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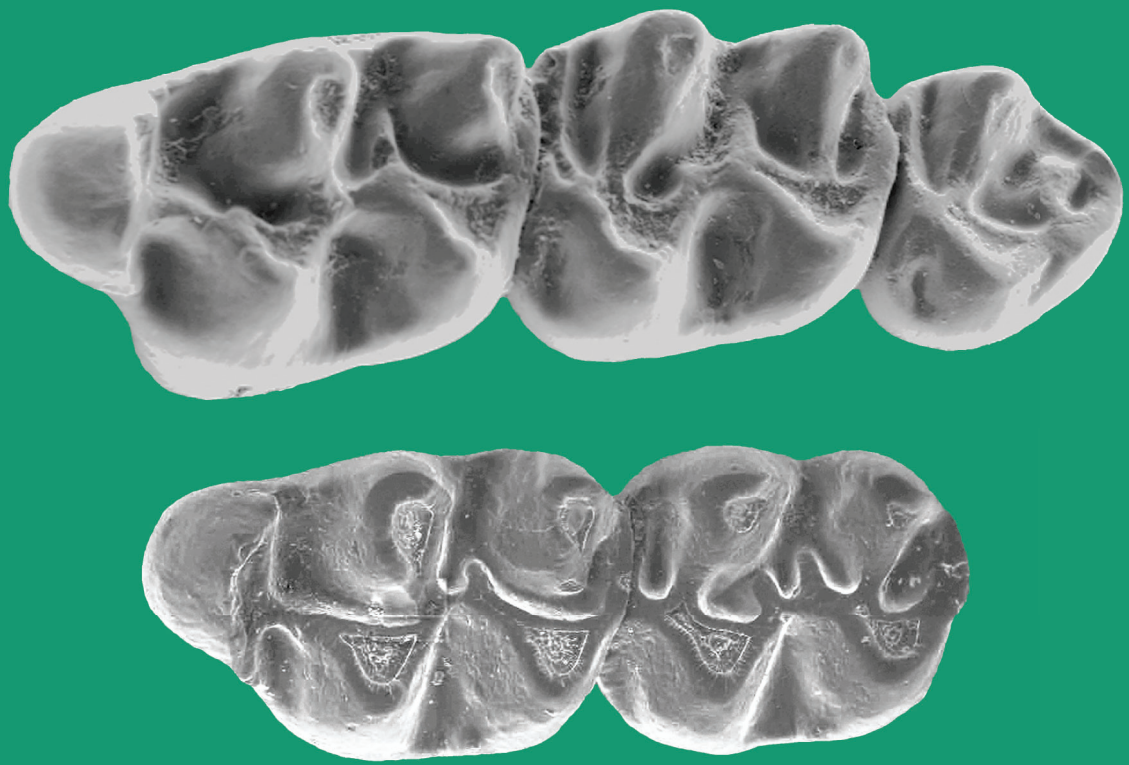

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Scanning electronic microscope (SEM) micrographs of early Miocene Cricetidae from different sites of the Vallès-Penedès Basin. *Democricetodon hispanicus* Freudenthal, 1967

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

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**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* Fahlbusch, 1964 and *Megacricetodon* Fahlbusch, 1964 in the Vallès-Penedès Basin (Catalonia, Spain). *Democricetodon* is represented by four species in the studied sites (*D. hispanicus* Freudenthal, 1967, *D.* cf. *decipiens* (Freudenthal & Daams, 1988), *D. gracilis* Fahlbusch, 1964 and a large-sized undetermined species) and *Megacricetodon* by one (*M. primitivus* (Freudenthal, 1963)). 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.

**KEY WORDS**
*Democricetodon*,
*Megacricetodon*,
early Miocene,
Iberian Peninsula,
biostratigraphy,
western Europe.

**RÉSUMÉ**
*Dispersion et évolution précoce des premiers rongeurs cricétidés modernes en Europe occidentale : nouvelles données du bassin de Vallès-Penedès (Catalogne).*
Les cricétidés modernes sont originaires d'Asie et se sont dispersés en Europe occidentale à la fin du Miocène inférieur. Nous passons ici en revue les signalements du Miocène inférieur des genres *Democricetodon* Fahlbusch, 1964 et *Megacricetodon* Fahlbusch, 1964 du bassin du Vallès-Penedès (Catalogne, Espagne). *Democricetodon* est représenté par quatre espèces (*D. hispanicus* Freudenthal, 1967, *D.* cf. *decipiens* (Freudenthal & Daams, 1988), *D. gracilis* Fahlbusch, 1964 et une espèce indéterminée de grande taille) et *Megacricetodon* par une (*M. primitivus* (Freudenthal, 1963)). La succession de cricétidés 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 révèle également des affinités avec des 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 durant le Miocène inférieur.

**MOTS CLÉS**
*Democricetodon*,
*Megacricetodon*,
Miocène inférieur,
péninsule Ibérique,
biostratigraphie,
Europe occidentale.

## 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 & 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 (Daams *et al.* 1999; Abdul Aziz *et al.* 2008, 2010; Kälin & Kempf 2009; Van der Meulen *et al.* 2012; Casanovas-Vilar *et al.* 2016a; Prieto & Rummel 2016). 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 (Mein 1999; Agustí *et al.* 2001; Hilgen *et al.* 2012).

*Democricetodon* and *Megacricetodon* are two of the first genera commonly referred to as "modern cricetids" (see comments on classification in section Classification of the cricetids) to distinguish them from older muroid taxa that had characterized the Oligocene faunas of Eurasia (e.g. the genera *Eucricetodon* Thaler, 1966, *Pseudocricetodon* Thaler, 1969 and *Melissiodon* Schaub, 1920). Modern cricetids, namely the genera *Spanocricetodon* Li, 1977 and *Primus* de Bruijn *et al.*, 1981, 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 (*c.* 22 Ma) from Anatolia, Pakistan and China (Meng *et al.* 2003; Maridet *et al.* 2011; Flynn & Wessels 2013; Flynn *et al.* 2013). On the other hand, *Megacricetodon* is also first recorded from the early Miocene (*c*. 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 & 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 & Peláez 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 & Freudenthal 1988; Freudenthal & Daams 1988; Van der Meulen *et al.* 2003; Oliver Pérez 2015; Oliver & Peláez-Campomanes 2014, 2016). These genera are also common in other Iberian basins, including the Foia de Bunyol (Daams & Freudenthal 1974; Adrover *et al.* 1987) or the Riu Magre Basin (Ruiz-Sánchez *et al.* 2003), both in Valencia, and 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 & 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.

## GEOLOGICAL SETTING AND AGE

The record of the Vallès-Penedès Basin (Barcelona, Catalonia) covers most of the Miocene, ranging from the Ramblian (*c*. 20 Ma) to the middle Turolian (*c*. 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 & Calvet 1996; Roca *et al.* 1999; Cabrera *et al.* 2004). Major features of the stratigraphic record of the Vallès-Penedès were controlled

