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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 similarities 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; Källin & 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 the 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; Adrovet et al. 1987) or the Riu Magre Basin (Ruiz-Sánchez et al. 2003), both in Valencia, and the Ébro 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 Valles-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 Valles-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 Valles-Penedès were controlled
by tectonic activity of the main limiting faults and sea level changes in the western Mediterranean. The sediment infill of the basin is mostly continental, except for brief episodes of marine transgression that occurred during the latest early Miocene and the beginning of the middle Miocene. The studied material was recovered from early and early middle Miocene localities that have been dated by means of litho- and biostratigraphy (Agustí 1982; Agustí et al. 1985; Casanovas-Vilar et al. 2011, 2016b).

The early Miocene record of the Vallès-Penedès starts at the Ramblian, biozone MN3 (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, 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 Mamer and Les Esclletes del Papio,
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; Agustí 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 coralal 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 Esclletxes del Papiol and Sant Mamat 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 Esclletxes 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 Mamat, 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 Mariet (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 CRICETIDAE

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’Elia 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 Tylomyinae; Steppan et al. 2004; Fabre et al. 2012, 2015; Steppan & Schenk 2017). Other muroid groups (e.g. Nesomyidae, Spalacidae, Platanthomysidae) 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; Källin 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
the Muridae (including murnines, 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 genera 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 labiobuccal 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 Moli de Can Calopa;
MOR1 Riera del Morral – level 1;
PA Les Esclertxes del Papiol;
SAB1 Sant Andreu de la Barca – level 1;
SM Sant Mamet – level 1;
TFR1 Turó de les Forques – level 1;
VI Vilobi del Penedès.

Other abbreviations
MN European Mammal Neogene zones.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer von Waldfheim, 1817
Genus Democricetodon Fahldieck, 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 protocone. In some specimens, there is a short ectoloph on the protocone. 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 varies from long to short but is more commonly long (Appendix 2l). 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 anteroloph, 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 hypolophid is short and merges with the entolophid anteriorly to the hypoconid. The metalophid, is absent in IPS19481 from CS74 (Fig. 4C). In the other specimens, the metalophid 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 protosinus id 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 metalophid. The mesolophid is absent in all the specimens. The entoconid is highly reduced being integrated into the hypolophid. 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% confidence 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 francniacus 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 frequently 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 regarding 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. lacombei 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.
Dispersal and early evolution of the first modern cricetid rodents in Western Europe

**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, IPS86864 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). *Democricetodon 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). *Democricetodon* sp. 4: P, IPS86688 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 metalophid is simple and very short, merging with the anterolophid anterior to the protoconid. The anterolophid is generally low where it joins the metalophid 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 entocristid just anterior to the hypoconid. The posterolophid is thin and long, it reaches the base of the entoconid and closes the posterosinusid.

m2 (Fig. 4J)
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 (IP585738) 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 posterosinusid 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. gracilis (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; Marider 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 (Marider 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; Marider 2003; Wessels & Reumer 2009), France (Marider 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 (Marider 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 (Casasovas-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).

| Locality | Species | m1 | m2 | m3 |
|----------|---------|----|----|----|
| SM       | D. cf. decipiens | 1.91 | 1 | 1 |
| VI       | D. cf. decipiens | 1.54 | 1 | 1 |
| CS74     | D. hispanicus | 1.58 | 1 | 1 |
| CMV3     | D. hispanicus | 1.47 | 1 | 1 |
| LCV1     | D. hispanicus | 1.61 | 1 | 1 |
| EC       | D. hispanicus | 1.63 | 1 | 1 |

**L**

| Locality | Species | min. | mean | max. | s.d. | N | min. | mean | max. | s.d. | N |
|----------|---------|------|------|------|------|---|------|------|------|------|---|
| SM       | D. cf. decipiens | 1.87 | 1   | 1.20 | 1   | 1 |
| VI       | D. cf. decipiens | 1.58 | 1.03 | 2   | 0.99 | 10 |
| CS74     | D. hispanicus | 1.69 | 1.19 | 2   | 0.99 | 10 |
| CMV3     | D. hispanicus | 1.52 | 1.08 | 3   | 1.04 | 10 |
| LCV1     | D. hispanicus | 1.64 | 1.09 | 3   | 0.93 | 10 |
| EC       | D. hispanicus | 1.17 | 1.17 | 1   | 1.17 | 10 |

