Fossil Record 28 (1) 2025, 187–218 | DOI 10.3897/fr.28.138478

The Early Miocene muroids (Muroidea, Rodentia) of the Ribesalbes-Alcora Basin (Spain): A thriving haven during a time of migration

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Academic editor: Johannes Müller ♦ **Received** 3 October 2024 ♦ **Accepted** 21 May 2025 ♦ **Published** 11 June 2025

Abstract

The Campisano Ravine in the Ribesalbes-Alcora Basin (Spain, Early Miocene, Biozone C, MN 4) yielded a diverse and abundant assemblage of muroids, comprising five distinct taxa, and nearly 700 remains. The assemblage yielded five muroid taxa: *Megacricetodon primitivus*, *Democricetodon decipiens*, *Eumyarion weinfurteri*, *Melissiodon* sp., and Muroidea indet. The most abundant taxa were *M. primitivus* and *D. decipiens*, with *M. primitivus* being the most prevalent in the oldest sites and *D. decipiens* in the most recent ones. *E. weinfurteri* was exclusively identified in the FS1, MAB3, and MAB5 sites of the most recent biozone (*L. ellipticus*, see Crespo et al. 2021). In contrast, *Melissiodon* sp. was confined to the BC-1 and MAB-3 sites. *M. primitivus* was present in all Iberian basins, whereas *D. decipiens* exhibited considerable variability, being recorded in the Ca biozone of the Calatayud-Montalbán Basin, the last part of the C biozone of the Vallès-Penedès Basin, and the Buñol site. It can be hypothesised that the studied basin may be a factor in the distribution of this species across the regions in question. *Eumyarion* was present in the Vallès-Penedès Basin from the first part of the C biozone, subsequently migrating to the studied basin and appearing in the Cb biozone in the Calatayud-Montalbán and Buñol basins. *Melissiodon* was absent from the latter basin from the MN3 biozone to the last part of the C biozone and from the MN5 biozone in the Vallès-Penedès Basin. The presence of muroid faunas in the Early Miocene suggests that the coastal Ribesalbes-Alcora Basin functioned as a transitional region between the forested areas of west and central Europe and the drier inner Iberian Peninsula basins.

Key Words

Aragonian, biostratigraphy, cricetids, Iberian Peninsula, muroids, palaeoecology

Introduction

The superfamily Muroidea constitutes the second-largest family of mammals, comprising more than 870 species, including hamsters, New World rats and mice, and arvicolids (Wilson and Reeder 2005). The hypothesis is that their arrival in Europe from Asia in the early Oligocene coincided with the closure of the Turgai Strait and the extinction of numerous vertebrate groups during the Eocene-Oligocene transition on this continent, also known as the Grande Coupure (Stehlin 1909; Vianey-Liaud 1985). These genera include *Eucricetodon*, *Paracricetodon*, *Pseudocricetodon*, *Atavocricetodon*, and *Melissiodon* (Mödden 1999; Dawson 2003). Consequently, at the beginning of the Early Miocene, only four genera of muroids survived in Europe: *Adelomyarion*, *Eucricetodon*, *Pseudocricetodon*, and *Melissiodon* (Cuenca-Bescós 1985; Hugueney 1999;

Mödden 1999). The genera, namely *Adelomyarion*, *Eucricetodon*, *Pseudocricetodon*, and *Melissiodon* (Cuenca-Bescós 1985; Hugueney 1999; Mödden 1999), are regarded as the most prominent survivors of the muroid group. Except for *Melissiodon*, these forms became extinct throughout the earliest Miocene. The genus *Adelomyarion* is exclusively documented from the Autol locality in the Ebro Basin (Cuenca-Bescós 1985), whereas *Pseudocricetodon* becomes increasingly scarce, with only the species *Pseudocricetodon thaleri* Hugueney, 1969 surviving (Hugueney 1969). The genus *Eucricetodon* underwent accelerated evolution in size and morphology during the initial part of the Early Miocene, until its extinction in the middle part of the Early Miocene (Hugueney 1999). Subsequently, only the genus *Melissiodon* survived until the conclusion of the MN4 (Hordijk et al. 2015; Jovells-Vaquè and Casanovas-Vilar 2018b). The apparent absence of representatives of this family, except for *Melissiodon*, in European faunas during part of MN3 is referred to as the *cricetid vacuum*. This phase would conclude with the migration of the genus *Democricetodon* at the end of MN3 (Daams and Freudenthal 1989). From MN4 onwards, several muroid subfamilies present in the record under study were established. In MN5, muroids became the dominant group in the Iberian rodent faunas, displacing the extinct eomyids and glirids (van der Meulen et al. 2012).

The faunal exchanges are particularly evident during the lower Aragonian, specifically in the lower part of MN4, due to the immigration of muroids of Asian origin. During this period, at least three migrations of muroids have been documented in the Iberian Peninsula, at least in the Calatayud-Montalbán Basin (García-Paredes et al. 2016). The initial migration is characterised by the arrival of one species of the genus *Democricetodon*, followed by those of the genus *Megacricetodon*. A third migration is marked by the entry of *Eumyarion* into the Iberian Peninsula (García-Paredes et al. 2016). These migrations appear to be driven by temperature and environmental humidity changes. Van Dam et al. (2006) and García-Paredes et al. (2016) observed that the MN4 period in the Calatayud-Montalbán Basin is characterised by aridification and cooling, attributed to the Mi-2 glacial event. This phenomenon has been identified as a significant driver of disruption in terrestrial biota, leading to habitat fragmentation and a reduction in food availability. This phenomenon has been shown to favour the new immigrants, which subsequently dominate the faunas, while being detrimental to the previously existing taxa (DeMiguel et al. 2010).

In the Ribesalbes-Alcora Basin, Agustí et al. (1988) cite the presence of *Megacricetodon primitivus* (Freudenthal, 1963), *Democricetodon hispanicus* (Freudenthal, 1963) and *Democricetodon* (*Fahlbuschia*) *koenigswaldi* (Fahlbusch, 1964). The latter two taxa exhibit similarities and fall within the range of variability described in this paper and those described by van der Meulen et al. (2003) as *Democricetodon decipiens* (Freudenthal and Daams 1988).

The study of the muroids in this basin provides further insight into the ecosystem of the Araia d'Alcora outcrop in the Ribesalbes-Alcora Basin at the end of the Early Miocene. Notable contributions to the field include the discovery of the new species *Plesiodimylus ilercavonicus* Crespo et al., 2018 (Crespo et al. 2018), the bat *Cuvierimops penalveri* Crespo et al., 2020a (Crespo et al. 2020a), and the snail *Pseudamnicola roblesi* Albesa et al., 2022 (Albesa et al. 2022). Furthermore, the southernmost documented record of the herpetotheriid *Amphiperatherium frequens erkertshofense* (von Meyer, 1846) (Furió et al. 2012; Crespo et al. 2020b) was identified, as were abundant remains of talpids (Crespo et al. 2019b), diverse soricids (Crespo et al. 2019c), erinaceids (Crespo et al. 2020b), squirrels (Crespo et al. 2021a), eomyids (Crespo et al. 2021b), dormice (Crespo et al. 2023), bats (Crespo et al. 2020a), lagomorphs, *Cainotherium* (Crespo et al. 2022), snails (Albesa et al. 2022), reworked Cretaceous batoids (Manzanares and Crespo 2023), and even a Konservat-Lagerstätte (Álvarez-Parra et al. 2021). This article constitutes the final contribution to a series of studies examining the taxonomy of the mammalian fauna present in the Ribesalbes-Alcora Basin.

Geological setting

The outcrop of Araia d'Alcora in the Ribesalbes-Alcora Basin is located in the eastern part of the Iberian Peninsula, encompassing the vicinity of the village of the same name in Castelló, Spain (see Fig. 1; Agustí et al. 1988; Crespo et al. 2019a). The study included a comprehensive evaluation of seven sections within the basin, namely Mas dels Coixos (MCX), Mas de Torner (MTR), Araia Cantera Sud (ACS), Barranc de Campisano (BC), Foieta la Sarra (FS), Mas d'Antolino B (MAB), and Corral de Brisca (CBR). The selection of areas was meticulously arranged in chronological order, ranging from the oldest to the youngest, with some sections exhibiting overlap.

The Campisano Ravine is composed of grey and yellow mudstones, limestones, and sandstones, with a total thickness of approximately 100 m (Crespo et al. 2019a). It is situated within 'Unit Three' of the Ribesalbes-Alcora Basin, by Anadón et al.'s (1989) classification (Fig. 1). For detailed descriptions of up to 45 related sites, according to the sections mentioned above, see Crespo (2017) and Crespo et al. (2019a).

The examined sections display a stratigraphic sequence that corresponds to part of the local biozone C in the Calatayud-Montalbán Basin (MN4, early Aragonian, Early Miocene), covering a time range from 16.5 to 15.94 million years, as established by Van der Meulen et al. (2012) (Crespo et al. 2019a). An alternative hypothesis has been proposed by Casanovas-Vilar et al. (2022), who suggest that the extinction limit of *Ligerimys florancei* lies within the MN4-MN5. According to this interpretation, the sites of the Ribesalbes-Alcora Basin associated with the local biozone *L. florancei* would correspond

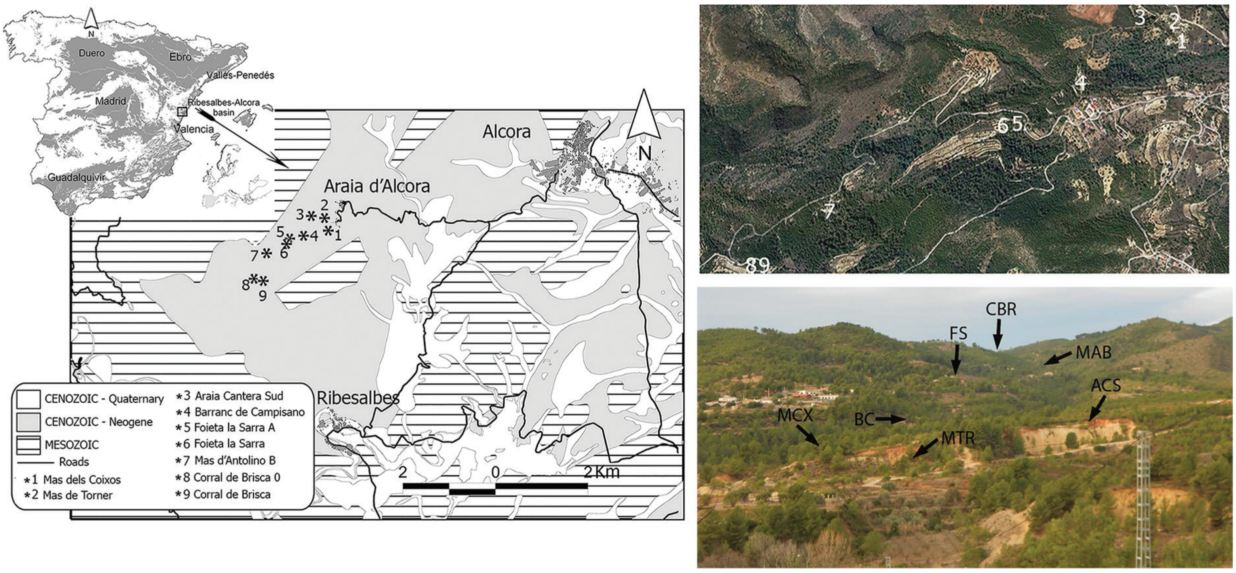

Figure 1. Left: Geographic and geological setting of the Ribesalbes-Alcora Basin; Right: Location of the outcrops of the Campisano Ravine, and the sections studied, and photography of the Campisano Ravine indicating the different sections. Modified from Crespo 2017 and Crespo et al. 2019a.

to the MN4. In contrast, those associated with the local biozone *L. ellipticus* would be assigned to the MN5.

Material and methods

The fossil material under study is currently stored at the Natural History Museum of the University of Valencia (MUVHN), bearing the label MGUV (see the Suppl. material 1). Images of the specimens were captured using a Scanning Electron Microscope HITACHI 4800 at the Servei Central de Suport a la Investigació Experimental (SCSIE) of the University of València Estudi General (UVEG). The terminology employed for the description is proposed by Oliver and Peláez-Campomanes (2013), with certain modifications. Following the methodology proposed by Kristkoiz (1992) for the genus *Melissiodon*, the mesoconid has been added to the m1. Moreover, the second protolophule has been modified to an axioloph (Freudenthal and Daams 1988) for the M3. The measurement criteria employed in this study are derived from the methodologies established by Daams and Freudenthal (1988b). The measurements are expressed in millimetres and were obtained through a Leica MZ75 binocular microscope, equipped with a mechanical stage and connected to a Sony Magnescale measuring device. This article employed the assistance of ChatGPT, in conjunction with DeepL Writer, to enhance the quality and clarity of the English language.

Abbreviations

Lower teeth are designated with lower-case letters (lower molars: **m1**, **m2**, and **m3**). Upper teeth are written in upper-case letters (upper molars: **M1**, **M2**, and **M3**). **MCX:** Mas dels Coixos; **MTR:** Mas de Torner; **ACS:** Araia Cantera Sud; **BC:** Barranc de Campisano; **FS:** Foieta la Sarra; **MAB:** Mas d'Antolino B; **CBR:** Corral de Brisca.

Institutional abbreviations

MUVHN: Museu de la Universitat de València d'Historia Natural. **MGUV:** Museu de Geologia de la Universitat de València.

Systematic palaeontology

Suborder Myomorpha Brandt, 1855
Infraorder Myodonta Schaub, 1955
Superfamily Muroidea Illiger, 1811
Subfamily Megacricetodontinae Mein & Freudenthal, 1971

Genus *Megacricetodon* Fahlbusch, 1964

Type species. *Megacricetodon gregarious* (Schaub, 1925), La Grive M, Upper Miocene.

***Megacricetodon primitivus* (Freudenthal, 1963)**
Figs 2–4

Localities. MCX2, MCX3, MCX4, MTR1, MTR2, MTR3, BC1, BC2, FS1, MAB0A, MAB0B, MAB2, MAB3, MAB4, MAB5, MAB11, MAB11B, MAB12, CBR0B, CBR0E, CBR0F, CBR1, CBR2, and CBR4.

Material (number of remains). Suppl. material 1; MCX2 (1): 1 mandible, 1 m1; MCX3 (62): 1 mandible, 12 m1, 9 m2, 9 m3, 10 M1, 12 M2, 9 M3; MCX4: 1 M1; MTR1 (3): 1 m1, 2 M2; MTR2 (47): 13 m1, 9 m2, 3 m3,

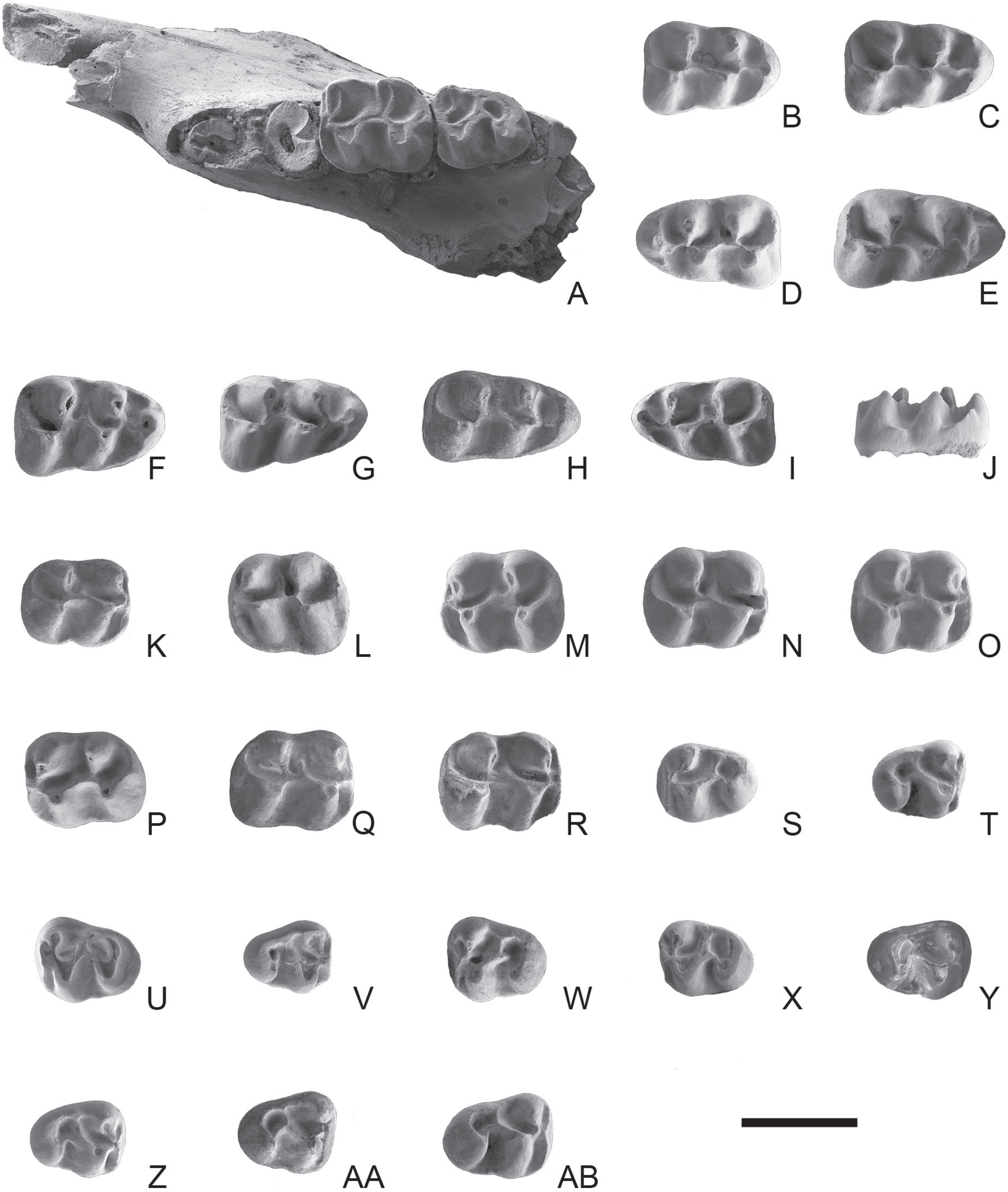

Figure 2. Lower teeth of *Megacricetodon primitivus* from the Ribesalbes-Alcora Basin. **A.** Left mandible+m2+m3 (MCX3-33); **B.** Right m1 (MCX3-73); **C.** Right m1 (MTR2-72); **D.** Left m1 (BC1-55); **E.** Right m1 (MAB0B-10); **F.** Right m1 (MAB5-9); **G.** Right m1 (MAB5-61); **H.** Right m1 (MAB5-499); **I.** Left m1 (MAB5-798); **J.** Right m1, labial view (MCX3-65); **K.** Right m2 (MCX3-78); **L.** Left m2 (BC1-70); **M.** Left m2 (MAB3-170); **N.** Right m2 (MAB3-171); **O.** Right m2 (MAB3-172); **P.** Left m2 (MAB3-173); **Q.** Right m2 (MAB5-540); **R.** Right m2 (CBR0B-13); **S.** Left m3 (MCX3-87); **T.** Right m3 (BC1-71); **U.** Left m3 (MAB2-2); **V.** Right m3 (MAB3-6); **W.** Left m3 (MAB3-209); **X.** Left m3 (MAB3-213); **Y.** Right m3 (MAB3-214); **Z.** Right m3 (MAB3-219); **AA.** Right m3 (MAB5-512); **AB.** Right m3 (MAB5-803). Scale bar: 1 mm.