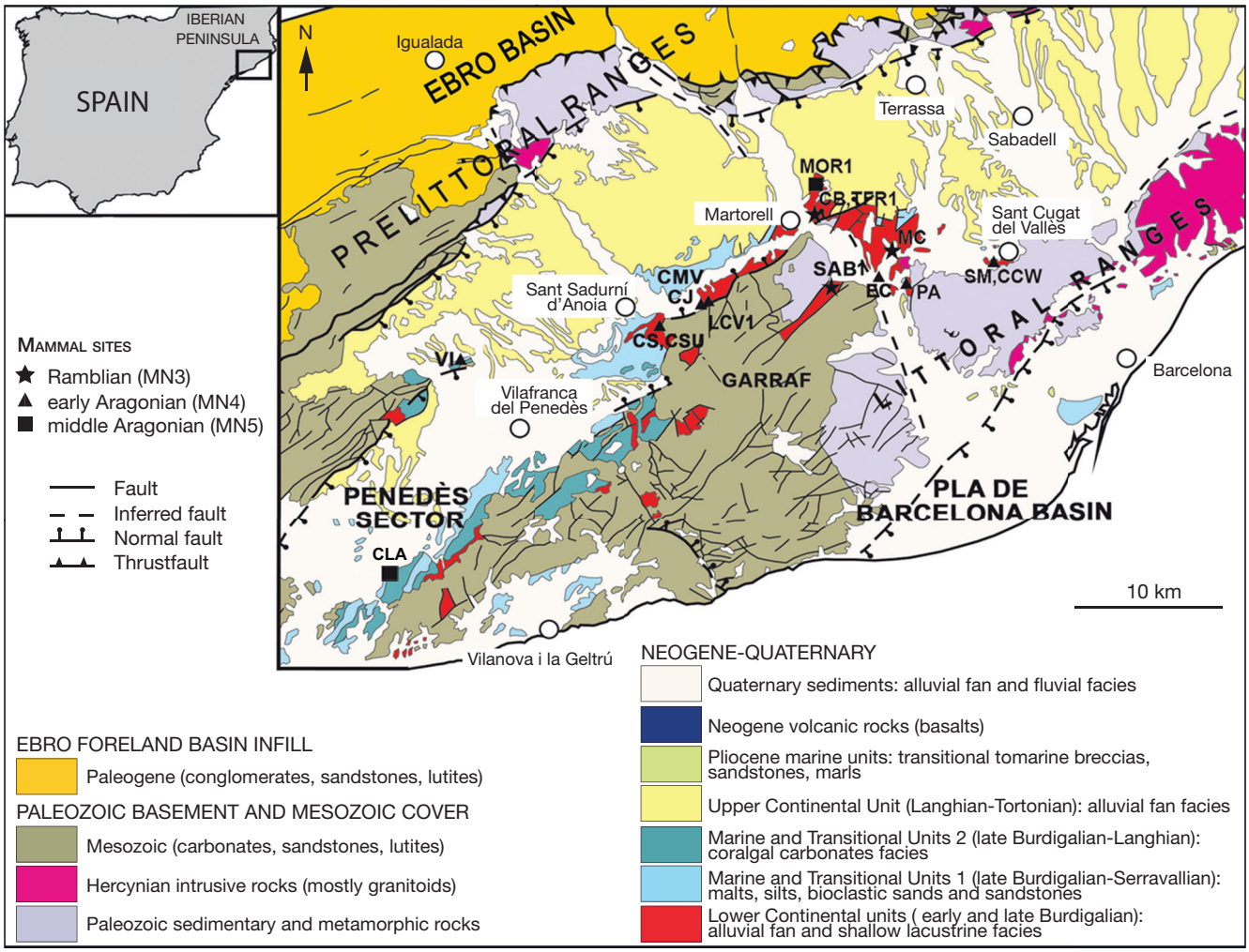


FIG. 1. — Geographical location and simplified geological map of the Vallès-Penedès Basin indicating the main mammal localities ranging from MN3 to MN5 (modified from Casanovas-Vilar *et al.* 2016a, b). For locality acronyms see section Abbreviations of the main text.

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 (*c.* 19.5-17.2 Ma). Ramblian sites correspond to the so-called "cricetid vacuum" (Daams & Freudenthal 1989) and do not include cricetids other than *Melissiodon* (Casanovas-Vilar *et al.* 2011, 2016b; Jovells-Vaqué & 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 & 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 (Cabrera 1979, 1981; Agustí & Cabrera 1980; 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 over 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 & Calvet 1996; de Gibert & Casanovas-Vilar 2011; Casanovas-Vilar *et al.* 2016b). 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 (Ortí & Pueyo 1976; Magné 1978; Agusti *et al.* 1990). 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 ostreids 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 & Calvet 1996; de Gibert & Casanovas-Vilar 2011; Casanovas-Vilar *et al.* 2016b). 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 & Robles 2005; Casanovas-Vilar & 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 Biostratigraphy and correlations). However, the age of these sites will be surely refined after ongoing magnetostratigraphical studies.

## MATERIAL AND METHODS

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* (Freudenthal, 1963) 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 & Peláez-Campomanes (2013), whereas measurement method is after Daams & Freudenthal (1988: 42, fig. 1). Morphotype coding follows Van der Meulen *et al.* (2003) and Maridet (2003) for *Democricetodon* and Oliver & 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).

### Classification of the cricetids

The contents and definition of the cricetid family are a matter of debate. McKenna & 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. Hartenberger 1998; Steppan *et al.* 2004; Wilson & Reeder 2005; Fabre *et al.* 2012, 2015; Steppan & Schenk 2017; D'Elía *et al.* 2019). Recent molecular phylogenetic analyses recognize the Cricetidae as a distinct family from the Muridae, both being part of the larger Muroidea superfamily (Steppan *et al.* 2004; Fabre *et al.* 2012, 2015; Steppan & 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; Steppan *et al.* 2004; Fabre *et al.* 2012, 2015; Steppan & 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* Wood, 1936 (Lindsay 2008). On the other hand, *Megacricetodon* is generally considered to be closer to

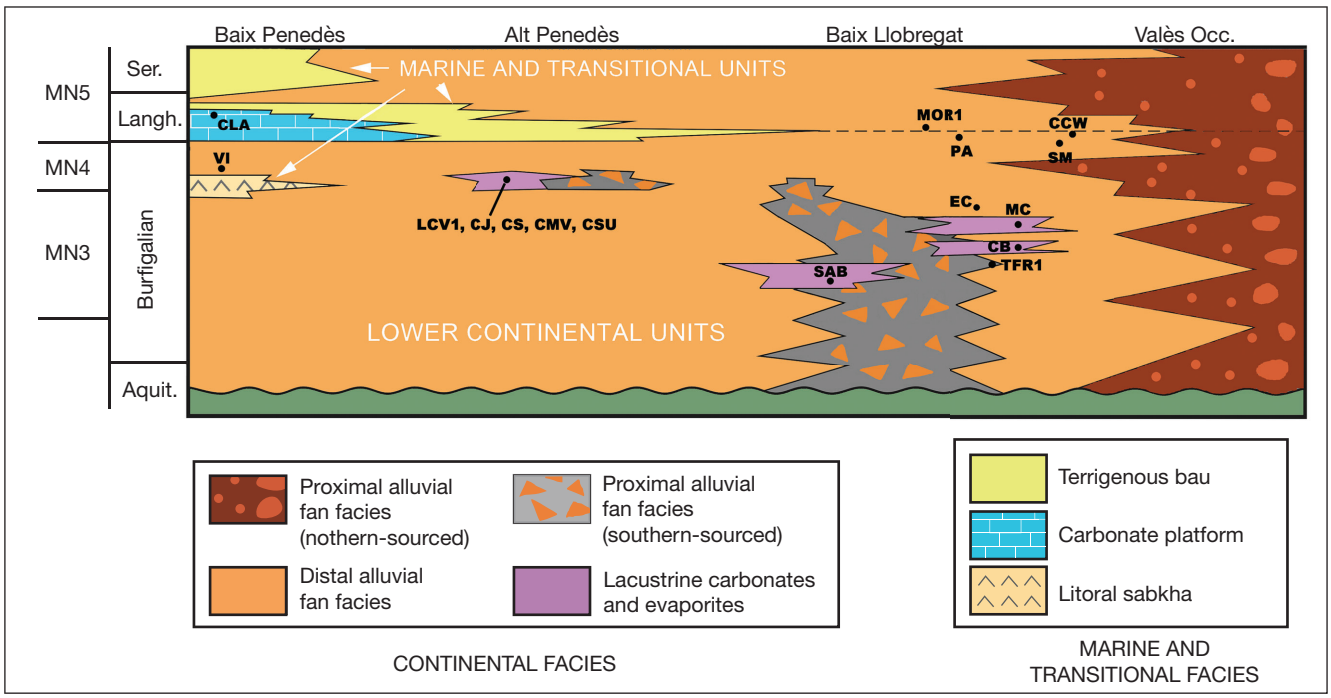


FIG. 2. — Generalized stratigraphic framework of the early to early middle Miocene sedimentary record of the Vallès-Penedès Basin showing the main lithostratigraphic units and their relationships (modified after Cabrera *et al.* 1991 and De Gibert & Casanovas Vilar 2011). Note the different early Miocene lacustrine systems (including most localities) as well as the marine deposits associated to the Langhian transgression. For locality acronyms see section Abbreviations of the main text.

the Muridae (including murines, gerbillines and other minor extant subfamilies) since its dental morphology resembles that of early murids such as *Potwarmus* Lindsay, 1988 and *Antemus* Jacobs, 1977 (Jacobs 1977; Flynn 1985; Lindsay 1988; Jacobs & Down 1994). *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.

## ABBREVIATIONS

*Institutions*

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

*Measurements*

| | |
|---|---|
| L | anteroposterior length; |
| W | labiolingual width. |

*Localities*

| | |
|---|---|
| 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. |

## SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer von Waldheim, 1817
Genus *Democricetodon* Fahlbusch, 1964

***Democricetodon hispanicus*** Freudenthal, 1967
(Figs 3, 4; Table 1; Appendix 2)

A catalog of the studied material and measurements is given in Appendix 1. See Table 1 for summary statistics

and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix 2.

