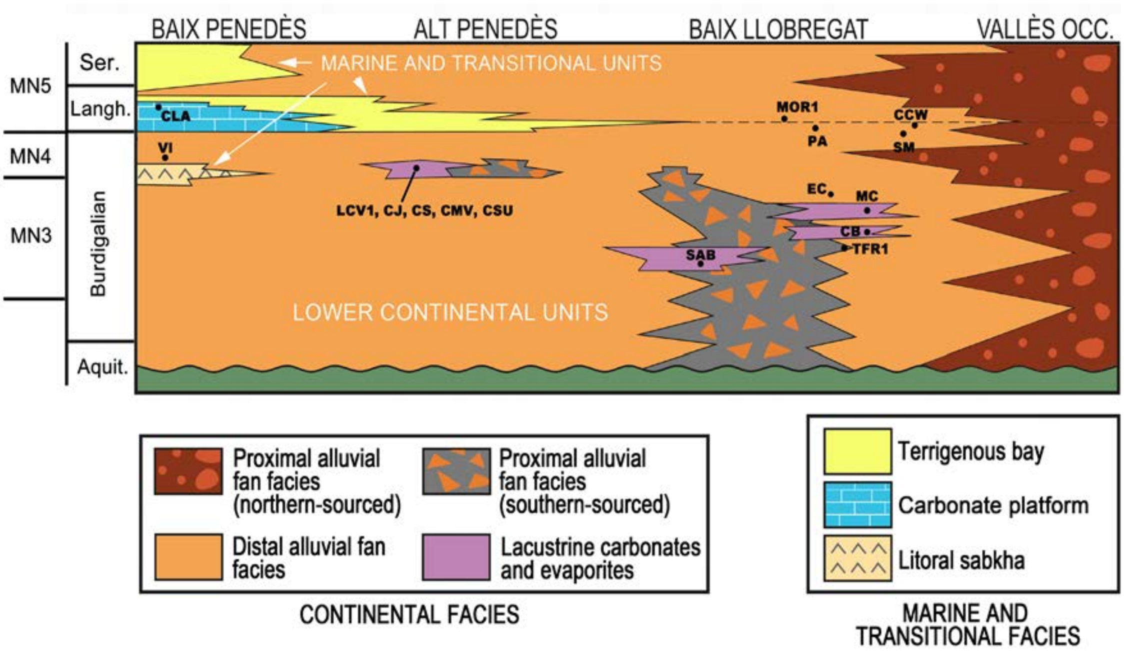


Figure 2: Generalized stratigraphic framework of the early to early middle Miocene sedimentary record of the Vallès-Penedès Basin showing the main lithostratigraphic units and their relationships (modified after Cabrera et al., 1991 and De Gibert and Casanovas Vilar, 2011). Note the different early Miocene lacustrine systems (including most localities) as well as the marine deposits associated to the Langhian transgression. For locality acronyms see section 3.2. of the main text.

Figure 2: Cadre stratigraphique généralisé des enregistrements sédimentaires du Miocène inférieur au Miocène moyen du Bassin de Vallès-Penedès montrant les principales unités lithostratigraphiques et leurs relations (modifié d'après Cabrera et al., 1991 et De Gibert et Casanovas Vilar, 2011). Notez les différents systèmes lacustres du Miocène inférieur (ils comprennent la plupart des localités) ainsi que les dépôts marins associés à la transgression du Langhien. Pour les acronymes des localités, voir la section 3.2. dans le texte principal.

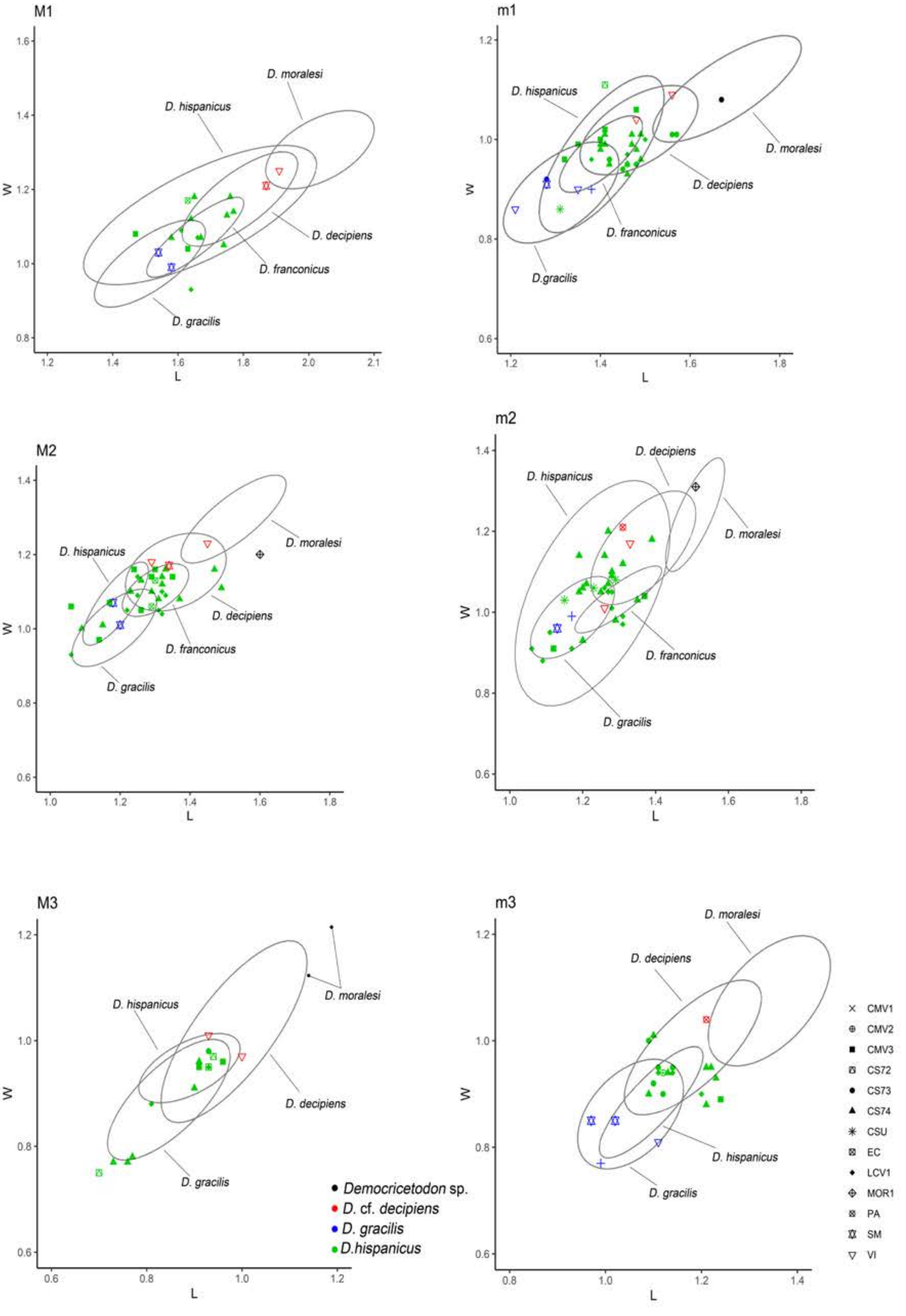

M1
W
L
1.6
1.4
1.2
1.0
0.8
1.2
1.4
1.6
1.8
2.0
2.1
D. moralesi
D. hispanicus
D. decipiens
D. franconicus
D. gracilis
m1
W
L
1.2
1.0
0.8
0.6
1.2
1.4
1.6
1.8
D. hispanicus
D. moralesi
D. decipiens
D. franconicus
D.gracilis
M2
W
L
1.4
1.2
1.0
0.8
0.6
1.0
1.2
1.4
1.6
1.8
D. hispanicus
D. moralesi
D. decipiens
D. franconicus
D. gracilis
m2
W
L
1.4
1.2
1.0
0.8
0.6
1.0
1.2
1.4
1.6
1.8
D. decipiens
D. hispanicus
D. moralesi
D. franconicus
D. gracilis
M3
W
L
1.2
1.0
0.8
0.6
0.6
0.8
1.0
1.2
D. hispanicus
D. moralesi
D. decipiens
D. gracilis
Democricetodon sp.
D. cf. decipiens
D. gracilis
D.hispanicus
m3
W
L
1.2
1.0
0.8
0.6
0.8
1.0
1.2
1.4
D. moralesi
D. decipiens
D. hispanicus
D. gracilis
CMV1
CMV2
CMV3
CS72
CS73
CS74
CSU
EC
LCV1
MOR1
PA
SM
VI

Figure 3: Length/width scatter plot for Democricetodon hispanicus, D. gracilis, D. cf. decipiens and D. sp. 4 from different Vallès-Penedès sites. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and Freudenthal (1988: 42, Fig. 1). The ellipses show the 95 % confience interval for the following species: Democricetodon hispanicus from Villafeliche 2A, D. moralesi from La Col D and D. franconicus from La Col D, (data provided by P. Peláez-Campomanes, Museo Nacional de Ciencias Naturales, Madrid), D. gracilis and D. mutilus from Sandelzhausen (Wessels and Reumer, 2009) and D. decipiens from Bunyol (Daams and Freudenthal, 1974).

Figure 3. Diagramme de dispersion de longueur/largeur pour Democricetodon hispanicus, D. gracilis, D. cf. decipiens et D. sp. 4 de différentes localités du Vallès-Penedès. Les acronymes des localités et les abréviations des mesures sont expliqués
dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1). Les ellipses indiquent l'intervalle de confiance de 95% pour les espèces suivantes: Democricetodon hispanicus de Villafeliche 2A, D. moralesi de La Col D et D. franconicus de La Col D, (données fournies par P. Peláez-Campomanes, Museo Nacional de Ciencias 1584 Naturales, Madrid). , D. gracilis et D. mutilus de Sandelzhausen (Wessels and Reumer, 2009) et D. decipiens de Bunyol (Daams and Freudenthal, 1974).

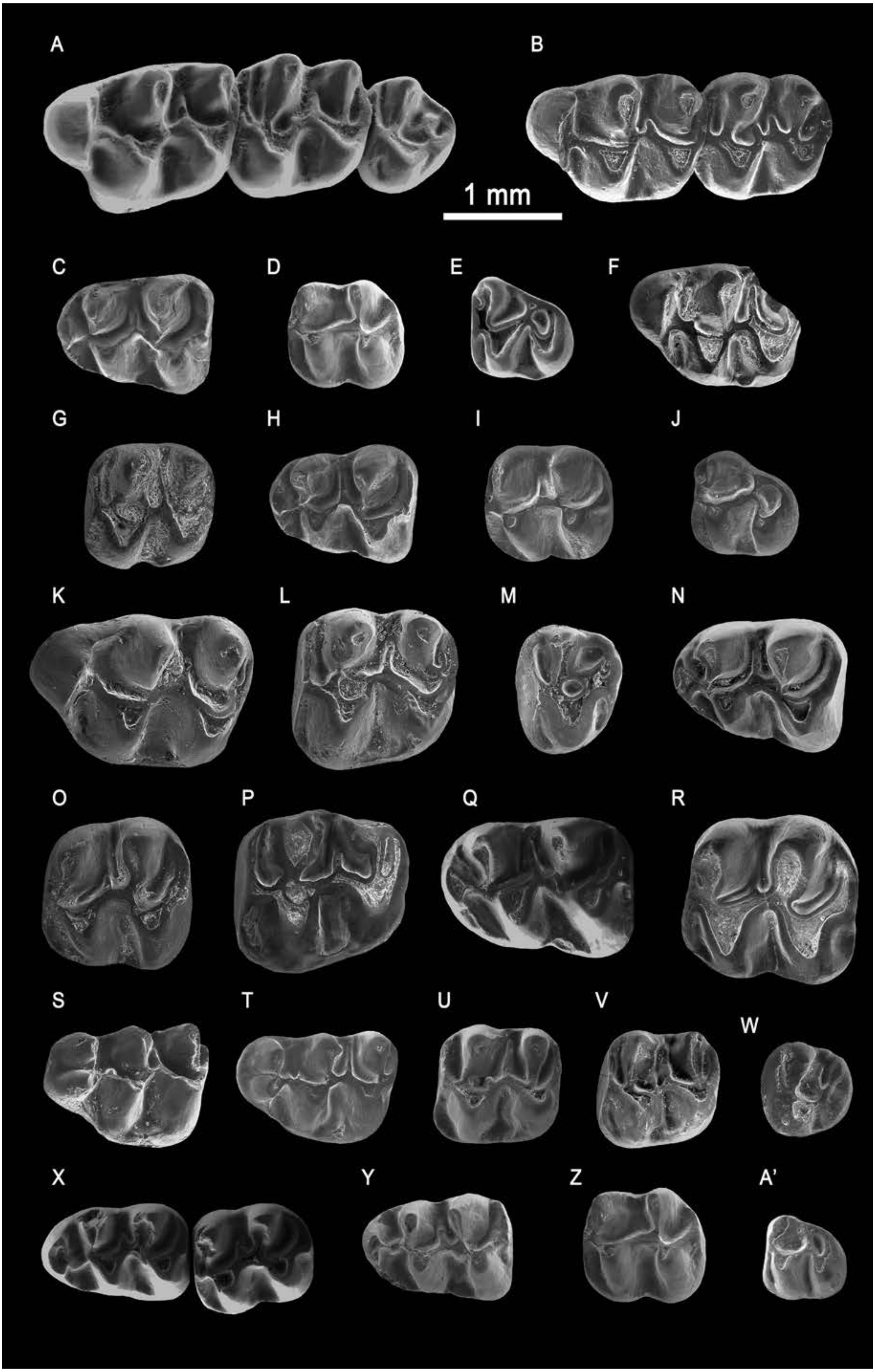

A
B
1 mm
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
A'

Figure 4: Scanning electronic microscope (SEM) micrographs of early Miocene Cricetidae from different sites (indicated in parentheses) of the Vallès-Penedès Basin. Democricetodon hispanicus A: IPS45008, right M1-M3 (reversed) (CS74); B: 1589 IPS19491, right M1-M2 (reversed) (CS74); C: IPS19481, left m1 (CS74); D: IPS88884 left m2 (LCV1); E: IPS86457, right m3 (reversed) (LCV1). Democricetodon gracilis, F: IPS103751 left M1 (SM); G: IPS103753 left M2 (SM); H: IPS103754 left m1 (SM); I: IPS103755, right m2 (reversed) (SM); J: IPS105145 left m3 (SM). Democriceton cf. decipiens, K: IPS19548, left M1(VI); L: IPS87106 left M2 (VI); M: IPS86941 left M3 (VI); N: IPS87109 left m1 (VI); O: IPS86387 left m2 (PA). Democriceton sp. 4, P: IPS88868 left M2 (MOR1); Q: IPS 45052 left m1 (CS73); R: IPS105188 left m2 (MOR1). Megacricetodon primitivus, S: IPS86997 left M1 (VI); T: IPS86432 right M1 (reversed) (LCV1); U: IPS86435 left M2 (LCV1); V: IPS87022 left M2 (VI); W: IPS19479 left M3 (CS74); X: IPS44950 right m1-m2 (reversed) (CS74); Y: IPS86440 left m1(LCV1); Z: IPS86444 left m2 (LCV1); A': IPS86451 right m3 (reversed) (LCV1). For the locality acronyms see section 3.2. of the main text.

Figure 4: Micrographies au microscope électronique à balayage (MEB) de Cricetidae du Miocène inférieur de différents localités (indiqués entre parenthèses) du Bassin de Vallès-Penedès. Democricetodon hispanicus A: IPS45008, M1-M3 droites (inversé) (CS74); B: IPS19491, M1-M2 droites (inversé) (CS74); C: IPS19481, m1 gauche (CS74); D: IPS88884 m2 gauche (LCV1); E: IPS86457, m3 droite (inversé) (LCV1). Democricetodon gracilis, F: IPS103751 M1 gauche (SM); G: IPS103753 M2 gauche (SM); H: IPS103754 m1 gauche (SM); I: IPS103755, m2 droite (inversé) (SM); J: IPS105145 m3 gauche (SM). Democriceton cf. decipiens, K: IPS19548, M1 gauche (VI); L: IPS87106 M2 gauche (VI); M: IPS86941 M3 gauche (VI); N: IPS87109 m1 gauche (VI); O: IPS86387 m2 gauche (PA). Democriceton sp. 4, P: IPS88868 M2 gauche (MOR1); Q: IPS 45052 m1 gauche (CS73); R: IPS105188 m2 gauche (MOR1). Megacricetodon primitivus, S: IPS86997 M1 gauche (VI); T: IPS86432 M1 droite 1613 (inversé) (LCV1); U: IPS86435 M2 gauche (LCV1); V: IPS87022 M2 gauche (VI); W: IPS19479 M3 gauche (CS74); X: IPS44950 m1-m2 droites (inversé) (CS74); Y: IPS86440 m1 gauche (LCV1); Z: IPS86444 m2 gauche (LCV1); A ': IPS86451 m3 droit (inversé) (LCV1). Pour les acronymes des localités, voir section 3.2. dans le texte principal.

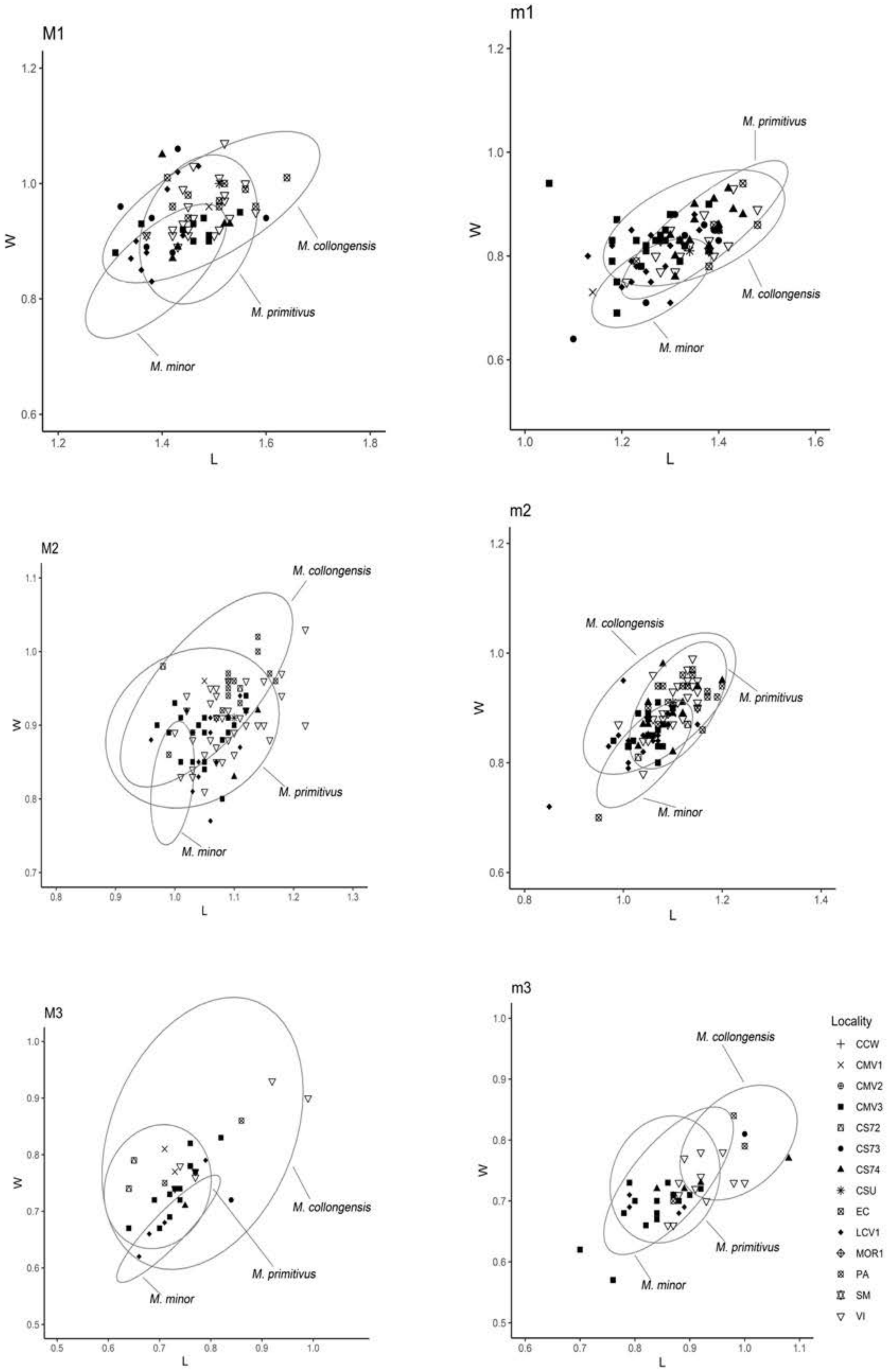

M1
W
L
1.2
1.0
0.8
0.6
1.2
1.4
1.6
1.8
M. collongensis
M. primitivus
M. minor
m1
W
L
1.2
1.0
0.8
0.6
1.0
1.2
1.4
1.6
M. primitivus
M. collongensis
M. minor
M2
W
L
1.1
1.0
0.9
0.8
0.7
0.8
0.9
1.0
1.1
1.2
1.3
M. collongensis
M. primitivus
M. minor
m2
W
L
1.2
1.0
0.8
0.6
0.8
1.0
1.2
1.4
M. collongensis
M. primitivus
M. minor
M3
W
L
1.0
0.9
0.8
0.7
0.6
0.5
0.5
0.6
0.7
0.8
0.9
1.0
M. collongensis
M. primitivus
M. minor
m3
W
L
1.0
0.9
0.8
0.7
0.6
0.5
0.6
0.7
0.8
0.9
1.0
1.1
M. collongensis
M. primitivus
M. minor
Locality
+ CCW
× CMV1
⊕ CMV2
■ CMV3
⊠ CS72
● CS73
▲ CS74
✳ CSU
⊠ EC
◆ LCV1
⊕ MOR1
⊠ PA
⌛ SM
▽ VI

Figure 5: Length/width scatter plot for Megacricetodon primitivus from different Vallès-Penedès sites. Locality acronyms and measurement abbreviations are explained in section 3.2. of the main text. For details on the measurement methods see section 3 and Daams and Freudenthal (1988: 42, Fig. 1). The ellipses show the 95 % confience interval for Megacricetodon primitivus (Oliver and Pelaez-Campomanes, 2014), M. minor (Wessels and Reumer, 2009) and M. collongensis (Mein, 1958).

Figure 5. Diagramme de dispersion de longueur/largeur pour Megacricetodon primitivus de différentes localités du Vallès-Penedès. Les acronymes des localités et les abréviations des mesures sont expliqués dans la section 3.2. du texte principal. Pour détails sur les méthodes de mesure, voir la section 3 et Daams and Freudenthal (1988: 42, Fig. 1). Les ellipses indiquent l'intervalle de confiance de 95% pour Megacricetodon primitivus (Oliver and Pelaez-Campomanes, 2014), M. minor (Wessels and Reumer, 2009) et M. collongensis (Mein, 1958).

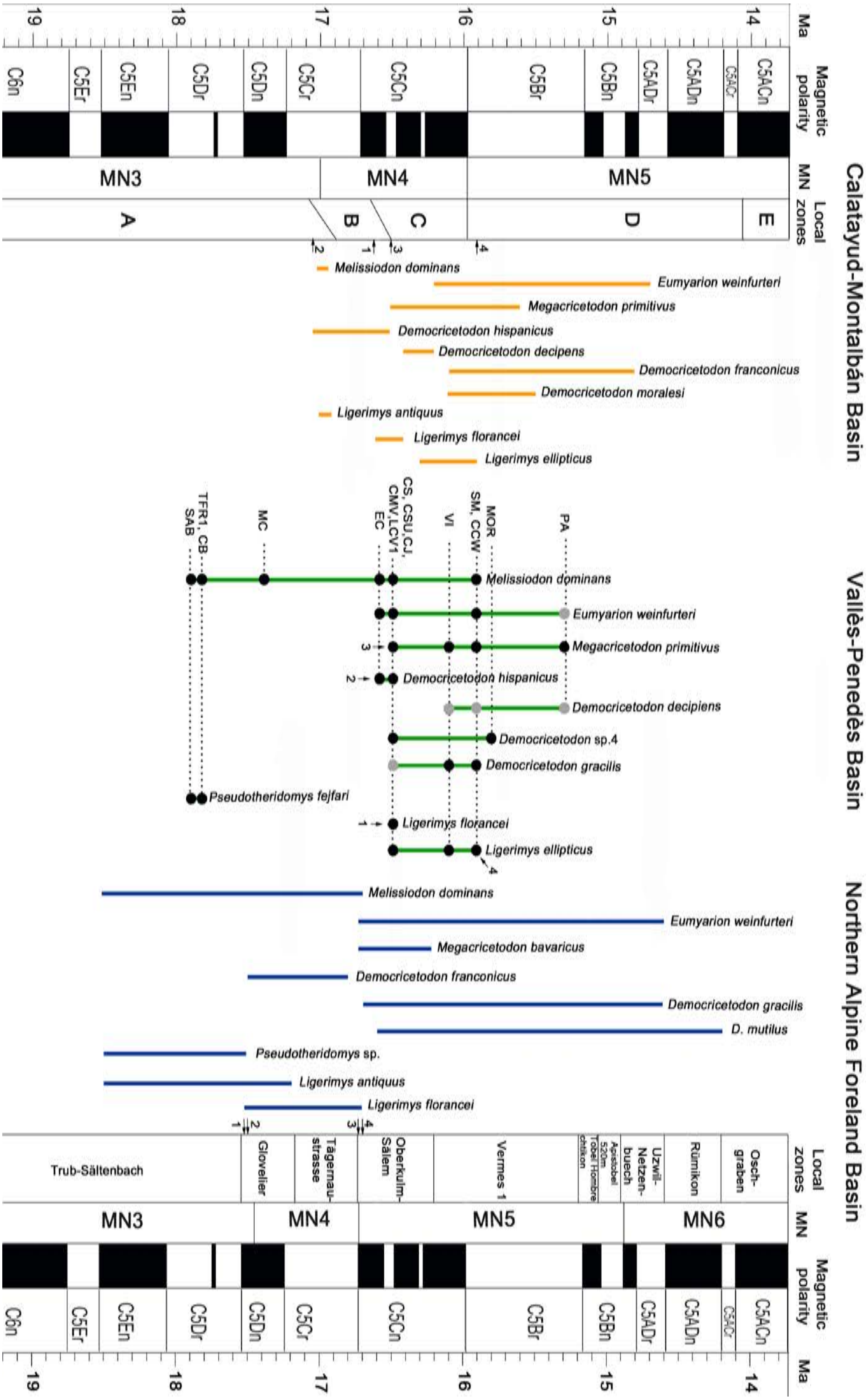
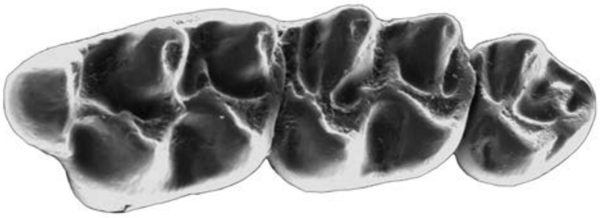

Ma
19
18
17
16
15
14
Magnetic polarity
C6n
C5Er
C5En
C5Dr
C5Dn
C5Cr
C5Cn
C5Br
C5Bn
C5ADr
C5ADn
C5ACr
C5ACn
MN
MN3
MN4
MN5
MN6
Local zones
A
B
C
D
E
Calatayud-Montalbán Basin
1
2
3
4
Melissiodon dominans
Eumyarion weinfurteri
Megacricetodon primitivus
Democricetodon hispanicus
Democricetodon decipens
Democricetodon franconicus
Democricetodon moralesi
Ligerimys antiquus
Ligerimys florancei
Ligerimys ellipticus
Vallès-Penedès Basin
SAB
TFR1, CB
MC
EC
CS, CSU,CJ, CMV,LCV1
VI
SM, CCW
MOR
PA
Melissiodon dominans
Eumyarion weinfurteri
Megacricetodon primitivus
Democricetodon hispanicus
Democricetodon decipiens
Democricetodon sp.4
Democricetodon gracilis
Pseudotheridomys fejfari
Ligerimys florancei
Ligerimys ellipticus
Northern Alpine Foreland Basin
Melissiodon dominans
Eumyarion weinfurteri
Megacricetodon bavaricus
Democricetodon franconicus
Democricetodon gracilis
D. mutilus
Pseudotheridomys sp.
Ligerimys antiquus
Ligerimys florancei
Trub-Sältenbach
Glovelier
Tägernau-strasse
Oberkulm-Sälem
Vermes 1
Tobel Hombrechtikon
Anwil 520m
Uzwil-Netzen-buech
Rümikon
Osch-graben

Figure 6: Biostratigraphic distribution of the early Miocene cricetid species in the Vallès-Penedès Basin. Selected eomyid taxa are also included because of their use in biostratigraphical correlation. Black dots represent the occurrence of a taxon in a given site while grey dots indicate uncertain attribution to that taxon. The Calatayud-Montalbán basin record and local biostratigraphy is after Van der Meulen et al. (2012) while those for the Swiss Molasse Basin is after Kälin and Kempf (2009). Four main biochronlogic events are distinguished: 1) First occurrence (FO) of the eomyid Ligerimys florancei; 2) FO of the cricetid Democricetodon; 3) FO of the cricetid Megacricetodon; 4) Last occurrence (LO) of the eomyid genus Ligerimys. Note the different order and timing of bioevents in the different regions. For locality acronyms see section 3.2. of the main text.

Figure 6: Distribution biostratigraphique des espèces de cricétidés du Miocène inférieur du Bassin du Vallès-Penedès. Des taxons d'éomyidés sélectionnés sont également inclus parce que de leur utilisation en les corrélations biostratigraphiques. Les points noirs représentent l'occurrence d'un taxon dans une localité, les points gris indiquent une attribution incertaine à ce taxon. Le registre et la biostratigraphie locale du Bassin du Calatayud-Montalbán sont d'après Van der Meulen et al., 2012, celles du Bassin de la Molasse suisse sont après Kälin and Kempf (2009). On distingue quatre événements biochronologiques principaux: 1) Première apparition (FO) de l'éomyide Ligerimys florancei; 2) FO du cricétidé Democricetodon; 3) FO du cricétidé Megacricetodon; 4) Dernière apparition (LO) du genre d'éomyidés Ligerimys. On remarque les différents ordres et chronologies d'évènements biologiques dans les différentes régions. Pour les acronymes des localités, voir section 3.2. dans le texte principal



Chapter 10: Discussion

CHAPTER 10: DISCUSSION

This dissertation reviews the cricetid rodent record from the early to early middle Miocene of the Vallès-Penedès Basin, further discussing its biostratigraphical, paleobiogeographical and paleoecological implications. The main body of the thesis, chapters 5 to 9, provides a systematic study of particular taxa and localities. These deal mostly with the description of dental remains in order to identify the species present and provide sound systematic and biostratigraphical conclusions. However, cranial and postcranial remains of *Democricetodon hispanicus* are also briefly described in chapter 8, and the whole small mammal fauna from les Cases de la Valenciana site is described in detail in chapter 6. Therefore, since every chapter includes its own discussion and conclusions, here only the systematic results for cricetid rodents will be briefly summarized. (chapter 10.1). On the other hand, greater attention will be devoted to biostratigraphy and biochronology (chapter 10.2-10.3), incorporating into the discussion unpublished results of recent magnetostratigraphic studies and the review of the large mammal fauna. In addition, a final section in which the small mammal faunas are used to reconstruct the paleoenvironmental changes that took place in the Vallès-Penedès Basin during the early and early middle Miocene is included (chapter 10.4).

10.1 SYSTEMATIC PALEONTOLOGY

Four cricetid genera are present in the early to early middle Miocene (late Ramblian-middle Aragonian, MN3-MN5) rodent record of the Vallès-Penedès Basin. Late Ramblian (zone A; ca. 19.3-17.2 Ma) sites are devoid of cricetids other than the archaic *Melissiodon dominans*, which is more abundant than in other Iberian basins. Crusafont et al. (1955) erected the species *Melissiodon arambourgi* based on a single specimen from el Fallol site, but after a revision of the holotype, we confirm earlier suggestions (Agustí, 1981) that the published figure and descriptions do not agree with it and this species is regarded as a junior subjective synonym of *Melissiodon dominans*. New specimens recovered from many different early and early middle Miocene sites confirm the attribution of all the Vallès-Penedès material to *M. dominans* (chapter 5).

Modern cricetids are a common component of the Vallès-Penedès early and middle Aragonian faunas (zone C and early zone D, between ca. 16.5 and 15 Ma) and include four species of the genus *Democricetodon* (*D. hispanicus*, *D.* cf. *decipiens*, *D. gracilis*, *D.* sp. 4) and one of the genus *Megacricetodon* (*M. primitivus*) (chapter 9). In turn, these modern forms co-occur with two archaic 'cricetids': *Eumyarion weinfurteri* and *M. dominans*, which is last recorded at about 15.9 Ma.

Concerning *Eumyarion*, it is scarce in the Vallès-Penedès being only present in some MN4 and MN5 sites. It is first recorded in the early Aragonian sites of les Cases de la Valenciana and Can Martí Vell (MN4, subzone Ca). Agustí (1981) reported an additional specimen from Sant Mamet (early MN5, subzone Cb; Agustí, 1981), but has not been found in the ICP collections. New field campaings have provided a few more specimens from Les Cases de la Valenciana and Can Martí Vell as well as from les Escletxes del Papiol (subzone Da). The material from Can Martí Vell is attributed to *E. weinfurteri* whereas that of other Vallès-Penedès sites is regarded as *Eumyarion* sp. *E. weinfurteri* is a common element in MN4 and MN5 Central European faunas (Germany, Switzerland and Austria).

Regarding *Democricetodon*, the oldest sites (MN4, subzone Ca) just include *D. hispanicus*. *D. hispanicus* is the most abundant *Democricetodon* species during the early Miocene in the Vallès-Penedès. It is present in most MN4 (subzone Ca) localities such as el Canyet, les Cases de la Valenciana, Can Martí Vell and also in some early MN5 (subzone Cb) localities such as Cal Sutxet and Els Casots. *Democricetodon hispanicus* persists for a significantly longer time interval in the Vallès-Penedès than in the Calatayud-Montalbán Basin. In the Calatayud-Montalbán Basin it is restricted to Aragonian zone B and uppermost zone A (ca 17-16.5 Ma; Van der Meulen et al. 2003, 2012), whereas in the Vallès-Penedès it is last recorded at 15.9 Ma (els Casots; see sections 10.2 and 10.3).

The other *Democricetodon* species are less abundant than *D. hipanicus* in the Vallès-Penedès Basin sites and they all first appear somewhat later, during Aragonian subzone Cb (MN5). *Democricetodon gracilis* is represented by a few specimens at els Casots (CS73), Vilobí del Penedès, Sant Mamet and Can Cabanes W. This species is smaller than all other *Democricetodon* species present in Western Europe at that time. At els Casots it coexists with *D. hispanicus*, whereas at the other sites it co-occurs with *Democricetodon decipiens*. *Democricetodon gracilis* is clearly distinguished from these two species by its clearly smaller size and shorter anteroconid, amongst other features. On the other hand, *D. decipiens* is larger species than both *D. gracilis* and *D. hispanicus* and further presents shorter mesoloph/ids. The fourth *Democricetodon* species found in the Vallès-Penedès Basin during the MN5 is a large-sized species represented by one m1 at els Casots (CS73) plus one M2 and one m2 at la Riera del Morral. The material is too scarce to be confidently ascribed at the species level and, although *Democricetodon moralesi* seems a likely choice, other species such as *Democricetodon koenigswaldi* and *Democricetodon mutilus* cannot be excluded.

All the early to early middle Miocene material of *Megacricetodon* from the Vallès-Penedès Basin is ascribed to a single species: *Megacricetodon primitivus*. This species overwhelmingly dominates the rodent assemblage of many MN5 (subzones Cb and Da) sites (e.g., Vilobí del Penedès, les Escletxes del Papiol). *Megacricetodon primitivus* is restricted to southwestern Europe (Iberia and southern France) and contrary to other contemporaneous cricetids (e.g., *Democricetodon*) is remarkably stable in size and morphology, showing no directional trends and displaying a high intraspecific variability (Oliver and Peláez-Campomanes, 2016). It is a small-sized species that presents a deeply split anterocone on the M1 and a predominantly simple anteroconid on the m1. Mesolophs are generally long to medium-sized and mesolophids medium-sized to short, rarely absent. Throughout its record in the Vallès-Penedès *M. primitivus* does not show clear trend in morphology or size except for the more common occurrence of subdivided anteroconids on the m1 and a tendency to reduce the posterosinus on the M1 in younger samples. These slight morphological trends are not observed in the material from the Calatayud-Montalbán Basin (Oliver and Peláez-Campomanes, 2016).

The Vallès-Penedès cricetid succession bears several similarities with that of the nearby Calatayud-Montalbán Basin (east-central Spain) to the point that the same detailed local biostratigraphy could be extended to the Catalan basin (see chapter 10.2). However, the temporal range of particular *Democricetodon* species differs, with *D. hispanicus* disappearing much earlier than in the Calatayud-Montalbán Basin and *D. decipiens* first occurring significantly later. The rare presence of certain cricetid species (*D. gracilis, E. weinfurteri*) reveals affinities with regions beyond the Iberian Peninsula (see chapters 10.2 and 10.4).

10.2 Early Miocene small mammal succession and biostratigraphy

The early Miocene Vallès-Penedès small mammal succession is more continuous than previously thought, covering the later part of the early Miocene as well as its transition with the middle Miocene (Figure 10.1). In addition, contrary to the situation during the later middle and late Miocene (see Casanovas-Vilar et al., 2016a, b), the rodent fauna in particular shows several affinities with that from the Aragonian type area, the Calatayud-Montalbán Basin of east-central Spain (Van der Meulen et al. 2012; for a detailed discussion see chapter 4.4.3). Previous works have remarked the similarity of the early Miocene Vallès-Penedès faunas with those of the Aragonian type area, further advocating for the use of the same local biozonation, with only minor differences (Casanovas-Vilar et al. 2011b, 2016a; chapters 5 to 9). On the other hand, the Vallès-Penedès faunas also show some similarities with the central European ones, such as from the Swiss Molasse Basin succession (Kälin and Kempf, 2009; see chapter 9). Nevertheless, these similarities appear to be fewer and generally involve faunal events, such as the 'cricetid vacuum', that characterize the western European early Miocene record as a whole. As already outlined in previous chapters (chapters 5 to 9), the following lines discuss the biostratigraphy of the Vallès-Penedès early to early middle Miocene record relying on their correlation to the local biozonation of the Aragonian type area.