12 M1, 5 M2, 5 M3; MTR3 (2): 1 M1, 1 M2; BC1 (51): 10 m1, 8 m2, 7 m3, 15 M1, 7 M2, 4 M3; BC2 (1): 1 M1; MAB0A (22): 3 m1, 4 m2, 1 m3, 7 M1, 4 M2, 3 M3; MAB0B (9): 2 m1, 3 m2, 2 m3, 2 M1; FS1 (15): 3 m1, 1 m3, 3 M1, 7 M2, 1 M3; MAB2 (2): 1 m1, 1 m3; MAB3 (92): 14 m1, 20 m2, 19 m3, 17 M1, 12 M2, 10 M3;

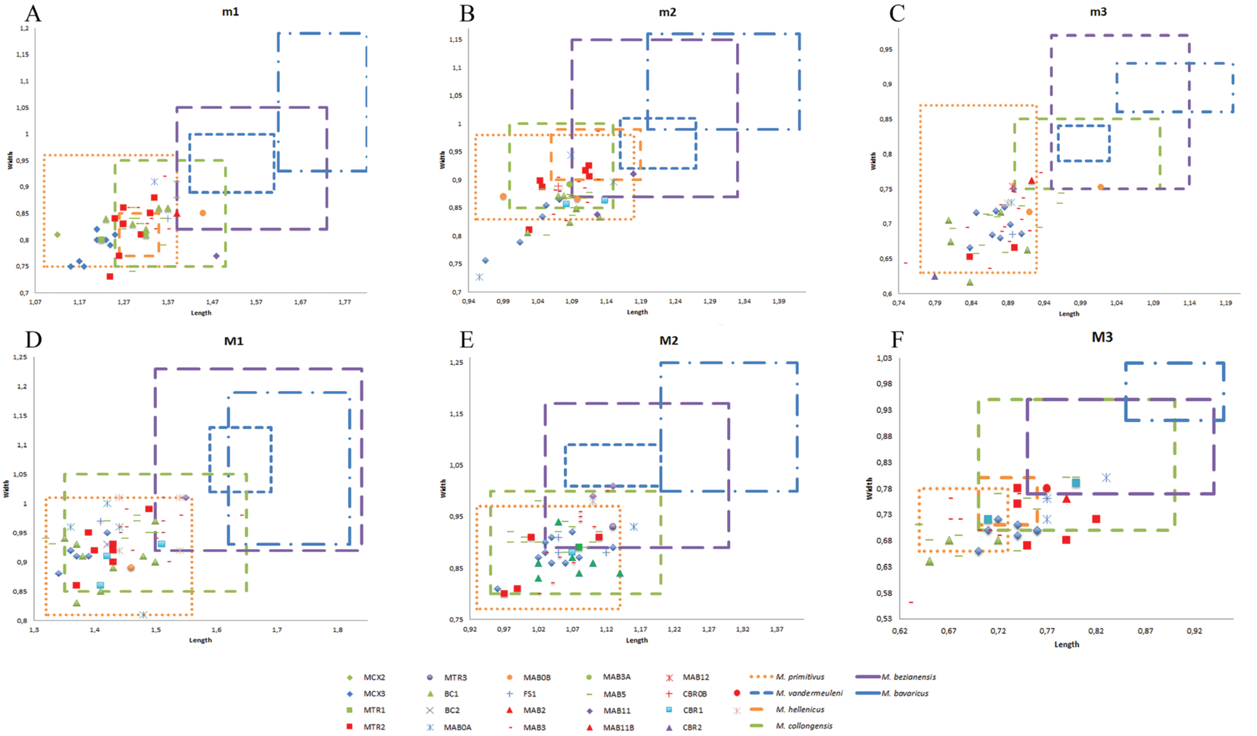

Figure 3. Comparison of length and width measurements (in mm) of *Megacricetodon primitivus* from Ribesalbes-Alcora Basin. *M. primitivus* from Valtorres (type locality (t.l.)); *M. vandermeuleni* from Fuente Sierra 4 (t.l.); *M. hellenicus* from Aliveri NQ (t.l.); *M. collongensis* from Vieux Collonges (l.t.); *M. bezianensis* from Bézian; *M. bavaricus* from Langenmoosen (t.l.); and the material from Ribesalbes-Alcora Basin (Fahlbusch 1964, Bulot 1972, Maridet 2003, Oliver and Peláez-Campomanes 2013, 2014, 2016; this publication).

MAB3A (1): 1 m2; MAB4 (1): 1 M2; MAB5 (85): 18 m1, 13 m2, 14 m3, 14 M1, 15 M2, 11 M3; MAB11 (10): 1 m1, 3 m2, 1 m3, 3 M1, 2 M2; MAB11B (1): 1 M3; MAB12 (1): 1 m3; CBR0B (1): 1 m2; CBR0E (1): 1 M1; CBR0F (1): 1 m2; CBR1 (19): 1 m1, 4 m2, 2 m3, 5 M1, 4 M2, 2 M3; CBR2 (1): 1 m3; CBR4 (1): 1 M1.

Measurements. Suppl. material 2.

Description. (See Suppl. material 3).

Mandible (MCX3; Fig. 2A): In occlusal view, the mandible exhibits a slight inclination, which does not obscure the mental foramen. This foramen is located between the incisor and the first molar on the labial side. The masseteric process is deep and originates at the level of the anterior part of the m1 with a ridge.

Concerning other sites, no significant disparities were observed in the material of MCX2.

m1 (MAB5; Fig. 2F–I): the anteroconid is simple and rounded, and slightly lower than the rest of the cusps (between morphology B and C as described by Oliver and Peláez-Campomanes (2016) (Fig. 2H)). The labial spur of the anterolophulid may be developed (1 out of 16), incipient (1 out of 16), or absent (14 out of 16). The metalophulid is positioned anteriorly and is directed forward, not connected to the protoconid. The mesolophid may be categorised as follows: long and developed to the lingual side (1 out of 16), long without reaching the lingual side (4 out of 16), medium (8 out of 16), or short (3 out of 16). The ectomesolophid is absent. The hypolophulid is directed forward. The posterolophid descends towards the base of the entoconid but does not connect to it.

Variability in other sites: In the remains of MCX2 and MCX3 (Fig. 2B), the anterolophulid is consistently absent, and the mesolophid is either short or medium. In MTR1, the anterolophulid is absent. In the remains from MTR2 (Fig. 2C), two specimens have a double metalophulid, one has no mesolophid, one has an ectomesolophid and one has the posterolophid attached to the entoconid. In BC1, the mesolophid is shorter (Fig. 2D). In one individual, the posterolophid is joined to the entoconid, and there is greater development of the labial ridge of the anterolophulid. In MAB0B (Fig. 2E), one individual is observed to possess two ridges at the lingual-anterior and labial side of the anteroconid; the anterolophulid is more developed, and in another, the metalophulid is isolated. In FS1, an individual is noted with the metalophulid isolated from the protoconid. In MAB3, a tooth with an incipient ectomesolophid is observed. The material from the other sites (MAB2, MAB0A, MAB11, and CBR1) shows no significant differences. Generally, there seems to be a slight tendency for the mesolophid to elongate over time. As illustrated in Fig. 3A, Suppl. material 4, the biometric values of *M. primitivus* from localities MCX2 and MCX3 are the smallest observed in this basin. In addition, there is a tendency for specimens to lengthen in time.

m2 (MAB3; Fig. 2M–P): the lingual anterolophid may terminate at the antero-lingual border of the metaconid (2 out of 16), fail to reach the corner (10 out of 16), or be absent (4 out of 16). The anterosinusid may be small and narrow (7 out of 16) or absent (9 out of 16). The labial anterolophid is long and descends towards the base of

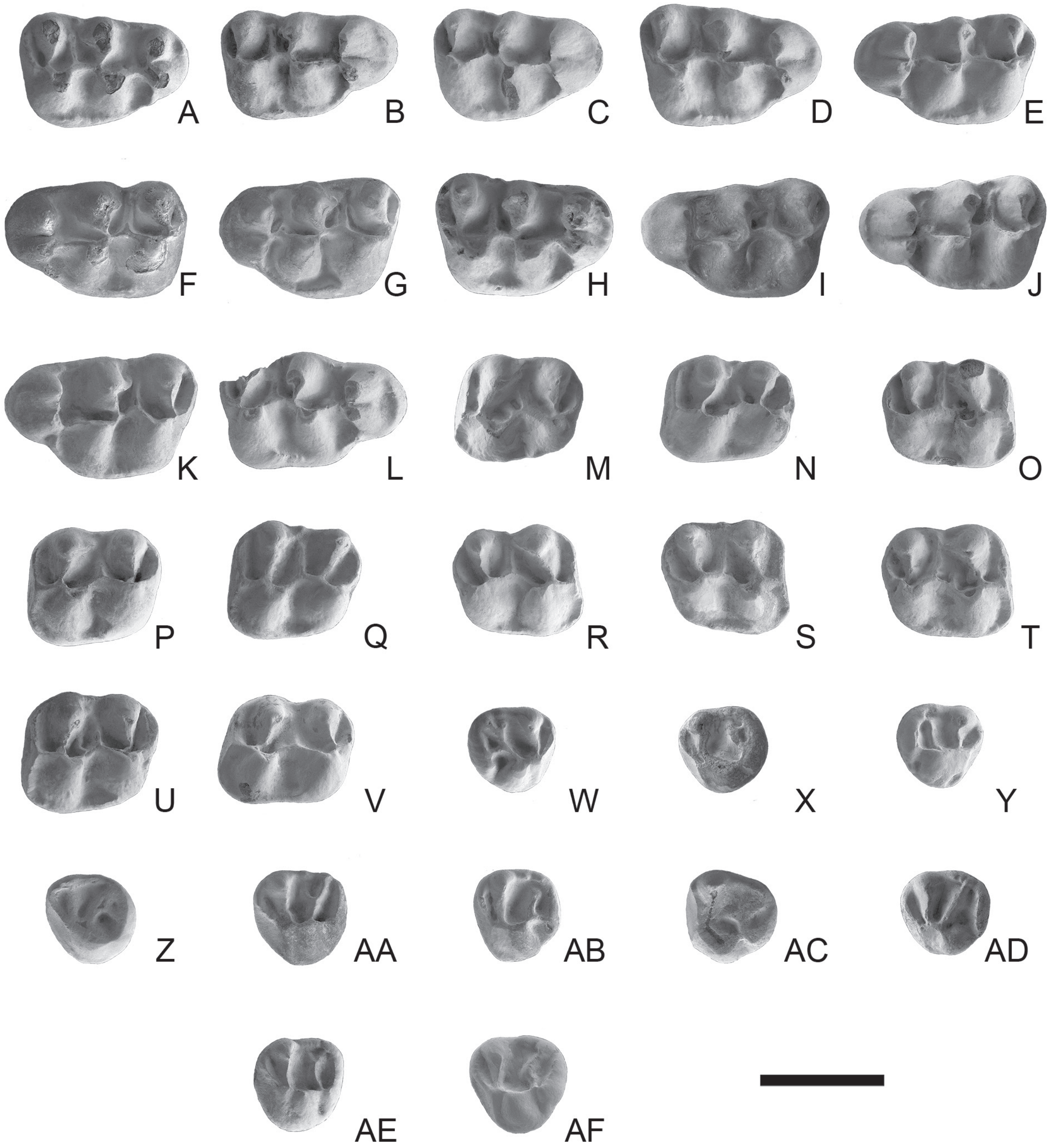

Figure 4. Upper teeth of *Megacricetodon primitivus* from the Ribesalbes-Alcora Basin. **A.** Right M1 (MTR2-47); **B.** Right M1 (BC1-33); **C.** Right M1 (BC1-36); **D.** Right M1 (MAB0A-22); **E.** Left M1 (MAB3-53); **F.** Left M1 (MAB3-57); **G.** Left M1 (MAB3-59); **H.** Right M1 (MAB3-62); **I.** Left M1 (MAB3-66); **J.** Left M1 (MAB5-78); **K.** Left M1 (MAB11-1); **L.** Right M1 (CBR1-12); **M.** Left M2 (MCX3-51); **N.** Left M2 (BC1-46); **O.** Right M2 (FS1-20); **P.** Left M2 (MAB3-87); **Q.** Left M2 (MAB5-65); **R.** Right M2 (MAB5-74); **S.** Right M2 (MAB5-489); **T.** Right M2 (MAB5-509); **U.** Left M2 (MAB11-31); **V.** Left M2 (CBR1-1); **W.** Left M3 (MCX3-59); **X.** Left M3 (MTR2-204); **Y.** Right M3 (BC1-53); **Z.** Left M3 (MAB3-112); **AA.** Left M3 (MAB3-114); **AB.** Left M3 (MAB3-118); **AC.** Left M3 (MAB5-13); **AD.** Left M3 (MAB5-62); **AE.** Left M3 (MAB5-494); **AF.** Left M3 (MAB5-809). Scale bar: 1 mm.

the protoconid. The mesolophid can be categorised into several distinct forms, including long and reaching the lingual margin (2 out of 18), long without reaching the lingual margin (3 out of 18), medium (6 out of 18), short (5 out of 18), or absent (3 out of 18). The ectolophid is continuous. The ectomesolophid is absent, and the posterolophid is not connected to the entoconid.

Variability in other sites: In MCX3 (Fig. 2K), the lingual anterolophid is always present and longer, and the mesolophid is short or medium in length. In BC1 (Fig. 2L), the lingual anterolophid is always present; in one specimen, the labial anterolophid joins the labial mesocingulum, and the mesolophid is usually longer. In MAB0A, the mesolophid is usually longer. In MAB0B, the posterolophid may be connected to the entoconid. In MAB5 (Fig. 2Q), the anterolophid is always present. In CBR1, the posterolophid is connected to the entoconid; in another specimen, the labial anterolophid is connected to the labial mesocingulum. The m2 morphology of MTR2, FS1, MAB3A, MAB11, CBR0B (Fig. 2R), and CBR0F does not differ significantly from that of MAB3. About the biometry (Fig. 3B, Suppl. material 4) between the material from the different sites of this species in the Ribesalbes-Alcora Basin, the material from MCX3 is slightly smaller, while that from MAB11 is slightly longer, and that from BC1 is slightly narrower. In addition, there is a slight tendency for specimens to become larger over time.

m3 (MAB3; Fig. 2V–Z): The lingual anterolophid may be of medium size (7 out of 19), short (6 out of 19), or absent (6 out of 19). A small anterosinusid is present in six specimens. The labial anterolophid may be long (9 out of 18) or short (9 out of 18), descending towards the base of the protoconid (9 out of 18). The metalophulid is short and complete, while the mesolophid is absent. The mesosinusid is narrow and transverse. The posterosinusid is medium to large in size. The protoconid and the hypoconid may be separate (6 out of 18) or not (12 out of 18). The metaconid, entoconid, and posterolophid form a continuous wall along the lingual margin (10 out of 17), or the metaconid is independent (7 out of 17).

Variability in other sites: In MCX3 (Fig. 2S), the lingual anterolophid is shorter and the labial is longer, with the anterosinusid occurring more frequently. In BC1 (Fig. 2T), there is a tooth with an anterior cingulum in front of the anterolophid. In MAB2 (Fig. 2U), an individual is observed with a developed mesolophid. In MAB5 (Fig. 2AA–AB), the lingual anterolophid is long in two individuals, while the metalophulid is absent in another and the mesolophid is present in a third specimen. In CBR1, in addition to the mesolophid, the metaconid has a ridge that contacts the lingual part of the ectolophid in one specimen. In the more modern sites of the basin, such as MAB5 and CBR1, the presence of mesolophids is more prevalent. The morphology of m3 from localities MTR2, MAB0A, MAB0B, FS1, MAB11, MAB12, and CBR2 does not differ significantly from that described in MAB3. The comparison of the biometry (Fig. 3C, Suppl. material 4) of the m3 of *M. primitivus* from the various localities of the Ribesalbes-Alcora Basin shows that the specimen from MAB0B is the largest, while that from CBR2 is the smallest (MAB0B). In addition, there is a slight tendency for specimens to become shorter and wider over time.

M1 (MAB3; Fig. 4E–I): the anterocone may be not subdivided (1 out of 15), be slightly subdivided and the sulcus shallow (1 out of 15), or deeply subdivided and have a deeply subdivided with a platform in front of the anterocone (10 out of 15) and with even a cingulum (3 out of 15). The labial part of the anterocone may be larger (13 out of 15) or equal (2 out of 15) to the lingual one. The protolophule may be posterior to the protocone (5 out of 15), posterior almost double, formed by the labial ridge of the anteroloph or by the front ridge of the paracone (10 out of 15). The anterolophule may connect over the lingual cusp (8 out of 15) or between the two cusps of the anterocone (7 out of 15). The labial spur of the anterolophule may be short (4 of 15), incipient (7 of 15), or absent (4 of 15). The lingual mesocingulum is present but poorly developed (8 of 16) or absent (8 out of 16). The ectoloph (or paracone ridge) may be long (8 out of 16) or short (8 out of 16). The length of the mesoloph is recorded as either long and reaching the labial margin (2 out of 17), long (11 out of 17), medium (2 out of 17), or short (2 out of 17). The connection between the mesoloph and ectoloph of the paracone is categorised as either present (4 out of 18) or absent (14 out of 18). The metalophule is directed backwards, thereby reducing the posterosinus. The posterosinus may be narrow (10 out of 17) or of medium width (7 out of 17), being either deep (8 out of 15) or deep (8 out of 15) or shallow (7 out of 15).

Variability in other sites: In the M1 of MCX3, there is a higher prevalence of uniform size anterocone cusps, the absence of a double protolophule, the anterolophule connection with the lingual cusp, the ectoloph is absent in one specimen, and the mesoloph is long and lack of contact with the posterior crest of the paracone. In M1 from MTR2 (Fig. 4A), the protolophule is posterior, the anterolophule connects to the lingual cusp, the labial crest of the anterolophule is absent, the lingual mesocingulum is rare, the mesoloph and ectoloph of the paracone never seem to be connected, and finally the metalophule usually connects to the most anterior part of the posteroloph. It may even be directed more posteriorly, even transversely. In BC1 (Fig. 4B, C), there are two specimens with a deeply divided anterocone without platform or cingulum, the protolophule is simple and posterior, the anterolophule connects with the lingual cusp, its labial crest is always absent, the lingual mesocingulum is less frequent, the mesoloph never connects with the ectoloph of the paracone and finally the metalophule connects with the posteroloph posterior to the hypocone in six out of fifteen cases. In MAB0A (Fig. 4D), most individuals have an anterior cingulum of the anterocone, the protolophule is usually posterior, the ectoloph is long in three out of six individuals, and in another, the metalophule does not reduce the posterosinus. In FS1, the anterocone is deeply divided and has no anterior platform or cingulum; in one individual, the protolophule is double; in another, the protolophule is double; in another, the ectoloph is absent. In MAB5 (Fig. 4J), the anterocone is less divided and there are no specimens with a cingulum, the proportion of material with anterocone cusps of equal size is higher, the lingual mesocingulum is less common, the protolophule is mostly posterior, the ectoloph is absent in one tooth, and there are four specimens with a metalophule that connects posteriorly but without reducing the posterosinus. In MAB11 (Fig. 4K), the anterocone is less divided; in another, the metalophule does not reduce the posterosinus. In CBR1 (Fig. 4L), the protolophule is posterior, the anterolophule touches the lingual cusp, and the metalophule does not reduce the posterosinus in three individuals and is transverse in another. In the remaining sites (MCX4, MTR3, BC2, MAB0B, CBR0E, and CBR4), no significant morphological differences were observed. About biometrics (Fig. 3D, Suppl. material 4), the material from the study sites belongs to the *L. florancei* local biozone, which is generally slightly smaller in size. In addition, there is a slight tendency for specimens to become larger over time.