**W**

| Locality | Species | min. | mean | max. | s.d. | N | min. | mean | max. | s.d. | N |
|----------|---------|------|------|------|------|---|------|------|------|------|---|
| SM       | D. cf. decipiens | 1.91 | 1   | 1.25 | 1   | 1 |
| VI       | D. cf. decipiens | 1.58 | 1.03 | 2   | 0.99 | 10 |
| CS74     | D. hispanicus | 1.69 | 1.19 | 2   | 0.99 | 10 |
| CMV3     | D. hispanicus | 1.52 | 1.08 | 3   | 1.04 | 10 |
| LCV1     | D. hispanicus | 1.64 | 1.09 | 3   | 0.93 | 10 |
| EC       | D. hispanicus | 1.17 | 1.17 | 1   | 1.17 | 10 |
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 ectloloph 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 ectloloph 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 posterolophus 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 anterocone 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 transverse 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 anteroloph 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 hypocone.

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 protoloph 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 metaloph 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 symmetric. The anterior valleys of the teeth are narrow, especially the anterolophid, 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 sinuclid 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 anterolophusid. On the contrary, the labial arm of the anterolophid is well developed and closes the protosinusid. The mesolophid is vestigial. The sinus 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 mutulus* (Fig. 3). Some characters of the M2 of MOR1 fit better with *D. moralesi* (Van der Meulen et al. 2003) or *D. mutulus* (Wessels & Reumer 2009) 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 middle 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. mutulus*, a species known from Serbia, Hungary, Austria, Germany, Switzerland and France, but not recorded in the Iberian Peninsula. This species co-occurs with *D. gracils* in certain Swiss (Källin & Kempf 2009) and German sites (Wessels & Reumer 2009), which is also present at CS73. While *D. mutulus* 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**

*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 anteroconid 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
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

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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
Dispersal and early evolution of the first modern cricetid rodents in Western Europe

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% confidence 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 posterosinusid. 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 paracorne 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 anterosinusid (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 recurred, being barely distinguishable in many specimens such in IPS45094 from CS72. The metalophule is anterior to the hypocone. The posterolophule 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 anterocone is simple and round in all the studied specimens but in a few teeth from PA and CS74 which show a slight subdivision of this cusp (Appendix 4P). In these cases, the two cusps of the anterocone 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 anterolophule (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 metalophidul and the hypolophidul 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 mesoloph 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 Megacricetodon 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.
The metalophule is simple in all M2. The mesolophids 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 posterior sinus on M1. In the younger localities, such as VI and PA, the metalophule is connected to the postero-loph more obliquely, thus delimiting a more reduced posterior sinus. While this is also observed in a significant number of specimens from older sites, such as those from CMV 3, it is by far more common in younger ones. Such pattern is not observed in the Calatayud-Montalbán material, the posterior sinus 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 *Melissodon* 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, 1966b; 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 Moli de Can Calopa (Casanovas-Vilar et al. 2011, 2016b). These have delivered a glirid-dominated fauna that also includes the cricetid *Melissodon* (Jovells-Vaqué & Casanovas-Vilar 2018) but no modern cricetids. Besides the absence of cricetids other than *Melissodon*, 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 *Ligerimy s 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* (Augst 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) andCb (16.3-15.93 Ma) according to the *Democricetodon* species present and the replacement of *Ligerimys floracesei* 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 andCb 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-Montblán, 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. fratconicus, Van der Meulen et al. 2003, 2012), which is not present in the Vallés-Penedès. On the contrary, D. gracilis is not recorded in Calatayud-Montblán, but is first recorded in the Swiss Molasse during the late MN4 (Kalin & Kempf 2009), more or less at the same time it is first recorded in the Vallés-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 Vallés-Penedès sites can be correlated to zone C of the Calatayud-Montblán 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. weinfensteri (Schaub & Zapf, 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 (Casteller i La Gornal, Penedès sector). Several fissures have delivered a rich sample comprising thousands of small mammals including insectivores, 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-Montblán, 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 & Agustí 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 Pyrenees) 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-Montblán 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 comyid Ligerimys and occasional terrestrial sciurids (see Van der Meulen & de Bruijn 1982). In addition, presumably arboreal glirids (characterized by long molars with many transverse ridges, e.g., Muscardinus Kaup, 1829, Glis Brisson, 1762, Grirolinus 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 dominate over those originating from Central Europe. Iberian taxa include certain ground-dwelling glirids, such as the hypsodont Armanontomyx De Bruijn, 1966, only recorded at Turó de les Forques – level 1 and Costablanca (Ramblian, MN3), and Simplusmys simplicident (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 cricetid genera of the Vallès-Penedès site present a 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-Campo- manes 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; Källin & 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 assignments 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 & Agustí 2007). The genera Democricetodon and Megacricetodon are medium to small-sized cricetids with brachyodont and bunodont molars often assumed to have been generalists (e.g. Van Dam & Weltje 1999; Casanovas-Vilar & Agustí 2007). However, Daams et al. (1988: 291) assigned different ecological preferences to the Iberian species of these genera, with small-sized forms with long mesolophs/ids (e.g. Democricetodon gaillardi (Schaub, 1925), Megacricetodon minor) presumably favoring more humid environments. Heshkovitz (1967) noted that 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 (pentalophodont) tend to prefer open country. All the Democricetodon and Megacricetodon species present at the Vallès-Penedès during the early Miocene present mesoloph/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 ecomesolophid 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 existence 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 Oherodof (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, palaeoecological 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 which 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. mutius. 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.

