

## EOMYIDS FROM THE RIBESALBES-ALCORA BASIN (EARLY MIOCENE, IBERIAN PENINSULA) AND THEIR BIOSTRATIGRAPHIC AND PALAEOECOLOGICAL IMPLICATIONS

VICENTE D. CRESPO<sup>1,2,3\*</sup>, ARTURO GAMONAL<sup>2</sup>, PLINI MONTOYA<sup>4</sup> & FRANCISCO J. RUIZ-SÁNCHEZ<sup>3,4,5</sup>

<sup>1</sup>Consejo Nacional de Investigaciones Científicas y Técnicas, División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina. E-mail: vidacres@gmail.com

<sup>2</sup>Museo Paleontológico de Alpuente, Av. San Blas 17, Alpuente, 46178 Valencia, Spain. E-mail: arturo-gamonal@hotmail.es

<sup>3</sup>Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, Alginet, 46230 Valencia, Spain.

<sup>4</sup>Departament de Botànica i Geologia, Universitat de València, Dr. Moliner 50, 46100, Burjassot, Valencia, Spain.

E-mail: p.montoya@uv.es, francisco.ruiz@uv.es

<sup>5</sup>Universidad Estatal Península de Santa Elena, 7047, Santa Elena, Ecuador.

\*Corresponding Author

To cite this article: Crespo V.D., Gamonal A., Montoya P. & Ruiz-Sánchez F.J. (2021) - Eomyids from the Ribesalbes-Alcora Basin (early Miocene, Iberian Peninsula) and their biostratigraphic and palaeoecological implications. *Rin. It. Paleontol. Strat.*, 127(3): 497-514.

**Keywords:** Eomyidae; Rodents; Biostratigraphy; Aragonian; Paleoecology; biochronology; Spain.

**Abstract.** Two species of the family Eomyidae are identified in the early Miocene localities of the Araia d'Alcora outcrop (Ribesalbes-Alcora Basin, Iberian Peninsula): *Ligerimys florancei* and *Ligerimys ellipticus*. The first is rarer than the second, which is one of the most abundant mammals in the Ribesalbes-Alcora Basin assemblages. Due to its abundance, we are able to describe its variability in dental morphology, showing characteristics never previously observed, including the presence of a mesoloph or other features previously described only in ancient assemblages of this species, such as the presence of the anteroloph, which appears in younger assemblages in the Araia sequence.

Furthermore, based on the eomyids, we divide the record of the Campisano Ravine section into two long local biozones, depending on the species present. In addition, each local biozone is divided into two smaller sub-biozones, depending on the abundance of each species. We retrospectively compare and correlate the assemblages studied here with other *Ligerimys* assemblages from the other basins in the Iberian Peninsula. We classify these sites based on the abundance and species of the genus *Ligerimys*. Additionally, we discuss the palaeoecological preferences of these species.

### INTRODUCTION

The Eomyidae are an extinct family of rodents with a distribution across a large part of the European Cenozoic; their origin is possibly North American (Flynn 2008). The European record begins in the early Oligocene and extends until the early Pleistocene, with maximum diversity between the late Oligocene and the early Miocene (Engesser 1999).

In the Iberian Peninsula, the recorded genera of this family are *Ritteneria*, *Ligerimys*, *Rhodanomys*, *Eomyops*, *Eomys*, *Keramidomys* and *Pseudotheridomys* (Agustí et al. 1987; Álvarez-Sierra 1987; Ruiz-Sánchez et al. 2009). Thanks to the diversity and faunal isolation of the Iberian Peninsula, a large number of endemic species have been described: *Pseudotheridomys lacombai* Álvarez-Sierra, 1987, *Ligerimys freudenthali* Álvarez-Sierra, 1987, *Ligerimys fabllbuschi* Álvarez-Sierra, 1987, *Ligerimys magnus* Álvarez-Sierra, 1987, *Ligerimys palomae* Álvarez-Sierra, 1987, *Ligerimys ellipticus* Daams, 1976, and *Eomyops noeliae* Ruiz-Sánchez et al., 2009

Received: October 19, 2020; accepted: June 09, 2021

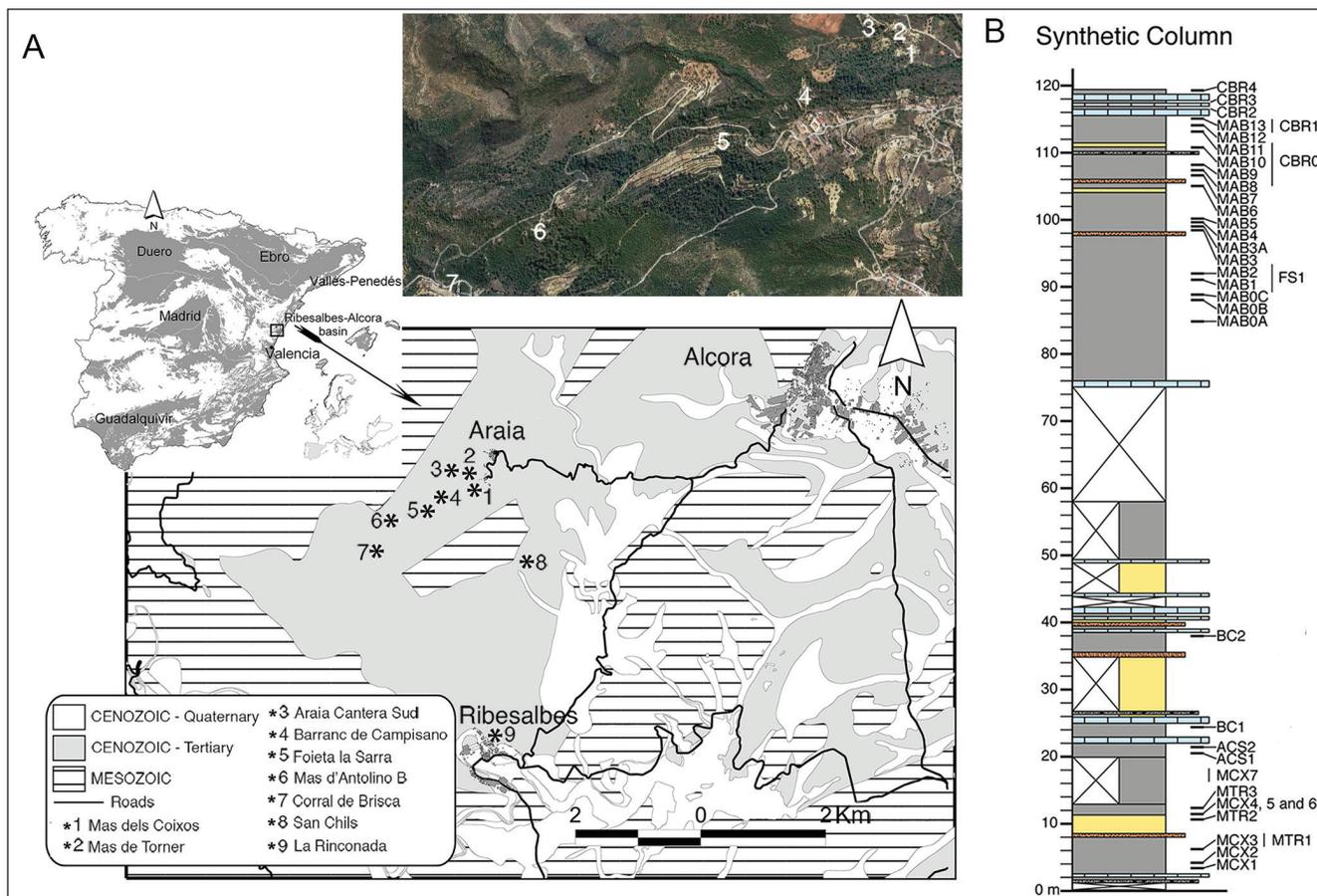


Fig. 1 - Geographic and geological setting of the Ribesalbes-Alcora Basin, showing the location of the outcrops of the Campisano ravine. Modified from Crespo et al. (2018).

(Álvarez-Sierra 1987; Engesser 1999; Ruiz-Sánchez et al. 2009).

The genus *Ligerimys* occurs in the early Miocene and the lowermost part of the middle Miocene (MN3-5) from Europe and Asia (MN2-3; Engesser 1999; Augé et al. 2002; Wang et al. 2009; Kimura et al. 2020). This genus has great importance from a local biostratigraphic perspective, since it shows maximum diversity during the MN3, becoming the most abundant genus in some MN4 small mammal assemblages (Engesser 1999).

Nine species comprise the record of this genus in Europe. Five of them are endemic to the Iberian Peninsula: *L. ellipticus*, *L. freudenthali*, *L. fahlbuschi*, *L. magnus*, and *L. palomae*. Two are present throughout Europe – *Ligerimys antiquus* Fahlbusch, 1970 and *Ligerimys florancei* Stehlin & Schaub, 1951 – and another two are endemic to Central Europe: *Ligerimys oberlii* Engesser, 1990 and *Ligerimys lophidens* (Dehm, 1950) – (Engesser 1999; Álvarez-Sierra 1987; Escarguel & Aguilar 1997).

In the Ribesalbes-Alcora Basin, two species of the genus *Ligerimys* have been found: *L. florancei* and *L. ellipticus*. The first appears in the MN3 of France, including some transitional assemblages with the ancestral species *L. antiquus* (Escarguel & Aguilar 1997; Augé et al. 2002). This species dispersed throughout Europe in the MN4 and became extinct at the end of the MN4. In the Iberian Peninsula, it appears at the end of local biozone B (Escarguel & Aguilar 1997; Van der Meulen et al. 2011; Ruiz-Sánchez et al. 2012; Richenbacher et al. 2013). The second species, *L. ellipticus*, is an endemism of the Iberian Peninsula. It appears locally in Calatayud-Montalbán Basin (Aragon, east-central Spain) in local biozone B and replaces other species of this genus in local zone C, before becoming extinct at the base of the MN5 (Álvarez-Sierra 1987; Van der Meulen et al. 2012). In this article, we study the *Ligerimys* remains found in the Ribesalbes-Alcora Basin (Valencia, eastern Spain), and assess their biostratigraphic and palaeoecological implications, in order to place them in an Iberian context.

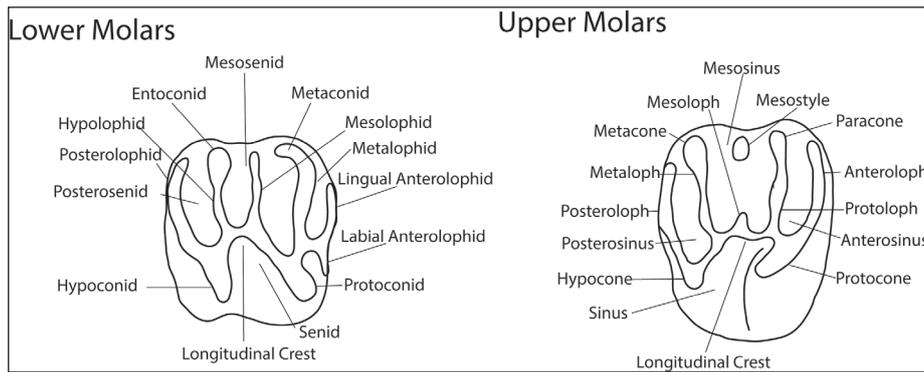


Fig. 2 - Terminology of the eomyid teeth modified from Álvarez-Sierra (1987).

**Institutional abbreviations.** The fossil material is stored at the Museu de la Universitat de València d'Història Natural (MUVHN) in Burjassot, Spain.