Ramblian zone A. This zone records the 'cricetid vacuum', which is the time interval between the last common occurrence (LCO) of *Eucricetodon* and the first common occurrence (FCO) of *Democricetodon*. This is a time span devoid of cricetids other than *Melissiodon* and characterized by faunas dominated by glirids and eomyids (*Ligerimys* and *Pseudotheridomys*). Ramblian zone A ranges from ca. 19.3 to 17.2 Ma (lower boundary after Larrasoaña et al., 2006; upper boundary after Agustí et al., 2001). The Vallès-Penedès sites correlated to zone A are Sant Andreu de la Barca, el Turó de les Forques, la Costablanca, and el Molí de Can Calopa (figure 10.1). Glirids are diverse and abundant, *Vasseuromys* and *Pseudodryomys* being particularly common. Other glirids include *Glirudinus modestus, Peridyromys murinus* and *Simplomys simplicidens*, which are all common components of zone A faunas in the Daroca-Calamocha area (type are of the Ramblian) in the Calatayud-Montalbán Basin (see Daams et al., 1999 a, b). The hypsodont glirid *Armantomys aragonensis*, an Iberian endemic previously not reported from the Vallès-Penedès Basin, is present at el Turó de les Forques and la Costablanca. Eomyids are also abundant and may be dominant in some sites (e.g., el Turó de les Forques). They include two species of *Ligerimys*, *Ligerimys antiquus* and *Ligerimys fahlbuschi*, plus much rarer remains of *Pseudotheridomys fejfari*, which is only recorded at el Turó de les Forques and Sant Andreu de la Barca (figrue 33). *Ligerimys antiquus* and *L. fahlbuschi* occur in Ramblian zones Z and A, while *P. fejfari* is restricted to the uppermost zone A in the type area (Álvarez-Sierra, 1987; see also Daams et al., 1999 a, b; Van der Meulen et al., 2012). Sciurids include *Heteroxerus*, *Palaeosciurus* and *Dehmisciurus*, which are generally rare. Regarding lagomorphs, the ochotonid *Lagopsis penai* is very common and present in all sites, while isolated finds of *Prolagus vascociensis* have been reported from the Rubí and el Papiol area (see López Martínez, 1989). Eulipotyphlans are more diverse in the Vallès-Penedès Basin than in Daroca-Calamocha area (see Van den Hoek Ostende et al., 2020 for a detailed study of this group), including dimylids, a family unknown from the Spanish inland at the time and represented by *Chainodus* and *Plesiodimylus* in the Vallès-Penedès Basin. In contrast, these genera are commonly recorded in central European faunas. Erinaceids include *Galerix remmerti* (figure 10.1), which is the oldest member of this genus hitherto reported from the Iberian Peninsula and characterizes Ramblian zones Z and A, being replaced by *Galerix symeonidisi* by the end of zone A in the Aragonian type area (Van den Hoek Ostende, 2003). The talpid *Desmanodon daamsi* is also a common element of the faunas. Finally, other insectivorans include the heterosoricid *Heterosorex neumayrianus*, only recorded at la Costablanca, and the rare soricids *Clapasorex alvarezae* and cf. *Florinia* sp. Notably, *Heterosorex* is absent from the Calatayud-Montalbán Basin at that time (its last occurrence being at lowermost Ramblian zone Z; Van der Meulen et al., 2012) and *Heterosorex neumayrianus* does not occur there until Aragonian subzone Ca. *Heterosorex* is a very common element in central European assemblages, but its occurrence in the Iberian Peninsula seems far more restricted and apparently discontinuous (Van den Hoek Ostende et al., 2016). In the Vallès-Penedès Basin, it seems to be continuously present (see below), likely because this taxon preferred more humid environments (Van den Hoek Ostende et al., 2020). Finally, as far as micromammals are concerned, the marsupial *Amphiperatherium frequens* occurs in many sites. Overall, the composition of the small mammal assemblages of the Vallès-Penedès Basin fits perfectly with that of zone A in the type area of the Ramblian. The only significant differences in the Vallès-Penedès Basin would be the noticeably more diverse eulipotyphlan fauna and the presence of some taxa, such as the glirid *Vasseuromys* or the sciurid *Dehmisiciurus*, which do not occur in the Calatayud-Montalbán Basin at that time.

Aragonian zone B. Even though *Democricetodon hispanicus* is already recorded during the uppermost zone A in the Calatayud-Montalbán Basin, its FCO defines the lower boundary of zone B as

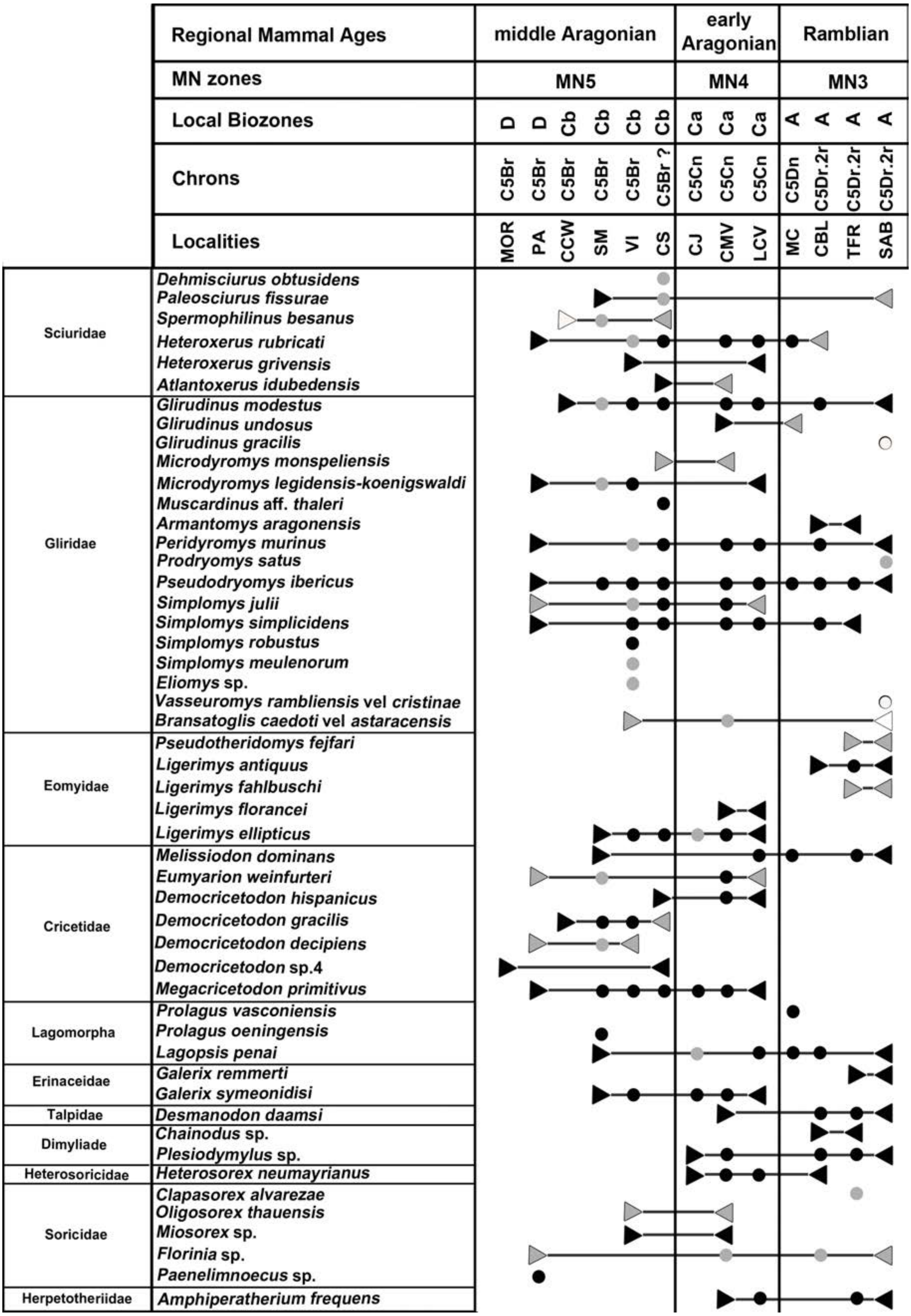


Figure 10.1: Early to early middle Miocene small mammal succession of the Vallès-Penedès Basin. For the locality acronyms see chapter 2.3 and appendix 1. Triangles indicate first and last occurrences. Grey dots and triangles indicate cf. species. White dots and triangles indicate aff. species.

well as that of the Aragonian age (Daams et al., 1999 a, b; Van der Meulen et al., 2012). The upper boundary is defined by the fist occurrence (FO) of *Megacricetodon primitivus*, so that during zone B *D. hispanicus* is the only cricetid species present. In the Vallès-Penedès Basin, this zone seems to be missing because the FO of *D. hispanicus* coincides with that of *M. primitivus* and *Eumyarion weinfurteri* (chapters 6, 9). Casanovas-Vilar et al. (2016a) preliminary assigned el Turó de les Forques to this zone because of the finding of a single *Democricetodon* molar, but this turned to be an unfortunate mixing with material from les Cases de la Valenciana during the sorting procedure (chapter 9). El Canyet is the only Vallès-Penedès site that might be correlated to zone B. Although exact stratigraphic position is unknown because the locality was apparently destroyed, it was located several meters in stratigraphic series above el Molí de Can Calopa (zone A) and clearly below Langhian marine deposits (Crusafont et al., 1955; Agustí et al., 1985; López-Martínez, 1989). This site has yielded scarce small mammal remains that only include the sciurid *Dh. obstusidens*, the glirid *Pseudodryomys ibericus*, and most notably the cricetid *Democricetodon hispanicus*. In addition, the erinaceid *G. symeonidisi*, the marsupial *A. frequens* (see Van den Hoek Ostende et al., 2020) and the ochotonid lagomorph *Prolagus* cf. *tobieni* (see López-Martínez, 1989) are recorded. *Democricetodon hispanicus* is the only cricetid present, which may be taken as an argument in favor of a correlation to zone B. However, it is worth noting that the collection includes just about 20 identifiable remains, so that the absence of other cricetid species is likely to be an effect of insufficient sampling and el Canyet may well correspond to the following Aragonian zone C. Therefore, given the present state of knowledge, no localities of the Vallès-Penedès Basin can be unambiguously atributed to Aragonian zone B.

Aragonian zone C. Daams et al. (1999a, b) characterized early Aragonian zone C by the predominance of the eomyid *Ligerimys ellipticus* along with the presence of *M. primitivus* (referred to as *Megacricetodon collongensis* in Daams et al., 1999a, b), *Eumyarion*, and various species of *Democricetodon* (included in *Fahlbuschia* in Daams et al., 1999a, b). Zone C was subdivided into the short-lasting subzones Ca and Cb by Van der Meulen et al. (2012). This subdivision mostly reflects changes in the cricetid faunas. Subzone Ca is characterized by the concurrent range of *M. primitivus* and *Democricetodon decipiens*, the FO of these two taxa marking the lower boundary of zone C. Subzone Cb is characterized by the concurrent range of *Democricetodon moralesi* and *L. ellipticus*, the FO of *D. moralesi*(the following member of the *Democricetodon hispanicus* – *Democricetodon lacombai* anagenetic lineage ; Van der Meulen et al., 2003), marking the lower boundary. Additional criteria allow distinguishing the two subzones in the type area, although they were not considered in their diagnoses. Remarkably, in subzone Ca two *Ligerimys* species (*Ligerimys florancei* and *L. ellipticus*) occur (albeit never in the same site), whereas in subzone Cb only *L. ellipticus* is recorded, the LCO of this species marking the boundary between zones C and D (Van der Meulen et al., 2012). In addition, *Eumyarion* first occurs within zone Cb in the Aragonian type area (Van der Meulen et al., 2012), although it is recorded earlier, during subzone Ca, in localities from Teruel and Valencia (Daams and Freudenthal, 1974). Zone C overlaps with two different MN zones, since the boundary between MN4 and MN5 is marked by the LO of *L. florancei* at ca. 16.4 Ma as defined in Hilgen et al., (2012). Most of the early Miocene Vallès-Penedès Penedès sites are correlated to zone C because of the presence of *M. primitivus* and *L. ellipticus*. The subdivision of this zone into two distinct subzones in the Vallès-Penedès Basin is debatable because the cricetid succession is clearly different (see chapter 9), and *D. hispanicus*, restricted to uppermost zone A and zone B in the Aragonian type area (Van der Meulen et al., 2012), persists for a longer time in the Catalan basin. Eomyids offer an additional, and perhaps better, criterion to distinguish subzones Ca and Cb. Localities that have delivered both *L. florancei* and *L. ellipticus* can be correlated to subzone Ca and are older than those with only *L. ellipticus*, which are here assigned to subzone Cb. Following this criterion, subzone Ca in the Vallès-Penedès Basin would include the sites from Gelida: les Cases de la Valenciana, Can Martí Vell and, perhaps Can Julià. On the other hand, Cal Sutxet, els Casots, Vilobí del Penedès, Sant Mamet and, probably, el Palau (located in Sant Andreu de la Barca) and Can Cabanes W would correlate to subzone Cb. It is worth noting that *D. hispanicus* persists into subzone Cb, being abundant at els Casots, although additional *Democricetodon* species are recorded for the first time within this subzone. These include the small-sized *Democricetodon gracilis*, an element more typical of roughly coeval central European faunas (see Kälin and Kempf, 2009) but also recorded in the Ebro Basin localities correlated to zones C and D (Suárez Hernando, 2017). *Democricetodon gracilis* is generally rare, but occurs at els Casots, Vilobí del Penedès, Sant Mamet and Can Cabanes W. At els Casots, a third, larger-sized species of *Democricetodon* is also represented by a single specimen. Finally, *D.* cf. *decipiens* has been also recovered at Vilobí del Penedès and Sant Mamet, two sites that have also yielded *D. gracilis* but not *D. hispanicus*. Furthermore, *L. ellipticus* is extremely rare at all the sites correlated to subzone Cb, which may indicate a younger age. Other differences in the cricetid succession as compared to the Aragonian type area include the more common occurrence of the genus *Eumyarion,* represented by *E. weinfurteri*, a species reported from Central Europe but not from inland Spain, which is recorded at les Cases de la Valenciana, Can Martí Vell and Sant Mamet. The latter locality also represents the LO of *Melissiodon dominans*, being one of the youngest records of this genus (see below and chapter 5). Glirids are not particularly abundant but they are very diverse, including presumably arboreal forms (see Van Dam, 2006) such as *Glirudinus undosus*, *Gl. modestus*, *Microdyromys legidensis-Mi. koenigswaldi*, *Muscardinus* aff. *thaleri* and *Bransatoglis cadeoti* vel *B. astaracensis*. However, ground-dwelling species such as *Peridyromys murinus*, *Ps. ibericus*, *S. simplicidens*, *Simplomys robustus*, *Simplomys julii* and *Simplomys meulenorum* are far more common. A good illustration of the glirid fauna is provided by the sites of les Cases de la Valenciana (see chapter 6) and Can Martí Vell (Agustí, 1983). The sciurid fauna is similar to that of the Ramblian, with a predominance of ground squirrels. The insectivoran faunas are similar to those of the Aragonian type area, being dominated by *Ga. symeonidisi* and *H. neumayrianus*. Additional soricid genera (*Oligosorex*, *Miosorex*) enter the assemblage. Dimylids are solely represented by *Plesiodimylus*, which appears to be restricted to subzone Ca. The marsupial *A. frequens* continues to be abundant. Lagomorph faunas are not well known but appear to be dominated by *Lagopsis penai.* It is worth noting that magnetostratigraphic data (see chapter 10.3) indicate that the LCO of *L. ellipticus* occurs slightly later in the Vallès-Penedès Basin (ca. 15.7 Ma) than in the Aragonian type area (15.9 Ma), which would imply slightly different zone boundaries.

Aragonian zone D. The long-lasting zone D covers most of the MN5 and is subdivided into four subzones (Da, Db, Dc, Dd) in the Aragonian type area, being mostly distinguished by the presence of different species of *Democricetodon* and *Megacricetodon* (Van der Meulen et al., 2012). Therefore, this zone belongs to the middle rather than the early Miocene. Two sites of the Vallès-Penedès Basin are correlated to zone D: les Escletxes del Papiol and la Riera del Morral. The correlation of la Riera del Morral is dictated more by its position in stratigraphic series, interbedded with Langhian marine and transitional facies, than by the recovered fauna, which solely includes a few molars attributed to a large-sized *Democricetodon* species (see chapter 9). In contrast, the site of les Escletxes del Papiol, which is located in lutite layers between Langhian marine deposits (figure 10.2), has delivered a rich fauna comprising more than 100 identifiable cheek teeth. The rodent fauna is surprisingly poor, being overwhelmingly dominated by the cricetid *M. primitivus* (see chapter 9). A few specimens of *D.* cf. *decipiens* and a single molar of *Eumyarion* sp. have also been recovered. Glirids are scarce and not very diverse; *Mi. koenigswaldi*, *Pe. murinus* and *Ps. ibericus* are the most common elements. Sciurids are solely represented by the genus *Heteroxerus*, while insectivorans only include cf. *Florinia* sp. and the first record of the soricid *Paenelimnoecus*. Most notably, the eomyid genus *Ligerimys* is entirely missing. Such a faunal composition agrees with the very short-lasting (ca. 15.9–15.85 Ma) subzone Da of the Calatayud-Montalbán Basin (Van der Meulen et al., 2012). This subzone comprises the time interval between the LCO of *L. ellipticus* and the first occurrence of *Megacricetodon vandermeuleni* (referred to as *Megacricetodon* n. sp. 1 in Van der Meulen et al., 2012). These low diversity faunas also agree with this tentative correlation to subzone Da, although magnetostratigraphic data (see chapter 10.3) indicate that les Escletxes del Papiol could be as young as 15.2 Ma, thus significantly postdating the youngest sites of this subzone in the Aragonian type area.

Finally, a few recently discovered sites in the Alt Penedès area, such as el Terral (Sant Pau d'Ordal) or the karstic sites of la Gornal (Castellet i la Gornal), have delivered middle Miocene small mammal faunas that are correlated to MN5. These sites overlie Langhian marine units, in the case of la Gornal in karstic fissures affecting a Miocene reef system. Additional, larger-sized *Megacricetodon* species have been recovered from these localities, thus indicating a younger age than les Escletxes del Papiol. In addition, at la Gornal the cricetid *Cricetodon* is first recorded in the Vallès-Penedès Basin, which could indicate a correlation to local zone E, thus corresponding to the latest MN5. These faunas have yet to be studied but allow bridging the gap between early middle Miocene sites and the late middle Miocene localities such as those from the Abocador de Can Mata series.

In conclusion, the local zonation of the Aragonian type area could well be extended to the Vallès-Penedès Basin for the early and early middle Miocene part of the record. However, a detailed subdivision into subzones (at least as currently defined in the type area) is questionable because of the different cricetid succession. Yet, other criteria, such as the presence of different *Ligerimys* species, could be used for correlation. In addition, there is a clear diachrony in the LOs of certain taxa, most notably for *D. hispanicus* but also for other species such as *L. ellipticus* (see also chapter 10.3).

10.3 Magnetostratigraphy and biochronology

The sequences studied for magnetostratigraphy include six main composite sections of more than 100 m in thickness; two of them, Gelida and Santa Maria de Vilalba, are particularly long (more than 300 m) and continuous (see figure 10.2). The section of els Casots, which was sampled by means of exploratory core drilling (see chapter 4.5), is conspicuously shorter, being 30 m thick. Fossil mammal sites occur in all sections but are particularly scarce in the Santa Maria de Vilalba one. In addition, shallow marine deposits, rich in marine micro- and macrofauna, also occur in most sections and provide additional means for correlation. The sections of Gelida, Santa Maria de Vilalba, Molí Calopa and la Costablanca show various polarity reversals, but shorter sections such as those of Rubí and els Casots do not. Correlation to the Geomagnetic Polarity Time Scale (GPTS) relies on the characteristic pattern of polarity reversals importantly supported by biostratigraphic data and correlation of intercalated shallow marine sediments (see figure 10.2 and 10.3). Marine deposits also allow positioning the Vilobí section, which was not sampled for magnetostratigraphy. Small mammal biostratigraphy helps constraining the age of Molí Calopa and Costablanca sections. Other sections were correlated after the unambiguous identification of the long reversed chron C5Br, which marks the beginning of the Langhian and further coincides with a major marine transgression in the Vallès-Penedès Basin (see figure 10.4). The overall magnetostratigraphic sequence represents about 3 million years, from about 18 to 15 Ma, thus covering part of the early Miocene and the beginning of the Mid-Miocene Climatic Optimum (MMCO; see Zachos et al., 2001). The early Miocene Vallès-Penedès record allows constraining the age of several regional to continental bioevents that occurred at that time (figure 10.4), which are discussed below.

***Anchitherium* event.** This three-toed equid first appears in the early Miocene of North America and it is widely recognized as an immigrant that dispersed into Europe in MN3 (e.g., Bernor and Armour-Chelu, 1999). In the Vallès-Penedès, *Anchitherium* is recorded in the zone A sites of la Costablanca, el Molí de Can Calopa and Sant Andreu de la Barca (figure 10.3) (for a description of the material see Rotgers and Alba, 2011), thus agreeing with its record

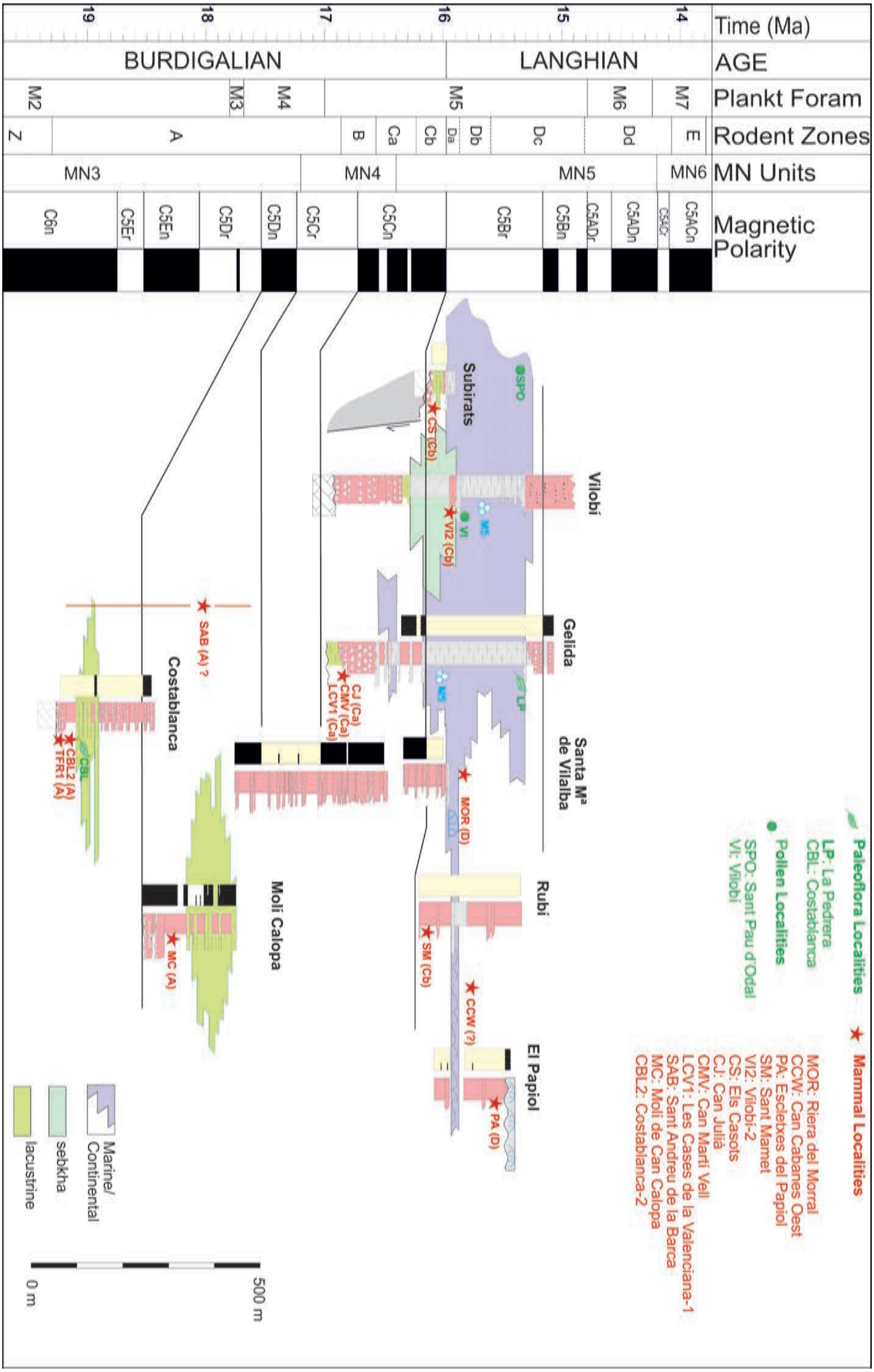

Time (Ma)
19
18
17
16
15
14
AGE
BURDIGALIAN
LANGHIAN
Plankt Foram
M2
M3
M4
M5
M6
M7
Rodent Zones
Z
A
B
Ca
Cb
Da
Db
Dc
Dd
E
MN Units
MN3
MN4
MN5
MN6
Magnetic Polarity
C6n
C5Er
C5En
C5Dr
C5Dn
C5Cr
C5Cn
C5Br
C5Bn
C5ADr
C5ADn
C5ACr
C5ACn
Subirats
SPO
CS (Cb)
Vilobí
VI
V12 (Cb)
M5
Gelida
LP
M5
CJ (Ca)
CMV (Ca)
LCV1 (Ca)
Santa Mª de Vilalba
MOR (D)
Rubí
SM (Cb)
CCW (?)
El Papiol
PA (D)
Costablanca
SAB (A) ?
CBL
CBL2 (A)
TFR1 (A)
Molí Calopa
MC (A)
Paleoflora Localities
LP: La Pedrera
CBL: Costablanca
Pollen Localities
SPO: Sant Pau d'Odal
VI: Vilobí
Mammal Localities
MOR: Riera del Morral
CCW: Can Cabanes Oest
PA: Esclebes del Papiol
SM: Sant Mamet
VI2: Vilobí-2
CS: Els Casots
CJ: Can Julià
CMV: Can Martí Vell
LCV1: Les Cases de la Valenciana-1
SAB: Sant Andreu de la Barca
MC: Molí de Can Calopa
CBL2: Costablanca-2
Marine/ Continental
sebkha
lacustrine
0 m
500 m

Figure 10.2 (previous page): Correlation of the early to early middle Miocene magnetostratigraphic sections of the Vallès-Penedès Basin. Light blue indicates marine transgressions. Ages, MN zone boundaries and planktonik foraminifera zones are after Hilgen et al. (2012). Geomagnetic Polarity Time Scale is after Ogg et al. (2012) and Ramblian and Aragonian biozones are after Van der Meulen et al. (2012) and García-Paredes et al. (2016). Figure courtesy of M. Garcés.

elsewhere in Iberia and Europe. In the Iberian Peninsula, the oldest occurrences of this equid correspond to zone A sites, such as Ágreda (Teruel Basin; Daams et al., 1998), Alto de Ballester 1 and Rubielos de Mora 1 (both in the Rubielos de Mora Basin; Van den Hoek Ostende et al., 2017). Unfortunately, there is no associated magnetostratigraphy to these sites, but Daams et al. (1998) estimated an age of about 18 Ma for Ágreda based on micromammal biostratigraphy. In the Vallès-Penedès Basin, la Costablanca is correlated to chron C5Dr.2r, which would imply a minimum age of 18.06–17.74 Ma for the FO of *Anchitherium* in Iberia. Molí de Can Calopa is slightly younger, being correlated to chron C5Dn (17.53–17.24 Ma). Sant Andreu de la Barca, which lacks associated magnetostratigraphic data, might be potentially older than both sites, up to about 19 Ma, the lower boundary of zone A. Other European localities agree with this age and point towards a dispersal of *Anchitherium* coinciding with the cricetid vacuum, but two sites are certainly older than Iberian occurrences. These are Wintershof-West (Franconian Jura, Germany), the reference site for biozone MN3 (see Hilgen et al., 2012), and Estrepouy (Aquitanian Basin, France), which have yielded remains of the cricetids *Pseudocricetodon thaleri* and *Eucricetodon infralactorensis* (the latter species only in Estrepouy; see Hugueney and Bulot, 2011). Assuming that Ramblian regional zones can be extended to other areas of Europe, these two localities would be correlated to zone Z (early MN3), which would imply an age of 19.3–19.7 Ma (age boundaries after Larrasoña et al., 2006 and Suárez-Hernando, 2017). In Asia, *Anchitherium* is first recorded during the early Shanwangian at the Xiacowan Formation, China, yielding an estimated age of about 18.5 Ma (Qiu et al., 2013). Therefore, Asian oldest records do not predate European ones and indicate that this equid quickly dispersed from North America into Eurasia during the late Arikareean North American land mammal age.

Proboscidean event. Proboscideans are an order of African origin represented by different groups in the early Miocene of Eurasia: gomphotherids (*Gomphotherium*), mammutids (*Zygolophodon*) and deinotherids (*Prodeinotherium*). These dispersed at different times, so indeed there are multiple proboscidean dispersals rather than a single event. The oldest record of proboscideans out of Africa is just a tip of an upper tusk of an elephantiform proboscidean from the latest Oligocene (ca. 25 – 24 Ma) of the Chitawarta Formation in the Bugti Hills (Zinda Pir area, Pakistan; Antoine et al., 2003, 2013). *Gomphotherium* and *Prodeinotherium* are recorded in somewhat younger sediments of the Chitawarta Formation, dating back to the early Miocene (ca. 22–21 Ma; Antonine et al., 2013). First occurrences of proboscideans in Europe are noticeably younger, and those of *Gomphotherium* and *Zygolophodon* predate that of *Prodeinotherium* (Göhlich, 1999; Mein, 1999; Sen, 2013). In the Vallès-Penedès Basin, oldest occurrences of *Gomphotherium* are at Sant Andreu de la Barca and Torrent de Vilaroc (figure 10.2). The first lacks magnetostratigraphic data but is unambiguously correlated to Ramblian zone A (late MN3), thus yielding an age of 19.3 to 17 Ma. Torrent de Vilaroc is a classical site from the Rubí area situated some meters above Molí de Can Calopa (Crusafont et al., 1955). Considering its stratigraphic position and the magnetostratigraphic data from Molí de Can Calopa, the age of Torrent de Vilaroc would be around 17 Ma (figure 10.2). Therefore, the Vallès-Penedès occurrences would represent the oldest record of this genus (and of proboscideans) in the Iberian Peninsula; its FO in inner Spain (Villafeliche 2a, Calatayud-Montalbán Basin; Mazo and Van der Made, 2012) dates back to Aragonian zone B (MN4, estimated age 16.63 Ma after Van der Meulen et al., 2012) and a similar age is inferred for localities from Unit IVb in the Tagus Basin of Portugal (Antunes et al., 1996, 1999). However, older records of proboscideans are known from the Aquitaine Basin in France. These comprise the sites of Marsolan and Le Casse-Richevoltes (Bulot and Ginsburg, 1993). Marsolan, included within the Calcaries de Pelléchaus unit, delivered a molar of *Zygolophodon turicensis*, whereas an isolated indeterminate mastodont molar fragment was recovered from Le Casse-Richevoltes, which is stratigraphically below Marsolan (Bulot and Ginsburg, 1993: 1015, figure). The small mammal fauna from Marsolan (see Bulot, 1989) includes the cricetid *Eucricetodon infralactorensis* together with the eomyid *Ligerimys antiquus*, thus predating the cricetid vacuum. If regional Ramblian zones can be extended to southern France, this would indicate a correlation to zone Z, implying an age of 19.3–19.7 Ma. Marsolan is located stratigraphically above Estrepouy (see above); thus, the FO of proboscideans in Western Europe would occur slightly later than that of the equid *Anchitherium*. In the Aquitaine Basin, *Gomphotherium* appears after *Zygolophodon*, its FO being at Navère (Bulot and Ginsburg, 1993), which is correlated to the cricetid vacuum interval (Ramblian zone A) and hence roughly contemporaneous with the Vallès-Penedès sites where *Gomphotherium* is first recorded. Regarding deinotheres, its FO in the Vallès-Penedès Basin dates back to chron C5Br, *Prodeinotherium* being present at els Casots, Can Cerdà and les Escletxes del Papiol, other chronologically close sites (Gasamans et al., unpublished data). Since els Casots is correlated to the early part of chron C5Br the age of this event can be estimated at 15.9–15.7 Ma (early MN5). This record is substantially younger than the FO of this genus in the Iberian Peninsula, corresponding to Artesilla (Calatayud-Montalbán Basin; see Azanza et al., 1993) which is correlated to Aragonian subzone Ca (MN4) with an estimated age of 16.49 Ma (see Van der Meulen et al., 2012). Deinotheres also first occur in MN4 sites in Portugal (Quinta das Pedreiras, Unit Va2 of the Tagus Basin; Antunes et al., 1996, 1999, Antunes and Ginsburg, 2003) and France (e.g., La Romieu, Chevilly). Older, potentially MN3, occurrences of *Prodeinotherium* in France (Clére-les-Pins, Savigné-sur-Lathan Basin), indeed mix material mostly belonging to MN5 (including *Prodeinotherium bavaricum*) with a few reworked fossils dating back to MN3 (see Ginsburg, 2001). However, radiometric

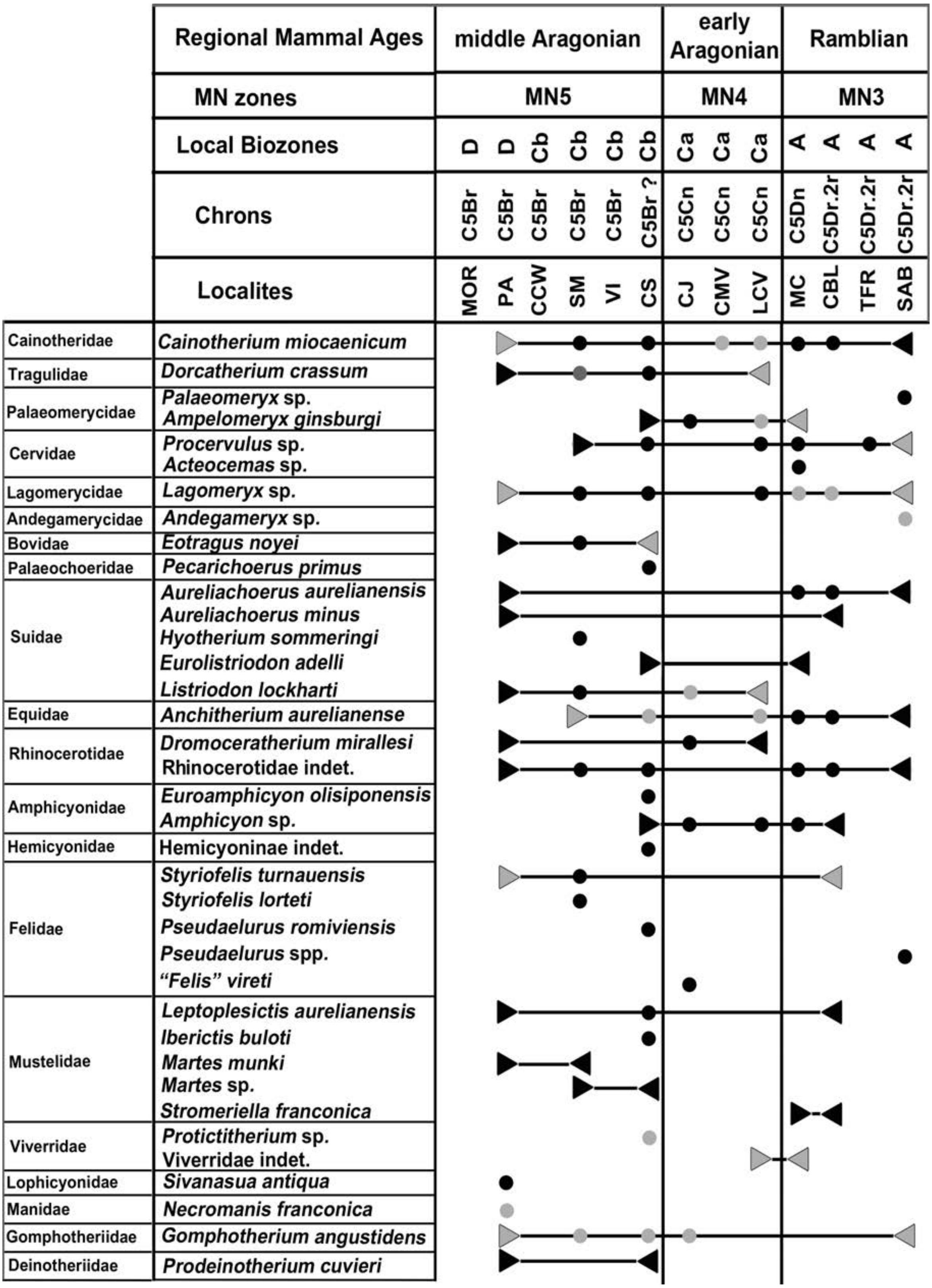


Figure 10.3: Early to early middle Miocene large mammal succession of the Vallès-Penedès Basin. For the locality acronyms see chapter 2.3 and appendix 1. Triangles indicate first and last occurrence. Grey dots and triangles indicate cf. species. White dots and triangles indicate aff. species.

dating of the first record of *Prodeinotherium* from Gavathas in Lesvos island (Greece) is 18.4 ± 0.5 Ma (Koufos, 2003), which would place the oldest European occurrence of deinotheres within MN3. Overall, eastern occurrences (either in Asia or the eastern Mediterranean) predate western first records of proboscideans, sometimes by several million years.