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

### APPENDIX 2B. — Anterolophule M1.

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

### APPENDIX 2C. — Protolophule M1.

| Species  | Site | N |
|----------|------|---|
| *D. decipiens* | SM | 1 |
|           | VI  | 1 |
| *D. gracilis* | SM | – |
| *D. hispanicus* | CS74 | 7 |
|            | CMV3 | 2 |
|            | LCV1 | 1 |
|            | EC  | – |
### APPENDIX 2D. — Ectoloph on the Paracone M1.

| Species      | Site | N  |
|--------------|------|----|
| D. decipiens | SM   | 1  |
|              | VI   | 1  |
| D. gracilis  | SM   | 2  |
| D. hispanicus| CS74 | 6  |
|              | CMV3 | 4  |
|              | LCV1 | 2  |
|              | EC   | 1  |

### APPENDIX 2E. — Mesoloph M1.

| Species      | Site | N  |
|--------------|------|----|
| D. decipiens | SM   | 1  |
|              | VI   | 1  |
| D. gracilis  | SM   | 2  |
| D. hispanicus| CS74 | 4  |
|              | CMV3 | 4  |
|              | LCV1 | 2  |
|              | EC   | 1  |

### APPENDIX 2F. — Metalophule M1.

| Species      | Site | N  |
|--------------|------|----|
| D. decipiens | SM   | 1  |
|              | VI   | 1  |
| D. gracilis  | SM   | 2  |
| D. hispanicus| CS74 | 9  |
|              | CMV3 | 4  |
|              | LCV1 | 2  |
|              | EC   | 1  |
### Appendix 2G. — Protolophule M2.

| Species        | Site    | N  |
|----------------|---------|----|
| *D. sp. 4*     | MOR1    | 1  |
| *D. decipiens* | SM      | 1  |
|                | PA      | 1  |
|                | VI      | 2  |
| *D. gracilis*  | SM      | 1  |
| *D. hispanicus*| CS74    | 6  |
|                | CMV3    | 2  |
|                | LCV1    | 2  |
|                | EC      | 1  |

### Appendix 2H. — Ectoloph on the Paracone M2.

| Species        | Site    | N  |
|----------------|---------|----|
| *D. sp. 4*     | MOR1    | 1  |
| *D. decipiens* | SM      | 1  |
|                | PA      | 1  |
|                | VI      | 2  |
| *D. gracilis*  | SM      | 2  |
| *D. hispanicus*| CS74    | 8  |
|                | CMV3    | 7  |
|                | LCV1    | 2  |
|                | EC      | 2  |

### Appendix 2I. — Mesoloph M2.

| Species        | Site    | N  |
|----------------|---------|----|
| *D. sp. 4*     | MOR1    | 1  |
| *D. decipiens* | SM      | 1  |
|                | PA      | 1  |
|                | VI      | 2  |
| *D. gracilis*  | SM      | 2  |
| *D. hispanicus*| CS74    | 6  |
|                | CMV3    | 6  |
|                | LCV1    | 2  |
|                | EC      | 1  |
### APPENDIX 2J. — Metalophule M2.