**Other abbreviations.** Lower teeth are designated with lower case letters (lower decidual premolar: dp4; lower premolar: p4; lower molars: m1, m2, and m3) and upper teeth are written in upper case letters (upper decidual premolar: DP4; upper premolar: P4; upper molars: M1, M2, and M3). Throughout the text, the names of the sections often appear abbreviated as follows: MCX (Mas dels Coixos); MTR (Mas de Torner); ACS (Araia Cantera Sud); BC (Barranc de Campisano); FS (Foietà la Sarra); MAB (Mas d'Antolino B); CBR (Corral de Brisca).

## GEOGRAPHIC AND GEOLOGICAL SETTING

The materials studied in this paper were recovered in the Ribesalbes-Alcora Basin, specifically near the village of Araia d'Alcora in the eastern Iberian Peninsula (Fig. 1; Agustí et al. 1988; Crespo et al. 2019a). Seven sections comprise the synthetic stratigraphic column; these have been named from oldest to youngest (with some overlap) as follows: Mas dels Coixos, Mas de Torner, Araia Cantera Sud, Barranc de Campisano, Foietà la Sarra, Mas d'Antolino B, and Corral de Brisca. Grey and yellow mudstones, limestones and sandstones are the primary sediment beds in this ravine, with almost 100m of thickness (Crespo et al. 2019a); these are included in 'Unit Three' of the Ribesalbes-Alcora Basin *sensu* Anadón et al. (1989) (Fig. 1).

Until now, up to 45 sites have been described from the seven sections detailed in Crespo et al. (2019a) and Crespo (2017). The first sites with mammalian remains from the Ribesalbes-Alcora Basin were reported by Agustí et al. (1988). Noteworthy published results, include the southernmost documented record of the herpetotheriid *Amphiperaterium frequens erkertshofense* (von Meyer 1846) (Furió et al. 2012; Crespo et al. 2020a); the new species *Plesiodimylus ilercavonicus* Crespo et al., 2018 (Crespo et al. 2018) and *Cuvierimops penalveri* Crespo et al. 2020a (Crespo

et al. 2020a); the abundant remains of talpids (Crespo et al. 2019b); and the diversity of sorcids (Crespo et al. 2019c), erinaceids (Crespo et al. 2020b), squirrels (Crespo et al. 2021), bats (Crespo et al. 2020a), and a Konservat-Lagerstätte (Álvarez-Parra et al. 2021).

The studied sections represent a stratigraphic succession corresponding to local biozone C from the Calatayud-Montalbán Basin (MN4, lower Aragonian, early Miocene), ranging from 16.5 to 16 Ma according to Van der Meulen et al. (2012) (Crespo et al. 2019a).

## MATERIALS AND METHODS

Pictures of the specimens were taken with 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).

We use the nomenclature and measuring methods of Álvarez-Sierra (1987), but with modifications (Fig. 2). In the upper teeth, the mesoloph is divided into two parts: a central part (the true mesoloph) and a labial part (the mesostyle). In the lower teeth, the anterolophid is divided into two parts –labial and lingual– because these parts of the crest may be reduced independently. Measurements are given in millimetres; they were taken using a Leica MZ75 binocular microscope by displacing of a mechanical stage, connected to Sony Magnescale measuring equipment.

We use the definition of local/regional biozones for Calatayud-Montalbán Basin provided by Van der Meulen et al. (2012), in which the early Aragonian (MN4) consists of three zones. First, the local biozone B is defined as the interval zone between the first common occurrence of *Democricetodon hispanicus* (Freudenthal, 1967) to the first occurrence of *Megacricetodon primitivus* (Freudenthal, 1963). Other faunal events (although not diagnostic for the zone) in this local/regional biozone include the first occurrences of *Ligerimys palomae* (it is replaced by *L. florancei* in the last part of this local/regional biozone) and *Atlantoxerus blacki* de Bruijn, 1967, along with the first common occurrence of *Galerix symeonidisi* Doukas, 1986. The assemblages are dominated by *Lagopsis penai* (Royo, 1928), while glirids and eomyids are less frequent than in other local biozones. Second, local/regional biozone Ca is defined by the concurrent range zone of *M. primitivus* and *Democricetodon decipiens* (Freudenthal & Daams, 1988). In this local biozone, there are also, (although not diagnostic for the zone), the last occurrences of *Praearmantomys crusafonti* de Bruijn, 1966, *Armantomys jasperi* Daams, 1991 and *L. florancei* (it is replaced by *L. ellipticus* in the last part of this

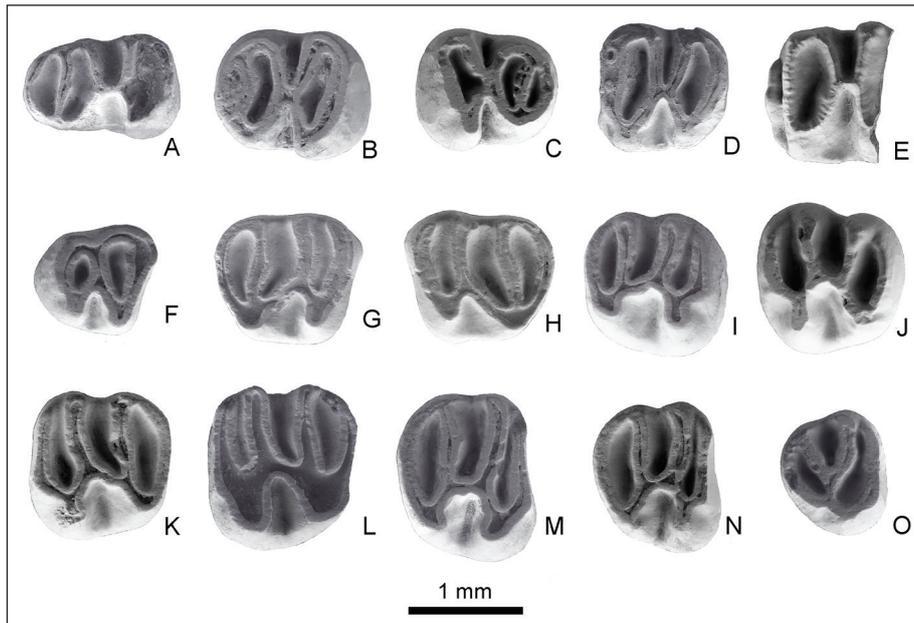


Fig. 3 - Teeth of *Ligerimys florancei* from the Ribesalbes-Alcora Basin.

A- Left dp4 (MAB0A-45); B- Left p4 (MAB0B-2); C- Right p4 (MAB0B-31); D- Left m1/2 (MTR2-4); E- Left m1/2 (MAB0A-52); F- Right m3 (MAB0A-58); G- Right DP4 (MTR2-149); H- Left DP4 (BC1-149); I- Right P4 (MAB0A-46); J- Left P4 (MAB0B-28); K- Left M1 (MAB0B-29); L- Left M1 (MAB0A-50); M- Right M2 (MAB0B-3); N- Right M2 (MAB0B-32); O- Right M3 (MAB0A-52).

local biozone). These assemblages are characterised by the reoccurrence of *Heterosorex*, the rareness of *Microdyromys legidensis-koegnivaldi*, and the decrease in the numbers of lagomorphs. Finally, local/regional biozone Cb is defined by the concurrent range zone of *Democricetodon moralesi* Van der Meulen, Peláez-Campomanes & Daams, 2004 and *L. ellipticus*. In this local/regional biozone, there are also (although not diagnostic for the zone), the first occurrences of *Democricetodon franconicus* Fahlbusch, 1966, *Eumyarion*, *Prolagus vargasensis* Hordijk & Van der Meulen, 2010 (*Prolagus* n. sp. 2 in Van der Meulen et al. 2012), and *Amphelchinus*, as well as *Prodryomys satus* Mayr, 1979 in the uppermost part. In this local biozone, there are the last occurrences of *Heterosorex*, *Peridyromys murinus* (Pomel, 1853), and *Simplomys meulenorum* García-Paredes et al. 2009. We differentiate regional biozones in the eastern Iberian Peninsula based on the Calatayud-Montalbán Basin – as described above – from the local biozones.

## SYSTEMATIC PALAEOLOGY

Order **Rodentia** Bowdich, 1821

Suborder **Supramyomorpha** D'Elía et al., 2019

Infraorder **Castorimorpha** Wood, 1955

Superfamily Geomyoidea Bonaparte, 1845

Family Eomyidae Winge, 1887

Genus *Ligerimys* Stehlin & Schaub, 1951

*Ligerimys florancei* Stehlin & Schaub, 1951

Fig. 3

**Localities:** MTR2, BC1, MAB0A and MAB0B.

**Material:** MTR2: 2 dp4, 1 p4, 1 m1/2, 2 DP4, 2 M1/2; BC1: 1 p4, 1 DP4; MAB0A: 2 dp4, 2 p4, 2 m1/2, 2 m3, 4 P4, 3 M1/2, 1 M3; MAB0B: 2 p4, 1 m1/2, 2 m3, 1 P4, 3 M1/2.

**Measurements:** Suppl. tab. 1; Fig. 4

**Stratigraphic and geographic range:** MN3-4 (early Miocene) of Western and Central Europe.

## Description

*dp4* (MAB0A; Fig. 3A): The anterolophid and metalophid are well-connected. They may form a closed ellipse (1 out of 2) or be open on the labial side (1 out of 2); this ellipse is the smallest of the tooth. The metalophid is straight and forms a closed ellipse with the mesolophid; the lingual connection is high in both, while the labial connection may be high (1 out of 2) or low (1 out of 2). The longitudinal crest is well-developed and slightly connects the mesolophid and the hypolophid on the labial side of the tooth. The mesosinusid and sinusid are open, although the sinusid is relatively narrow. The hypolophid and posterolophid form a closed ellipse with a low lingual connection.

**Variability in other sites** (see Suppl. tab. 2): The dp4 from MTR2 has a medial connection between the anterolophid and metalophid; this last crest is sinuous.

*p4* (MAB0B; Figs. 3B-C): The connection between the anterolophid and metalophid may be low on the lingual side (1 out of 2) or on the labial side (1 out of 2) of the ellipse. The metalophid is curved. This last crest and the mesolophid form the largest ellipse and their connections are well-developed. The longitudinal crest may be well developed (1 out of 2) or absent (1 out of 2); if it is present, it is positioned slightly towards the labial side of the tooth. The mesosinusid is open. The sinusid is open and narrow. The hypolophid and the posterolophid form a closed ellipse. The lingual connection may be low (1 out of 2) or high (1 out of 2).

**Variability in other sites** (see Suppl. tab. 2):

The p4 from BC1 has a low anterior elliptical connection, a connection in the middle of the anterior ellipse, a sinuous metalophid, and an interrupted mesolophid. The specimens from MTR2, BC1, and MAB0A are smaller than those from MAB0B. Two flattened roots, anterior and posterior, are present.

*m1/2* (MTR2; Fig. 3D): Both anterolophids are present. The metalophid and the mesolophid form a complete and slightly rhomboidal ellipse; the labial connection of this ellipse is well-developed. The protoconid and the hypoconid are well-developed. The hypolophid and the posterolophid form another rhomboidal ellipse with a high labial connection. The ellipses are connected by a low longitudinal crest (compared to other crests) with a slightly labial position. The sinusid and the mesosinusid are transverse with a similar size. Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2):

In the material from MAB0A (Fig. 3E), the labial anterolophid may be absent or both anterolophids may be present, albeit independent of the metalophid. In the material from MAB0B, the longitudinal crest is longer than in the material previously described.