M2 (MAB5; Fig. 4Q–T): the protolophule may be single and transverse, connected to the protocone (11 out of 14), or double with an incomplete posterior protolophule (3 out of 14). The ectoloph may be long and contact the labial side (4 out of 13), long (2 out of 13), short (4 out of 13), or absent (3 out of 13). The mesoloph is long and reaches the labial edge (4 out of 13), long without reaching the labial edge (6 out of 13), or medium length (3 out of 13). The ectoloph and the mesoloph may be connected (5 out of 13) or not (6 out of 13), with two specimens in which the ectoloph is connected to the labial border. The sinus may be directed slightly anteriorly (2 out of 16) or perpendicular (14 out of 16). The metalophule may be directed posteriorly, connecting with the posteroloph posterior to the hypocone (3 out of 13), or directed forward and connecting with the entoloph (10 out of 13). The posteroloph may be connected to the posterior part of the metaconid (8 out of 13) or not (5 out of 13). The posterosinus may be either long (8 out of 13) or short (5 out of 13).

Variability in other sites: In MCX3 (Fig. 4M), there is one individual with a double protolophule, another with a lingual mesocingulum, and the ectoloph is usually longer. In BC1 (Fig. 4N), the morphology of the protolophule is more variable, even with a double protolophule, a double protolophule with both protolophules complete in one individual, the mesoloph is short in another. It does not appear to be connected to the ectoloph. In MAB0A, the protolophule may be directed either anteriorly or posteriorly. In FS1 (Fig. 4O), there is one individual with a double protolophule and another with a metalophule attached to the posteroloph. In MAB3 (Fig. 4P) there are three individuals with the protolophule attached to the anteroloph anterior to the protocone another with a double protolophule, the ectoloph always present, another with a short mesoloph, and three others with a transverse metalophule. In MAB11 (Fig. 4U) has one specimen with an anterior protolophule and another with a transverse metalophule. In CBR1 (Fig. 4V), there is one individual with an incomplete anterior protolophule, an oblique sinus in three out of four specimens, another with a transverse metalophule, and another with a reduced posterosinus. No significant differences exist in MTR1, MTR2, MTR3, and MAB4. Regarding biometry (Fig. 3E, Suppl. material 4), the examined material belonging to local biozone *L. florancei* tends to be smaller than that belonging to local biozone *L. ellipticus*. In addition, there is a slight tendency for specimens to become larger over time.

M3 (MAB5; Fig. 4AC–AF): the lingual anteroloph and the protosinus may be poorly developed (2 out of 11) or absent (9 out of 11). The labial anteroloph may be short (5 out of 11) or long (6 out of 11), connecting with the paracone (7 out of 11) or not (4 out of 11). This morphology of the labial anteroloph influences the presence of a short but relatively wide anterosinus (2 out of 11), a long anterosinus (6 out of 11), or the absence of an anterosinus (3 out of 11). The metalophule (centroloph) may be connected to the neo-entoloph (3 out of 11), to the anterior ridge of the hypocone (4 out of 11), to the anterior ridge of the hypocone and protolophule (2 out of 11), to the posterior ridge of the protocone (1 out of 11) or the axioloph (1 out of 11). The sinus may be shallow (4 out of 11) or deep (7 out of 11). The mesoloph may be long (2 out of 11), short (4 out of 11), incipient (2 out of 11), or absent (3 out of 11). The neo-entoloph may be short and connected to the protocone and hypocone (8 out of 11) or absent (3 out of 11). The axioloph may be incipient (3 out of 11) or absent (8 out of 11). The posteroloph may be long and curved (10 out of 11) or straight (1 out of 11), forming a labial wall together with the metacone and the posterior wall of the paracone (7 out of 11), and may not connect with the metacone (4 out of 11).

Variability in other sites: In MCX3 (Fig. 4W), the labial anteroloph is shorter; in two out of eight individuals, the neo-entoloph is absent, and the protocone and hypocone are directly connected. In MTR2 (Fig. 4X), there is one individual without a labial anteroloph, and the metaloph seems more often connected to the hypocone. In BC1 (Fig. 4Y), there is one individual without a metalophule; the sinus is always deep, and the mesoloph is absent. In MAB3 (Fig. 4Z–AA), the metalophule disappears in some individuals, while the mesoloph is less common. There are no significant differences in FS1, MAB0A, MAB11B, and CBR1. Regarding biometry (Fig. 3F, Suppl. material 4), no significant differences can be observed between the different sites in the Ribesalbes-Alcora basin. In addition, there is a slight tendency for specimens to become larger over time.

Remarks. The genus *Megacricetodon* has been the focus of significant research interest due to its abundance and wide distribution during the Early and Middle Miocene (Daams and Freudenthal 1988; Lazzari and Aguilar 2007; Wessels and Reumer 2009; Maridet et al. 2011; Oliver and Peláez-Campomanes 2013, 2014, 2016; Bonilla-Salomón et al. 2021; Jovells-Vaqué and Casanovas-Vilar 2021; Čermák et al. 2023, among others). The probable origin of this genus is in Asia, with the possibility of *Megacricetodon beijiangensis* Maridet et al., 2011 in China (Maridet *et al.* 2011) or *Megacricetodon dzhungaricus* (Kordikova and de Bruijn, 2001) in Kazakhstan (Kordikova and de Bruijn 2001), being possibly the oldest species described so far. An alternative hypothesis proposes an origin in Turkey, with an indeterminate form found in Keseköy (Wessels et al. 2001). These localities correlate with the European MN3 (Wessels et al. 2001; Wessels 2009; Maridet et al. 2011; Flynn and Wessels 2013). The temporal range of this genus extends to the island site of Gargano (MN13). However, the karstic origin of the latter site means that the record is a mixture of materials of different ages, according to Freudenthal and Martín Suárez (2010). Therefore, it can be concluded that the most recent record is that cited from the MN9 by Kälin (1999).

The species *M. primitivus*, in conjunction with *Megacricetodon bezianensis* Bulot, 1980, represents the most primitive species identified in south-western Europe (Oliver and Peláez-Campomanes 2014; Čermák et al. 2023). Furthermore, the existence of multiple species of this genus in the Iberian Peninsula dates back to the Middle Miocene, as evidenced by the coexistence of *M. primitivus* with other species of the same genus during this period (Sesé 2006; van der Meulen et al. 2012; Casanovas-Vilar et al. 2016). In the Early Miocene of France, *M. primitivus* undoubtedly coexists with other species of the same genus, including *M. bezianensis* and *Megacricetodon aunayi* Lazzari & Aguilar, 2007 (Antoine et al. 2000; Ginsburg and Bulot 2000; Bulot et al. 2009).

The populations of the Calatayud-Montalbán Basin, as meticulously documented by Oliver and Peláez-Campomanes (2014), provide a detailed understanding of the morphology of M. primitivus. This understanding is defined by specific characteristics: the m1 with a rounded and generally simple anteroconid, a short anterolophulid, and an ectomesolophid that is typically absent; the m3 mesolophids are usually present at low frequency; the m1 has double anteroconid, which are typically accompanied by a small anterior platform, a strong lingual mesocingulum that is present in 20% of specimens, and a mesoloph that is usually short to medium length. This detailed morphology is comparable to that observed in the material studied here, although with some minor variations, which will be discussed in further detail below.

The material under study is distinguished from other small and medium-sized species of this genus from Europe and Turkey by its relatively smaller size, *Megacricetodon andrewsi* Peláez-Campomanes & Daams, 2002, *Megacricetodon similis* (Fahlbusch, 1964), and *Megacricetodon grueneri* Čermák et al., 2022 (Peláez-Campomanes and Daams 2002; Čermák et al. 2023). The material under study exhibits significant distinguishing characteristics in comparison with *Megacricetodon collongensis* (Mein, 1958), including a higher frequency of double anteroconids, longer anterolophs/lophids, more symmetrical anterocones of M1, and a greater prevalence of protolophs and double metalophs in M1 and M2. It differs from *Megacricetodon debruijni* Freudenthal, 1968, in that it exhibits split anteroconids on M1 and short mesolophids. It is also distinguished from *Megacricetodon freudenthali* García Moreno (in Álvarez-Sierra and García Moreno, 1986), *Megacricetodon lopezae* García Moreno (in Álvarez-Sierra and García Moreno, 1986), *Megacricetodon minor* (Lartet, 1851), *Megacricetodon minutus* Daxner, 1967, and *Megacricetodon rafaeli* Daams & Freudenthal, 1988. The material under study differs from these in possessing an undivided anterocone. Furthermore, it differs from *Megacricetodon tautavelensis* Lazzari & Aguilar, 2007 in terms of its smaller size, a higher percentage of divided anterocones, shorter mesolophs/ids, and a higher percentage of representation of crescent-shaped anteroconids. Finally, *Megacricetodon hellenicus* Oliver and Peláez-Campomanes, 2016 differs from the aforementioned material by having the M1 in that it has a less deeply divided anterocone, longer mesolophs and entolophs; M2 has a higher percentage of ectolophs; M3 has longer entolophs; the anteroconid of m1 is lower, and the mesolophids and lingual anterolophid of m2 are the longest (Oliver and Peláez-Campomanes 2014, 2016).

Given the substantial number of localities in which this species is present, a comparison was made between the present material and that from the localities of the Calatayud-Montalbán Basin. The most numerous population from each of the localities, Ca (Artesilla), Cb (Vargas 1a), and the type locality (Valtorres, MN5, local area Db), was selected for analysis (Oliver and Peláez-Campomanes 2014).

In the M1s of the Calatayud-Montalbán Basin, the anterocone generally exhibits a small anterior platform; however, in a smaller proportion of specimens, this feature is absent, and in a lesser degree, the anterocones display a small cingulum or the anterocone is barely divided. In the material studied, this form is dominant only in MTR2. In the remaining localities, the presence of this anterior platform or the cingulum is exceedingly rare. It is noteworthy that MAB5 contains multiple specimens exhibiting a slight division of the anterocone. About the symmetry of the anterocone of M1, the prevailing morphology in the populations used for comparisons is that in which the labial cusp is larger than the lingual cusp, except Artesilla, where the two cusps are almost of the same size. A similar phenomenon is observed in the localities of the Ribesalbes-Alcora Basin, where something similar occurs, where three sites (MCX3, MAB5, and CBR1) exhibit comparable sizes between the anterocone cusps. In the type locality, the connection of the anteroloph of M1 to the anterocone occurs at similar frequencies along the middle part of the cusps of the anterocone or on the lingual cusp, with a slightly higher frequency in the latter case.

In the Ribesalbes-Alcora Basin, except MAB3 and MAB5, where both morphologies are represented in equal proportions, there is a striking prevalence of the anteroloph attached to the lingual cusp in the remaining materials. The presence of the partially developed or incipient labial ridge of the anteroloph of M1 is an infrequent occurrence in the localities with which it is compared. In contrast, it is similar in our localities, with the incipient stage slightly more common. The protoloph of M1 in the localities used for comparisons of the Calatayud-Montalbán Basin is predominantly single and posterior, with a lesser prevalence of complete or interrupted double forms. These also occur in our material, although in MAB3 the dominant form is that with the small unconnected ridge.

Concerning the lingual mesocingulum of M1, the number of individuals exhibiting a robust lingual mesocingulum was documented in the populations utilised for comparisons. This character is not particularly prevalent in the material under consideration. However, when only the presence or absence of the mesocingulum-anteroloph connection is considered, the proportions are similar or even higher. The ectoloph is typically longer in the localities of the Ribesalbes-Alcora Basin than in the localities used for comparisons of the Calatayud-Montalbán Basin, and a comparable development is observed solely at the Artesilla site. In contrast, the number of connections with the mesoloph is very similar in both groups of localities. The mesoloph of M1 demonstrates a comparable development, except for MCX3, where they are longer. At the same time, the metalophule of M1 is predominantly connected to the base of the posteroloph in the localities used for comparisons. In the localities of the Ribesalbes-Alcora Basin, there is material where a posteriorly directed metalophule dominates, thereby reducing the size of the posterosinus.

Regarding the development of the M2 protolophule, in most of the populations utilised for comparisons, it is anterior, or an incomplete posterior protolophule manifests with significantly reduced frequency, and the transverse, double, or posterior forms are residual. Conversely, within the material studied, the proportions observed in the sites belonging to the *L. florancei* biozone are consistent with those seen in other populations, while in the sites belonging to the *L. ellipticus* biozone, the transverse forms predominate. The ectoloph's length and percentage of connections with the mesoloph are comparable. Notably, the ectoloph-mesoloph junction is generally less frequent in the oldest deposits belonging to the local *L. florancei* biozone of the Ribesalbes-Alcora Basin. The development of the M2 metalophule is very similar in both populations, with the anterior form dominating, although the transverse form predominates in MCX3 and the posterior metalophule in MAB0A.

The morphology of the metalophule of M3 is similar in both basins, predominantly connected to the anterior ridge of the hypocone, except for the exception of BC1, where the majority of specimens are devoid of a metalophule.

In m1, the anteroconid is consistently simple, although at very low frequencies, the populations employed for comparisons from the Calatayud-Montalbán Basin may be slightly divided. The labial ridge of the m1 anterolophulid is predominantly absent in both basins, although incipient ridges are well represented in BC1 and well-developed ridges are present in Vargas 1A. The anterior metalophulid of m1 is present in the majority of specimens from both basins, more frequently separated from the protoconid in the Ribesalbes-Alcora Basin than in the populations used for comparisons of the Calatayud-Montalbán Basin. The mesolophid lengths of m1, m2, and m3 are similar in the localities of both basins, although in m2 of the localities studied, there are proportionally more specimens that reach the labial edge. On the other hand, the mesolophids of m3 occur only in the more modern deposits belonging to local biozone *L. ellipticus* in the Ribesalbes-Alcora Basin. The absence of ectomesolophids in m1 and the length of the anterolophid of m2 (short) are similar in both basins. Although in the latter case, the length of the m2 anterolophid is shorter, the well-developed form is more abundant in the MCX3, BC1, and MAB5 sites.

The specimens from the Calatayud-Montalbán and the Ribesalbes-Alcora basins studied here are similar in size (see Fig. 3). However, minor discrepancies do emerge: the m1 is similar to those of the populations utilised for comparisons of local biozone C (Ca and Cb), though with some shorter specimens in MCX2, MCX3, and MTR2; the m2 are also more similar to the local biozone C populations, with maximum length values slightly higher than in the material under study; the m3 the sizes are similar to those of the deposits of the same local biozone, except for one specimen found in MAB0B; the M1, although similar, is generally closer to the range of the locality used for comparisons in local biozone Cb; the M2 are identical to those of this locality, only the material from MAB0A is longer; and finally, regarding the M3, there is one specimen from BC1 and one from MAB3 that are narrower than those from this locality, while the rest are of similar size.

In relation to the Buñol zone, the Barranco de Candel site is distinguished by the following features in comparison with our material: one specimen with a slightly bilobed anteroconid of the M1; the anterolophid of the M2 is typically more developed; the M2 mesolophid is longer; the M1 ectolophs are more prevalent; and the M1 mesolophs are longer. Regarding biometrics, the specimens from the Barranco del Candel site are broadly similar to those studied from the Ribesalbes-Alcora Basin, although the M1s are slightly smaller (Adrover et al. 1987). Furthermore, the morphology of the material from the Buñol site is comparable to that of the Ribesalbes-Alcora Basin sites, with the exception of the mesolophid of m1, which is slightly longer, and the anterolophid of m1, which is somewhat shorter. Also, the lingual anterolophid of m2 is more developed, the protolophule is almost double in half of the specimens, which is the same as in MAB3, and the mesoloph of M1 is shorter. The measurements are similar, except M2 is slightly smaller and M3 is slightly broader (Daams and Freudenthal 1974).

In the Morteral section (1–20A), within the Magro Basin (including *M. primitivus* and some taxa in open nomenclature (*Megacricetodon* sp. 1 and 2), the morphology of these taxa is similar. However, there are some differences when compared to our sites. In the more modern sites, there are representatives with a slightly doubled anteroconid of m1 and shorter mesolophids. The m2 exhibits a slightly shorter mesolophid, and the labial ridge of the anterolophid of M1 is less frequently observed. The ectoloph of the M1 is longer. In M2, there is a reduction in the number of partially double and transverse protolophids. Furthermore, in the more modern deposits, the ectoloph is more frequently attached to the mesoloph. The metalophule of M2 exhibits a comparable morphology, with the exception of MCX3, where it is transverse. Biometrically, they are similar, except for *Megacricetodon* sp. 2, which has larger lower molars, and the upper molars are of a similar size (Ruiz-Sánchez 1999; Ruiz-Sánchez et al. 2003).

In the Vallès-Penedès Basin, the remains analysed in this study demonstrate notable similarities to those exhibited by the material found in the following sites: Can Julià 6 and Can Martí Vell I and II, Els Casots 73 and 76. However, a distinguishing feature emerges in the analysis of Can Martí Vell I, where the protolophid is consistently located posteriorly, and the mesolophid of m1 is typically shorter. Biometrically, the material from Catalonia corresponds with the material studied here, including the *Megacricetodon* sp. described by Agustí (1983), for which he emphasized its larger size. While the most recent publications from this basin indicate an increase in size in the more recent deposits, similar to what occurred in the present basin, the measurements are, on average, slightly larger than those of the material studied (Jovells-Vaqué and Casanovas-Vilar 2021).

In the Loranca Basin, particularly at the La Retama site, the mesoloph of M1 is characterised by a reduction in length, the lingual mesocingulum exhibits increased prevalence, the protolophule is posteriorly positioned, and the metalophule is anteriorly situated. In the M2, the mesoloph is shorter; in the M1, there is a higher prevalence of divided anteroconids. In the m2, the lingual anterolophid is less prevalent, and the mesolophids are shorter in length. Biometrically, M2, m2, and m3 are typically smaller in size (Álvarez-Sierra et al. 2006).

Therefore, the morphological and biometric study of the material of *M. primitivus* is in accordance with the findings of Oliver and Peláez-Campomanes (2014), which indicate that the species is highly stable over time, exhibiting intraspecific variability. Additionally, there is no evident evolutionary trend in either size or morphology. Furthermore, the distribution of dental characters varies considerably across different sites, yet they always retain a resemblance to the type of material.

Subfamily Copemyinae Jacobs & Lindsay, 1984

Genus *Democricetodon* Fahlbusch, 1964

Type species. *Democricetodon crassus* Freudenthal, 1969. Sansan, Middle Miocene.

Democricetodon decipiens (Freudenthal & Daams, 1988)

Figs 5–7

Localities. MCX1, MCX3, MTR1, MTR2, BC1, FS1, MAB0A, MAB0B, MAB3, MAB5, MAB10, MAB11, MAB13, CBR0B, and CBR1.

Material (number of remains). Suppl. material 1; MCX1 (2): 2 M1; MCX3 (1): 1 m1; MTR1 (2): 2 m2; MTR2 (11): 1 m1, 3 m2, 1 m3, 2 M1, 3 M2, 1 M3; BC1 (2): 1 M3, 1 m1; MAB0A (3): 1 m1, 1 m2, 1 M2; MAB0B (1): 1 m3; FS1 (3): 1M2, 1M3, 1 m3; MAB3 (85): 15 m1, 10 m2, 13 m3, 15 M1, 19 M2, 13 M3; MAB5 (69): 15 m1, 11 m2, 4 m3, 12 M1, 14 M2, 13 M3; MAB10 (1): 1 m1; MAB11 (31): 4 m1, 7 m2, 2 m3, 6 M1, 8 M2, 4 M3; MAB13 (1): 1 M3; CBR0B (4): 1 m2, 3 M2 (2); CBR1: 1 m1, 1 m2.