| Species       | Site | N   |
|---------------|------|-----|
| *D. sp. 4*    | MOR1 | 1   |
| *D. decipiens* | SM   | 1   |
|               | PA   | 1   |
|               | VI   | 2   |
| *D. gracilis* | SM   | 1   |
| *D. hispanicus* | CS74 | 11  |
|               | CMV3 | 7   |
|               | LCV1 | 2   |
|               | EC   | 1   |

### APPENDIX 2K. — Lingual Anterolophid m1.

| Species       | Site | N   |
|---------------|------|-----|
| *D. sp. 4*    | CS73 | –   |
| *D. decipiens* | VI   | –   |
| *D. gracilis* | SM   | –   |
|               | VI   | –   |
|               | CS73 | –   |
|               | CCW  | –   |
| *D. hispanicus* | CS74 | 8   |
|               | CS72 | 2   |
|               | CSU  | 1   |
|               | CMV3 | 4   |
|               | CMV1 | 1   |
|               | LCV1 | 6   |

### APPENDIX 2L. — Metalophulid m1.

| Species       | Site | N   |
|---------------|------|-----|
| *D. sp. 4*    | CS73 | 1   |
| *D. decipiens* | VI   | 2   |
| *D. gracilis* | SM   | 1   |
|               | VI   | 2   |
|               | CS73 | 1   |
|               | CCW  | 1   |
| *D. hispanicus* | CS74 | 5   |
|               | CS72 | 7   |
|               | CSU  | –   |
|               | CMV3 | 4   |
|               | CMV1 | 1   |
|               | LCV1 | 5   |
### APPENDIX 2M. — Metaconid ridge m1.

| Species          | Site   | N  |
|------------------|--------|----|
| D. sp. 4         | CS73   | 1  |
| D. decipiens     | VI     | 2  |
| D. gracilis      | SM     | 1  |
|                  | VI     | 2  |
|                  | CS73   | 1  |
|                  | CCW    | 1  |
| D. hispanicus    | CS74   | 12 |
|                  | CS72   | 8  |
|                  | CSU    | 1  |
|                  | CMV3   | 4  |
|                  | CMV1   | 1  |
|                  | LCV1   | 6  |

### APPENDIX 2N. — Mesolophid m1

| Species          | Site   | N  |
|------------------|--------|----|
| D. sp. 4         | CS73   | 1  |
| D. decipiens     | VI     | 2  |
| D. gracilis      | SM     | 1  |
|                  | VI     | 2  |
|                  | CS73   | 1  |
|                  | CCW    | 1  |
| D. hispanicus    | CS74   | 12 |
|                  | CS72   | 8  |
|                  | CSU    | 1  |
|                  | CMV3   | 4  |
|                  | CMV1   | 1  |
|                  | LCV1   | 6  |
APPENDIX 2O. — Anterosinusid m2

| Species      | Site       | N |
|--------------|------------|---|
| *D. sp. 4*   | MOR1       | 1 |
| *D. decipiens* | PA         | 1 |
|              | VI         | 2 |
| *D. gracilis* | SM         | 1 |
|              | CCW        | 1 |
| *D. hispanicus* | SM         | 2 |
|              | CS74       | 5 |
|              | CSU        | 3 |
|              | CMV3       | 2 |
|              | CMV2       | -- |
|              | LCV1       | 5 |

APPENDIX 2P. — Metaconid ridge m2

| Species      | Site       | N |
|--------------|------------|---|
| *D. sp. 4*   | MOR1       | 1 |
| *D. decipiens* | PA         | 1 |
|              | VI         | 2 |
| *D. gracilis* | SM         | 1 |
|              | CCW        | 1 |
| *D. hispanicus* | SM         | 2 |
|              | CS74       | 3 |
|              | CSU        | -- |
|              | CMV3       | 2 |
|              | CMV2       | 1 |
|              | LCV1       | 6 |