*m3* (MAB0A; Fig. 3F): The anterolophid is absent. The metalophid and the mesolophid form a closed ellipse (as with the hypolophid and the posterolophid), with the last ellipse being smaller. Both ellipses have a wide connection, lingually displaced. The hypoconid and protoconid are labially displaced in the ellipse. The sinusid is slightly displaced to the posterior side, and the mesosinusid is absent.

*DP4* (MTR2; Fig. 3G): The anteroloph and protoloph are not connected on the labial side. The protoloph is connected to the protocone. The longitudinal crest is lingually displaced, convex, long, and connected to the hypocone. The mesosinus is open and curves posteriorly on its lingual end. The mesoloph is absent. The sinus is markedly proverse. The metaloph and posteroloph form a closed ellipse, the first crest is sinuous. The posterosinus is relatively narrow. Three flattened roots are present, one at each corner of the subrectangular tooth.

**Variability in other sites** (see Suppl. tab. 2):

The material from BC1 (Fig. 3H) has a small mesostyle and is longer.

*P4* (MAB0A; Fig. 3I): The crests are wide. The anteroloph and protoloph may be joined labially by

a low connection (1 out of 2) or may lack a connection (1 out of 2). The protoloph is connected to the longitudinal crest posterior to the protocone. The hypocone is smaller than the protocone. The longitudinal crest may be situated in the middle of the tooth and may be directed to the posterolingual side (2 out of 4), or it may be straight (2 out of 4) and connected with the metaloph. The mesosinus may be open on the labial side (1 out of 2) or closed by a low crest (1 out of 2). The sinus is well developed and slightly directed to the anterior side. The mesosinus is open and curved posteriorly on its lingual end. A small crest may be present on the anterolabial side of the metacone (1 out of 2) or absent (1 out of 2). The metaloph is curved and has a low connection on the labial side of the posteroloph. The posterosinus is relatively wide. At least three roots are present, two occurring on the lingual side.

**Variability in other sites** (see Suppl. tab. 2):

The material from MAB0B is similar to that described previously.

*M1/2* (MAB0B; Fig. 3K-L): There is a vestigial lingual anterolophid. The protocone has a well-developed contact with the protoloph (2 out of 3) or is low (1 out of 3). The anteroloph and protoloph have no contact on the labial side; the first crest is shorter and narrower than the second. The protoloph is sinuous. In one specimen, there is a small central mesoloph. In another, there is a low crest that closes the mesosinus. The mesostyle is not present. The longitudinal crest is low and convex; it contacts the metaloph; in one specimen, this contact is low. The longitudinal crest is lingually displaced; the metaloph is sinuous. This crest and the posteroloph form a closed ellipse; their labial contact is either low (1 out of 3) or well-developed (2 out of 3). The posteroloph may be relatively short and narrow (1 out of 3) or have a length similar to the other crests (2 out of 3). The posterior side of the tooth is slightly rounded and is narrower than the anterior side. Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2):

In the material from MAB0A (Fig. 3J), the mesoloph is absent and the mesostyle is small. The anterior ellipse is not closed labially, and it is larger.

*M3* (MAB0A; Fig. 3M): subtriangular occlusal shape. The protocone has complete contact with the anteroloph and is isolated from the protoloph. The anteroloph and the protoloph have a low labial

connection. The protoloph and metaloph are connected, forming a Y-shape. The mesoloph is absent, and a crest partially closes the mesosinus. The metacone has an anterolabial spur. The sinus is absent. The metaloph is reduced and contacts the labial side on the postero-lingual corner of the tooth. The metaloph and the posteroloph form a small, closed ellipse. The posteroloph is short and curved. The posterior side of the tooth is rounded and reduced. Two roots are present, anterior and posterior.

**Remarks.** *Ligerimys florancei* is proportionally less common than the other species of this genus described in the Ribesalbes-Alcora Basin. Overall, this species is clearly distinguished from the other species of the early Aragonian from the Iberian Peninsula by its larger size and its crests with rhomboidal form in the lower molars (Álvarez-Sierra 1987). On the contrary, *Ligerimys lophidens*, the other contemporary European species, differs from, *L. florancei* in having a well-developed longitudinal crest in the m1/2 (among other characteristics), which gives this part of the tooth an H shape (Álvarez-Sierra 1987). The absence of this morphology in the specimens from the oldest sites of the studied basin indicates that they belong to *L. florancei*.

This species, which has a Central European origin and is present in the assemblages from the Ribesalbes-Alcora Basin, does not differ greatly from the samples described by Álvarez-Sierra (1987) from the Calatayud-Teruel Basin. Nevertheless we note the lower morphological variability and greater development of the central crests of the M1, as well as the presence of a simpler dp4. These are all common differences between the assemblages of this species.

Compared to other European assemblages, such as those from French sites, there are several differences: a better-developed m1/2 anterolophid – with respect to material from the sites in the south of France (Escarguel & Aguilar 1997; Aguilar et al. 2010) – or a less-developed mesoloph than specimens from the site of Suèvres (Hugueney & Mein 1968). In the other Central European assemblages, there are no major differences with the material studied here (Fejfar 1989), although the specimens from Rembach and Forsthart present a less developed anterolophid of the m1/2 (Ziegler & Fahlbusch 1986).

The measurements of this species (Fig. 4) show small differences between the representati-

ves of the Iberian Peninsula and those of Central Europe (Álvarez-Sierra 1987). Overall, the studied specimens are larger than those from Villafeliche 2A from the Calatayud-Montalbán Basin; they are similar to those from the sites of Can Martí Vell 1, Vieux Collonges, Erkertshofen and Olmo Redondo 3 (Álvarez-Sierra 1987).

### *Ligerimys ellipticus* Daams, 1976

Fig. 5 and 6

**Localities:** FS1, MAB1, MAB2, MAB3, MAB4, MAB5, MAB6, MAB8, MAB11, MAB12, CBR0B, CBR0D and CBR1.

**Material:** FS1: 2 dp4, 1 p4, 2 m1/2, 2 m3, 1 DP4; 3 P4; 5 M1/2; 2 M3; MAB1: 2 m3; MAB2: 1 P4, 5 M1/2; MAB3: 18 dp4, 8 p4, 36 m1/2, 14 m3, 26 DP4, 13 P4, 54 M1/2, 16 M3; MAB4: 1 M1/2; MAB5: 11 dp4, 12 p4, 47 m1/2, 21 m3, 20 DP4, 23 P4, 63 M1/2, 28 M3; MAB6: 1 M1/M2; MAB8: 2 m1/2, 2 M1/2; MAB11: 2 m1/2, 1 m3, 1 P4, 2 M1/2, 2 M3; MAB12: 1p4; CBR0B: 4 m1/2, 1 m3, 1 DP4, 2 M1/2, 1 M3; CBR0D: 1 m1/2, 1 M3; CBR1: 2 M1/2.

**Measurements:** Suppl. tab. 1; Fig. 4

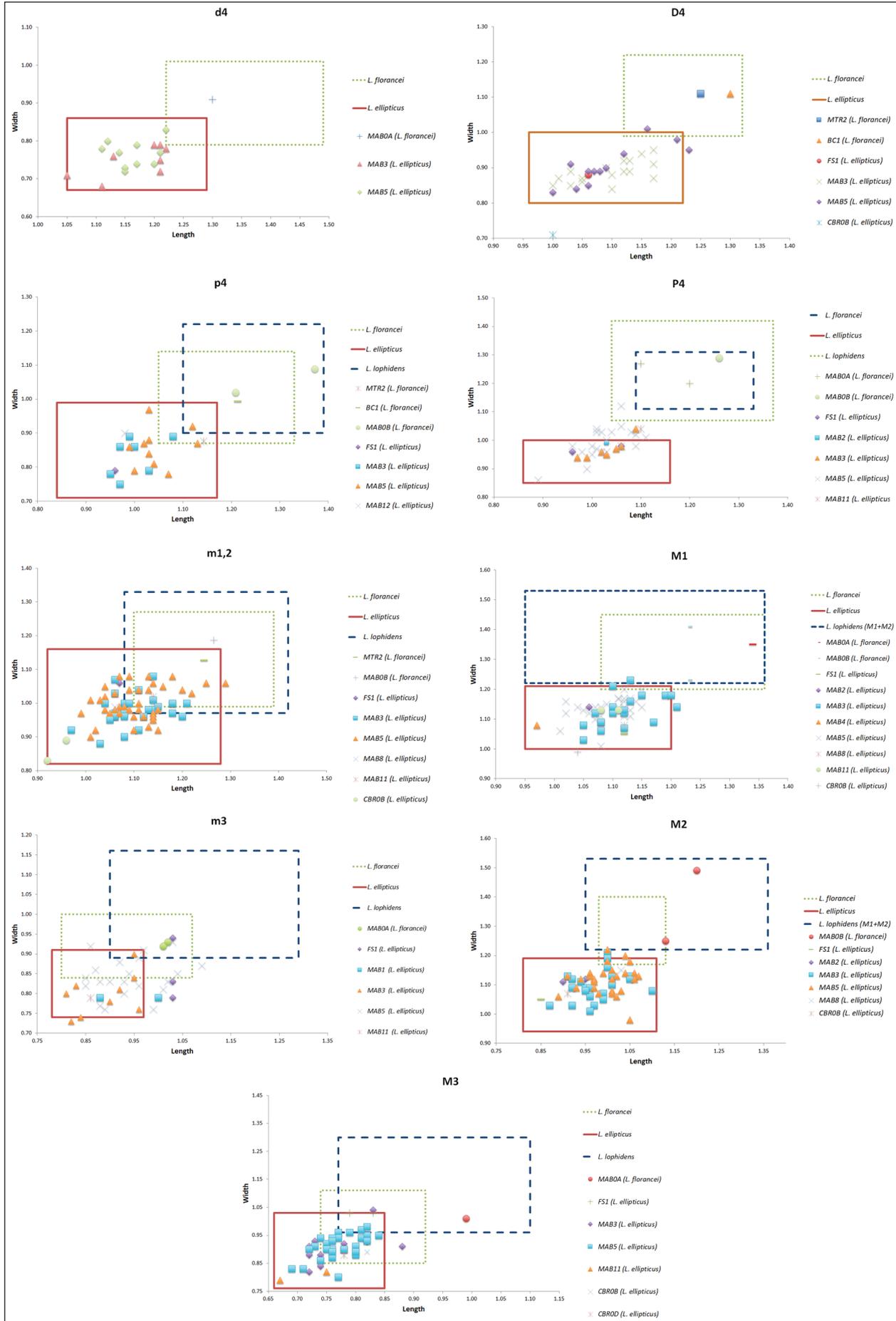
**Stratigraphic and geographic range:** MN4-5 (early-middle Miocene) of Iberian Peninsula

### Description

*dp4* (MAB5; Fig 5A-B): The anterolophid and metalophid may be well-connected (2 out of 10) or the contact may be low on the lingual side (3 out of 10), only on the labial side (2 out of 10), or on both sides (1 out of 10); alternatively, it is low on the lingual side and open on the labial side (2 out of 10). These crests form a closed ellipse; this ellipse is smaller than the next one; in one specimen, there is a medial connection within the ellipse via a low crest. The metalophid may be straight (4 out of 10) or sinuous (6 out of 10). The metalophid and mesolophid form a closed ellipse. The lingual connection between them may be high (7 out of 11) or low (4 out of 11). The longitudinal crest may be well-developed (3 out of 11) but is more frequently low, connecting the mesolophid and hypolophid in the middle of the tooth, slightly to the labial side. The mesosinusid is open. The sinusid is open and

---

Fig. 4 - Comparison of length and width measurements (in mm) of dp4, DP4, p4, P4, m1, 2, M1, m3, M2, and M3 of the genus *Ligerimys*. *L. florancei* from Villafeliche 2A; *L. ellipticus* from Buñol (type locality); *L. lophidens* from Bissingen; and the material from Ribesalbes-Alcora Basin (Fahlbusch, 1970; Álvarez-Sierra 1987; this publication).



