THE LATE MIOCENE AND EARLY PLIOCENE MICROMAMMAL FAUNAS FROM THE ALCOY AND CABRIEL BASINS (SPAIN)

SAMUEL MANSINO PARÍS

Tesis Doctoral, 2015

Universitat de València, Departament de Geologia

Programa de Doctorado: Biodiversidad, RD 1393/2007

Tesis Doctoral codirigida por los Dres. Francisco Javier Ruiz Sánchez y Plinio Montoya Belló

Los Dres. Francisco Javier Ruiz Sánchez y Plini Montoya Belló hacen constar que la Tesis Doctoral titulada "The Late Miocene and Early Pliocene micromammal faunas from the Alcoy and Cabriel basins (Spain)", presentada por D. Samuel Mansino París y realizada dentro del Programa de Doctorado de Biodiversidad, reúne, a su juicio, todos los requisitos necesarios para su defensa y aprobación.

Fdo: Dr. Francisco Javier Ruiz Sánchez	Fdo. Dr. Plini Montoya Belló
Codirector de la Tesis Doctoral	Codirector de la Tesis Doctoral

Fdo. D. Samuel Mansino París

*Both the cover and the back cover images have been yielded by María Soledad París Meco.

A mis padres

A unos ojos claros, serenos…

CONTENTS

CHAPTER I. INTRODUCTION.

I.1. General introduction and structure of the thesis

This thesis is the result of the work carried out in the area of Venta del Moro (Cabriel Basin, Valencia) and the Gormaget ravine (Alcoy Basin, Alicante) by the vertebrate palaeontology group of the Departament de Geologia of the Universitat de València. I started my collaboration in the Department in the years 2007/2008, when I began my master's degree project, and at some point of 2009 I started working on this PhD. The Gormaget Ravine had been the subject of a previous, unfinished PhD, which means some of the levels of interest had been already sampled, and even washed in some cases, but no collections were assembled. Later we decided to include in my thesis an unpublished collection from the localities of La Bullana (Cabriel Basin), which was enlarged by processing more material kept at the Departament de Geologia. All this implies that part of the fieldwork was already done when I started, but it also resulted in some problems like the misidentification of some of the levels sampled in the years prior to the beginning of this thesis (see chapter VI).

Regarding the site of Venta del Moro, the excavation of this locality for nearly thirty years (Morales 1984, Montoya *et al*. 2006a) has produced a great amount of fossil remains, which were stored at the Department de Geologia. The study of the micromammal remains from Venta del Moro alone could result in one or more thesis, so we decided to focus on two taxa that were especially relevant in our opinion: the genera *Eliomys* (chapter X) and *Apocricetus* (chapter XI). These remains can be related with the material that had been previously studied in the localities from Alcoy and La Bullana.

The localities of the Gormaget ravine range in age from the Late Miocene (López-Martínez 1989) to the Early Pliocene (López-Martínez 1989, Montoya *et al*. 2006b, Mansino *et al*. 2009a and 2013). The concentration of several localities of a similar age in northern and southern sides of the Gormaget ravine (see chapter VIII) has allowed obtaining a great resolution in the evolution of the faunas and environmental conditions of the Early Pliocene, possibly recording the Mio-Pliocene boundary. The resolution achieved for the Early Pliocene is only comparable in the Iberian Peninsula to that of the Teruel Basin (see Mein *et al.* 1990). In addition, the localities of La Bullana 2B and 3, placed near the site of Venta del Moro, have yielded an abundant fauna of rodents, among which it is to be noted the presence of the gerbil *Debruijnimys* cf. *julii*, which allows us to hypothesize about the phylogenetic relationships of the genus (chapter VII). Finally, the well-known locality of Venta del Moro has yielded a huge collection of micromammal remains, most of them yet unassembled. The study of a great number of specimens is necessary to correctly assess the morphological and biometrical variability of a given species (chapter XI) and, if necessary, to erect a new species with the certainty of having enough material to provide an accurate differential diagnosis (chapter X).

I have opted to present my thesis as a compendium of publications, because this format allows the pre-doctoral student entering the publication world much faster than the classical thesis. In this sense, I feel that the interaction with the several referees and editors who have participated with their corrections and suggestions in the making of the articles have greatly raised the overall quality of this work.

I am the first author of all the papers presented in this compendium, and therefore I carried out the majority of the writing in all of them, including the description of the specimens and most of the discussions and the conclusions. However, some parts of the articles comprising this thesis were made by the co-authors, such as the geological setting and stratigraphic logs of the Alcoy area, performed by Ignacio Fierro, the geological setting and stratigraphic logs of La Bullana area, carried out by Luis de Luque, and the palaeomagnetic analysis of La Bullana 2B and La Bullana 3, performed by Luis Gibert and Gary Scott. In addition, despite dealing with the fauna from these latter localities, the paper "*Apocricetus barrierei* (Rodentia, Mammalia) from La Bullana 2B and La Bullana 3 (Cabriel Basin, Valencia, Spain). Revision of the Late Miocene–Early Pliocene forms of the genus *Apocricetus*", by Ruiz-Sánchez, F.J., Freudenthal, M., Mansino, S., Crespo-Roures, V.D., Montoya, P., was not included in this thesis since I did not carry out the bulk of the work. However, we continued that working line in the article "New approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain)", which has been included in chapter XI and in its published form as an appendix.

According to the regulation by the Universitat de València, in a thesis that is a compendium of publications there must be a general introduction, discussion and conclusions. Between the introduction and the discussion, a copy of the papers already published or admitted for publication must be attached, or they must be included as an appendix. Since the works dealing with the fossil assemblages from the Alcoy and Cabriel basins have similar introductions, I have chosen to write a common introduction for each of these basins, and to attach the accepted or published files as appendixes at the end of the thesis.

The articles used in the making of this thesis comprise:

- Mansino, S., Fierro, I., Ruiz-Sánchez, F.J., Montoya, P. The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of Alcoy-Mina. ***Status: published (2013)***, *Journal of Iberian Geology* 39 (2), 261–284. **Corresponds to chapter IV.**

- Mansino, S., Fierro, I., Montoya, P., Ruiz-Sánchez, F.J. Micromammal faunas from the Mio-Pliocene boundary in the Alcoy Basin (SE Spain): biostratigraphical and palaecological inferences. ***Status: accepted (in press, 2015)***, *Bulletin of Geosciences* 90 (3), xxx–xxx. **Corresponds to chapter V.**

- Mansino, S., Fierro, I., Montoya, P., Ruiz-Sánchez, F.J. Mio-Pliocene rodent assemblages from Alcoi Forn (Alcoy Basin, Eastern Spain). Biostratigraphical and palaeoclimatical inferences ***Status: to be submitted***. **Corresponds to chapters VI and IX.**

- Mansino, S., Ruiz-Sánchez, F.J., Luque, L. de, Montoya, P., Gibert, L., Morales, J., Abella, J., Crespo, V.D., Scott, G. R. First Early Pliocene micromammal faunas from the Venta del Moro area (Cabriel Basin, Spain): new data on the Messinian dispersal of *Debruijnimys*. ***Status: accepted (in press, 2015)***. *Journal of Iberian Geology*. **Corresponds to chaptes II.2.3. and VII.**

- Mansino, S., Fierro, I., Tossal, A., Montoya, P., Ruiz-Sánchez, F.J. Micromammal biostratigraphy of the Late Miocene-Early Pliocene of the Alcoy Basin (Eastern Spain): Considerations on the Mio-Pliocene boundary. ***Status: to be submitted***. **Corresponds to chapters II.1. and VIII.**

- Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J., Montoya, P. A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. ***Status: accepted (in press, 2015)***, *Acta Palaeontologica Polonica,* 60 (X): xxx–xxx. **Corresponds to chapter X.**

- Mansino, S., Ruiz-Sánchez, F.J., Freudenthal, M., Montoya, P. A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain). ***Status: published (2014).*** *Proceedings of the Geologists' Association* 125, 392–405. **Corresponds to chapter XI.**

A small chapter dealing with methodology has been included (chapter III), as well as a short section comparing the palaeoenvironmental data inferred from chapters V to VIII with other studies dealing with the climatic evolution of the Mio-Pliocene boundary and Early Ruscinian (chapter IX). I have tried to avoid redundancies in the text, so I have placed the segments that were similar in the different chapters in common sections. In that sense, the geological setting is explained in chapter II, the general methodology in chapter III, and the faunal lists of the localities from the Alcoy Basin (chapters IV to VI) are compared with those from other localities of similar age in Fig. VIII.1. However, I have maintained the sections dealing with the palaeoecology of each locality separate, as they form part of the conclusions of each chapter. Finally, chapter XII summarizes the conclusions of all the papers comprising this thesis.

I.2. Historical context

The first fossil mammal locality described in the Alcoy Basin, which was also one of the first sites known in the Iberian Peninsula, was Alcoy-Mina. This site yielded macromammal remains during the exploitation of the lignite beds from 1841 to 1862; these works were resumed in 1917 and later in 1937, as a consequence of the scarcity of coal because of the World War I and the Spanish Civil War, respectively (Adrover 1969).

The resulting fossil collections were scattered in a number of institutions, such as the Muséum national d'Histoire naturelle (Paris), Museo GeoMinero (Madrid), Museo Nacional de Ciencias Naturales (Madrid), Museo de Ciencias Naturales de Valencia and the Museu Arqueològic Municipal "Camil Visedo Moltó" (Alcoy) (Montoya *et al.* 2006b). Although the material from Alcoy-Mina was studied by several authors during the late 19th and early 20th centuries (Ezquerra 1850, Verneuil and Collomb 1852, Gervais 1852, Botella 1854, Vilanova 1867, Nicklés 1893, Boscá 1911, Hernández-Pacheco 1914, Novo 1915, Visedo 1922, Royo-Gómez 1922, among others), it was not until the second half of the 20th century that a precise list was given, with the revisions of several authors such as Crusafont and Villalta (1955), Alberdi (1974), Mazo (1977), Gromolard (1980), Guérin (1980), Morales (1984), Made and Belinchón (1991) and Montoya *et al.* (2006b).

Initially, the site of Alcoy-Mina was regarded as Late Miocene by Gervais (1852). Subsequent authors, among which are Thaler *et al.* (1965) and Adrover (1969), placed Alcoy-Mina in the Pliocene. However, the discovery of the locality of La Alberca led Montenat (1973) to consider this site as Late Miocene, since the faunas from both localities share some similarities and La Alberca is enclosed within two marine levels with Late Miocene microfauna. In addition, the presence in the Late Miocene locality of Venta del Moro of the genera *Parabos* and *Agriotherium*, which also appeared in Alcoy-Mina and were considered typically Pliocene, led Morales (1984) to give a Late Miocene age for Alcoy-Mina.

The study of the micromammal remains did not help to solve this question. The washing of sediment from the former lignite Mine resulted in a single diagnostic remain (Adrover 1969), which made Adrover search for more fossiliferous levels in the area, finding a richer site near an abandoned furnace (Thaler *et al.* 1965, Adrover *et al.* 1969), which is called Alcoy Barranco by Morales (1984). However, the presence of both Late Miocene (Alcoy-N, López-Martínez 1989) and Early Pliocene (Alcoy 4B, Freudenthal *et al.* 1998; Alcoy 2, Esteban Aenlle and Lacomba 1988) sites near the old lignite mine prevented ascribing Alcoy-Mina to any of these ages (Montoya *et al.* 2006b).

Nevertheless, the works performed in the Alcoy Basin by the vertebrate palaeontology group of the Departament de Geologia of the Universitat de València from 2005 to 2008, and in the years 2011 and 2012, have allowed us to provide a biostratigraphical frame for these localities (see chapters IV, V, VI and VIII of this thesis). Based on the similarities of their faunal lists, we consider Alcoy-Barranco to be of a similar age to the Early Pliocene locality of AC-0 (chapters V and VIII). In the latest revision of the macrofauna from Alcoy-Mina, Montoya *et al.* (2006b) considered that the most appropriate age for this fauna was Early Ruscinian (MN14), and Mansino *et al.* (2013, chapters IV and VIII) suggested an equivalent stratigraphic position for Alcoy-Mina, Alcoy 2, AL2-C and AL2-D, placing these sites in the end of MN14 or in the MN14-MN15 boundary (Mansino *et al.* 2013, chapter IV).