Modern cricetid event. *Democricetodon* is the first 'modern cricetid' (for the usage of this informal term see chapter 3.3) to appear in Western Europe after the 'cricetid vacuum'. In the Iberian Peninsula it is first recorded at 17.2 Ma in the Ebro Basin (La Naja 145; Agustí et al., 2011) and 17.0 Ma in the Calatayud-Montalbán Basin (San Roque 4A; Van der Meulen et al., 2003, 2012). Agustí et al. (2011) used the FO of this cricetid to define the Ramblian/Aragonian boundary, whereas Van der Meulen et al. (2012) preferred to use the first common occurrence of *Democricetodon* and placed the localities where this genus is scarcely recorded (San Roque 4A and 4B) in the latest Ramblian zone A. The FO of *Democricetodon* in Central Europe is estimated to be somewhat older, dating back to 17.6–17.05 Ma (Kälin and Kempf, 2009; see also Van der Meulen et al., 2011, 2012). This record corresponds to the Swiss site of Glovelier, a karstic fissure which has yielded *Democricetodon franconicus* (and not *Democricetodon hispanicus*, which is the species present at Iberian sites). The first occurrences of this genus from Austria (Oberdorf; see Steininger et al., 1998) and southern Germany (Pippèrr et al., 2007) are consistent with these older ages. Yet, there is a diachrony of about 0.3 million years with the FO of *Democricetodon* in the Iberian record (see Van der Meulen et al., 2011). The FO of *Democricetodon* precedes that of other 'modern cricetids' in Europe (see Van der Meulen et al., 2011). The oldest *Democricetodon* species in the Vallès-Penedès Basin is *D. hispanicus*, as in other Iberian sites. Additional *Democricetodon* species do not occur until the lowermost chron C5Br, at about 15.9 Ma. These include *Democricetodon* cf. *decipiens* and *Democricetodon gracilis*, which are recorded significantly later than in other regions. *Democricetodon decipiens* is an Iberian species that ranges between 16.5 and 16.2 Ma in the Calatayud-Montalbán Basin, being restricted to subzone Ca (Van der Meulen et al., 2012). It is also present in Valencia, where it persists until subzone Cb (Crespo Roures, 2017). Regarding *D. gracilis*, this is a species of central European origin (see chapter 9) that has also been recorded from the Bardenas Reales (Navarra) in the Ebro Basin (Loma Negra 64 and Pico del Fraile 2 sites), also from chron C5Br (Suárez Hernando, 2017). *Democricetodon gracilis* first occurs in the Swiss Molasse Basin by the end of chron C5Cr, almost one million years earlier than in the Vallès-Penedès and Ebro basins (see Kälin and Kempft, 2009). It is also worth noting that the last occurrence (LO) of *D. hispanicus* in the Vallès-Penedès is at els Casots site, which is correlated to the earliest part of chron C5Br (ca. 15.9 Ma). This record postdates by about 0.5 million years the LO of this species in the Aragonian type area (Daams et al., 1999a, b; Van der Meulen et al., 2012). *Democricetodon* is the only 'modern cricetid' present at Aragonian zone B, the FO of *Megacricetodon* marking the lower boundary of zone C. In the Vallès-Penedès Basin both genera are first recorded at the same time because no zone B sites are known (see chapter 10.2). *Megacricetodon* first occurs at les Cases de la Valenciana and Can Martí Vell, which are correlated to subzone Ca (figure 10.1). Therefore, the first record of this taxon would be coherent with that of the Calatayud-Montalbán Basin and would occur between 16.5 and 16.3 Ma. As for *Democricetodon*, the FO of *Megacricetodon* in Central Europe is confidently placed within chron C5Cr in the Swiss Molasse Basin (Kälin and Kempf, 2009), yielding an estimated age of 17.1 Ma. Its FO in other European regions, such as Bavaria, may be even older (see Van der Meulen et al., 2011). Finally, a third cricetid genus, *Eumyarion*, first dispersed into central and western Europe by the end of the early Miocene. Its FO in the Vallès-Penedès Basin is also at les Cases de la Valenciana and Can Martí Vell, which are close in age to its other Iberian FOs from Valencia and the Teruel area (Daams and Freudenthal, 1974; Van der Meulen et al., 2012). In Central Europe, the FO of *Eumyarion* coincides with that of *Megacricetodon* in the Swiss Molasse Basin (Kälin and Kempf, 2009). In conclusion, even though the Vallès-Penedès record does not provide new data regarding the dispersal of 'modern cricetids' it is perfectly coherent with the record from other Iberian basins.

***Ligerimys* last occurrence event.** The eomyid *Ligerimys* is a characterstic element of MN3 and MN4 of Europe. In Central Europe, the replacement of this genus by *Keramidomys* is used as a diagnostic criterion for the MN4/MN5 boundary (Kälin and Kempf, 2009). The well-calibrated Swiss Molasse record shows that this event occurred between 16.7 and 16.35 Ma (Kälin and Kempf, 2009) and perhaps earlier in Bavaria, at ca. 17.2 Ma (Abdul Aziz et al., 2009). Remarkably, in the Iberian Peninsula this genus disappears substantially later, which precludes using this event as an MN-boundary marker. Such discrepancy is explained by regional endemism. *Ligerimys florancei* is the last *Ligerimys* species recorded in Central Europe, but in Spain this species is followed by *Ligerimys ellipticus*, which first occurs at 16.3 Ma and persists until 15.9 Ma (Daams et al., 1999a, Van der Meulen et al., 2011, 2012). However, the LO of *L. florancei* occurs in both Switzerland and Spain at around 16.4 Ma (Van der Meulen et al., 2011, 2012) and is currently used to define the MN4/MN5 boundary (see Hilgen et al., 2012). In the Vallès-Penedès record, the LO of *L. florancei* is at les Cases de la Valenciana and Can Martí Vell, where it coexists with *L. ellipticus*. Such coexistence is not observed in the Aragonian type area, where *L. ellipticus* simply replaces *L. florancei* within subzone Ca (Van der Meulen et al., 2012) but occurs in other Iberian sites such as Bunyol (Valencia; Robles et al., 1991; Crespo Roures, 2017). Many Vallès-Penedès sites traditionally correlated to MN4, such as els Casots and Sant Mamet, only include *L. ellipticus* (see figure 10.1) and should instead be correlated to MN5, therefore belonging to the earliest middle Miocene rather than the late early Miocene. The LO of *L. florancei* in the Vallès-Penedès is at Can Martí Vell, and certainly occurred before chron C5n.1n, which would imply a minimum age of 16.2 Ma for the event, which largely agrees with other records. Regarding the LO of *L. ellipticus*, it occurs at Sant Mamet, which is placed just a few meters below the Langhian transgressive deposits and is correlated to the lower part of chron C5Br (see figure 10.2 and 10.4). Therefore, Sant Mamet would be somewhat younger than 15.9 Ma, so the LO of *L. ellipticus* fits perfectly with the age of

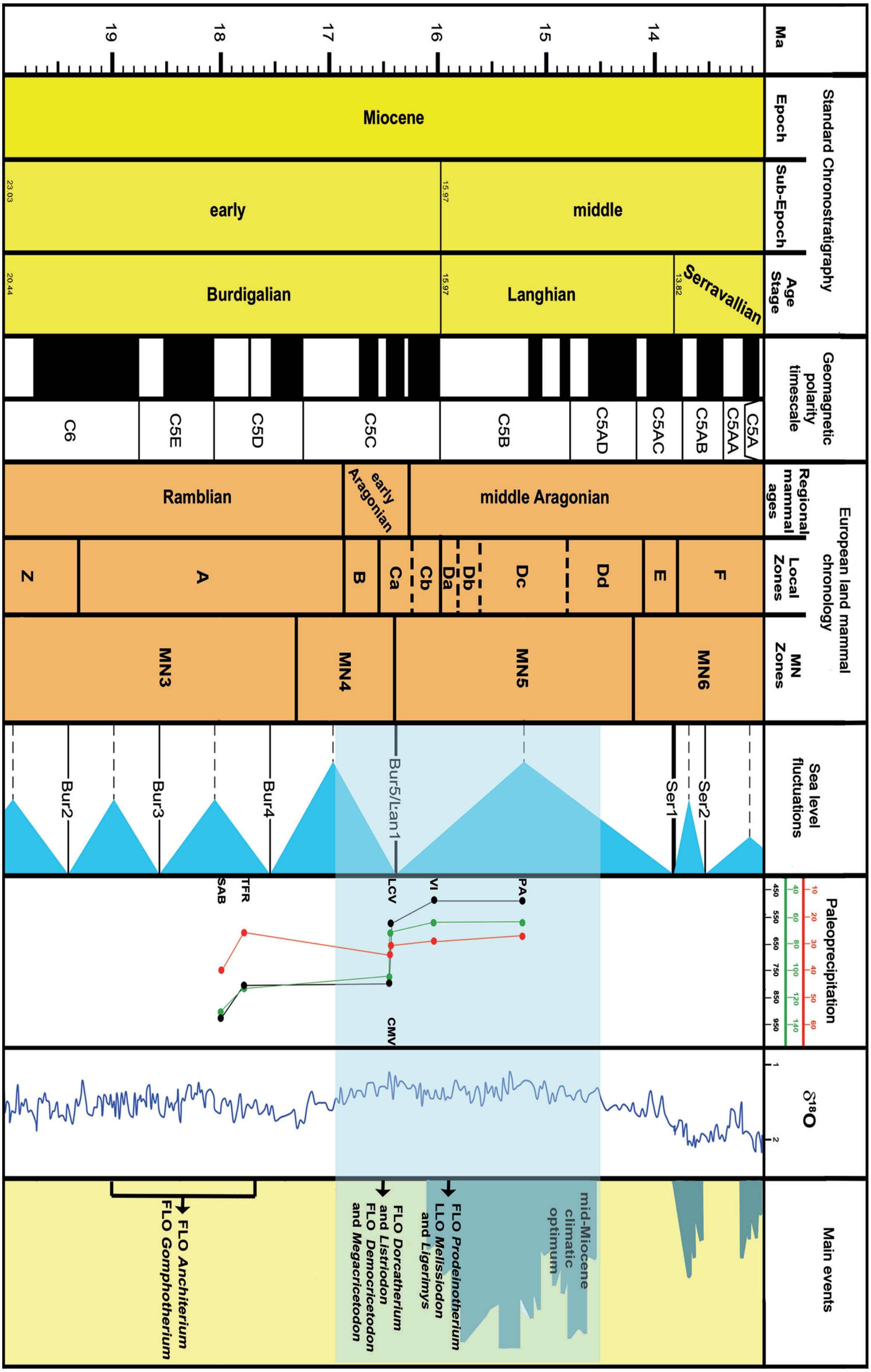

Ma
19
18
17
16
15
14
Standard Chronostratigraphy
Epoch
Miocene
Sub-Epoch
23.03
early
15.97
middle
Age Stage
20.44
Burdigalian
15.97
Langhian
13.82
Serravallian
Geomagnetic polarity timescale
C6
C5E
C5D
C5C
C5B
C5AD
C5AC
C5AB
C5AA
C5A
European land mammal chronology
Regional mammal ages
Ramblian
early Aragonian
middle Aragonian
Local Zones
Z
A
B
Ca
Cb
Da
Db
Dc
Dd
E
F
MN Zones
MN3
MN4
MN5
MN6
Sea level fluctuations
Bur2
Bur3
Bur4
Bur5/Lan1
Ser1
Ser2
Paleoprecipitation
10 20 30 40 50 60
40 60 80 100 120 140
450 550 650 750 850 950
SAB
TFR
LCV
VI
PA
CMV
δ18O
1
2
Main events
FLO Anchitherium
FLO Gomphotherium
FLO Dorcatherium and Listriodon
FLO Democricetodon and Megacricetodon
FLO Prodeinotherium
LLO Melissiodon and Ligerimys
mid-Miocene climatic optimum

Figure 10.4 (previous page): Small-mammal-based paleoprecipitation estimates for the early and early middle Miocene record of the Vallès-Penedès Basin. Main local bioevents, registered marine transgressions (in blue) and their age are also indicated. Global sea-level changes and the global isotopic curve are also included for comparison. The pale blue area indicates the Mid-Miocene Climatic Optimum. For the locality acronyms see chapter 2.3 and appendix 1. In the paleoprecipitation section, red line indicates precipitation in the driest month (LMP), green precipitation in the wettest month (HMP) and black mean anual precipitation (MAP) (see table 10.1). Miocene chronology and climatic data after Hilgen et al. (2012) and generated with the software Time Scale Creator 7.1. (Ogg and Lugowski, 2020 and references therein).

this event in the Aragonian type area, or occurs only slightly later.

Other large mammal events. Several artiodactyl groups that will persist for most of the Miocene are first recorded during the early Miocene. These include listriodontine suids as well as several groups of ruminants, such as tragulids, cervids and bovids. Cervids are first represented by *Procervulus*, which is first recorded in the Vallès-Penedès Basin during Ramblian zone A (late MN3), occurring at all known sites of this age (see figure 10.3). This record is consistent with the oldest occurrences of this genus in the Iberian Peninsula, which also date back to zone A in the Ebro (La Nasa 1 and 3; Larrasoaña et al., 2006) and Rubielos de Mora basins (Rubielos de Mora 1, Alto de Ballester 1; Montoya et al., 1996). However, *Procervulus* first appears slightly earlier in Germany (Wintershof-West) and France (Estrepouy). Although these sites are also correlated to MN3, the presence of the cricetids *Pseudocricetodon* and *Eucricetodon* (Hugueney and Bulot, 2011) points towards an older age than the Spanish sites (see above). The listriodontine suids *Eurolistriodon* and *Listriodon*, the tragulid *Dorcatherium* and the early bovid *Eotragus* are all first recorded in the Iberian Peninsula during MN4. The oldest record of listriodontines and the tragulid *Dorcatherium* at the Vallès-Penedès Basin is at les Cases de la Valenciana, which is correlated to subzone Ca, yielding roughly the same age as other records of these taxa from the Iberian Peninsula (Bunyol, Artesilla; Pickford and Morales, 2003; correlations after Van der Meulen et al., 2012). Similarly, the FO of listridontines in France is in sites that still contain *L. florancei* (Béon 1 = Montreal-du-Gers, Pellechaus; Orliac, 2006) and are correlated to MN4 (Bulot, 1989; Bulot and Ginsburg, 1993; Bulot et al., 2009). Therefore, the FO of listriodontines in Western Europe can confidently be placed at around 16.5 Ma. Regarding *Dorcatherium*, recent revisions of German occurrences indicate that this genus is recorded earlier in Central Europe. Its FO is at Eggingen-Mittelhart (South German Molasse Basin) which would be older than 17 Ma (Rössner, 2017), but still placed within MN4 because of existing diachrony in MN zone boundaries between Iberia and Central Europe (see Van der Meulen et al., 2011, 2012). Finally, *Eotragus* is the oldest bovid possessing true horn cores. Its oldest record in Eurasia corresponds to *Eotragus minus* from Bugti Hills, Northern Pakistan, which is correlated to chron C5En, thus yielding an estimated age of about 18 Ma (Antoine et al., 2013). In Western Europe *Eotragus* first occurs in MN4 sites that still include *L.*

florancei, such as Artenay in France or sites correlated to Aragonian subzone Ca in Iberia (Bunyol), thus implying a maximum age of ca. 16.5 Ma for its dispersal. In the Vallès-Penedès its FO is slightly later, at about 16 Ma at els Casots site. The dispersal into Western Europe of listriodontines, tragulids and bovids occurred at approximately the same time only shortly after that of modern cricetids.

Other small mammal events. Agustí et al. (2011) concluded that the occurrence of the eomyid *Pseudotheridomys fejfari* was a short-lasting event that took place during the latest part of Ramblian zone A (or late MN3). Indeed, in the Calatayud-Calamocha area this species occurs in Moratilla and Bañón 11, which are correlated to the latest zone A (Álvarez Sierra, 1987), while in the Ebro Basin, it is only recorded from chron C5Dr.2r at ca. 17.9–17.8 Ma (Agustí et al., 2011). In the Vallès-Penedès *P. fejfari* is present at Sant Andreu de la Barca and la Costablanca (figure 10.1). While the age of Sant Andreu de la Barca cannot be adequately constrained, la Costablanca is correlated to chron C5Dr.2r, thus being perfectly congruent with the data from the Ebro Basin. The LO of the long-lived cricetid genus *Melissiodon* is also a remarkable bioevent. In the Vallès-Penedès it is at Sant Mamet, which is correlated to chron C5Br and has an estimated age of about 15.9–15.7 Ma, thus representing the youngest record of *Melissiodon* known to date (early MN5, subzone Cb). In the Iberian Peninsula, *Melissiodon* is last recorded from the Aragonian type area during the late Ramblian (zone A; Van der Meulen et al., 2011, 2012), although this is a likely local phenomenon because it persists until subzone Ca in the Teruel Basin (Montalvos 2; Hordijk et al., 2015) and Bunyol-Xiva Basin (Valencia; Daams, 1976; Robles et al., 1991). Its record at Mas d'Antolino B3 (MAB3) at the Ribesalbes-Alcora Basin (Valencia) is comparable to that of Sant Mamet, which is also correlated to subzone Cb (Crespo et al., 2014; Crespo Roures, 2017). However, the rodent fauna of MAB3 includes abundant remains of *L. ellipticus*, which may indicate an older age than Sant Mamet, where this eomyid is rare. The LO of *Melissiodon* in France is in sites that are correlated to MN4 (e.g., Béon 2, Artenay, La Romieu Bulot, 1989; Bulot and Ginsburg, 1993; Bulot et al., 2009). In Central Europe *Melissiodon* also disappears during MN4, its last occurrence being well constrained in the Swiss Molasse Basin to the uppermost part of chron C5Cr (ca. 16.8 Ma; Kälin and Kempf, 2009).

The Vallès-Penedès early to middle Miocene record has delivered both micro- (figure 10.1) and macromammals (figure 10.3). This contrasts with other Iberian regions, such as the Calatayud-Montalbán and Teruel Basins, that show a comparatively richer record for this time interval but have mostly delivered just small mammals. Thanks to a combination of bio- and magnetostratigraphic data it is possible to provide a robust chronology for some major bioevents. These include the dispersal of the equid *Anchitherium* or that of the proboscidean *Gomphotherium* (figure 10.4). The Vallès-Penedès record provides a minimum age (at around 18 Ma) for these two events, although they certainly occurred earlier, probably during the early Ramblian, as they are associated to clearly older faunas in France. In addition, the record indicates that a second wave of immigrants, which included deinotheres, listriodontine suids, tragulids and bovids, entered Iberia at around 16.5 Ma. As far as small mammals are concerned, the main faunal events, such as the dispersal of modern cricetids or the extinction of the eomyid *Ligerimys* occurred at approximately the same time as in other Iberian basins.

10.4 PALEOECOLOGY AND PALEOCLIMATOLOGY

10.4.1 REGIONAL PATTERNS

The early Miocene small mammal faunas of the Vallès-Penedès Basin include multiple sites that have delivered rich samples (of more than 100 identified specimens) which are suitable for paleoenvironmental inferences. The mean annual precipitation (MAP), precipitation in the driest month (LMP) and the wettest month (HMP) was inferred using the transfer functions devised by Van Dam (2006) and Van Dam and Utescher (2016) that consider diversity of arboreal and invertivore small mammals (see chapter 4.6.3). Paleoprecipitation estimates are carried out for the following sites: Sant Andreu de la Barca, el Turó de les Forques, les Cases de la Valenciana, Can Martí Vell, Vilobí del Penedès and les Escletxes del Papiol (see table 10.1, figure 10.3). Other sites were necessarily excluded either because recovered sample sizes were not large enough or because part of the small mammal community had not been studied. Anyway, small-mammal-based paleoprecipitation estimates range from about 18 to 15 Ma and show main trends during this time interval. Late Ramblian (zone A, MN3) sites show high MAP values, well over 800 mm/year. Inferred precipitation seasonality is important, nearing 100 mm difference between the driest and wettest month in Sant Andreu de la Barca (39 mm vs. 131 mm; see table 10.1). During the early Aragonian subzone Ca (MN4) estimates are variable, showing values close to that of Ramblian sites for Can Martí Vell and significantly lower for les Cases de la Valenciana (MAP near 540 mm/year). Such difference is due to the much diverse insectivore fauna at Can Martí Vell, and probably reflects local conditions rather than regional ones. A marked decrease in MAP is observed in later Aragonian sites such as Vilobí del Penedès (subzone Cb, MN5) and les Escletxes del Papiol (subzone Da, MN5), with estimates of 490 mm/year for both sites. LMP precipitation is similar to that recorded during zones A and Ca (about 30 mm), but HMP precipitation is significantly lower, being of just 63 mm. This indicates a significant regional aridification coinciding with the latest Burdigalian and the Langhian, or between 16 and 15 Ma, that coincides with the maximum of the Mid-Miocene Climatic Optimum (MCO; see Zachos et al., 2001). Earlier sites, dating back to around 16.5 Ma may already show this increased aridity, but results are ambiguous.

Additional paleoclimatic information can be gathered from the rest of the vertebrate fauna. To this regard thermophilic ectothermic vertebrates (freshwater fishes, amphibians and reptiles) are particularly valuable. Representatives of certain groups, including crocodiles, monitor lizards, chameleons or giant turtles that are currently restricted to tropical and subtropical regions provide valuable clues on paleotemperature range (Böhme, 2003). The early Miocene herpetofauna is currently

Locality	Basin	MN	MAP	LMP	HMP
les Escletxes del Papiol	Vallès-Penedès	MN5	490	28	63
Vilobí del Penedès	Vallès-Penedès	MN5	490	29	63
Can Martí Vell	Vallès-Penedès	MN4	490	28	63
Les Cases de la Valenciana 1	Vallès-Penedès	MN4	791	34	107
el Turó de les Forques	Vallès-Penedès	MN3	538	30	69
Sant Andreu de la Barca	Vallès-Penedès	MN3	664	32	88
Olmo Redondo 9	Calatayud-Montalbán	MN5	628	23	87
Olmo Redondo 8	Calatayud-Montalbán	MN5	509	24	69
Olmo Redondo 5	Calatayud-Montalbán	MN5	509	24	69
Vargas 1A	Calatayud-Montalbán	MN5	616	26	83
Artesilla	Calatayud-Montalbán	MN4	453	21	62
Villafeliche 2A	Calatayud-Montalbán	MN4	556	29	72
Olmo Redondo 3	Calatayud-Montalbán	MN4	582	30	76
San Roque 2	Calatayud-Montalbán	MN4	455	23	61
Olmo Redondo 2	Calatayud-Montalbán	MN4	595	29	79
Olmo Redondo 1	Calatayud-Montalbán	MN4	525	23	72
San Roque 1	Calatayud-Montalbán	MN4	666	31	88
San Roque 4B	Calatayud-Montalbán	MN3	719	32	96
San Roque 4A	Calatayud-Montalbán	MN3	595	29	79
Aspitobel 520m	Swiss N. Alpine Foreland	MN5	762	31	103
Rämisgraben	Swiss N. Alpine Foreland	MN5	455	23	61
Tobel Hombrechtikon	Swiss N. Alpine Foreland	MN5	768	37	104
Vermes 2	Swiss N. Alpine Foreland	MN5	860	33	118
Hüllistein	Swiss N. Alpine Foreland	MN5	663	27	90
Vermes 1	Swiss N. Alpine Foreland	MN5	695	33	92
Martinsbrünneli	Swiss N. Alpine Foreland	MN5	686	37	92
Buchberg-Erlistrasse	Swiss N. Alpine Foreland	MN5	608	34	79
Oberkulm-Sämlen	Swiss N. Alpine Foreland	MN5	719	32	96
Hubertingen	Swiss N. Alpine Foreland	MN4	476	33	59
Hüenerbach	Swiss N. Alpine Foreland	MN4	540	32	69
Tägernaustrasse	Swiss N. Alpine Foreland	MN4	879	39	122
Glovelier	Swiss N. Alpine Foreland	MN4	743	35	100
Trub-Sältenbach	Swiss N. Alpine Foreland	MN3	820	40	114
Pontlevoy	Southern France	MN5	512	31	65
La Romieu	Southern France	MN4	717	38	97
Beaulieu	Southern France	MN3	864	39	120
Engelswies	Southern Germany	MN5	781	39	107
Sandelzhausen	Southern Germany	MN5	670	29	90
Petersbuch 11	Southern Germany	MN4	726	34	98
Wintershof-West	Southern Germany	MN3	821	39	114
Bunyol	Foia de Bunyol	MN5	781	33	106
Barranc de Campisano	Ribesalbes-Alcora	MN4	747	34	100
Alto de Ballester	Rubielos de Mora	MN3	511	2	84
Rubielos de Mora	Rubielos de Mora	MN3	762	31	103

Table 10.1: Small-mammal paleoprecipitation estimates inferred using Van Dam (2006) and Van Dam and Utescher, (2016) transfer functions. Locality estimates are averaged by MN zone and represented in the paleogeographic maps for MN3 to MN5 (see figure 10.6).

under study, but some thermophilic taxa, such as crocodiles and giant turtles have been recovered in almost all the studied sites (Luján, 2015). Small crocodiles of the genus *Diplocynodon* are particularly common in early Miocene sites (Luján et al., 2018), and even complete skulls have been recovered els Casots (Díaz-Aráez et al., 2017). On the other hand, giant turtle shell fragments and occasionally more complete material belonging to the genus *Titanochelon* (e.g., from les Cases de la Valenciana; see Luján et al., 2017) have been recovered in almost all sites. In addition, other thermophilic taxa include phytonid snakes (Ivanov, 2001), which are present at les Cases de la Valenciana, and monitor lizards (*Varanus* sp.), which have been recovered from Can Mas (el Papiol; Delfino et al., 2013). Overall, the presence of giant turtles and crocodiles points towards mean annual temperatures (MAT) above 17 ºC and reaching a maximum of ca. 27 ºC (see Böhme, 2003). Significantly large samples of macromammals have only been recovered at a few sites (Sant Andreu de la Barca, les Cases de la Valenciana, els Casots), generally associated with lacustrine facies. Again, detailed studies are yet to be performed, but the absence of grazing herbivores or mixed feeders points to the presence of forested environments, at least close to these humid areas.

Finally, paleobotanical data complete the paleoenvironmental picture. Rich macrofloral assemblages have been recovered at several points of the basin, sometimes in layers just a few meters above or below mammal-bearing strata. Major macrofloral sites comprise la Costablanca (in layers just a few meters above the mammal site) and la Pedrera (Sant Llorenç d'Hortons), which dates back to the Langhian (Sanz de Síria Catalán, 1993, 1996, 2001; see figure 10.2). Further macrofloral sites include localities at Sant Sadurní d'Anoia, Martorell and Rubí (Sanz de Síria Catalán, 2001). However, the stratigraphical position and age of these sites is uncertain, although they are generally correlated to the late Langhian (e.g., Sanz de Síria Catalán, 2001). In addition, fossil pollen has been recovered from Vilobí del Penedès in lutites above the coquina oyster layer (thus a few meters above the micomammal-bearing levels; Bessedik, 1984), from the Langhian layers at la Rierussa (Sant Llorenç d'Hortons, Bessedik, 1985; Jiménez-Moreno and Suc, 2007) and from the Langhian shallow marine facies at Sant Pau d'Ordal, near els Casots site (Bessedik and Cabrera, 1985; Jiménez-Moreno and Suc, 2007; figure 10.2). The Costablanca flora, dating back to ca. 18 Ma (late Ramblian), includes more than 30 % of xerophytic and microphyllous leguminose bushes and trees (e.g., *Acacia*, *Cassia*, *Caesalpina*, *Mimosa*) which would indicate a tropical to subtropical climate with marked rainfall seasonality (Sanz de Síria Catalán, 1993, 1996; Kovar-Eder, 2003). Additional remains include aquatic plants (reeds such as *Phragmites* and *Typha*), the palm *Sabal* (palmetto) and other subtropical to tropical taxa such as *Bumelia* (bully tree), *Ficus* (fig tree) and *Sapindus* (soapberry), which would have defined the riverine vegetation (Sanz de Síria Catalán, 1993, 1996). Away from the humid areas, the environment would likely correspond to less dense woodland dominated by leguminose trees. Sanz de Síria Catalán (1993, 1996) estimates MAT of 20-25 ºC and protracted dry seasons on the basis of la Costablanca flora. Undetermined plant remains, presumably belonging to aquatic plants, have been recovered in some early Aragonian (subzone Ca) sites, such as les Cases de la Valenciana, but in practice there are no paleobotanical data for this time interval. The more recent palynofloras from Vilobí del Penedès, La Rierussa and Sant Pau d'Ordal, which range between about 16 and 15 Ma, offer a detailed picture of the regional vegetation (Bessedik, 1984, 1985; Bessedik and Cabrera, 1985; Jiménez-Moreno and Suc, 2007). The pollen profiles of these three localities are all similar and include abundant *Avicennia* pollen, thus indicating the presence of impoverished coastal mangroves. The palynoflora also includes several mega- and mesothermic taxa, such as: Taxodiacea (swamp cypress family), Sapotaceae, *Bombax* (cotton tree), *Myrica* (bayberry), *Engelhardia* and *Platycarya* (tropical members of the walnut and hickory family), amongst others. Temperate elements, such as *Buxus sempervirens* type (common box) or *Carya* (hickory) are rare. However, most of the pollen spectra is dominated by herbs (Poaceae, Asteraceae). Leguminose trees, such as *Acacia*, are surprisingly rare. The palynoflora suggests the presence of scattered forest rich in tropical to subtropical elements developing at low altitudes near humid areas and also at mid altitudes (Jiménez-Moreno and Suc, 2007). MAT estimates for la Rierussa range from 17 to 25 ºC, whereas MAP would be 900-1300 mm with moderate rainfall seasonality (Jiménez-Moreno et al., 2010). These results generally agree with the presumably Langhian macroflora recovered at the Vallès-Penedès Basin (Sant Sadurní d'Anoia, Martorell, Rubí), except for the higher presence of leguminose trees in these sites (Sanz de Síria Catalán, 2001). Overall, Ramblian and middle Aragonian macrofloras are very similar to one another, indicating the prevalence of tropical to subtropical and seasonally dry conditions (Sanz de Síria Catalán, 1993, 1996, 2001). Plant-based paleoprecipitation estimates are notably higher than those based on small mammals and do not show major variations throughout the interval. The reasons for such disagreement are not known. Maybe small mammals record more local environmental conditions, or the studied sites coincide with short-lasting arid episodes. Be that as it may, small-mammal-based MAP estimates reach their minimum during the Langhian, coinciding with the major transgressive pulses (figure 10.4). At these particularly warm moments, when coral reefs developed in the shallow sea that flooded part of the basin (Permanyer, 1990; de Gibert and Casanovas-Vilar, 2011; Domènech et al., 2011), annual rainfall decreased markedly.

Considering the range of MAT and MAP as inferred from different proxies, early to early middle Miocene major biome types in the Vallès-Penedès Basin are in the range of savannahs and tropical deciduous woodlands and forests (Whittaker, 1962; Prentice et al. 1992). Small mammals show an ample difference in precipitation between the driest and wettest month, so apparently a savannah or woodland is more likely than forest, at least far from humid areas.

10.4.2 CONTINENTAL PATTERNS

Small-mammal based paleo-precipitation estimates were calculated for several European regions besides the Vallès-Penedès Basin: Calatayud-Montalbán Basin, Rubielos de Mora Basin, Ribesalbes-Alcora Basin, Foia de Bunyol, Southern France, Swiss North Alpine Foreland Basin and Southern Germany. Data were primarily taken from Van der Meulen et al. (2012) for Calatayud-Montalbán, from Crespo Roures (2017) for the Ribesalbes-Alcora and Foia de Bunyol basins (Valencia), from Van den Hoek Ostende et al. (2017) for Rubielos de Mora Basin (Teruel) and from Kälin and Kempf (2009) for Switzerland. Data from selected French and German sites were downloaded from the NOW database of fossil mammals (The NOW Community, 2020). Considering the coarse temporal resolution of French and German sites, locality estimates were averaged by MN zone and represented in paleogeographic maps for MN3 to MN5 (see figure 10.6). For a complete list of localities, age and calculated parameters see table 10.1.

MAP shows a consistent pattern of lower values in southern latitudes, particularly in the inner Iberian Peninsula. During MN3, MAP is high in all regions, well above 800 mm/year, except in Rubielos de Mora (ca. 760 mm/year) and the Calatayud-Montalbán Basin (ca. 650 mm/year) (figure 10.6A). Inferred MAP in the Vallès-Penedès Basin is as high as in Central Europe. MN4 seems to reflect higher continental aridity, MAP being only above 800 mm/year in Germany (figure 10.6B). In Switzerland and France it ranges from about 660 to 720 mm/year, while in the Vallès-Penedès it is slightly lower, of just about 600 mm/year. In the Ribesalbes-Alcora, MAP is significantly high, of about 750 mm/year, showing locally humid conditions. Once more, the Calatayud-Montalbán shows the lowest MAP values, of about 550 mm/year. MAP values during the Langhian (MN5) decrease in all areas but in Valencia, the site of Bunyol showing MAP of about 780 mm/year (figure 10.6C). This may either reflect a locally humid environment, or be attributed to the older age of this site (Aragonian subzone Cb, early MN5) as compared to other localities. Latitudinal paleoprecipitation patterns are the same as in previous intervals, with Central Europe showing higher values than southern regions, but this time estimated MAP is just of about 730 mm/year in Germany and 690 mm/year in Switzerland. Southern France, the Vallès-Penedès and the Calatayud-Montalbán basins show very low MAP estimates ranging from about 500 to 550 mm/year. It is worth noting that MN5 sites of the Vallès-Penedès just correspond to the lowermost part of this biozone (see chapters 10.2 and 10.3), which is known to correspond to a particularly warm phase (the height of the MCO; Zachos et al., 2001). Therefore, it is likely that if younger, post-MMCO localities were present they would have resulted in higher MAP estimates for the MN5 record in this basin.

The generally high paleo-precipitation estimates for southern France and Central Europe are in agreement with paleobotanical data. Pollen profiles from the late Burdigalian and Langhian of southern France (Estagel, Bayanne, Les Mées; see Jiménez-Moreno and Suc, 2007) are characterized by the dominance of termophilous elements (Sapotaceae, Taxodiaceae, *Engelhardia*, *Myrica*) and even include mangroove pollen (*Avicennia*). Mesothermic elements (*Carya*, *Liquidambar* [sweetgum], *Quercus* [oak] deciduous type, *Zelkova*) are also present and herbs (mostly Poaceae) can be important, but contrary to Iberian records they do not dominate the

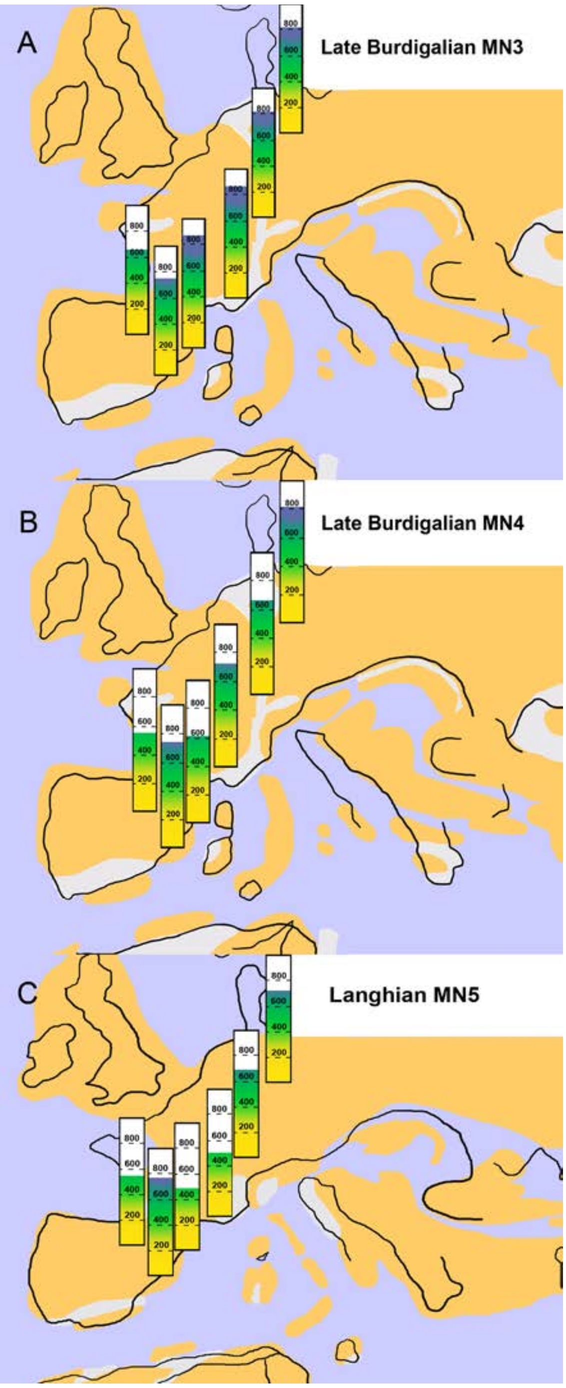
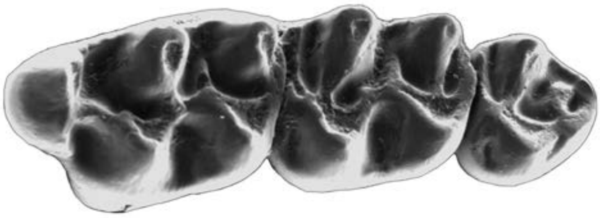


Figure 10.6: Small-mammal based paleoprecipitation estimates for different European regions averaged by MN zone and represented in paleogeographic maps for MN3 to MN5. For a complete list of localitites, age and calculated parameters see table 10.1.

pollen assemblage. In east-central France (Ecotet) and Switzerland (Le Locle) the pollen profiles show low abundances of herbs and shrubs (Jiménez-Moreno and Suc, 2007). In these sites megathermic elements (Taxodiaceae, *Engelhardia*) are still common, although some taxa, such as *Avicennia*, are not recorded. Mesothermic taxa, mostly deciduous *Quercus*, are dominant components of the assemblage. The pollen assemblage, which always includes a significant proportion of megathermic elements, indicates high temperatures and the regional environment is interpreted as evergreen and mixed forests. MAP would have been high and with little to no seasonality (Jiménez-Moreno and Suc, 2007). Macrofloral data support these interpretations and show that assemblages comparable to modern evergreen broad-leafed forests were predominant in Central Europe during the early and early middle Miocene (Kovar-Eder, 2003). These forest environments, today thriving in certain regions of eastern Asia (southeast China, Taiwan) are characterized by a warm-temperate humid climate, with mild winters (MAT between 16-19 ºC and no months with temperature below 0 ºC) and high rainfall (MAP well over 1400 mm/year, even higher at particular locations), without marked precipitation seasonality. *Taxodium* swamps would have developed in organic-rich wetlands (Kovar-Eder, 2003). Overall, the Iberian Peninsula appears to have been more arid and seasonal than higher latitudes, as reflected in pollen spectra and macrofloral assemblages by the occurrence of a higher proportion of herbs and also leguminose trees and shrubs such as *Acacia* (Jiménez-Moreno and Suc, 2007; Jiménez Moreno et al., 2010; Sanz de Síria Catalán, 1993, 1996, 2001). Because of their proximity to the sea, coastal regions of Catalonia and Valencia would have been significantly more humid than more inland areas such as the Calatayud-Montalbán Basin (Jiménez-Moreno and Suc, 2007; Jiménez Moreno et al., 2010).