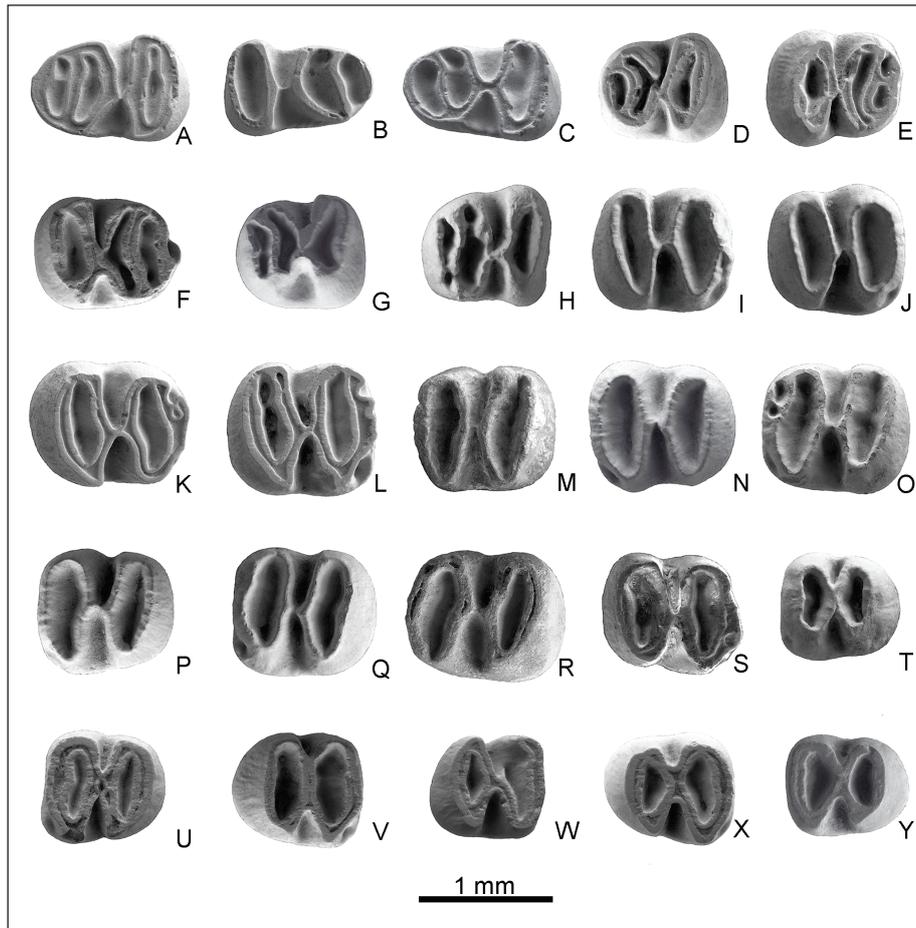


Fig. 5 - Lower teeth of *Ligerimys ellipticus* from the Ribesalbes-Alcora Basin.

A- Left dp4 (MAB5-23); B- Right dp4 (MAB5-672); C- Left dp4 (MAB3-598); D- Left p4 (MAB5-327); E- Right p4 (MAB5-674); F- Right p4 (MAB3-607); G- Left p4 (FS1-60); H- Left p4 (MAB12-2); I- Right m1/2 (MAB5-299); J- Right m1/2 (MAB5-310); K- Right m1/2 (MAB5-682); L- Right m1/2 (MAB5-688); M- Left m1/2 (MAB5-698); N- Left m1/2 (MAB3-614); O- Left m1/2 (MAB3-617); P- Left m1/2 (MAB3-620); Q- Left m1/2 (MAB8-3); R- Left m1/2 (MAB11-91); S- Right m1/2 (CBR0B-48); T- Left m3 (MAB5-315); U- Left m3 (MAB5-703); V- Right m3 (MAB5-704); W- Right m3 (MAB3-646); X- Right m3 (MAB3-647); Y- Left m3 (CBR0B-50).

may be relatively narrow (3 out of 11) or wide (8 out of 11). The lingual connections of the posterior ellipse may be high (5 out of 11), low (3 out of 11), or absent (1 out of 11), or both connection of the posterior ellipse may be low (2 out of 11). Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2): In MAB3 (Fig. 5C), the low connection between the anterolophid and the metalophid, along with the presence of a sinuous metalophid is more frequent. The high labial connection between the metalophid and the mesolophid is dominant. The longitudinal crest is not present in one specimen; it is doubled in another. Generally, the development of this crest is larger in this site than in MAB5. Finally, the sinusid is narrower and smaller. The material from FS1 is similar to that described from MAB5.

*p4* (MAB5; Fig. 5D-E): The anteroloph is very reduced, although it is better developed in four specimens. The connection between the anterolophid and the metalophid may be low (8 out of 10) or well-developed (2 out of 10), forming a closed ellipse. The metalophid is curved. The metalophid and mesolophid form a closed ellipse; in one speci-

men, it is interrupted (Fig. 5D). The lingual connection between the anterior crests may be low (8 out of 10) or well-developed (2 out of 10), while the labial connection may be high (6 out of 10) or low (4 out of 10). The longitudinal crest may be absent, with a direct connection between the mesolophid and hypolophid (2 out of 11), a low connection (4 out of 11), or a well-developed connection (5 out of 11). This connection, if present, is always closer to the labial side of the tooth. The mesosinusid is open. The sinusid is narrow and open. The hypolophid and posterolophid form a closed ellipse. Both connections may be low (6 out of 11); otherwise only the lingual connection is low (1 out of 11) or well-developed (4 out of 11). Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2): In MAB3 (Fig. 5.F), a small valley in the antero-lingual side of the anterolophid is present in one specimen. The connection between the anterolophid and metalophid in the lingual side is low in one specimen and absent in two; in three specimens there is a connection between both crests in the medial part of the tooth. The metalophid is straight in one

specimen. In another specimen, the mesolophid is absent, and the metalophid has a low connection with the hypolophid; the mesolophid is absent in another specimen. The longitudinal crest is near the labial side in one specimen, and the sinusid is reduced in another. The specimens from MAB3 are generally smaller than from MAB5. The material from FS1 (Fig. 5G) and MAB12 (Fig. 5H) is similar to that described from MAB5.

*m1/2* (MAB5; Fig. 5I-M): Both the lingual and labial anterolophids may be present (14 out of 45); alternatively only the labial anterolophid is present (29 out of 45), or both are absent (2 out of 45). The metalophid and the mesolophid form a closed ellipse. The lingual connection of this ellipse may be high (21 out of 35) or low (14 out of 35); the labial connection may be low (13 out of 36) or high (23 out of 36). The mesolophid in two specimens has a posterior spur. The hypolophid and posterolophid form a closed ellipse. The lingual connection is generally low, except in four specimens where it is high; the labial connection is high in half of the teeth. The ellipses are connected by a longitudinal crest, which may be short (40 out of 46) or relatively long (6 out of 46). Its position may be central or slightly labial. The sinusid and the mesosinusid are transverse and similar in size. Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2): At MAB3 (Fig. 5O-P), two specimens have no longitudinal crest, and (generally) the specimens from CBR0B (Fig. 5S) are slightly smaller than those from other sites. The material from FS1, MAB8, MAB11 (Fig. 5S), and CBR0D are similar to those described previously.

*m3* (MAB5; Fig. 5T-V): The anterolophid may be present (3 out of 19), be only a labial spur (9 out of 19), or be absent (8 out of 19). The metalophid and mesolophid form a closed ellipse, as do the hypolophid and posterolophid. Four specimens have a medial contact in the middle of the anterior ellipse. In two specimens, the lingual connection of the posterior ellipse is low, while in another two, the labial connection is also low. In half of the teeth, the anterior ellipse is larger than the posterior ellipse; in the other half, they are of similar size. Both ellipses may have a wide connection (15 out of 22), a narrow connection (6 out of 22), or a double connection (1 out of 22) (Fig. 5U). This connection may be slightly lingually displaced (16 out of 21) or

labially displaced (5 out of 21). The sinusid and mesosinusid are transverse. The sinusid may be larger than the mesosinusid (14 out of 21) or similar in size (7 out of 21). Two circular roots are present in an antero-posterior position.

**Variability in other sites** (see Suppl. tab. 2): In the material from MAB3 (Fig. 5W-X) in one specimen (Fig. 5W) the lingual side of the mesolophid is only a spur and the ellipse is not closed. In another, the posterolophid is open; and in yet another, the labial connection between metalophid and mesolophid is absent. Generally, in specimens from this site, the anterior ellipse is larger and the connection between both ellipses is narrower and in the labial position; the sinusid and mesosinusid are more transversal, and the specimens are slightly smaller. The material from FS1, MAB1, MAB11, and CBR0B (Fig. 5Y) are similar to those described from MAB5.

*DP4* (MAB5; Fig. 6A-C): The anteroloph and the protoloph are not connected on the labial side, except in one specimen. In the other specimen, there is an anterior spur on the anteroloph. The protoloph is connected to the longitudinal ridge posteriorly to the protocone. The longitudinal crest is convex, long, and lingually displaced; it may be connected to the metaloph (14 out of 18) or the hypocone (4 out of 18). The longitudinal crest may be continuous (13 out of 19) or interrupted (6 out of 19). In one specimen, the protocone has no contact with the protoloph. The mesoloph is small in eight specimens, and the mesostyle is small in seven. The sinus is slightly directed towards the anterior part. The mesosinus is transverse and open. The metaloph and posteroloph form a closed ellipse, although it is open in three specimens. The metaloph may be sinuous (15 out of 19) or nearly straight (4 out of 19). In two specimens, the metaloph and the posteroloph are connected in the middle of the tooth by a low crest. The posterosinus is relatively narrow. Three roots are present, one at each corner of the subrectangular tooth.

**Variability in other sites** (see Suppl. tab. 2): At MAB3 (Fig. 6D), the anteroloph and the protoloph are never connected on the labial side. The mesostyle is less common. The material from FS1 (Fig. 6E) and CBR0B (Fig. 6F) are similar to those described from MAB5.

*P4* (MAB5; Fig. 6G-I): The crests of this tooth are wide and irregular. The anteroloph and

protoloph are not connected on the labial side, except in two specimens. The protoloph is connected to the protocone. The protocone and the hypocone are well-developed. The longitudinal crest is slightly lingually displaced, convex, and short; it may be connected to the metaloph (17 out of 22) or to the hypocone (4 out of 22); or the connection is absent (1 out of 22). The mesoloph is absent. The mesostyle may be small (7 out of 22) or absent (15 out of 22). The sinus is slightly directed to the anterior side (8 out of 22) or is transverse (14 out of 22). The mesosinus is transverse and open, although in one specimen it is closed. The metaloph and posteroloph form a closed ellipse in eight specimens. The posteroloph is reduced in two teeth. The metaloph is straight. Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2): In MAB3 (Fig. 6J), the anteroloph and protoloph are not connected on the labial side. The longitudinal crest is connected to the metaloph; in one specimen it is double. The mesoloph is small in two teeth, and the mesostyle is present in six. The mesosinus is more commonly closed than in MAB5 specimens. In the sites of FS1 (Fig. 6K) and MAB11 (Fig. 6L), the lingual cusps are less developed. The material from MAB2 is similar to that the described from MAB5.