Regarding Venta del Moro, this locality is one of the most interesting sites near the Mio-Pliocene boundary because of the richness and diversity of its fossil assemblage (Morales 1984, Montoya *et al*. 2006a). The age of this site has been estimated at 6.23 Ma (Gibert *et al.* 2013), and it was described for the first time by Aguirre *et al*. (1973) and Robles (1974). From 1970 to 1980, the excavation work was performed by researchers from the Museo Nacional de Ciencias Naturales, and it is there where the collections from this period are housed. The excavations were interrupted from 1980 to 1995, when they were restarted by researchers from the Departament de Geologia de la Universitat de València, in collaboration with the Museo Nacional de Ciencias Naturales, stopping again in 2013. The collections from this latter period are kept at the Museu de Geologia de la Universitat de València.

The faunal list of Venta del Moro includes more than 100 species, of which over 40 are mammals. Of these, it is the type locality of *Agriotherium roblesi* Morales and Aguirre, 1976, *Paracamelus aguirrei* Morales, 1984, *Tragoportax ventiensis* (Morales, 1984), *Parabos soriae* Morales, 1984, *Eucyon debonisi* Montoya, Morales and Abella, 2009, *Martes ginsburg*i Montoya, Morales and Abella, 2011, and *Eliomys yevesi*

Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. In addition, the site was proposed as type locality of a new mammal age, the Ventian (Aguirre *et al.* 1976, Alberdi *et al.* 1977, Alberdi and Bonadonna 1988), although it has had little acceptance (Montoya *et al.* 2006a). Still, Morales *et al*. (2013) made an attempt to vindicate the Ventian, although the subzonation proposed by these authors has some troubles (see chapter VIII.3 of this thesis).

In addition, two new localities were discovered in 2005 during the prospection works performed in the Venta del Moro area: La Bullana 2B and La Bullana 3. These sites have been also included in this thesis, and their biostratigraphical and chronostratigraphical implications are discussed in chapters VII and VIII.

I.3 Introduction to micromammal palaeontology

The term micromammal comprises four different groups of animals: rodents (Order Rodentia), rabbits and hares (Order Lagomorpha), bats (Order Chiroptera) and insectivores (Order Lipotyphla). Since this thesis deals only with fossil remains of rodents and insectivores, these two groups will be further explained in sections I.3.1 and I.3.2. The main common feature between these taxa is their small size, and other mammals of reduced dimensions, such as the Herpetotheriidae, an extinct family closely related to marsupials present in Paleogene and Lower Miocene of Europe, can be regarded as micromammals too. However, some representatives of these orders have grown to impressive sizes, such as the giant Pliocene South American rodent *Josephoartigasia monesi*, with an estimated weight of approximately 1000 kg. (Rinderknecht and Blanco 2008), or the giant insular forms *Deinogalerix koenigswaldi*, from the Upper Miocene of Gargano (Italy), the largest erinaceidae ever with a skull over 20 cm. long (Freudenthal 1972) and the lagomorph *Nuralagus rex*, from the Late Neogene of Minorca, with an average weight of about 12 kg. (Quintana *et al.* 2011). Nevertheless, these bigger species are usually studied by the same specialists who work with their smaller relatives, and very small ungulates and carnivores like tragulids and the smaller mustelids are left for the experts in those groups, making the concept of micromammal purely conventional.

Except in the rare cases of the giant forms, micromammal palaeontology focus mainly on the dentition, with a particular emphasis on the molars. Teeth are more likely to be preserved than bones, because enamel is the hardest part of vertebrate skeleton, and show a wide morphological variability. The basic patterns of the different families are easily discriminated from each other, and minor deviations from the general pattern of each family distinguish genera and species, allowing to achieve a great accuracy in the taxonomic determination and dating of stratigraphical levels. In addition, molars do not grow with age, which allows comparing the measurements of all the specimens of a certain dental element, and since teeth form part of the digestive system, functional morphology makes possible to infer the palaeoecology and palaeobiology of a given taxon.

I.3.1. Rodents

Rodents are the most abundant and diverse mammals of terrestrial ecosystems, comprising over 42 % of all extant mammal species, about 2000 (MacDonald 2001). This order is widespread, being present in all continents except the Antarctica. Most rodents are herbivores, eating a range of plants, fruits, leaves and small invertebrates, but some of them are specialized carnivores such as the Australian water rat (*Hydromys chysogaster*) and the grasshopper mice (genus *Onychomys*).

The earliest rodents appeared in Late Paleocene, about 57 Ma (MacDonald 2001). The order diversified rapidly during the Eocene, and by the Miocene most extant families have already appeared.

Because rodents have evolved in similar niches, they show a great deal of convergence, which obscure their systematics. There has been many attempts to clarify this issue since Linnaeus created the order Glires (Linnaeus 1740) including both rodents and lagomorphs. Brandt (1885) divided the rodents in three suborders, Sciuromorpha, Hystricomorpha and Myomorpha, based in the development of the masseteric musculature. Subsequent authors proposed their own versions of the systematics of rodents (Schlosser 1884, Tullberg 1899, Ellerman 1940, Simpson 1945, Chaline and Mein 1979, McKenna and Bell 1997, among others). The use of molecular analysis has not fully resolved the question, although it has confirmed the monophyly of the suborder Hystricognathi (Huchon *et al*. 2002).

The term rodent derives from the Latin verb “rodere”, which means “to gnaw” (MacDonald 2001). This name reflects one of the most characteristic anatomical features of the order, the presence of chisel-like, ever-growing incisors used to gnaw food, excavate burrows or defend themselves. Immediately behind the incisors lies a gap with no teeth known as diastema (see Fig. I.1), which allows sealing the mouth from inedible fragments produced by gnawing. There are no canines and usually no premolars, therefore many rodent have just 16 teeth. Rodent molars show a great diversity of forms, and they have taxonomic significance.

In this thesis, we have studied fossil remains of the families Muridae, Cricetidae, Gliridae, Sciuridae, Trilophomyidae and Gerbillidae.

The systematics of murids is problematic for both neontologists and palaeontologists. The group has been considered a superfamily (Muroidea) with several subfamilies, or a family (Muridae), in which case these subfamilies are promoted to families. Many palaeontologists have chosen the latter alternative, and so have we.

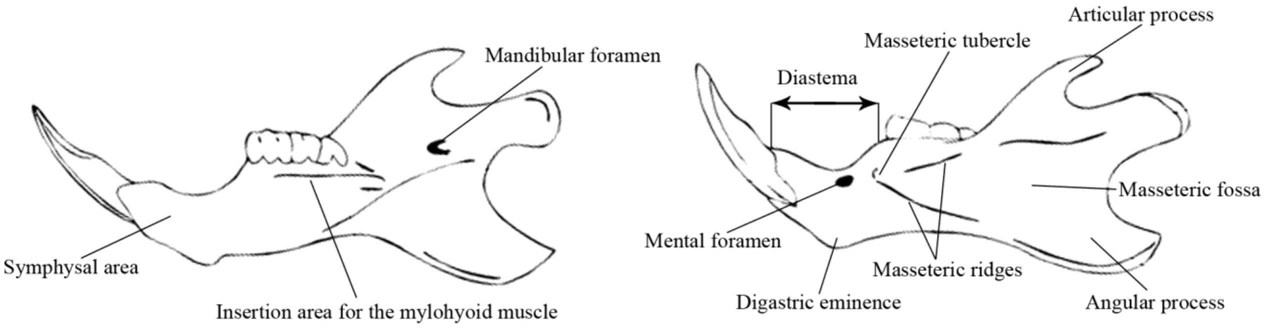


Figure I.1. Nomenclature of the elements of the mandible of rodents in lingual (left) and labial (right) view (modified from Casanovas-Vilar 2007).

Muridae is the largest family of all mammals, with over 100 genera and 500 species (Freudenthal and Martín-Suárez 1999, Musser and Carleton 2005). Murids have a great diversity of body types, and nowadays this group is adapted to all kinds of biotopes, including aquatic environments. The dental formula is 1.0.0.3 for both upper and lower molars, and the third molars are reduced with respect the first and second molars. These molars are rooted and not ever-growing, ranging from brachyodont to hypsodont. They display the typical “cricetid plan” (Schaub 1925), which consists in four major cups besides additional cusps (anterocone or anteroconid) at the mesial part of the first molars (see Figs. I.2 and I.3). The upper dentition is characterized by a fully functional set of extra lingual cusps (Freudenthal and Martín-Suárez 1999) and cusps placed in 3 chevrons in M1 and M2. In lower molars a third row of accessory cusps may be developed labially (Fig. I.2), but they are usually low and only worn down in advance stages of wear.

Murids are thought to be derived from cricetids, which were the dominant faunas in the European Oligocene and most of the Miocene. Their origin is probably Asian, and by Late Miocene they had become the dominant European faunas. They maintained this preeminent position until the arrival of the Microtidae at the end of the Pliocene, which greatly reduced their importance (Freudenthal and Martín-Suárez 1999). In the time interval studied in this thesis, murids are the most abundant group in all the assemblages (see Table IX.1 for the percentages of the localities from the Alcoy Basin and La Bullana 2B).

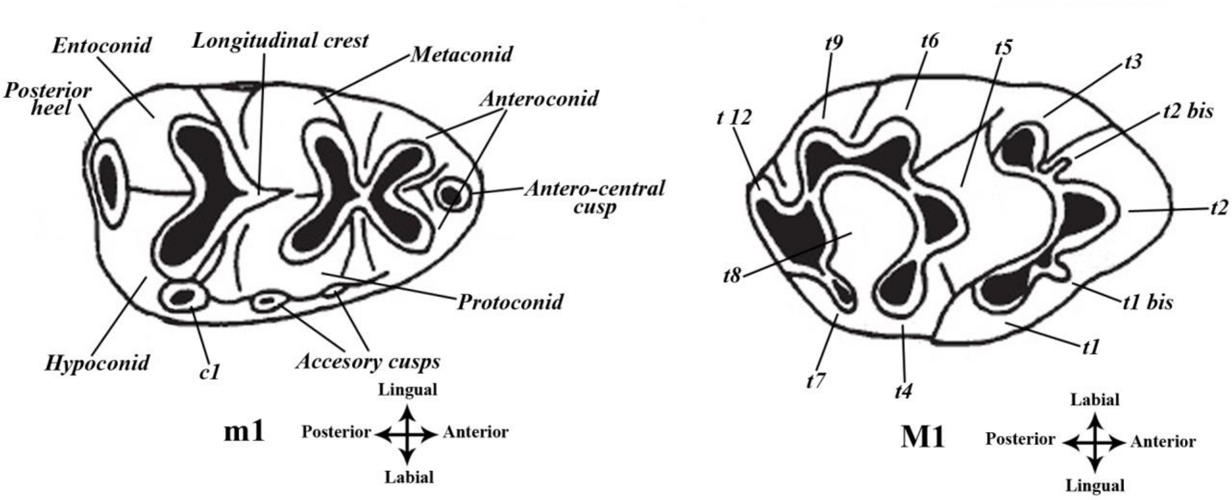


Figure I.2. Dental nomenclature of the Family Muridae after Martín-Suárez and Freudenthal (1993). Modified after Weerd (1976).