Paleobiogeographic patterns in early to middle Miocene mammal faunas reflect this increased aridity and rainfall seasonality in Iberia. Eulitpotyphlans clearly illustrate this and show a consistent latitudinal diversity gradient throughout the Miocene in Western Europe, lower latitudes always showing an impoverished insectivore fauna because of the absence of certain genera or even entire families (Furió et al. 2011, Madern and Van den Hoek Ostende, 2015). The early Miocene insectivore faunas of the Vallès-Penedès, particularly Ramblian ones, are more diverse in the Vallès-Penedès Basin than those of the Calatayud-Montalbán Basin (Van den Hoek Ostende et al., 2020; see chapter 10.2) and for example include dimylids, a family unknown from the Spanish inland at the time but commonly recorded in central European faunas. Perhaps not surprisingly, dimylids such as *Chainodus* and a diverse insectivore assemlage have been recovered from the Ribesalbes-Alcora and Rubielos de Mora basins (Crespo Roures et al., 2017; Van den Hoek Ostende et al., 2017). Similarly, the rodent faunas of the Vallès-Penedès Basin include a higher proportion of inferred forest-dwellers, such as certain sciurids (*Dehmisciurus*) and glirids (*Vasseuromys, Bransantoglis, Muscardinus* and *Glirudinus*; see chapter 9 and section 10.2). The presence of certain cricetid species unknown from the Calatayud-Montalbán Basin, namely *Democricetodon gracilis* and *Eumyarion weinfurteri*, further supports this interpretation (see chapter 9). Presumably arboreal glirids are also more common in the Ribesalbes-Alcora, Foia de Bunyol and Rubielos de Mora basins. Furthermore, flying squirrels (*Aliveria*, *Blackia*, *Miopetaurista*), unknown from the Vallès-Penedès at that time, have been reported from these basins (De Bruijn and Moltzer, 1974; Daams, 1977; Crespo Roures, 2017). Finally, larger mammals also show consistent paleobiogeographic patterns, so that during the early Miocene (MN3–MN4) Vallès-Penedès assemblages are distinct from those of other Iberian basins, and include a slightly higher diversity of herbivores, particularly suiforms (Costeur and Legendre 2008a, b). In this regard, they are closer to contemporary faunas from southern France and Germany. On the other hand, Fortelius et al. (2002) used degree of hypsodonty in large herbivores as an aridity proxy for the Eurasian Neogene and found that during the early Miocene (24-15 Ma) brachyodont (low-crowned) taxa dominated European faunas except in central Spain. In this region mesodont and hypsodont rhinoceroses (such as *Hispanotherium*) provide evidence of incipient aridity (Fortelius et al., 2002).

During the early Miocene the Vallès-Penedès was a transitional area between two distinct bioprovinces: central European and inner Iberian. MAP and rainfall seasonality is apparently the main distinguishing climatic variable between these provinces, with inner Iberia being consistently recognized as drier and more seasonal. Evergreen broad-leafed forests covered much of Central Europe at that time, while more seasonal and open dry tropical/subtropical forests and woodlands occurred in Iberia. This is reflected in the mammal faunas, which include a higher diversity of forest elements at higher latitudes. The Vallès-Penedès faunas and those of other basins of eastern Spain (Rubielos de Mora, Ribesalbes-Alcora, Foia de Bunyol) present higher affinities with inland basins, but still include a significant amount of Central European taxa. De Bruijn and Moltzer (1974) already recognized this pattern while comparing the Rubielos de Mora rodent faunas with those of Calatayud-Montalbán. Later on, Agustí (1990) even distinguished and Ibero-Levant subprovince, including eastern coastal basins, although noting at the same time that during the early Miocene Iberia appears to have been a rather homogenous biogeographic unit. Back to that time, this was a rather precipitate conclusion because it was based in very few data and localities, however, new data and analyses show that it was largely correct. The position of the Vallès-Penedès as a transitional region between the Iberian and Central European bioprovinces during the middle and late Miocene is well known (see Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2005, 2008), but, as shown here, this situation already existed during the early Miocene. Interestingly, at that time this transitional character extended to other basins of east-coastal Spain, which would define the Ibero-Levant subprovince of Agustí (1990). Unfortunately, the middle and early late Miocene record in these regions is almost exclusively restricted to the Vallès-Penedès Basin, so it is impossible to evaluate the geographical extension of the Ibero-Levant subprovince at that time.



Chapter 11: Conclusions

11. CONCLUSIONS

I. The early to early middle Miocene cricetid rodent fauna from the Vallès-Penedès is more diverse than previously thought, including four different genera and up to seven species.

II. Late Ramblian (zone A; ca. 19.3-17.2 Ma) is devoid of cricetids other than the archaic *Melissiodon dominans*, which is more abundant in the Vallès-Penedès Basin than in other Iberian basins. The old material was first attributed to the species *Melissiodon arambourgi*, but after reviewing it as well as thanks to the recovery of new specimens from additional sites of the basin, earlier suggestions that this species is a junior subjective synonym of *Melissiodon dominans* are confirmed. The last occurrence of *Melissiodon* is at Sant Mamet (Aragonian subzone Cb, early MN5), with an estimated age of 15.9-15.7 Ma, and is one of the youngest records of this genus.

III. Along with *Melissiodon dominans,* another archaic cricetid genus is found in the Vallès-Penedès Basin during the early Aragonian age (zone C and early zone D, ca. 16.5 - 15 Ma): *Eumyarion weinfurteri. Eumyarion* is present in some MN4 and MN5 sites of the basin, but it is always scarcely represented. It is first recorded in early Aragonian (subzone Ca) sites of les Cases de la Valenciana and Can Martí Vell. *Eumyarion weinfurteri* is a common element in MN4 and MN5 sites from Central Europe but it is unknown from other Iberian basins.

IV. Modern cricetids are major components of the Aragonian faunas of the Vallès-Penedès Basin. These include four species of the genus *Democricetodon* and one of the genus *Megacricetodon*, thus significantly increasing previously known diversity.

V. *Democricetodon hispanicus* is present in almost all the early Aragonian sites (subzone Ca), thus being the most abundant *Democricetodon* species during the early Miocene in the Vallès-Penedès Basin. In this basin D. hispanicus persists for a significantly longer time than in the Aragonian type area (the Calatayud-Montalbán Basin, east-central Spain), being last recorded during Aragonian subzone Cb at els Casots site, with an estimated age of 15.9 Ma. In the Calatayud-Montalbán Basin, it is restricted to zone B and uppermost zone A, its last occurrence being at 16.5 Ma.

VI. Additional *Democricetodon* species are less abundant than *D. hispanicus* and first appear somewhat later, in the early Aragonian (subzone Cb) and are more common in middle Aragonian (early zone D) sites . These are *Democricetodon gracilis,* which is a small-sized species far more common and widespread in Central Europe than in the Iberian Peninsula. *Democricetodon decipiens* is larger than both *D. gracilis* and *D. hispanicus* and is further distinguished by its shorter mesolophs/ids. Finally, a large-sized *Democricetodon* species is represented by scarce material (just a few specimens that preclude even a tentative species attribution) in a few MN5 sites.

VII. The early Miocene Vallès-Penedès small mammal succession is more continuous than previously thought, covering the later part of the early Miocene as well as its transition with the middle Miocene. Besides, the rodent fauna in particular shows several affinities with that from the Aragonian type area, the Calatayud-Montalbán Basin of east-central Spain and also a few affinities with Central European regions such as Swiss Molasse Basin.

VIII. The local zonation for the Ramblian and Aragonian type areas can be extended to the Vallès-Penedès Basin during the early and early middle Miocene. The Vallès-Penedès record for this time interval comprises Ramblian zone A as well as Aragonian zone C and early zone D. Sites that could be correlated to Aragonian zone B remain elusive, but there are no evidences for major hiatuses coinciding with this time interval.

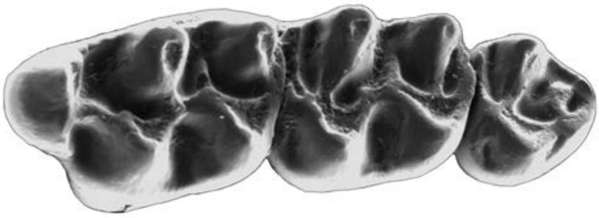
IX. The extension of Ramblian and Aragonian zones to the Vallès-Penedès record has some difficulties. While major zones can be applied without problems, the detailed subdivision into subzones is questionable because of the different cricetid succession, especially regarding the *Democricetodon* species from the type area, which show slightly different temporal ranges in the Vallès-Penedès Basin or, in some cases, are completely absent. Yet, additional criteria can be used to distinguish particular subzones, such as the occurrence of different species of the eomyid *Ligerimys* in early Aragonian subzones Ca and Cb.

X. Magnetostratigraphic data have been compiled for several early to middle Miocene fossiliferous sections. These, combined with litho- and biostratigraphic data allow providing a robust chronology for some major bioevents, such as the dispersal of the equid *Anchitherium* from North America or that of the proboscidean *Gomphotherium* from Africa. The Vallès-Penedès record provides a minimum age (ca. 18 Ma) for these two events in the Iberian Peninsula. A second wave of immigrants, which included deinotheres, listriodontine suids, tragulids and bovids dispersed into Iberia at ca. 16.5 Ma. Concerning small mammals, the main faunal events, such as the dispersal of modern cricetids or the extinction of the eomyid *Ligerimys*, occurred at approximately the same time as in other Iberian basins.

XI. The new robust chronology for the early and early middle Miocene Vallès-Penedès record allows for the reconstruction of regional climatic dynamics during this interval using different proxies. This period coincided with the onset of the Mid-Miocene Climatic Optimum (MCO), implying higher global temperatures and worldwide sea level rise specially between 17 and 15 Ma. Small-mammal community structure is used to infer rainfall patterns and show a marked decrease in mean annual precipitation (MAP) between ca. 16.5 and 15 Ma, that is, during the height of the MCO. Considering the inferred range in mean annual temperatures, the early to early middle Miocene major biome types in the Vallès-Penedès Basin are in the range of savannahs and tropical deciduous woodlands and forests. Small mammals show an ample difference in precipitation between the driest and wettest month, so a savannah or woodland is more likely than a forest, at least far from humid areas which would have presented a denser vegetation cover. This conclusion is supported by available paleobotanical evidence.

XII. Small mammals indicate an important decrease in MAP in other Western

European regions during the maximum of the MCO. Aridification, was significantly higher in peri-Mediterranean regions, particularly in inner Iberia.The small mammal fauna indicates that during the early and early middle Miocene the Vallès-Penedès was a transitional area between two distinct bioprovinces: central European and inner Iberian. MAP and rainfall seasonality is the main distinguishing climatic variable between these provinces, with inner Iberia being consistently recognized as drier and more seasonal. Such situation, which had previously been recognized for the middle and early late Miocene already existed at the beginning of this epoch.



Chapter 12: References

REFERENCES

This reference list only comprises references cited in chapters 1 to 4 and chapter 10. Chapters 5 to 9 correspond to published scientific papers including references cited therein in their corresponding reference section.

Abdul Aziz, H., Böhme, M., Rocholl, A., Prieto, J., Wijbrans, J. R., Bachtadse, V., & Ulbig, A. 2010. Integrated stratigraphy and 40Ar/39Ar chronology of the early to middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences, 99, 1859–1886.

Abdul Aziz, H., Böhme, M., Rocholl, A., Zwing, A., Prieto, J., Wijbrans, J. R., & Bachtadse, V. 2008. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). International Journal of Earth Sciences, 97, 115–134.

Adkins, R. M., Gelke, E. L., Rowe, D., & Honeycutt, R. L. 2001. Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes. Molecular Biology and Evolution, 18, 777–791.

Aguilar, J-P. 1981. Evolution des rongeurs miocènes et paleogeographie de la Méditerranée occidentale. [Ph.D. dissertation]. Montpellier: Université des Sciences et Techniques de Montpellier II.

Agustí, J. 1981. Roedores Miomorfos del Neógeno de Cataluña. Director: Crusafont, Miquel. [Ph.D. dissertation]. Barcelona: Universitat de Barcelona, Departament de Paleontologia.

Agustí, J. 1982. Biozonación del Neógeno continental de Cataluña mediante roedores (Mamm.). Acta Geol*ó*gica Hisp*á*nica, 17, 21–26.

Agustí, J. 1983. Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallés-Penedés, Cataluña, España). Estudios Geológicos, 39, 417–430.

Agustí, J. 1989. On the peculiar distribution of some muroid taxa in the Western Mediterranean. Bolletino Della Società Paleontologica Italiana, 28, 147–154.

Agustí, J., & Antón, M. 2002. Mammoths, sabertooths, and hominids: 65 million years of mammalian evolution in Europe. New York: Columbia University Press.

Agustí, J., & Cabrera, L. 1980. Nuevos datos sobre la biozonación del Burdigaliense continental de la cuenca del Vallés-Penedés. Acta Geológica Hispánica. Barcelona: Universitat de Barcelona, 15, 81–84.

Agustí, J., Cabrera, L., & Moyà-Solà, S. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. Paleontologia i Evolució, 18, 57–81.

Agustí, J., & Galobart, A. 1997. Noves localitats amb mamífers fòssils en el Miocè de la

Conca del Vallès-Penedès. Tribuna d'Arqueologia. Barcelona: Generalitat de Catalunya. Departament de Cultura, 1996-1997, p. 9–22.

Agustí, J., & Llenas, M. 1993. Los roedores del Mioceno inferior de Els Casots (Vallés-Penedés). Nota preliminar. In: González Donoso, J.M. (Ed.), Comunicaciones de las IX Jornadas de Paleontología, Málaga, 28-30 de octubre de 1993. Màlaga: Universidad de Málaga, pp. 70–72.

Agustí, J., & Moyà-Solà, S. 1990. Mammal extinctions in the Vallesian (Upper Miocene). Lecture Notes in Earth Science, 30, 425-432.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., & Parés, J. M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth-Science Reviews, 52, 247–260.

Agustí, J., Cabrera, L., Domènech, R., Martinell, J., MoyàSolà, S., Ortí, F., & de Porta, J. 1990. Neogene of Penedès area (Prelittoral Catalan depression, NE Spain). In: J. Agustí, J., Domènech, R., Julià, R. & Martinell, J. (Eds.). Iberian Neogene basins. Paleontologia i Evolució memòria especial 2, 187-207.

Agustí, J., Moyà-Solà, S., & Gibert, J. 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. Paléobiologie Continentale, 14, 33-46.

Agustí, J., Cabrera, L., Garcés, M., & Parés, J.M. 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. Palaeogeography, Palaeoclimatology, Palaeoecology, 133, 149–180.

Agustí, J., Pérez-Rivarés, F. J., Cabrera, L., Garcés, M., Pardo, G., & Arenas, C. 2011. The Ramblian-Aragonian boundary and its significance for the European Neogene continental chronology. Contributions from the Ebro Basin record (NE Spain). Geobios, 44, 121–134.

Alba, D. M., Moyà-Solà, S., Malgosa, A., Casanovas-Vilar, I., Robles, J. M., Almécija, S., & Mengual, J. V. B. 2010. A new species of Pliopithecus Gervais, 1849 (Primates: Pliopithecidae) from the Middle Miocene (MN8) of Abocador de Can Mata (els Hostalets de Pierola, Catalonia, Spain). American Journal of Physical Anthropology, 141, 52–75.

Alba, D. M., Almecija, S., DeMiguel, D., Fortuny, J., de los Rios, M. P., Pina, M., & Moya-Sola, S. 2015. Miocene small-bodied ape from Eurasia sheds light on hominoid evolution. Science, 350, aab2625–aab2625.

Alba, D. M., Casanovas-Vilar, I., Garcés, M., & Robles, J. M. 2017. Ten years in the dump: An updated review of the Miocene primate-bearing localities from Abocador de Can Mata (NE Iberian Peninsula). Journal of Human Evolution, 102, 12–20.

Alba, D. M., Casanovas-Vilar, I., Furió, M., García-Paredes, I., Angelone, C., Jovells-Vaqué, S., & Moyà-Solà, S. 2018. Can Pallars i Llobateres: A new hominoid-bearing locality from the late Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula). Journal of Human Evolution, 121, 254–259.

Aldana Carrasco, E. J. 1991. Roedores Esciuromorfos del Neógeno de Cataluña. [Ph.D. dissertation]. Bellaterra: Universitat Autònoma de Barcelona.

Aldana Carrasco, E. J. 1992. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedès (Cataluña, España). Treballs del Museu de Geologia de Barcelona, 2, 69–97.

Almera, J. 1891. Mapa geológico y topográfico de la provincia de Barcelona subvencionado por la Excma. Diputación provincial. Región primera ó de contornos de la capital. Escala 1:40.000. Barcelona: Diputación Provincial de Barcelona.

Almera, J. 1898. Sobre la serie de mamíferos fósiles descubiertos en Cataluña: memoria leída por el académico numerario canónigo Dr. D. Jaime Almera, Pbro. en la junta general ordinaria celebrada el día 30 de abril de 1896. Memorias de la Real Academia de las Ciencias y las Artes de Barcelona, 2, 351–357.

Almera, J. 1899. Compte rendu de l'excursion (du Samedi 8 Octobre 1898) à Castellví de la Marca, au Vallon de Sant Pau d'Ordal et à Sant Sadurní d'Anoia. Bulletin de la Société Géologique de France, 26, 840–852.

Álvarez Sierra, M. Á. 1987. Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia) del Oligoceno superior y el Mioceno inferior español. Scripta Geologica, 86, 1–207.

Anadón, P., & De Villalta, J.F. 1975. Caracterización de terrenos de edad estampiense en Campins (Vallés Oriental). Acta Geológica Hispánica, 10, 6–9.

Andrews, P., Lord, J. M., & Nesbit Evans, E. M. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. Biological Journal of the Linnean Society, 11, 177–205.

Andrews, P. 1990. Owls, Caves and Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas From Westbury-Sub-Mendip, Somerset, U.K. University of Chicago Press, Chicago.

Andrews, P., & Kelley, J. 2007. Middle Miocene dispersals of apes. Folia Primatologica, 78, 328–343.

Andrews, P. 2015. An ape's view of human evolution. Cambridge ; New York: Cambridge University Press.

Antoine, P.-O., Welcomme, J.-L., Marivaux, L., Baloch, I., Benammi, M., & Tassy, P. 2003. First record of Paleogene Elephantoidea (Mammalia, Proboscidea) from the Bugti Hills of

Pakistan. Journal of Vertebrate Paleontology, 23(4), 977–980.

Antoine, P.-O., Marivaux, L., Croft, D. A., Billet, G., Ganerød, M., Jaramillo, C., & Gismondi, R. S. 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proceedings of the Royal Society B: Biological Sciences, 279, 1319–1326.

Antoine, P.-O., Métais, G., M. J., Crochet, J.-Y., Flynn, L. J., Marivaux, L., Rahim Rajpar, A., Roodhi, G., & Welcomme, J-L. 2013. Mammalian Neogene Biostratigraphy of the Sulaiman Province, Pakistan. In: Fossil Mammals of Asia. Neogene Bisotratigraphy and chronology. Wang, X., Flynn L.J., Fortelius, M. (Eds.). Columbia University press. New York. pp. 400-422.

Antunes, M. T., Legoinha, P., Nascimento, A., & Pais, J. 1996. The evolution of the Lower Tagus basin (Lisbon and Setúbal Peninsula, Portugal) from Lower to early Middle Miocene. Géologie de La France, 4, 59–77.

Antunes, M. T., Elderfield, H., Legoinha, P., Nascimento, A., & Pais, J. 1999. A stratigraphic framework for the Miocene from the Lower Tagus Basin (Lisbon, Setúbal Peninsula, Portugal) depositional sequences, biostratigraphy and isotopic ages. Revista de La Sociedad Geológica de España, 12, 3–15.

Antunes, M. T., & Ginsburg, L. 2003. The Deinotherium (Proboscidea, Mammalia): an abnormal tusk from Lisbon, the Miocene record in Portugal and the first appearance datum. Evidence from Lisbon, Portugal. Ciências Da Terra, 15, 173–189.

Archibald, J. D., & Deutschman, D. H. 2001. Quantitative analysis of the timing of the origin and diversification of extant placental orders. Journal of Mammalian Evolution, 8, 107–124.

Asher, R. J., Meng, J., Wible, J. R., McKenna, M. C., Rougier, G. W., Dashzeveg, D., & Novacek, M. J. 2005. Stem lagomorpha and the antiquity of glires. Science, 307, 1091–1094.

Asher, R. J., Smith, M. R., Rankin, A., & Emry, R. J. 2019. Congruence, fossils and the evolutionary tree of rodents and lagomorphs. Royal Society Open Science, 6, 190387.

Azanza, B., Cerdeño, E., Ginsburg, L., Van der Made, J., Morales, J., & Tassy, P. 1993. Les grands mammifères du Miocène inférieur d'Artesilla, bassin de Calatayud-Teruel (province de Saragosse, Espagne). Bulletin Museé Nationale Histoire Naturelle Paris. Section C: Sciences de la Terre, 15, 105–153.

Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J. M., Alcalde-Olivares, C., Vieira, M., Castro, L., & Valle-Hernández, M. 2010. The Cenozoic vegetation of the Iberian Peninsula: A synthesis. Review of Palaeobotany and Palynology, 162(3), 382–402.

Bartrina, M. T., Cabrera, L., Jurado, M. J., Guimerà, J., & Roca, E. 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). Tectonophysics, 203(1), 219–247.

Bataller, J. R. 1918. Mamífers fòssils de Catalunya. Treballs de la Institució Catalana d'Història Natural, 4, 111-272. Barcelona.

Bataller, J. R. 1924. Contribució a l'estudi de nous mamífers fòssils de Catalunya. Arxius de l' Institut de Ciències, 13, 36-41

Bataller, J. R. 1928. Los yacimientos de vertebrados fósiles de Cataluña. Comptes-rendus XIV^{e} Congrès Geologiqué International 1926, 3, 1009-1015.

Bataller, J. R. 1938. Els ratadors fòssils de Catalunya. Impremta de la Casa d'Assistència President Macià. Barcelona.

Bernor R. L., & Armour-Chelu, M. 1999. Family Equidae. In: Rössner, G., Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich. pp. 193-202.

Bessedik, M. 1985. Reconstitution des énvironnéments Miocènes de régions nord-ouest méditerranéennes à partir de la palynologie. [Ph.D. dissertation]. Montpellier: Université de Montpellier.

Bessedick, M. & Cabrera, L. 1985. Le couple récif-mangrove à Sant Pau d'Ordal (Vallès-Pénédès, Espagne), témoin du maximum transgressif en Méditerranée nord occidentale (Burdigalien supérieur - Langhien inférieur). Newsletters in Stratigraphy, 14, 20-35.

Bi, S., Meng, J., & Wu, W. 2008. A new species of *Megacricetodon* (Cricetidae, Rodentia, Mammalia) from the middle Miocene of northern Junggar Basin, China. American Museum Novitates, 3602, 1–23.

Blanga-Kanfi, S., Miranda, H., Penn, O., Pupko, T., DeBry, R. W., & Huchon, D. 2009. Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. BMC Evolutionary Biology, 9, 71.

Blumenbach, J. F. 1779. Handbuch der Naturgeschichte. Göttingen: Johann Christian Dieterich.

Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology, 195, 389–401.

Bolliger, T. 1999. Family Anomalomyidae. In: Rössner, G., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich, pp. 411- 420.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. Paris: J. Smith.

Brandt, J. F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. Mémoires de l'Academie Imperiale des Sciences de St Pétersbourg, Sixième Série, 9, 1–375.

Brenchley, P., & Harper, D. 1998. Palaeoecology: Ecosystems, Environments and Evolution. Chapman and Hall, London.

Bulot, C. 1989. Biostratigraphie des formations continentales de l'Orléanien du Haut-Armagnac (France). Bulletin Museé Nationale Histoire Naturelle Paris. Section C: Sciences de la Terre, 11, 133–139.

Bulot, C., & Ginsburg, L. 1993. Gisements à Mammifères miocènes du Haut-Armagnac et âge des plus anciens Probiscidiens d'Europe occidentale. Comptes Rendus Académie des Sciences de Paris. Série II, 316, 1011–1016.

Bulot, C., Antoine, P.-O., & Duranthon, F. 2009. Rongeurs et lagomorphes du Miocène inférieur de Béon 2 (MN4, Montréal-du-Gers, SW France). Annales de Paléontologie, 95, 197–215.

Cabrera, L. 1979. Estudio Estratigráfico i Sedimentológico de los Depósitos Basales del Mioceno de la Depresión del Vallès-Penedès. [Ph.D. dissertation]. Barcelona: Universitat de Barcelona.

Cabrera, L. 1981. Estratigrafía y características sedimentológicas generales de las formaciones continentales de la cuenca del Vallès-Penedès (Barcelona, España). Estudios Geológicos, 37, 35-43.

Cabrera, L., & Calvet, F. 1996. E8 onshore Neogene record in NE Spain: Vallès-Penedès and El Camp half-grabens (NW Mediterranean). In Friend, P. & Dabrio, C.J. (Eds.). Tertiary Basins of Spain: Record of Crustal Kinematics. Cambridge, United Kingdom: Cambridge University Press. pp. 97–105.

Cabrera, L., Calvet, F., Guimerà, J., & Permanyer, A. 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: organización secuencial y relaciones tectónica sedimentación. In: Colombo, F. (Ed.). Libro-guía excursión nº. 4, I Congreso del Grupo Español del Terciario, Barcelona. Universitat de Barcelona. pp. 1-132.

Cabrera, L., Roca, E., Garcés, M., & de Porta, J. 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera, J. A. (Ed.). Geología de España. Madrid: SGE-IGME. pp. 569-573.

Cabrera, L., Muñoz, J.A., Bordonau, J., Calvet, M., Liesa, M., & Losantos, M. 2010. El registre geològic. 25-0 milions d'anys: l'obertura de la Mediterrània. In: Atles Geològic Catalunya. Roca i Adrover, A. Miranda i Canals, J. (coords.). Barcelona: Generalitat de Catalunya. pp. 110-111.

Casanovas-Vilar, I. 2007. The rodent assemblages from the late Aragonian and the Vallesian (middle to late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). [Ph.D.

dissertation]. Bellaterra: Universitat Autònoma de Barcelona.

Casanovas-Vilar, I., & Agustí, J. 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, 248, 169–189.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J.M., Köhler, M., & Angelone, C. 2008. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). Journal of Human Evolution, 55, 589-603

Casanovas-Vilar, I., & DeMiguel Cascán, D. 2013. Memòria de la intervenció paleontològica als dipòsits del Miocè Inferior de la Conca del Vallès-Penedès i àrees properes. Campanya 2011 [unpublished field report]. Bellaterra: Institut Català de Paleontologia Miquel Crusafont.

Casanovas-Vilar, I., Alba, D.M., & Moyà-Solà, S. 2011a. Parada 1. Panorámica general de la cuenca y yacimiento de els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. Paleontologia i Evolució, Mem. espec. 6, 81–88.

Casanovas-Vilar, I., Alba, D. M., Garcés, M., Robles, J. M., & Moyà-Solà, S. 2011b. Updated chronology for the Miocene hominoid radiation in Western Eurasia. Proceedings of the National Academy of Sciences, 108, 5554–5559.

Casanovas-Vilar, I., Alba, D. M., Robles, J. M., & Moyà-Solà, S. 2011c. Registro paleontológico continental del Mioceno de la Cuenca del Vallès-Penedès. Paleontologia i Evolució, Mem. espec. 6, 55–80.

Casanovas-Vilar, I., DeMiguel, D., Galindo, J., Robles, J.M., Garcés, M., & Cabrera, L. 2011d. The continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). In: Viajando a mundos pretéritos (eds. A. Pérez-García, F. Gascó, J.M. Gasulla & F. Escaso). Morella: Ayuntamiento de Morella. pp. 93-100.

Casanovas-Vilar, I., DeMiguel Cascán, D., & Madurell-Malapeira, J. 2014. Informe sobre la intervenció paleontològica al jaciment de Les Cases de la Valenciana (Gelida, l'Alt Penedès). Campanya 2014 [unpublished field report]. Bellaterra: Institut Català de Paleontologia Miquel Crusafont.

Casanovas-Vilar, I., Madern, A., Alba, D. M., Cabrera, L., García-Paredes, I., van den Hoek Ostende, L. W., & Moyà-Solà, S. 2016a. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). Comptes Rendus Palevol, 15, 791–812.

Casanovas-Vilar, I., Garcés, M., Van Dam, J., García-Paredes, I., Robles, J.M., & Alba, D.M. 2016b. An updated biostratigraphy for the late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). Geologica Acta, 14, 195–217.

Casanovas-Vilar, I., DeMiguel, D., Madurell-Malapeira, J., & Jovells-Vaqué, S. 2017. Memòria de la intervenció paleontològica al jaciment de Les Cases de la Valenciana (Gelida, l'Alt Penedès). Campanyes 2014-2015 [unpublished field report]. Bellaterra: Institut Català de Paleontologia Miquel Crusafont.

Casanovas-Vilar, I., Garcia-Porta, J., Fortuny, J., Sanisidro, Ó., Prieto, J., Querejeta, M., Llácer, S., Robles, J.M., Bernardini, F., & Alba, D. M. 2018. Oldest skeleton of a fossil flying squirrel casts new light on the phylogeny of the group. eLife, 7, e39270.

Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V., & Ehleringer, J. R. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature, 389, 153–158.

Chaline, J., & Mein, P. 1979. Les Rongeurs et l'évolution. Paris: Doin.

Chaline, J., Mein, P., & Petter, F. 1977. Les grandes lignes d'une classification évolutive des Muroidea. Mammalia, 41, 245–252.

Coster, P. M. C., Beard, K. C., Salem, M. J., Chaimanee, Y., & Jaeger, J.-J. 2015. New fossils from the Paleogene of central Libya illuminate the evolutionary history of endemic African anomaluroid rodents. Frontiers in Earth Science, 3, 56.

Costeur, L., & Legendre, S. 2008a. Spatial and temporal variation in European Neogene large mammals diversity. Palaeogeography, Palaeoclimatology, Palaeoecology, 261, 127–144.

Costeur, L., & Legendre, S. 2008b. Mammalian Communities Document a Latitudinal Environmental Gradient during the Miocene Climatic Optimum in Western Europe. PALAIOS, 23(5), 280–288.

Cox, P. G., & Jeffery, N. 2015. The muscles of mastication in rodents and the function of medial pterygoid. In: Cox, P. G., & Hautier, L. (Eds.). Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press.

Cox, P. G., & Hautier, L. (Eds.). 2015. Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press.

Cox, P. G., Rayfield, E. J., Fagan, M. J., Herrel, A., Pataky, T. C., & Jeffery, N. 2012. Functional evolution of the feeding system in rodents. PLoS ONE, 7, e36299.

Crespo, V. D., Ruiz Sánchez, F. J., Freudenthal, M., & Montoya, P. 2014. Primer registro del género Melissiodon (Mammalia, Cricetidae) en la cuenca de Ribesalbes-Alcora (Castelló, España). In:, XXX Jornadas de Paleontología: Teruel. R. Royo Torres, F. Javier Verdú, & L. Alcalá (Eds.). Teruel: Fundación Conjunto Paleontológico de Teruel, Dinópolis. pp. 53–55.

Cox, P. G., Faulkes, C. G., & Bennett, N. C. 2020. Masticatory musculature of the African mole-rats (Rodentia: Bathyergidae). PeerJ, 8, e8847.

Crespo Roures, V. D. 2017. Los mamíferos del Mioceno inferior de la Cuenca de Ribesalbes-Alcora (Castelló, España) [Ph.D. dissertation]. València: Universitat de València.

Croft, D. A., Su, D. F., & Simpson, S. W. (Eds.). 2018. Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities New York, Springer.

Crusafont Pairó, M. 1950. La cuestión del llamado Meótico español. Arrahona, 1–2, 41–48.

Crusafont Pairó, M., & Truyols Santonja, J. 1954. Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología. Sabadell: Museo de la Ciudad de Sabadell.

Crusafont, M., De Villalta, J. F., & Truyols, J. 1955. El Burdigaliense continental de la Cuenca del Vallés-Penedés. Memorias y Comunicaciones del Instituto Geológico, 12, 11–272.

Crusafont, M., Valenciano, A., & Sanz, E. 1968. Un nuevo yacimiento de Vertebrados en el Burdigaliense de Martorell (Provincia de Barcelona). Acta Geológica Hispánica, 3, 44–47.

Cuvier, G. 1798. Tableau Élémentaire de l'Histoire Naturelle des Animaux. Paris: J.B. Bailière.

Cuvier, G. 1800. Leçons d'Anatomie Comparée. Paris: Bauduin.

D'Elía, G., Fabre, P.-H., & Lessa, E. P. 2019. Rodent systematics in an age of discovery: recent advances and prospects. Journal of Mammalogy, 100, 852–871.

D'Erchia, A. M., Gissi, C., Pesole, G., Saccone, C., & Arnason, U. 1996. The guinea-pig is not a rodent. Nature, 381, 597–600.

Daams, R. 1977. Aragonian sciuroptera (Sciuridae, Rodentia, Mammalia) from Spain. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, 80, 356–359.

Daams, R. 1999. Family Gliridae. In: Rössner, G. E. & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich. pp. 301–318.

Daams, R., & Freudenthal, M. 1974. Early Miocene Cricetidae (Rodentia, Mammalia) from Buñol (Prov. Valencia), Spain. Scripta Geologica. 24: 1-19.

Daams, R., & Freudenthal, M. 1981. Aragonian: the Stage concept versus Neogene Mammal Zones. Scripta Geologica, 62, 42736

Daams, R., & Freudenthal, M. 1988a. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*. Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud-Teruel Basin (Spain). Ed. M. Freudenthal. Scripta Geologica, Special Issue., 1, 39–132.

Daams, R., & Freudenthal, M. 1988b. Synopsis of the Dutch-Spanish collaboration program in the Aragonian type area, 1975-1986. Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud-Teruel Basin (Spain). Ed. M. Freudenthal. Scripta Geologica, Special Issue., 1, 43160.

Daams, R., & Freudenthal, M. 1989. The Ramblian and the Aragonian: límits, subdivision, geographical and temporal extentsion. In: Lindsay, E. H., Fahlbusch, V. & Mein, P. (Eds.), European Neogene Mammal Chronology. New York: Springer US, pp. 51–59.

Daams, R., & Van der Meulen, A.J. 1984. Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of North Central Spain. Paléobiologie Continentale, 14, 241-257.

Daams, R., Freudenthal, M., & Álvarez Sierra, M. Á. 1987. Ramblian; A new stage for continental deposits of early Miocene age. Geologie en Mijnbouw, 65, 297–308.

Daams, R., Alcalá, L., de los Angeles Alvarez Sierra, M., Azanza, B., Arie van Dam, J., van der Meulen, A.-J., Morales, J., Nieto, M., Peláez-Campomanes, P., & Soria, D. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of Central Spain. Comptes Rendus de l'Académie Des Sciences - Series IIA - Earth and Planetary Science, 327, 625–631.

Daams, R., Van der Meulen, A. J., Sierra, M. A., Peláez-Campomanes, P., & Krijgsman, W. 1999a. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters, 165, 287–294.

Daams, R., Van der Meulen, A. J., Álvarez Sierra, M. de los Á., Peláez-Campomanes, P., Calvo, J. P., Alonso Zarza, M. A., & Krijgsman, W. 1999b. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy, 37, 103–139.

Damuth, J. 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology. 8, 434-446.

Dawson, M. R. 2003. Paleogene rodents of Eurasia. In: Reumer, J.W.F. & Wessels, W. (Eds.). Distribution and Migration of Tertiary Mammals in Eurasia. DEINSEA, 10, 97–126.

Dawson, M. R., Tsubamoto, T., Takai, M., Egi, N., Tun, S. T., & Sein, C. 2003. Rodents of the family Anomaluridae (Mammalia) from Southeast Asia (Middle Eocene, Pondaung Formation, Myanmar). Annals of the Carnegie Museum., 72, 203–213.

De Bruijn, H. 1998. Vertebrates from the Early Miocene lignite deposits of opencast mine Oberdorf (Western Styrian Basin, Austria). 6. Rodentia 1 (Mammalia). Ann. Naturhist. Mus. Wien, 99 A, 99–137.

De Bruijn, H., & Moltzer, J. G. 1974. The rodents of Rubielos de Mora; the first evidence of the existence of different biotopes in the early Miocene of eastern Spain. Proceedings of the Koninklijke Akademie van Wetenschappen. Series B, 77, 130–145.

De Bruijn, H., & Saraç, G. 1991. Early Miocene rodent faunas from the eastern Mediterranena area. Part I. The genus *Eumyarion*. Proceedings of the Koninklijke Akademie van Wetenschappen, 94, 13150.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Morales, J., Heinzmann, E., Mayhew, D.F., Van der Meulen, A.J., Schmidt-Kittler, N., & Telles Antunes, M. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. Newsletters on Stratigraphy, 26, 65-118.

De Bruijn, H., Ünay, E., Yïlmaz, A., & Saraç, G. 2003 A rodent assemblage from the Eo/Oligocene boundary interval near Süngülü, Lesser Caucasus, Turkey. Coloquios de Paleontología, Special Issue. 1, 47-76.

De Bruijn, H., Marković, Z., Wessels, W., & van de Weerd, A. A. 2019. Pappocricetodontinae (Rodentia, Muridae) from the Paleogene of south-east Serbia. Palaeobiodiversity and Palaeoenvironments, 99, 511–526.

De Gibert, J. M., & Robles, J. M. 2005. Firmground ichnofacies recording high-frequency marine flooding events (Langhian transgression, Vallès-Penedès Basin, Spain). Geologica Acta, 3, 295–305.

De Gibert, J. M., & Casanovas-Vilar, I. 2011. Contexto geológico del Mioceno de la Cuenca del Vallès-Penedès. Paleontologia i Evolució, Special Issue. 6, 39–45.