*M1/2* (MAB5; Fig. 6M-O, T-X): A small antero-lingual valley may be present (14 out of 61); the crest that encloses this valley may be only a small spur (33 out of 61), or the valley and the crest may be absent (14 out of 61). The protocone may have well-developed contact with the longitudinal ridge posterior to the protocone (50 out of 57), or poorly developed contact (7 out of 57). The anteroloph and protoloph are not connected on the labial side; the first crest is similar to the second, although in five specimens, it is shorter and narrower. The protoloph has a sinuous course. The mesoloph is small in nine specimens, while the mesostyle is present in 28. A low crest closes the mesosinus, except in 25 teeth. A small- to medium-sized spur of the metacone appears in 41 specimens. The longitudinal crest is low, convex, and connected to the metaloph, although it is divided in 11 teeth. The longitudinal crest is lingually displaced. A cingulum closes the sinus in one tooth. The metaloph has a sinuous course. The metaloph and posteroloph form a closed ellipse; the contact may be complete (12 out of 57), low (42 out of 57), or incomplete (3 out of 57). In two speci-

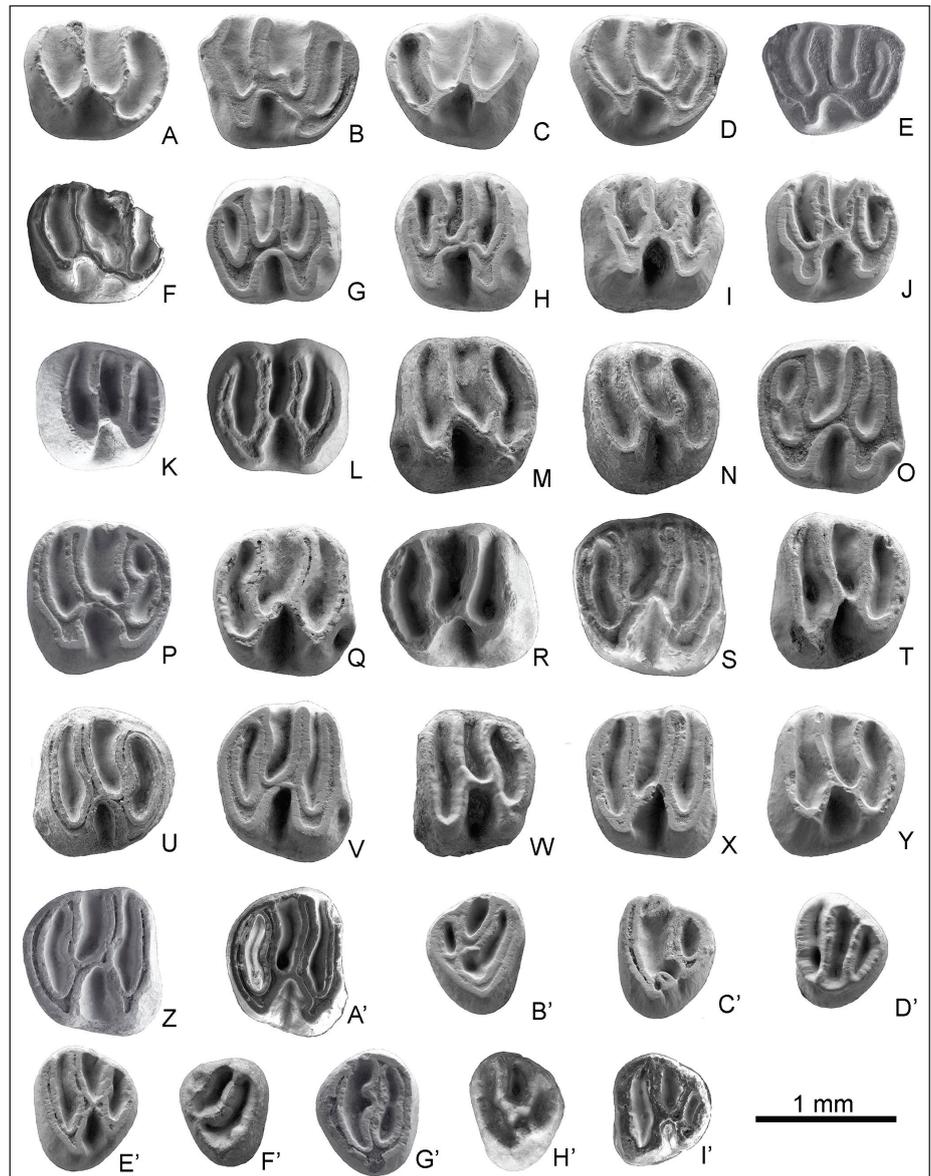
mens, there is a longitudinal connection between the metaloph and posteroloph in the middle of the ellipse. The posteroloph may be similar to the anterior crests, although it is shorter and narrower in three specimens. In one tooth, the posteroloph has no contact with the hypocone. The posterior side is rounded and more narrow than the anterior side, especially on M2. Two flattened roots, anterior and posterior, are present.

**Variability in other sites** (see Suppl. tab. 2): At MAB3 (Figs. 6P-Q, Y), the mesoloph is less common, while the metastyl is more common. The metaloph is discontinuous in one tooth. In another, the metaloph is directly connected to the protocone and the longitudinal crest is discontinuous; in this specimen, the connection between the hypocone and metaloph is low. At MAB11 (Fig. 6S), the anterolabial spur of the metacone is not present. The material from FS1 (Fig. 6Z), MAB2, MAB6, MAB8 (Fig. 6R), CBR0B (Fig. 6A'), and CBR1 is similar to that described before.

*M3* (MAB5; Fig. 6B'-F'): Subtriangular tooth with a very variable morphology. One specimen presents a spur in the anterolingual side of the anteroloph. The protocone may be isolated (one specimen), may not contact the protoloph (9 out of 28), may only show a low contact (9 out of 28), or may only show a high contact (10 out of 28). In one tooth, the protoloph is absent; in another two, it connects with the labial side. The relationship between the anteroloph and protoloph is highly variable: they may be connected on the labial side (Fig. 6F'; 5 out of 28), have a low connection between both crests (Fig. E'; 12 out of 28), be isolated (Fig. 6D'; 8 out of 28), or be completely fused (Fig. 6C'; 1 out of 28); otherwise, the protocone is absent (Fig. 6B'; 1 out of 28). One tooth has a low anteroloph-protoloph connection. The protoloph is connected to the longitudinal crest; it may be a spur of the protoloph (3 out of 27), be well-developed and connect the protoloph and metaloph (4 out of 27), or have a low connection (10 out of 27), a double connection (1 out of 27) or no connection (9 out of 27). The metaloph and protoloph are fused in six specimens. In another five, the protoloph connects directly to the metaloph. The mesoloph is absent. A crest closes the mesosinus, except in seven teeth. A small anterolabial spur appears in the metacone. The sinus may be closed by a crest (18 out of 29), open (6 out of 29), or absent (5 out of 29). The metaloph

Fig. 6 - Upper teeth of *Ligerimys ellipticus* from the Ribesalbes-Alcora Basin.

A- Right DP4 (MAB5-81); B- Right DP4 (MAB5-628); C- Left DP4 (MAB5-629); D- Left DP4 (MAB3-429); E- Right DP4 (FS1-48); F- Right DP4 (CBR0B-47); G- Left P4 (MAB5-351); H- Left P4 (MAB5-359); I- Right P4 (MAB5-644); J- Right P4 (MAB3-520); K- Right P4 (FS1-49); L- Left P4 (MAB11-90); M- Left M1 (MAB5-84); N- Left M1 (MAB5-328); O- Right M1 (MAB5-346); P- Left M1 (MAB3-526); Q- Right M1 (MAB3-540); R- Right M1 (MAB8-4); S- Right M1 (MAB11-89); T- Left M2 (MAB5-88); U- Left M2 (MAB5-333); V- Right M2 (MAB5-348); W- Left M2 (MAB5-635); X- Right M2 (MAB5-642); Y- Left M2 (MAB3-517); Z- Right M2 (FS1-52); A'- Right M2 (CBR0B-49); B'- Right M3 (MAB5-102); C'- Left M3 (MAB5-669); D'- Left M3 (MAB5-715); E'- Left M3 (MAB5-869); F'- Right M3 (MAB5-874); G'- Right M3 (MAB3-16); H'- Left M3 (MAB11-95); I'- Left M3 (CBR0B-2).



is reduced and goes from the lingual side to the labial side. The metaloph and posteroloph generally form a closed ellipse; the contact may be well-developed (15 out of 26), low (10 out of 26), or entirely absent (2 out of 26). In one specimen, there is contact in middle of the tooth between the metaloph and posteroloph. The posteroloph is short, narrow and connected to the labial side. The posterior side is rounded and may be very reduced (10 out of 27) or less reduced (16 out of 27); or the posteroloph may even be residual (1 out of 27). In one tooth, the anteroloph and metaloph connect to form an ellipse, with the protoloph situated in the middle of the tooth and the posteroloph reduced to only a posterior spur (Fig. 6F'). Three cylindrical roots are present: one on the labial side, another on the lingual side, and the last one on the anterior side.

**Variability in other sites** (see Suppl. tab. 2): At MAB3 (Fig. 6G'), the protocone has a low contact with the anteroloph in three teeth. One specimen has a low connection between the anteroloph and the protoloph at their medial zone. In another tooth, the protoloph is divided in two, forming the sinus, while the metaloph is separated from the protoloph. A closed sinus is less frequent. The metaloph and posteroloph form a small, closed ellipse; this contact is always present. The posterior side of the tooth is often more reduced. At CBR0D, the longitudinal crest is absent; there is a small antero-labial spur of the metacone; the sinus is absent; and the metaloph is reduced. One tooth from MAB11 (Fig. 6H') is smaller than the other specimens. The material from FS1 and CBR0B (Fig. 6I') is similar to that described from MAB5.

**Remarks.** The morphological characteristics and size of the specimens from the various sites of the Ribesalbes-Alcora Basin are similar. Compared to other *Ligerimys ellipticus* assemblages from the Calatayud-Montalbán and Magro basins, the studied material has generally and supposedly primitive characteristics (after Álvarez-Sierra 1987), such as the presence (and the grade of development) of the anterolophid, which appears more frequently in the older species of the genus *Ligerimys*. Moreover, the remains studied here are more similar to the assemblages from the Vallès-Penedès Basin (Agustí 1983).

In the specimens from the Ribesalbes-Alcora Basin, the presence of a primitive mesostyle in the upper molars is common, though it is less frequent in the central part of the tooth. In other assemblages, this characteristic is uncommon or absent or the mesoloph does not appear. In other species of this genus, it only appears in this frequency in *Ligerimys antiquus*, although in this species and *Ligerimys falibuschi*, the mesoloph is better developed (Álvarez-Sierra 1987).

The labial connection between the M1/2 ellipses is generally open on the anterior side and closed on the posterior side (Álvarez-Sierra 1987). Nevertheless, in the Araia material, the anterior connection is more developed, with a low connection. This characteristic can be observed in the teeth with slight wear. This kind of connection – and its proportion of occurrence – is typical in primitive species such as *Ligerimys palomae* (Álvarez-Sierra, 1987) and some assemblages of *L. ellipticus*, such as the sample from Morteral 1 (Ruiz-Sánchez et al. 2012). The lingual connection in *L. ellipticus* is well-developed, although it very rarely presents a low connection or an absent connection. In other primitive species, this appears as a low lingual connection in the anterior valley (*L. florancei* and *L. palomae*) or is absent (*Ligerimys magnus* and *L. falibuschi*; Álvarez-Sierra 1987). In the studied material, two principal kinds of connections occur: a well-developed connection and a low and central connection. A low and anterior connection occurs rarely.