Measurements. Suppl. material 2.

Description. (See Suppl. material 3).

m1 (MAB3; Fig. 5C–F): the anteroconid is simple and it may be located close to the metaconid (8 out of 13) or slightly further away (5 out of 13), and they may be contacting (2 out of 13) or not (11 out of 13). The labial anterolophid is low and may be in contact with the base of the protoconid (11 out of 12) or not (1 out of 12). The anterolophulid may be short (10 out of 15), connected to the protoconid (3 out of 15), or absent (2 out of 15). The metalophulid may be anterior (13 out of 15) or transverse (2 out of 15). The hypolophulid is anterior. The mesolophid may be short (2 out of 15), medium (4 out of 15), long (7 out of 15), or absent (2 out of 15). The ectomesolophid is absent. The sinusid is directed anteriorly, and may be closed by a ridge (5 out of 12), not closed by a ridge (1 out of 12), or have neither ridge nor cusp (6 out of 12). The posterolophid may connect with the entoconid (5 out of 13) or not (8 out of 13).

Variability in other sites: In MCX3 the metalophulid is absent and the hypolophulid is transverse. In MTR2 (Fig. 5A), the hypolophulid is transverse. In BC1 (Fig. 5B), the posterolophid has a posterior ridge; in MAB5 (Fig. 5G, H), the anteroconid is typically closer to the protoconid. In one specimen, the anterolophulid contacts the metaconid. The metalophulid is anterior or absent, and the mesolophid is invariably present. In MAB10 (Fig. 5I), the anterolophulid does not contact the metalophulid. In MAB0A, MAB11 (Fig. 5J), and CBR1, there are no significant morphological differences from the m1 of MAB3. Biometrically, the earliest material from the Ribesalbes-Alcora Basin, categorised as belonging to the local *L. florancei* biozone, exhibits a slightly larger size relative to more recent material classified as the *L. ellipticus* biozone (Fig. 6A, Suppl. material 4).

m2 (MAB3; Fig. 5O–R): the labial anterolophid contacts the anterolabial edge of the protoconid. The lingual anterolophid may be weak and fused to the metaconid (7 out of 10) or absent (3 out of 10). The metalophulid and hypolophulid are anterior. The mesolophid may be short (7 out of 9) or medium (2 out of 9) in length. The ectomesolophid is absent. The sinusid is directed anteriorly. The labial mesocingulum may be a ridge (5 out of 7), cusp-shaped (1 out of 7), or neither cusp-shaped nor ridge (1 out of 7). The posterolophid may be either connected to the entoconid (5 out of 8) or not (3 out of 8). The posterolophid has a posterior ridge.

Variability in other sites: In MTR2 (Fig. 5L–N), there is one specimen with an incipient ectomesolophid. In MAB5 (Fig. 5S), the labial anterolophid may or may not contact the labial mesocingulid around the protoconid, in another the lingual anterolophid is long, in another the sinusid is perpendicular. Finally, two specimens have no posterior crest of the posterolophid. In MAB11 (Fig. 5T, U), there is one specimen in which the labial anterolophid contacts the mesocingulum. There are no significant morphological

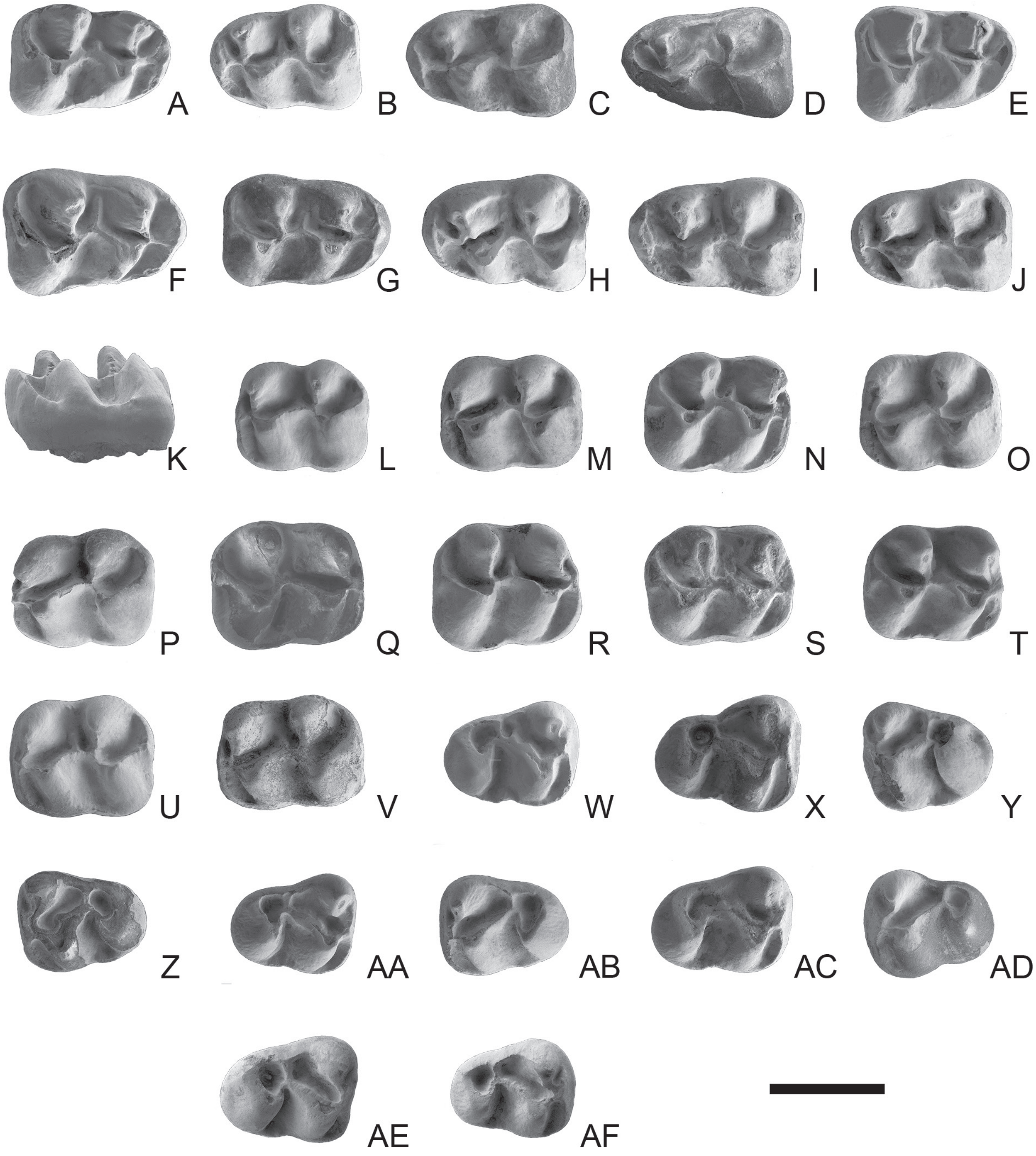

Figure 5. Lower teeth of *Democricetodon decipiens* from the Ribesalbes-Alcora Basin. **A.** Right m1 (MTR2-80); **B.** Left m1 (BC1-57); **C.** Left m1 (MAB3-152); **D.** Left m1 (MAB3-154); **E.** Right m1 (MAB3-156); **F.** Right m1 (MAB3-164); **G.** Right m1 (MAB5-188); **H.** Left m1 (MAB5-530); **I.** Left m1 (MAB10-1); **J.** Left m1 (MAB11-39); **K.** Left m1, labial view (MAB3-157); **L.** Left m2 (MTR2-3); **M.** Left m2 (MTR2-93); **N.** Right m2 (MTR2-94); **O.** Left m2 (MAB3-191); **P.** Left m2 (MAB3-195); **Q.** Right m2 (MAB3-196); **R.** Right m2 (MAB3-201); **S.** Right m2 (MAB5-197); **T.** Right m2 (MAB11-2); **U.** Left m2 (MAB11-45); **V.** Left m2 (CBR0B-1); **W.** Right m3 (MTR2-98); **X.** Right m3 (MAB0B-15); **Y.** Left m3 (FS1-31); **Z.** Left m3 (MAB3-224); **AA.** Right m3 (MAB3-228); **AB.** Left m3 (MAB3-231); **AC.** Right m3 (MAB3-233); **AD.** Left m3 (MAB5-544); **AE.** Right m3 (MAB5-545); **AF.** Right m3 (MAB11-53). Scale bar: 1 mm.

differences in MTR1, MAB0A, CBR1, and CBR0B (Fig. 5V). Biometrically, the older material from the Ribesalbes-Alcora Basin, belonging to the local *L. florancei* biozone, is similar to the more modern material belonging to the *L. ellipticus* biozone (Fig. 6B, Suppl. material 4).

m3 (MAB3; Fig. 5Z–AC): the labial anterolophid may connect to the antero-labial edge of the protoconid (10 out of 11) or connect to the labial mesocingulum (1 out of 11). The lingual anterolophid may be medium (1 out of 11), short (6 out of 11), or incipient (4 out of 11). The mesolophid is

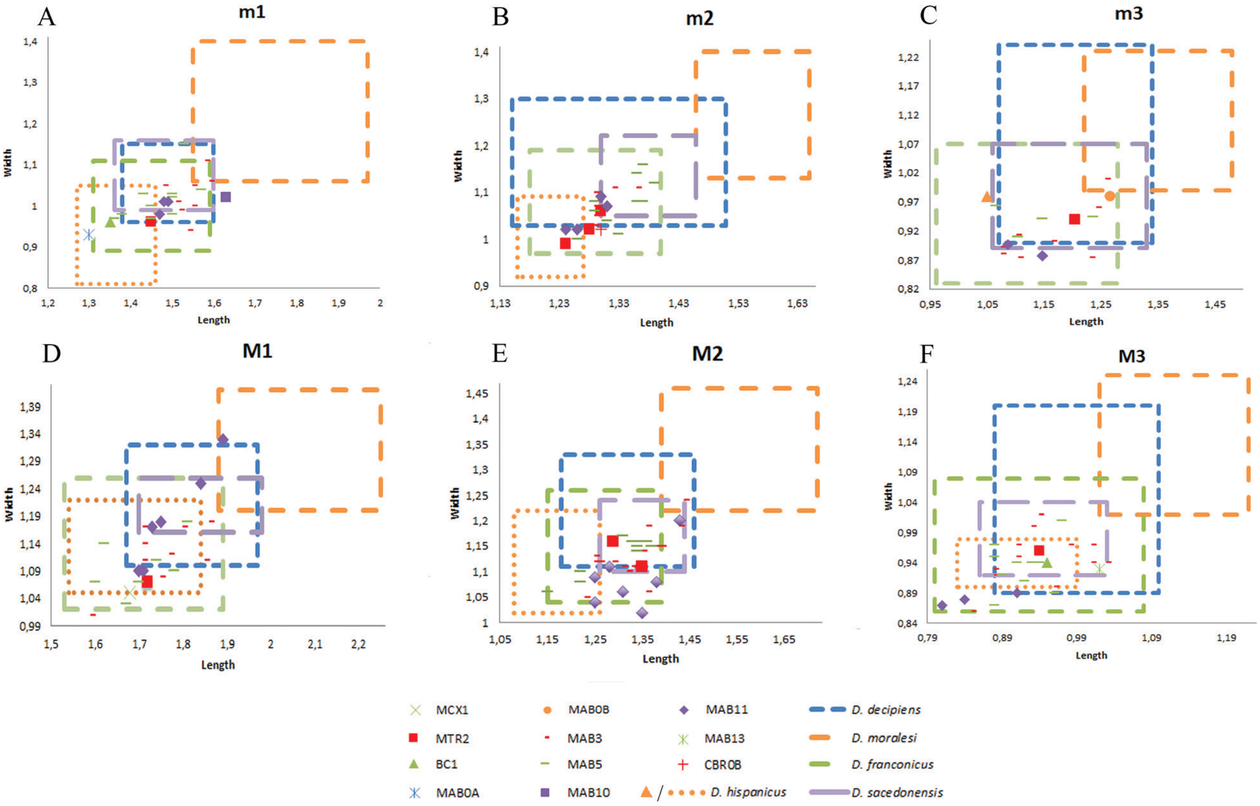

Figure 6. Comparison of length and width measurements (in mm) of *Democricetodon decipiens* from Ribesalbes-Alcora Basin. *D. hispanicus* from Villafeliche 2A (type locality (t.l.)); *D. decipiens* from Buñol (t.l.); *D. moralesi* from La Col (l.t.); *D. franconicus* from Erkertshofen (l.t.); *D. sacedonensis* from Córcoles; and the material from Ribesalbes-Alcora Basin (Fahlbusch 1966, van der Meulen et al. 2003, Freudenthal 2006, this publication).

mostly absent, with only one specimen showing an incipient one. The metaconid and posterolophid are connected. The mesosinusid is occluded by a ridge (6 out of 10) or opens to the labial side unobstructed (4 out of 10).

Variability in other sites: In MTR2 (Fig. 5W), the mesolophid is double, with the anterior one being incipient. In MAB0B (Fig. 5X), the mesolophid is incipient, with the posterior part of the tooth narrower than in other sites. In FS1 (Fig. 5Y), there is an incipient mesolophid, and the sinusid has a cusp on the labial edge. In MAB5 (Fig. 5AD–AE), the labial anterolophid may be short or absent as well as long, the lingual anterolophid may be long, and the metaconid and posterolophid are not connected in two specimens. In MAB11 (Fig. 5AF), there is one specimen with a strong lingual anterolophid, and the mesosinusid has a cusp on the labial margin. A biometric analysis reveals a decrease in size of the specimens over time in the Ribesalbes-Alcora Basin (Fig. 6C, Suppl. material 4).

M1 (MAB3; Fig. 7C–F): The anterocone may be simple (13 out of 14) or shallowly divided (1 out of 14), with a platform on the anterior side. The labial part of the anterocone may be larger than the lingual part (12 out of 13) or they are of similar size (1 out of 13). The labial anteroloph may connect to the paracone (12 out of 13), but in one specimen, the labial anteroloph runs from the anterocone to the mesosinus. The lingual anteroloph may connect with the protocone (7 out of 13) or not (6 out of 13). The anteroloph connects the lingual part of the anterocone with the protocone. The labial ridge of the anterolophule may be incipient (4 out of 15) or absent (11 out of 15). The protoloph may be double (1 out of 14), almost double with incipient or short anterior protoloph (3 out of 14), or posterior, connecting with the longitudinal ridge near the protocone (10 out of 14). The metaloph may connect with the posteroloph (11 out of 13) or the hypocone (2 out of 13). The mesoloph may be short (3 out of 13), medium (3 out of 13), or long (7 out of 13). The mesostyle may be present (6 out of 9) or not present (3 out of 9). The ectoloph may be incipient (6 out of 13) or absent (7 out of 13). The metacone ridge is absent. The entostyle may take the form of a cusp (3 out of 11) or a cingulum (8 out of 11). The posterosinus may be small (4 out of 9), medium (1 out of 9), long (2 out of 9), or absent (2 out of 9). The posteroloph may be connected with the metacone (6 out of 9) or not (3 out of 9).

Variability in other sites: In MCX1 (Fig. 7A), the metalophule is absent. In MTR2 (Fig. 7B), a ridge may be present in front of the anterocone. In MAB5 (Fig. 7G), there is a decrease in the number of individuals where the contact between the lingual anteroloph and protocone is present, and there is one specimen with a short labial crest of the anteroloph. The ectoloph is less common; there is one M1 with a metacone ridge, and the posterosinus is smaller. In MAB11 (Fig. 7H–J), two specimens were observed with a ridge in front of the anterocone, the lingual anteroloph consistently contacts the protocone, and the labial ridge of

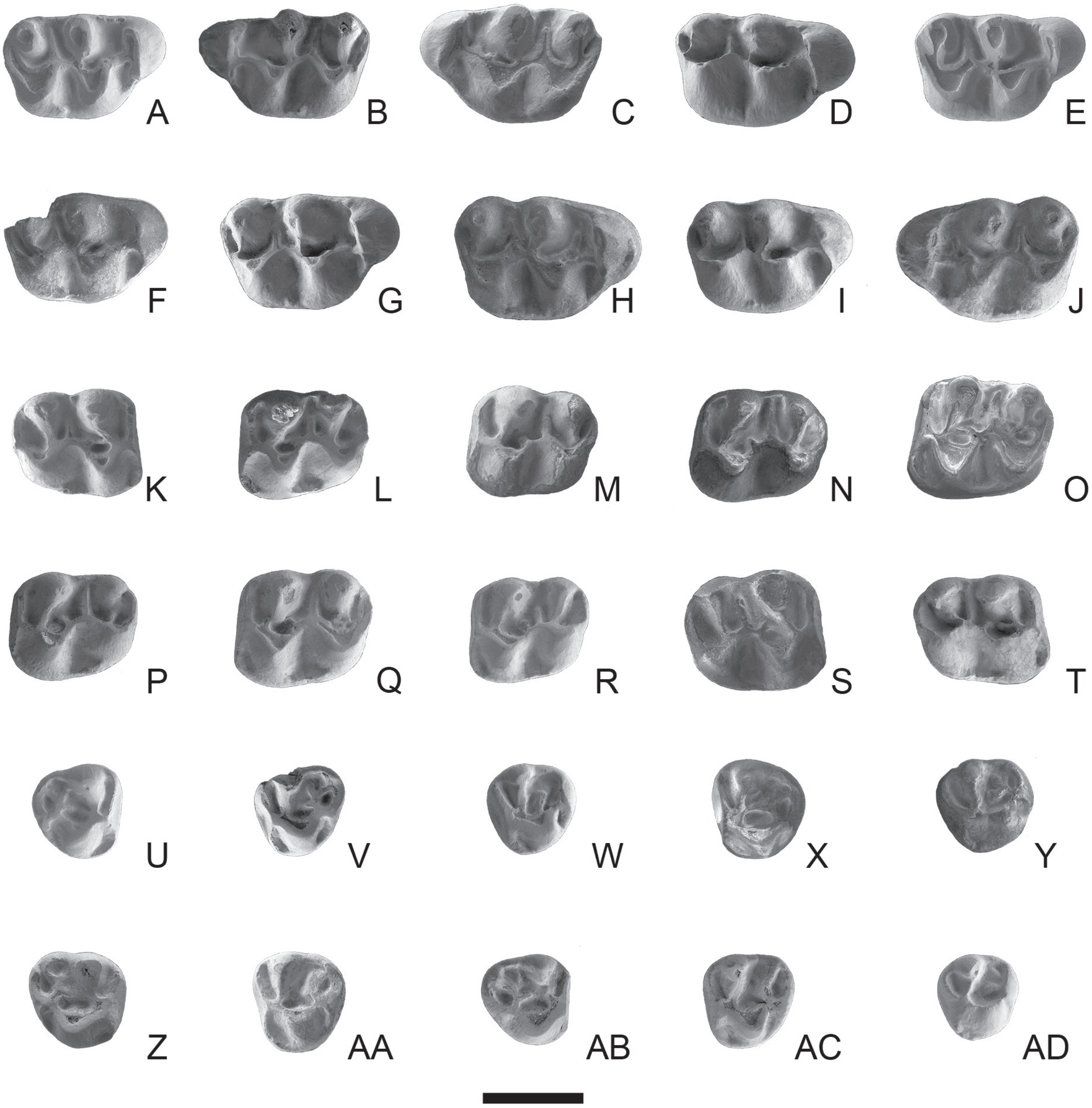

Figure 7. Upper teeth of *Democricetodon decipiens* from the Ribesalbes-Alcora Basin. **A.** Right M1 (MCX1-1); **B.** Left M1 (MTR2-56); **C.** Left M1 (MAB3-70); **D.** Right M1 (MAB3-74); **E.** Right M1 (MAB3-77); **F.** Right M1 (MAB3-78); **G.** Right M1 (MAB5-516); **H.** Right M1 (MAB11-18); **I.** Right M1 (MAB11-19); **J.** Left M1 (MAB11-20); **K.** Right M2 (MTR2-62); **L.** Left M2 (MTR2-63); **M.** Left M2 (MAB3-96); **N.** Left M2 (MAB3-105); **O.** Left M2 (MAB3-110); **P.** Left M2 (MAB3-194); **Q.** Left M2 (MAB5-520); **R.** Left M2 (MAB11-3); **S.** Right M2 (MAB11-25); **T.** Right M2 (MAB11-28); **U.** Right M3 (MTR2-69); **V.** Left M3 (BC1-51); **W.** Left M3 (MAB3-124); **X.** Left M3 (MAB3-125); **Y.** Left M3 (MAB3-127); **Z.** Right M3 (MAB3-128); **AA.** Left M3 (MAB5-227); **AB.** Right M3 (MAB5-228); **AC.** Left M3 (MAB5-229); **AD.** Left M3 (MAB11-37). Scale bar: 1 mm.

the anteroloph may be double (2 out 6), with the anterior one developed and the posterior one incipient (2 out 6) or absent (2 out 6). There are two specimens with a double protolophule. Two specimens exhibit a double metalophule, one of these with the formation of a double mesoloph, and the other one surrounding the mesoloph. In the latter, the surrounding mesoloph is longer. The ridge of the metacone is present in two specimens, and the posterosinus is smaller. Biometrically, there is a slight tendency for specimens to become larger over time (Fig. 6D, Suppl. material 4).