Delfino, M., Rage, J-C., Bolet, A. & Alba D.M. 2013. Early Miocene dispersal of the lizard Varanus into Europe: Reassessment of vertebral material from Spain. Acta Palaeontologica Polonica, 58, 731-735.

Díaz Aráez, J. L., Delfino, M., Luján, À. H., Fortuny, J., Bernardini, F., & Alba, D. M. 2017. New remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the Early Miocene of the Iberian Peninsula. Comptes Rendus Palevol, 16, 12–26.

Domènech, R., Martinell, J., & de Gibert, J. M. 2011. Registro paleontológico marino del Mioceno de la Cuenca del Vallès-Penedès. Paleontologia i Evolució, 47–54.

Druzinsky, R. E. 2010. Functional anatomy of incisal biting in aplodontia rufa and sciuromorph rodents – Part 2: Sciuromorphy is efficacious for production of force at the incisors. Cells, Tissues, Organs, 192, 50–63.

Druzinsky, R. E. 2015. The oral apparatusof rodents: variations on the theme of a gnawing Machine. In: Cox, P. G., & Hautier, L. (Eds.). Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom:

Cambridge University Press. pp. 323-349.

Duranthon, F., Moyà-Solà, S., & Köhler, M. 1995. *Ampelomeryx ginsburgi* nov. gen., nov. sp. (Artiodactyla, Cervoidea) et la famille des Palaeomerycidae. Compte rendus de l'Académie des Sciences. Paris Série II, 321, 339–346.

Ellerman, J. R. 1940. The Families and Genera of Living Rodents with a list of Named Forms (1758-1936). London: British Museum.

Emry, R. J. 1981. New material of the Oligocene muroid rodent *Nonomys*, and its bearing on muroid origins. American Museum novitates ; 2712, 1-14.

Emry, R. J., & Thorington, R. W. 1982. Descriptive and comparative osteology of the oldest fossil squirrel Protosciurus (Rodentia: Sciuridae). Smithsonian Contributions to Paleobiology, 47, 1–35.

Engesser, B. 1979. Relationships of some insectivores and rodents from the Miocene of North America and Europe. Bulletin of Carnegie Museum of Natural History, 14, 1-68.

Engesser, B. 1999. Family Eomyidae. In: Rösner, G.E. & Heissig, K. (Eds.) The Miocene Land Mammals of Europe. Verlag Dr. Friedrick Pfeil, Munich. pp. 319–335.

Eronen, J. T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C., & Fortelius, M. 2010. Precipitation and large herbivorous mammals II: application to fossil data. Evolutionary Ecology Research, 12, 235–248.

Escarguel, G. 1999. Les rongeurs de l'Eocène inférieur et moyen d'Europe occidentale. Systématique, phylogenie, biochronologie et paléobiogéographie des niveaux-repères MP7 a MP14. Palaeovertebrata, 28, 89–351.

Fabre, P.-H., Hautier, L., Dimitrov, D., & P Douzery, E. J. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. BMC Evolutionary Biology, 12, 88.

Fabre, P. H., Hautier, L., & Cox, P. 2015. A synopsis of rodent molecular phylogenetics, systematics and biogeography. In: Cox, P. G. & Hautier, L. (Eds.). Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press. pp. 19-69.

Fahlbusch, V. 1964. Die Cricetiden (Mamm.) der Oberen Sübwasser-Molasse Bayerns. Bayerische Akademie Der Wissenschaften Mathematisch-Natur Wissenschaftliche Klasse Abhandlungen, 118, 136 pp., 7 làm.

Fahlbusch, V. 1967. Die Beziehungen zwischen einigen Cricetiden (Mamm. Rodentia) des nordamerikanischen und europäischen Jungtertiärs. Palaeont. Z., 41:154-164.

Fahlbusch, V. 1976. Report on the International Symposium on Mammalian Biostratgraphy of the European Tertiary. Newsletters on Stratigraphy. 5, 160-167.

Fahlbusch, V. 1985. Origin and evolutionary relationships among Geomyoids. In: Luckett, W. P & Hartenberger, J.-L. (Eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis New York: Plenum Press. pp. 617–629.

Faith, J. T., & Lyman, R. L. 2019. Paleozoology and Paleoenvironments. Cambridge ; New York: Cambridge University Press.

Flynn, L. J. 1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In: Luckett, W. P & Hartenberger, J.-L. (Eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis New York: Plenum Press. pp. 589–616.

Flynn, L. J., & Jacobs, L. L. 2008. Aplodontoidea. In: Janis, C. M., Gunnell, G. F. & Uhen, M. D. (Eds.). Evolution of Tertiary Mammals of North America: Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge ; New York: Cambridge University Press. pp. 377–390.

Flynn, L. J., & Wessels, W. 2013. Paleobiogeography and South Asian mammals. Neogene latitudinal faunal variation. In: Wang, X., Flynn, L. J. & Fortelius M. (Eds.). Fossil Mammals of Asia. Neogene Biostratigraphy and chronology. New York, NY: Columbia University Press. pp. 445–460.

Flynn, L.J., Lindsay, E.H., Pilbeam, D., Raza, S.M., Morgan, M.E., Barry, J.C., Badgley, C.E., Behrensmeyer, A.K., Cheema, I.U., Rajpar, A.R., & Opdyke, N.D. 2013. The Siwaliks and Neogene evolutionary biology in South Asia. In: Wang, X., Flynn, L.J., Fortelius, M. (Eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York. pp. 353-372.

Flynn, L. J., Jacobs, L. L., Kimura, Y., & Lindsay, E. H. 2019. Rodent Suborders. Fossil Imprint, 75, 292–298.

Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, Z., Zhang, Z. & Zhou, L. 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. Evolutionary Ecology Research, 4, 1005–1016.

Freudenthal, M. 1994. Cricetidae (Rodentia, Mammalia) from the Upper Oligocene of Mirambueno and Vivel del Río (prov. Teruel, Spain). Scripta Geologica, 104, 1-55.

Freudenthal, M., Hugueney, M., & Moissenet, E. 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). Scripta Geologica, 104, 57–114.

Freudenthal, M. 2006. The status of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* (Cricetidae, Mammalia). A reply to Van der Meulen et al. (2004). Geobios, 39, 43–55.

Freudenthal, M., & Daams, R. 1988. Cricetidae (Rodentia) from the type-Aragonian;

the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen., and *Renzimys*. Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud-Teruel Basin (Spain). Ed. M. Freudenthal. Scripta Geologica, Special Issue., 1, 133–252.

Freudenthal, M., Lacomba, J. I., & Sacristán, M. A. 1992. Classification of European Oligocene cricetids. Revista Española de Paleontología, Num. Ext. 1992, 49–57.

Furió, M., Casanovas-Vilar, I., & van den Hoek Ostende, L. W. 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. Palaeogeography, Palaeoclimatology, Palaeoecology, 304, 219–229.

Gallart, F. 1981. Neógeno superior y Cuaternario del Penedès (Catalunya, España). Acta Geològica Hispànica, 16, 151-157.

Garcés Crespo, M. 1995. Magnetoestratigrafía de las sucesiones del Mioceno medio y superior del Vallès Occidental (Depresión del Vallès-Penedès, N. E. de España): Implicaciones biocronológicas y cronoestratigráficas. [Ph.D. dissertation]. Barcelona: Universitat de Barcelona, Departament de Geologia Dinàmica, Geofísica i Paleontologia.

Garcés, M., & Beamud, E. 2016. La magnetoestratigrafía y la escala del tiempo geológico basada en las inversiones del campo magnético terrestre. Enseñanza de las Ciencias de la Tierra, 24, 282-293.

Garcés, M., Agustí, J., Cabrera, L., & Parés, J.M. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (northeast Spain). Earth and Planetary Science Letters, 142, 381-396.

Garcés, M., Cabrera, L., Agustí, J., & Parés, J. M. 1997. Old World first appearance datum of *Hipparion* horses: Late Miocene large-mammal dispersal and global events. Geology, 25, 19–22.

García-Paredes, I., Álvarez-Sierra, M.A., Van den Hoek Ostende, L.W., Hernández-Ballarín, V., Hordijk, K., López-Guerrero, P., Oliver, A., & Peláez-Campomanes, P. 2016. The Aragonian and Vallesian high-resolution micromammal succession from the Calatayud-Montalbán Basin (Aragón, Spain). Comptes Rendus Palevol, 15, 781-789.

Gidley, J.W. 1912. The lagomorphs an independent order. Science, 36, 285-286.

Ginsburg, L. 2001. Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lathan (France). Geodiversitas, 23, 381–394.

Göhlich, U. B. 1999. Order Proboscidea. In: Rössner, G. & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich. pp. 157-168.

Golpe Posse, J. M. 1974. Faunas de yacimientos con suïformes en el Terciario español.

Paleontología y Evolución, 8, 1-87.

Gomes Rodrigues, H. 2015. The great variety of dental structures and dynamics in rodents: new insights into their ecological diversity. In: Cox, P. G., & Hautier, L. (Eds.). Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press. pp. 424-447.

Gómez Cano, A.R. 2013. Análisis biocimático y paleoecológico de las faunas de roedores del Mioceno Medio Superior ibérico [Ph.D. dissertation]. Madrid: Universidad Autónoma de Madrid.

Graur, D., Hide, W. A., & Li, W. H. 1991. Is the guinea-pig a rodent? Nature, 351, 649–652.

Harrison, T. M., Copeland, P., Kidd, W. S. F., & Yin, A. 1992. Raising Tibet. Science, 255, 1663–1670.

Hartenberger, J.-L. 1967. Contributions à l'étude de l'anatomie crânienne des Rongeurs. I. - Principaux types de Cricétodontinés. Palaeovertebrata, 1, 47–64.

Hartenberger J.L., Crusafont i Pairó M., 1979. Rongeurs Miocènes dans le valles-Penedes 1: Les rongeurs de Can Ponsic 1. Palaeovertebrata 9, 1-15.

Hartenberger, J.-L. 1985. The order Rodentia: major questions on their evolutionary origin, relationships and suprafamilial systematics. In Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis, eds. W. P. Luckett and J.-L.Hartenberger. New York: Plenum Press. pp. 1–33.

Hartenberger, J.L. 1998. Description de la radiation des Rodentia (Mammalia) du Paléocène supérieur au Miocène; incidences phylogénétiques. Comptes Rendus de l'Acad*émie des sciencies.* Paris Sciences de La Terre et Des Planètes, 326, 439–444.

Harzhauser, M., & Piller, W. E. 2007. Benchmark data of a changing sea — Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology, 253, 8–31.

Hautier, L., Cox, P. G., & Lebrun, R. 2015. Grades and clades among rodents: the promise of geomètric morphometrics. In: Cox, P. G., & Hautier, L. (Eds.) Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press. pp. 277-299.

Hautier, L., Michaux, J., Marivaux, L., & Vianey-Liaud, M. 2008. Evolution of the zygomasseteric construction in Rodentia, as revealed by a geometric morphometric analysis of the mandible of Graphiurus (Rodentia, Gliridae). Zoological Journal of the Linnean Society, 154, 807–821.

Hautier, L., Lebrun, R., Saksiri, S., Michaux, J., Vianey-Liaud, M., & Marivaux, L. 2011.

Hystricognathy vs Sciurognathy in the Rodent Jaw: A New Morphometric Assessment of Hystricognathy Applied to the Living Fossil Laonastes (Diatomyidae). PLoS ONE, 6, e18698.

Hernández Fernández, M. 2001. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico. [Ph.D. dissertation]. Madrid: Universidad Complutense de Madrid.

Hernández Fernández, M. 2006. Rodent paleofaunas as indicators of climatic change in Europe during the last 125,000 years. Quaternary Research, 65, 308–323.

Hernández Fernández, M., & Peláez-Campomanes, P. 2003. The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. Global Ecology and Biogeography, 12, 507-517.

Hernandez-Fernandez, M., & Pelaez-Campomanes, P. 2005. Quantitative palaeoclimatic inference based on terrestial mammal faunas. Global Ecology and Biogeography, 14, 81-87.

Hershkovitz, P. 1967. Dynamics of rodent molar evolution: a study based on new world Cricetinae, family Muridae. Journal of Dental Research, 5, 829-842.

Hilgen, F. J., Lourens, L. J., & Van Dam, J. A. 2012. The Neogene Period. In: Gradstein F. M., Ogg J. G., Schmitz M. & Ogg G. (Eds.). The Geologic Time Scale 2012. Amsterdam: Elsevier. pp. 923–978.

Hoffstetter, R. 1972. Origine et dispersion des rongeurs hystricognathes. Comptes Rendus de l'Académie des Sciences (Paris), 274, 2867-2870.

Hordijk, K., Bosma, A., de Bruijn, H., van Dam, J., Geraedts, C., van den Hoek Ostende, L., & Wessels, W. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos2, Teruel Basin, Spain. Palaeobiodiversity and Palaeoenvironments, 95, 321–346.

Hotinski, R. M., & Toggweiler, J. R. 2003. Impact of a Tethyan circumglobal passage on ocean heat transport and "equable" climates. Paleoceanography, 18.

Hrubesch, K. 1957. Zahnstudien an tertiären Rodentia als Beitrag zu deren Stammesgeschichte. Über die Evolution der Melissiodontidae, eine Revision der Gattung Melissiodon. Bayerische Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Klasse, 83, 1–101.

Hsü, K. J., Ryan, W. B. F., & Cita, M. B. 1973. Late Miocene desiccation of the Mediterranean. Nature, 242, 240–244.

Hsü, K. J., Montadert, L., Bernoulli, D., Cita, M. B., Erickson, A., Garrison, R. E., & Wright, R. 1977. History of the Mediterranean salinity crisis. Nature, 267(5610), 399–403.

Huchon, D., Catzeflis, F. M., & Douzery, E. J. 1999. Molecular evolution of the nuclear von Willebrand factor gene in mammals and the phylogeny of rodents. Molecular Biology and Evolution, 16, 577–589.

Huchon, D., Madsen, O., Sibbald, M. J. J. B., Ament, K., Stanhope, M. J., Catzeflis, F., & Douzery, E. J. P. 2002. Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. Molecular Biology and Evolution, 19, 1053–1065

Hugueney, M., & Bulot, C. 2011. Les petits Mammifères du Burdigalien (MN3; Miocène) d'Estrepouy (Gers, France): liste faunique actualisée. Estudios Geológicos, 67, 427–442.

International Comission on Zoological Nomenclature (ICZN). 1999. Interantional Code of Zoological Nomenclature. Fourth Edition. London: The International Trust for Zoological Nomenclature.

Illiger, C. 1811. Prodromus Systematis Mammalium et Avium Additus Terminis Zoographis Utriudque Classis. Berlin: C. Salfeld.

Ivanov, M. 2001. Changes in the composition of the European snake fauna during the Early Miocene and at the Early / Middle Miocene transition. Paläontologische Zeitschrift, 74, 563–573.

Jacobs, L. L. 1977. A new genus of murid rodent from the Miocene of Pakistan and comments on the origin of the Muridae. PaleoBios, 25, 39753.

Jacobs, L. L., & Lindsay, E. H. 1984. Holarctic Radiation of Neogene Muroid Rodents and the Origin of South American Cricetids. Journal of Vertebrate Paleontology, 4, 265–272.

Jacobs, L. L., & Downs, W. R. 1994. The evolution of murine rodents in Asia. In: Tomida, Y., Li, C. & Setoguchi, T. (Eds.). Rodent and Lagomorph Families of Asian Origins and Diversification. National Science Museum Monographs, 8, 149–156.

Janis, C. M., Dawson, M. R., & Flynn, L. J. 2008. Glires summary. In: Janis, C. M., Gunnell, G. F. & Uhen M. D. (Eds.). Evolution of Tertiary Mammals of North America: Volume 2, Small Mammals, Xenarthrans, and Marine Mammals. Cambridge ; New York: Cambridge University Press. pp. 377–390.

Jansa, S. A., & Weksler, M. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. Molecular Phylogenetics and Evolution, 31, 256–276.

Jiménez-Moreno, G., & Suc, J.-P. 2007. Middle Miocene latitudinal climatic gradient in Western Europe: Evidence from pollen records. Palaeogeography, Palaeoclimatology, Palaeoecology, 253, 208–225.

Jiménez-Moreno, G., Fauquette, S., & Suc, J.-P. 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Review of Palaeobotany and Palynology, 162, 403–415.

Joniak, P., Peláez-Campomanes, P., Ostende, L. W. van den H., & Rojay, B. 2017. Early Miocene rodents of Gökler (Kazan Basin, Central Anatolia, Turkey). Historical Biology, 31, 982–1007.

Jovells-Vaqué, S., Ginestí, M., & Casanovas-Vilar, I. First cranial of *Democricetodon hispanicus* Freudenthal, 1967 (Rodentia, Cricetidae) from els Casots site (Vallès-Penedès Basin, Catalonia). Preliminary results.2017. In: Barrios de Pedro,S.; Blanco Moreno, C; de Celis, A; Colmenar,J.; Cuesta, E.; García-Martínez, D.; Gascó, F.; Jacinto, A; Malafaia, E; Marín JImenez, M.; de Miguel Chaves, C.; Mocho, P.; Pais, V.; Parámo Blázquez, A.; Pereira, S.; Serrano Martínez, A.; Vidal, D. (Eds.), A Glimpse of the Past. Book of abstracts XV meeting of Young researchers in Paleontology. Pombal (Portugal). pp. 223-226.

Jovells-Vaqué, S., & Casanovas-Vilar, I. 2018. A review of the genus *Melissiodon* (Cricetidae, Rodentia) in the Vallés-Penedès Basin (Catalonia). Journal of Vertebrate Paleontology, 38, e1520714.

Kälin, D. 1999. Tribe Cricetini. In: Rössner, G. E., & Heissig K. (Eds.). The Miocene Land Mammals of Europe. Munich. pp. 373-387.

Kälin, D., & Kempf, O. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch Für Geologie Und Paläontologie - Abhandlungen, 254, 177–235.

Kay, R. F., & Madden, R. H. 1997. Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). Journal of Human Evolution, 32, 161–199.

Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J. T., Hui, T., & Fortelius, M. 2018. The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. Nature Ecology & Evolution, 2, 241-246.

Korth, W. W. 1994. The Tertiary Record of Rodents in North America. New York: Plenum Press.

Koufos, G. D. 2003. Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean. In: Reumer, J.W.F. & Wessels, W. Distribution and Migration of Tertiary Mammals in Eurasia. DEINSEA, 10, 343–371.

Kovar-Eder, J. 2003. Vegetation dynamics in Europe during the Neogene. In: Reumer, J.W.F. & Wessels, W. Distribution and Migration of Tertiary Mammals in Eurasia. DEINSEA, 10, 373–392.

Kovarovic, K., Su, D.F., & Lintulaakso, K. 2018. Mammal community structure analysis.

In: Croft, D.A., Su, D.F, Simpson, S.W. (Eds.). Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities. New York: Springer Nature. pp. 351-372.Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., van Dam, J., van der Meulen, A.J., Agustí, J., Cabrera, L. 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth and Planetary Science Letters, 142, 367–380.

Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., van Dam, J., van der Meulen, A.J. Agustí, J., & Cabrera, L. 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth and Planetary Science Letters, 142, 367–380.

Kutzbach, J. E., Prell, W. L., & Ruddiman, W. F. 1993. Sensitivity of Eurasian Climate to Surface Uplift of the Tibetan Plateau. The Journal of Geology, 101, 177–190.

Langereis, C. G., Krijgsman, W., Muttoni, G., & Menning, M. 2010. Magnetostratigraphy concepts, definitions, and applications. Newsletters on Stratigraphy, 207–233.

Larrasoaña, J. C., Murelaga, X., & Garcés, M. 2006. Magnetobiochronology of Lower Miocene (Ramblian) continental sediments from the Tudela Formation (western Ebro basin, Spain). Earth and Planetary Science Letters, 243, 409–423.

Lavocat, R., & Parent, J.-P. 1985. Phylogenetic analysis of middle ear features in fossil and living rodents. In: Luckett, W. P & Hartenberger, J.-L. (Eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis New York: Plenum Press. pp. 333–354.

Lazzari, V., Charles, C., Tafforeau, P., Vianey-Liaud, M., Aguilar, J.-P., Jaeger, J.-J., & Viriot, L. 2008. Mosaic convergence of rodent dentitions. PLoS ONE, 3, e3607.

Legendre, S., Montuire, S., Maridet, O., & Escarguel, G. 2005. Rodents and climate: A new model for estimating past temperatures. Earth and Planetary Science Letters, 235, 408–420.

Li, C.-K., & Ting, S.-Y. 1985. Possible phylogenetic relationship of asiatic eurymilids and rodents, with comments on mimotonids. In: Luckett, W. P & Hartenberger, J.-L. (Eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. New York: Plenum Press. pp. 35–58.

Li, C., Zheng, J., & Ting, S. 1989. The skull of *Cocomys lingchaensis*, an Early Eocene ctenodactyloid rodent of Asia. In: Black, C.C. & Dawson, M.R. (Eds.). Papers on fossil rodents in honor of Albert Elmer Wood. Los Angeles, California: Natural History Museum of Los Angeles County. pp. 179-192.

Li, Q., & Meng, J. 2010. Erlianomys combinatus, a primitive myodont rodent from the Eocene Arshanto Formation, Nuhetingboerhe, Nei Mongol, China. Vertebrata PalAsiatica, 48, 133–144

Lilljeborg, W. 1866. Systematisk Öfversigt af de Gnagande Däggdjuren. Upsala: Kogl. Akad. Boktryckeriet.

Lindsay, E.H. 1972. Small mammal fossils from the Barstow Formation, California. University of California Publications in Geological Sciences, 93, 1-104.

Lindsay, E. H. 1977. *Simimys* and origin of the Cricetidae (Rodentia: Muroidea). Geobios, 10, 597–623.

Lindsay, E. H. 1987. Cricetid rodents of lower Siwalik deposits, Potwar Plateau, Pakistan and Miocene mammal dispersal events. Annales Instituti Geologici Publici Hungarici, 70, 483–488.

Lindsay, E. H. 1988. Cricetid rodents from Siwalik deposits near Chinji village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae. Palaeovertebrata, 18, 95–154.

Lindsay, E. H. 1994. The fossil record of Asian Cricetidae with emphasis on Siwalik cricetids. In: Tomida, Y., Li, C. & Setoguchi, T. (Eds.). Rodent and Lagomorph Families of Asian Origins and Diversification. National Science Museum Monographs, 8, 131–147.

Lindsay, E.H. 2008. Cricetidae. In: Janis, C.M., Gunnell, G.F., Uhen, M.D. (Eds.). Evolution of Tertiary Mammals of North America. Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambirdge, UK: Cambirdge University Press. pp. 456-479.

Lindsay, E.H., & Tedford, R.H. 1989. Developement and application of land mammal ages in North America and Europe, a comparison. In: European Neogene Mammal Chronology. Lindsay, E.H., Fahlbusch, V. & Mein, P. (Eds.). New York: Plenum Press.. pp.601-624.

Lindsay, E. H., Flynn, L. J., Cheema, I. U., Barry, J. C., Downing, K., & Mahmood Raza, S. 2005. Will Downs and the Zinda Pir Dome. Palaeontologia Electronica, 8, 18.

Linnaeus, C. 1735. Systema Naturae, Sive Regna Tria Naturae Systematice Proposita per Classes, Ordines, Genera et Species. Leiden: Fol. Lugduni Batavorum.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima, Reformata. Sotckholm: Laurentius Salvius, 1-824.

Llenas Avellaneda, M. 2015. Memòria de la intervenció paleontològica d'urgència al jaciment de les Cases de la Valenciana 2- (Gelida-Alt Penedès) [unpublished field report] Bellaterra: Institut Català de Paleontologia Miquel Crusafont.

Llenas Avellaneda, M., Casanovas-Vilar, I., Jovells-Vaqué, S., Furió Bruno, M., Robles Giménez, J.M., Berrocal Barberà, M., Hernández Luján, À., & Méndez Rodríguez, J. M. 2016. Memòria de la intervenció paleontològica d'urgència al jaciment de Can Martí Vell (Gelida-Alt Penedès). [unpublished field report] Bellaterra: Institut Català de Paleontologia Miquel Crusafont.

López Martínez, N. 1989. Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. Zaragoza: Diputación General de Aragón, Departamento de Cultura y Educación.

Luckett, W. P., & Hartenberger, J.-L. 1985. Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. New York: Plenum Press.

Luckett, W. P. 1985. Superordinal and intraordinal affinities of rodents: developmental evidence from the dentition and placentation. In: Lucket, W. P. & Hartenberger, J. L. (Eds.). Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis, eds.W. P. Luckett and J.-L. Hartenberger. New York: Plenum Press, pp. 227–276

Luján, A.H. 2015. Les tortugues (Testudines) del Neogen i Quaternari de Catalunya (NE de la Península Ibèrica). [unpublised Ph.D. dissertation] Bellaterra: Universitat Autònoma de Barcelona.

Luján, À. H., DeMiguel, D., Ivanov, M., Madurell-Malapeira, J., Jovells-Vaqué, S., & Casanovas-Vilar, I. 2017. Paleoherpetofauna from the early Miocene locality of Les Cases de la Valenciana (Catalonia, Spain). Zitteliana, 91, 55.

Luján, À. H., Delfino, M., Díaz-Aráez, J. L., Ivanov, M., Casanovas-Vilar, I., & Alba, D. M. 2018. Fossil crocodylians from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula). In M. Marzola, O. Mateus, & M. Moreno-Azanza (Eds.), Abstract book of the XVI Annual Meeting of the European Association of Vertebrate Palaeontology (p. 97). Caparica, Portugal: DCT, Departamento de Ciências da Terra, Faculdade Ciências e Tecnología, Universidade Nova de Lisboa.

Magné, J. 1978. Études microstratigraphiques sur le Néogéne de la Méditerranée Nord-Occidentale. Vol. I: les bassins néogènes catalans. [unpublished Ph.D. dissertation]. Toulousse: Unversité Paul Sabatier, CNRS.

Maridet, O. 2003. Révision du genre Democricetodon (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d’Europe occidentale: évolution, paléobiodiversité et paléobiogéographie. [unpublised Ph.D. dissertation]. Lyon: Université Claude Bernard-Lyon I.

Maridet, O., & Ni, X. 2013. A new cricetid rodent from the early Oligocene of Yunnan, China, and its evolutionary implications for early Eurasian cricetids. Journal of Vertebrate Paleontology, 33, 185–194.

Maridet, O., Wu, W.-Y., Ye, J., Bi, S.-D., Ni, X.-J., & Meng, J. 2011a. Early Miocene cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological implications. Geobios, 44, 445–459.

Maridet, O., Wu, W.-Y., Ye, J., Bi, S.-D., Ni, X.-J., & Meng, J. 2011b. Earliest occurrence of Democricetodon in China, in the early Miocene of the Junggar Basin (Xinjiang), and comparison with the genus Spanocricetodon. Vertebrata PalAsiatica, 49, 393–405.

Maridet, O., Costeur, L., & Legendre, S. 2013. European Neogene rodent communities: explaining family-level replacements through a spatiotemporal approach. Historical Biology, 25(5–6), 655–677.

Marivaux, L., Vianey-Liaud, M., & Jaeger, J.-J. 2004. High-level phylogeny of early Tertiary rodents: dental evidence. Zoological Journal of the Linnean Society, 142, 105–134.

Martin, L. D. 1980. The early evolution of the Cricetidae in North America. The University of Kansas Paleontological Contributions, 102, 1–42.

Martinell, J. 1988. An overview of the marine Pliocene of N.E. Spain. Géologie Méditerranéenne, 15, 227–233.

Martini, E. 1990. The Rhinegraben system, a connection between northern and southern seas in European Tertiary. Veröff Übersee-Museum Bremen, 1, 10: 83-98.

Mason, M. J. 2015. Functional morphology of rodent middle ears. In: Cox P. G. & Hautier L. (Eds.). Evolution of the rodents: advances in phylogeny, functional morphology, and development. Cambridge, United Kingdom: Cambridge University Press. pp. 373–404.

Mazo, A. V., & Van der Made, J. 2012. Iberian mastodonts: Geographic and stratigraphic distribution. Quaternary International, 255, 239–256.

McKenna, M. C. 1975. Towards a phylogeny and classification of the Mammalia. In: Luckett, W. P. & Szalay, F.S. (Eds.) Phylogeny of the Primates: a Multidisciplinary Approach. New York: Plenum Press. pp. 21–46.

McKenna, M. C. and Bell, S. J. 1997. Classification of Mammals Above the Species Level. New York: Columbia University Press.

Mein, P. 1967. Determination de l'Humérus de quelques Cricetidae fossiles. Colloques Internationaux Du Centre National de La Recherche Scientifique (C.N.R.S.). Problèmes Actuels de Paléontologie (Évolution Des Vertébres), 163, 515–521.

Mein, P. 1975. Une forme de transition entre deux familles de rongeurs. Colloques Internationaux Du Centre National de La Recherche Scientifique (C.N.R.S.). Problèmes Actuels de Paléontologie (Évolution Des Vertébres), 218, 759–763.

Mein, P. 1989 [imprint date 1990]. Updating of MN zones. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.). European Neogene Mammal Chronology. New York: Plenum Press. pp. 73-90.

Mein, P. 1999. European Miocene mammal biochronology. In: Rössner, G. E. & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedich Pfeil. Munich. pp.

25-38.

Mein, P., & Freudenthal, M. 1971a. Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. Partie 1: Le genre *Cricetodon* Lartet, 1851. Scripta Geologica, 5, 1-51.

Mein, P., & Freudenthal, M. 1971b. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. Scripta Geologica, 2, 1–37.

Mein, P., & Romaggi, J.-P. 1991. Un gliridé (mammalia, rodentia) planeur dans le miocène supérieur de l'ardèche: Une adaptation non retrouvée dans la nature actuelle. Geobios, 24, Supplement 1, 45–50.

Meng, J. 2004. Phylogeny and divergence of basal Glires. Bulletin of the American Museum of Natural History, 285, 93–109.

Meng, J., & Wyss, A. R. 2005. Glires (Lagomorpha, Rodentia). In: Rose, K. D. & Archibald, D. D. (Eds.). The Rise of Placental Mammals Baltimore, Md: Johns Hopkins University Press. pp. 145–158.

Meng, J., Hu, Y., & Li, C. 2003. The osteology of rhombomylus (mammalia, glires): implications for phylogeny and evolution of glires. Bulletin of the American Museum of Natural History, 275, 1–247.

Mercer, J. M., & Roth, V.L. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science, 299, 1568–1572.

Michaux, J., Reyes, A., & Catzeflis, F. 2001. Evolutionary history of the most speciose mammals: molecular phylogeny of muroid rodents. Molecular Biology and Evolution, 18, 2017–2031.

Miller, K.G, Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S, Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., & Pekar, S.F. 2005. The Phanerozoic record of global sea-level change. Science, 310, 1293-1298.

Miller, G. S., Jr., & Gidley, J. W. 1918. Synopsis of the supergeneric groups of Rodents. Journal of the Washington Academy of Sciences, 8, 431–448.

Mödden, C. 1999. Family Melissiodontidae. In: Rössner G. E. & Heissig K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedich Pfeil. Munich. pp. 343–346.

Montgelard, C., Matthee, C. A., & Robinson, T. J. 2003. Molecular systematics of dormice (Rodentia: Gliridae) and the radiation of Graphiurus in Africa. Proceedings of the Royal Society of London B: Biological Sciences, 270, 1947–1955.

Montgelard, C., Forty, E., Arnal, V., & Matthee, C. A. 2008. Suprafamilial relationships among Rodentia and the phylogenetic effect of removing fast-evolving nucleotides in mitochondrial, exon and intron fragments. BMC Evolutionary Biology, 8, 321.

Montoya, P., Peñalver, E., Ruiz-Sánchez, F.J., De Santiesteban, C., Alcalá, L., Belinchón, M., & Lacomba, J.I. 1996. Los yacimientos paleontológicos de la cuenca terciaria contientnal de Rubielos de Mora (Aragón). Revista Española de Paleontología, Núm. Ext., 215–224.

Moyà-Solà, S., & Rius Font, L. 1993. El jaciment paleontològic dels Casots (Subirats, Alt Penedès). Tribuna d'Arqueologia. pp. 7–12.

Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., & Galindo, J. 2004. *Pierolapithecus catalaunicus*, a new middle Miocene great ape from Spain. Science, 306, 1339–1344.

Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., Galindo, J., Robles, J. M., & Beamud, E. 2009a. First partial face and upper dentition of the Middle Miocene hominoid Dryopithecus fontani from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. American Journal of Physical Anthropology, 139, 126–145.

Moyà-Solà, S., Alba, D. M., Almécija, S., Casanovas-Vilar, I., Köhler, M., DeEsteban-Trivigno, S., & Fortuny, J. 2009b. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. Proceedings of the National Academy of Sciences, 106, 9601–9606.

Murphy, W. J., Eizirik, E., Johnson, W. E., Zhang, Y. P., Ryder, O. A., & O'Brien, S. J. 2001. Molecular phylogenetics and the origins of placental mammals. Nature, 409, 614–618.

Norris, R. W., Zhou, K., Zhou, C., Yang, G., William Kilpatrick, C., & Honeycutt, R. L. 2004. The phylogenetic position of the zokors (Myospalacinae) and comments on the families of muroids (Rodentia). Molecular Phylogenetics and Evolution, 31, 972–978.

Novacek, M. J. 1985. Cranial evidence for rodent affinities. In: Luckett, W.P. & Hartenberger, J. L. (Eds.). Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis. New York: Plenum Press. pp. 59–82.

Novacek, M. J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bulletin of the American Museum of Natural History, 183, 1–111.

Ogg, J.G. 2012. Geomagnetic Polarity Time Scale. In: the Geologic Time Scale. Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (Eds.). Amsterdam, ElSevier. pp. 84-113.

Ogg J & Lugowski A. 2020. TSCreator visualization of enhanced Geologic Time Scale 2004 database (Version 7.1; 2020) http://www.tscreator.org

Oliver Pérez, A. 2015. Evolution of *Megacricetodon* from the Aragonian and Vallesian (Miocene) of the Iberian Peninsula. [Ph.D. Dissertation]. Madrid: Universidad Complutense de Madrid.

Oliver, A., & Peláez-Campomanes, P. 2013. *Megacricetodon vandermeuleni* , sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for Megacricetodon. Journal of Vertebrate Paleontology, 33, 943–955.

Oliver, A., & Pelaez-Campomanes, P. 2016. Early Miocene evolution of the genus Megacricetodon in Europe and its paleobiogeographical implications. Acta Palaeontologica Polonica, 61(1), 211-219

Orliac, M. J. 2006. *Eurolistriodon tenarezensis*, Sp. Nov., from Montreal-Du-Gers (France): Implications for the Systematics of the European Listriodontinae (Suidae, Mammalia). Journal of Vertebrate Paleontology, 26, 967–980.

Ortí, F., & Pueyo, J.J. 1976. Yeso primario y secundario del depósito de Vilobí (Provincia de Barcelona, España). Revista del Instituto de Investigaciones Geológicas de la Diputación de Barcelona, 31, 5-34.

Parcerisa i Duocastella, D. 2002. Petrologia i diagénesi en sediments de l'Oligocè superior i del Miocè inferior i mitjà de la Depressió del Vallès i del Pla de Barcelona. Evolució de l'àrea font i dinàmica dels fluids. [unpublishec Ph.D. dissertation]. Bellaterra: Universitat Autònoma de Barcelona.

Parcerisa, D., Gómez-Gras, D., Roca, E., Malapeira, J. M. I., & Ballester, J. A. 2007. The Upper Oligocene of Montgat (Catalan Coastal Ranges, Spain): New age constrains to the western Mediterranean Basin opening. Geologica Acta, 5, 3–18

Pardiñas, U., Myers, P., León-Paniagua, Ordóñez Garza, N., Cook, J., Kryštufek, B., Haslauer, R., Bradley, R., Shenbrot, G., & Patton, J. 2017. Family Cricetidae. In: Wilson, D.E., Mittermeier, R.S., Lacher, T.E. (Eds.). Handbook of the Mammals of the World – Volume 7. Rodents II. Bellaterra: Lynx Edicions. pp. 204-280.

Pareto, L. 1865. Note sur les subdivisions que l'on purrait etablir dans les terrains tertiaires de l'Apénin septentrional. Bulletin de la Société Géologique de France, 22, 210-277.

Peppe, D.J., Baumgartner, A., Flynn, A & Blonder, B. 2018. Reconstructing paleoclimate and paleoecology using fossil leaves. In: Croft, D.A., Su, D.F, Simpson, S.W. (Eds.). Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities. New York: Springer Nature. pp. 289-317.

Permanyer, A. 1990. Sedimentologia i diagènesi dels esculls miocènics de la Conca del Penedès. Arxius de la Secció de Ciències de l'Institut d'Estudis Catalans, 92, 1-320.

Petter, F. 1966. L'origine des murides. Plan cricetin et plans murins. Mammalia, 30 (2), 205–225.

Pickford, M., & Morales, J. 2003. New Listriodontinae (Mammalia, Suidae) from Europe and a review of listriodont evolution, biostratigraphy and biogeography. Geodiversitas, 25, 347–404.

Pickford, M., & Moyà-Solà, S. 1994. *Taucanamo* (Suoidea, Tayassuidae) from the Middle Miocene (MN04a) of Els Casots, Barcelona, Spain. Comptes Rendus de l'Académie des Sciences, 319, 1569–1575.

Pickford, M. & Moyà-Solà, S. 1995. Eurolistriodon gen. nov., (Suoidea, Mammalia) from Els Casots, early middle Miocene, Spain. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen., 98, 343–360.

Pickford, M., & Morales, J. 1994. Biostratigraphy and paleobiogeography of East Africa and the Iberian Peninsula. Palaeogeography, Palaeoclimatology, Palaeoecology, 112, 297–322.

Pippèrr, M., Reichenbacher, B., Witt, W., & Rocholl, A. 2007. The middle and upper Ottnangian of the Simssee area (SE Germany): micropalaeontology, biostratigraphy and chronostratigraphy. Neues Jahrbuch Fur Geologie Und Paläontologie Abhandlungen, 245, 353–378.

Popov, S. V., Shcherba, I. G., Ilyina, L. B., Nevesskaya, L. A., Paramonova, N. P., Khondkarian, S. O., & Magyar, I. 2006. Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology, 238, 91–106.

Pound, M. J., Haywood, A. M., Salzmann, U., & Riding, J. B. 2012. Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33Ma). Earth-Science Reviews, 112, 1–22.

Poux, C., Chevret, P., Huchon, D., De Jong, W.W., & Douzery, P. 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Systematic Biology, 55, 228-244.