Following the classification of the M3 morphotypes after Álvarez-Sierra (1987), in the studied material, morphotypes 2 (crests in an H-shape) and 3 (crests in a Y-shape) are dominant. Morphotypes 4 (parallel crests), 5 (one anterior ellipse and two posterior crests), and 6 (a simplified

molar with only two ellipses and one central crest) appear less commonly. According to Álvarez-Sierra (1987), this dominance is typical of *L. falibuschi*, while in the type locality of *L. ellipticus*, the dominant morphotype is 4, followed by 2.

The morphology of the p4 in the Ribesalbes-Alcora Basin is similar to that of the type locality of *L. ellipticus*. The dominant morphotype shows a complete anterolophid and – to a lesser degree – the presence of an incomplete one. The complete mesolophid of the p4 is dominant in this species, and this crest is absent in only one tooth in the type locality (Álvarez-Sierra 1987). In the Araia material, the presence of a complete metalophid is dominant, although two morphotypes appear with relative frequency: a discontinuous mesolophid and a short mesolophid that originates from the hypolophid. This second morphology only appears in *L. antiquus* from Bañón 11A, *L. falibuschi* from Ramblar 7, and *L. aff. magnus* from Ramblar 3B and 4. While, the third morphology appears rarely in *L. palomae* from Olmo Redondo 2 and in *L. antiquus* from Moratilla. The connection between the mesolophid and posterolophid observed in the studied sites resembles the morphotypes of *L. ellipticus* from Vargas 1A (Álvarez-Sierra 1987).

The anterolophid of the m1/2 is highly variable, although it is always reduced in the studied material. This variability is considered to be higher in older species of this genus (Álvarez-Sierra 1987), although, as noted above, it does not occur in the material studied here. Álvarez-Sierra (1987) does not describe the labial anterolophid, which is described in Escarguel and Aguilar (1997) for *L. florancei* and *L. antiquus* from the Early Miocene of southern France. In particular, this characteristic is quite frequent in the specimens studied here. The longitudinal crest is just a low contact between the two ellipses and is never well-developed. This occurs in other assemblages of this species, even in the type locality where this crest is more frequently absent. The contact between the hypolophid and the posterolophid is variable: The more common morphotype in the studied material is with low contact, resembling the older species of this genus, in contrast to what occurs in *L. ellipticus*, in which it shows a complete connection (Álvarez-Sierra 1987). The position of the longitudinal crest may be labial or lingual, although it lacks a clear tendency in the studied material, as it is usually located in the middle

of the tooth. Even so, it can be observed that, in MAB3, this crest tends to be placed in the labio-central position. In other species, the trend is clearly towards the labial side, except in *L. freudenthali*, where it is placed lingually (Álvarez-Sierra 1987).

Regarding the m3, the anterolophid is more variable in the studied material than in other assemblages of *L. ellipticus*, where it is absent. The morphology of the mesolophid is highly variable as well; in the studied specimens, it usually originates from the hypolophid, as in the older species of this genus (Álvarez-Sierra 1987).

Regarding measurements, the studied material fits the variability observed in the type locality (Buñol), although the P4 are wider and the m3 are longer.

Despite the morphological differences discussed here, the material studied should be ascribed to the species *Ligerimys ellipticus*, considering its size and general morphology. Nevertheless, this study shows that this species is characterized by great morphological variability.

## Discussion

### Palaeoecology

The palaeoecology of this group has traditionally been inferred from two aspects: the accompanying fauna and the percentages of *Ligerimys* found in each site (Álvarez-Sierra 1987). The genus *Ligerimys* is found in large numbers in lignitiforous sites from Central Europe; for this reason, a wooded and moist habitat has been inferred for eomyids in general (Álvarez-Sierra 1987; Daams et al. 1988; Van Dam & Weltje 1999). Nevertheless, Engesser (1999) questions this assignment, at least for some genera of this family. In fact, only two specimens of eomyids with complete skeletal remains and impressions of soft tissues, are known: *Eomys queryi* Comte & Vianey-Liaud, 1987 and *Eomyodon volkeri* Engesser, 1987. The first species shows typical anatomy of a gliding animal and certainly dwelled in dense forests, while the other species does not show this gliding adaptation and seems to have been a more generalized terrestrial/scansorial rodent (Storch et al. 1996; Engler & Martin 2015). On the other hand, Freudenthal et al. (2014) remark that the assumption of a moist and forest environment stems mostly from the general co-occurrence of eomyids with dormice. Thus, if the assignment of the second family fails, that of eomyids turns out

to be wrong. Indeed, in Engesser (1999), Huguency (1984), and Van der Meulen & Daams (1992), this assignment is due, in part, to the interpretation of the frequency curves of the different groups in the faunal sequences, the fact that they are totally coincident with the frequencies of certain dormice, and the fact that their absence coincides with intervals when ground squirrels are very abundant. However, other authors (Maridet et al. 2011) associate them (at least the brachyodont genera of this family) with humid and wooded environments. This is because their abundance is correlated to the pattern of fluctuation and progressive disappearance of forests during the late Miocene in Asia. The disappearance of this family occurs earlier in Asia and America (at the end of the Pliocene) than in Europe (at the beginning of the Pleistocene), likely because of the persistence in the latter continent of more warm-temperate forests (Kimura et al. 2020).

The presence of both species in a wide range of facies (see lithologies in Crespo et al. 2019a) would indicate that these species are eurytopic taxa and that their abundance may have been conditioned by temperature and humidity conditions. Although possibly this presence would be modified by the presence of a forest around the lake that defined the Ribesalbes-Alcora Basin. This is demonstrated by the *Konservat-Lagerstätten* of Foietà la Sarra A (FSA) and the presence of different groups of small mammals. The palaeovegetation of FSA is typical of a riparian assemblage, similar to the near forested sites of La Rinconada and San Chils, with presence of, poales, *Dicotylophyllum* sp. and *Salix?* (Álvarez-Parra et al. 2021; Postigo-Mijarra and Barrón 2013). The palaeolake of FSA in the base of the *L. ellipticus* biozone indicates an increase of the humidity of this biozone in contrast of *L. florancei* biozone. The forested habitat is also demonstrated by the other small mammal assemblage: unusual bat association, because the high diversity with a few number individuals of molossid bats is not typical in a European Early Miocene assemblage, where prevails the current European association, it is common in present day Neotropical, Ethiopian, and Indo-Australian molossid faunas. By this reason, this unusual assemblage is more typical of a tropical forested habitat although this family tends to avoid thickly forested habitats or subcanopy areas (Crespo et al. 2020a; and references therein). Other small mammals indicators of forested habitats founded in the Ribesalbes-Alco-

ra Basin are: the glider squirrel *Aliveria* cf. *luteyni* de Bruijn et al. 1980, the cricetid *Eumyarion*, the dormice *Prodryomys*, *Brasantoglis*, *Glirudinus*, and *Myoglis* the metatherian *Amphiperatherium frequens*, the gymnures, and the abundance of shrews (Crespo 2017; Crespo et al. 2019c, 2020b, 2021).

In particular, as indicated by the rest of the assemblage where each species appears, *L. florancei* could cope with drier environments than *L. ellipticus* in the Ribesalbes-Alcora Basin. This conclusion is supported by three lines of evidence: a preliminary study conducted by Crespo (2017) on the palaeoecological preferences of the mammals found in Campisano Ravine, a preliminary isotopic study performed by Ríos (2013) in which the drier sites coincide with the presence of *L. florancei*, and the presence of gypsum layers in some sites where *L. florancei* appears and *L. ellipticus* is absent.

#### Biostratigraphy

The members of the family Eomyidae are often used as biostratigraphic markers for the late Oligocene and Early Miocene (Álvarez-Sierra 1987; Ruiz-Sánchez et al. 2012; Van der Meulen et al. 2012). For example, in the Calatayud-Montalbán Basin (see Van der Meulen et al., 2012), along the Ramblian (regional zone A, MN3) there is a high abundance of eomyids, represented by the species *Ligerimys antiquus* and *L. fahlbuschi*, among others. During the earliest Aragonian (regional zone B, MN4), *Ligerimys palomae* appears in the first part of the local biozone. Within this zone, it is later substituted by *Ligerimys florancei*; in this local biozone, the remains of eomyids are scarce compared to local biozones A and C. Van der Meulen et al. (2012) divide regional biozone C of the Aragonian into two local biozones (Ca and Cb). In the first subzone, the species *L. florancei* is replaced by *L. ellipticus*; the latter species becomes extinct in the earliest part of the MN5 (middle Miocene) in local biozone Da. Another alternative regional biozonation has been proposed by Ruiz-Sánchez et al. (2012) for the Magro Basin. While one or more species of the genus *Ligerimys* occur in regional biozone B, during regional zone C, there is a period of coexistence and later replacement of *L. florancei* by *L. ellipticus*. This is similar to what occurs in the Vallès-Penedès Basin, in the localities of Can Martí Vell I and II (Agustí 1981, 1983) and Les Cases de la Valenciana (Jovells-Vaquè et al. 2018). This genus becomes extinct at the end of the MN4 after the

alternative regional biozonation of Ruiz-Sánchez et al. (2012).

Casanovas-Vilar et al. (2016) propose that the assemblages from the early Aragonian Vallès-Penedès Basin are to be correlated to local biozone C, as indicated above, but with the presence of only *L. ellipticus* in the younger sites, with no other species coexisting during this time period, while in the older sites as Cases de la Valenciana or Can Martí Vell 1 and 2 both species occur (Jovells-Vaquè et al. 2018).

Based on the data obtained from the study of eomyids, as well as the proportions in which they occur (Suppl. tab. 3), the sequence of Araia deposits can be divided into two long local biozones, with each biozone further subdivided into two subzones (Fig. 7):

1 - *Ligerimys florancei* Taxon-range local biozone (*L. ellipticus* is not present):

a - Sub-biozone *L. florancei* abundance range A: without this species, or less representing less than 5% of the recovered remains, such as in the sites MCX3 (132 mammal teeth found, extracted from Crespo et al. (2019a)), MTR2 (187), and BC1 (180).

b - Sub-biozone *L. florancei* abundance range B: with a scarce presence of eomyids (5 -20% of the total fauna), represented by the species *L. florancei*. This biozone is present in sites MAB0A (80) to MAB0B (75).

2 - *Ligerimys ellipticus* Taxon range local biozone (*L. florancei* is not present):

a - Sub-biozone *L. ellipticus* abundance range A: with a high abundance of eomyids (more than 20%), represented by the species *L. ellipticus*. This is present in the zone between FS1 to MAB9. In this sub-biozone, the principal sites are FS1 (63), MAB3 (807), and MAB5 (874).

b - Sub-biozone *L. ellipticus* abundance range B: with a scarce presence of the species *L. ellipticus* (less than 20%). This biozone includes all sites between MAB10 and the end of the synthetic stratigraphic column (CBR4). In this sub-biozone, the principal sites are MAB11 (145), CBR0B (56), and CBR1 (47).