M2 (MAB3; Fig. 7M–P): the lingual anteroloph may be of three distinct lengths: it may be long and reach the antero-lingual border of the protocone (9 out of 16), of medium length (1 out of 16), or short (9 out of 16). The labial anteroloph may either be long and connect to the paracone (15 out of 17) or be disconnected (2 out of 17). The protolophule may be double (7 out of 17), and there are two protolophule, but the posterior one is incomplete (9 out of 17) or simple and connected to the antero-labial part of the protocone (1 out of 17). The metalophule may be anterior (9 out of 18), posterior (2 out of 18), or there are two metalophules, but the anterior one is incomplete (1 out of 18), double (1 out of 18), or disconnected from the metaconule (1 out of 18). The mesoloph may be long, contacting the labial border (3 out of 18), long (12 out of 18), or medium (3 out of 18). The ectoloph may be present (5 out of 16) or absent (11 out of 16). The metaconal ridge may be present (2 out of 17) or not (15 out of 17). The lingual mesocingulum may close the sinus (10 out of 15) or not (5 out of 15). The mesostyle is present in 9 of 16 specimens. The sinus is transverse. The posteroloph may either connect to the metacone (15 out of 17) or not (2 out of 17).

Variability in other sites: In MTR2 (Fig. 7K, L), the sinus is posterior in one specimen. In MAB5 (Fig. 7Q), the lingual anteroloph is shorter, and the metalophule may be transverse. MAB11 (Fig. 7R–T) has one specimen with a posterior metalophule. No significant morphological differences were observed in MAB0A, CBR0B, and FS1. Biometrically, the Ribesalbes-Alcora Basin sites were found to be similar, except for MAB11, where they were generally narrower (Fig. 6E, Suppl. material 4).

M3 (MAB3; Fig. 7W–Z): The labial anteroloph may reach the antero-labial side of the paracone (6 out of 12), or not (6 out of 12), it may be long (7 out of 11) or of medium length (4 out of 11). The lingual anteroloph reaches the protocone base; it may be long (2 out of 12), medium in length (5 out of 12), short (4 out of 12), or platform-shaped (1 out of 12). The hypocone may be either large (3 out of 12) or small (9 out of 12). The metacone's position relative to the tooth's ridge is another distinguishing factor: it may be incorporated within the ridge surrounding the tooth (8 out of 10) or not (2 out of 10). The metalophule is connected to the anterior ridge of the hypocone (7 out of 11), does not reach the metacone (1 out of 11), is connected to the neo-entoloph (2 out of 11), or connects to the anterior ridge of the hypocone and the axioloph (1 out of 11). The mesoloph may be long (1 out of 13), short (7 out of 13), incipient (1 out of 12), or absent (2 out of 12). The axioloph may be long (3 out of 12), long with contact to the paracone/protolophule (3 out of 12), short (3 out of 12), incipient (1 out of 12), or absent (2 out of 12). The sinus may be relatively long (3 out of 12), medium (4 out of 12), or short (5 out of 12). The mesosinus may be wide (4 out of 12) or narrow (8 out of 12).

Variability in other sites: The mesoloph contacts the paracone in MTR2 (Fig. 7U). In MAB5 (Fig. 7AA–AC), the hypocone may be absent, and the mesoloph is more often absent. In MAB11 (Fig. 7AD), there is one specimen without a hypocone, and the mesoloph is shorter. No significant morphological differences were observed in BC1 (Fig. 7V), MAB13, and FS1. A biometric analysis reveals that the different sites in the Ribesalbes-Alcora Basin are morphologically similar (Fig. 6F, Suppl. material 4).

Remarks. The taxonomic status of the genus *Democricetodon* has been the subject of extensive debate in the literature (Kälin 1999; van der Meulen et al. 2003; Casanovas-Vilar 2007; Jovells-Vaquè and Casanovas-Vilar 2018a). This debate has encompassed a range of perspectives, including the proposal of the existence of multiple genera, such as *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia*, and *Renzimys* (Freudenthal and Daams 1988; Freudenthal 2006; Ruiz-Sánchez et al. 2013). Conversely, alternative perspectives advocate for the exclusive consideration of *Democricetodon* and *Fahlbuschia* as synonyms (Aguilar 1981; Aguilar et al. 2010a). A third viewpoint suggests the avoidance of such deliberations (Murelaga et al. 2008; de Bruijn 2010; Prieto et al. 2010, among others). However, some scholars have proposed that all the aforementioned genera be subsumed under the genus *Democricetodon* (van der Meulen et al. 2003; Álvarez-Sierra et al. 2006; Fejfar et al. 2011; Casanovas-Vilar et al. 2016; García-Paredes et al. 2016; among others). The latter hypothesis is the one that is more widely accepted, and, as a consequence, will be followed in this publication, as it is not a topic of discussion.

The provenance of the genus under consideration may be located in Anatolia, with the first records in Turkey immediately following the MN1. In contrast, the earliest evidence of the genus in China and Europe is not until MN3/4 (Fejfar et al. 2011). Alternatively, the genus may have originated in Central Asia (Maridet et al. 2011; Flynn and Wessels 2013) and arrived in Europe at the end of MN3 (van der Meulen et al. 2012; among others).

This genus is clearly distinguishable from the species of muroids present in the Ribesalbes-Alcora Basin, which are assigned to *Megacricetodon* and *Eumyarion*, by virtue of its intermediate size and more rounded teeth. Furthermore, *Democricetodon* differs from *Megacricetodon* in having an undivided anterocone of M1 and a generally more complex tooth pattern. Compared to *Eumyarion*, it exhibits a more simplified and advanced pattern (Fejfar 1999). A further distinction is the development of the cusps of the labial side of the upper molars and the lingual part of the lower molars, which are higher than those of the other region (Figs 2J, 5K). In the remaining genera, there is typically less variation in the height of the cusps.

The material under discussion is compared with that described by Freudenthal and Daams (1988), van der Meulen et al. (2003), Freudenthal (2006), and Jovells-Vaquè and Casanovas-Vilar (2021). In addition, a comparison is made with the measurements of *Democricetodon franconicus* Fahlbusch, 1966 by Fahlbusch (1966).

In the M1 from the localities of the Ribesalbes-Alcora Basin, the anterocones are simple, as in the species *D. hispanicus*, *D. decipiens*, *Democricetodon moralesi* van der Meulen et al., 2003, *Democricetodon sacedonensis* Freudenthal, 2006, and *D. franconicus*. About the protolophid, while this character is predominantly double in *D. hispanicus* and the older populations of *D. franconicus*, it is less represented ("morphotype double") in *D. moralesi* and *D. sacedonensis*, the percentages of representation or morphotypes in the Ribesalbes-Alcora Basin are very different in *D. moralesi* and *D. sacedonensis*, similar to those described for *D. decipiens* by van der Meulen et al. (2003) for the Calatayud-Montalbán and Buñol basins. The length of the mesoloph is very similar to that described for *D. decipiens*. It differs from that of *D. hispanicus*, *D. sacedonensis*, and *D. franconicus*, where it is usually medium-long, and also from that of *D. moralesi*, which is shorter. With regard to size (see Fig. 6), the material studied is generally larger than *D. hispanicus* from Villafeliche 2A, smaller than *D. moralesi* from La Col D, slightly smaller than *D. sacedonensis* from Córcoles, and very similar to those of *D. decipiens* from Buñol and *D. franconicus* from Erkertshofen. About the L/W index of M1, the studied material is within the range of variability observed in each of the aforementioned species (Table 1).

Table 1. Relation Length/Width of *Democricetodon decipiens* from the Ribesalbes-Alcora Basin. *D. hispanicus* from Villafeliche 2A (type locality (t.l.)); *D. decipiens* from Buñol (t.l.); *D. moralesi* from La Col (l.t.); *D. franconicus* from Erkertshofen (l.t.); *D. sacedonensis* from Córcoles; and the material from Ribesalbes-Alcora Basin (Fahlbusch 1966; Van der Meulen et al. 2003; Freudenthal 2006; this publication).

Element	Site	n	Min.	Med.	Max.
m1	MTR2	1		1.51	
	BC1	1		1.41	
	MAB0A	1		1.40	
	MAB3	11	1.39	1.49	1.64
	MAB5	10	1.33	1.44	1.53
	MAB10	1		1.60	
	MAB11	3	1.47	1.48	1.50
	Villafeliche 2			1.41	
	Buñol			1.42	
	La Col D			1.47	
	Erkertshofen			1.45	
	Córcoles			1.46	
M1	MCX1	1		1.60	
	MTR2	1		1.62	
	MAB3	10	1.46	1.56	1.67
	MAB5	7	1.42	1.55	1.63
	MAB11	6	1.42	1.50	1.57
	Villafeliche 2			1.46	
	Buñol			1.5	
	La Col D			1.55	
	Erkertshofen			1.5	
	Córcoles			1.53	

In the M2, the mesolophs of the material from the Ribesalbes-Alcora Basin are of a medium-long length, as observed in *D. franconicus*, *D. hispanicus*, and *D. decipiens*. In this regard, the former exhibits a longer length than that observed in *D. moralesi* and *D. sacedonensis*. The ectoloph is absent in *D. hispanicus* and is very poorly represented in *D. franconicus*, *D. decipiens*, and *D. moralesi*, as observed in the localities studied. In the material under consideration, protolophules are predominantly double and metalophules are primarily anterior, as seen in *D. decipiens*, *D. franconicus*, and *D. sacedonensis*. The size of the material from the Ribesalbes-Alcora Basin is generally larger than that of *D. hispanicus* from Villafeliche 2A, smaller than that of *D. moralesi* from La Col D, and similar to that of *D. decipiens* from Buñol, *D. franconicus* from Erkertshofen, and *D. sacedonensis* from Córcoles.

The M3 from the Ribesalbes-Alcora Basin is comparable in size to *D. hispanicus*, *D. franconicus*, and *D. decipiens*, with a narrower width than *D. sacedonensis* and a smaller overall size than *D. moralesi*.

For the m1, while in *D. hispanicus* the anteroconid-metaconid contact is invariably present, in *D. decipiens* it is present in approximately half of the examined remains. At the same time, in *D. franconicus* it is highly variable. In *D. moralesi* and *D. sacedonensis*, the contact is present in only a few specimens. In the material studied, something similar to *D. decipiens* occurs, tending to have a higher percentage of connections in the localities belonging to the *L. florancei* local biozone. However, there are only a few specimens in these sites. On the other hand, in the Ribesalbes-Alcora Basin, the metalophulid is anterior, rarely transverse or absent, whereas in *D. franconicus*, the metalophulid is usually transverse, in *D. sacedonensis* transverse or anterior, and variable in the rest. The mesolophid of the material from the Ribesalbes-Alcora Basin is typically long, as in *D. hispanicus*, and shorter in *D. decipiens*, *D. franconicus*, *D. sacedonensis*, and *D. moralesi*. The remaining morphologies of m1 are analogous to those previously documented for *D. hispanicus*, *D. franconicus*, *D. sacedonensis*, *D. decipiens*, and *D. moralesi*. With regard to size, the material from the Ribesalbes-Alcora Basin is typically larger than *D. hispanicus* from Villafeliche 2A, smaller than *D. moralesi* from La Col D, and of the same size as *D. decipiens* from Buñol, *D. sacedonensis* from Córcoles, and *D. franconicus* from Erkertshofen. The L/W index indicates that the studied material falls within the variability of one of the described species (Table 1).

The mesolophid m2 from the Ribesalbes-Alcora Basin material is characterised by either a short or, on rare occasions, a long form, with a length comparable to that of the species *D. franconicus*, *D. hispanicus*, *D. decipiens*, and *D. moralesi*, and shorter than that of *D. sacedonensis*. The size of the m2 from the Ribesalbes-Alcora Basin is typically larger than those of *D. hispanicus* from Villafeliche 2A, smaller than those of *D. moralesi* from La Col D, and *D. sacedonensis* from Córcoles, and very similar to those of *D. decipiens* from Buñol and *D. franconicus* from Erkertshofen.

The m3 from the Ribesalbes-Alcora Basin exhibits mesolophids in the local *L. florancei* biozone localities, although the number of identified remains of this element is limited. Such occurrences are absent in *D. sacedonensis* and observed only infrequently in *D. hispanicus* and *D. decipiens*. The size of the m3 in this study is generally larger than that of *D. hispanicus* from Villafeliche 2A, smaller than that of *D. moralesi* from La Col D, not as wide as that of *D. sacedonensis* from Córcoles, and very similar in size to that of *D. decipiens* from Buñol and *D. franconicus* from Erkertshofen.

The material under study exhibits notable disparities compared with other European species of the genus

Democricetodon of the same age. It is distinguished from *Democricetodon anatolicus* Theocharopoulos, 2000 by its larger size and more robust anteroconid (Theocharopoulos 2000); and from *Democricetodon doukasi* Theocharopoulos, 2000 by its larger size, less developed M1-2 ectoloph of the M1-2, and longer mesolophids (Theocharopoulos 2000); from *Democricetodon affinis* (Schaub, 1925) is distinguished for being smaller, having shorter mesolophs, longer mesolophids and the anterocone exhibiting a slight division (Maridet 2003); from *Democricetodon brevis* (Schaub, 1925) from MN6, of which there is a citation in MN4 from Port la Nouvelle (Aguilar et al. 1999) for having a less divided anterocone and shorter mesoloph/phids (Maridet 2003); from *Democricetodon gracilis* (Fahlbusch 1964) for having shorter mesolophs and larger size (Maridet 2003); and from *Democricetodon mutilus* (Fahlbusch, 1964) because the protolophule of M1 is usually double or nearly double, the mesolophule is shorter, the lingual valleys of m1 and 2 are not as anterior, and m3 usually has an entoconid and is smaller (Maridet 2003); from *Democricetodon gaillardi* (Schaub, 1925) due to the smaller size, the shorter mesoloph/ids, the less elongated m1, and because the anteroconid is weaker (Maridet, 2003); from *Democricetodon freudenthali* (Antunes and Mein 1981) because of the smaller size and the longer mesolophs (Antunes and Mein 1981); from *Democricetodon romieviensis* (Freudenthal, 1963) for being larger, having a less developed double protolophule of M1 and metalophule of M2, and for having shorter mesoloph/ids (Daams and Freudenthal 1974).

Compared with all previously documented *Democricetodon* species, it can be concluded that the *Democricetodon* material from the Ribesalbes-Alcora Basin localities can be assigned to *D. decipiens*. Its morphology and size fall within the range of intrapopulation variability, and it exhibits novel morphological features not observed in any other species of the genus, including the mesolophs and the double labial ridges of the anteroloph of MAB11.

Subfamily Eumyarioninae Onay, 1989

Genus *Eumyarion* Thaler, 1966

Type species. *Cricetodon medium* Lartet, 1851 (=*Cricetodon helveticum* Schaub, 1925). Sansan, Middle Miocene.

Eumyarion weinfurteri (Schaub & Zapfe, 1953)

Figs 8A–T, 9

Localities. FS1, MAB3, and MAB5.

Material (number of remains). Suppl. material 1; FS1 (1): 1 m2; MAB3 (21): 3 M1, 1 M2, 3 M3, 3 m1, 6 m2, 5 m3; MAB5 (8): 1 M1, 1 M3, 2 m1, 2 m2, 2 m3.

Measurements. Suppl. material 2.

Description. ***m1*** (MAB3; Fig. 8A, B): the anteroconid is simple. The anterolophulid may be complete (1 out of 3), low (1 out of 3), or incomplete (1 out of 3). In the latter case, the anterolophulid is a ridge that starts from the protoconid. A ridge begins from the metaconid and may contact the anteroconid (2 out of 3) or not (1 out of 3). The anterior metalophulid is directed slightly forward, and it may either connect with the anterolophulid (2 out of 3) or not (1 out of 3). The posterior metalophulid may contact with the posterior ridge of the protoconid (1 out of 3), there is only a spur (1 out of 3), or absent (1 out of 3). The protosinusid is almost closed by a low ridge coming from the anteroconid. The anterosinusid may be well developed (1 out of 3) or practically disappear by the anterior spur of the metaconid (2 out of 3). The posterior ridge of the protoconid may be short, and does not connect with the mesolophid (1 out of 3) or is of medium size and contacts the mesolophid (2 out of 3). The mesolophid is of medium length. The ectomesolophid may reach the labial margin (2 out of 3) or be absent (1 out of 3). The hypolophulid is transverse and connects with the ectolophid. The posterior ridge of the hypoconid may be present (2 out of 3) or not (1 out of 3), resulting in a high posterolophid connected to the entoconid, which encloses the posterosinusid.

Variability in other sites: in MAB5 (Fig. 8C, D), the anterior ridge of the metaconid does not contact the anteroconid, the anterior metalophulid is a spur, while the posterior one is directed towards the mesolophid in one specimen. In one, the mesolophid is long, while the ectomesolophid is either a spur or absent. The m1 from MAB5 is comparatively larger than that of MAB3 (Fig. 9A).

m2 (MAB3; Fig. 8F, G): the lingual anterolophid is of medium length, and it may not reach the lingual margin (4 out of 5) or be absent (1 out of 5). The anterosinusid is closed by the anterolophid (4 out of 5) or absent (1 out of 5). The labial anterolophid connects to the base of the protoconid. The metalophulid is simple and connects to the anterolophid. On the lingual side, the posterior ridge of the metaconid connects with the lingual part of the posterior ridge of the protoconid (4 out of 5), or not (1 out of 5), almost completely enclosing the mesosinusid. The posterior ridge of the protoconid is of medium length, and two specimens contact the mesolophid. The mesolophid is medium length (1 out of 6), short (4 out of 6), or absent (1 out of 6). The ectomesolophid may be short (1 out of 5), medium (1 out of 5), or absent (3 out of 5). The posterior crest of the hypoconid is long (2 out of 6) or only a spur (4 out of 6). The posterolophid is high and connects with the entoconid, enclosing the posterosinusid (4 out of 6) or not contacting the entoconid (2 out of 6).