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 2C). 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 2E), 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 2G). 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 2H). 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 2I). 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 2M). 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 2Q). 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* Freudenthal, 1967

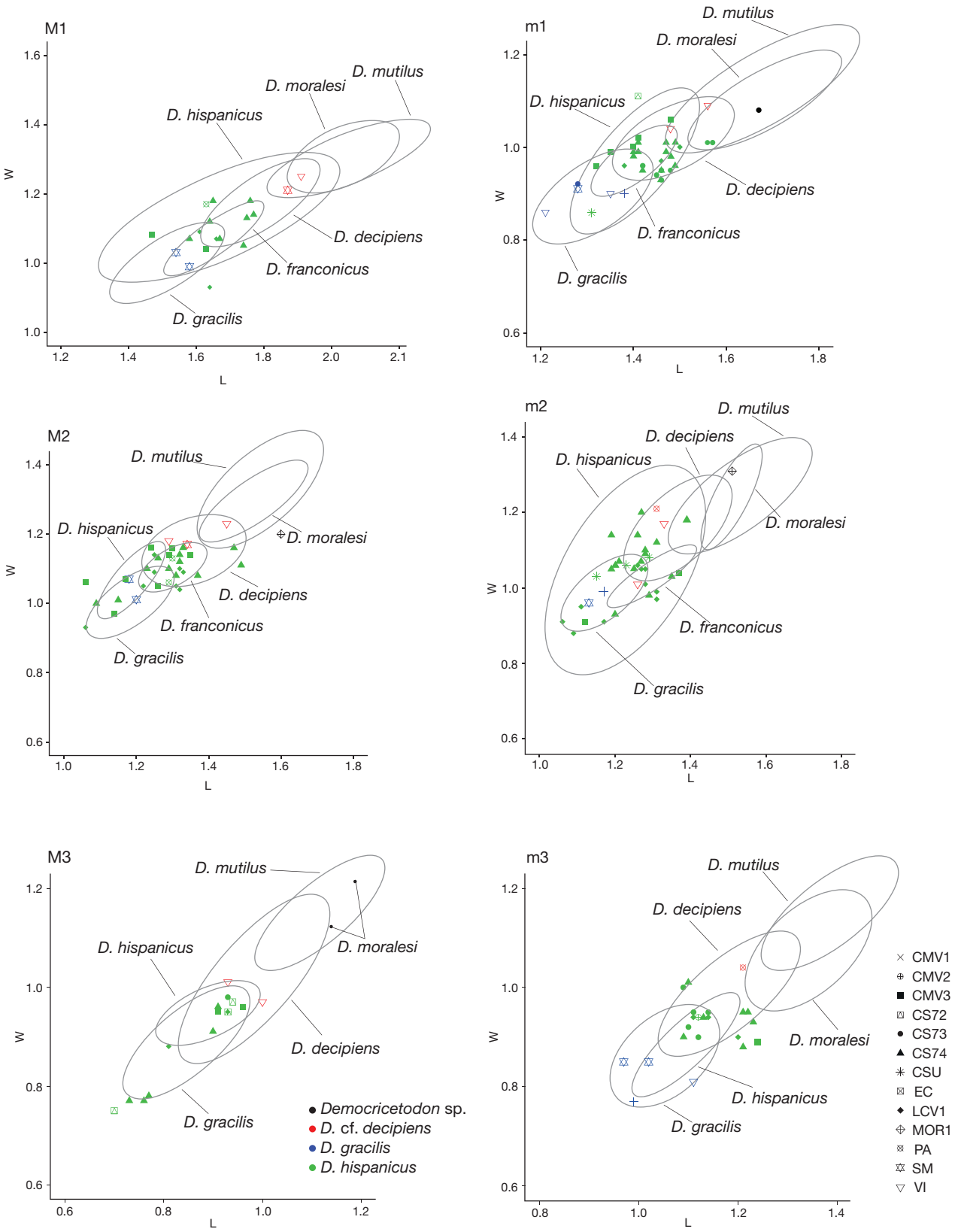


FIG. 3. — Length/width scatter plot for *Democricetodon hispanicus* Freudenthal, 1967, *D. gracilis* Fahlbusch, 1964, *D.* cf. *decipiens* (Freudenthal & Daams, 1988) and *D.* sp. 4 from different Vallès-Penedès sites. Locality acronyms and measurement abbreviations are explained in section Abbreviations of the main text. For details on the measurement methods see section Material and methods, and Daams & Freudenthal (1988: 42, Fig. 1). The ellipses show the 95% confience interval for the following species: *Democricetodon hispanicus* from Villafeliche 2A, *D. moralesi* Van der Meulen *et al.*, 2003 from La Col D and *D. franconicus* Fahlbusch, 1966 from La Col D (data provided by P. Peláez-Campomanes, Museo Nacional de Ciencias Naturales, Madrid), *D. gracilis* and *D. mutilus* Fahlbusch, 1964 from Sandelzhausen (Wessels & Reumer 2009) and *D. decipiens* from Bunyol (Daams & Freudenthal 1974).

(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 & 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 1). 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 2C, G). 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 2C). 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 2E, I). 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 & Daams 1988; Van der Meulen *et al.* 2003), whereas in the Vallès-Penedès material they predominate (Appendix 2C, G). 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 & 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
(Figs 3, 4; Table 1; Appendix 2)

A catalog of the studied material and measurements is given in Appendix 1. See Table 1 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix 2.

#### 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 2C). 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 2E). 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 2G). 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.

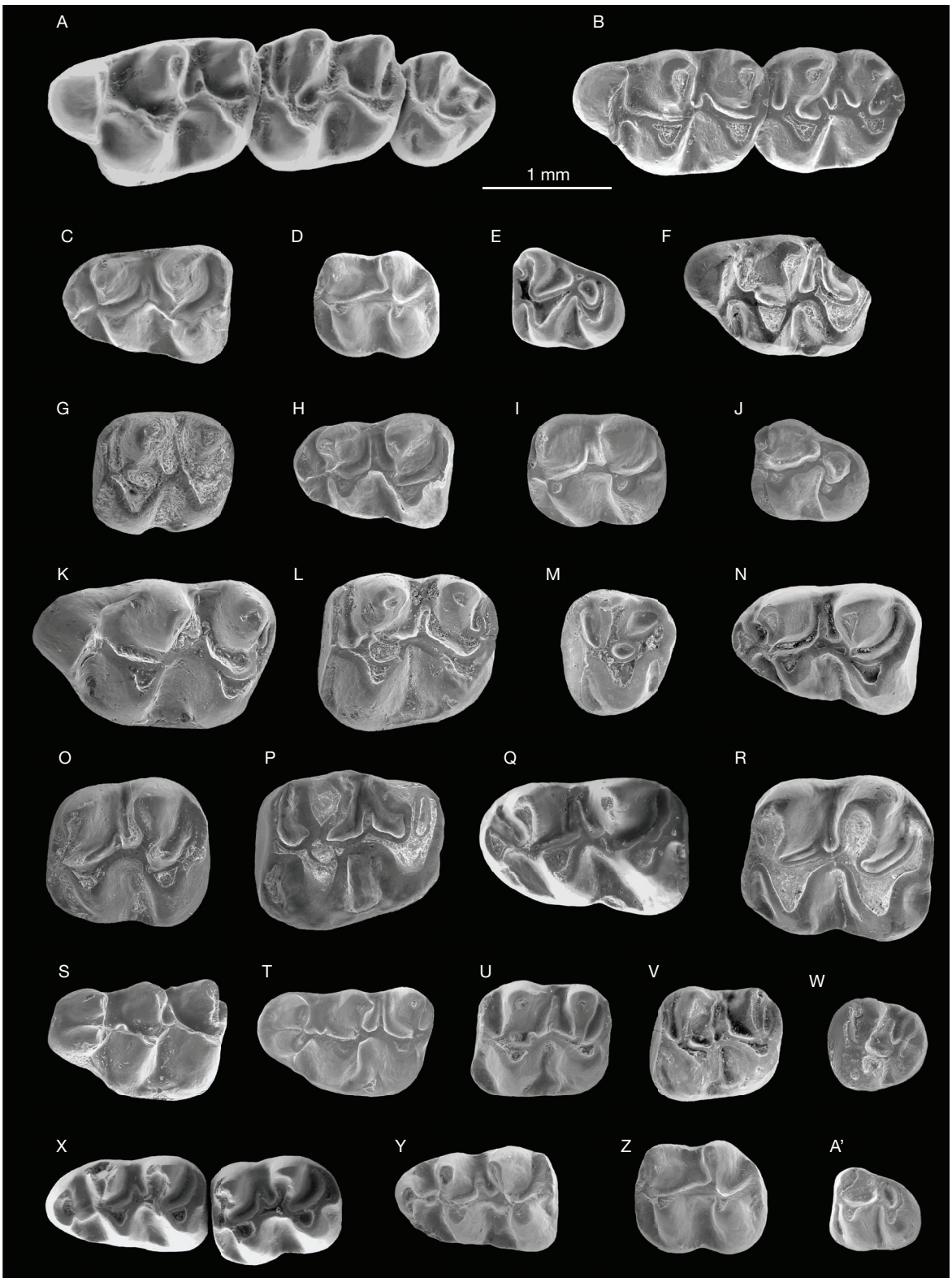


FIG. 4. — Scanning electronic microscope (SEM) micrographs of early Miocene Cricetidae from different sites (indicated in parentheses) of the Vallès-Penedès Basin. *Democricetodon hispanicus* Freudenthal, 1967*:* **A**, IPS45008, right M1-M3 (reversed) (CS74); **B**, IPS19491, right M1-M2 (reversed) (CS74); **C,** IPS19481, left m1 (CS74); **D**, IPS88884 left m2 (LCV1); **E**, IPS86457, right m3 (reversed) (LCV1). *Democricetodon gracilis* Fahlbusch, 1964; **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* (Freudenthal & Daams, 1988); **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* (Freudenthal, 1963); **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 Abbreviations of the main text. Scale bar: 1 mm.