Prieto, J., & Rummel, 2016. Some considerations on small mammal evolution in Southern Germany, with emphasis on Late Burdigalian-Earliest Tortonian (Miocene) cricetid rodents. Comptes Rendus Palevol, 15, 837-854.

Prieto, J., Angelone, C., Casanovas-Vilar, I., Gross, M., Hír, J., Van den Hoek Ostende, L.W., Maul, L.C., & Vailyan, D. 2014. The small mammals from Gratkorn: an overview. Palaeobiodiversity and Palaeoenvironments, 94, 135-162.

Prothero, D. R. 2006. After the Dinosaurs: The Age of Mammals. Bloomington, Indiana University Press.

Qiu, Z.-X., Qiu, Z.-D., Deng, T., Li, C.-K., Zhang, Z., Wang, B.-Y., & Wang, X. 2013. Neogene Land Mammal Stages/Ages of China. Toward the Goal to Establish an Asian Land Mammal Stage/Age Scheme. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology (pp. 29–90). New York, N.Y:

Columbia University Press.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. https://www.R-project.org.

Reed, K. E., & Fleagle, J. G. 1995. Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences, 92, 7874–7876.

Reguant i Serra, S. 2004. Josep Ramon Bataller i Calatayud, semblança biogràfica. Barcelona: Institut d'Estudis Catalans. Secció de Ciències i Tecnologia.

Reumer, J. W. F. 1995. The effect of paleoclimate on the evolution of the Soricidae (Mammalia, Insectivora). In: Vrba E.S., Denton, G.H. Partridge, T.C. & Burckle L.H. (Eds.). Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press. pp.135–147.

Rinderknecht, A., & Blanco, R. E. 2008. The largest fossil rodent. Proceedings of the Royal Society B: Biological Sciences, 275, 923–928.

Robles, F., Belinchón, M., García-Flor, J., & Morales, J. 1991. El Neógeno continental de Buñol y del Valle del Rio Cabriel. Revista Española de Paleontología, 205–215.

Roca, E., & Guimerà, J. 1992. Geology and Geophysics of the Valencia through Western Mediterranean The Neogene structure of the eastern Iberian margin: Structural constraints on the crustal evolution of the Valencia trough (western Mediterranean). Tectonophysics, 203, 203–218.

Roca, E., Sans, M., Cabrera, L., & Marzo, M. 1999. Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). Tectonophysics, 315, 209–229.

Rögl, F. 1999. Circum-Mediterranean Miocene paleogeography. In: Rössner, G.E., & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedich Pfeil. Munich. pp. 39-48.

Rose, K. D., & Archibald, J. D. (Eds.). 2005. The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades. Baltimore: Johns Hopkins University Press.

Rössner, G. E. 2017. New palaeontological and geological age constraints for the arrival and dispersal of Miocene tragulids (Tragulidae, Artiodactyla) in Europe. Zitteliana, 89, 351–359.

Rotgers, C., & Alba, D.M. 2011. The genus Anchitherium (Equidae: Anchitheriinae) in the Vallès-Penedès Basin (Catalonia, Spain). In Pérez García, A., Gascó, F., Gasulla, J.M., & Escaso, F. (Eds.), Viajando a Mundos Pretéritos (pp. 347–354). Morella: Ayuntamiento de Morella.

Sahni, A. 1985. Enamel structure of Early Mammals and its role in evaluting relationships among rodetns. In Luckett, W. P., & Hartenberger, J.-L. (Eds.). Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. New York: Plenum Press. pp. 133-150.

Salvador, A. 1994. International stratigraphic guide. Boulder. CO: Geological Society of America.

Sanisidro, Ó., DeMiguel, D., Madurell-Malapeira, J., Jovells-Vaqué, S., & Casanovas-Vilar, I. 2018. Revalidation of the genus *Dromoceratherium* (Perissodactyla, Rhinocerotidae) and its key role within Rhinocerotinae. In: Farke, A., MacKenzie, A. & Miller-Camp, J. (Eds.). Society of vertebrate paleontology. October 2018. Abstarcts of papers. 78th Annual meeting. Alburquerque, New Mexico. p. 209.

Sanz de Siria Catalán. 1981. La flora Burdigaliense de los alrededores de Martorell (Barcelona). Paleontologia i Evolució, 16, 3-13.

Sanz de Siria Catalán, A. 1993. Datos sobre la paleoclimatología y la paleoecología del Neógeno del Vallès-Penedès según las macrofloras halladas en la cuenca y zonas próximas. Paleontologia i Evolució. Sabadell: Institut Paleontològic Dr. M. Crusafont (Diputació de Barcelona), 26–27, 281–289.

Sanz de Siria Catalán, A. 1996. La evolución de las paleofloras en las cuencas cenozoicas catalanas. Acta Geologica Hispanica, 29, 169–189.

Schaub, S. 1925. Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. Eine systematisch-odontologische studie. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft, 45, 1–114.

Schaub, S. 1933. Neue Funde von *Melissiodon*. Eclogae Geologicae Helvetiae, 26, 241-247.

Schenk, J. J., Rowe, K. C., & Steppan, S. J. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. Systematic Biology, 62, 837–864.

Sen, S. 2013. Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys. Geobios, 46, 159–172.

Sierra, A., San Miguel, M., Marcet, J., & Cerezo, R. 1930. Memoria explicativa de la hoja núm. 420 (San Baudilio del Llobregat) del Mapa Geológico de España. geological map, Madrid: Instituto Geológico y Minero de España.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85, 1–350.

Springer, M.S., Murphy, W. J., Eizirik, E., & O'Brien, S. J. 2003. Placental mammal diversification and the Cretaceous–Tertiary boundary. Proceedings of the National Academy of Sciences, 100, 1056–1061.

Steininger, F. F., Daxner-Höck, G., Haas, M., Kovar-Eder, J., Mauritsch, H., Meller, B., &

Scholger, R. M. 1998. Stratigraphy of the “Basin Fill” in the early Miocene lignite opencast mine Oberdorf (N Voitsberg, Styria, Austria). Jahrbuch Der Geologischen Bundesanstalt, 140, 491–496.

Steininger, F. F. 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene “European Land Mammal Mega-Zones” (ELMMZ) and the Miocene “Mammal-Zones (MN-Zones)”. In: Rössner, G.E. & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. Verlag Dr. Friedich Pfeil. Munich. pp. 9-24.

Steppan, S. J., & Schenk, J. J. 2017. Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. PLoS ONE, 12, e0183070.

Steppan, S. J., Storz, B. L., & Hoffmann, R. S. 2004a. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Molecular Phylogenetics and Evolution, 30, 703–719.

Steppan, S., Adkins, R., & Anderson, J. 2004b. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology, 53, 533–553.

Storch, G., Engesser, B., & Wuttke, M. 1996. Oldest fossil record of gliding in rodents. Nature, 379, 439–441.

Strömberg, C. A. E. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences, 39, 517–544.

Suárez-Hernando, Oier. 2017. Magnetobiocronología y paleoecología del Mioceno inferior-medio en las Bardenas Reales de Navarra (cuenca del Ebro) [Ph.D. dissertation]. Leioa: Euskal Herriko Unibertsitatea.

Swanson, M. T., Oliveros, C. H., & Esselstyn, J. A. 2019. A phylogenomic rodent tree reveals the repeated evolution of masseter architectures. Proceedings of the Royal Society B: Biological Sciences, 286, 20190672.

Thaler, L. 1965. Une échelle de zônes biochronologique pour les mammifères de Tertiaire de l’Europe. Compte Rendus Sommaires de la Sóciété Géologique de France, 118.

Thaler, L. 1966. Les rongeurs fossils du Bas-Languedoc dans leurs rapports avec l’histoire des faunes et la stratigraphie du Tertiare d’Europe. Mémoires du Muséum National d’Histoire Naturelle, 17, 1–295.

The NOW community 2020. New and Old Words Database of Fossil Mammals (NOW). Licenced under CCBY 4.0.

Theocharopoulos, C. D. 2000. Late Oligocene-middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the Eastern Mediterranean area. Gaia, 8, 1–92.

Tullberg, T. 1899. Über das System der Nagethiere: eine phylogenetische Studie. Nova Acta Regiae Societatis Scientarium Upsaliensis Series 3, 18, 1–514.

Turnbull, W. D. 1970. Mammalian masticatory aparatus. Fieldiana: Geology, 18 (2), 1–356.

Ünay-Bayraktar, E. 1989. Rodents from the middle Oligocene of Turkish Thrace. Utrecht Micropaleontological Bulletins. Special Publication, 5, 5-119.

Valenciano, A., Abella, J., Alba, D. M., Robles, J. M., Álvarez-Sierra, M. A., & Morales, J. 2020. New early Miocene material of *Iberictis*, the oldest member of the wolverine lineage (Carnivora, Mustelidae, Guloninae). Journal of Mammalian Evolution, 27, 73–93.

Van Dam, J. A. 2003. European Neogene mammal chronology: past, present and future. In: Reumer, J.W.F. & Wessels, W. (Eds.). Distribution and Migration of Tertiary Mammals in Eurasia. DEINSEA, 10, 85–95.

Van Dam, J. A. 2006. Geographic and temporal patterns in the late Neogene (12-3 Ma) aridification of Europe. The use of small mammals as paleoprecipitation proxies. Paleogeography, Paleoclimatology, Paleoecology, 238, 190–218.

Van Dam, J. A. V., & Weltje, G. J. 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity succession: an application of end-member modelling. Palaeogeography, Palaeoclimatology, Palaeoecology, 151, 267–305.

Van Dam, J. A., & Utescher, T. 2016. Plant- and micromammal-based paleoprecipitation proxies: Comparing results of the Coexistence and Climate-Diversity Approach. Palaeogeography, Palaeoclimatology, Palaeoecology, 443, 18–33.

Van Dam, J.A., Krijgsman, W., Abels, H.A., Álvarez-Sierra, M.Á., García-Paredes, I., López-Guerrero, P., Peláez-Campomanes, P., & Ventra, D. 2014. Updated chronology for Middle to Late Miocene mammal sites of the Daroca area (Calatayud-Montalbán Basin, Spain). Geobios, 47, 325-334.

Van den Hoek Ostende, L.W. 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area. Coloquios de Paleontología, vol. ext. 1, 281-31.

Van den Hoek Ostende, L.W., Furió, M., Madern, A., & Prieto, J. 2016. Enters the shrew, some considerations on the Miocene palaeobiogeography of Iberian insectivores. Comptes Rendus Palevol, 15, 813-823.

Van den Hoek Ostende, L.W., Álvarez-Sierra,M.A., García-Paredes, I., Montoya, P., Ruiz-Sánchez, F.J., & Peláez-Campomanes, P. 2017. Alto de Ballester, biogeographical consequences of atypical MN 3 micromammal assemblages from eastern Spain Palaeontographica Abteilung A., 308, 127-175.

Van den Hoek Ostende, L. W., Casanovas-Vilar, Furió, M. 2020. Stuck in the middle. A geographical appraisal of the oldest insectivores – and a marsupial – from the Vallès-Penedès (early Miocene, Catalonia, Spain). Comptes Rendus Palevol, 19, 1-25.

Van der Made, J. 1999. Intercontinental relationships Europe-Africa and the indian subcontinent. In: Rössner, G & Heissig, K. (Eds.). The Miocene Land Mammals of Europe. München. pp. 457-472.

Van der Meulen, A.J., & De Bruijn, H. 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece): Part 2. The Gliridae. Proceedings of the Koninklijke Akademie van Wetenschappen, B, 485–524.

Van der Meulen, A. J., & Daams, R. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. Palaeogeography, Palaeoclimatology, Palaeoecology, 93, 227–253.

Van der Meulen, A. J., Pélaez-Campomanes, P., & Daams, R. 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in The Calatayud-Teruel basin (Zaragoza, Spain). Coloquios de Paleontologia, vol. ext. 1, 385–441.

Van der Meulen, A. J., Peláez-Campomanes, P., & Levin, S. A. 2005. Age structure, residents, and transients of Miocene rodent communities. The American Naturalist, 165(4), E108–E125.

Van der Meulen, A. J., García-Paredes, I., Álvarez-Sierra, M. Á., van den Hoek Ostende, L. W., Hordijk, K., Oliver, A., Lopez-Guerrero, P., Hernandez-Ballarín, V., & Peláez-Campomanes, P. 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. Geobios, 44, 309–321.

Van der Meulen, A. J., García-Paredes, I., Álvarez Sierra, M. Á., Van den Hoek Ostende, L. W., Hordijk, K., Oliver, A., & Pélaez-Campomanes, P. 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European chronology. Geologica Acta, 10, 159–179.

Van Weerd, A., & Daams, R. 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications (I/II). Proceedings of the Koninklijke Akademie van Wetenschappen, B, 448–473.

Vianey-liaud, M. 1974. L’anatomie crânienne des genres *Eucricetodon* et *Pseudocricetodon* (Cricetidae, Rodentia, Mammalia) ; essai de systématique des Cricétidés oligocènes d’Europe occidentale. Géologie Méditerranéenne, 1, 111–131.

Vianey-Liaud, M. 1985. Possible evolutionary relationships among Eocene and Lower Oligocene rodents of Asia, Europe, and North America. In: Luckett, W. P., & Hartenberger, J.-L. Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. New York:

Plenum Press. pp. 277-310.

Vincent, E., & Berger, W. H. 1985. Carbon Dioxide and Polar Cooling in the Miocene: The Monterey Hypothesis. In E. T. Sundquist & W. S. Broecker (Eds.), The Carbon Cycle and Atmospheric CO2: Natural Variations Archean to Present (pp. 455–468). Washington DC: American Geophysical Union (AGU).

Von Koenigswald, W. 1985. Evolutionary trends in the enamel of rodent incisors. In: Luckett W.P. & Hartenberger J. L. (Eds.). Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis. New York: Plenum Press, pp. 403–422.

Wahlert, J. H. 1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorpha) : skull and upper teeth of Kansasimys. American Museum novitates ; no. 2645.

Walter, H. 1998. Vegetació i zones climàtiques del món. L'estructuració ecològica de la geobiosfera (segona). Barcelona: PPU (Promociones y Publicaciones Universitarias).

Wang, B.-Y., & Dawson, M. R. 1994. A primitive cricetid (Mammalia: Rodentia) from the Middle Eocene of Jiangsu Province, China. Annals of Carnegie Museum, 63, 239–256.

Ward C.V. 2007. Postcranial and Locomotor Adaptations of Hominoids. In: Handbook of Paleoanthropology. Henke, W. & Tattersall, I. (Eds.). Springer, Berlin, Heidelberg

Waterhouse, G. R. 1839. Observations on the Rodentia with a view to point out groups as indicated by the structure of the crania in this order of mammals. Magazine of Natural History, 3, 90–96, 184–188, 274–279, 593–600.

Weksler, M. 2006. Phylogenetic relationships of oryzomine [i.e. oryzomyine] rodents (Muroidea, Sigmodontinae) : separate and combined analyses of morphological and molecular data. Bulletin of the AMNH ; no. 296.

Wessels, W., Theocharopoulos, K. D., De Bruijn, H., & Ünay, E. 2001. Myocricetodontinae and Megacricetodontini (Rodentia) from the lower Miocene of NW Anatolia. Lynx, n. S., 32, 371–388.

Wessels, W., Van de Weerd, A. A., De Bruijn, H., & Markovic, Z. 2018. New Melissiodontinae (Mammalia, Rodentia) from the Paleogene of sout-east Serbia. Palaeobiodiversity and Palaeoenvironments, 98(3), 471–487.

Whittaker, R. 1962. Classification of Natural Communities. Botanical Review, 28(1), 1-239.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., & Solomon, A. M. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19(2), 117–134.

Wilson, D., & Reeder, D. 2005. Mammal Species of the World. Baltimore: Johns Hopkins

University Press.

Wood, A.E. 1936. Cricetid rodents described by Leidy and Cope from the Tertiary of North America. American Museum Novitates, 822, 1-8.

Wood, A. E. 1955. A revised classification of the rodents. Journal of Mammalogy, 36, 165–187.

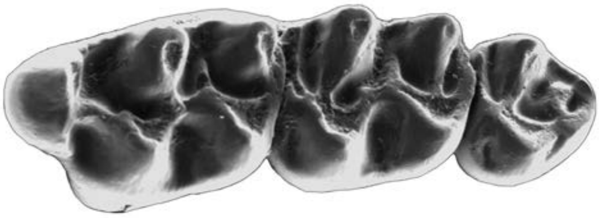
Wood, A.E. 1965. Grades and clades among rodents. Evolution, 19, 115-130.

Wood, A.E. 1974. The evolution of the Old World and New World Hystricomorphs. In: Rowlands, B.J. (Ed.). Symposium of the Zoological Society on the Biology of Hystricomorph Rodents. London: Zoological Society of London. pp. 21-54.

Woodburne, M. O. 2004. Global Events and the North American Mammalian Biochronology. In: Woodburne, M. O. (Ed.). Late Cretaceous and Cenozoic Mammals of North America. New york. Columbia University Press. pp. 315-344.

Zachos, J. C., Pagani, M., Sloan, L., Thomas, E., & Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 292(5517), 686–693

Zisheng, A., Kutzbach, J. E., Prell,W. L., & Porter, S. C. 2001. Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. Nature, 411, 62–66.



Appendix 1: Small mammal faunal lists for the Vallès-Penedès sites studied in this work

APPENDIX 1

Small mammal faunal lists for the Vallès-Penedès sites studied in this work. GPTS refers to Geomagnetic Polarity Time Scale, see Ogg (2012) for chron boundaries. Locality coordinates are given using the Universal Transverse Mercator (UTM) system (grid zone 31N) with European Terrestrial Reference System (ETRS89).

SANT ANDREU DE LA BARCA

Acronym: SAB

Fossiliferous levels: SAB1, SAB2, SAB3, SABS, SABi, SAB3B

Municipality: Sant Andreu de la Barca(el Baix Llobregat, Barcelona)

Coordinates UTM (easting, northing): 413288, 4588727

MN zonation: MN3

Regional/local zone: Ramblian zone A

Correlation to GPTS: C5Dr.2r

Faunal list: *Paleosciurus* cf. *fissurae, Glirudinus modestus, Glirudinus* aff. *gracilis, Peridyromys murinus, Prodryomy* cf. *satus, Pseudodryomys ibericus, Vasseuromys* aff. *ramblensis, Bransantoglis* aff. *caedoti, Pseudotheridomys* cf. *fejfari, Ligerimys antiquus, Ligerimys* cf. *fahlbuschi, Melissiodon dominans, Lagopsis penai, Galerix remmerti, Desmanodon daamsi, Plesiodymylus* sp., *Florinia* sp., *Amphiperatherium frequens.*

References: Agustí, 1981; Agustí and Galobart, 1997, Van den Hoek Ostende et al.,2020, this work

TURÓ DE LES FORQUES

Acronym: TFR

Levels: TFR1, TFR2

Municipality: Castellbisbal (el Vallès-Occidental, Barcelona)

Coordinates UTM (easting, northing): 422025, 4591970

MN zonation: MN3

Regional/local zones: Ramblian zone A

Correlation to GPTS: C5Dr.2r

Faunal list: *Armantomys aragonensis, Pseudodryomys ibericus, Simplomys simplicidens, Pseudotheridomys* cf. *fejfari, Ligerimys antiquus, Ligerimys* cf. *fahlbuschi, Melissiodon dominans, Galerix remmerti, Desmanodon daamsi, Chainodus* sp., *Plesiodymylus* sp., *Clapasorex* cf. *alvarezae, Amphiperatherium frequens.*

References: Casanovas-Vilar and DeMiguel, 2013, Van den Hoek Ostende et al. 2020, this work

LA COSTABLANCA

Acronym: CBL or CB (used in chapter 9)

Levels: CB, CB2A,CB2A, CB2B

Municipality: Castellbisbal (el Vallès-Occidental, Barcelona)

Coordinates UTM (easting, northing): 411750, 4592250

MN zonation: MN3

Regional/local zone: Ramblian zone A

Correlation to GPTS: C5Dr.2r

Faunal list: *Heteroxerus* cf. *rubricati, Glirudinus modestus, Glirudinus* cf. *undosus, Armantomys aragonensis, Peridyromys murinus, pseudotheridomys ibericus, Simplomys simplicidens, Ligerimys antiquus, Lagopsis penai, Desmanodon daamsi, Chainodus* sp., *Plesiodymylus* sp., *Heterosorex neumayrianus, Florinia* sp.

References: Crusafont et al., 1968; Sanz de Siria 1981, 1993; Rotgers and Alba, 2011, Casanovas-Vilar et al., 2016c, Van der Hoek Ostende et al. 2020, this work

MOLÍ DE CAN CALOPA

Acronym: MC

Other names: Molí Calopa

Levels: MC1, MC2

Municipality: Rubí (el Vallès-Occidental, Barcelona)

Coordinates UTM (easting, northing): 417600, 4590700

MN zonation: MN3

Regional/local zone: Ramblian zone A

Correlation to GPTS: C5Dn

Faunal list: *Heteroxerus rubricati, Pseudodryomys ibericus, Melissiodon dominans, Prolagus vasconensis, Lagopsis penai,*

References: Almera, 1891, 1898, 1899; Crusafont et al., 1955, Llenas Avellaneda, 1996, Casanovas-Vilar et al. 2016, this work.

EL CANYET

Acronym: EC or CNY

Levels: EC

Municipality: Castellbisbal (el Vallès Occidental, Barcelona)

Coordinates UTM (easting, northing): 416150, 4589600

MN zonation: MN4

Regional/local zones: Aragonian zone Ca

Correlation to GPTS: -

Faunal list: *Dehmisciurus obtusidens, Pseudodryomys ibericus, Democricetodon hispanicus.*

References: Crusafont et al., 1955; Agustí, 1981; Aldana Carrasco, 1991, 1992.

LES CASES DE LA VALENCIANA

Acronym: LCV

Levels: LCV1, LCV2

Municipality: Gelida (l'Alt Penedès, Barcelona)

Coordinates UTM (easting, northing): 404340, 4587030

MN zonation: MN4

Regional/local zones: Argonian zone Ca

Correlation to GPTS: C5Cn

Faunal list: *Heteroxerus rubricati, Heteroxerus* cf. *grivensis, Glirudinus modestus, Microdyromys legidensis* vel *koenigswaldi, Peridyromys murinus, Pseudodryomys ibericus, Simplomys* cf. *julii, Simplomys simplicidens, Ligerimys florancei, Ligerimys ellipticus, Melissiodon dominans, Eumyarion* cf. *weinfurteri, Democricetodon hispanicus, Megacricetodon primitivus, Lagopsis penai, Galerix symeonidisi, Heterosorex neumayrianus, Amphiperatheium frequens.*

References: Crusafont et al., 1955; Agustí and Cabrera, 1980; Llenas Avellaneda, 2015.; Casanovas-Vilar et al., 2014, 2017; Luján et al., 2017; Sanisidro et al., 2018, Van der Hoek Ostende et al. 2020, this work.

CAN MARTÍ VELL

Acronym: CMV

Levels: CMV1, CMV2, CMV3

Municipality: Gelida (l'Alt Penedès, Barcelona)

Coordinates UTM (easting, northing): 403760, 4586830

MN zonation: MN4

Regional/local zone: Aragonian zone Ca

Correlation to GPTS: C5Cn

Faunal list: *Heteroxerus rubricati, Atlantoxerus idubedensis, Glirudinus modestus, Glirudinus undosus, Microdyromys monspeliensis, Peridyromys murinus, Pseudodryomys ibericus, Simplomys julii, Simplomys simplicidens, Bransantoglis caedoti, Ligerimys florancei, Ligerimys* *ellipticus, Eumyarion weinfurteri, Democricetodon hispanicus, Megacricetodon primitivus, Galerix symeonidisi, Desmanodon daamsi, Plesiodymylus* sp., *Heterosorex neumayrianus, Oligosorex thauensis, Miosorex* sp., *Florinia* sp., *Amphiperatherium frequens.*

References: Agustí and Cabrera, 1980; Agustí et al., 1985; Agustí, 1983; Casanovas-Vilar et al., 2016c; Van den Hoek Ostende 2020., this work.

CAN JULIÀ

Acronym: CJ

Levels: CJ6

Municipality: Gelida (l'Alt Penedès, Barcelona)

Coordinates UTM (easting, northing): 403680, 4586600

MN zonation: MN4

Regional/local zones: Aragonian zone Ca

Correlation to GPTS: C5Cn

Faunal list: *Ligerimys* cf. *ellipticus, Megacricetodon primitivus, Lagopsis* cf. *penai, Galerix symeonidisi, Plesiodymylus* sp., *Heterosorex neumayrianus.*

References: Crudafont and Villata, 1952; Crusafont et al., 1955; Agustí and Cabrera, 1980; Agustí, 1981, Van der Hoek Ostende et al., 2020, this work.

ELS CASOTS, CAL SUTXET AND FONSANTA COAL MINES

Acronym: CS (els Casots) and CSU (Cal Sutxet)

Levels: CS72, CS73, CS74

Municipality: Subirats (l'Alt Penedès, Barcelona)

Coordinates UTM (easting, northing): 400685, 4585580

MN zonation: MN5

Regional/local zone: Aragonian zone Cb

Correlation to GPTS: C5Br

Faunal list: *Dehmisciurus* cf. *obtusidens, Palaeosciurus* cf. *fissurae, Spermophillinus* cf. *besanus, Heteroxerus rubricati, Atlantoxerus idubedensis, Glirudinus modestus, Microdyromys* cf. *mosnpeliensis, Muscardinus* aff. *thaleri, Peridyromys murinus, Pseudodryomys ibericus, Simplomys julii, Simplomys simplicidens, Bransantoglis* cf. *caedoti, Ligerimys ellipticus, Democricetodon hispanicus, Democricetodon gracilis, Democricetodon* sp., *Megacricetodon primitivus.*

References Moya-Solà and Rius Font, 1993; Casanovas-Vilar et al., 2011 a, c; Crusafont et al. 1955; Aldana Carrasco, 1991, 1992, this work.

VILOBÍ DEL PENEDÈS

Acronym: VI

Levels: VI1, VI2, VIO

Municipality: Vilobí del Penedès (l'Alt Penedès, Barcelona)

Coordinates UTM (easting, northing): 387508, 4582561

MN zonation: MN5

Regional/ local zone: Aragonian zone Cb

Correlation to GPTS: C5Br

Faunal list: *Heteroxerus* cf. *rubricati, Heteroxerus* cf. *grivensis, Glirudinus modestus, Microdyromys legidensis* vel *koenigswaldi, Peridyromys* cf. *murinus, Pseudodryomys ibericus, Simplomys* cf. *julii, Simplomys simplicidens, Simplomys robustus, Simplomys* cf. *meulenorum, Eliomys* sp.*, Ligerimys ellipticus, Democricetodon gracilis, Democricetodon* cf. *decipiens, Megacricetodon primitivus, Galeix symeonidisi, Oligosorex* cf. *thauensis, Miosorex* sp.

References: Ortí and Pueyo, 1976; Aguilar, 1981, 1985; Magné, 1978; Bessadick and Cabrera, 1985; Agustí et al., 1990, Casanovas-Vilar et al. 2016a, this work.

SANT MAMET

Acronym: SM

Levels: SM1, SM2

Municipality: Sant Cugat del Vallès (el Vallès-Occidental, Barcelona)

Coordinates UTM (easting, northing): 421251, 4592653

MN zonation: MN5

Regional/ local zone: Aragonian zone Cb

Correlation to GPTS: C5Br

Faunal list: *Palaeosciurus fissurae, Spermophillinus besanus, Glirudinus modestus, Microdyromys legidensis* vel *koenigswaldi, Pseudodryomys ibericus, Ligerimys ellipticus, Melissiodon dominans, Eumyarion weinfurteri, Democricetodon gracilis, Democricetodon decipiens, Megacricetodon primitivus, Prolagus oeningensis, Lagopsis penai, Galerix symeonidisi*

References: Crusafont et al. 1955, Agustí et al., 1985, Garcés Crespo, 1995, Van der Hoek Ostende et al., 2020, this work.

CAN CABANES WEST

Acronym: CCW

Levels: -

Municipality: Sant Cugat del Vallès (el Vallès-Occidental, Barcelona)

Coordinates UTM (easting, northing): 422812.4, 4592667.2

MN zonation: MN5

Regional/local zone: Aragonian zone Cb

Correlation to GPTS: C5Br

Faunal list: *Spermophillinus* cf. *besanus, Glirudinus modestus, Democricetodon gracilis.*

References: De Gibert and Robles, 2005, this work.

LA RIERA DEL MORRAL

Acronym: MOR

Levels: MOR1

Municipality: Abrera (el Baix Llobregat, Barcelona)

Coordinates UTM (easting, northing): 411391, 4596140

MN zonation: MN5

Regional/local zone: Aragonian zone D

Correlation to GPTS: C5Br

Faunal list: *Democricetodon* sp.

References: Casanovas-Vilar and Jovells-Vaqué, 2017, this work.

LES ESCLETXES DEL PAPIOL

Acronym: PA, EPA

Levels: -

Municipality: El Papiol (el Baix Llobregat, Barcelona)

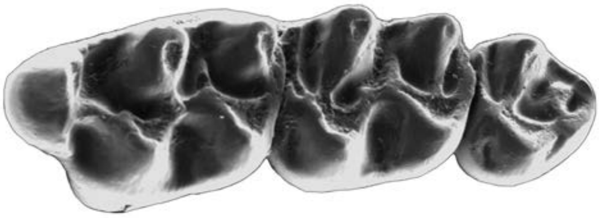
Coordinates UTM (easting, northing): 418000, 4587900

MN zonation: MN5

Correlation to GPTS: C5Br

Faunal list: *Heteroxerus rubricati, Microdyromys legidensis* vel *koeningswaldi, Peridyromus murinus, Pseudodyromus ibericus, Simplomys* cf. *julii, Simplomys simplicidens, Eumyarion* cf. *weinfurteri, Democricetodon* cf. *decipiens, Megacricetodon primitivus, Florinia* sp., *Paenelimnoecus* sp.

References: Agustí et al. 1985, Crusafont et al., 1955; Permanyer, 1990, this work.



Appendix 2: Catalogue of the studied material and measurements

APPENDIX 2

Catalogue of the studied cricetid material from the Vallès-Penedès Basin including length (L) and width (W) measurements. Estimated measurements are given within brackets, whereas '>' indicates that the measurement certainly exceeds the reported value but could not be reliably taken. Collection acronyms are as follows: IPS, Institut de Paleontologia de Sabadell (now ICP, Institut Català de Paleontologia Miquel Crusafont), Sabadell, Spain; MGB, Museu de Geologia de Barcelona (now Museu de Ciències Naturals de Barcelona), Barcelona, Spain, 'V' preceding collection number indicates that the specimen belongs to the Villalta Collection, donated to the museum in the 1980s. For locality acronyms see chapter 9 and Appendix 1.

LOCALITY	TAXON	COLLECTION NUMBER	ELEMENT	L	W
TFR1	*Melissiodon dominans*	IPS85463	M1	3.48	2.46
TFR1	*Melissiodon dominans*	IPS85464	M1	3.37	2.15
TFR1	*Melissiodon dominans*	IPS85465	M2	2.57	[2.13]
TFR1	*Melissiodon dominans*	IPS85466	M2	>2.11	[2.32]
TFR1	*Melissiodon dominans*	IPS85467	m2	-	[1.87]
MC	*Melissiodon dominans*	IPS20721	M1	-	-
MC	*Melissiodon dominans*	IPS22935	m2	[2.43]	[1.97]
MC	*Melissiodon dominans*	IPS22935	m3	[2.58]	[1.90]
SAB	*Melissiodon dominans*	IPS19219	m1	2.94	2.05
SAB	*Melissiodon dominans*	IPS86077	m3	2.82	1.88
SAP	*Melissiodon dominans*	MGB V7859	m1	-	>1.72
EF	*Melissiodon dominans*	IPS18269	m2	[2.60]	[2.03]
EF	*Melissiodon dominans*	IPS18269	m3	[2.64]	[2.12]
SM	*Melissiodon dominans*	IPS85757	M1	2.96	1.99
LCV1	*Eumyarion* sp.	IPS8885	M1	1.91	1.41
EC	*Democricetodon hispanicus*	V7846	M1	1.63	1.17
EC	*Democricetodon hispanicus*	V7846	M2	1.31	1.13
EC	*Democricetodon hispanicus*	V7845	M2	1.29	1.06
LCV1	*Democricetodon hispanicus*	IPS88883	M1	1.61	1.09
LCV1	*Democricetodon hispanicus*	IPS86452	M2	1.31	1.05
LCV1	*Democricetodon hispanicus*	IPS86453	M2	1.25	1.09
LCV1	*Democricetodon hispanicus*	IPS86454	M3	0.81	0.88
LCV1	*Democricetodon hispanicus*	IPS86455	m1 fragment	-	0.90
LCV1	*Democricetodon hispanicus*	IPS88884	m2	1.31	0.97
LCV1	*Democricetodon hispanicus*	IPS86456	m2 fragment	1.26	1.06
LCV1	*Democricetodon hispanicus*	IPS86457	m3	1.11	0.94
LCV1	*Democricetodon hispanicus*	IPS116921	M1	1.64	0.93
LCV1	*Democricetodon hispanicus*	IPS116919	M1	1.69	1.07
LCV1	*Democricetodon hispanicus*	IPS116922	M1 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116920	M1	-	0.93
LCV1	*Democricetodon hispanicus*	IPS116926	M2	1.25	1.14
LCV1	*Democricetodon hispanicus*	IPS116927	M2	1.32	1.10
LCV1	*Democricetodon hispanicus*	IPS116928	M2 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116929	M2	1.33	1.09
LCV1	*Democricetodon hispanicus*	IPS116930	M2	1.22	1.05
LCV1	*Democricetodon hispanicus*	IPS116931	M2 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116932	M2	1.06	0.93
LCV1	*Democricetodon hispanicus*	IPS116933	M2	1.32	1.04
LCV1	*Democricetodon hispanicus*	IPS116934	M3	0.93	0.95
LCV1	*Democricetodon hispanicus*	IPS116935	M3	0.90	0.92
LCV1	*Democricetodon hispanicus*	IPS116936	m1	1.50	0.99
LCV1	*Democricetodon hispanicus*	IPS116937	m1	1.38	0.96
LCV1	*Democricetodon hispanicus*	IPS116938	m1	1.46	0.97
LCV1	*Democricetodon hispanicus*	IPS116939	m1 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116940	m1 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116941	m2	1.17	0.91

LCV1	*Democricetodon hispanicus*	IPS116942	m2	1.09	0.88
LCV1	*Democricetodon hispanicus*	IPS116943	m2	1.28	1.05
LCV1	*Democricetodon hispanicus*	IPS116944	m2	1.11	0.95
LCV1	*Democricetodon hispanicus*	IPS116945	m2	1.27	1.05
LCV1	*Democricetodon hispanicus*	IPS116946	m2	1.28	1.09
LCV1	*Democricetodon hispanicus*	IPS116947	m2 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116948	m2	1.31	0.99
LCV1	*Democricetodon hispanicus*	IPS116949	m2 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116950	m2	1.27	1.01
LCV1	*Democricetodon hispanicus*	IPS116951	m3	1.19	0.89
LCV1	*Democricetodon hispanicus*	IPS116952	m3	1.14	0.94
LCV1	*Democricetodon hispanicus*	IPS116953	M1 fragment	-	-
LCV1	*Democricetodon hispanicus*	IPS116954	M1 fragment	-	-
CMV1	*Democricetodon hispanicus*	IPS96842	m1 fragment	-	-
CMV2	*Democricetodon hispanicus*	IPS102015	m2	1.36	1.04
CMV2	*Democricetodon hispanicus*	IPS102016	m3	1.12	0.94
CMV3	*Democricetodon hispanicus*	IPS86265	M1	1.48	1.05
CMV3	*Democricetodon hispanicus*	IPS89774	M1	1.63	1.04
CMV3	*Democricetodon hispanicus*	IPS89775	M1 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89776	M1	1.47	1.08
CMV3	*Democricetodon hispanicus*	IPS89777	M1 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89778	M1 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89779	M2	1.30	1.16
CMV3	*Democricetodon hispanicus*	IPS89780	M2	1.26	1.05
CMV3	*Democricetodon hispanicus*	IPS89781	M2	1.14	0.97
CMV3	*Democricetodon hispanicus*	IPS89782	M2	1.06	1.06
CMV3	*Democricetodon hispanicus*	IPS89783	M2	1.29	1.14
CMV3	*Democricetodon hispanicus*	IPS89784	M2	1.35	1.14
CMV3	*Democricetodon hispanicus*	IPS89785	M2 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89786	M2	1.24	1.16
CMV3	*Democricetodon hispanicus*	IPS89787	M2	1.17	1.07
CMV3	*Democricetodon hispanicus*	IPS89788	M2 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89789	M3	0.96	0.96
CMV3	*Democricetodon hispanicus*	IPS89790	M3	0.91	0.95
CMV3	*Democricetodon hispanicus*	IPS89621	m1	1.48	1.06
CMV3	*Democricetodon hispanicus*	IPS89791	m1	1.41	1.02
CMV3	*Democricetodon hispanicus*	IPS89792	m1	1.32	0.97
CMV3	*Democricetodon hispanicus*	IPS89793	m1	1.35	0.99
CMV3	*Democricetodon hispanicus*	IPS89794	m1	1.40	1.00
CMV3	*Democricetodon hispanicus*	IPS89795	m1 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89796	m1 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89797	m2	1.12	0.91
CMV3	*Democricetodon hispanicus*	IPS89798	m2 fragment	-	-
CMV3	*Democricetodon hispanicus*	IPS89799	m3	1.24	0.89
CSU	*Democricetodon hispanicus*	IPS86295	M1 fragment	-	-
CSU	*Democricetodon hispanicus*	IPS86296	m1	1.31	0.86
CSU	*Democricetodon hispanicus*	IPS86281	m2	1.15	1.03
CSU	*Democricetodon hispanicus*	IPS86282	m2 fragment	-	-