Variability at other sites: FS1 (Fig. 8E) exhibits no notable differences. However, in MAB5, the lingual anterolophid is shorter (Fig. 8H, I). Additionally, the m2 of the study material appears to lengthen with time in terms of biometry (Fig. 9B).

m3 (MAB3; Fig. 8J, K): the lingual anterolophid is short, and the labial one connects with the base of the protoconid. The metalophulid contacts obliquely

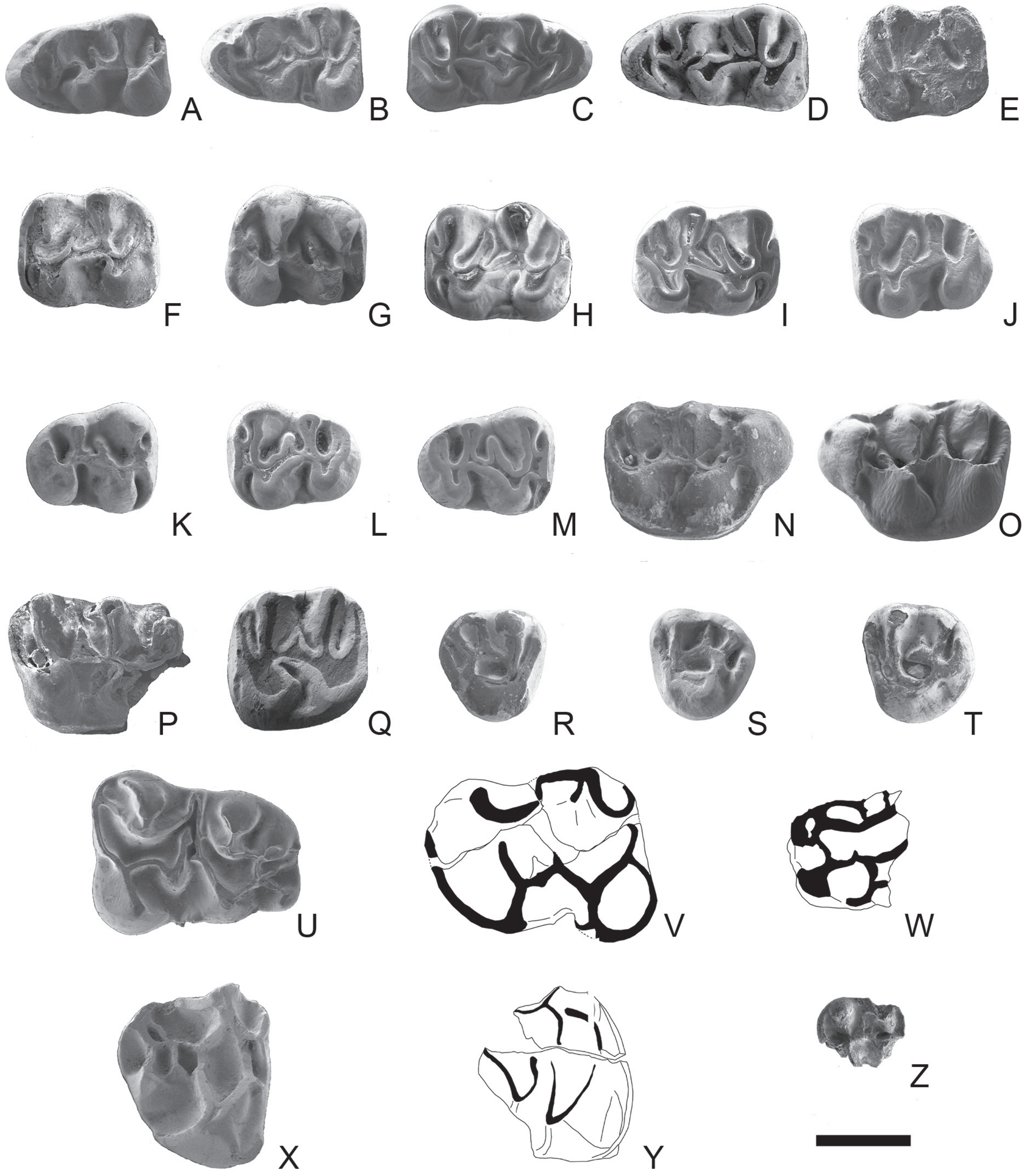

Figure 8. Teeth of *Eumyarion weinfurteri*, *Melissiodon* sp., and Muroidea indet. From the Ribersalbes-Alcora-Basin. *Eumyarion weinfurteri*: **A.** Left m1 (MAB3-161); **B.** Left m1 (MAB3-162); **C.** Right m1 (MAB5-75); **D.** Left m1 (MAB5-76); **E.** Right m2 (FS1-29); **F.** Left m2 (MAB3-203); **G.** Right m2 (MAB3-206); **H.** Left m2 (MAB5-53); **I.** Right m2 (MAB5-54); **J.** Left m3 (MAB3-241); **K.** Right m3 (MAB3-242); **L.** Left m3 (MAB5-56); **M.** Right m3 (MAB5-57); **N.** Right M1 (MAB3-82); **O.** Left M1 (MAB3-83); **P.** Right M1 (MAB5-515); **Q.** Left M2 (MAB3-111); **R.** Right M3 (MAB3-133); **S.** Left M3 (MAB3-134); **T.** Left M3 (MAB3-135). *Melissiodon* sp.: **U.** Right m1 (MAB3-168); **V.** Left m3 (MAB3-169); **W.** Left M1 (BC1-32); **X.** Left M3 (BC1-31); **Y.** Left M3 (MAB3-727). Muroidea indet.: **Z.** Right M2 (MAB0A-43). Scale bar: 1 mm.

forward. On the lingual side, the posterior ridge of the metaconid connects with the anterior ridge of the protoconid and with the entoconid, enclosing the mesosinusid. The posterior ridge of the protoconid is of medium-long length. The ectomesolophid may be short (1 out of 5) or absent (4 out of 5). The hypolophulid is transverse and complete. The posterolophid is high and connects with the entoconid, enclosing the posterosinusid.

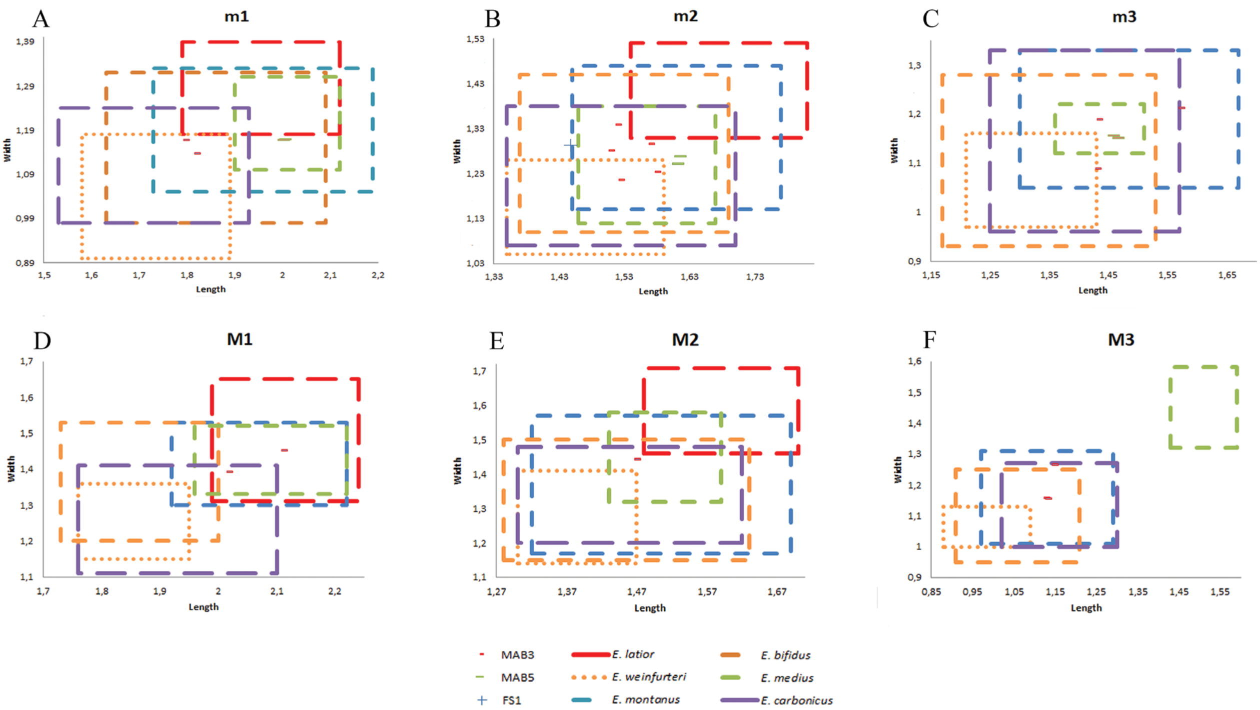

Figure 9. Comparison of length and width measurements (in mm) of *Eumyarion weinfurteri* from Ribesalbes-Alcora Basin. *E. latior* from Neudorf (type locality (t.l.); *E. weinfurteri* from Puttenhausen (t.l.); *E. montanus* from Keseköy (l.t.); *E. bifidus* from Sandelzhausen (t.l.); *E. medius* from Untereichen Altenstadt 565; *E. carbonicus* from Harami 1 (t.l); and the material from Ribesalbes-Alcora Basin (Hartenberger 1965, Wu 1982, de Bruijn and Saraç 1991, Prieto et al. 2008, de Buijn 2009, this publication).

Variability in other sites: in MAB5 (Fig. 8L, M), the posterior ridge of the protoconid is more delayed. However, no difference in size is apparent (Fig. 9C).

M1 (MAB3; Fig. 8N, O): The tooth surface is rough. The anterocone is simple and extends transversely. One specimen has an anterior ridge on the labial side of the anterocone. The postero-labial ridge of the anterocone is attached to the labial side of the tooth in one individual, and in another it is isolated. The anterocone has a central posterior ridge: in one specimen it is directed towards the labial side, in another towards the protocone, and in the last one it is straight. The anteroloph may be present (2 out of 3) or absent (1 out of 3). The labial ridge of the anterolophule may be incipient (1 out of 3) or absent (2 out of 3). The anterior ridge of the protocone is directed forward and, in one specimen, connects with the median ridge of the anterocone. The posterior protoloph is transverse and connects labially to the entoloph, posterior to the protocone. The ectoloph may be present (2 out of 3) or absent (1 out of 3). In one individual, there is a double mesoloph. In the latter case, the anterior mesoloph is incipient and is directed towards the posterior mesoloph. The posterior or main mesoloph is long. The ectomesoloph may be absent (2 out of 3) or only a spur (1 out of 3). The sinus is relatively narrow and directed forward. The metaloph is connected to the entoloph. The posteroloph is long, and it may connect to the base of the metacone (1 out of 3) or not (2 out of 3).

Variability is present in other sites: in MAB5 (Fig. 8P), the absence of a posterior ridge of the anterocone is observed, and the metaloph is connected to the anterior part of the hypocone. No significant disparities in size are detected (Fig. 9D).

M2 (MAB3; Fig. 8Q): The surface is rough. The lingual anteroloph is short. The protoloph is transverse and connects with the protocone. The mesoloph is of medium length. The ectomesoloph is absent. The sinus is narrow and directed forward. The metaloph is transverse and connects with the hypocone. The posteroloph is long and isolated labially.

M3 (MAB3; Fig. 8R–T): the labial anteroloph is characterised as either long (2 out of 3) or medium (1 out of 3) in length, with the possibility of either connecting to the protocone (1 out of 3) or the protoloph (2 out of 3). The lingual anteroloph is either small (2 out of 3) or absent (1 out of 3). The protoloph is simple, transverse, or shifted slightly forward, connecting to the anterior part of the protocone. The posterior ridge of the paracone connects to the base of the metacone, forming a labial cingulum that closes the mesosinus. The neo-entoloph may be complete and high (1 out of 3), short and weak (1 out of 3), or incomplete (1 out of 3). The axioloph may be complete and located in the central part of the tooth (2 out of 3), or long and incomplete (1 out of 3). The mesoloph may be medium (1 out of 3) or long and connects to the labial cingulum (2 out of 3). The metaloph is long and directed forward. The metaloph may connect to the metacone and the neo-entoloph through the axioloph (1 out of 3), the metacone and the posterior part of the protocone (1 out of 3), or the anterior part of the hypocone (1 out of 3). The hypocone may be well developed (1 out of 3) or absent (2 out of 3). The posteroloph may be high and short, connecting the neo-entoloph and the metacone, enclosing a small posterosinus (1 out of 3), which is small and isolated (1 out of 3), or high, short, and not connected to the metacone (1 out of 3).

Variability is present in other sites: the tooth from MAB5 is similar to the one described before.

Remarks. The genus *Eumyarion* is a small to medium-sized muroid characterized by primitive dental features (Thaler 1966). The origins of this genus are complex and likely related to *Eucricetodon* from the Oligocene and Early Miocene (Kälin 1999). A comprehensive revision of both genera could potentially result in their synonymy, encompassing some basal forms of *Eumyarion* (Kälin 1999; de Bruijn et al. 2013).

The provenance of this genus has been the subject of considerable debate among scholars, with various authors proposing a range of potential locations. These include the upper Oligocene in Turkey (Ünay et al. 2003), the MN1 in Asia (Lopatin 2004a; Maridet et al. 2011), and the upper Oligocene in Europe, more specifically in Bosnia and Herzegovina, have all been proposed as potential locations for the origin of this genus. (de Bruijn et al. 2013). The earliest known fossil of this species from Central and Western Europe was discovered at Dolnice 1 in the Cheb Basin in the Czech Republic and dates back to the first half of the lower Aragonian (MN4; Fejfar 1989). During the Early-Middle Miocene in Europe, a variety of species of *Eumyarion* were present, namely *Eumyarion bifidus* (Fahlbusch, 1964), *Eumyarion latior* (Schaub & Zapfe, 1953), *Eumyarion medius* (Lartet, 1851), and *E. weinfurteri* (which may be a synonym of *E. latior*, according to de Bruijn (2009)). In addition, within the geographical confines of Turkey, the following species have been identified: *Eumyarion carbonicus* de Bruijn & Saraç, 1991, *Eumyarion orhani* de Bruijn et al., 2006, *Eumyarion montanus* de Bruijn & Saraç, 1991, *Eumyarion beyderensis* Bilgin et al., 2023, *Eumyarion aegeaniensis* Bilgin et al., 2023, and *Eumyarion gordesensis* Peláez-Campomanes et al., 2019 were also discovered (de Bruijn 2009; Peláez-Campomanes et al. 2019; Bilgin et al. 2023).

In the Iberian Peninsula, the earliest fossil records date from the lower Aragonian (upper part of the MN4), specifically at the localities of Buñol (Cerro de la Cruz, Magro River Basin, last part of the local biozone C; Daams and Freudenthal (1974); local biozone according to Crespo et al. 2019), Montalvos 2 (Teruel Basin, local biozone Ca, Hordijk et al. 2015), Vargas 4A (Calatayud-Montalbán Basin, local biozone Cb, van der Meulen et al. 2012), and Les Cases de la Valenciana, Can Martí Vell, Els Casots or San Mamet (Vallès-Penedès Basin, local biozone C, Casanovas-Vilar et al. 2016, Jovells-Vaquè et al. 2017). During the Early Miocene appear in the Iberian Peninsula, the species *E. medius*, *Eumyarion valencianum* Daams & Freudenthal, 1974 (*nomem dubium* in de Bruijn and Saraç (1991), probably *E. weinfurteri* or *E. latior* according to de Bruijn 2009) and *E. weinfurteri* (Daams and Freudenthal 1974; Ruiz-Sánchez et al. 2003; Casanovas-Vilar et al. 2016), and subsequently, *Eumyarion leemani* (Hartenberger, 1965) (Hartenberger 1965; Casanovas-Vilar 2007).

The classification of medium-sized *Eumyarion* poses a considerable challenge, primarily due to the extensive intraspecific variation observed in their morphology and size. This observation has prompted several researchers to synonymise species and question the homogeneity of populations (Engesser 1972; Vasileiadou and Zouros 2012). A particularly illustrative example of this phenomenon is *E. weinfurteri*, a species initially synonymised with *E. latior* by de Bruijn and Saraç (1991), and subsequently by Schötz (1993). However, de Bruijn (2009) subsequently raised questions regarding its status, albeit identifying differences between the two in M1 and M2 of Sandelzhausen.

The material of the genus *Eumyarion* recovered from the Ribesalbes-Alcora Basin exhibits a larger size compared to the smaller species of the genus (namely *Eumyarion intercentralis* de Bruijn & Saraç, 1991, *Eumyarion microps* de Bruijn & Saraç, 1991), *E. gordensensis*, and *E. orhani*. It is slightly larger than the type population of *E. weinfurteri* (although resembling other populations of this species), *E. bifidus*, and *E. carbonicus*, and exhibits similarities with *E. aegeaniensis*, *E. beyderensis*, *E. montanus*, and *E. medius*. However, in comparison to *E. latior*, it is similar or slightly smaller, depending on the specific element (Fig. 9).

The MAB3 sample exhibits a combination of primitive and derived features in the m1 morphology, with one specimen displaying an anteroconid that is strikingly similar to that of *E. orhani* or *Eumyarion tremulus* Lopatin, 1996, and lacking protoconid-anteroconid contact. In the remaining material, the anteroconid has a decreasing crescent shape and it is connected to the metaconid and protoconid by a well-developed anterolophulid, a feature typical of *E. carbonicus* or *E. latior*/*weinfurteri* (Daams and Freudenthal 1974; Bulot 1979; de Bruijn et al. 2006). It differs from *E. beyderensis* because in this species the anteroconid is near to be isolated, and *E. aegeaniensis* by this more developed anteroconid (Bilgin et al. 2023). One specimen displays the distinctive characteristics of *E. montanus* from Keseköy, i.e., a short mesolophid and a posterior ridge of the protoconid (de Bruijn and Saraç 1991). Conversely, the remaining specimens exhibit a convergence of both ridges, a morphology consistent with that of *E. latior*/*weinfurteri* as observed in Buñol, Aliveri, and Dolnice (Daams and Freudenthal 1974; Hofmeijer and de Bruijn 1988; Fejfar 1989), or *E. orhani* (de Bruijn et al. 2006). The occurrence of the posterior crest of the hypoconid varies significantly within the genus *Eumyarion*. It is present in our material in a comparable percentage to *E. montanus*, *E. tremulus*, or *E. latior*/*weinfurteri* (de Bruijn and Saraç 1991; Lopatin 2004a; de Bruijn 2009). The morphological similarity of the m1 of MAB5 to the *E. latior*/*weinfurteri* populations from Buñol or Aliveri (Daams and Freudenthal 1974; Hofmeijer and de Bruijn 1988) is remarkable. This element is biometrically smaller than the type population of *E. latior*, and only MAB5 is larger than the type population of *E. weinfurteri*, while the remains of MAB3 are smaller than the type population of *E. medius* (Fig. 9A).