*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 2N). 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 2O). 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 2Q). 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* Fahlbusch, 1964 (see Fahlbusch 1964; Maridet 2003; Wessels & 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 & 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 & 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* (Schaub, 1925) and *D. crusafonti* (Agustí, 1978) (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 Biostratigraphy and correlations), *D. franconicus*, the oldest member of this lineage, appears to be absent.

### *Democricetodon* cf. *decipiens*
(Freudenthal & Daams, 1988)
(Figs 3, 4; Table 1; Appendix 2)

A catalog of the studied material and measurements is given in Appendix 1. See Table 1 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix 2.

TABLE 1. — Summary measurements (in mm) of *Democricetodon hispanicus* Freudenthal, 1967, *D. gracilis* Fahlbusch, 1964, *D.* cf. *decipiens* (Freudenthal & Daams, 1988) 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 Abbreviations of the main text. For details on the measurement methods see section Material and methods, and Daams & Freudenthal (1988: 42, Fig. 1).

| | | L | | | | | W | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Locality** | **Species** | **min.** | **mean** | **max.** | **s.d.** | **N** | **min.** | **mean** | **max.** | **s.d.** | **N** |
| **M1** | | | | | | | | | | | |
| SM | *D.* cf. *decipiens* | – | 1.87 | – | – | 1 | – | 1.20 | – | – | 1 |
| VI | *D.* cf. *decipiens* | – | 1.91 | – | – | 1 | – | 1.25 | – | – | 1 |
| SM | *D. gracilis* | 1.54 | – | 1.58 | – | 2 | 0.99 | – | 1.03 | – | 2 |
| CS74 | *D. hispanicus* | 1.58 | 1.69 | 1.77 | 0.07 | 8 | 1.05 | 1.12 | 1.19 | 0.05 | 10 |
| CMV3 | *D. hispanicus* | 1.47 | 1.52 | 1.63 | – | 3 | 1.04 | 1.05 | 1.08 | – | 3 |
| LCV1 | *D. hispanicus* | 1.61 | 1.64 | 1.66 | – | 3 | 0.93 | 1.03 | 1.09 | – | 3 |
| EC | *D. hispanicus* | – | 1.63 | – | – | 1 | – | 1.17 | – | – | 1 |
| **M2** | | | | | | | | | | | |
| MOR1 | *D.* sp. 4 | – | 1.6 | – | – | 1 | – | 1.2 | – | – | 1 |
| SM | *D.* cf. *decipiens* | – | 1.34 | – | – | 1 | – | 1.17 | – | – | 1 |
| PA | *D.* cf. *decipiens* | – | 1.39 | – | – | 1 | – | – | – | – | - |
| VI | *D.* cf. *decipiens* | 1.29 | – | 1.45 | – | 2 | 1.18 | – | 1.23 | – | 2 |
| SM | *D. gracilis* | 1.18 | – | 1.2 | – | 2 | 1.01 | - | 1.07 | – | 2 |
| CS74 | *D. hispanicus* | 0.93 | 1.25 | 1.49 | 0.16 | 13 | 0.84 | 1.07 | 1.16 | 0.09 | 14 |
| CMV3 | *D. hispanicus* | 1.06 | 1.22 | 1.35 | 0.10 | 8 | 0.97 | 1.09 | 1.16 | 0.07 | 8 |
| LCV1 | *D. hispanicus* | 1.06 | 1.25 | 1.33 | 0.09 | 8 | 0.93 | 1.06 | 1.14 | 0.06 | 8 |
| EC | *D. hispanicus* | 1.29 | – | 1.30 | – | 2 | 1.06 | – | 1.13 | – | 2 |
| **M3** | | | | | | | | | | | |
| VI | *D.* cf. *decipiens* | – | 0.93 | – | – | 1 | – | 1.01 | – | – | 1 |
| CS74 | *D. hispanicus* | 0.73 | 0.84 | 0.91 | – | 3 | 0.77 | 0.88 | 0.96 | – | 3 |
| CS73 | *D. hispanicus* | – | 0.93 | – | – | 1 | – | 0.98 | – | – | 1 |
| CS72 | *D. hispanicus* | 0.7 | – | 0.94 | – | 2 | 0.75 | – | 0.97 | – | 2 |
| CMV3 | *D. hispanicus* | 0.91 | – | 0.96 | – | 2 | 0.95 | – | 0.96 | – | 2 |
| LCV1 | *D. hispanicus* | 0.81 | 0.88 | 0.93 | – | 3 | 0.88 | 0.91 | 0.95 | – | 3 |
| **m1** | | | | | | | | | | | |
| CS73 | *D.* sp. 4 | – | 1.67 | – | – | 1 | – | 1.08 | – | – | 1 |
| VI | *D.* cf. *decipiens* | 1.48 | – | 1.56 | – | – | 0.80 | 0.98 | 1.09 | – | 3 |
| VI | *D. gracilis* | 1.21 | – | 1.35 | – | 2 | 0.86 | – | 0.89 | – | 2 |
| SM | *D. gracilis* | – | 1.28 | – | – | 1 | – | 0.91 | – | – | 1 |
| CS73 | *D. gracilis* | – | 1.28 | – | – | 1 | – | 0.92 | – | – | 1 |
| CCW | *D. gracilis* | – | 1.37 | – | – | 1 | – | 0.90 | – | – | 1 |
| CS74 | *D. hispanicus* | 1.4 | 1.44 | 1.49 | 0.03 | 12 | 0.93 | 0.97 | 1.01 | 0.02 | 12 |
| CS73 | *D. hispanicus* | 1.42 | 1.48 | 1.57 | 0.05 | 8 | 0.94 | 0.98 | 1.11 | 0.05 | 8 |
| CSU | *D. hispanicus* | – | 1.31 | – | – | 1 | – | 0.86 | – | – | 1 |
| CMV3 | *D. hispanicus* | 1.32 | 1.39 | 1.48 | – | 5 | 0.96 | 1.01 | 1.06 | – | 5 |
| LCV1 | *D. hispanicus* | 1.38 | 1.45 | 1.50 | - | 3 | 0.96 | 0.98 | 1.00 | - | 3 |
| **m2** | | | | | | | | | | | |
| MOR1 | *D.* sp. 4 | – | 1.51 | – | – | 1 | – | 1.31 | – | – | 1 |
| PA | *D.* cf. *decipiens* | – | 1.31 | – | – | 1 | – | 1.21 | – | – | 1 |
| VI | *D.* cf. *decipiens* | 1.26 | – | 1.33 | – | 2 | 1.01 | 1.12 | 1.17 | – | 3 |
| SM | *D. gracilis* | – | 1.13 | – | – | 1 | – | 0.96 | – | – | 1 |
| CCW | *D. gracilis* | – | 1.17 | – | – | 1 | – | 0.99 | – | – | 1 |
| CS74 | *D. hispanicus* | 1.19 | 1.26 | 1.39 | 0.06 | 15 | 0.93 | 1.07 | 1.20 | 0.07 | 15 |
| CSU | *D. hispanicus* | 1.15 | 1.22 | 1.29 | – | 3 | 1.03 | 1.05 | 1.07 | – | 3 |
| CMV3 | *D. hispanicus* | – | 1.12 | – | – | 1 | – | 0.91 | – | – | 1 |
| LCV1 | *D. hispanicus* | 1.06 | 1.21 | 1.31 | 0.1 | 10 | 0.88 | 0.97 | 1.05 | 0.07 | 10 |
| **m3** | | | | | | | | | | | |
| PA | *D.* cf. *decipiens* | – | 1.21 | – | – | 1 | – | 1.04 | – | – | 1 |
| VI | *D. gracilis* | – | 1.11 | – | – | 1 | – | 0.81 | – | – | 1 |
| SM | *D. gracilis* | 0.97 | – | 1.02 | – | 2 | – | 0.85 | – | – | 2 |
| CCW | *D. gracilis* | – | 0.99 | – | – | 1 | – | 0.77 | – | – | 1 |
| CS74 | *D. hispanicus* | 1.09 | 1.17 | 1.23 | 0.05 | 7 | 0.88 | 0.92 | 0.95 | 0.02 | 6 |
| CS73 | *D. hispanicus* | 1.09 | 1.11 | 1.14 | 0.02 | 5 | 0.9 | 0.94 | 1 | 0.03 | 5 |
| CMV3 | *D. hispanicus* | – | 1.24 | – | – | 1 | – | 0.89 | – | – | 1 |
| CMV2 | *D. hispanicus* | – | 1.12 | – | – | 1 | – | 0.94 | – | – | 1 |
| LCV1 | *D. hispanicus* | 1.11 | 1.14 | 1.19 | – | 3 | 0.899 | 0.92 | 0.94 | – | 3 |

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 2B). 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 2G). 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 2K), 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 2K-N).