Murids are very important in the biostratigraphy of Late Miocene and Pliocene (Weerd 1976, Mein *et al.* 1990, Martín-Suárez and Freudenthal 1998, Minwer-Barakat *et al.* 2012, among others). The biozonation of the Alcoy Basin, which is mainly based on murid faunas, is discussed in chapter VIII of this thesis. In addition, the study of fossil murids provides important hints of the palaeogeography of the family and the faunal interchanges between Asia, Africa and Europe, like the dispersion of the genus *Paraethomys* from Africa to Europe during the Messinian (Bruijn 1974, Jaeger *et al.* 1975, Agustí *et al.* 2006, Gibert *et al.* 2013), and the reconstruction of past environments (see chapter IX).

Cricetids have the same dental formula as the murids. This family occupy today a wide spectrum of habitats in the Palearctic region (Nowak 1999). Modern cricetids appeared in Europe for the first time in latest Early Miocene (base of MN4), becoming quickly a significant part of micromammal assemblages, which remained stable for more than 8 Myr. (Kälin 1999). After the appearance of murids in Europe in the MN10, the group suffered an important reduction in both diversity and abundance. However, cricetids remained common in the Late Miocene and Pliocene ecosystems, and some of them, like the genus *Apocricetus*, are especially important for the biostratigraphy of this period (Freudenthal *et al.* 1998, Ruiz-Sánchez *et al.* 2014, Mansino *et al.* 2014, chapter XI).

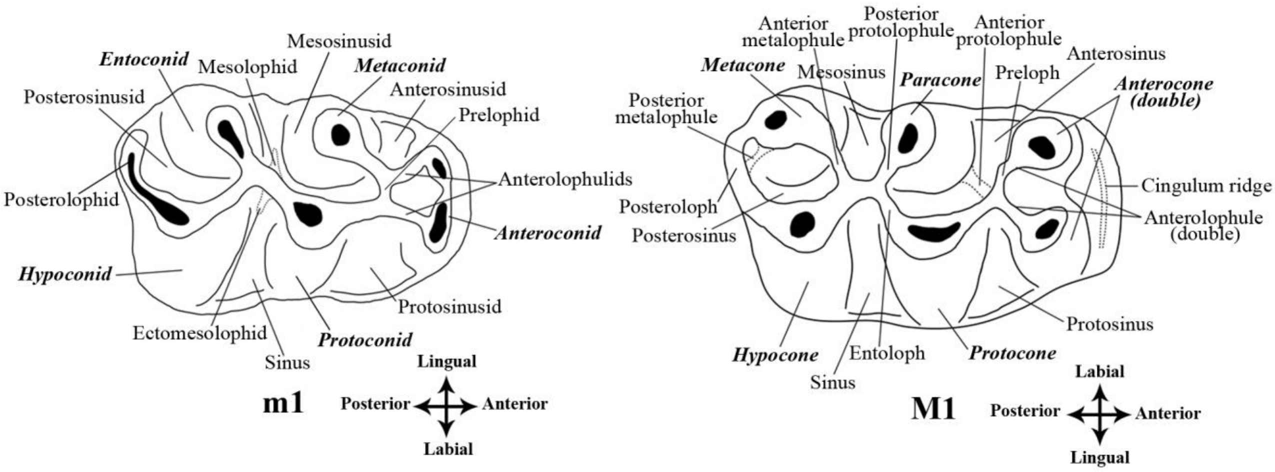


Figure I.3. Dental nomenclature of the cricetid *Apocricetus*, after Freudenthal *et al*. (1994). Modified after Mansino *et al.* (2014).

At the end of the Miocene, cricetids experienced a radiation in which some forms with hypsodont and simple molars (microtoid cricetids) appeared linked to strong climatic changes (Fejfar 1999, Kälin 1999). The genera *Blancomys* (chapters IV and VI) and *Ruscinomys* (IV, V and VII) are two of them.

Similar forms appeared in Early Pliocene, such as the Trilophomyidae. This family reached the Iberian Peninsula as a result to a dispersal event of Palaearctic origin, dwelling southern Europe during the cooling events that preceded the onset of the glacial–interglacial dynamics (Agustí and Antón 2002). The dental formula of this group is 1.0.0.3 for both upper and lower teeth, and their dental nomenclature is shown in Fig. I.4. Their appearance in Western Europe has a great relevance for biostratigraphy (Mein *et al.* 1990, Minwer-Barakat *et al.* 2012, Morales *et al.* 2013, chapter VIII).

The dental formula of the family Gliridae is 1.0.1.3 for both upper and lower teeth. Their molars are usually flat or slightly concave, although some representatives of the subfamily Myomiminae present hypsodont molars (Daams 1990, Ruiz-Sánchez *et al.* 2012). Their dental pattern is usually complex, with several transverse main and extra ridges (see Fig. I.5). The geographical range of the family (both extant and fossil forms) comprises Africa, Asia and Europe.

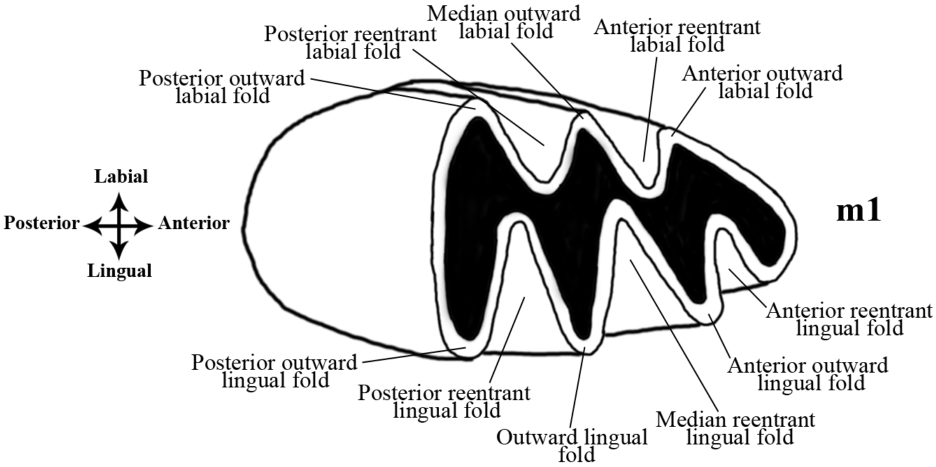


Figure I.4. Dental nomenclature of the family Trilophomyidae (modified after Adrover 1986).

The earliest known glirid is *Eogliravus wildi*, from the Early Eocene of France. The group diversified during the Eocene and Oligocene, reaching a maximum from MN3 to MN5 (Early-Middle Miocene), when they seem to occupy many different ecological niches (Daams 1999).

From MN5 onwards modern cricetids became the dominant group, and the diversity and abundance of glirids declined (Daams and Bruijn 1995). Extant glirids are a shadow of its former diversity and abundance, comprising just eight genera and 14-15 species

(Daams 1999). In the localities studied in this thesis, glirids are very scarce (see Table IX.1) with relative abundances of less than 4 %. These remains comprise the genera *Glis* (chapter IV) and *Eliomys* (chapters IV, V, VI, VII and X). The phylogeny of the latter genus is discussed in the light of the findings from Venta del Moro and the Alcoy Basin in chapter X.

With respect to sciurids, many extinct forms of this rodent group are only known from isolated molars and fragmentary maxillas and jaws. However, these remains are very characteristic. The dental formula of sciurids is 1.0.1-2.2-3 for the upper molars, and 1.0.1.3 for the lower teeth (Bruijn 1999). Cheek teeth are rooted, usually brachyodont, and have three main cusps in the upper molars and four main cusps in the lower molars (see Fig. I.6). The earliest sciurid remains date from the Eocene of Europe (Bruijn 1999). The diversity of sciurids reached a maximum in Miocene, suffering a decline in Late Pliocene and Pleistocene due to changes in climatic conditions.

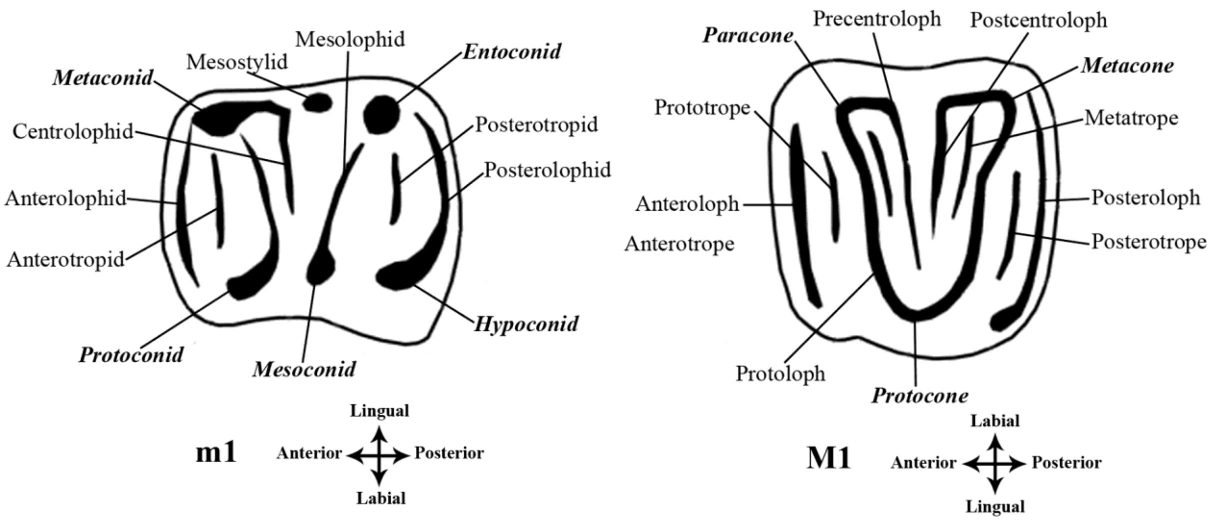


Figure I.5. Dental nomenclature of the family Gliridae after Daams (1981) and Freudenthal (2004). Modified after Freudenthal (2004).

Three adaptive types, with very different lifestyles, are recognized within sciurids: ground squirrels (burrowing and diurnal), tree squirrels (arboreal and diurnal), and flying squirrels (arboreal and nocturnal) (Bruijn 1999). These groups, present since Eocene, have been traditionally identified by dental characters. However, Thorington *et al.* (2005) noted that there is not a certain dental pattern that differentiates flying squirrels from the others groups, and that this discrimination should be made by the study of postcranial remains alone. One of the few remains of the genus *Pliopetaurista* in the Iberian Peninsula, considered a flying squirrel on the base of its dental morphology (Bruijn 1999), is described in chapter IV.

Extant Gerbillidae are typical dwellers of desert or sub-desert environments, comprising 103 species spread over 16 genera (Musser and Carleton 2005). Although nowadays gerbils are present just in Africa, Arabian Peninsula and Asia, some representatives of this group were present in the Late Miocene and Pliocene of Europe (see chapter VIII), with relevant biogeographical and biostratigraphical consequences (Agustí and Galobar 1986, Castillo and Agustí 1996, Agustí and Casanovas-Vilar 2003, Agustí *et al*. 2006, Minwer-Barakat *et al.* 2009a), although their importance in these ecosystems seems to have been limited (Wessels 1999). Their dental formula is 1.0.0.3 for both upper and lower teeth. In this work we have used the same dental nomenclature described for the Cricetidae.