The morphology of m2 is distinctive. In 33% of the specimens, the posterior ridge of the protoconid is present, a feature that is more commonly seen in more recent species. Conversely, the short or absent mesolophid is a characteristic of more primitive species. This combination of morphologies is a characteristic of *E. latior*/*weinfurteri* from Aliveri and *Eumyarion margueritae* from de Bruijn et al. 2013, from Banovići (Hofmeijer and de Bruijn 1988; de Bruijn et al. 2013). In terms of size, the specimens from the Ribesalbes-Alcora Basin are smaller than the type population of *E. latior*, somewhat larger than *E. weinfurteri*, and fall within the type variability shown for each species (Fig. 9B).

The m3 has no mesolophid, the posterior crest of the hypoconid is absent, and the posterior crest of the protoconid is medium to long. These characteristics are comparable to those found in *E. latior*/*weinfurteri* de Aliveri and *E. margueritae*, yet still shorter than those of the Buñol population (Daams and Freudenthal 1974; Hofmeijer and de Bruijn 1988; de Bruijn et al. 2013). With regard to dimensions, they are marginally larger than the *E. weinfurteri* type population (Fig. 9C).

The M1 is distinguished by the variability and complexity of the posterior spurs of the anterocone, exhibiting a morphology analogous to that observed in *E. latior*/*weinfurteri* populations from Aliveri or Dolnice 1 (Hofmeijer and de Bruijn 1988; Fejfar 1989). The number of specimens with the paracone spur not attached to the mesoloph is comparable to that observed in *E. montanus* and *E. tremulus*, exhibiting a medium mesoloph consistent with that seen in *E. montanus* (de Bruijn and Saraç 1991; Lopatin 2004a). De Bruijn (2009) regards this as one of the distinguishing elements between *E. latior* and *E. weinfurteri*. According to the classification system proposed by de Brujin (2009), the material from the Ribesalbes-Alcora Basin's "BBB" morphotype exhibits the characteristic morphologies of *E. weinfurteri*, including a lingual spur on the anterocone, no connection between mesoloph and metacone, and no paracone spur and mesoloph. The MAB3 specimen is slightly larger than the *E. weinfurteri* type population and longer than *E. bifidus* (Fig. 9D).

A single M2 has been identified at the MAB3 locality, and it is characterised by a small posterior paracone spur. This morphology is similar to that described in *E. montanus* from Keseköy and *E. weinfurteri* from Sandelzhausen or Bézian (Bulot 1979; de Bruijn and Saraç 1991; de Bruijn 2009), while in *E. latior* from Sandelzhausen or *E. latior*/*weinfurteri* from Buñol, this crest is more developed (Daams and Freudenthal 1974; de Bruijn 2009). The protoloph is single, in contrast to the double protoloph observed in *E. orhani* or *E. bifidus* (de Bruijn et al. 2006; de Bruijn 2009). The mesoloph is of medium length, a feature that is analogous to that of *E. montanus* (de Bruijn and Saraç 1991), yet it is comparatively shorter than in *E. latior*/*weinfurteri* (Daams and Freudenthal 1974; de Bruijn 2009). This morphology is another distinguishing factor between *E. latior* and *E. weinfurteri* (de Bruijn 2009; Vasileiadou and Zouros 2012). According to the classification proposed by Bruijn (2009), the material under study falls into the category "BBB": characterised by a simple protoloph, with no connection between the metacone and mesoloph, nor between the paracone spur and the mesoloph. This category is typical of *E. weinfurteri*. The specimen of MAB3 is of a size that falls between the type populations of *E. weinfurteri* and *E. latior*, coinciding with the variability of the rest of the species shown (Fig. 9E).

The morphology of the third molar exhibits considerable variation, with the axioloph potentially being either complete with a long mesoloph or incomplete with a short mesoloph. The former combination has been observed in *E. montanus* or early populations of *E. latior*/*weinfurteri* (Daams and Freudenthal 1974; de Bruijn and Saraç 1991), while the latter is exclusively found in the MAB3 specimens. With regard to biometrics, the M3 of MAB3 is larger than the type population of *E. weinfurteri* and smaller than that of *E. medius*, which is in agreement with the other species shown (Fig. 9F).

As posited by de Bruijn (2009), in his seminal work on the subject, the material of the genus *Eumyarion* from the Ribesalbes-Alcora Basin must be ascribed to *E. weinfurteri*, albeit with a slightly larger size than that of the type population.

Subfamily Melissiodontinae Schaub, 1925

Genus *Melissiodon* Schaub, 1925

Type species. *Melissiodon dominans* Schaub, 1925. Wintershof-West. Early Miocene.

Melissiodon sp.

Figs 8U–Y, 10

Localities. BC1 and MAB3.

Material (number of remains). Suppl. material 1; BC1 (2): 1 M1, 1 M3; MAB3 (3): 1 m1, 1 m3, 1 M3.

Measurements. Suppl. material 2.

Description. ***m1*** (MAB3; Fig. 8U): The tooth is elongated, with a subtriangular outline, and high, sharp cusps. The anteroconid has a lingual cusp, and the labial ridge is short. The lingual cusp has an anterior spur. The metaconid complex connects to the lingual anteroconid and is slightly connected to the posterior metalophulid. The anterior metalophulid connects with both anteroconids, developing a small ridge between the two. The protoconid has a short ectostylid. The posterior metalophulid is long and contacts the anterior ridge of the entoconid on the lingual side of the tooth. The posterior metalophulid has a posterior cusp and does not connect with the mesoconid. The mesolophid

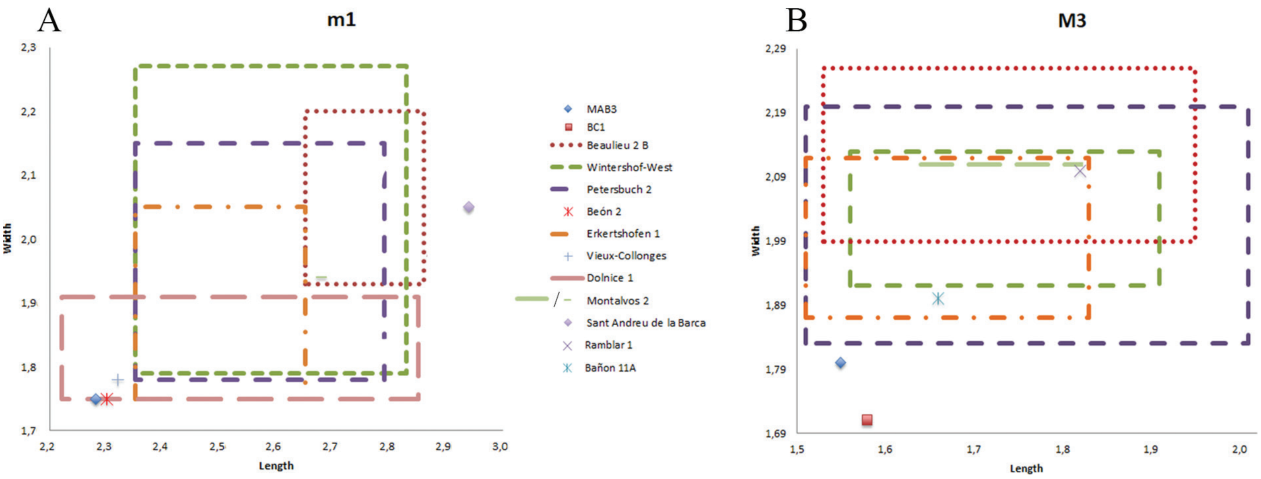

Figure 10. Comparison of length and width measurements (in mm) of *Melissiodon* sp. from Ribesalbes-Alcora Basin. *M. dominans* from Erkertshofen 1, Dolnice 1, Montalvos 2, Petersbuch 2, Sant Andreu de la Barca, and Wintershof West (type locality (t.l.); *M.* aff. *dominans* from Beaulieu 2B, and Vieux Collonges; *Melissiodon* sp. from Beón 2; and the material from Ribesalbes-Alcora Basin (Hrubesch 1957, Mein and Freudenthal 1981, Mein 1989, Ziegler and Fahlbusch 1986, Fejfar 1989, Bolliger 1992; Bulot et al. 2009, Hordijk et al. 2015, Jovells-Vaqué and Casanovas-Vilar 2018b, this publication).

is medium in size and isolated. The mesoconid is well-developed. The entoconid complex connects with a well-developed posterolophid.

m3 (MAB3; Fig. 8V): fragmented molar, with high, sharp cusps. The anterolophid connects the lingual side of the tooth with the metaconid, enclosing a small lingual anterosinusid. The metaconid has a small posterior spur. The anterior metalophulid is connected to the anterolophid and encloses a small, deep labial anterosinusid. The tooth has a small mesolophid and an incipient ectomesolophid. The hypolophid is medium-sized and isolated. The posterolophid does not connect with the entoconid.

M1 (BC1; Fig. 8W): tooth fragment, with both anterocones. The labial anterocone has an anterior ridge. A posterior ridge connects both anterocones. The lingual anterocone contacts the protocone complex. The anterior protolophule reaches the metacone complex.

M3 (BC1; Fig. 8X): The molar is subquadrangular, with high, sharp cusps, and a complex morphology. The tooth has a short anteroloph connected to the paracone complex. The anterosinus is short and deep. The anterior protoloph is connected to the paracone complex, and in addition, it has a posterior spur. The posterior protoloph is connected to the posterior part of the paracone complex, where two posterior ridges begin, connecting the lingual ridge with the anterior metaloph. A small entoloph starts at the protocone, but without reaching the hypocone. Both metalophs are connected, and the posterior one reaches the hypocone.

Variability in other sites: In MAB3 (Fig. 8Y), variability is evident in the configuration of the anteroloph, which does not connect with the paracone. The protolophs are separated and connect forming a V-shape. The posterior protoloph is short and does not connect to the hypocone, and the latter does not connect to the metacone, with the anterior crest of the hypocone being isolated. The posterior crest of the hypocone ends at the posterior part of the tooth. The specimen of BC1 is slightly narrower than that of MAB3 (Fig. 10B).

Remarks. The Melissiodontinae family is thought to have a primitive origin, as it probably first appeared in the early-middle Eocene of Asia (Wessels et al. 2018). The genus includes eight species: *Melissiodon chatticus* Freudenberg, 1941, *Melissiodon emmerichi* Schaub, 1925, *Melissiodon schalki* Hrubesch, 1957, *Melissiodon schroderi* Hrubesch, 1957, *Melissiodon quercyi* Schaub, 1920, *Melissiodon dominans* Dehm, 1950, *Melissiodon schlosseri* Schaub, 1925, and *Melissiodon schaubi* Dehm, 1935. The genus *Edirnella* was proposed by de Bruijn et al. (2013) as the ancestor of this genus. The earliest known record of *Melissiodon* dates back to the early Oligocene, most likely from Ehingen in the MP23 (Hrubesch 1957), and the most recent one in the Early Miocene, probably from Forsthart in the upper MN4 (Mödden 1999). The number of records from this period is limited, with only a few examples from Central Europe, France, Germany, Turkey, and the Iberian Peninsula. In these areas, the presence of only the *M. dominans* and *M. schlosseri* species has been documented (Antunes and Mein 1986; Mödden 1999; Ünay et al. 2003; Jovells-Vaquè and Casanovas-Vilar 2018b; Jovells-Vaquè and Mörs 2023). Another species of the genus *Melissiodon* was discovered in the Miocene area of El Fallol, situated in the Vallès-Penedès Basin. Crusafont et al. (1955) originally named it *Melissiodon arambourgi*. However, subsequent research by Mein and Freudenthal (1981) and Jovells-Vaquè and Casanovas-Vilar (2018b) posited that it should be regarded as a synonym of *M. dominans*. Utilising the MN4 material from Beon 2 (France), Bulot et al. (2009) proposed the designation of a new species, basing this assertion on the comparatively diminutive size of the MN4 material in relation to the MN3 populations. Nevertheless, no formal description has been provided due to the limited quantity of available material.

The fossil record of *Melissiodon* in the Early Miocene of the Iberian Peninsula is mainly limited to a few isolated teeth or tooth fragments recovered from several sites in the eastern part of the Iberian Peninsula. These sites include Level Q of Barranco del Candel (Magro Basin; Adrover et al. 1987), Ramblar 1, 3B and 7, Bañon 2 and 11A (Calatayud-Montalbán Basin; Sesé 1987), and Sant Andreu de la Barca, Molí de Can Calopa, Sant Andreu de la Barca 1, San Mamet, Turó de les Forques 1, El Fallol (Vallès-Penedès Basin, Jovells-Vaquè and Casanovas-Vilar 2018b), and Montalvos 2 (Teruel Basin; Hordijk et al. 2015).

The material from the Ribesalbes-Alcora Basin (Fig. 10) exhibits a smaller size than that of the populations of this genus from MN1-3, and falls within the variability presented in MN4, as observed in Beón 2. Conversely, Montalvos 2 exhibits a greater quantity of material than that of the other MN4 sites, and a larger size (Bulot et al. 2009; Hordijk et al. 2015). In comparison to the material from Central European and Vallés-Penedés Basin sites, the size of the material studied here is typically smaller (Jovells-Vaquè and Casanovas-Vilar 2018b; Jovells-Vaquè and Mörs 2023).

The m1 of MAB3 is notably intricate, exhibiting a distinctive set of characters that are not observed in any population of the genus *Melissiodon*. The mesolophid is isolated, making contact exclusively with the mesoconid. Additionally, there is direct contact between the posterior metalophulid and the entoconid, and no contact between the metaconid and the posterior metalophulid. This differs from the descriptions provided by Ziegler and Fahlbusch (1986) and Fejfar (1989) for other Central European MN4 populations. The Montalvos 2 population exhibits a markedly elongated labial part (Hordijk et al. 2015). The anteroconid complex closely resembles that observed in the Wintershof West population of *M. dominans* (Hrubesch 1957), except for the labial part, which is slightly less extended. The high variability in M3 morphology falls within the range observed in the Wintershof West population (Hrubesch 1957).

The primary concerns regarding the lower Aragonian collections of this genus pertain to the scarcity of remains (less than 1% of all mammals), the substantial degree of fragmentation of the remains, and the challenge in discerning the morphology of the small tooth fragments belonging to this genus. Consequently, the classification of these specimens is often uncertain (Mödden 1999). Notwithstanding the aforementioned challenges, two species of the genus have been formally described from the European Early Miocene. One of the species, *M. schlosseri*, is known only from its type locality, Haslach (Mödden 1999). In other localities, such as Mokrá-Quarry La Chaux 7 or Ulm Uniklinik, taxa that are related (aff.) to the former species have been recorded (Werner 1994; Engesser and Mödden 1997; Bonilla-Salomón et al. 2022). The second species is *M. dominans* (or its related forms (aff.)), regarded as a problematic taxon, given that most of the remains discovered in Europe are attributed to this species, despite the lack of definitive evidence or the scarcity of the remains. A third species, a descendant of *M. dominans*, has been identified in the lower Aragonian, distinguished by its smaller size relative to its ancestor. However, the scarcity of remains has precluded its formal description (Bulot et al. 2009).

The distinguishing characteristics between *M. schlosseri* and *M. dominans* are as follows: the former exhibits greater cusp thickness, while the latter possesses a squarer m1 with a labial anteroconid that is slightly extended in the latter. The labial anteroconid of *M. dominans* from Wintershof West (Hrubesch 1957) and the new species from Beón (Bulot et al. 2009) exhibit a ridge-form, which is even more elongated in the lower Aragonian species. In contrast, *M. schlosseri* is characterised by a labial anteroconid with a cusp-form. A further noteworthy distinction emerges in the diagnosis of *M. schlosseri*, where an elevation in the posterolophid is documented (Schaub, 1925). As Werner (1994) observes, this feature is likely attributable to intraspecific variation. It is noteworthy that the morphology of the m1 from the Ribesalbes-Alcora Basin is similar to that described by Bonilla-Salomón et al. (2022; Fig. 3Q), although in the present case, it is considerably smaller in size.

Consequently, upon thorough review of extant literature from multiple European localities, it was determined that specific populations of *M.* aff. *dominans* could be re-assigned to *M. schlosseri*, as evidenced by the findings in Vieux Collonges (Mein and Freudenthal 1981). This underscores the imperative for a comprehensive re-evaluation of the genus and its potential re-classification. Furthermore, the m1 from the Ribesalbes-Alcora Basin exhibits a smaller size compared to those previously described by Mein and Freudenthal (1981). The m1 from Ribesalbes-Alcora Basin is distinguished by an isolated mesolophid with an isolated on the anterior part and a slightly elongated labial anteroconid. These characteristics differentiate it from *M. dominans* from Central Europe and the Vallès-Penedès Basin. It is a closer alignment with *M.* aff. *dominans* (Jovells-Vaquè and Casanovas-Vilar 2018b; Jovells-Vaquè and Mörs 2023) is also noteworthy.

In consideration of the aforementioned morphological characteristics, the specimen exhibits primitive traits analogous to those observed in the Wintershof West population. It is comparable in size to the recently discovered but as yet unnamed species from Beon. Furthermore, the characteristics of the genus *Melissiodon* exhibit a high degree of variability, and the available comparative material is exceedingly scarce (Mödden 1999). Consequently, the *Melissiodon* material from the Ribesalbes-Alcora Basin will be assigned open nomenclature until a more substantial collection of remains becomes available for formal description.

Muroidea indet.

Fig. 8Z

Localities. MAB0A.

Material (number of remains). MAB0A (1): 1 M2.

Description. ***M2*** (MAB0A; Fig. 8Z): small broken tooth. The protoloph is double, the anterior one being transverse and connected to the protocone, and the posterior one incomplete, without contacting the paracone. The mesoloph is double: the anterior is short and the posterior is medium, both parallel. The crest of the protocone is short and does not contact the mesoloph. The ectomesoloph is absent. The sinus is narrow and directed forward. The metaloph is anterior and connects with the entoloph. The posteroloph is long and isolated labially. There is a small posterior ridge of the hypocone, in the posterosinus.

Remarks. The tooth fragment displays characteristics consistent with those observed in *Eumyarion*, *Pseudocricetodon*, or *Eucricetodon*, including the presence of double mesolophs and the posterior crest of the hypocone. Given its diminutive dimensions and the presence of a double protoloph, it seems not plausible that this specimen can be attributed to the *Eumyarion* species identified at other localities. The Turkish fossil record is replete with small *Eumyarion* species, yet one m1 has been described from the Blanquàtere 1 location, which belongs to one of these species (Aguilar et al. 2010b). It is imprudent to draw comparisons between the two, as they represent distinct elements. However, this combination of characteristics is absent in *E. intercentralis* or *E. microps* from Keseköy (de Bruijn and Saraç 1991). A specimen from Sabuncubeli exhibits some resemblance but displays a longer mesoloph, and the two crests are fused. Additionally, it is larger in *E. orhani* (de Bruijn et al. 2006). The presence of double mesolophs or the posterior crest of the hypocone has been documented in *Eucricetodon aquitanicus* Baudelot & Bonis, 1968 from the Early Miocene (Hugueney 1999b), and in addition, the presence of double mesolophs has been documented in *Eucricetodon atavoides* Freudenthal, 1996 from the early Oligocene (Freudenthal 1996; Gomes-Rodrigues et al. 2013), within the *Eucricetodon* genus. The species *Sindemys aguilari* (Lindsay, 1988) from Pakistan and certain Asian *Eucricetodon* forms (see plate 7.3, fig. 12; Wessels 2009; Gomes-Rodrigues et al. 2012) exhibit this or a similar configuration, despite originating from outside the European and Turkish regions.