CSU	*Democricetodon hispanicus*	IPS86283	m2	1.29	1.07
CSU	*Democricetodon hispanicus*	IPS86284	m2	1.23	1.06
CS72	*Democricetodon hispanicus*	IPS45092	M3	0.70	0.75
CS72	*Democricetodon hispanicus*	IPS45093	M3	0.94	0.97
CS72	*Democricetodon hispanicus*	IPS94650	M3	0.93	0.95
CS72	*Democricetodon hispanicus*	IPS19522	m1	1.41	1.11
CS73	*Democricetodon hispanicus*	IPS19517	m1	1.56	1.01
CS73	*Democricetodon hispanicus*	IPS45051	m1	1.42	0.96
CS73	*Democricetodon hispanicus*	IPS45054	m1	1.45	0.94
CS73	*Democricetodon hispanicus*	IPS45055	m1	1.48	0.95
CS73	*Democricetodon hispanicus*	IPS45056	m1	1.46	0.95
CS73	*Democricetodon hispanicus*	IPS45057	m1	1.57	1.01
CS73	*Democricetodon hispanicus*	IPS45058	m1	1.45	0.94
CS73	*Democricetodon hispanicus*	IPS19519	m3	1.12	0.90
CS73	*Democricetodon hispanicus*	IPS94653	m3	1.14	0.95
CS73	*Democricetodon hispanicus*	IPS94698	m3	1.10	0.92
CS73	*Democricetodon hispanicus*	IPS94700	m3	1.09	1.00
CS73	*Democricetodon hispanicus*	IPS94701	m3	-	-
CS73	*Democricetodon hispanicus*	IPS94637	m3	1.11	0.95
CS73	*Democricetodon hispanicus*	IPS94638	m3	-	-
CS73	*Democricetodon hispanicus*	IPS19503	M3	0.93	0.98
CS74	*Democricetodon hispanicus*	IPS19141	M1	1.65	1.18
CS74	*Democricetodon hispanicus*	IPS19141	M2	1.02	0.97
CS74	*Democricetodon hispanicus*	IPS45000	M1	-	1.13
CS74	*Democricetodon hispanicus*	IPS45001	M1	1.76	1.18
CS74	*Democricetodon hispanicus*	IPS45002	M1	1.58	1.07
CS74	*Democricetodon hispanicus*	IPS45003	M1	1.67	1.07
CS74	*Democricetodon hispanicus*	IPS45004	M1	1.77	1.14
CS74	*Democricetodon hispanicus*	IPS45005	M1	1.74	1.05
CS74	*Democricetodon hispanicus*	IPS45006	M1	1.75	1.13
CS74	*Democricetodon hispanicus*	IPS45006	M2	1.33	1.16
CS74	*Democricetodon hispanicus*	IPS45006	M3	0.76	0.77
CS74	*Democricetodon hispanicus*	IPS45007	M1	-	1.19
CS74	*Democricetodon hispanicus*	IPS45007	M2	-	1.16
CS74	*Democricetodon hispanicus*	IPS45008	M1	1.64	1.12
CS74	*Democricetodon hispanicus*	IPS45008	M2	1.09	1.00
CS74	*Democricetodon hispanicus*	IPS45008	M3	0.77	0.78
CS74	*Democricetodon hispanicus*	IPS19475	M2	1.49	1.11
CS74	*Democricetodon hispanicus*	IPS45019	M2	1.47	1.16
CS74	*Democricetodon hispanicus*	IPS45020	M2	1.32	1.14
CS74	*Democricetodon hispanicus*	IPS45021	M2	1.32	1.12
CS74	*Democricetodon hispanicus*	IPS45022	M2	1.29	1.10
CS74	*Democricetodon hispanicus*	IPS45023	M2	1.31	1.08
CS74	*Democricetodon hispanicus*	IPS45024	M2	1.23	1.10
CS74	*Democricetodon hispanicus*	IPS45025	M2	1.15	1.01
CS74	*Democricetodon hispanicus*	IPS45026	M2	1.37	1.08
CS74	*Democricetodon hispanicus*	IPS19490	M2	0.93	0.84
CS74	*Democricetodon hispanicus*	IPS45027	M2	1.26	1.13

CS74	*Democricetodon hispanicus*	IPS45027	M3	0.90	0.91
CS74	*Democricetodon hispanicus*	IPS94602	M3	0.91	0.96
CS74	*Democricetodon hispanicus*	IPS94652	M3	0.73	0.77
CS74	*Democricetodon hispanicus*	IPS19481	m1	1.41	1.01
CS74	*Democricetodon hispanicus*	IPS45040	m1	1.42	0.95
CS74	*Democricetodon hispanicus*	IPS45041	m1	1.40	0.99
CS74	*Democricetodon hispanicus*	IPS45042	m1	1.46	0.93
CS74	*Democricetodon hispanicus*	IPS45043	m1	1.41	0.99
CS74	*Democricetodon hispanicus*	IPS45044	m1	1.48	0.98
CS74	*Democricetodon hispanicus*	IPS45045	m1	1.49	0.96
CS74	*Democricetodon hispanicus*	IPS45046	m1	1.43	1.01
CS74	*Democricetodon hispanicus*	IPS45047	m1	1.47	0.99
CS74	*Democricetodon hispanicus*	IPS45048	m1	1.40	0.98
CS74	*Democricetodon hispanicus*	IPS45049	m1	1.49	1.01
CS74	*Democricetodon hispanicus*	IPS45050	m1	1.46	0.95
CS74	*Democricetodon hispanicus*	IPS19474	m2	1.39	1.18
CS74	*Democricetodon hispanicus*	IPS45059	m2	1.35	1.03
CS74	*Democricetodon hispanicus*	IPS45060	m2	1.20	0.93
CS74	*Democricetodon hispanicus*	IPS45061	m2	1.25	1.05
CS74	*Democricetodon hispanicus*	IPS45062	m2	1.21	1.07
CS74	*Democricetodon hispanicus*	IPS45063	m2	1.20	1.06
CS74	*Democricetodon hispanicus*	IPS45064	m2	1.31	1.12
CS74	*Democricetodon hispanicus*	IPS45065	m2	1.27	1.07
CS74	*Democricetodon hispanicus*	IPS45066	m2	1.19	1.14
CS74	*Democricetodon hispanicus*	IPS45067	m2	1.26	1.14
CS74	*Democricetodon hispanicus*	IPS45068	m2	1.27	1.20
CS74	*Democricetodon hispanicus*	IPS45069	m2	1.28	1.09
CS74	*Democricetodon hispanicus*	IPS45069	m3	1.10	1.01
CS74	*Democricetodon hispanicus*	IPS45070	m2	1.29	0.98
CS74	*Democricetodon hispanicus*	IPS45071	m2	1.28	1.10
CS74	*Democricetodon hispanicus*	IPS94609	m2	1.19	1.05
CS74	*Democricetodon hispanicus*	IPS19473	m3	1.13	0.94
CS74	*Democricetodon hispanicus*	IPS45082	m3	1.22	0.95
CS74	*Democricetodon hispanicus*	IPS45083	m3	1.21	0.95
CS74	*Democricetodon hispanicus*	IPS45084	m3	1.23	0.93
CS74	*Democricetodon hispanicus*	IPS45085	m3	1.21	0.88
CS74	*Democricetodon hispanicus*	IPS45086	m3	1.15	-
CS74	*Democricetodon hispanicus*	IPS45087	m3	1.09	0.90
CS73	*Democricetodon gracilis*	IPS45053	m1	1.28	0.92
CCW	*Democricetodon gracilis*	IPS19627	m1	1.38	0.91
CCW	*Democricetodon gracilis*	IPS85738	m2	1.17	0.987
CCW	*Democricetodon gracilis*	IPS85739	m1/m2 frag.	-	-
CCW	*Democricetodon gracilis*	IPS85740	m3	0.99	0.77
SM	*Democricetodon gracilis*	IPS103742	M1	1.54	1.03
SM	*Democricetodon gracilis*	IPS103751	M1	1.58	0.99
SM	*Democricetodon gracilis*	IPS103752	M2	1.2	1.01
SM	*Democricetodon gracilis*	IPS103753	M2	1.18	1.07
SM	*Democricetodon gracilis*	IPS105142	m2	> 1,08	> 0,90

SM	*Democricetodon gracilis*	IPS105143	m2 fragment	-	-
SM	*Democricetodon gracilis*	IPS103754	m1	1.28	0.91
SM	*Democricetodon gracilis*	IPS103755	m2	1.13	0.96
SM	*Democricetodon gracilis*	IPS105145	m3	0.97	0.85
SM	*Democricetodon gracilis*	IPS105144	m3	1.02	0.85
VI	*Democricetodon gracilis*	IPS87111	m1	1.35	0.89
VI	*Democricetodon gracilis*	IPS87112	m1	1.21	0.86
VI	*Democricetodon gracilis*	IPS87117	m3	1.11	0.81
VI	*Democricetodon* cf. *decipiens*	IPS86941	M3	0.93	1.01
VI	*Democricetodon* cf. *decipiens*	IPS86942	m1 fragment	-	-
VI	*Democricetodon* cf. *decipiens*	IPS86943	m2 fragment	-	1.12
VI	*Democricetodon* cf. *decipiens*	IPS86944	m2 fragment	-	1.16
VI	*Democricetodon* cf. *decipiens*	IPS19548	M1	1.91	1.25
VI	*Democricetodon* cf. *decipiens*	IPS87106	M2	1.45	1.23
VI	*Democricetodon* cf. *decipiens*	IPS87107	M2	1.29	1.18
VI	*Democricetodon* cf. *decipiens*	IPS87108	M3	1.00	0.97
VI	*Democricetodon* cf. *decipiens*	IPS87109	m1	1.48	1.04
VI	*Democricetodon* cf. *decipiens*	IPS87110	m1	1.56	1.09
VI	*Democricetodon* cf. *decipiens*	IPS87115	m2	1.26	1.09
VI	*Democricetodon* cf. *decipiens*	IPS87116	m2	1.33	1.17
VI	*Democricetodon* cf. *decipiens*	IPS87113	m1 fragment	-	-
VI	*Democricetodon* cf. *decipiens*	IPS87114	m1 fragment	-	0.80
PA	*Democricetodon* cf. *decipiens*	IPS86386	M2	1.39	-
PA	*Democricetodon* cf. *decipiens*	IPS86387	m2	1.31	1.21
PA	*Democricetodon* cf. *decipiens*	IPS86388	m3	1.21	1.04
SM	*Democricetodon* cf. *decipiens*	IPS19368	M1	1.87	1.21
SM	*Democricetodon* cf. *decipiens*	IPS85743	M2	1.34	1.17
CS73	*Democricetodon* sp. 4	IPS45052	m1	1.67	1.08
MOR1	*Democricetodon* sp. 4	IPS88868	M2	1.6	1.2
MOR1	*Democricetodon* sp. 4	IPS105188	m2	1.51	1.31
LCV1	*Megacricetodon primitivus*	IPS86432	M1	1.36	0.85
LCV1	*Megacricetodon primitivus*	IPS86433	M1	1.38	0.83
LCV1	*Megacricetodon primitivus*	IPS86434	M1	1.47	1.03
LCV1	*Megacricetodon primitivus*	IPS86435	M2	1.05	0.85
LCV1	*Megacricetodon primitivus*	IPS86436	M2	1.03	0.81
LCV1	*Megacricetodon primitivus*	IPS86437	M2 fragment	-	0.96
LCV1	*Megacricetodon primitivus*	IPS86439	M3	0.68	0.66
LCV1	*Megacricetodon primitivus*	IPS86440	m1	1.30	0.71
LCV1	*Megacricetodon primitivus*	IPS86441	m1	1.30	0.82
LCV1	*Megacricetodon primitivus*	IPS86442	m1	1.35	0.88
LCV1	*Megacricetodon primitivus*	IPS86443	m1	1.22	0.75
LCV1	*Megacricetodon primitivus*	IPS86444	m2	1.07	0.85
LCV1	*Megacricetodon primitivus*	IPS86445	m2	0.99	0.85
LCV1	*Megacricetodon primitivus*	IPS86446	m2	1.09	0.87
LCV1	*Megacricetodon primitivus*	IPS86447	m2 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS86448	m2 fragment	0.85	0.72
LCV1	*Megacricetodon primitivus*	IPS86449	m3	0.79	0.71
LCV1	*Megacricetodon primitivus*	IPS86451	m3	0.79	0.69

LCV1	*Megacricetodon primitivus*	IPS116859	M1	1.34	0.86
LCV1	*Megacricetodon primitivus*	IPS116860	M1	1.44	0.91
LCV1	*Megacricetodon primitivus*	IPS116861	M1	1.38	0.94
LCV1	*Megacricetodon primitivus*	IPS116862	M1	1.35	0.90
LCV1	*Megacricetodon primitivus*	IPS116863	M1	-	0.93
LCV1	*Megacricetodon primitivus*	IPS116864	M1	1.91	0.89
LCV1	*Megacricetodon primitivus*	IPS116865	M1	1.41	0.99
LCV1	*Megacricetodon primitivus*	IPS116866	M1	1.43	1.02
LCV1	*Megacricetodon primitivus*	IPS116867	M1	1.37	0.88
LCV1	*Megacricetodon primitivus*	IPS116868	M1	-	0.87
LCV1	*Megacricetodon primitivus*	IPS116869	M2	1.06	0.77
LCV1	*Megacricetodon primitivus*	IPS116870	M2	1.04	0.85
LCV1	*Megacricetodon primitivus*	IPS116871	M2	1.06	0.91
LCV1	*Megacricetodon primitivus*	IPS116872	M2	1.07	0.85
LCV1	*Megacricetodon primitivus*	IPS116873	M2	1.06	0.88
LCV1	*Megacricetodon primitivus*	IPS116874	M2	1.11	0.87
LCV1	*Megacricetodon primitivus*	IPS116875	M2	1.02	0.92
LCV1	*Megacricetodon primitivus*	IPS116876	M2	1.03	0.89
LCV1	*Megacricetodon primitivus*	IPS116877	M2	1.04	0.83
LCV1	*Megacricetodon primitivus*	IPS116878	M2	0.96	0.88
LCV1	*Megacricetodon primitivus*	IPS116879	M2	1.1	0.94
LCV1	*Megacricetodon primitivus*	IPS116880	M2 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116881	M2	1.04	0.85
LCV1	*Megacricetodon primitivus*	IPS116882	M2 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116884	M2 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116883	M2	1.00	0.95
LCV1	*Megacricetodon primitivus*	IPS116885	M3	0.71	0.68
LCV1	*Megacricetodon primitivus*	IPS116886	M3	0.79	0.79
LCV1	*Megacricetodon primitivus*	IPS116887	m1	-	0.86
LCV1	*Megacricetodon primitivus*	IPS116889	m1	1.22	0.85
LCV1	*Megacricetodon primitivus*	IPS116888	m1	1.23	0.78
LCV1	*Megacricetodon primitivus*	IPS116890	m1	1.26	0.75
LCV1	*Megacricetodon primitivus*	IPS116891	m1	1.22	0.79
LCV1	*Megacricetodon primitivus*	IPS116892	m1	1.29	0.78
LCV1	*Megacricetodon primitivus*	IPS116893	m1	-	0.82
LCV1	*Megacricetodon primitivus*	IPS116894	m1	1.18	0.86
LCV1	*Megacricetodon primitivus*	IPS116895	m1	1.25	0.77
LCV1	*Megacricetodon primitivus*	IPS116897	m1	1.28	0.83
LCV1	*Megacricetodon primitivus*	IPS116896	m1	1.36	0.85
LCV1	*Megacricetodon primitivus*	IPS116899	m1	1.20	0.74
LCV1	*Megacricetodon primitivus*	IPS116898	m1	1.26	0.84
LCV1	*Megacricetodon primitivus*	IPS116901	m1	1.13	0.80
LCV1	*Megacricetodon primitivus*	IPS116902	m1	1.18	0.82
LCV1	*Megacricetodon primitivus*	IPS116903	m2	1.01	0.80
LCV1	*Megacricetodon primitivus*	IPS116904	M1 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116905	m2	1.06	0.91
LCV1	*Megacricetodon primitivus*	IPS116906	m1 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116907	m2 fragment	-	-

LCV1	*Megacricetodon primitivus*	IPS116908	m2	1.06	0.84
LCV1	*Megacricetodon primitivus*	IPS116909	m2	1.01	0.84
LCV1	*Megacricetodon primitivus*	IPS116910	m2 fragment	-	-
LCV1	*Megacricetodon primitivus*	IPS116911	m2	0.97	0.83
LCV1	*Megacricetodon primitivus*	IPS116912	m2	1.15	0.87
LCV1	*Megacricetodon primitivus*	IPS116913	m2	1.04	0.82
LCV1	*Megacricetodon primitivus*	IPS116914	m2	1.04	0.85
LCV1	*Megacricetodon primitivus*	IPS116915	m2	1.01	0.79
LCV1	*Megacricetodon primitivus*	IPS116916	m2	1.07	0.84
LCV1	*Megacricetodon primitivus*	IPS116917	m2	1.09	0.89
LCV1	*Megacricetodon primitivus*	IPS116918	m3	0.88	0.68
CMV3	*Megacricetodon primitivus*	IPS89646	M1	1.46	0.90
CMV3	*Megacricetodon primitivus*	IPS89647	M1	1.49	0.91
CMV3	*Megacricetodon primitivus*	IPS89648	M1	1.31	0.88
CMV3	*Megacricetodon primitivus*	IPS89649	M1	1.36	0.93
CMV3	*Megacricetodon primitivus*	IPS89650	M1	1.44	0.92
CMV3	*Megacricetodon primitivus*	IPS89651	M1 fragment	-	0.97
CMV3	*Megacricetodon primitivus*	IPS89652	M1 fragment	-	0.92
CMV3	*Megacricetodon primitivus*	IPS89653	M1 fragment	-	0.94
CMV3	*Megacricetodon primitivus*	IPS89654	M1 fragment	-	0.89
CMV3	*Megacricetodon primitivus*	IPS89655	M1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89656	M1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89657	M2	1.05	0.84
CMV3	*Megacricetodon primitivus*	IPS89658	M2	1.12	0.92
CMV3	*Megacricetodon primitivus*	IPS89659	M2	1.01	0.91
CMV3	*Megacricetodon primitivus*	IPS89660	M2	1.12	0.94
CMV3	*Megacricetodon primitivus*	IPS89661	M2	1.01	0.85
CMV3	*Megacricetodon primitivus*	IPS89662	M2	1.05	0.91
CMV3	*Megacricetodon primitivus*	IPS89663	M2	1.05	0.89
CMV3	*Megacricetodon primitivus*	IPS89664	M2	1.03	0.85
CMV3	*Megacricetodon primitivus*	IPS89665	M2	1.08	0.80
CMV3	*Megacricetodon primitivus*	IPS89666	M2	1.08	0.88
CMV3	*Megacricetodon primitivus*	IPS89667	M2	-	-
CMV3	*Megacricetodon primitivus*	IPS89668	M2	-	-
CMV3	*Megacricetodon primitivus*	IPS89669	M2	1.09	0.91
CMV3	*Megacricetodon primitivus*	IPS89670	M2	1.04	0.9
CMV3	*Megacricetodon primitivus*	IPS89671	M2 fragment	-	0.86
CMV3	*Megacricetodon primitivus*	IPS89672	M2 fragment	-	0.85
CMV3	*Megacricetodon primitivus*	IPS89673	M2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89674	M2 d	1.05	0.85
CMV3	*Megacricetodon primitivus*	IPS89675	M2 d	-	-
CMV3	*Megacricetodon primitivus*	IPS89676	M2	0.99	0.93
CMV3	*Megacricetodon primitivus*	IPS89677	M2	0.99	0.89
CMV3	*Megacricetodon primitivus*	IPS89678	M2	0.97	0.90
CMV3	*Megacricetodon primitivus*	IPS89679	M2	-	-
CMV3	*Megacricetodon primitivus*	IPS89680	M2	-	-
CMV3	*Megacricetodon primitivus*	IPS89681	M2	-	-
CMV3	*Megacricetodon primitivus*	IPS89682	M3	0.76	0.78

CMV3	*Megacricetodon primitivus*	IPS89683	M3	0.70	0.67
CMV3	*Megacricetodon primitivus*	IPS89684	M3	0.76	0.82
CMV3	*Megacricetodon primitivus*	IPS89685	M3	0.74	0.74
CMV3	*Megacricetodon primitivus*	IPS89686	M3	-	-
CMV3	*Megacricetodon primitivus*	IPS89687	M3	0.77	0.77
CMV3	*Megacricetodon primitivus*	IPS89688	M3	0.82	0.83
CMV3	*Megacricetodon primitivus*	IPS89689	M3	0.64	0.67
CMV3	*Megacricetodon primitivus*	IPS89690	M3	-	-
CMV3	*Megacricetodon primitivus*	IPS89691	M3	0.69	0.72
CMV3	*Megacricetodon primitivus*	IPS89692	M3	0.73	0.69
CMV3	*Megacricetodon primitivus*	IPS89693	M3	0.73	0.74
CMV3	*Megacricetodon primitivus*	IPS89694	M3	0.74	0.72
CMV3	*Megacricetodon primitivus*	IPS89695	M3	0.72	0.73
CMV3	*Megacricetodon primitivus*	IPS89696	M3	0.73	0.74
CMV3	*Megacricetodon primitivus*	IPS89697	M3 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89698	m1	1.29	0.83
CMV3	*Megacricetodon primitivus*	IPS89698	m2	1.05	0.94
CMV3	*Megacricetodon primitivus*	IPS89699	m1	1.27	0.83
CMV3	*Megacricetodon primitivus*	IPS89700	m1	1.28	0.84
CMV3	*Megacricetodon primitivus*	IPS89701	m1	1.30	0.88
CMV3	*Megacricetodon primitivus*	IPS89702	m1	1.18	0.83
CMV3	*Megacricetodon primitivus*	IPS89703	m1	1.25	0.82
CMV3	*Megacricetodon primitivus*	IPS89704	m1	1.25	0.81
CMV3	*Megacricetodon primitivus*	IPS89705	m1	-	0.90
CMV3	*Megacricetodon primitivus*	IPS89706	m1	1.19	0.69
CMV3	*Megacricetodon primitivus*	IPS89707	m1	1.24	0.78
CMV3	*Megacricetodon primitivus*	IPS89708	m1	1.19	0.87
CMV3	*Megacricetodon primitivus*	IPS89709	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89710	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89711	m1	1.32	0.79
CMV3	*Megacricetodon primitivus*	IPS89712	m1	1.33	0.82
CMV3	*Megacricetodon primitivus*	IPS89713	m1	1.23	0.83
CMV3	*Megacricetodon primitivus*	IPS89714	m1	1.28	0.83
CMV3	*Megacricetodon primitivus*	IPS89715	m1	1.32	0.83
CMV3	*Megacricetodon primitivus*	IPS89716	m1	1.29	0.85
CMV3	*Megacricetodon primitivus*	IPS89717	m1	1.19	0.75
CMV3	*Megacricetodon primitivus*	IPS89718	m1	1.18	0.79
CMV3	*Megacricetodon primitivus*	IPS89719	m1	-	-
CMV3	*Megacricetodon primitivus*	IPS89720	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89721	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89722	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89723	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89724	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89725	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89726	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89727	m1 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89728	m2	1.05	0.89
CMV3	*Megacricetodon primitivus*	IPS89729	m2	1.02	0.84

CMV3	*Megacricetodon primitivus*	IPS89730	m2	1.08	0.83
CMV3	*Megacricetodon primitivus*	IPS89731	m2	1.07	0.80
CMV3	*Megacricetodon primitivus*	IPS89732	m2	1.01	0.83
CMV3	*Megacricetodon primitivus*	IPS89733	m2	1.03	0.89
CMV3	*Megacricetodon primitivus*	IPS89734	m2	0.98	0.84
CMV3	*Megacricetodon primitivus*	IPS89735	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89736	m2	-	0.82
CMV3	*Megacricetodon primitivus*	IPS89737	m2	1.07	0.91
CMV3	*Megacricetodon primitivus*	IPS89738	m2	1.08	0.87
CMV3	*Megacricetodon primitivus*	IPS89739	m2	1.07	0.83
CMV3	*Megacricetodon primitivus*	IPS89740	m2	1.05	0.85
CMV3	*Megacricetodon primitivus*	IPS89741	m2	1.07	0.86
CMV3	*Megacricetodon primitivus*	IPS89742	m2	1.05	0.88
CMV3	*Megacricetodon primitivus*	IPS89743	m2	1.06	0.85
CMV3	*Megacricetodon primitivus*	IPS89744	m2	1.07	0.86
CMV3	*Megacricetodon primitivus*	IPS89745	m2	1.1	0.9
CMV3	*Megacricetodon primitivus*	IPS89746	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89747	m2	1.02	0.84
CMV3	*Megacricetodon primitivus*	IPS89748	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89749	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89750	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89751	m2 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89752	m3	0.88	0.70
CMV3	*Megacricetodon primitivus*	IPS89753	m3	0.88	0.70
CMV3	*Megacricetodon primitivus*	IPS89754	m3	0.76	0.57
CMV3	*Megacricetodon primitivus*	IPS89755	m3	0.84	0.68
CMV3	*Megacricetodon primitivus*	IPS89756	m3	0.70	0.62
CMV3	*Megacricetodon primitivus*	IPS89757	m3	0.92	0.72
CMV3	*Megacricetodon primitivus*	IPS89758	m3	0.84	0.67
CMV3	*Megacricetodon primitivus*	IPS89759	m3	0.80	0.7
CMV3	*Megacricetodon primitivus*	IPS89760	m3	0.82	0.66
CMV3	*Megacricetodon primitivus*	IPS89761	m3	-	0.74
CMV3	*Megacricetodon primitivus*	IPS89762	m3	-	0.70
CMV3	*Megacricetodon primitivus*	IPS89763	m3	-	0.67
CMV3	*Megacricetodon primitivus*	IPS89764	m3 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89765	m3	0.83	-
CMV3	*Megacricetodon primitivus*	IPS89766	m3 fragment	-	-
CMV3	*Megacricetodon primitivus*	IPS89767	m3	0.78	0.68
CMV3	*Megacricetodon primitivus*	IPS89768	m3	0.92	-
CMV3	*Megacricetodon primitivus*	IPS89769	m3	0.87	0.71
CMV3	*Megacricetodon primitivus*	IPS89770	m3	0.86	0.73
CMV3	*Megacricetodon primitivus*	IPS89771	m3	0.84	0.7
CMV3	*Megacricetodon primitivus*	IPS89772	m3	0.90	0.71
CMV3	*Megacricetodon primitivus*	IPS89773	m3	0.79	0.73
CMV3	*Megacricetodon primitivus*	IPS86264	M1	-	-
CSU	*Megacricetodon primitivus*	IPS86289	M1	1.51	0.99
CSU	*Megacricetodon primitivus*	IPS86290	M1	-	1.02
CSU	*Megacricetodon primitivus*	IPS86291	M2	-	0.98

CSU	*Megacricetodon primitivus*	IPS86292	m1	1.34	0.82
CSU	*Megacricetodon primitivus*	IPS86293	m2	1.10	0.91
CSU	*Megacricetodon primitivus*	IPS86294	m3 fragment	-	-
CS72	*Megacricetodon primitivus*	IPS45094	M1 fragment	-	-
CS72	*Megacricetodon primitivus*	IPS45094	M2	0.98	0.98
CS72	*Megacricetodon primitivus*	IPS45094	M3	0.64	0.74
CS72	*Megacricetodon primitivus*	IPS44995	m1	1.39	0.85
CS72	*Megacricetodon primitivus*	IPS44996	m1	1.31	0.88
CS72	*Megacricetodon primitivus*	IPS19514	m1	1.37	0.86
CS72	*Megacricetodon primitivus*	IPS19515	m2	1.01	0.83
CS72	*Megacricetodon primitivus*	IPS44997	m2	1.03	0.81
CS72	*Megacricetodon primitivus*	IPS19523	m2	1.13	0.87
CS72	*Megacricetodon primitivus*	IPS45089	M2	1.11	0.95
CS72	*Megacricetodon primitivus*	IPS45089	M3	0.65	0.79
CS72	*Megacricetodon primitivus*	IPS94648	m1 fragment	-	-
CS72	*Megacricetodon primitivus*	IPS94648	m2 fragment	-	-
CS72	*Megacricetodon primitivus*	IPS94649	M1 fragment	-	-
CS73	*Megacricetodon primitivus*	IPS44963	M1	1.42	0.88
CS73	*Megacricetodon primitivus*	IPS44964	M1	1.37	0.89
CS73	*Megacricetodon primitivus*	IPS44965	M1	1.38	0.94
CS73	*Megacricetodon primitivus*	IPS44966	M1	1.32	0.96
CS73	*Megacricetodon primitivus*	IPS44967	M1	1.60	0.94
CS73	*Megacricetodon primitivus*	IPS44968	M1	1.43	1.06
CS73	*Megacricetodon primitivus*	IPS44969	m1	1.25	0.71
CS73	*Megacricetodon primitivus*	IPS44970	m1	1.33	0.84
CS73	*Megacricetodon primitivus*	IPS44971	m1	1.40	0.83
CS73	*Megacricetodon primitivus*	IPS44972	m1	1.10	0.64
CS73	*Megacricetodon primitivus*	IPS44973	m1	1.32	0.83
CS73	*Megacricetodon primitivus*	IPS44974	m1	-	0.83
CS73	*Megacricetodon primitivus*	IPS94639	M3	0.84	0.72
CS73	*Megacricetodon primitivus*	IPS94640	m3	1.00	0.81
CS73	*Megacricetodon primitivus*	IPS94641	M1	1.64	1.16
CS74	*Megacricetodon primitivus*	IPS44936	M1	1.40	1.05
CS74	*Megacricetodon primitivus*	IPS44937	M1	1.42	0.87
CS74	*Megacricetodon primitivus*	IPS44938	M1	1.52	0.93
CS74	*Megacricetodon primitivus*	IPS44939	M1	1.43	0.89
CS74	*Megacricetodon primitivus*	IPS44940	M1	1.53	0.93
CS74	*Megacricetodon primitivus*	IPS44941	M1 fragment	-	-
CS74	*Megacricetodon primitivus*	IPS44961	M2	1.10	0.83
CS74	*Megacricetodon primitivus*	IPS44984	M2	1.14	0.92
CS74	*Megacricetodon primitivus*	IPS19479	M3	0.75	0.71
CS74	*Megacricetodon primitivus*	IPS44942	m1	1.42	0.93
CS74	*Megacricetodon primitivus*	IPS44943	m1	1.45	0.88
CS74	*Megacricetodon primitivus*	IPS44944	m1	1.38	0.82
CS74	*Megacricetodon primitivus*	IPS44945	m1	1.40	0.85
CS74	*Megacricetodon primitivus*	IPS44946	m1	-	-
CS74	*Megacricetodon primitivus*	IPS44947	m1	1.38	0.81
CS74	*Megacricetodon primitivus*	IPS44948	m1	1.31	0.80

CS74	*Megacricetodon primitivus*	IPS44948	m2	1.05	0.85
CS74	*Megacricetodon primitivus*	IPS44949	m1	1.30	0.84
CS74	*Megacricetodon primitivus*	IPS44949	m2	1.05	0.91
CS74	*Megacricetodon primitivus*	IPS44949	m3	0.89	0.76
CS74	*Megacricetodon primitivus*	IPS44950	m1	1.31	0.76
CS74	*Megacricetodon primitivus*	IPS44950	m2	1.04	0.87
CS74	*Megacricetodon primitivus*	IPS44951	m1	1.39	0.91
CS74	*Megacricetodon primitivus*	IPS44951	m2	1.08	0.98
CS74	*Megacricetodon primitivus*	IPS44952	m1	1.32	0.83
CS74	*Megacricetodon primitivus*	IPS44953	m1	1.35	0.87
CS74	*Megacricetodon primitivus*	IPS44954	m1	1.34	0.83
CS74	*Megacricetodon primitivus*	IPS44955	m1	1.43	0.89
CS74	*Megacricetodon primitivus*	IPS44956	m1	-	0.87
CS74	*Megacricetodon primitivus*	IPS44957	m1	1.35	0.90
CS74	*Megacricetodon primitivus*	IPS44958	m1	1.40	0.86
CS74	*Megacricetodon primitivus*	IPS44959	m2	1.10	0.89
CS74	*Megacricetodon primitivus*	IPS44960	m2	1.03	0.83
CS74	*Megacricetodon primitivus*	IPS44962	m2	1.12	0.91
CS74	*Megacricetodon primitivus*	IPS44981	m2	1.12	0.89
CS74	*Megacricetodon primitivus*	IPS44982	m2	1.15	0.94
CS74	*Megacricetodon primitivus*	IPS44983	m2	1.05	0.87
CS74	*Megacricetodon primitivus*	IPS44985	m2	1.10	0.82
CS74	*Megacricetodon primitivus*	IPS44991	m3	1.08	0.77
CS74	*Megacricetodon primitivus*	IPS44992	m3	0.92	0.73
CS74	*Megacricetodon primitivus*	IPS44993	m3	0.89	0.72
CS74	*Megacricetodon primitivus*	IPS44994	m3	0.84	0.72
CS74	*Megacricetodon primitivus*	IPS94255	m2 fragment	-	-
CS74	*Megacricetodon primitivus*	IPS94256	m2	1.20	0.95
CS74	*Megacricetodon primitivus*	IPS94587	m2	-	-
CS74	*Megacricetodon primitivus*	IPS94588	m2	-	-
VI	*Megacricetodon primitivus*	IPS86871	M1 fragment	1.28	-
VI	*Megacricetodon primitivus*	IPS86872	M1 fragment	-	0.99
VI	*Megacricetodon primitivus*	IPS86873	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86874	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86875	M1 fragment	-	0.99
VI	*Megacricetodon primitivus*	IPS86876	M1 fragment	1.37	-
VI	*Megacricetodon primitivus*	IPS86877	M1 fragment	1.43	-
VI	*Megacricetodon primitivus*	IPS86878	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86879	M1 fragment	-	0.92
VI	*Megacricetodon primitivus*	IPS86880	M1 fragment	-	0.99
VI	*Megacricetodon primitivus*	IPS86881	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86882	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86883	M2	1.03	0.88
VI	*Megacricetodon primitivus*	IPS86884	M2	1.07	0.91
VI	*Megacricetodon primitivus*	IPS86885	M2	1.02	0.94
VI	*Megacricetodon primitivus*	IPS86886	M2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86887	M2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86888	M2	1.22	1.03

VI	*Megacricetodon primitivus*	IPS86889	M2	1.01	0.83
VI	*Megacricetodon primitivus*	IPS86890	M2 fragment	-	0.89
VI	*Megacricetodon primitivus*	IPS86891	M2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86892	M2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86893	M3	0.73	0.74
VI	*Megacricetodon primitivus*	IPS86894	M3	0.74	0.78
VI	*Megacricetodon primitivus*	IPS86895	M3	0.77	0.77
VI	*Megacricetodon primitivus*	IPS86896	M3	0.99	0.9
VI	*Megacricetodon primitivus*	IPS86897	M3 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86898	M3	0.76	0.76
VI	*Megacricetodon primitivus*	IPS86899	M1/2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86900	M1/2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86901	m1	1.38	0.83
VI	*Megacricetodon primitivus*	IPS86902	m1 fragment	-	0.85
VI	*Megacricetodon primitivus*	IPS86903	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86904	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86905	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86906	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86907	m1 fragment	-	0.85
VI	*Megacricetodon primitivus*	IPS86908	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86909	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86910	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86911	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86912	m1 fragment	-	0.77
VI	*Megacricetodon primitivus*	IPS86913	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86914	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86915	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86916	m2 fragment	-	0.99
VI	*Megacricetodon primitivus*	IPS86917	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86918	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86919	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86920	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86921	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86922	m2	1.05	0.88
VI	*Megacricetodon primitivus*	IPS86923	m2	1.13	0.92
VI	*Megacricetodon primitivus*	IPS86924	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86925	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86926	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86927	m3	0.92	0.74
VI	*Megacricetodon primitivus*	IPS86928	m3	0.88	0.73
VI	*Megacricetodon primitivus*	IPS86929	m3	0.87	0.66
VI	*Megacricetodon primitivus*	IPS86930	m3 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86931	m3 fragment	-	-
VI	*Megacricetodon primitivus*	IPS86932	m3	0.89	0.77
VI	*Megacricetodon primitivus*	IPS86933	m3	0.98	0.73
VI	*Megacricetodon primitivus*	IPS19559	M1	1.57	0.95
VI	*Megacricetodon primitivus*	IPS86997	M1	1.45	0.91

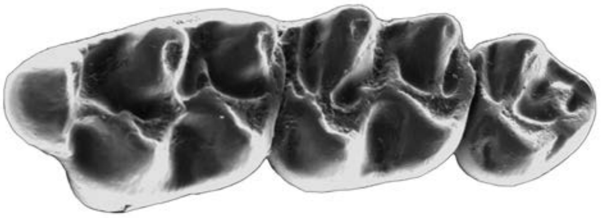
VI	*Megacricetodon primitivus*	IPS86998	M1	1.43	0.89
VI	*Megacricetodon primitivus*	IPS86999	M1	1.56	0.99
VI	*Megacricetodon primitivus*	IPS87000	M1	1.51	0.92
VI	*Megacricetodon primitivus*	IPS87001	M1	1.45	0.92
VI	*Megacricetodon primitivus*	IPS87002	M1	1.59	0.98
VI	*Megacricetodon primitivus*	IPS87003	M1	1.42	0.92
VI	*Megacricetodon primitivus*	IPS87004	M1	1.50	0.91
VI	*Megacricetodon primitivus*	IPS87005	M1	1.51	1.01
VI	*Megacricetodon primitivus*	IPS87006	M1	1.44	0.93
VI	*Megacricetodon primitivus*	IPS87007	M1	1.37	0.91
VI	*Megacricetodon primitivus*	IPS87008	M1	1.53	0.94
VI	*Megacricetodon primitivus*	IPS87009	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87010	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87011	M1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS19557	M1	1.46	0.94
VI	*Megacricetodon primitivus*	IPS87012	M1	1.52	0.97
VI	*Megacricetodon primitivus*	IPS87013	M1	1.52	1.07
VI	*Megacricetodon primitivus*	IPS87014	M1	1.45	0.96
VI	*Megacricetodon primitivus*	IPS87015	M1	1.43	0.99
VI	*Megacricetodon primitivus*	IPS87016	M1	1.46	1.02
VI	*Megacricetodon primitivus*	IPS87017	M1	1.42	0.91
VI	*Megacricetodon primitivus*	IPS87018	M1	-	-
VI	*Megacricetodon primitivus*	IPS19552	M2	1.18	0.97
VI	*Megacricetodon primitivus*	IPS87019	M2	1.09	0.87
VI	*Megacricetodon primitivus*	IPS87020	M2	1.08	0.85
VI	*Megacricetodon primitivus*	IPS87021	M2	1.11	0.91
VI	*Megacricetodon primitivus*	IPS87022	M2	1.12	0.92
VI	*Megacricetodon primitivus*	IPS87023	M2	1.15	0.96
VI	*Megacricetodon primitivus*	IPS87024	M2	1.03	0.84
VI	*Megacricetodon primitivus*	IPS87025	M2	1.16	0.88
VI	*Megacricetodon primitivus*	IPS87026	M2	1.07	0.85
VI	*Megacricetodon primitivus*	IPS87027	M2	1.18	0.97
VI	*Megacricetodon primitivus*	IPS87028	M2	1.15	0.90
VI	*Megacricetodon primitivus*	IPS87029	M2	1.18	0.94
VI	*Megacricetodon primitivus*	IPS87030	M2	1.10	0.86
VI	*Megacricetodon primitivus*	IPS87031	M2	1.08	0.91
VI	*Megacricetodon primitivus*	IPS19551	M2	1.12	0.96
VI	*Megacricetodon primitivus*	IPS87032	M2	1.09	0.92
VI	*Megacricetodon primitivus*	IPS87033	M2	1.10	0.89
VI	*Megacricetodon primitivus*	IPS87034	M2	1.067	0.95
VI	*Megacricetodon primitivus*	IPS87035	M2	1.03	0.83
VI	*Megacricetodon primitivus*	IPS87036	M2	1.08	0.92
VI	*Megacricetodon primitivus*	IPS87037	M2	1.06	0.93
VI	*Megacricetodon primitivus*	IPS87038	M2	1.06	0.86
VI	*Megacricetodon primitivus*	IPS87039	M2	-	-
VI	*Megacricetodon primitivus*	IPS87040	M2	1.08	0.96
VI	*Megacricetodon primitivus*	IPS19553	M2	1.12	0.89
VI	*Megacricetodon primitivus*	IPS87041	M2	1.22	0.90