In this way, if we only consider the genus *Ligerimys* and its abundance in the assemblages of the MN4/5 sites of the Iberian Peninsula, the next sequence can be obtained (Fig. 8; percentages obtained from Adrover et al. (1987), Agustí and Llenas (1993), Freudenthal et al. (2014), Hordijk et al. (2015), Jovells-Vaquè et al. (2018), and Crespo et al. (2019a)):

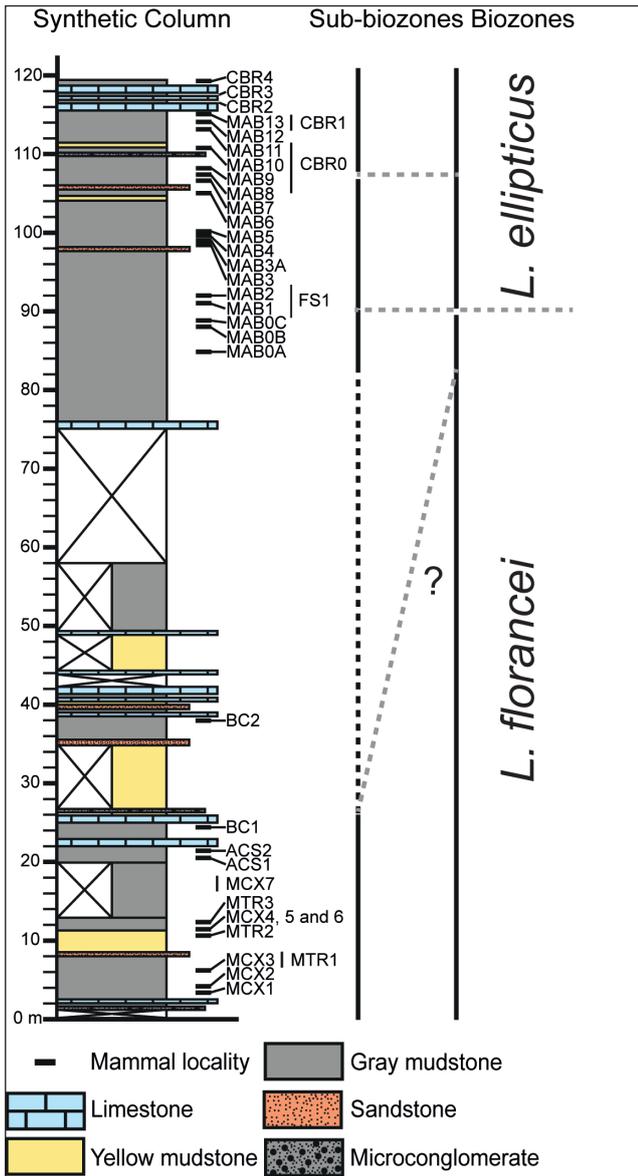


Fig. 7 - Composite column of the Campisano Ravine with positions of the studied sites and the different local biozones and sub-biozones present in this section. Modified from Crespo et al. (2019a). MCX: Mas dels Coixos; MTR: Mas de Torner; ACS: Araia Cantera Sud; BC: Barranc de Campisano; FS: Foietà la Sarra; MAB: Mas d'Antolino B; CBR: Corral de Brisca.

a - A first biozone with the presence of *L. palomae*, with more than 5% abundance. This biozone is represented by the sites of San Roque 1 and 2 and Olmo Redondo 1 and 2 from the Calatayud-Montalbán Basin. This biozone is not present in the Ribesalbes-Alcora Basin.

b - The second biozone shows more than 5% abundance for *L. florancei*. This biozone is represented by the Olmo Redondo 3 and Villafeliche 2 sites in the Calatayud-Montalbán Basin. This biozone is not present in the Ribesalbes-Alcora Basin.

c - The third biozone has an abundance of less than 5% for the species *L. florancei*, or it simply lacks the genus *Ligerimys*. This is represented by Artesilla from the Calatayud-Montalbán Basin and by MCX3, MTR2, and BC1 from the Ribesalbes-Alcora Basin.

d - In the fourth biozone *L. florancei* represents more than 5% of the recovered remains. This biozone is represented in the Ribesalbes-Alcora Basin by the sites MAB0A and MAB0B, although it is not recognized in other Iberian basins. This is because the Calatayud-Montalbán Basin has a gap in the record between the Artesilla sites and San Roque 3 (see Van der Meulen et al., 2012) and because, in the Levantine basins (excepting the Ribesalbes-Alcora Basin), there are no older sites than these.

e - The fifth biozone shows the presence of the species *L. florancei* and *L. ellipticus*. This biozone is present in the Barranco de Candel site in the Magro Basin and in Les Cases de la Valenciana and Can Martí Vell 1 and 2 in the Vallès-Penedès Basin. This biozone apparently is not recorded in the Ribesalbes-Alcora Basin.

f - In the sixth biozone *L. ellipticus* represents more of the 20% of the recovered remains. This biozone is represented by the sites of Buñol (Cerro de la Cruz; Magro Basin), Vargas 1A, and Olmo Redondo 5 and 8 (Calatayud-Montalbán Basin). In the Ribesalbes-Alcora Basin, it is represented by FS1, MAB3, and MAB5 sites.

g - The seventh biozone has an abundance of less than 20% for *L. ellipticus*. This is represented by Morteral 1 (Magro Basin), Montalvos 2 (Teruel Basin), Els Casots (Vallès-Penedès Basin), and MAB11, CBR0B, and CBR1 (Ribesalbes-Alcora Basin).

h - The eighth biozone has a residual presence of *L. ellipticus*, present only in La Col A from the Calatayud-Montalbán Basin.

## 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 two species of the genus *Ligerimys*. The most abundant species is *Ligerimys ellipticus*, which occurs in the youngest sites of this basin, while the other

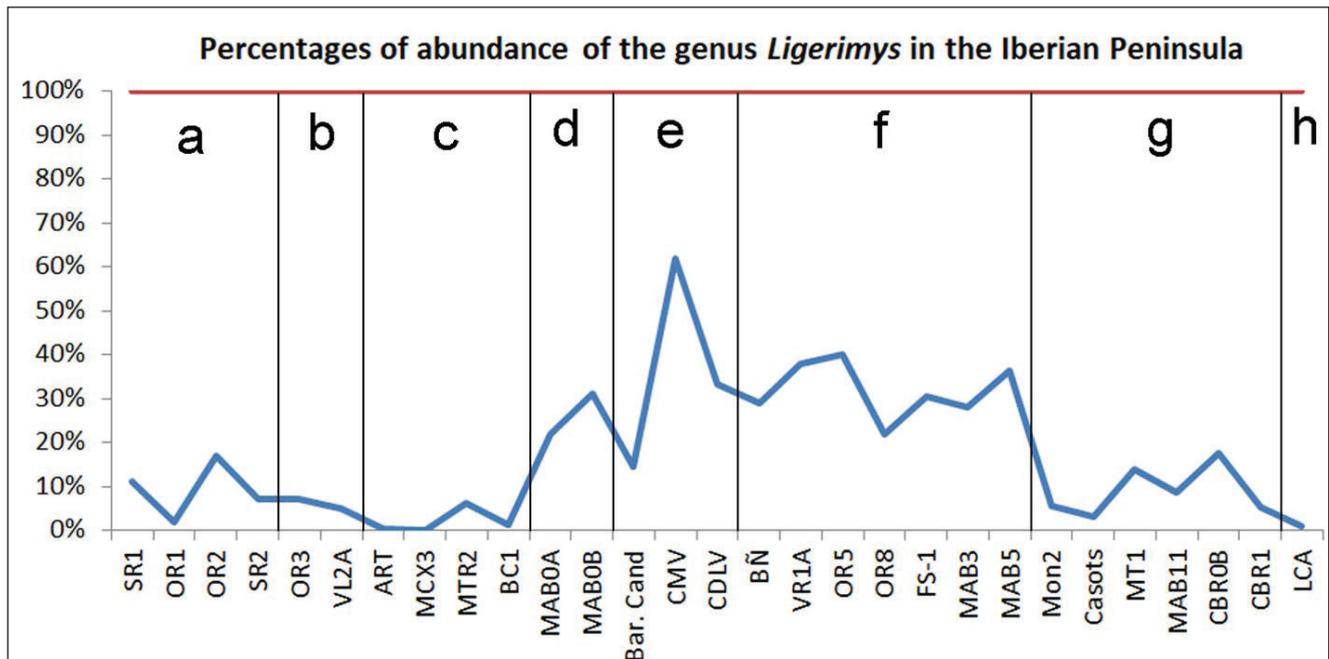


Fig. 8 - Relative abundance of the genus *Ligerimys* as compared to the rest of the rodents in the most representative sites of the Iberian Peninsula, together with the main sites studied in this publication. a: Biozone *L. palomae* with more than 5% of abundance; b: Biozone *L. florancei* with more than 5% of abundance; c: Biozone *L. florancei* with less than 5% or without presence of the genus; d: Subzone *L. florancei* with more than 5% of abundance; e: Biozone with presence of *L. florancei* and *L. ellipticus*; f: Biozone *L. ellipticus*, with more than 20% of abundance; g: Biozone *L. ellipticus*, with less than 20% of abundance; h: Biozone *L. ellipticus* with less than 1% of abundance. 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.: Barranco de Candel; CMV: Can Martí Vell; CDLV: Les Cases de la Valenciana; BÑ: Buñol; VR: Vargas; FS: Foieta la Sarra; Mon2: Montalvos 2; CBR: Corral de Brisca; MT1: Morteral 1; LCA: La Col A. From Adrover et al. (1987), Agustí and Llenas (1993), van der Meulen et al. (2011; 2012), Freudenthal et al. (2014), Hordijk et al. (2015), Jovells-Vaqué et al. (2018) and Crespo et al. (2019a).

species, *Ligerimys florancei*, appears in the oldest sites. Due to the large collection of *L. ellipticus* recovered, we can assess the morphological variation in this species. Notable newly reported features include the presence of a mesoloph, as well as features previously described only in ancient assemblages of this species, such as the presence of an anteroloph in the M1/2.

The palaeoecology of this genus is uncertain, and we consider that the abundance of this genus is influenced by the presence of a forest around the lake that defined the Ribesalbes-Alcora Basin. We infer that *L. florancei* could survive in drier environments than *L. ellipticus*. On the other hand, this genus is vital for biostratigraphy, because it allows for a subdivision the Ribesalbes-Alcora record into two long local biozones, depending on the species of *Ligerimys* present. Each local biozone can be divided into two local sub-biozones depending on the abundance (or absence) of the different species of this genus. Finally, we extend these local biozonation to the early Miocene record of other Iberian basins.

*Acknowledgements.* The survey and excavation campaigns in the area of 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 PGC2018-094122-B100 (AEI/ FEDER, UE). We also thank Dr. Isaac Casanovas-Vilar and the anonymous reviewers of the original manuscript for their invaluable comments. The authors sincerely thank Isaac Toenies, who revised the translation of the text into English. V.D.C. is the beneficiary of a postdoctoral fellowship from the Argentinian Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

#### REFERENCES

- Adrover R., Mein P. & Belinchón M. (1987) - La fauna de roedores en el Aragoniense medio del Barranco del Candel, Buñol (provincia de Valencia, España). *Paleontología i Evolució*, 21: 43-61.
- Aguilar J.P., Michaux J., Bertrand A., Calvet M. & Lazzari V. (2010) - Compléments à l'étude des rongeurs (Mammalia, Rodentia, Cricetidae, Eomyidae, Sciuridae) du gisement karstique de Blanquatière 1 (Miocène Moyen, sud de la France). *Geodiversitas*, 32: 515-533.