*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 2). 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 2N, Q). 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* (Freudenthal & Daams, 1988), *Democricetodon jordensi* Van der Meulen *et al.*, 2003 and *Democricetodon lacombai* (Freudenthal & Daams, 1988). 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

(Figs 3, 4; Table 1; Appendix 2)

A catalog of the studied material and measurements is given in Appendix 1. See Table 1 for summary statistics and comparisons. See also Figure 3 for measurements and comparisons. Morphotype frequency tables are given in Appendix 2.

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 & 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 & Reumer 2009). Interestingly, the CS73 m1 had been previously ascribed to the genus *Fahlbuschia* Mein & Freudenthal, 1971 (Agustí & 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 Biostratigraphy and correlations) *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 & Kempf 2009) and German sites (Wessels & 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
(Figs 4, 5; Table 2; Appendix 4)

A catalog of the studied material and measurements is given in Appendix 3. See Table 2 for summary statistics and comparisons. See also Figure 5 for measurements and comparisons. Morphotype frequency tables are given in Appendix 4.

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 4A). 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

TABLE 2. — Summary measurements (in mm) of *Megacricetodon primitivus* (Freudenthal, 1963) from different early Miocene sites of the Vallès-Penedès Basin. Only complete specimens were measured. Locality acronyms and measurement abbreviations are explained in section Abbreviations of the main text. For details on the measurement methods see section Material & methods, and Daams & Freudenthal (1988: 42, Fig. 1).

| | L | | | | | W | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Locality** | **min.** | **mean** | **max.** | **s.d.** | **N** | **min.** | **mean** | **max.** | **s.d.** | **N** |
| **M1** | | | | | | | | | | |
| 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 |
| **M2** | | | | | | | | | | |
| 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 |
| **M3** | | | | | | | | | | |
| 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 |
| **m1** | | | | | | | | | | |
| 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 |
| **m2** | | | | | | | | | | |
| 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 |
| **m3** | | | | | | | | | | |
| 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 |

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 4C). 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

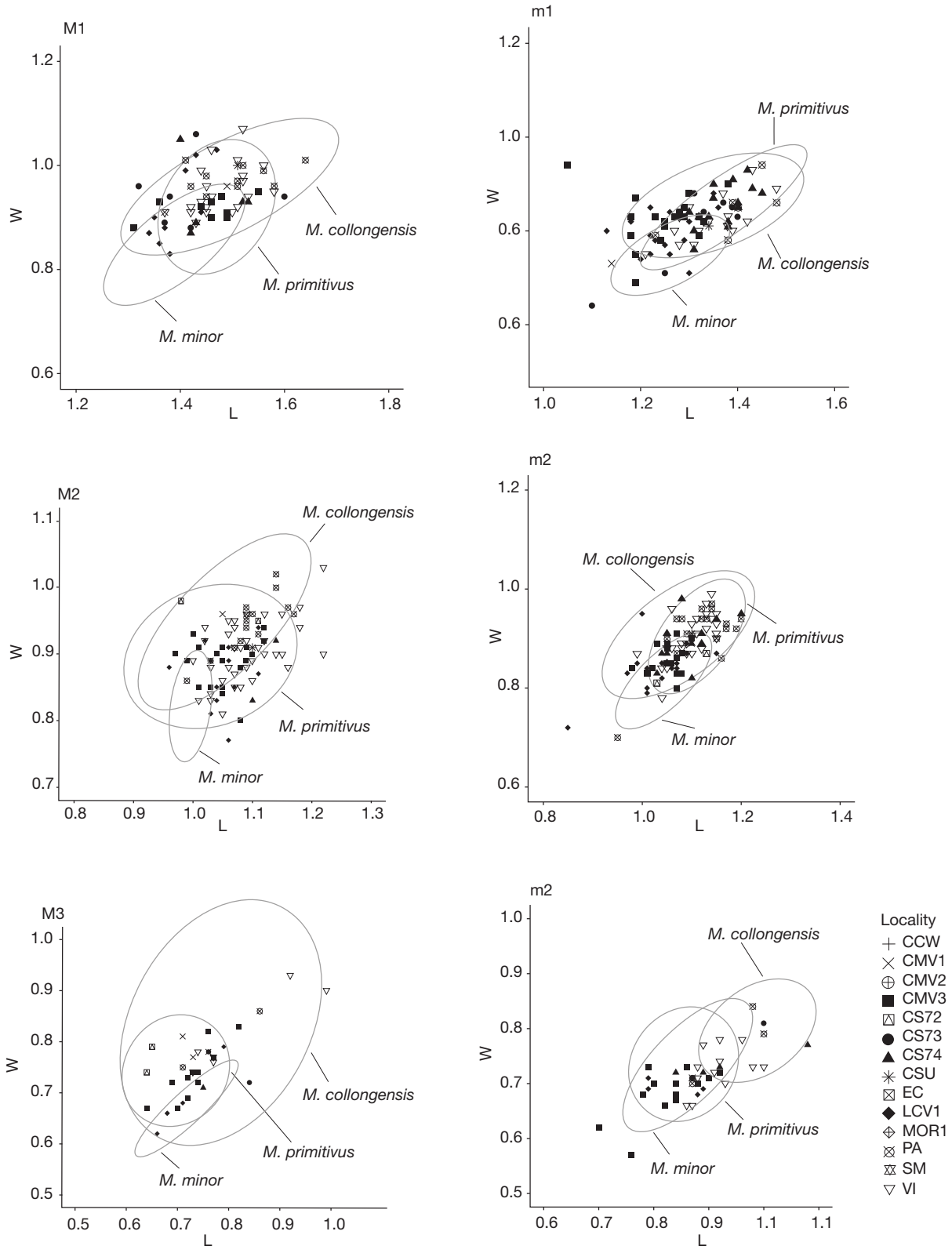


FIG. 5. — Length/width scatter plot for *Megacricetodon primitivus* (Freudenthal, 1963) from different Vallès-Penedès sites. Locality acronyms and measurement abbreviations are explained in section Abbreviations of the main text. For details on the measurement methods see section Material and methods, and Daams & Freudenthal (1988: 42, fig. 1). The ellipses show the 95% confience interval for *Megacricetodon primitivus* (Oliver & Peláez-Campomanes 2014), *M. minor* (Lartet, 1851) (Wessels & Reumer 2009) and *M. collongensis* (Mein, 1958).

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 4L), 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 4O). 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 4N).

*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 4P). 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 4Q). 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 & Freudenthal 1988; Oliver Pérez 2015; Oliver & 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 & 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 & 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.