VI	*Megacricetodon primitivus*	IPS87042	M2	1.06	0.88
VI	*Megacricetodon primitivus*	IPS87043	M2	1.00	0.89
VI	*Megacricetodon primitivus*	IPS87044	M2	1.07	0.87
VI	*Megacricetodon primitivus*	IPS87045	M2	1.07	0.94
VI	*Megacricetodon primitivus*	IPS87046	M2	1.06	0.95
VI	*Megacricetodon primitivus*	IPS87047	M2	1.05	0.81
VI	*Megacricetodon primitivus*	IPS87048	M2	1.08	0.85
VI	*Megacricetodon primitivus*	IPS87049	M2	1.14	0.90
VI	*Megacricetodon primitivus*	IPS87050	M2	1.02	0.92
VI	*Megacricetodon primitivus*	IPS87051	M3	0.92	0.93
VI	*Megacricetodon primitivus*	IPS19556	m1	1.43	0.93
VI	*Megacricetodon primitivus*	IPS87052	m3	0.96	0.92
VI	*Megacricetodon primitivus*	IPS87053	m1	1.29	0.84
VI	*Megacricetodon primitivus*	IPS87054	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87055	m1	1.31	0.77
VI	*Megacricetodon primitivus*	IPS87056	m1	1.48	0.89
VI	*Megacricetodon primitivus*	IPS87057	m1	1.28	0.83
VI	*Megacricetodon primitivus*	IPS87058	m1	1.37	0.88
VI	*Megacricetodon primitivus*	IPS87059	m1 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87060	m1	1.28	0.77
VI	*Megacricetodon primitivus*	IPS19558	m1	1.21	0.75
VI	*Megacricetodon primitivus*	IPS87061	m1	1.30	0.85
VI	*Megacricetodon primitivus*	IPS87062	m1	1.32	0.80
VI	*Megacricetodon primitivus*	IPS87063	m1	1.34	0.82
VI	*Megacricetodon primitivus*	IPS87064	m1	1.32	0.82
VI	*Megacricetodon primitivus*	IPS87065	m1	1.31	0.76
VI	*Megacricetodon primitivus*	IPS87066	m1	1.31	0.77
VI	*Megacricetodon primitivus*	IPS87067	m1	1.26	0.79
VI	*Megacricetodon primitivus*	IPS87068	m1	1.38	0.81
VI	*Megacricetodon primitivus*	IPS87069	m1	1.39	0.80
VI	*Megacricetodon primitivus*	IPS87070	m1	1.42	0.82
VI	*Megacricetodon primitivus*	IPS87071	m1	1.39	0.79
VI	*Megacricetodon primitivus*	IPS19555	m2	1.05	0.84
VI	*Megacricetodon primitivus*	IPS87072	m2	1.07	0.89
VI	*Megacricetodon primitivus*	IPS87073	m2	1.08	0.88
VI	*Megacricetodon primitivus*	IPS87074	m2	1.09	0.93
VI	*Megacricetodon primitivus*	IPS87075	m2	1.08	0.86
VI	*Megacricetodon primitivus*	IPS87076	m2	1.12	0.88
VI	*Megacricetodon primitivus*	IPS87077	m2	1.07	0.89
VI	*Megacricetodon primitivus*	IPS87078	m2	1.13	0.95
VI	*Megacricetodon primitivus*	IPS87079	m2	1.09	0.90
VI	*Megacricetodon primitivus*	IPS87080	m2	0.98	0.87
VI	*Megacricetodon primitivus*	IPS87081	m2	1.04	0.84
VI	*Megacricetodon primitivus*	IPS87082	m2	1.10	0.94
VI	*Megacricetodon primitivus*	IPS87083	m2	1.05	0.88
VI	*Megacricetodon primitivus*	IPS87084	m2	1.06	0.88
VI	*Megacricetodon primitivus*	IPS19554	m2	1.09	0.87
VI	*Megacricetodon primitivus*	IPS87085	m2	1.15	0.91

VI	*Megacricetodon primitivus*	IPS87086	m2	1.13	0.97
VI	*Megacricetodon primitivus*	IPS87087	m2	1.09	0.88
VI	*Megacricetodon primitivus*	IPS87088	m2	1.11	0.91
VI	*Megacricetodon primitivus*	IPS87089	m2	1.09	0.86
VI	*Megacricetodon primitivus*	IPS87090	m2	1.15	0.93
VI	*Megacricetodon primitivus*	IPS87091	m2	1.14	0.98
VI	*Megacricetodon primitivus*	IPS87092	m2	1.13	0.93
VI	*Megacricetodon primitivus*	IPS87093	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87094	m2	1.05	0.87
VI	*Megacricetodon primitivus*	IPS87095	m2	1.15	0.89
VI	*Megacricetodon primitivus*	IPS87096	m2	1.15	0.95
VI	*Megacricetodon primitivus*	IPS87097	m2	1.04	0.78
VI	*Megacricetodon primitivus*	IPS19549	m2	1.06	0.96
VI	*Megacricetodon primitivus*	IPS87098	m2	1.08	0.88
VI	*Megacricetodon primitivus*	IPS87099	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS19550	m3	0.86	0.65
VI	*Megacricetodon primitivus*	IPS87100	m3	1.00	0.73
VI	*Megacricetodon primitivus*	IPS87101	m3	0.96	0.78
VI	*Megacricetodon primitivus*	IPS87102	m3	0.88	0.71
VI	*Megacricetodon primitivus*	IPS87103	m3	0.91	0.72
VI	*Megacricetodon primitivus*	IPS87104	m3	0.93	0.70
VI	*Megacricetodon primitivus*	IPS87105	m3	0.92	0.78
VI	*Megacricetodon primitivus*	IPS19542	M2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87181	M3 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87182	m2 fragment	-	-
VI	*Megacricetodon primitivus*	IPS87183	m2 fragment	-	-
SM	*Megacricetodon primitivus*	IPS105146	m1	[1.37]	[0.92]
SM	*Megacricetodon primitivus*	IPS105147	m1	-	-
PA	*Megacricetodon primitivus*	IPS19622	M1	1.53	1.07
PA	*Megacricetodon primitivus*	IPS19623	M1	1.51	0.96
PA	*Megacricetodon primitivus*	IPS19624	M1	1.63	1.01
PA	*Megacricetodon primitivus*	IPS19625	M1	1.58	0.96
PA	*Megacricetodon primitivus*	IPS19626	M1	1.45	0.98
PA	*Megacricetodon primitivus*	IPS19628	M1	1.52	0.99
PA	*Megacricetodon primitivus*	IPS19629	M1	1.51	0.96
PA	*Megacricetodon primitivus*	IPS86308	M1	-	1.03
PA	*Megacricetodon primitivus*	IPS86309	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86310	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86311	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86312	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86313	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86314	M1	1.42	0.96
PA	*Megacricetodon primitivus*	IPS86315	M1	1.45	0.94
PA	*Megacricetodon primitivus*	IPS86316	M1	1.41	1.01
PA	*Megacricetodon primitivus*	IPS86317	M1	1.56	0.99
PA	*Megacricetodon primitivus*	IPS86318	M1	1.48	-
PA	*Megacricetodon primitivus*	IPS86319	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86320	M1 fragment	-	-

PA	*Megacricetodon primitivus*	IPS86321	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86322	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86323	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86324	M1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86325	M2	1.14	1.01
PA	*Megacricetodon primitivus*	IPS86326	M2 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86327	M2	1.15	0.96
PA	*Megacricetodon primitivus*	IPS86328	M2	1.11	0.93
PA	*Megacricetodon primitivus*	IPS86329	M2	0.99	0.86
PA	*Megacricetodon primitivus*	IPS86330	M2	1.07	0.91
PA	*Megacricetodon primitivus*	IPS86331	M2 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86332	M2	1.08	0.93
PA	*Megacricetodon primitivus*	IPS86333	M2	1.16	0.95
PA	*Megacricetodon primitivus*	IPS86334	M2	1.07	0.91
PA	*Megacricetodon primitivus*	IPS86335	M2	1.09	0.95
PA	*Megacricetodon primitivus*	IPS86336	M2	1.03	0.88
PA	*Megacricetodon primitivus*	IPS86337	M2	1.14	0.99
PA	*Megacricetodon primitivus*	IPS86338	M2	1.09	0.97
PA	*Megacricetodon primitivus*	IPS86339	M2	1.08	0.96
PA	*Megacricetodon primitivus*	IPS86340	M2	1.09	0.95
PA	*Megacricetodon primitivus*	IPS86341	M2	-	-
PA	*Megacricetodon primitivus*	IPS86342	M3	0.75	0.78
PA	*Megacricetodon primitivus*	IPS86343	M3	0.85	0.86
PA	*Megacricetodon primitivus*	IPS86344	M3	0.70	0.75
PA	*Megacricetodon primitivus*	IPS86345	m1	1.40	0.85
PA	*Megacricetodon primitivus*	IPS86346	m1	1.48	0.86
PA	*Megacricetodon primitivus*	IPS86347	m1	1.38	0.86
PA	*Megacricetodon primitivus*	IPS86348	m1	1.23	0.79
PA	*Megacricetodon primitivus*	IPS86349	m1	1.38	0.78
PA	*Megacricetodon primitivus*	IPS86350	m1	1.38	0.81
PA	*Megacricetodon primitivus*	IPS86351	m1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86352	m1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86353	m1 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86354	m1	1.45	0.94
PA	*Megacricetodon primitivus*	IPS86355	m2	1.16	0.92
PA	*Megacricetodon primitivus*	IPS86356	m2	1.12	0.94
PA	*Megacricetodon primitivus*	IPS86357	m2	1.14	0.96
PA	*Megacricetodon primitivus*	IPS86358	m2	1.19	0.92
PA	*Megacricetodon primitivus*	IPS86359	m2	1.08	0.93
PA	*Megacricetodon primitivus*	IPS86360	m2	1.12	0.93
PA	*Megacricetodon primitivus*	IPS86361	m2	1.17	0.93
PA	*Megacricetodon primitivus*	IPS86362	m2	1.15	0.90
PA	*Megacricetodon primitivus*	IPS86363	m2	1.05	0.90
PA	*Megacricetodon primitivus*	IPS86364	m2	-	-
PA	*Megacricetodon primitivus*	IPS86365	m2	-	-
PA	*Megacricetodon primitivus*	IPS86366	m2 fragment	-	-
PA	*Megacricetodon primitivus*	IPS86367	m2	1.14	0.96
PA	*Megacricetodon primitivus*	IPS86368	m2	1.14	0.96

PA	*Megacricetodon primitivus*	IPS86369	m2	1.16	0.86
PA	*Megacricetodon primitivus*	IPS86370	m2	1.07	0.94
PA	*Megacricetodon primitivus*	IPS86371	m2	1.07	0.87
PA	*Megacricetodon primitivus*	IPS86372	m2	1.21	0.94
PA	*Megacricetodon primitivus*	IPS86373	m2	1.09	0.91
PA	*Megacricetodon primitivus*	IPS86374	m2	1.12	0.96
PA	*Megacricetodon primitivus*	IPS86375	m2	0.95	0.70
PA	*Megacricetodon primitivus*	IPS86376	m2	-	0.87
PA	*Megacricetodon primitivus*	IPS86377	m2	-	-
PA	*Megacricetodon primitivus*	IPS86378	m2	-	0.95
PA	*Megacricetodon primitivus*	IPS86379	m3	0.87	0.70
PA	*Megacricetodon primitivus*	IPS86380	m3	0.87	0.70
PA	*Megacricetodon primitivus*	IPS86381	m3	0.98	0.84
PA	*Megacricetodon primitivus*	IPS86382	m3	1	0.79
PA	*Megacricetodon primitivus*	IPS86385	M3 fragment	0.72	0.70



Appendix 3: *Democricetodon* and *Megacricetodon* morphotype frequency tables

APPENDIX 3

Morphotype frequency tables for *Democricetodon* and *Megacricetodon* from the early and early middle Miocene of the Vallès-Penedès Basin. These are the appendices B and D from Jovells-Vaqué and Casanovas-Vilar, in press (chapter 9). For locality acronyms see chapter 9 and appendix 1.

Appendix B: Morphotype frequency tables for *Democricetodon*

Table 1: Anterocone M1

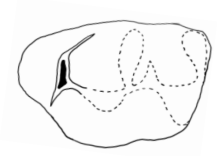
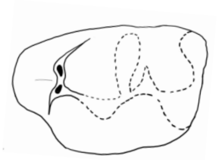
		Anterocone M1		
	Site			N
D.decipiens	**SM**	1		1
	VI	1		1
D.gracilis	**SM**	2		2
D.hispanicus	**CS74**	8	1	9
	CMV3	5		5
	LCV1	1		1
	EC	1		1

Table 2: Anterolophule M1

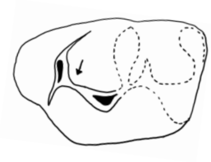
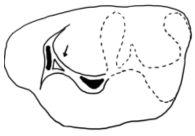
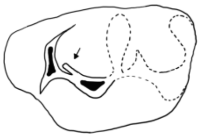
		Anterolophule M1			
	Site				N
D.decipiens	**SM**		1		1
	VI	1			1
D.gracilis	**SM**	2			2
D. hispanicus	**CS74**	8	1		9
	CMV3	5			5
	LCV1			1	1
	EC	1			1

Table 3: Protolophule M1

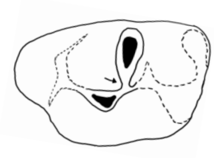
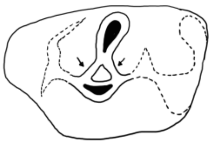
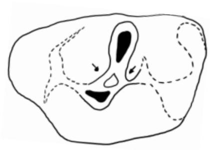
		Protolophule M1			
	Site				N
D.decipiens	**SM**	1			1
	VI	1			1
D.gracilis	**SM**		2		2
D.hispanicus	**CS74**	7	2		9
	CMV3	2	3		5
	LCV1	1			1
	EC		1		1

Table 4: Ectoloph on the paracone M1

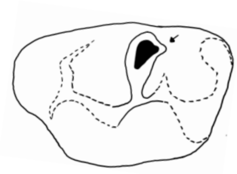
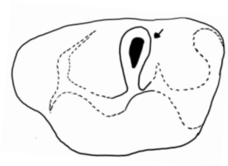
	Ectoloph on the Paracone M1			
	Site			N
D.decipiens	**SM**	1		1
	VI		1	1
D.gracilis	**SM**	2		2
D.hispanicus	**CS74**	6	3	9
	CMV3		4	4
	LCV1		2	2
	EC	1		1

Table 5: Mesoloph M1

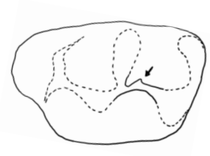
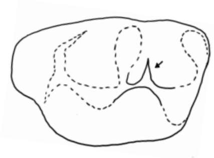
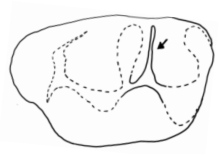
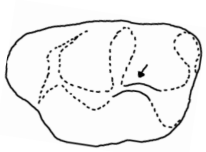
	Mesoloph M1					
	Site					N
D.decipiens	**SM**	1				1
	VI	1				1
D.gracilis	**SM**			2		2
D.hispanicus	**CS74**	4	5			9
	CMV 3			4		4
	LCV1			2		2
	EC		1			1

Table 6: Metalophule M1

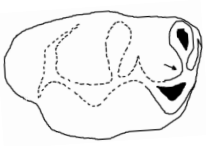
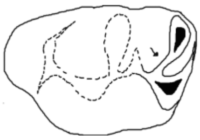
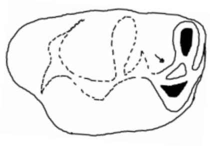
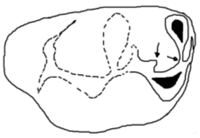
		Metalophule M1				
	Site					N
D.decipiens	**SM**	1				1
	VI	1				1
D.gracilis	**SM**	2				2
D.hispanicus	**CS74**	9				9
	CMV3	4				4
	LCV1	2				2
	EC			1		1

Table 7: Protolophule M2

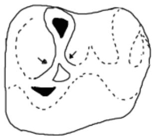
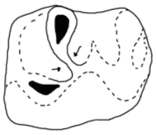
		Protolophule M2					
	Site						N
D.,sp. 4	**MOR1**			1			1
D.decipiens	**SM**			1			1
	PA			1			1
	VI		2				2
D.gracilis	**SM**	1		1			2
D.hispanicus	**CS74**	6		6			12
	CMV3			7			7
	LCV1	2	1	6			9
	EC	1	2				3

Table 8: Ectoloph on the Paracone M2

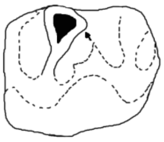
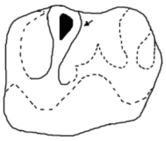
		Ectoloph on the Paracone M2		
	Site			N
D. sp. 4	**MOR1**	1		1
D.decipiens	**SM**		1	1
	PA			1
	VI		2	2
D.gracilis	**SM**	2		2
D.hispanicus	**CS74**	8	4	12
	CMV3		7	7
	LCV1	2		2
	EC	2	1	3

Table 9: Mesoloph M2

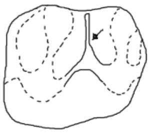
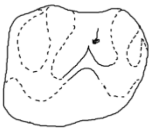
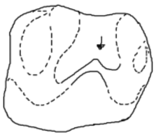
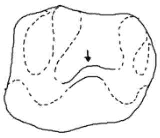
		Mesoloph M2				
	Site					N
D. sp. 4	**MOR1**		1			1
D.decipiens	**SM**	1				1
	PA			1		1
	VI		2			2
D.gracilis	**SM**	2				2
D.hispanicus	**CS74**	6	5	1		
	CMV3	6	1			7
	LCV1	2				2
	EC	1		2		3

Table 10: Metalophule M2

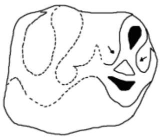
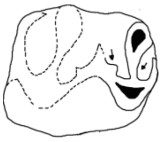
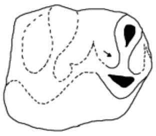
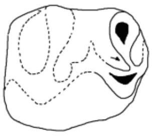
		Metalophule M2					
	Site						N
D. sp. 4	**MOR1**	1					1
D.decipiens	**SM**	1					1
	PA				1		1
	VI	2					2
D.gracilis	**SM**	1					1
D.hispanicus	**CS74**	11	1				12
	CMV3	7					7
	LCV1	2					2
	EC	2			1		3

Table 11: Lingual Anterolophid m1

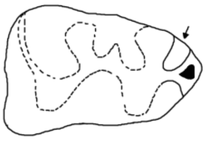
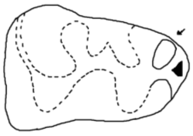
		Lingual Anterolophid m1		
	Site			N
D. sp. 4	**CS73**		1	1
D.decipiens	**VI**		2	2
D.gracilis	**SM**		1	1
	VI		2	2
	CS73		1	1
	CCW		1	1
D.hispanicus	**CS74**	8	4	12
	CS72	2	6	8
	CSU	1		1
	CMV3	4		4
	CMV1	1		1
	LCV1	6		6

Table 12: Metalophulid m1

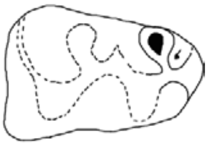
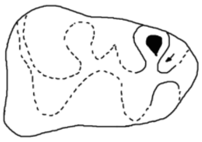
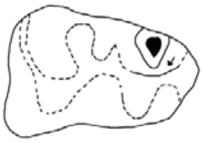
			Metalophulid m1		
	Site				N
D. sp. 4	**CS73**	1			1
D.decipiens	**VI**	2			2
D.gracilis	**SM**	1			1
	VI	2			2
	CS73	1			1
	CCW	1			1
D.hispanicus	**CS74**	5	6	1	12
	CS72	7	1		8
	CSU		1		1
	CMV3	4			4
	CMV1	1			1
	LCV1	5	1		6

Table 13: Metaconid ridge m1

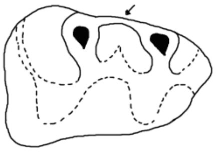
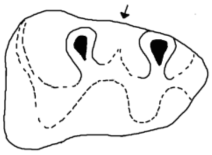
		Metaconid ridge m1		
	Site			N
D. sp. 4	**CS73**	1		1
D.decipiens	**VI**		2	2
D.gracilis	**SM**	1		1
	VI		2	2
	CS73		1	1
	CCW		1	1
D.hispanicus	**CS74**		12	12
	CS72		8	8
	CSU		1	1
	CMV3		4	4
	CMV1	1		1
	LCV1		6	6

Table 14; Mesolophid m1

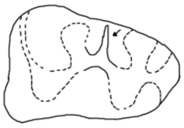
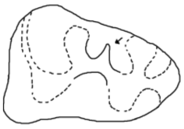
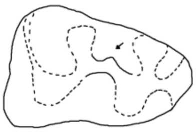
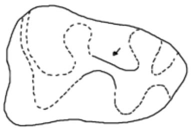
		Mesolophid m1				
	Site					N
D. sp. 4	**CS73**	1				1
D.decipiens	**VI**		2			2
D.gracilis	**SM**	1				1
	VI	2				2
	CS73	1				1
	CCW	1				1
D.hispanicus	**CS74**	3	6	3		12
	CS72		5	3		8
	CSU		1			1
	CMV3	1	2	1		4
	CMV1		1			1
	LCV1		3	3		6

Table 15: Anterosinusid m2

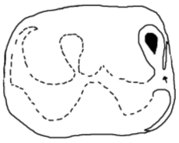
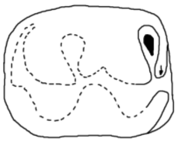
		Anterosinusid m2		
	Site			N
D. sp. 4	**MOR1**	1		1
D.decipiens	**PA**	1		1
	VI	2	1	3
D.gracilis	**SM**	1		1
	CCW	1		1
D.hispanicus	**SM**		2	2
	CS74	5	11	16
	CSU	3	1	4
	CMV3	2	2	4
	CMV2		1	1
	LCV1	5	6	11

Table 16: Metaconid ridge m2

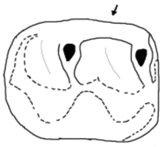
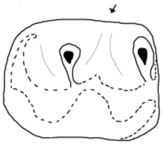
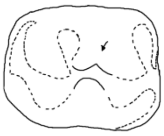
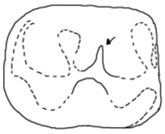
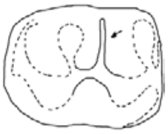
		Metaconid ridge m2		
	Site			N
D. sp. 4	**MOR1**		1	1
D.decipiens	**PA**		1	1
	VI		3	3
D.gracilis	**SM**		1	1
	CCW		1	1
D.hispanicus	**SM**		2	2
	CS74	3	13	16
	CSU		4	4
	CMV3	2	2	4
	CMV2	1		1
	LCV1	6	4	10

Table 17: Mesolophid m2

		Mesolophid m2				
	Site					N
D. sp. 4	**MOR1**	1				1
D.decipiens	**PA**	1				1
	VI	1			2	3
D.gracilis	**SM**		1			1
	CCW		1			1
D.hispanicus	**SM**	2				2
	CS74	8	4		4	16
	CSU	3			1	4
	CMV3		2	1	1	4
	CMV2			1		1
	LCV1	4	2	6		12

Appendix D: Morphotype frequency tables for *Megacricetodon primitivus*

Table 1: Anterocone M1

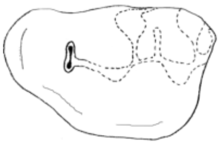
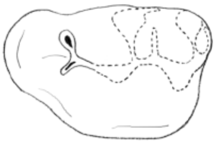
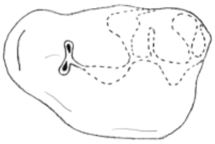
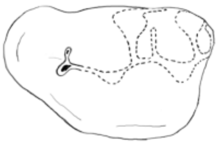
Anterocone M1					
Site					N
PA		6	15		21
VI		4	12	9	25
CS74		4	1		5
CS73		5			5
CSU		1			1
CMV3		6	6	1	13
CMV2		2			2
CMV1			1		1
LCV1		9	4		13

Table 2: Anterior platform of the M1 anterocone

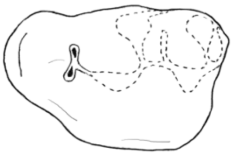
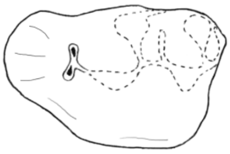
Anterior platform of the M1 anterocone M1			
Site			N
PA	8	6	14
VI	14	9	23
CS74	4	1	5
CS73	4	4	8
CSU		1	1
CMV3	7	6	13
CMV2	2		2
CMV1	1		1
LCV1	6	4	10

Table 3: Labial spur of the M1 anterolophule

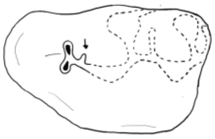
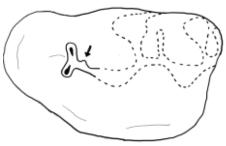
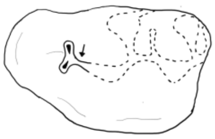
Labial spur of the M1 anterolophule				
Site				N
PA	1	3	16	20
VI	7	7	16	30
CS74	1	1	4	6
CS73		3	3	6
CSU		1		1
CMV3	1	4	5	10
CMV2			2	2
CMV1			1	1
LCV1	2	4	9	15

Table 4: Protolophule M1

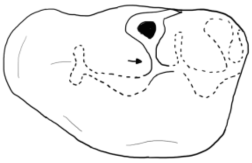
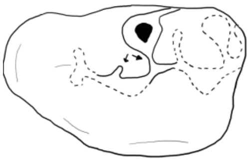
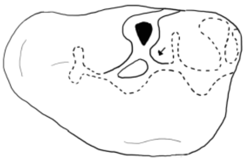
Protolophule M1				
Site				N
PA	20			20
VI	29		1	31
CS74	5			5
CS73	6			6
CSU	2			2
CMV3	12			12
CMV2	2			2
CMV1	1			1
LCV1	14			14

Table 5: Ectoloph M1

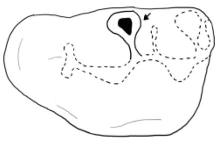
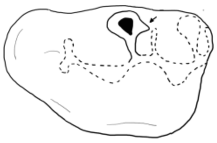
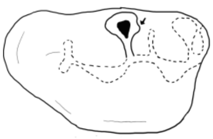
Ectoloph M1				
Site				N
PA	3	5	13	21
VI	10	6	12	28
CS74		2	1	3
CS73	1	1	4	6
CSU			2	2
CMV3	5	3	5	13
CMV2	1	1		2
CMV1			1	1
LCV1	3	8	3	14

Table 6: Ectoloph-Mesoloph connection M1

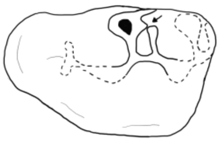
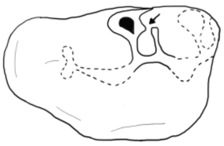
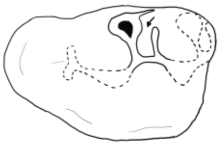
Ectoloph – Mesoloph connection M1				
Site				N
PA		1	19	20
VI		22	7	22
CS74			5	5
CS73			6	6
CSU		2		2
CMV3		12		12
CMV2			2	1
CMV1			1	1
LCV1			14	14

Table 7: Mesoloph M1

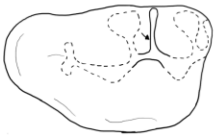
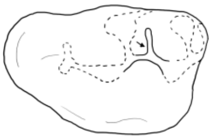
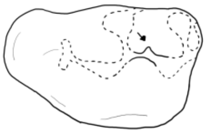
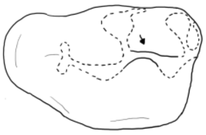
Mesoloph M1					
Site					N
PA	11	6	3		20
VI	18	7	5		30
CS74	1	3	2		5
CS73	2	3	1		6
CSU		2			2
CMV3	8	8	1		17
CMV2	1	1			2
CMV1		1			1
LCV1	9	4	1		14

Table 8: Metalophule M1

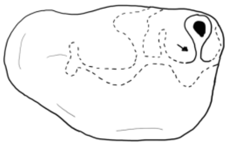
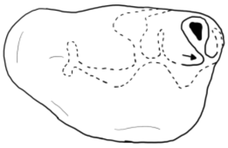
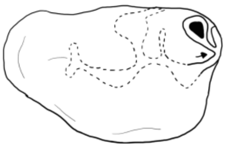
Metalophule M1				
Site				N
PA	1	4	12	17
VI	3	6	19	28
CS74	1	3	1	5
CS73		2	4	6
CSU		2		2
CMV3		6	8	14
CMV2		1	1	2
CMV1		1		1
LCV1		14		14

Table 9: Posterosinus M1

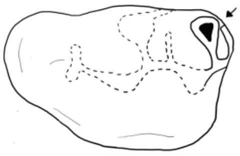
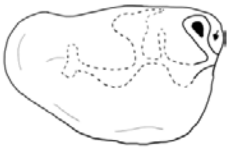
Posterosinus M1				
Site				N
PA	1	19		20
VI	12	16		28
CS74	2	3		5
CS73		6		6
CSU		2		2
CMV3	5	6	3	14
CMV2		2		2
CMV1		1		1
LCV1	7	5	1	13

Table 10: Protolophule M2

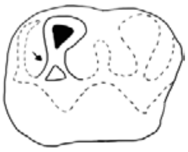
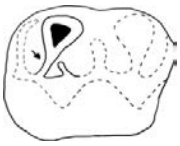
Protolophule M2						
Site						N
PA	13			3	3	16
VI	22	13	3	2	2	38
CS74	1	1				2
CS72	1	1				2
CSU	1					1
CMV3	8	4	1			13
CMV1		1				1
LCV1	10	6			1	17

Table 11: Ectoloph M2

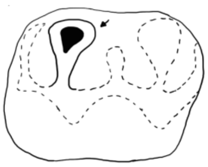
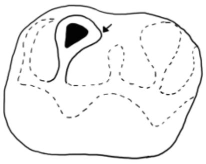
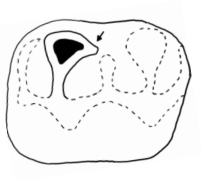
Ectoloph M2				
Site				N
PA	2	7	7	16
VI	14	11	10	35
CS74		2		2
CS72		1	1	2
CSU	1			1
CMV3	4	8	1	13
CMV1			1	1
LCV1	4	9	3	16

Table 12: Ectoloph-Mesoloph connection M2

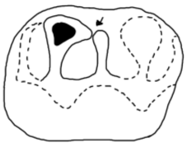
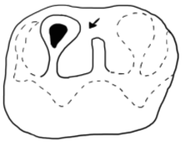
Ectoloph-Mesoloph connection M2			
Site			N
PA	5	11	11
VIO	8	31	39
CS74		2	2
CS72		2	2
CSU		1	1
CMV3		13	13
CMV1		1	1
LCV1		17	17

Table 13: Mesoloph M2

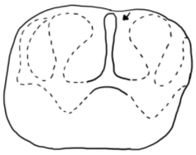
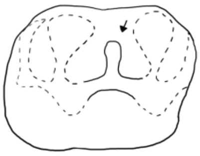
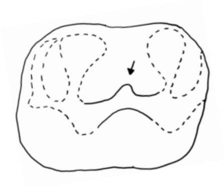
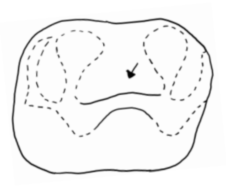
Mesoloph M2					
Site					N
PA	7	9			16
VI	19	20	6		35
CS74		2			2
CS72		2			2
CSU			1		1
CMV3	3	8	3		14
CMV1		1			1
LCV1	7	5	4	1	17

Table 14: Sinus M2

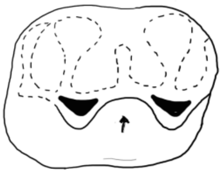
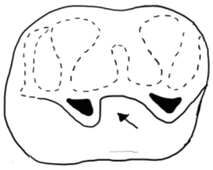
	Sinus M2		
Site			N
PA	12	4	16
VI	30	9	39
CS74	1	1	2
CS72	2		2
CSU	1		1
CMV3		13	13
CMV1	1		1
LCV1		16	16

Table 15: Metalophule M2

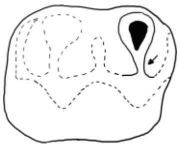
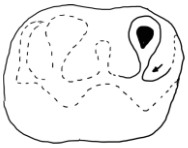
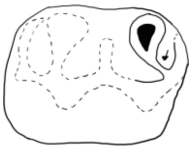
			Metalophule M2		
Site					N
PA	6	6	4		16
VI	7	21	7		35
CS74	1	1			2
CS72	2				2
CSU	1				1
CMV3	12	2			14
CMV1		1			1
LCV1	17				17

Table 16: Anteroconid m1

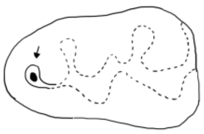
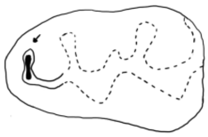
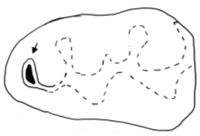
		Anteroconid m1		
Site				N
SM	1			1
PA	4	3		7
VI	25			25
CS74	13	2		15
CS73	3			3
CS72	5			5
CSU	1			1
CMV3	17			17
CMV1	5			5
LCV1	11			11

Table 17: Labial spur on m1 anterolophulid

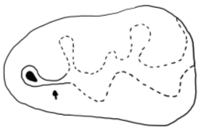
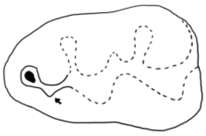
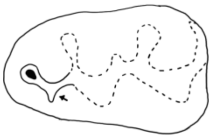
		Labial spur on m1 anterolophulid		
Site				N
SM	1			1
PA	10			10
VI	29			29
CS74	11	6		17
CS73	3			3
CS72	6			6
CSU	1			1
CMV3	21			21
CMV1	5			5
LCV1	17			17

Table 18: Metalophulid m1

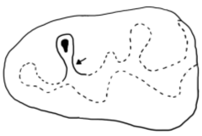
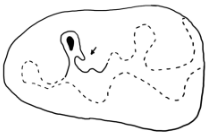
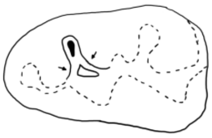
		Metalophulid m1		
Site				N
SM	1			1
PA	10			10
VI	32			32
CS74	17			17
CS73	3			3
CS72	6			6
CSU	1			1
CMV3	20			20
CMV1	5			5
LCV1	17			17

Table 19: Mesolophid m1

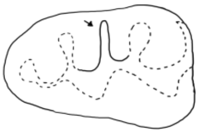
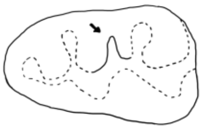
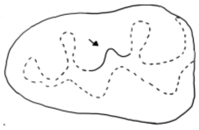
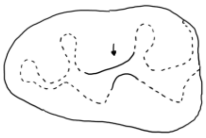
			Mesolophid m1		
Site					N
SM			2		2
PA	6	3	1		10
VI	1	17	7	4	29
CS74	1	2	13	1	17
CS73		2	1		3
CS72		1	4	1	6
CSU			1		1
CMV3		11	7		18
CMV1		4	1		5
LCV1	1	9	7		17

Table 20: Lingual anterolophid lingual m2

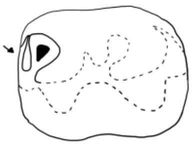
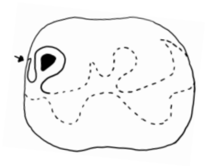
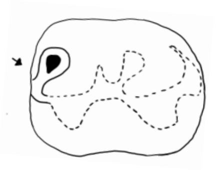
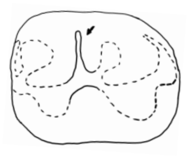
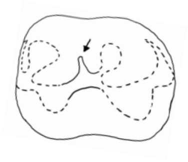
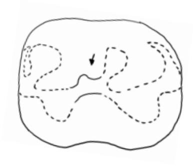
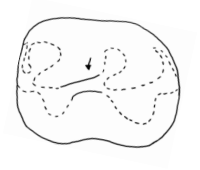
Lingual anterolophid m2				
Site				N
PA	5	10	2	17
VI	8	21	2	31
CS74	2	7	2	11
CS72		3		3
CSU		1		1
CMV3	4	5	2	11
CMV2	1			1
CMV1	1			1
LCV1	3	6	8	17

Table 21: Mesolophid m2

Mesolophid m2					
Site					N
PA	4	12	4		20
VI		24	6	4	34
CS74		2	7	2	11
CS72		2	1		3
CSU		1			1
CMV3		4	5	2	11
CMV2	3				3
CMV1		1			1
LCV1	3	8	5	1	17