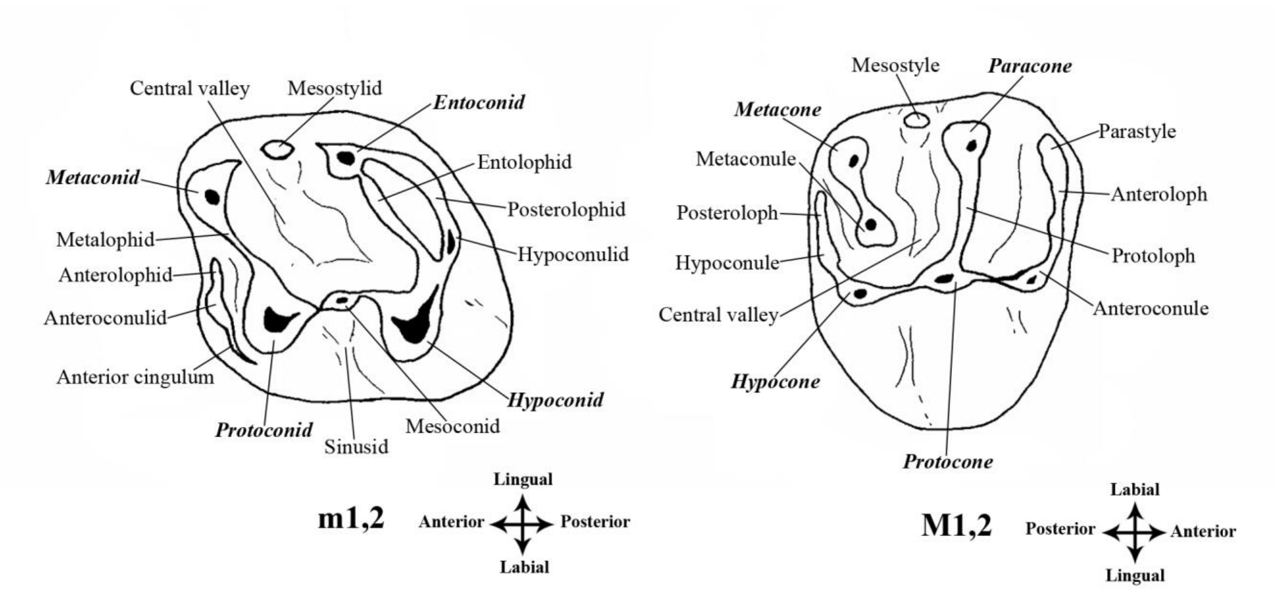


Figure I.6. Dental nomenclature of the family Sciuridae after Reumer and Hoek Ostende (2003). Modified after Cuenca (1988).

I.3.2. Insectivores

Insectivores are extremely diverse anatomically. This makes difficult to define the group, except for the lack of specializations present in other orders (Butler 1972). The extant forms are included in the order Lypotyphla Haeckel, 1866, which refers to the lack of caecum.

Generally, insectivores are found less frequently than rodents in the fossil record, and their taxonomic determination is more difficult since more complete parts are usually needed (Ziegler 1999). In addition, insectivores have been traditionally overlooked in palaeoecological reconstructions dealing with mammals, although their value as palaeoenvironmental indicators was recognized and they have been included in these kind of analysis from 2000s onwards (Furió *et al.* 2011).

In the localities studied in this thesis insectivores are scarce (see Table IX.1), and their contribution to the palaecological inferences discussed in chapter IX is reduced. They belong to the families Soricidae and Erinaceidae.

Soricids are the most diverse family of the order Lypotyphla, with more than 300 species in 26 genera (Wilson and Reeder 2011). The oldest record of the group has been found in the middle Eocene of North America (45 Ma, MacDonald 2001) and are probably close to the first mammals. Their actual range of distribution includes Eurasia, Africa, North America and northern South America. The dental formula is 3.1.1-3.3 for the upper molars, and 1-2.0-1.1-3.3 for the lower ones. The dental nomenclature for this group is shown in Fig. I.7.

Erinaceids are a relatively primitive group of placental mammals, and their origin can be traced to the Eocene. Many extinct forms have a complete eutherian dentition (3.1.4.3 in both upper and lower molars), which may be reduced in extant species (Ziegler 1999).

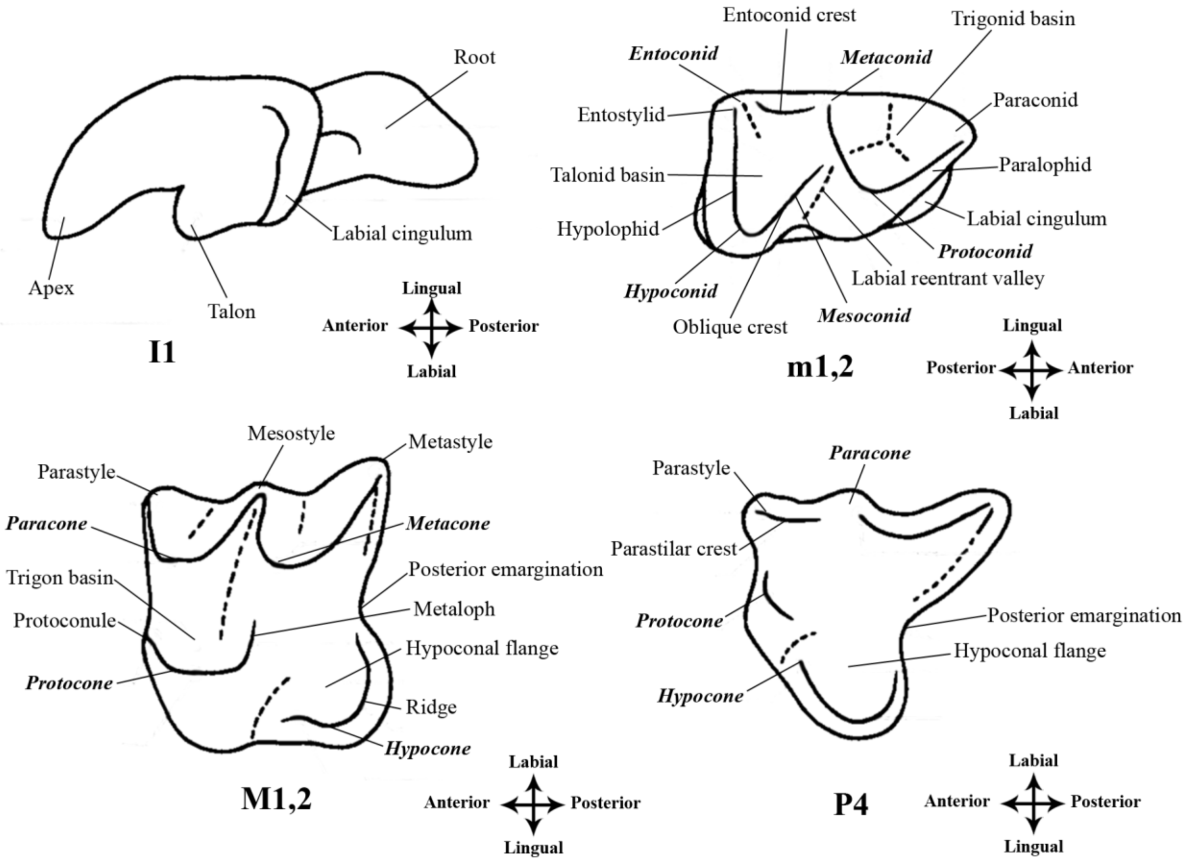


Figure I.7. Dental nomenclature of insectivores after Reumer (1984) and Furió (2007). Modified after Reumer (1984).

I.3.3. Historical background and importance

The study of fossil micromammals is relatively recent, although rodent remains in fossiliferous levels have been known since the 19th century (Blainville 1826, Pomel 1853, Filhol 1879, Schlosser 1884, Depéret 1890, Nehring 1898, among others). However, the main part of the work from these authors dealt with fissure fillings, since the chances of finding micromammals in excavations for large vertebrate remains is usually low (Hoek Ostende 2003). The assemblages from karstic fissure filling are habitually regarded as accumulations by predation, normally by birds of prey (Andrews 1990, Agustí and Martín-Suárez 1986). Since fluvio-lacustrine localities incorporate remains from a variety of sources, they are more representative of the environment in which they were formed, because the bias produced by the selective prey picking by the predator is reduced. In addition, the sedimentation rate is less constant in karstic fillings, which may undergo non-sedimentation periods, causing the mixing of remains from relatively long time spans and obscuring the palaeoenvironmental conditions of the formation of the site (Bolliger 1997). Furthermore, reworking is also common in karstic fillings (Bolliger 1997) and since they usually hold no correlation with the surrounding geology, the best way to date a certain site is by its faunal content, which may be composed of fossils from different time slices (Hoek Ostende 2003).

For these reasons, it was only after the sieving techniques for processing large amounts of sediments from fluvio-lacustrine localities were developed in the 1960s (see Freudenthal *et al*. 1976 and Daams and Freudenthal 1988) that the field really matured, becoming quickly a vital tool for understanding the terrestrial ecosystems of the Cenozoic (Hoek Ostende 2003). The widespread use of these techniques led to the publishing of a great number of works dealing with micromammal fossil remains in late 1960s and 1970s, many of them focusing on systematics. This provided the base for other kind of studies, such as the development of a micromammal-based stratigraphic framework (Hoek Ostende 2003), enabled by the fast evolution, cosmopolitan distribution, great abundance and relatively easy sampling of fossil micromammals.

Thaler (1966) was the first to propose a biozonation for Tertiary continental localities based on mammal remains, using mainly rodents. Other authors tried to create their own stages from the 1970s onwards, since usually there is no direct correlation between marine and continental localities because of the lack of common fossils. This has led to the establishment of several local zonations (see chapter VIII), and Mein (1975) proposed the division of the Neogene in 17 subzones, called “Mammal Neogene zones” or “MN zones” using both macro and micromammals. Although controversial, this system has reached a great popularity among stratigraphers, resulting in a similar division for the Paleogene (MP zones, Schmidt-Kittler 1987 and Aguilar *et al.* 1997) and Early Quaternary (MmQ zones, Agustí *et al.* 1987).

Besides their importance as biostratigraphical markers, the other main use of micromammal remains is palaeoenvironmental reconstructions. Some extant micromammals show very concrete ecological requirements, and these kinds of studies rely on the assumption that these preferences have been maintained over time. However, these postulates have to be taken with care, since recent representatives of a taxonomic category may occupy only a part of the niches held by its relatives in the past (see

Freudenthal and Martín-Suárez (2013) for a discussion on the palaeoecology of extinct Gliridae compared with their less diverse extant relatives).

Another proxy that has been widely used in palaeoecology is dental pattern (Meulen and Bruijn 1982, Daams *et al*. 1988 and 1999, Hernández-Fernández and Peláez-Campomanes 2003, among others). However, this approach is risky. Freudenthal *et al.* (2014) showed that the length of the mesolophid in extant cricetids and the number of crests in extant glirids could not be correlated with humidity. These authors also found a negative correlation between the climatic conditions inferred from the dental pattern of cricetids, glirids and eomyids in central Spanish Aragón and the data from the more reliable isotopic analysis of $\delta^{13}C$ of incisor enamel. This tissue is a solid source of palaeoenvironmental data, since the ever-growing rodent incisors (and the ever-growing molars of unrooted Pleistocene arvicolids) reflect the conditions during the last weeks of life of the animal (Klevezal *et al*. 1990 and Klevezal 2002), while non-growing tissues like the enamel of the molars of murids, glirids and cricetids may show perturbations created by weaning (Lindars *et al*. 2001).

In addition, dealing with whole assemblages can provide a better insight into the palaeoecological affinities of a certain taxon, since a positive correlation with other taxa of known preferences suggest similar requirements, while a negative correlation implies opposite affinities.

Another approach used in the reconstruction of past environments is the analysis of the weight structure of the communities of both macro and micromammals, proposed by Legendre (1986 and 1989), in which the body mass of a certain taxon is deduced from the measurements of the first molar (Legendre 1989). This method has been widely used (Aguilar *et al.* 1999, Hernández-Fernández *et al.* 2006, Gómez-Cano *et al.* 2006 among others) although some of its interpretations remain controversial (see Rodriguez 1999 and 2000).

1.3.4. Future goals

Since most studies dealing with fossil micromammals have been made in Europe and North America, the record of this group is strongly biased. Fortunately, the number of works from other parts of the world is increasing, which eventually will lead to a biostratigraphical frame with a resolution comparable to that of the European basins.