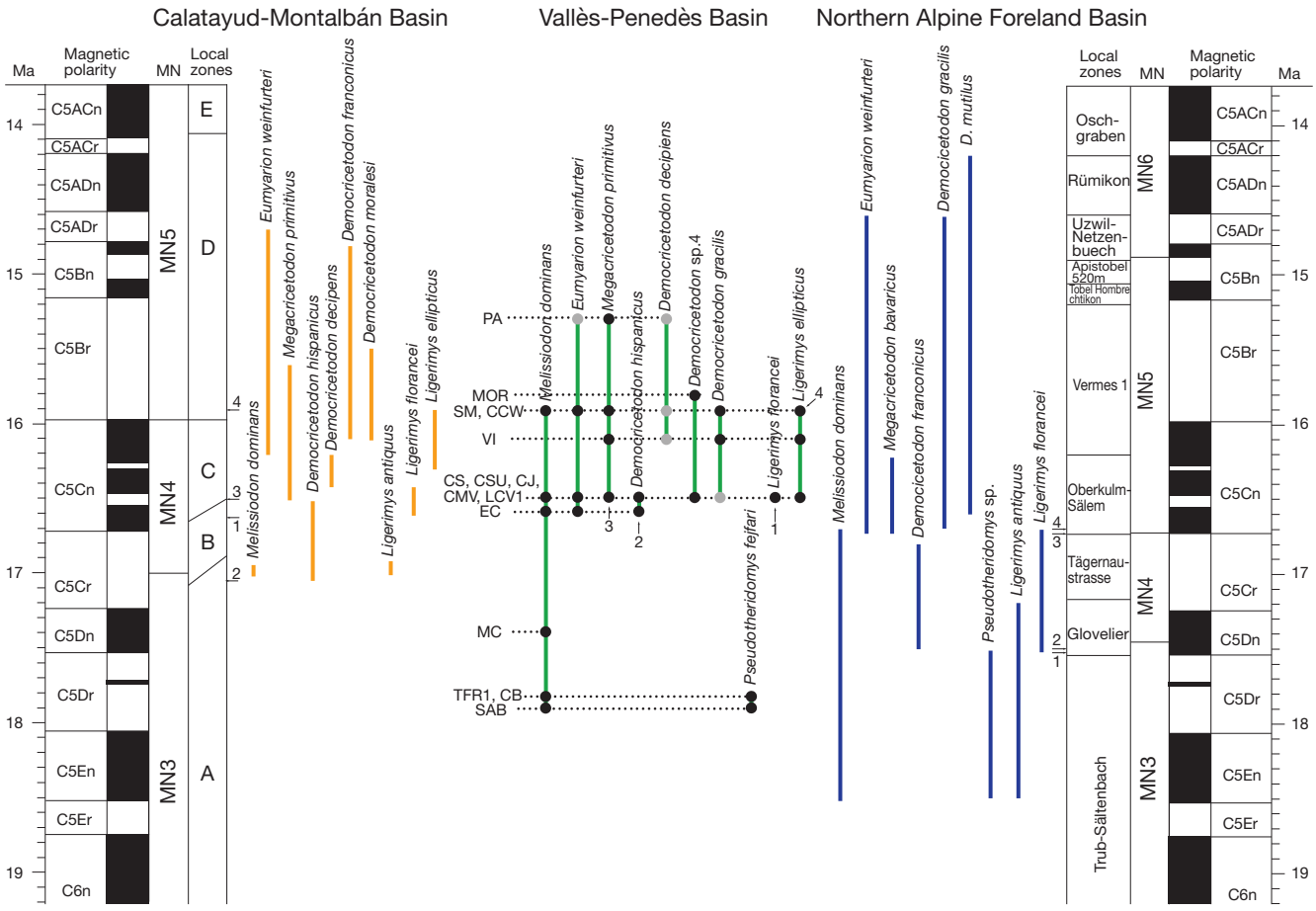


FIG. 6. — Biostratigraphic distribution of the early Miocene cricetid species in the Vallès-Penedès Basin. Selected eomyid taxa are also included because of their use in biostratigraphical correlation. Black dots represent the occurrence of a taxon in a given site while grey dots indicate uncertain attribution 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 & 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 Abbreviations of the main text. Black indicate normal magnetic polarity chrons, white indicate inversed magnetic polarity chrons.

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 & Freudenthal 1988; Oliver & 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 & Freudenthal 1988; Oliver & 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 & 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 *et al.* 2008, 2015; Oliver & 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 & Peláez-Campomanes 2014). Its disappearance coincides with the first record of additional, larger-sized *Megacricetodon* species in the region, such as *Megacricetodon vandermeuleni* (Oliver & 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 (Oliver & 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 & Peláez-Campomanes 2014: table 10).

## DISCUSSION

### 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 & 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 & 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* Thaler, 1966; and 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 & 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 (*c.* 19.5-16.77 Ma; Daams & 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 & 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* Stehlin & Schaub, 1951 and (more infrequently) *Pseudotheridomys* Schlosser, 1926.

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 & 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* Daams, 1976 characterizes zone C (16.49-15.93 Ma) together with the first appearance of *Megacricetodon* (*M. primitivus*) and *Eumyarion* (Daams & 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* Stehlin & Schaub, 1951 by *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 & 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* (Schaub & Zapfe, 1953)) 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.

## 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 *et al.* 2005, 2008; Casanovas-Vilar & Agusti 2007; 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 & 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 & 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 insectivores (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 & 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* Pomel, 1848 and the talpid *Desmanodon* Engesser, 1980 besides a few more genera (such as *Heterosorex* Gaillard, 1915 and *Miosorex* Kretzoi, 1959) (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.* 2020). 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.* 2020). The presence of dimylids (*Plesiodimylus* Gaillard, 1897, *Chainodus* Ziegler, 1990), 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 & 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* Marković *et al.*, 2016, *Miopetaurista* Kretzoi, 1962), semiaquatic castorids (*Steneofiber* Geoffroy-Saint-Hilaire, 1833), and several other "cricetids" including *Anomalomys* Gaillard, 1900, *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 & Casanovas-Vilar 2018). In addition, presumably arboreal glirids (characterized by molars with many transverse ridges, e.g. *Muscardinus* Kaup, 1829, *Glis* Brisson, 1762, *Glirudinus* De Bruijn, 1966; see Van der Meulen & 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* De Bruijn, 1966, only recorded at Turó de les Forques – level 1 and Costablanca (Ramblian, MN3), and *Simplomys simplicidens* (de Bruijn, 1966), 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* Ognev, 1924; see Van der Meulen & 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 & Peláez-Campomanes 2016). On the other hand, *Democricetodon gracilis* is a common component of central European faunas (Daxner-Höck *et al.* 1998; Maridet 2003; Abdul Aziz *et al.* 2008, 2010; Kälin & Kempf 2009; Wessels & Reumer 2009). Other "cricetids" shared with central Europe include *Eumyarion weinfurteri* and *Melissiodon dominans* Dehm, 1950. 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* Daams & Freudenthal, 1974, which also occurs in Valencia (Daams & 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 & 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 & Daams 1992; Van Dam & Weltje 1999; Van Dam 2006; Casanovas-Vilar & Agusti 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 & Weltje 1999; Casanovas-Vilar & 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* (Schaub, 1925), *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; Van Dam 2006; Casanovas-Vilar & Agustí 2007). 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 & 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 & 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.

## 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 (crown) 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 & 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 *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. By contrast, *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.

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Appendix 1. — Catalogue number and length and width measurements (in mm) of *Democricetodon hispanicus* Freudenthal, 1967*, D. gracilis* Fahlbusch, 1964, *D.* cf. *decipiens* (Freudenthal & Daams, 1988) and *Democricetodon* sp. 4 from different early Miocene sites of the Vallès-Penedès Basin. Locality acronyms and measurement abbreviations are explained in section Abbreviations of the main text. For details on the measurement methods see section Material and methods, and Daams & Freudenthal (1988: 42, fig. 1): https://doi.org/10.5852/cr-palevol2021v20a22_s1

Appendix 2. — Morphotype frequency tables for the *Democricetodon* Fahlbusch, 1964 species. For locality acronyms see section Abbreviations of the main text. For details on morphotype coding see section Material and methods, and references therein.

Appendix 2A. — Anterocone M1.

| | | Anterocone M1 | | |
|---|---|---|---|---|
| **Species** | **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 |

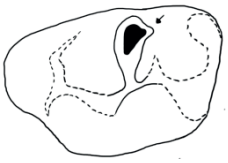
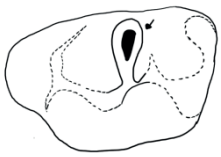
Appendix 2B. — Anterolophule M1.

| | | Anterolophule M1 | | | |
|---|---|---|---|---|---|
| **Species** | **Site** | | | | **N** |
| | SM | – | 1 | – | 1 |
| ***D. decipiens*** | VI | 1 | – | – | 1 |
| ***D. gracilis*** | SM | 2 | – | – | 2 |
| | CS74 | 8 | 1 | – | 9 |
| | CMV3 | 5 | – | – | 5 |
| ***D. hispanicus*** | LCV1 | – | – | 1 | 1 |
| | EC | 1 | – | – | 1 |

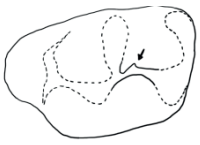
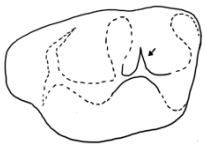
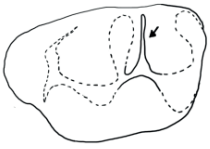
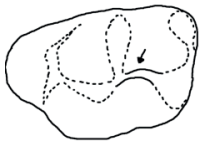
Appendix 2C. — Protolophule M1.

| | | Protolophule M1 | | | |
|---|---|---|---|---|---|
| **Species** | **Site** | | | | **N** |
| ***D. decipiens*** | SM | 1 | – | – | 1 |
| | VI | 1 | – | – | 1 |
| ***D. gracilis*** | SM | – | 2 | – | 2 |
| | CS74 | 7 | 2 | – | 9 |
| | CMV3 | 2 | 3 | – | 5 |
| ***D. hispanicus*** | LCV1 | 1 | – | – | 1 |
| | EC | – | 1 | – | 1 |