APPENDIX 2Q. — Mesolophid m2

| Species      | Site       | N |
|--------------|------------|---|
| *D. sp. 4*   | MOR1       | 1 |
| *D. decipiens* | PA         | 1 |
|              | VI         | 1 |
| *D. gracilis* | SM         | -- |
|              | CCW        | -- |
| *D. hispanicus* | SM         | 2 |
|              | CS74       | 8 |
|              | CSU        | 3 |
|              | CMV3       | -- |
|              | CMV2       | -- |
|              | LCV1       | 4 |
**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.

| Site | N  | N  |
|------|----|----|
| PA   | 6  | 15 |
| VI   | 4  | 12 |
| CS74 | 4  | 1  |
| CS73 | 5  | –  |
| CSU  | 1  | –  |
| CMV3 | 6  | 6  |
| CMV2 | 2  | –  |
| CMV1 | –  | 1  |
| LCV1 | 9  | 4  |

**APPENDIX 4B.** — Anterior platform of the M1 anterocone.

| Site | N  | N  |
|------|----|----|
| PA   | 8  | 6  |
| VI   | 14 | 9  |
| CS74 | 4  | 1  |
| CS73 | 4  | 4  |
| CSU  | –  | 1  |
| CMV3 | 7  | 6  |
| CMV2 | 2  | –  |
| CMV1 | 1  | –  |
| LCV1 | 6  | 4  |
### APPENDIX 4C. — Labial spur of the M1 anterolophule.

| Site  | N  |  |  |  |
|-------|----|---|---|---|
| PA    | 1  | 3 | 16 | 20 |
| VI    | 7  | 7 | 16 | 30 |
| CS74  | 1  | 1 | 4  | 6  |
| CS73  | –  | 3 | 3  | 6  |
| CSU   | –  | 1 | –  | 1  |
| CMV3  | 1  | 4 | 5  | 10 |
| CMV2  | –  | – | 2  | 2  |
| CMV1  | –  | – | 1  | 1  |
| LCV1  | 2  | 4 | 9  | 15 |

### APPENDIX 4D. — Protolophule M1.

| Site  | 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  | 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     | 19 |
| VI     | 7  |
| CS74   | 5  |
| CS73   | 6  |
| CSU    | 2  |
| CMV3   | 12 |
| CMV2   | 2  |
| CMV1   | 1  |
| LCV1   | 14 |

APPENDIX 4G. — Mesoloph M1.

### Mesoloph M1

| Site   | N  |
|--------|----|
| PA     | 11 |
| VI     | 18 |
| CS74   | 1  |
| CS73   | 2  |
| CSU    | –  |
| CMV3   | 8  |
| CMV2   | 1  |
| CMV1   | –  |
| LCV1   | 9  |

APPENDIX 4H. — Metalophule M1.

### Metalophule M1

| Site   | N  |
|--------|----|
| PA     | 4  |
| VI     | 6  |
| CS74   | 1  |
| CS73   | 2  |
| CSU    | 2  |
| CMV3   | 6  |
| CMV2   | 1  |
| CMV1   | 1  |
| LCV1   | 14 |
### APPENDIX 4I. — Posterosinus M1

| Site | PA | VI | CS74 | CS73 | CSU | CMV3 | CMV2 | CMV1 | LCV1 |
|------|----|----|------|------|-----|------|------|------|------|
| N    | 19 | 16 | 3    | 6    | 2   | 6    | 2    | 1    | 5    |
| N    | 20 | 28 | 5    | 6    | 2   | 14   | 2    | 1    | 13   |

### APPENDIX 4J. — Protolophule M2

| Site | PA | VI | CS74 | CS72 | CSU | CMV3 | CMV1 | LCV1 |
|------|----|----|------|------|-----|------|------|------|
| N    | 13 | 16 | 2    | 2    | 1   | 1    | 1    | 13   |
| N    | 16 | 38 | 2    | 2    | 1   | 13   | 1    | 17   |