As explained above, traditionally teeth have been the main object of study of micromammal palaeontologists. On the contrary, postcranial remains have received little attention, except in the rare cases where a complete specimen appears in anatomical connection, like the murid *Paraethomys* in Calvo *et al.* (1978) (Late Miocene), the eomyid *Eomys quercyi* in Storch *et al*. (1996) (Late Oligocene), and the glirids *Eogliravus wildi* in Storch and Seiffert (2007) (Early Middle Eocene), *Hypnomys* in Bover *et al.* (2010) (Late Pliocene-Early Holocene) and *Muscardinus cyclopeus* in Quintana (2015) (Pliocene).

The study of micromammalian postcranial skeleton is common in zooarchaeological contexts, since these remains are much more complete and can be directly compared with reference collections of the same species. On the contrary, bones are much more fragmented in palaeontological localities, and they usually belong to extinct species, which do not have a direct correlation with extant forms. However, this approach has been successfully used in Pleistocene remains (Condis-Fernández and Berovides 2002, Ubilla 2008, among others), and it is to be hoped that the study of postcranial remains in older localities will provide abundant information on the palaeobiology and palaeoecology of extinct micromammals.

Finally, the methodologies used in fossil micropalaeontology are being updated, since many techniques used for macromammals have been adapted to the (usually) small size of micromammals. In this regard, analysis of dental microwear, usually performed on fossil primates and ungulates, have been successfully used in murids (Gomes-Rodrigues *et al.* 2009 and 2013), glirids (Kaya and Kaymakçi 2013, Oliver *et al.* 2014) and insectivores (Silcox and Teadford 2002), and the use of geometric morphometrics has allowed achieving a greater resolution in systematics (Barciová and Macholán 2006, Barciová 2009) and morphological changes of lineages along time (Renaud and Dam 2002). Other techniques, such as finite element analysis (FEA) and synchrotron X-ray tomography can provide new insights into the biomechanics of micromammals (see Gill *et al.* 2014 for a combined use of these methodologies), increasing our understanding on the palaeobiology of this group. Other studies have gone a step further, identifying the genetic bases behind the development of certain phenotypes, like the stephanodont dental pattern (Gomes-Rodrigues *et al.* 2013). In summary, the combination of different approaches can expand our knowledge of past faunas and environments, and the capacity of palaeontologists to answer the questions raised in the study of fossils will be increased, as new technologies are adapted to specific groups.

CHAPTER II. GEOLOGICAL SETTING.

II.1. Alcoy Basin

II.1.1. Introduction

The Alcoy Basin (SE Spain) belongs to the inner Prebetic of the Betic chain, and it is surrounded by the mountain ranges of Menejador, Mariola and Benicadell (Fig. II.1). Previously, the geology of this area was studied by Durand Delga *et al.* (1964), Montenat (1973: 1009-1014, fig.153), Aguirre *et al.* (1975) and Pierson d'Autrey (1987). A number of vertebrate localities have been described in this basin, among which, only the classic locality of Alcoy-Mina, known since the 19th century (see Montoya *et al*. 2006b), has yielded macromammal remains.

Regarding the micromammals, previous works have described the sites of Alcoy (Thaler *et al*. 1965, Adrover 1969), denominated in this thesis Alcoy-Barranco (following Morales 1984), Alcoy-N (López-Martínez 1989), Alcoy-4B (Freudenthal *et al.* 1998), Alcoy-2 (Esteban Aenlle and Lacomba 1988) and Alcoi Cotes Altes-2 (Mansino *et al*. 2009a). While the location of the classic locality of Alcoy-Mina is known after Montoya *et al.* (2006b), the position of the rest of mammal localities in the area is doubtful. Although the locality of Alcoy-2 (Esteban Aenlle and Lacomba 1988) has been rediscovered, the level of Alcoy-4B (Freudenthal *et al*. 1998) is now under a newly built residence, while the location of the rest (Alcoy-Barranco and Alcoy-N) is uncertain because the intense erosion in the zone has extended the ravine in both margins, changing the references in the terrain. Adrover (1969) placed the locality of Alcoy-Barranco near an abandoned furnace, close to the house *El Gormaget de Torretes.* Unfortunately, the erosive processes and vegetal covering occurring in the Gormaget ravin make impossible to know the exact location of this site. The age of the localities from the Alcoy Basin ranges from Late Miocene to Late Pliocene (MN13 to MN16) (López-Martínez 1989, Mansino *et al*. 2009a), and their approximate locations are shown in Fig. II.1.

II.1.2. Betic context

In the area, Mesozoic rocks of the inner Prebetic are characterized by a widespread detachment, in which plastic Triassic rocks are involved. This has generated an abundance of folds and large structures. In the context of the Betic Range, Neogene postorogenic basins provide important information, essential to understanding the final evolution of the Atlantic-Mediterranean communication. The closure of the seaway and the isolation of the basins are diachronic, so marine to continental transition occurs in different a time depending on its geographical location.

II.1.3. Prebetic basins

In the Alcoy environment, the Betic context allowed the development of vast synclinal depressions, WSW-ENE oriented. Over them were deposited the characteristic marine marls in “Tap” facies during the marine Miocene. Isolation of the sea occurred very early in the North Prebetic basins of Alicante (Tortonian, Vallesian-Early Turolian), and marine sediments are only represented in the Unit I of Viseras *et al.* (2004). In this manner, a marine basal Tortonian with carbonate facies and limited thickness (always lower than 30 m) was deposited over “Tap” facies in angular discordance. Over this material, we find the continental facies, constituted essentially by lacustrine and fluvial sediments. These first continental deposits belong to Unit II of Viseras *et al.* (2004). They are represented by alluvial fan facies in the margin and fluvio-lacustrine facies in the centre. In this context, the Miocene-Pliocene transition takes place in a continental environment (Aguirre *et al.* 1975).

II.1.4. Alcoy Basin environment

The central part of Alcoy Basin is constituted by a depression that disrupts the normal development of the Betic mountain chain direction. This depression can be subdivided in some quadrangular grabens, being the Almudaina Graben where the studied deposits are located. Two sedimentary associations in continental facies are present in the marine lower Tortonian (Pierson d´Autrey 1987): a lacustrine white series and a fluvial red one that fills all the central part of the Alcoy Basin, covering the ancient sediments. Deposits of Alcoy Basin have a very important role to study the palaeoenvironmental evolution of this area, since they provide interesting fossil sites.

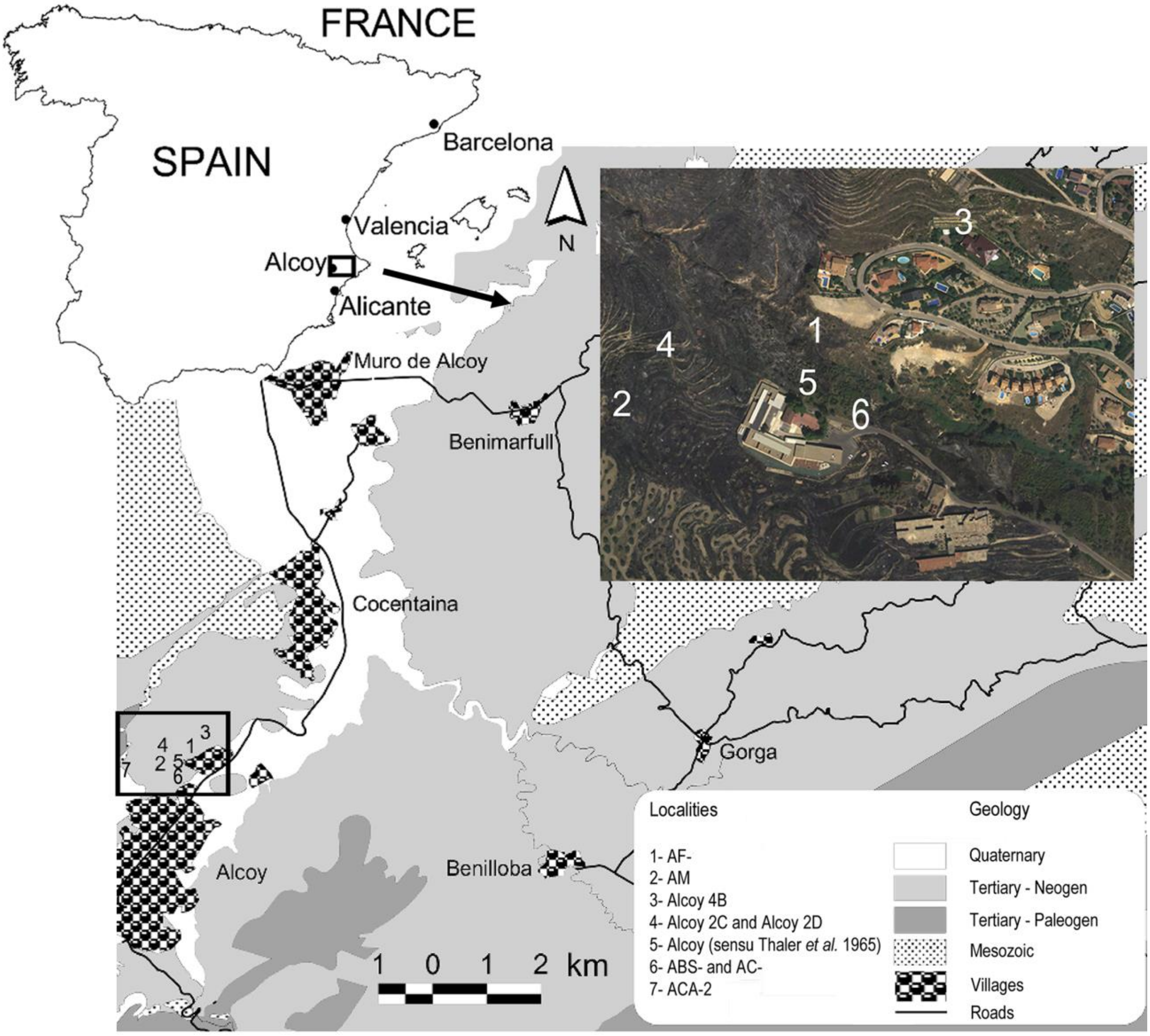


Figure II.1. Geographic and geological setting of the Alcoy Basin, showing the location of the outcrops of the Gormaget ravine (1 to 7 fossil levels). Acronyms: ABS-, Alcoi Barranc Sud; AC-, Alcoi Cristian; ACA-, Alcoi Cotes Altes; AF-, Alcoi Forn.

According to Ballesteros *et al*. (2007), continental fossil sites in lignite deposits (like Alcoy-Mina) belong to fluvial conglomerates, silts and clays unit, inside synthem V of the same authors. This synthem covers, in angular discordance, different Paleogene and Miocene units, so all the studied deposits are discordant with older material and their direction and dip are related with a normal fault (Ballesteros *et al*. 2007).

II.1.5. Methodology and general description

Fieldwork is very complicated in the studied area due to the soil development, great escarpment of the zone and coverage by cultivation terraces. The measured stratigraphic sequence comprises about 68 meters (Fig. II.2). This series includes materials located very close to the outcrop of Alcoy-Mina, related to two sections, Alcoi Cristian (AC) and Alcoi Barranc Sud (ABS) in Gormaget ravine (Fig. II.3, A), which faunal lists are summarized in Table VIII.1. To obtain the stratigraphic data presented in Fig. II.2 we dug some trenches in different places to look for the fresh rock, interpreting this information accordingly to the environment of the Gormaget ravine.

The studied series are located SE of Alcoy fault (N30-N50 55ºSSE) and are influenced by its movement. This fault cuts obliquely the WSW-ENE syncline that lies between the Mariola and Menejador ranges, injecting versicoloured Triassic marls and separating this syncline in two different buckets since upper Burdigalian. The effect of the Alcoy fault can be seen in the arrangement of the studied materials, which are tilted in the direction of the fault scarp, changing its natural dip towards the centre of the basin.