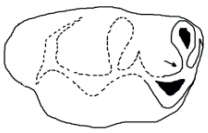
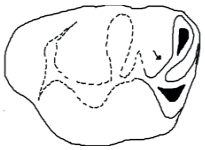
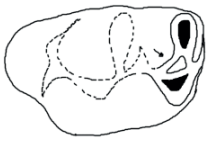
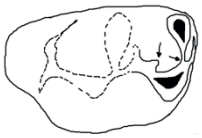
Appendix 2D. — Ectoloph on the Paracone M1.

| | | Ectoloph on the Paracone M1 | | |
|---|---|---|---|---|
| | |  |  | |
| **Species** | **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 |

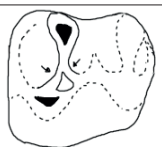
Appendix 2E. — Mesoloph M1.

| | | Mesoloph M1 | | | | |
|---|---|---|---|---|---|---|
| | |  |  |  |  | |
| **Species** | **Site** | | | | | **N** |
| ***D. decipiens*** | SM | 1 | – | – | – | 1 |
| | VI | 1 | – | – | – | 1 |
| ***D. gracilis*** | SM | – | – | 2 | – | 2 |
| ***D. hispanicus*** | CS74 | 4 | 5 | – | – | 9 |
| | CMV3 | – | – | 4 | – | 4 |
| | LCV1 | – | – | 2 | – | 2 |
| | EC | – | 1 | – | – | 1 |

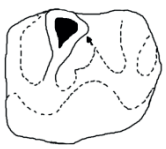
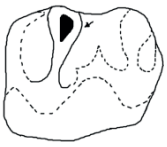
Appendix 2F. — Metalophule M1.

| | | Metalophule M1 | | | | |
|---|---|---|---|---|---|---|
| | |  |  |  |  | |
| **Species** | **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 |

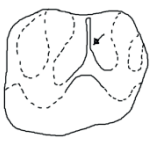
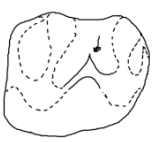
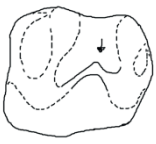
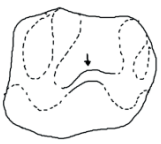
Appendix 2G. — Protolophule M2.

| | | Protolophule M2 | | | | | |
|---|---|---|---|---|---|---|---|
| | |  |  |  |  |  | |
| **Species** | **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 |

Appendix 2H. — Ectoloph on the Paracone M2.

| | | Ectoloph on the Paracone M2 | | |
|---|---|---|---|---|
| | |  |  | |
| **Species** | **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 |

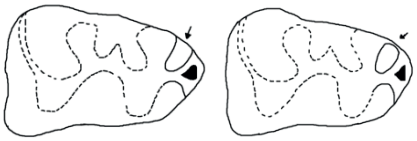
Appendix 2I. — Mesoloph M2.

| | | Mesoloph M2 | | | | |
|---|---|---|---|---|---|---|
| | |  |  |  |  | |
| **Species** | **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 | – | 12 |
| | CMV3 | 6 | 1 | – | – | 7 |
| | LCV1 | 2 | – | – | – | 2 |
| | EC | 1 | – | 2 | – | 3 |

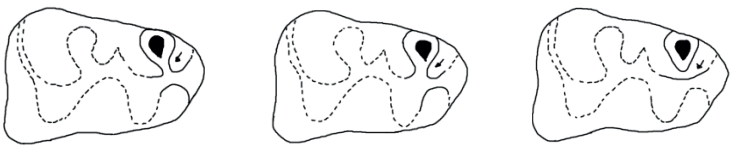
Appendix 2J. — Metalophule M2.

| | | Metalophule M2 | | | | | |
|---|---|---|---|---|---|---|---|
| | |  | | | | | |
| **Species** | **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 |

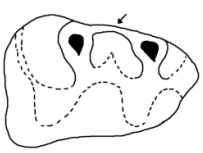
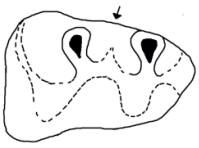
Appendix 2K. — Lingual Anterolophid m1.

| | | Lingual Anterolophid m1 | | |
|---|---|---|---|---|
| | |  | | |
| **Species** | **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 | – |
| | CS72 | 2 | 6 | 8 |
| | CSU | 1 | – | 1 |
| | CMV3 | 4 | – | 4 |
| | CMV1 | 1 | – | 1 |
| | LCV1 | 6 | – | 6 |

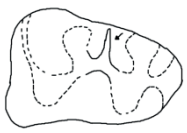
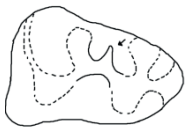
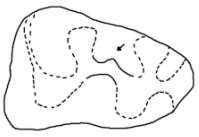
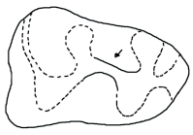
Appendix 2L. — Metalophulid m1.

| | | Metalophulid m1 | | | |
|---|---|---|---|---|---|
| | |  | | | |
| **Species** | **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 |

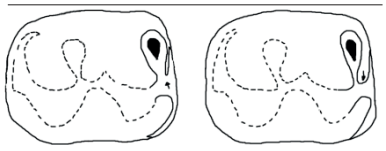
Appendix 2M. — Metaconid ridge m1.

| | | Metaconid ridge m1 | | |
|---|---|---|---|---|
| | |  |  | |
| **Species** | **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 |
| | CS74 | – | 12 | 12 |
| ***D. hispanicus*** | CS72 | – | 8 | 8 |
| | CSU | – | 1 | 1 |
| | CMV3 | – | 4 | 4 |
| | CMV1 | 1 | – | 1 |
| | LCV1 | – | 6 | 6 |

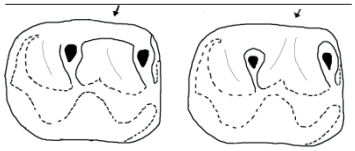
Appendix 2N. — Mesolophid m1

| | | Mesolophid m1 | | | | |
|---|---|---|---|---|---|---|
| | |  |  |  |  | |
| **Species** | **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 |

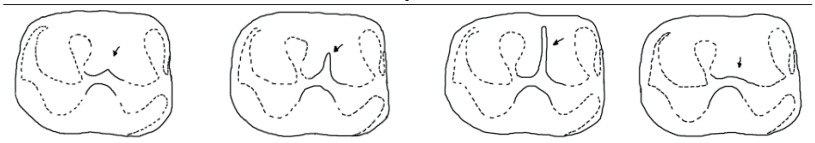
Appendix 2O. — Anterosinusid m2

| Species | Site | Anterosinusid m2 | | 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 |

Appendix 2P. — Metaconid ridge m2

| Species | Site | Metaconid ridge m2 | | 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 |

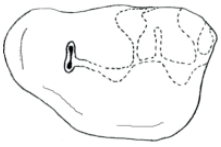
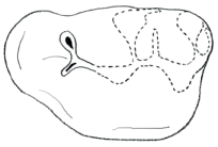
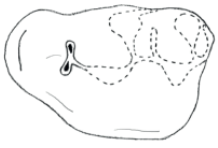
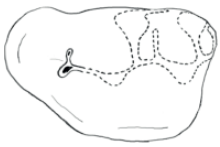
Appendix 2Q. — Mesolophid m2

| Species | Site | Mesolophid m2 | | | | 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 |

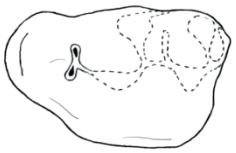
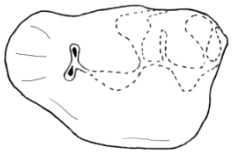
Appendix 3 — Catalogue number and length and width measurements (in mm) of *Megacricetodon primitivus* (Freudenthal, 1963) from different early Miocene sites of the Vallès-Penedès Basin. Locality acronyms and measurement abbreviations are explained in section Abbreviations of the main text. For details on the measurement methods see section Material and methods, and Daams & Freudenthal (1988: 42, fig. 1): https://doi.org/10.5852/cr-palevol2021v20a22_s2

Appendix 4. — Morphotype frequency tables for *Megacricetodon primitivus* (Freudenthal, 1963). For locality acronyms see section Abbreviations of the main text. For details on morphotype coding see section Material and methods, and references therein.