- Agustí J. (1981) - Roedores miomorfos del Neógeno de Cataluña. PhD thesis, Universitat de Barcelona, Spain, 288 pp.
- Agustí J. (1983) - Roedores (Mammalia) del Mioceno Inferior de Can Martí Vell (Vallés-Penedés, Cataluña, España). *Estudios Geológicos*, 39: 417-430.
- Agustí J., Anadón P., Arbiol S., Cabrera L., Colombo F. & Sáez A. (1987). Biostratigraphical characteristics of the Oligocene sequences of north-eastern Spain (Ebro and Campins basins). *Münchner Geowissenschaften Abhandlungen (A)*, 10: 35-42.
- Agustí J., Anadón P., Ginsburg L., Mein P. & Moissenet E. (1988) - Araya et Mira: nouveaux gisements de mammifères dans le Miocène Inférieur-Moyen des Chaînes Ibériques orientales et méditerranéennes. Conséquences stratigraphiques et structurales. *Paleontologia i evolució*, 22: 83-101.
- Agustí J. & Llenas M. (1993) - Los roedores del Mioceno inferior de Els Casots (Vallés-Penedès). Nota preliminar. *Comunicaciones de las IX Jornadas de Paleontología*: 70-72.
- Álvarez-Parra S., Albesa J., Gouiric-Cavalli S., Montoya P., Peñalver E., Sanjuan J. & Crespo V. D. (2021) - The early Miocene lake of Foietta la Sarra-A and its relevance for the reconstruction of the Ribesalbes-Alcora Basin palaeoecology (E Iberian Peninsula). *Acta Palaeontologica Polonica*. Accepted.
- Álvarez-Sierra M.A. (1987) - Estudio sistemático y bioestratigráfico de los Eomyidae (Rodentia, Mammalia) del Oligoceno Superior y Mioceno Inferior español. *Scripta Geologica*, 86: 1-206.
- Anadón P., Cabrera L., Julià R., Roca E. & Rosell L. (1989) - Lacustrine oil-shale basins in tertiary grabens from NE Spain (Western European rift system). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 70: 7-28.
- Augé M., Ginsburg L., de Lapparent de Broin F., Makinsky M., Mourer C., Pouit D. & Sen S. (2002) - Les vertébrés du Miocène Moyen de Contres (Loir-et-Cher, France). *Revue de Paléobiologie*, 21: 819-852.
- Casanovas-Vilar I., Madern A., Alba D.M., Cabrera L., García-Paredes I., Van den Hoek Ostende L.W., DeMiguel D., Robles J.M., Furió M., Van Dam J., Garcés M., Angelone C. & Moyà-Solà S. (2016) - The Miocene mammal record of the Vallés-Penedès Basin (Catalonia). *Comptes Rendus Palevol*, 15: 791-812.
- Crespo V.D. (2017) - Los mamíferos del Mioceno Inferior de la Cuenca de Ribesalbes Alcora (Castelló, España). PhD thesis. Universitat de València, Valencia, Spain, 695 pp. Available in: <http://roderic.uv.es/handle/10550/60982>
- Crespo V.D., Fagoaga A., Montoya P. & Ruiz-Sánchez F.J. (2019c) - Old-timers and newcomers: The shrews and heterosoricids from the Ribesalbes-Alcora Basin (East of Spain). *Palaeontologia Electronica*, 22.3.64: 1-22.
- Crespo V.D., Fagoaga A., Ruiz-Sánchez F. J. & Montoya P. (2021) - Diggers, gliders and runners: The squirrels from the Ribesalbes-Alcora Basin (East of Spain). *Bulletin of Geosciences*, 96: 83-97.
- Crespo V.D., Furió M., Ruiz-Sánchez F.J. & Montoya P. (2018) - A new species of *Plesiodimylus* (Dimylidae, Eulipotyphla, Mammalia) from the early Miocene of Spain. *Historical Biology*, 30: 360-371.
- Crespo V.D., Goin F.J., Montoya P. & Ruiz-Sánchez F.J. (2020b) - Early Miocene marsupialiforms, gymnures and hedgehogs from southernmost Western Europe. *Journal of Paleontology*: 1-15.
- Crespo V. D., Marquina-Blasco R., Ruiz-Sánchez F.J. & Montoya P. (2019b) - An unusual insectivore assemblage from the early Miocene of southwestern Europe: the talpids and dimylids from the Ribesalbes-Alcora Basin (Spain). *Comptes Rendus Palevol*, 18: 407-416.
- Crespo V.D., Sevilla P., Montoya P. & Ruiz Sánchez F.J. (2020a) - A relict tropical forest bat assemblage from the early Miocene of the Ribesalbes-Alcora Basin (Castelló, Spain). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 111: 247-258.
- Crespo V.D., Suárez-Hernando O., Murelaga X., Ruiz-Sánchez F.J. & Montoya P. (2019a) - Early Miocene mammal assemblages from the Campisano ravine in the Ribesalbes-Alcora Basin (E Spain). *Journal of Iberian Geology*, 45: 181-194.
- Daams R., Freudenthal M. & Van der Meulen J.A. (1988) - Ecostratigraphy of micromammal faunas from the Neogene of the Calatayud-Teruel Basin. In: Freudenthal M. (Ed.) - Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain): 287-302. *Scripta Geologica, Special Issue 1*.
- Engesser B. (1999) - Family Eomyidae. In: Rössner G. E. & Heissig K. (Eds.) - The Miocene land mammals of Europe: 319-335. Verlag Dr. Friedrich Pfeil, München.
- Engler T. & Martin T. (2015) - A partial skeleton of the eomyid *Eomyodon volkeri* Engesser, 1987 (Mammalia: Rodentia) from the late Oligocene Fossil- Lagerstätte of Enspel, Germany. *Palaeobiodiversity and Palaeoenvironments*, 95(1): 133-147.
- Escarguel G. & Aguilar J.P. (1997) - Les éomyidés *Pseudotheridomys* et *Ligerimys* (Rodentia, Mammalia) du Miocène Inférieur du Sud de la France. Evolution et biostratigraphie. *Palaeontographica Abteilung, Serie A*, 247: 25-58.
- Fejfar O. (1989) - The Neogene VP sites of Czechoslovakia: a contribution to the Neogene terrestrial biostratigraphy of Europe based on rodents. In: Lindsay E.H., Fahlbusch V. & Mein P. (Eds.) - European Neogene Mammal Chronology: 211-236. Plenum Press, Nueva York.
- Flynn L. J. (2008) - Eomyidae. In: Janis C.M., Gunnell G.F. & Uhen M.D. (Eds) - Evolution of Tertiary Mammals of North America: Volume 2, Small Mammals, Xenarthrans, and Marine Mammals: 415-427. Cambridge University Press, New York.
- Freudenthal M., García-Alix A., Ríos M., Ruiz-Sánchez F.J., Martín-Suárez E. & Huertas A.D. (2014) - Review of paleo-humidity parameters in fossil rodents (Mammalia): Isotopic vs. tooth morphology approach. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 395: 122-130.
- Furió M., Ruiz-Sánchez F.J., Crespo V.D., Freudenthal M. & Montoya P. (2012) - The southernmost Miocene occurrence of the last European herpetothetiid *Amphipera-therium frequens* (Metatheria, Mammalia). *Comptes Rendus*

- Palevol*, 11: 371-377.
- Hordijk K., Bosma A., de Bruijn H., Van Dam J., Geraedts C., Van den Hoek Ostende L.W., Reumer J. & Wessels W. (2015) - Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos2, Teruel Basin, Spain. *Palaeobiodiversity and Palaeoenvironments*, 95: 321-346.
- Hugueney M. (1984) - Evolution du paléoenvironnement dans le tertiaire de Limagne (Massif Central, France) à partir des faunes de mammifères. *Geobios*, 17: 385-391.
- Hugueney M. & Mein P. (1968) - Les Eomyidés (Mammalia, Rodentia) néogènes de la région lyonnaise. *Geobios*, 1: 187-203.
- Jovells-Vaqué S., García-Paredes I., Furió M., Angelone C., Van den Hoek Ostende L. W., Berrocal Barberà M., Demiguel D., Madurell-Malapeira J. & Casanovas-Vilar I. (2018) - Les Cases de la Valenciana, a new early Miocene small-mammal locality from the Vallès-Penedès Basin (Catalonia, Spain). *Historical Biology*, 30: 404-421.
- Kimura Y., Casanovas-Vilar I., Maridet O., Kalthoff D.C., Mörs T. & Tomida Y. (2020). The Eomyidae in Asia: Biogeography, diversity and dispersals. *Fossil Imprint*, 76: 181-200.
- Maridet O., Wu W.Y., Ye J., Ni X.J. & Meng J. (2011) - New discoveries of glirids and eomyids (Mammalia, Rodentia) in the Early Miocene of the Junggar basin (Northern Xinjiang province, China). *Swiss Journal of Palaeontology*, 130: 315-323.
- Postigo-Mijarra J.M. & Barrón E. (2013) - Zonal plant communities of the Ribesalbes-Alcora Basin (La Rinconada mine, eastern Spain) during the early Miocene. *Botanical Journal of the Linnean Society*, 172: 153-174.
- Reichenbacher B., Krijgsman W., Lataster Y., Pipperr M., Van Baak C.G., Chang L., Kálin D., Jost J., Doppler G., Jung D., Prieto J., Abdul-Aziz H., Böhme M., Garnish Kirscher U. & Bachtadse V. (2013) - A new magnetostratigraphic framework for the lower Miocene (Burdigalian/Ottangian, Karpatian) in the North Alpine Foreland Basin. *Swiss Journal of Geosciences*, 106: 309-334.
- Ríos M. (2013) - Estudio multi-isotópico de la paleoecología y la paleoclimatología de la Cuenca de Ribesalbes-Alcora (Castellón, España) durante el Óptimo Climático del Mioceno. Unpublished MSc Thesis, Universitat de València, Valencia, Spain, 76 pp.
- Ruiz-Sánchez F.J., Freudenthal M. & Mansino S. (2012) - Eomyidae fauna turnover at the Early-Middle Miocene boundary in the Morteral section (Magro Basin, Valencia, Spain). *Geobios*, 45: 387-396.
- Ruiz-Sánchez F.J., Lázaro-Calatayud B. & Freudenthal M. (2009) - *Eomyops noeliae* sp. nov., a new Eomyidae (Mammalia, Rodentia) from the Aragonian of Spain. *Comptes Rendus Palevol*, 8: 375-384.
- Storch G., Engesser B. & Wuttke M. (1996) - Oldest fossil record of gliding in rodents. *Nature*, 379: 439-441.
- Van Dam J.A. & Weltje G.J. (1999) - Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of endmember modelling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 151: 267-305.
- Van der Meulen A.J. & Daams R. (1992) - Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 93: 227-253.
- Van der Meulen A.J., García-Paredes I., Álvarez-Sierra M.Á., Van den Hoek Ostende L.W., Hordijk K., Oliver A., López-Guerrero P., Hernández-Ballarín V. & Peláez-Campomanes P. (2011) - Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small mammal events in Europe. *Geobios*, 44: 309-321.
- Van der Meulen A.J., García-Paredes I., Álvarez-Sierra M.Á., Van den Hoek Ostende L.W., Hordijk K., Oliver A. & Peláez-Campomanes P. (2012) - Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. *Geologica acta*, 10: 159-179.
- Wang X. M., Qiu Z.D., Li Q., Tomida Y., Kimura Y., Tseng Z. J. & Wang H.J. (2009) - A new Early to Late Miocene fossiliferous region in Central Nei Mongol: Lithostratigraphy and Biostratigraphy in Aocerban Strata. *Vertebrata Palasiatica*, 47: 111-134.
- Ziegler R. & Fahlbusch V. (1986) - Kleinsäuger-Faunen aus der basalen Oberen Süßwasser-Molasse Niederbayerns. Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, *Zitteliana*, 14: 3-80.