### APPENDIX 4K. — Ectoloph M2

| Site | PA | VI | CS74 | CS72 | CSU | CMV3 | CMV1 | LCV1 |
|------|----|----|------|------|-----|------|------|------|
| N    | 2  | 14 | 2    | 1    | 1   | 4    | 1    | 4    |
| N    | 7  | 11 | 2    | 2    | 1   | 8    | 1    | 3    |
| N    | 7  | 10 | 2    | 2    | 1   | 1    | 1    | 17   |

| Site | PA | VI | CS74 | CS72 | CSU | CMV3 | CMV1 | LCV1 |
|------|----|----|------|------|-----|------|------|------|
| N    | 2  | 14 | 2    | 1    | 1   | 4    | 1    | 4    |
| N    | 7  | 11 | 2    | 2    | 1   | 8    | 1    | 3    |
| N    | 7  | 10 | 2    | 2    | 1   | 1    | 1    | 17   |

| Site | PA | VI | CS74 | CS72 | CSU | CMV3 | CMV1 | LCV1 |
|------|----|----|------|------|-----|------|------|------|
| N    | 2  | 14 | 2    | 1    | 1   | 4    | 1    | 4    |
| N    | 7  | 11 | 2    | 2    | 1   | 8    | 1    | 3    |
| N    | 7  | 10 | 2    | 2    | 1   | 1    | 1    | 17   |
### APPENDIX 4L. — Ectoloph-Mesoloph connection M2.

| Site   | N  | N  |
|--------|----|----|
| PA     | 5  | 11 |
| VIO    | 8  | 31 |
| CS74   | 2  | 2  |
| CS72   | 2  | 2  |
| CSU    | 1  | 1  |
| CMV1   | 1  | 1  |
| LCV1   | 17 | 17 |

### APPENDIX 4M. — Mesoloph M2.

| Site   | N  | N  | N  |
|--------|----|----|----|
| PA     | 7  | 9  | 16 |
| VI     | 19 | 20 | 6  |
| CS74   | –  | 2  | –  |
| CS72   | –  | 2  | –  |
| CSU    | –  | –  | 1  |
| CMV3   | 3  | 8  | 3  |
| CMV1   | –  | 1  | –  |
| LCV1   | 7  | 5  | 1  |

### APPENDIX 4N. — Sinus M2.

| Site   | N  | N  |
|--------|----|----|
| PA     | 12 | 4  |
| VI     | 30 | 9  |
| CS74   | 1  | 1  |
| CS72   | 2  | 2  |
| CSU    | 1  | –  |
| CMV3   | –  | 13 |
| CMV1   | 1  | –  |
| LCV1   | –  | 16 |
APPENDIX 4O. — Metalophule M2.

| Site   | N  |
|--------|----|
| PA     | 6  |
| VI     | 7  |
| CS74   | 1  |
| CS72   | 2  |
| CSU    | 1  |
| CMV3   | 12 |
| CMV1   | 1  |
| LCV1   | 17 |

APPENDIX 4P. — Anteroconid m1.

| Site   | N  |
|--------|----|
| SM     | 1  |
| PA     | 4  |
| VI     | 25 |
| CS74   | 13 |
| CS73   | 3  |
| CS72   | 5  |
| CSU    | 1  |
| CMV3   | 17 |
| CMV1   | 5  |
| LCV1   | 11 |

APPENDIX 4Q. — Labial spur on m1 anterolophulid.

| Site   | N  |
|--------|----|
| SM     | 1  |
| PA     | 10 |
| VI     | 29 |
| CS74   | 11 |
| CS73   | 3  |
| CS72   | 6  |
| CSU    | 1  |
| CMV3   | 21 |
| CMV1   | 5  |
| LCV1   | 17 |

Dispersal and early evolution of the first modern cricetid rodents in Western Europe
### APPENDIX 4R. — Metalophulid m1

| Site | N  |
|------|----|
| SM   | 1  |
| PA   | 10 |
| VI   | 32 |
| CS74 | 17 |
| CS73 | 3  |
| CS72 | 6  |
| CSU  | 1  |
| CMV3 | 20 |
| CMV1 | 5  |
| LCV1 | 17 |

### APPENDIX 4S. — Mesolophid m1.

| Site | N  |
|------|----|
| SM   | 2  |
| PA   | 10 |
| VI   | 4  |
| CS74 | 29 |
| CS73 | 3  |
| CS72 | 6  |
| CSU  | 1  |
| CMV3 | 18 |
| CMV1 | 5  |
| LCV1 | 17 |
**APPENDIX 4T. — Lingual anterolophid lingual m2.**

| Site | N  |  | N  |  | N  |  | 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.**

| Site | N  |  | N  |  | N  |  | 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 |   |   |   |