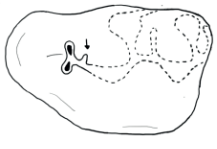
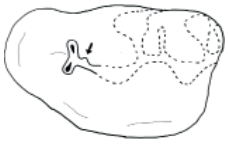
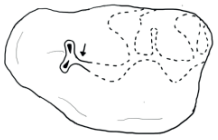
Appendix 4A. — Anterocone M1.

| | 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 |

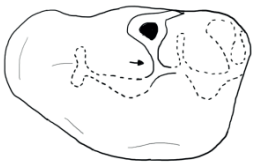
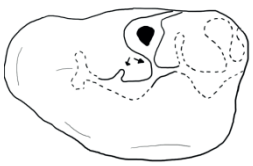
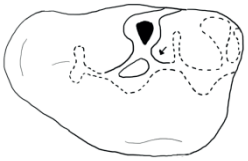
Appendix 4B. — Anterior platform of the M1 anterocone.

| | 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 |

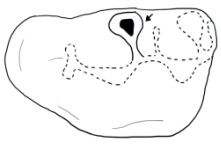
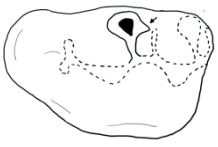
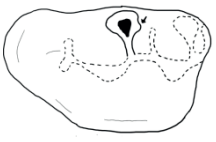
Appendix 4C. — Labial spur of the M1 anterolophule.

| Site | Labial spur of the M1 anterolophule | | | 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 |

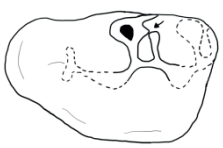
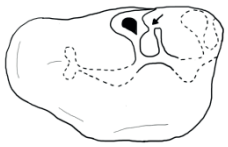
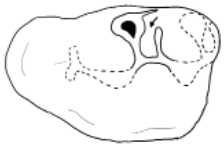
Appendix 4D. — Protolophule M1.

| Site | Protolophule M1 | | | N |
|---|---|---|---|---|
| |  |  |  | |
| **PA** | 20 | – | – | – |
| **VI** | 29 | – | 1 | – |
| **CS74** | 5 | – | – | 5 |
| **CS73** | 6 | – | – | 6 |
| **CSU** | 2 | – | – | 2 |
| **CMV3** | 12 | – | – | – |
| **CMV2** | 2 | – | – | 2 |
| **CMV1** | 1 | – | – | 1 |
| **LCV1** | 14 | – | – | – |

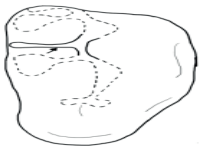
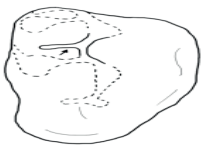
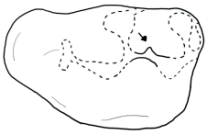
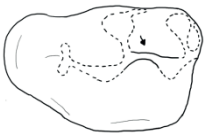
Appendix 4E. — Ectoloph M1.

| Site | Ectoloph M1 | | | 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 |

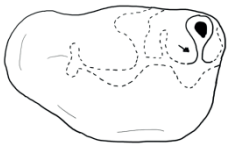
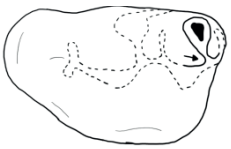
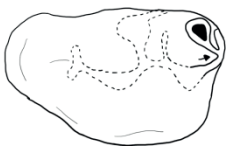
Appendix 4F. — Ectoloph-Mesoloph connection M1.

| | 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 |

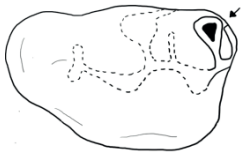
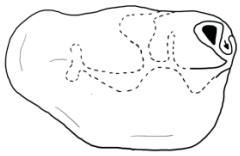
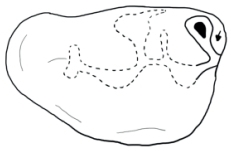
Appendix 4G. — Mesoloph M1.

| | 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 |

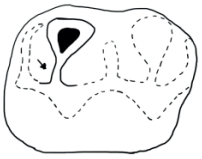
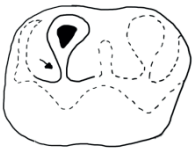
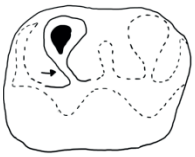
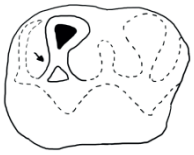
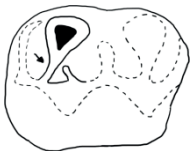
Appendix 4H. — Metalophule M1.

| | 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 |

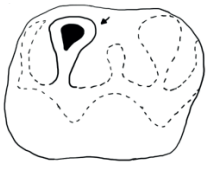
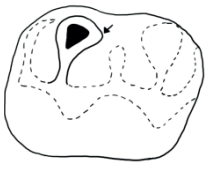
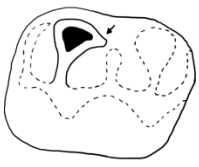
Appendix 4I. — Posterosinus M1

| | 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 |

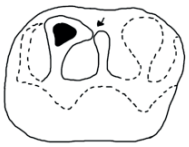
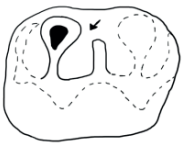
Appendix 4J. — Protolophule M2.

| | 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 |

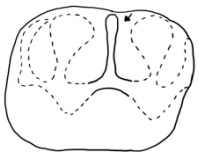
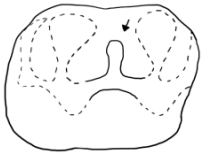
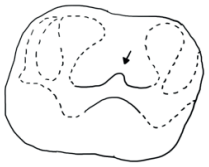
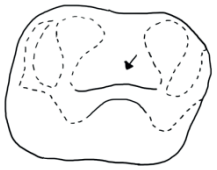
Appendix 4K. — Ectoloph M2.

| | 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 |

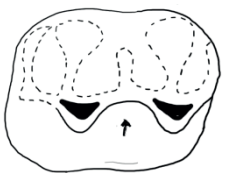
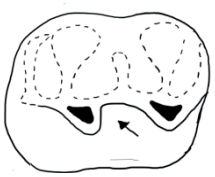
Appendix 4L. — Ectoloph-Mesoloph connection M2.

| Site | Ectoloph-Mesoloph connection M2  |  | 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 |

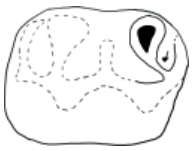
Appendix 4M. — Mesoloph M2.

| Site | Mesoloph M2  |  |  |  | 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 |

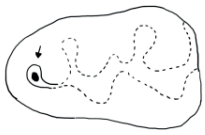
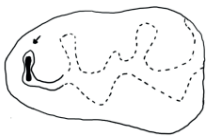
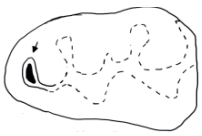
Appendix 4N. — Sinus M2.

| Site | Sinus M2  |  | 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 |

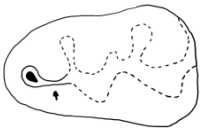
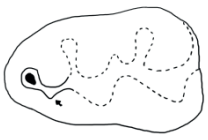
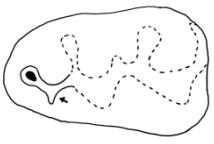
Appendix 4O. — Metalophule M2.

| | 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 |

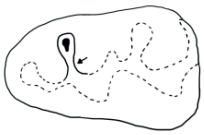
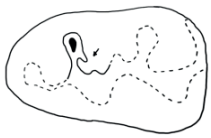
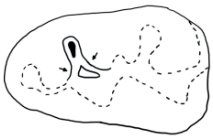
Appendix 4P. — Anteroconid m1.

| | 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 |

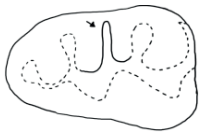
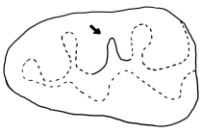
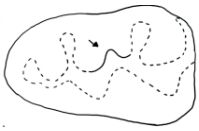
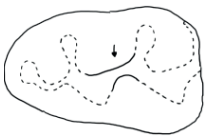
Appendix 4Q. — Labial spur on m1 anterolophulid.

| | 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 |

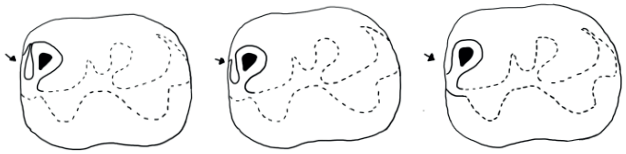
Appendix 4R. — Metalophulid m1

| | 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 |

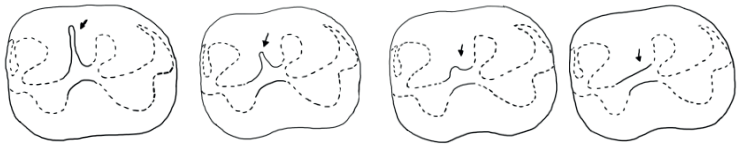
Appendix 4S. — Mesolophid m1.

| | 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 |

Appendix 4T. — 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 |

Appendix 4U — 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 |