Gormaget ravine series are related to fluvial series that develop without discontinuity above the lacustrine facies of the basin, arranged at the foot of the southern slopes of the Benicadell and Mariola ranges and the northern slopes of the Menejador range. The studied series, with alluvial facies included in sandy marls with organic layers, present lacustrine and floodplain deposits features. Upwards, conglomerates take more importance (thickness and grain size), organic marls are not present and reddish colours are predominant.

The alluvial systems present complex landforms in which take part an orographic-dynamic environment and the availability of a solid charge in a fluvial stream (Pedraza 1996). Stratigraphic series described below seem to be the transition between the organic marls with sporadic conglomerates (more distal and in a lower stratigraphic position) and conglomerate units (more proximal and in an upper stratigraphic position). This is the typical context in which subsidence has less importance than contributions.

II.1.6. Stratigraphy and sedimentology of the sites

In the studied area, the sandy-marls deposits with gray to brownish colours, which can be several meters thick, are generally dominant. In marls, there are frequently isolated pebbles or sandy to conglomerate linear intercalations. Conglomerate levels are relatively common, reaching a thickness of a meter or more. The presence of organic levels of intense dark colour is also remarkable.

Lignite deposits from Alcoi Barranc Sud (ABS) present the greater lateral continuity of the series, with several tens of meters visible in the outcrop. They form the basis of the studied series where in about 20 meters we identify up to 10 organic levels (ABS1 to ABS10, Figs. II.2 and II.3, B) that have been sampled.

In ABS the conglomeratic intercalations are frequent, with a slightly erosive base and a yellow sandy matrix. Organic levels are always present in the middle or upper part of the sandy marls, which are arranged above each conglomeratic intercalation. In this sense, these deposits seem to respond to specific events that are repeated.

Some of the conglomerates present in ABS are coarsening upwards and some sandy intercalations show the existence of sedimentary structures that indicate the direction of the current. In some organic and sandy-marl levels, the remains of continental gastropods are common. These cited conglomerates strata are light coloured (often yellow) with a sandy matrix, and often lack internal structure. In some of them we check coarsening-upwards pebbles and minor erosive base. They differ from those in the top of the Gormaig ravine (stratigraphically higher), which have a reddish matrix, a bigger average size of the pebbles and greater thickness of the strata.

A few meters above ABS, we find the organic levels named as Alcoi Cristian (AC, Figs. II.2 and II.4, A). In AC we confirm the existence of little differences in facies association from previous deposits. Some of the organic levels are in the same position that we explained before (to the middle or upper part of the sandy marls, which are arranged above each conglomeratic intercalation), but in two cases we can put the organic levels just in contact with the top of conglomerates. On the other hand, AC shows evidence of paedological development in marly intervals. Irregular carbonate precipitates are also common around AC-1 and throughout the entire series of AC.

The level AC-0 and the lost locality of Alcoy Barranco (Adrover 1969) are possibly of a similar age. The uppermost organic layer is Alcoy 2D (AL2-D, Figs. II.2 and II.4, B), although other organic levels are present above AC deposits, like Alcoy-Mina inferior, being of little importance and without fossil remains. The levels AL2-C and AL2-D are considered equivalent to the fossiliferous levels of the classic locality of Alcoy-Mina (Mansino *et al*. 2013, chapter IV).

AL2-D has a thickness of more than 60 centimetres, only visible in a small outcrop. At first sight, we can find abundant shell gastropod fragments. In the lower part of AL2-D, there is a fine clay level with intense ochre colour (AL2-C). In addition, in the middle and lower part of the organic layer we detect two light coloured limestone marls levels.

AL2-D seems to be a palaeosoil of organic nature (histosol) which must have developed in a flooded area of low energy. The lenticular shape of some of the organic levels in the studied area is probably related to the existence of depressions of limited extension in which some drainage occurred.

Alcoi Forn (AF, Figs. II.1, II.5, A and II.5, B) series cannot be correlated with the rest of the synthetic series presented in this thesis. However, the materials are very similar to those previously described, and their faunal context suggest a slightly older age for these localities.

Also in the northern side of the Gormaget ravine has been relocated the locality of Alcoy 4B (Freudenthal *et al.* 1998), which yielded abundant remains of gerbils. Its faunal list comprises *Apocricetus* cf. *barrierei*, *Ruscinomys lasallei*, *Eliomys intermedius*, *Blancomys neglectus*, *Debruijnimys* sp., *Apodemus* sp., *Stephanomys* cf. *cordii*, *Paraethomys* cf. *jaegeri* and *Castillomys crusafonti* (Agustí, personal comment). This assemblage is consistent with an Early Ruscinian age, and probably the *Castillomys* present in Alcoy 4B is *Castillomys crusafonti gracilis* (Agustí, personal comment, synonymized to *C. gracilis* in Martín-Suárez and Mein 1991). This site could not be resampled because it lies now under a dwelling, but it is likely close in age to the levels of the AC section, maybe slightly younger, but clearly older than the localities of AL2-C and AL2-D.

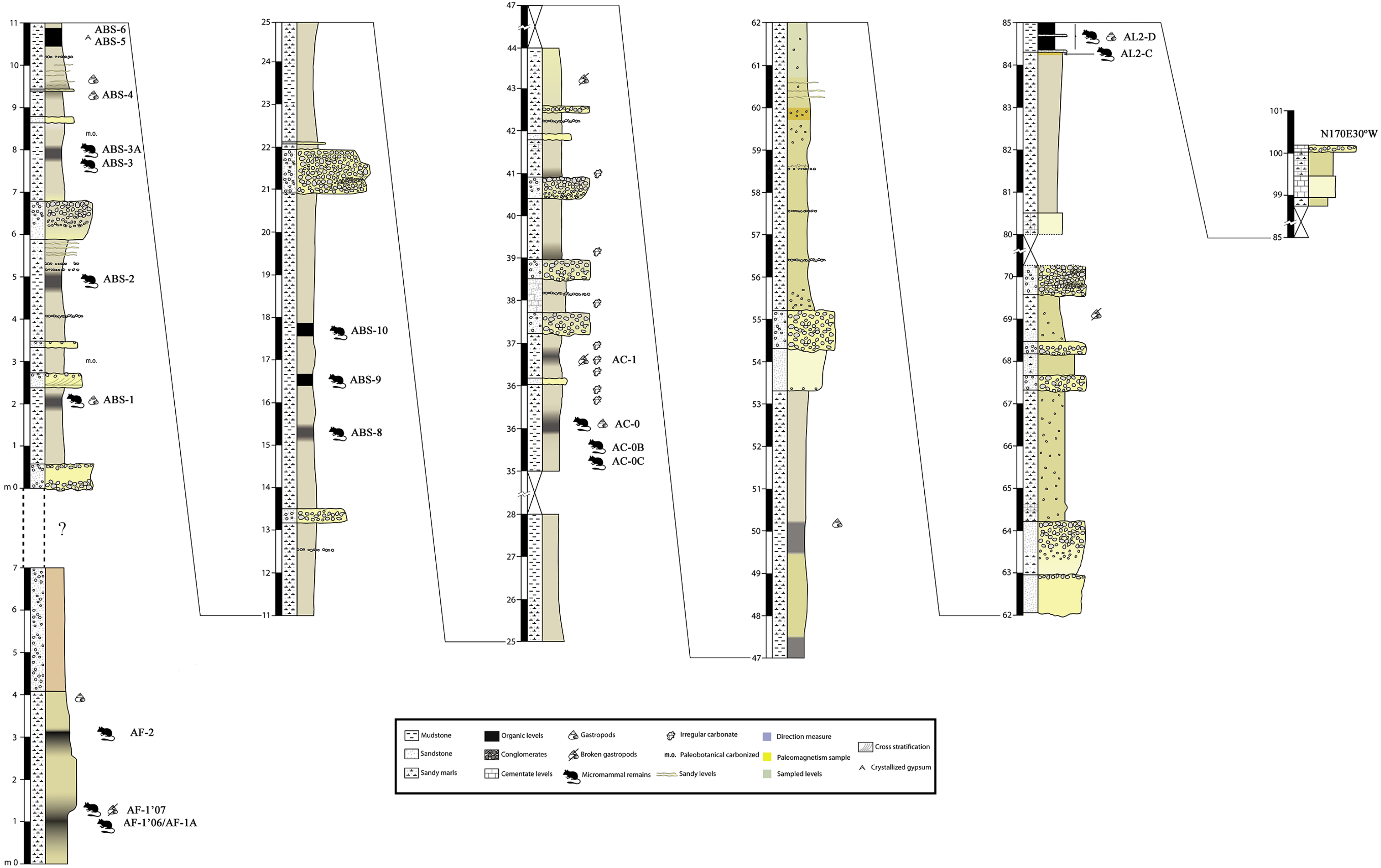


Figure II.2. Lithostratigraphic logs of the AF, ABS, AC and AL2 sections of the Gormaget ravine (Alcoy Basin), showing the position of the localities ABS-1 to 10, AC-0C, 0B and 0, AL2-C and D, and AF-1’06, A, 1’07 and 2. The dashed lines connect the ABS section to the supposed stratigraphic position of AF deposits. Scale in meters.

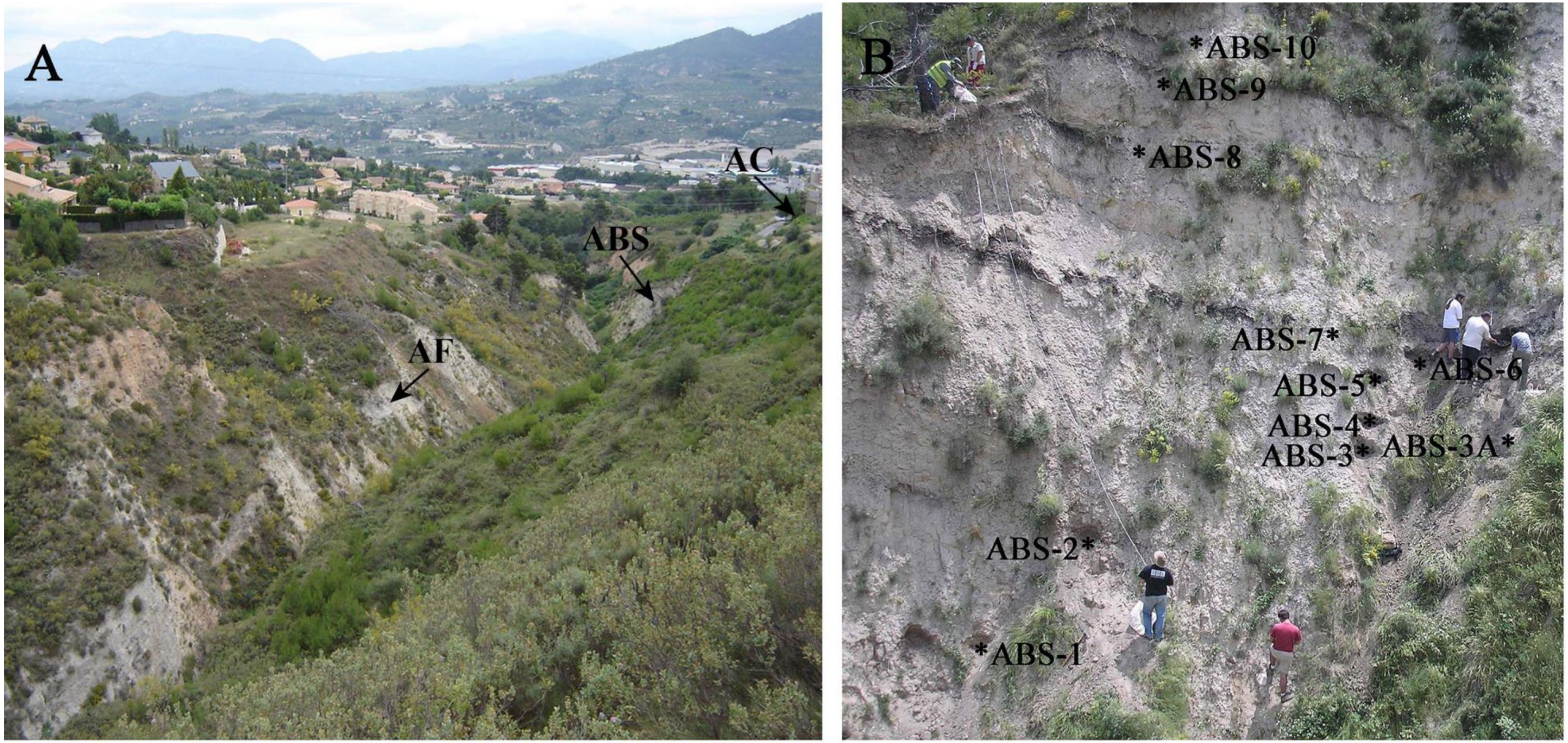


Figure II.3. **A**, Northeastern view of the Gormaget ravine. **B**, detail of the sampled localities in Alcoi Barranc Sud (ABS) section.