The complicated primitive morphology of the taxon precludes its categorisation within any specific genus. If the specimen were determined to belong to *Eumyarion*, it would represent the earliest known appearance of this genus in the Levantine basins from the Iberian Peninsula. Conversely, if the specimen belonged to *Eucricetodon*, it would represent the surviving member of the genus following the absence of representatives of the European MN3 following the *Cricetid Vacuum* (Hugueney 1999b). Alternatively, it could be an exotic immigrant species from Asia or another continent during a period of widespread intercontinental migration.

Discussion

Biostratigraphy

The muroid family is a frequently employed biostratigraphic indicator for the Neogene period (Daams and Freudenthal 1988; Freudenthal and Daams 1988; Hugueney 1999b; Rummel 1999; van der Meulen et al. 2012; Casanovas-Vilar et al. 2016, among others). During the MN4 biochronological unit, there was a notable increase in the proportion of this rodent group across the study sites. Initially scarce in local zone B, their percentage increased with certain variations within local zone C (Fig. 11), potentially due to site-specific climatic conditions. At the outset of local zone D during

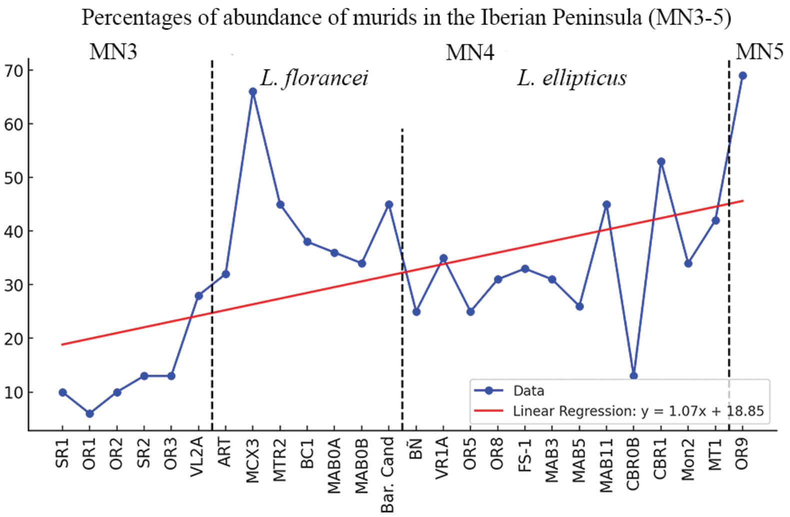

Figure 11. Percentages of relative abundance of muroids per site with respect to the total number of rodents in the most representative sites of the Iberian Peninsula from MN4-5, together with the main sites studied here. The graph shows the increase in abundance towards the end of MN4 and the beginning of MN5 (OR9). The order of the sites is hypothesised from the literature, the alteration of the order within each group, does not alter the trend. SR: San Roque; OR: Olmo Redondo; VL: Villafeliche; ART: Artesilla; MCX: Mas dels Coixos; MTR: Mas de Torner; BC: Barranc de Campisano; MAB: Mas d'Antolino B; Bar. Cand: Barranc de Candel; BÑ: Buñol; VR: Vargas; FS: Foieta la Sarra; Mon2: Montalvos 2; MT1: Morteral 1; CBR: Corral de Brisca. Taken from Adrover et al. (1987), van der Meulen et al. (2012), Freudenthal et al. (2014), Hordijk et al. (2015), and this publication.

MN5, these rodents became the dominant group within the rodent faunas, at least in the Calatayud-Montalbán Basin (van der Meulen et al. 2012). However, they do not constitute the majority of the rodents in the sites under study, except MCX3, where their prevalence is higher. This may be attributed to climatic factors.

As illustrated in Fig. 12, the temporal sequence under scrutiny reveals a decline in the abundance percentages of this family, with the exception of MAB11, where a marginal increase is observed. The graph further elucidates the variations in abundance among the depicted genera. Notably, there is an increase in the presence of *Democricetodon*, accompanied by a decline in *Megacricetodon*. Consequently, the former becomes the dominant genus in the muroid faunas in the MAB11 and CBR0B sites.

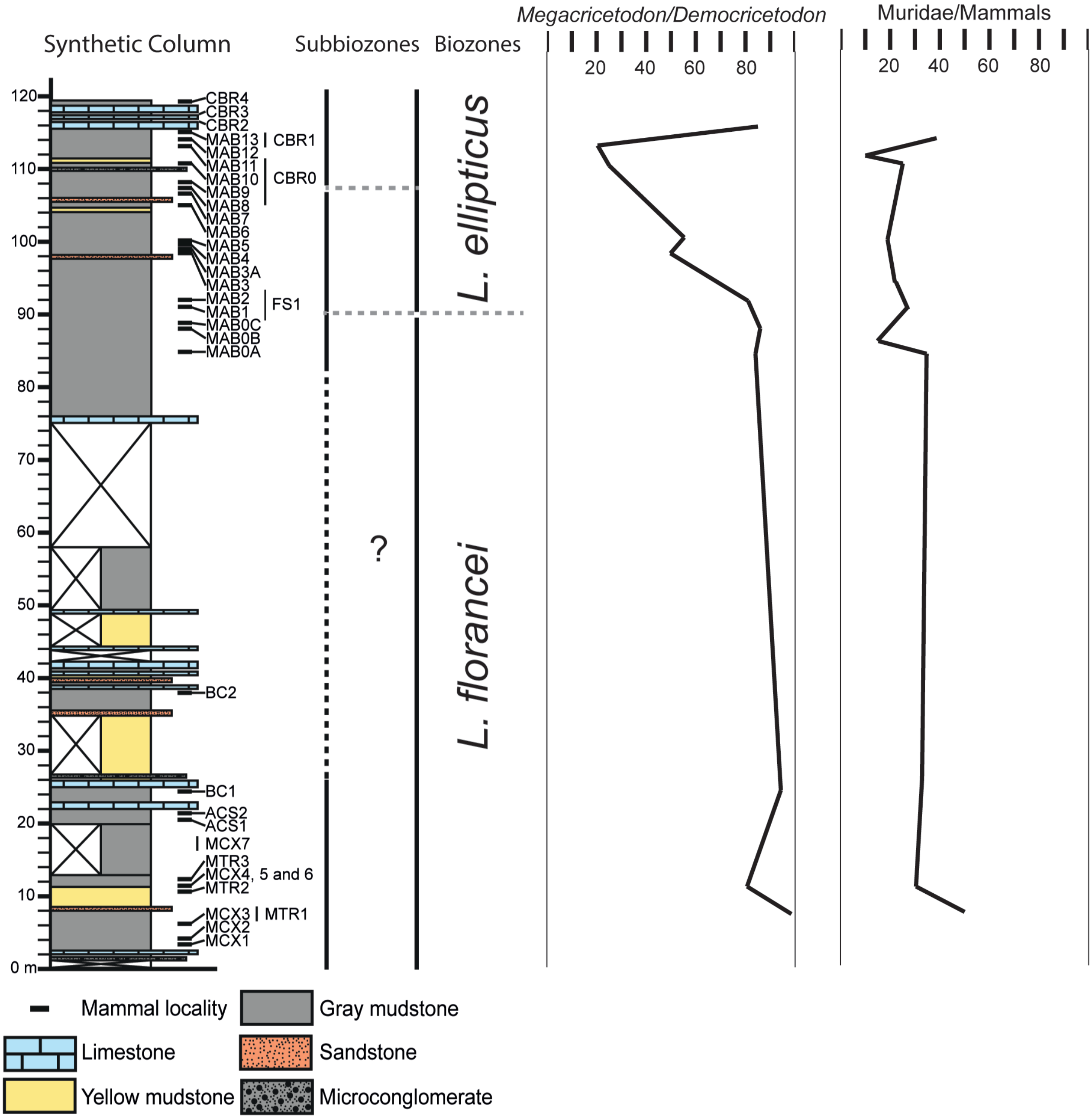

Figure 12. Composite column of the Campisano Ravine with positions of the studied sites and the different local biozones and subbiozones present in this section, with percentage abundance of *Megacricetodon*/*Democricetodon* and Muridae/Mammals at the different sites under study (only sites with a significant collection of small mammal remains are represented). *Megacricetodon primitivus* is present in the sites: MCX2, MCX3, MCX4, MTR1, MTR2, MTR3, BC1, BC2, FS1, MAB0A, MAB0B, MAB2, MAB3, MAB4, MAB5, MAB11, MAB11B, MAB12, CBR0B, CBR0E, CBR0F, CBR1, CBR2, and CBR4; *Democricetodon decipiens* is present in the sites: MCX1, MCX3, MTR1, MTR2, BC1, FS1, MAB0A, MAB0B, MAB3, MAB5, MAB10, MAB11, MAB13, CBR0B, and CBR1; *Eumyarion weinfurteri* is present in the sites: FS1, MAB3, and MAB5; *Melissiodon* sp. is present in the sites: BC1 and MAB3; and Muroidea indet. is present in the site: MAB0A. Modified from Crespo et al. (2019a, 2021). MCX: Mas dels Coixos; MTR: Mas de Torner; ACS: Araia Cantera Sud; BC: Barranc de Campisano; FS: Foieta la Sarra; MAB: Mas d'Antolino B; CBR: Corral de Brisca.

The record of the muroids in the Calatayud-Montalbán Basin, in the MN3-4 (van der Meulen et al. 2012; García-Paredes et al. 2016; partially Daams and Freudenthal 1988) shows a sequential replacement from *Democricetodon hispanicus* (biozone B) to *D. decipiens* (Ca), followed by *D. moralesi* and *D. franconicus* (Cb), with *Megacricetodon primitivus* persisting until Db. A comparable sequence of events has been observed in the Vallès-Penedès Basin (Casanovas-Vilar et al. 2016; Jovells-Vaquè and Casanovas-Vilar 2017, 2021), where contemporary muroids emerge in the early local biozone C and undergo diversification within this biozone. In the Buñol zone, the record of this family appears in the site of Cerro de la Cruz (classic Buñol site) with the species *D. decipiens*, *M primitivus*, and *E. latior*/*weinfurteri* (Daams and Freudenthal 1974; de Bruijn 2009). Furthermore, the species found in the Barranco de Candel site are: *Democricetodon* aff. *hispanicus*, *M. primitivus*, and *Melissiodon* aff. *dominans* (Adrover et al. 1987).

In Central Europe, specifically in the Swiss basins, the occurrence of *Democricetodon* as identified by Kälin and Kempf (2009) marks the MN3/4 boundary and constitutes the first local area of MN4. Subsequently, the taxa *Democricetodon*, *Megacricetodon*, and *Eumyarion* are recorded together, forming the last local biozone of MN4.

The record of the *Melissiodon* in the Calatayud-Montalbán Basin stops at the end of local zone B, according to van der Meulen et al. (2012). In contrast, in the Levantine and Teruel basins (Hordijk et al. 2015), the species persists until the last part of the local biozone C, both zones in MN4. In contrast, in the Vallès-Penedès Basin, the last occurrence of this genus is dated to the beginning of the MN5, in San Mamet and Can Cabanes W (Jovells-Vaqué and Casanovas-Vilar 2018b; Casanovas-Vilar et al. 2021). Consequently, it can be deduced that the remains of the Ribesalbes-Alcora Basin represent the most recent finds in the Levantine basins.

In the Ribesalbes-Alcora Basin (Fig. 12), the record of the muroids comprises *D. decipiens* and *M. primitivus* in all localities, and *Melissiodon* is present in both local biozones described by Crespo et al. (2021). In contrast, *Eumyarion* is only present in the *L. ellipticus* local biozone within the basin.

Ecological preferences and habitat distribution of early miocene muroids

Daams et al. (1988) hypothesised that *Megacricetodon* species may demonstrate a proclivity for either wet or dry habitats, with *M. primitivus* being a particularly ubiquitous species. In Central Europe, particularly within the Swiss Molasses, it is hypothesised that the larger species of the genus would inhabit the more distal areas of the floodplains, while the smaller species would have no clear preference for either humidity or temperature (Kälin 1999).

It has been traditionally assumed that the MN4 forms of *Democricetodon* and *Megacricetodon* exhibit a preference for humid ecological conditions, mainly due to the mesoloph length. In the case of a shorter length, the environment is believed to be more arid (Daams et al. 1999). However, this hypothesis has been refuted by Freudenthal et al. (2014), who found no correlation between mesoloph length and the palaeoecology of extant *Reithrodontomys* hamsters. Consequently, they argue that this methodology is an insufficient means of identifying ecological preferences.

In the local biozone *L. florancei* (MCX3 to MAB0B), the genus *Megacricetodon* is unquestionably predominant within the muroid faunas, with *Democricetodon* appearing scarcely. The genus *Democricetodon* becomes increasingly prevalent at the sites within the local biozone *L. ellipticus* (MAB3 to CBR1). Indeed, it is the most abundant muroid taxon at the MAB11 and CBR0B sites (as illustrated in Fig. 12). This phenomenon may be associated with a comparatively arid environment (or open areas) in the sites belonging to the *L. florancei* local biozone (after Crespo 2017; Crespo et al.2023, and references therein), which would make *Megacricetodon* a taxon more associated with arid or open environments, similar to the Anatolian site of Çapak (Bilgin et al. 2021). Conversely, the *L. ellipticus* local biozone is characterised by higher humidity and a predominance of forest cover (after 2023, and references therein), which would align the preferences of the taxon *Democricetodon* more closely with those of the aforementioned species. The genus *Eumyarion* has traditionally been believed to favour humid and wooded habitats, particularly in the Iberian Peninsula (van der Weerd and Daams 1978; Daams et al. 1988; Duncan 2012). However, in Swiss Molasses sites, the species has been observed to prefer the most proximal parts of the floodplains, indicating that there is no specific preference for moisture or temperature (Kälin 1999).

Melissiodon was traditionally assigned a frugivorous diet based on its tooth morphology, which resembles the Oligocene flying squirrel *Plesispermophilus* (Mein and Freudenthal 1981). However, the aberrant, frail, and slim mandible of *Melissiodon*, as previously observed by Schaub (1920), is accompanied by an extensive, cylindrical diastema that has weak incisors situated below the m2, in addition to delicately-ridged and brittle teeth (Hordijk et al. 2015). These structural characteristics are shared by shrew rats that inhabit the Philippines and Sulawesi regions and feed mainly on soft-bodied invertebrates (Musser 1990; Esselstyn et al. 2012), and other insectivorous rodents (Jovells-Vaquè and Mörs 2023). This combination of traits suggests an ecologically insectivorous diet for this rodent (Wessels et al. 2018), which may explain its survival during the Early Miocene *cricetid vacuum* (Hordijk et al. 2015), contradicting the conventional view of its dietary habits. Furthermore, the aforementioned authors observe that this genus is seldom found in lacustrine deposits but is more frequently present in karstic fills of that age, suggesting that this species inhabited the dry highlands of Europe. The discovery of the species in abundance at the karstic sites provides compelling evidence to suggest its preference for less wet upland habitats (Bonilla-Salomón et al. 2022; Jovells-Vaquè and Mörs 2023).

Conclusions

The Ribesalbes-Alcora Basin has a continental time sequence that is comparable to the regional biozone C (early Miocene) of the larger Calatayud- Montalbán Basin. It has yielded abundant remains of muroids, including five taxa: *Megacricetodon primitivus*, *Democricetodon decipiens*, *Eumyarion weinfurteri*, *Melissiodon* sp., and Muroidae indet. The most abundant species, *M. primitivus* and *D. decipiens*, were found in nearly all the sites under study. The first species was more prevalent in the oldest sites (*L. florancei* local biozone). In contrast, the second was more abundant in the most modern ones (*L. ellipticus* local biozone). Conversely, *E. weinfurteri* was only observed in the FS1, MAB3, and MAB5 sites, which are part of the most recent local biozone, *L. ellipticus*, in the basin. In contrast, *Melissiodon* sp. has been found exclusively in the BC-1 and MAB-3 sites, likely to have experienced drier climatic conditions.

While *M. primitivus* has been identified in all Early Miocene Iberian basins, the genus *Democricetodon* is highly variable. The species of this genus have been identified in the Ribesalbes-Alcora Basin (*D. decipiens*), appear in the Ca biozone of the Calatayud-Montalbán Basin, the last part of the C biozone of the Vallès-Penedès Basin, and the Buñol site. The basin under study may represent a link between the distribution of this species in these two regions. Concerning *Eumyarion*, this genus has been present in the Vallès-Penedès basin since the beginning of the early part of the C biozone. However, it is not until the final part of the C biozone that it begins to migrate towards the basin under study. It only appears in the Cb in the Calatayud-Montalbán Basin and Buñol zone. Conversely, *Melissiodon* is absent in the latter basin from the MN3 biozone to the last part of the C biozone in Cerro de la Cruz and from the MN5 biozone in the Vallès-Penedès Basin.

Consequently, the muroid faunas imply that during the early Miocene, the coastal Ribesalbes-Alcora Basin functioned as a transitional region between the forested areas of west and central Europe and the drier inner Iberian Peninsula basins.

Acknowledgments

The survey and excavation campaigns in Araia d'Alcora were funded by the Conselleria de Cultura i Esports of the Generalitat Valenciana from 2008 to 2011, by projects 2008/0433-CS, 2010/0528-CS, 2011/0230-CS, GV06/304, and GVPRE/2008/320. This research was also supported by the Spanish Ministerio de Ciencia, Innovación y Universidades PID2023-151089NB-I00 (MCIU / AEI / 10.13039/501100011033 / FEDER, UE). Thanks are also due to the helpful comments of Dr. López-Guerrero and anonymous reviewers, which improved the original manuscript, and Jarrid Muhlenberg for the English revision of the manuscript. V.D.C. thanks the Stimulus of Scientific Employment, Individual Support – 2021 Call grant by the Fundação para a Ciência e a Tecnologia (Portugal, CEECIND/03080/2021; DOI: 10.54499/2021.03080.CEECIND/CP1657/CT0007) and GeoBioTec; M.R. thanks the Stimulus of Scientific Employment, Individual Support – 2018 Call grant by the Fundação para a Ciência e a Tecnologia (Portugal, CEECIND/02199/2018) and GeoBioTec. This work was funded by National funding, FCT – Fundação para a Ciência e a Tecnologia, within the framework of UID GeoBioTEC UIDB/04035/2020 (DOI: 10.54499/UIDB/04035/2020). RMB thanks the CIAPOS postdoctoral grant (CIAPOS/2023/160, Generalitat Valenciana), co-financed by the European Social Fund.

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Supplementary material 1

Museum numbers

Authors: Vicente D. Crespo, María Ríos, Rafael Marquina-Blasco, Plini Montoya

Data type: pdf

Explanation note: These are the museum entry numbers of the fossils studied, as well as their identification, site and field numbers.

Link: https://doi.org/10.3897/fr.28.138478.suppl1

Supplementary material 2

Measuremets of the muroids from the Ribesalbes-Alcora Basin

Authors: Vicente D. Crespo, María Ríos, Rafael Marquina-Blasco, Plini Montoya

Data type: docx

Link: https://doi.org/10.3897/fr.28.138478.suppl2

Supplementary material 3

Megacricetodon primitivus from Ribesalbes-Alcora Basin

Authors: Vicente D. Crespo, María Ríos, Rafael Marquina-Blasco, Plini Montoya

Data type: xlsx

Link: https://doi.org/10.3897/fr.28.138478.suppl3

Supplementary material 4

M. primitivus and *D. decipiens*

Authors: Vicente D. Crespo, María Ríos, Rafael Marquina-Blasco, Plini Montoya

Data type: xlsx

Explanation note: Text

Link: https://doi.org/10.3897/fr.28.138478.suppl4