Figure II.4. **A**, detail of Alcoi Cristian (AC) section. **B**, detail of Alcoy 2 (AL2) section.

Figure II.5. **A**, Overview of AF section. **B**, detail of AF section, with levels AF-1, AF-1A and AF-2.

II.1.7. Interpretation

Upper Miocene continental deposits of Alcoy Basin show the existence of a large lake surrounded by the mountain ranges of Benicadell to the north, Cantauco to the south and west and Mariola to the west (Fig. II.1). These reliefs provided abundant detrital sediment that went to the lacustrine basin where river floodplains developed, containing organic episodes with vertebrate remains. The red series seems to correspond to an intensification of erosion (Pierson d´Autrey 1987).

Alluvial facies like those present in the context of the sites are located in the margins of the basin. Conglomeratic bodies were interpreted as meandering channels within a marly to silty floodplain, more or less braided (Pierson d´Autrey 1987). The uppermost massive conglomerates have been interpreted as subaerial deposits, formed by gravitational flows in mass (Santisteban *et al*. 1997).

The studied series and the context in which they are included show the evolution of the Alcoy Basin at the base of a mountain range. The bulk of the studied materials belong to a fluvial environment in which floodplain deposits are dominant. Towards the base, there is evidence of lacustrine environments, over which powerful red conglomeratic banks are developed. They show the progress of the detrital material towards the centre of the basin.

The bulk of sediments of alluvial plains are overbank deposits laid down during floods, when the system often inundates extensive areas (Kukal 1971). We can think that alluvial systems are formed, to a large degree, by fluviatile processes with the influence of mudflows produced by the downslope movement of solid debris.

The organic marls represent lacustrine deposits that could be interpreted like expansive periods of a lake or be placed between river branches, at the margins of alluvial plains or in an area between two fans. In this sense, organic deposits could collect vertebrate remains representing different palaeoenvironments around them (Santisteban *et al*. 1997)

II.2. Cabriel Basin

II.2.1 Introduction

The Cabriel Basin, in the East of the Iberian Peninsula, is a mid-sized Neogene basin located between the Iberian platform to the north and the Betic Cordillera to the south. The watershed of the Cabriel Basin is mostly composed of Cenozoic limestones with detrital sediments (Fig. II.6). The sedimentary record of this basin contains several mammal sites ranging from Late Aragonian to Villanyian (MN7/8 to MN17) (Aguirre *et al.* 1973, Alberdi *et al.* 1982 and 1997, Benavent *et al.* 2008, Freudenthal *et al.* 1998, Lacomba *et al.* 1986, López-Martínez 1989, Mansino *et al.* 2009b, Martín-Suárez *et al.* 2000, Mein *et al.* 1978, Mein and Martín-Suárez 1993, Montoya *et al.* 2006b, Morales 1984, Opdyke *et al.* 1990 and 1997, Robles *et al.* 1974, Ruiz-Sánchez *et al.* 1994 and 2011).

II.2.2. Venta del Moro

This site is located in an abandoned train trench (Fig. II.7, A), nearby the town of Venta del Moro. It is situated in the upper part of the Detrital Unit of Los Isidros, in the Venta del Moro-Villatoya Formation, according the stratigraphy of the area defined by Robles (1970). In this locality are represented at least two cycles of carbonated lacustrine facies, which intercalate palaeosoils and lignitiferous clays. These facies are covered in a discordant way by several meters thick layers of sands and canaliform conglomerates intercalated with floodplain clays (Mathisen and Morales 1981, Gibert *et al*. 2013). In the last of these lacustrine cycles are found the rich fossil-bearing levels studied in this thesis (Fig. II.7, B: Venta del Moro A, AB, B, BC, C and D, sensu Montoya *et al*. 2006a). Levels A, AB, B and BC comprise a single marly layer, darker and more detrital to the bottom and clearer and more carbonated to the top. Level C is a single black layer of lignitous marls. Finally, level D is formed by biodetrital grey sandy marls.

II.2.3. La Bullana

The sites of La Bullana 2B and La Bullana 3 are located approximately 3 km southwest of the classic locality of Venta del Moro (Fig. II.6), about 10 m below La Molata (Fig. II.8). However, the dip slope of these outcrops suggests that they may be the same carbonated unit. These sites were discovered during the systematic prospecting works in the area of Venta del Moro, framed within the project of excavation and study of this latter locality.

The cross section of La Bullana 2, from where micromammal remains have been obtained, is very detrital, although it is crowned by a layer of several decimetres of limestone (Fig. II.9) This outcrop includes several lignite levels and abundant fluvial sands, resting on red clays with intercalations of sandy channels. One kilometre to southeast of La Bullana 2B is found La Bullana 3 (30SXJ6404368), which probably represents an outcrop of equivalent deposits.

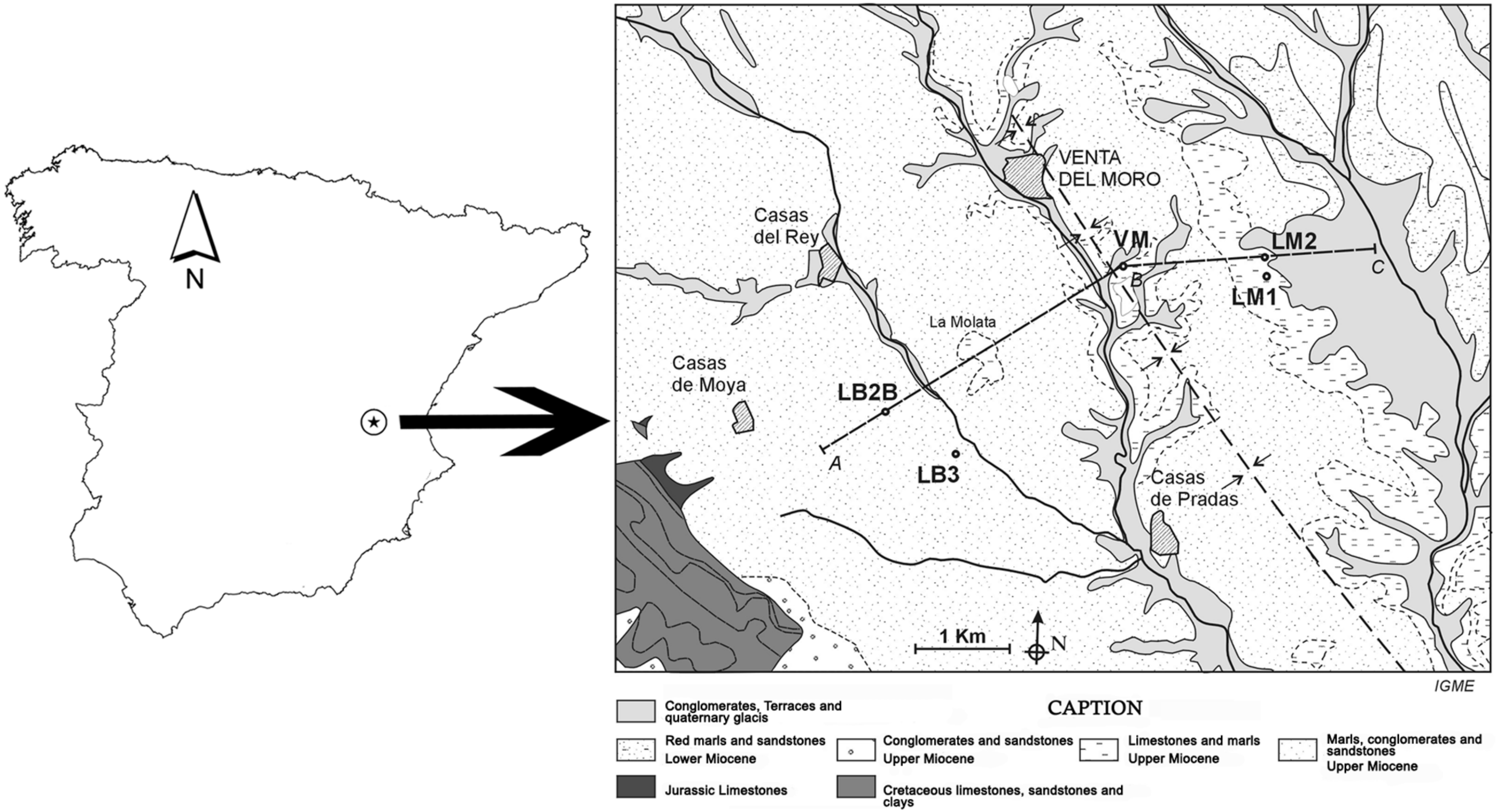


Figure II.6. Geographical and geological setting of the surroundings of Venta del Moro (VM, chapters IX and X), showing the location of the sites Los Mingos 1 (LM1) (Benavent *et al.* 2008), Los Mingos 2 (LM2), LB2B and LB3 (chapter VIII).

Figure II.7. **A**, Overview of the locality of Venta del Moro. **B**, detail of the levels VVm-A, VVm-AB, VVm-B, VVm-BC and VVm-C sensu Montoya *et al*. (2006a).

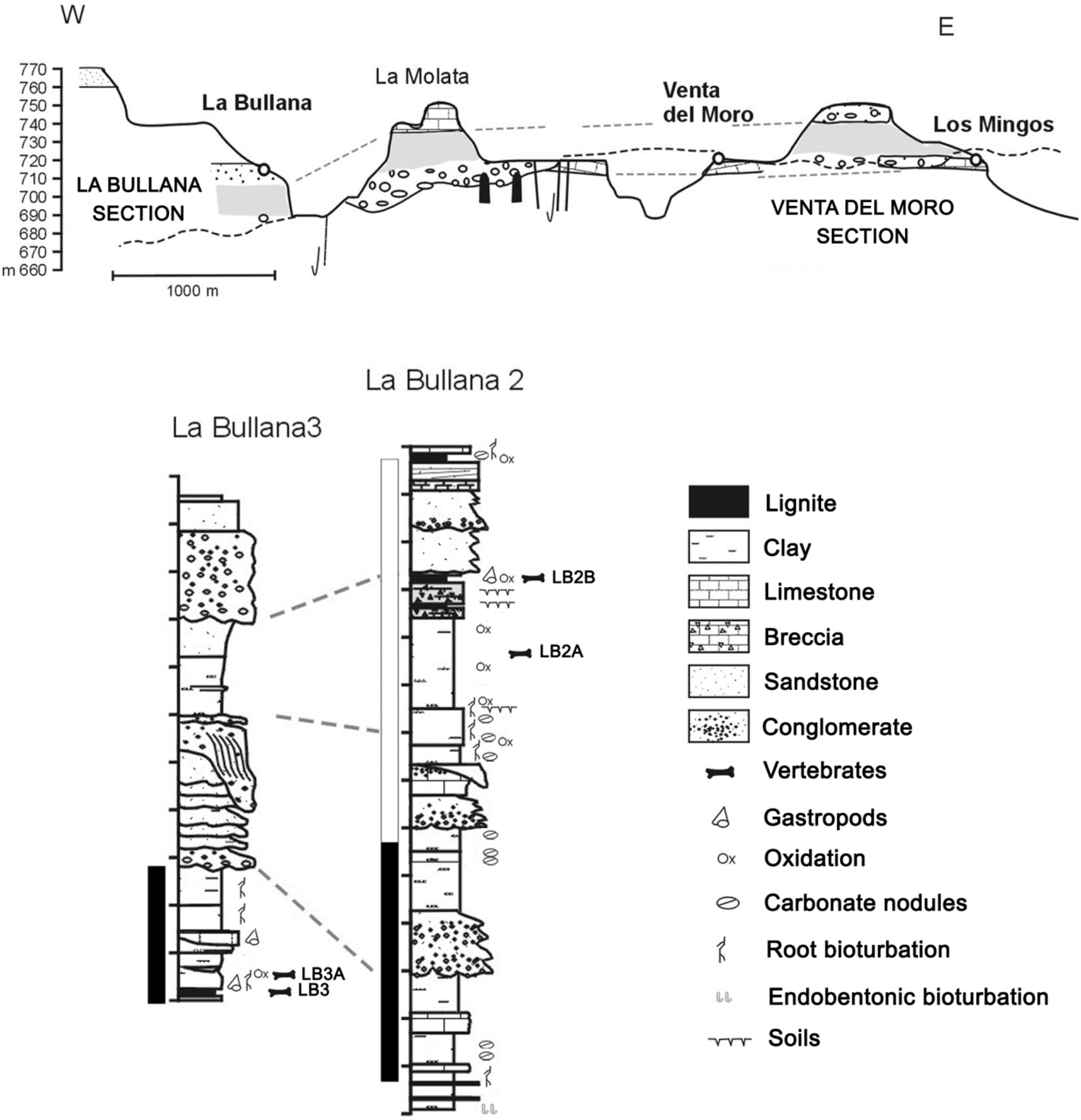


Figure II.8. Geological sketch in the Venta del Moro area with location of the La Bullana and Venta del Moro sections, their correlation and, on left, the available palaeomagnetic data.

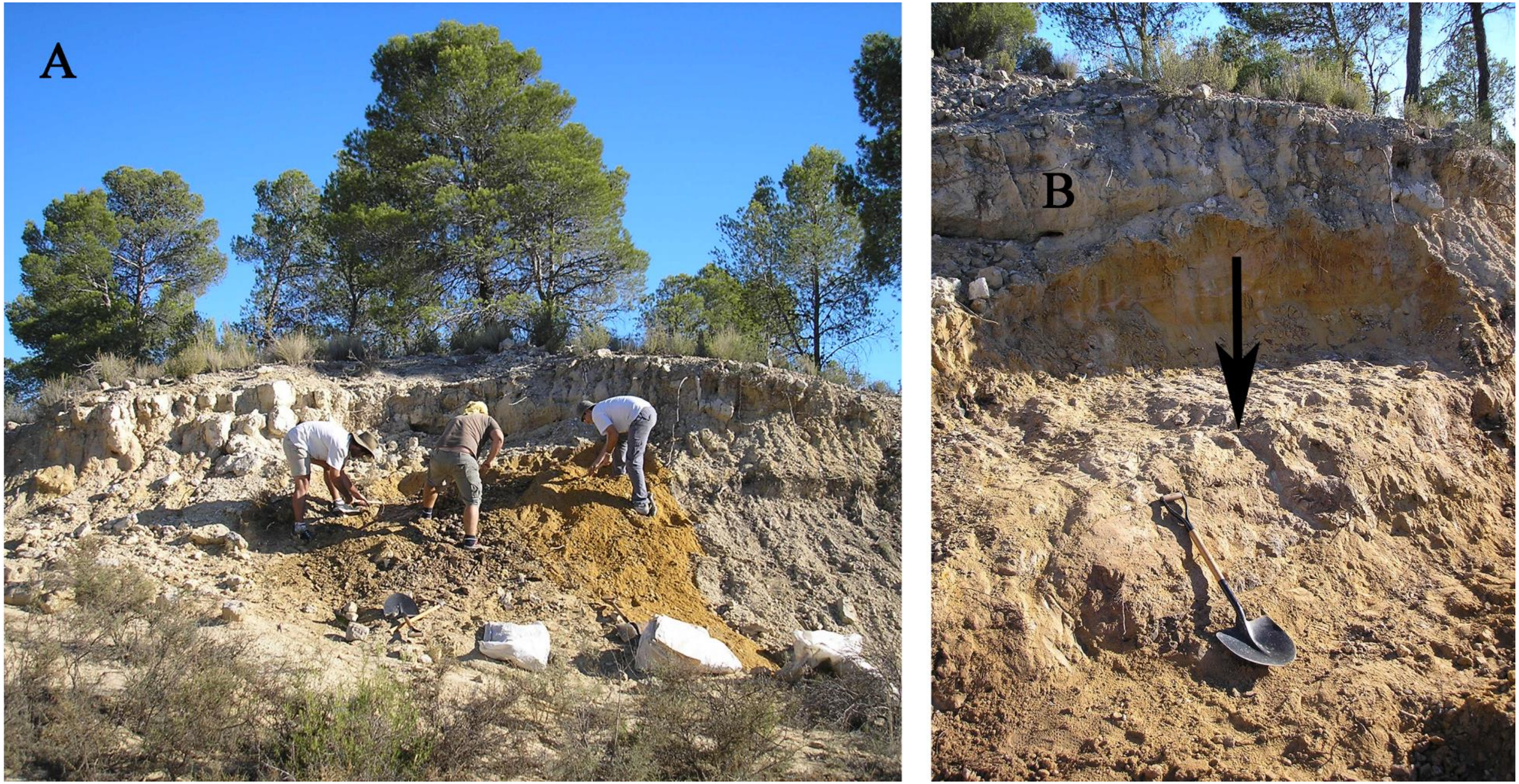


Figure. II. 9. **A**, Overview of the locality LB2B. **B**, Detail of the fossiliferous level LB2B.

CHAPTER III. METHODOLOGY.

III.1. Introduction

Because of their small size and low incidence in fluvio-lacustrine sediments, the techniques required in the study of fossil microvertebrates differ from those used when working with bigger remains. Specifically, the study of micromammal fossils is relatively new in palaeontology, although remains of rodents have been known since the 19th century (see section I.3.3). These first attempts dealt mainly with karstic fissure fillings, where there may be a huge concentration of fossils, sometimes mixing remains from a wide temporal range, or casual findings in regular excavations. The study of fluvio-lacustrine localities implies the processing of great volumes of sediment, preferably in a short time. Although wet sieving techniques had been used before (see McKenna *et al*. 1994), the development of new methodologies in the 1960s allowed the progress of the discipline (Daams and Freudenthal 1988).

The techniques used in the assembling and study of the collections can be divided in three groups: field techniques, laboratory techniques and office techniques.

III.2. Field techniques

Direct observation of micromammal fossils on the field is rare due to their small size and low incidence, although bone fragments of vertebrates may be discerned in some levels. Because of this, micromammal palaeontologists use indirect evidences that suggest that a certain level may yield fossil remains, such as a dark coloration due to organic matter and the presence of gastropod fossils. However, promising levels may be completely sterile, while others without gastropods or with a clearer coloration might be indeed rich localities. To prevent wasting time and effort in sterile or poor levels, a sample of two or three sacks containing 15-20 kg each is taken. If the sample shows an acceptable richness of fossils, which may vary according to the expectations of the researcher, a bigger sample is then taken for its study (Table II.1).

Locality	Sacks	Kg.	Identifiable remains	Remains/sack	Remains/Kg.
ABS-1	3	45	1	0.33	0.02
ABS-2	33	395	20	0.61	0.05
ABS-3	33	395	47	1.42	0.12
ABS-3A	34	510	35	1.03	0.07
ABS-6	3	45	1	0.33	0.02
ABS-7	2	30	1	0.50	0.03
ABS-8	2	30	1	0.50	0.03
ABS-9	2	30	3	1.50	0.10
ABS-10	2	30	2	1.00	0.10
AC-0	50	750	91	1.82	0.12
AC-0B	22	345	12	0.55	0.04
AC-0C	21	330	10	0.48	0.03
AF-1’06	99	1485	139	1.40	0.10
AF-1’07	90	1359	38	0.42	0.03
AF-1A	21	315	18	0.86	0.06
AF-2	2	30	2	1.00	0.07
AL2-C	11	165	79	7.18	0.48
AL2-D	43	645	275	6.40	0.43
LB2B	80	1200	253	3.16	0.21
LB3	100	1500	34	0.03	$2x10^{-3}$
VVm	≈280	4200	≈4000	-	-

Table II.1. Sample size (number of sacks and estimated sample weight, considering an average of 15 kg/sack) and relative richness of rodent and insectivore identifiable remains (remains/sack and kg) of each of the localities studied in this thesis. The number of specimens from the locality of Venta del Moro (VVm) is an estimation, since some micromammal groups like the insectivores and the microtoid cricetids are not assembled yet. Abbreviations: ABS, Alcoi Barranc Sud; AC, Alcoi Cristian; AF, Alcoi Forn; AL2, Alcoy 2; LB, La Bullana; VVm, fossil collection from Venta del Moro housed at the Universitat de València.

The sediment extracted from levels containing fossil evidences is now air-dried. This step is necessary to carry out the washing of sediment on the field, since sediments with a high degree of humidity will not disaggregate correctly, hindering the whole process. The drying is usually performed on the field, near the place where the washing will be carried out. Once dried, the sediment is placed in washing-up bowls with water, which creeps into the pores, disaggregating the sample. The resulting water-saturated mud is now ready to be sieved. We used a foldable sieve (Daams and Freudenthal 1988), consisting of three-four sieves with decreasing mesh size of 5, 2.5, 0.7 and 0.5 mm. The sieve with the coarser mesh size protects the other sieves from the bigger stones and other objects, while the finer sieve will collect the remains bigger than 0.5 mm, enough to gather most micromammal molars but some m3/M3 of the smaller species. This method requires an abundant water supply, and it is usually performed in the shores of rivers or lakes. A pump with several water hoses is then introduced in the water, and while three or four people are washing sediment in the table, others carry the washing-up bowls and drop the mud on the sieve with the bigger mesh size. This teamwork allows processing great volumes of sediment in a relatively short time, reducing the volume of the sample up to 99 % (Hoek Ostende 2003, Minwer-Barakat 2005).

III.3. Laboratory techniques

This set of techniques is used in order to reduce the volume of the sample as much as possible before screening it under the binocular lens. The ideal scenario would be to eliminate all the remains except the fossils, but in some cases this would involve the use of expensive methodologies, like the elimination of quartz remains using heavy liquids. Because of this, we use the techniques that allow us to reduce the first concentrate to an acceptable volume.

III.3.1 Re-washing

Generally, the first concentrate obtained on the field has remains of clays, which are eliminated in a second wash in the laboratory. For that purpose, the sample is usually first dried in a heater, and then washed in a sieve with a mesh size of 0.5 mm. However, each wash involves a greater risk of breaking the fossils, since they are pressed against the sieve by the water. Therefore, a low water pressure is preferred if a second wash is needed.

III.3.2. Acid treatment

Usually, the concentrates obtained on the field from all fossil sites have a great amount of calcium carbonate. To eliminate the carbonated fraction a solution of acetic acid at 20 % is used. The apatite of the fossils is not affected by the acetic acid, while the calcium carbonate reacts with the acid to form carbon dioxide and acetate, which is soluble in water and can be eliminated in further washings.

III.3.3. Magnetic separation

The samples which had a ferromagnetic fraction, like the sediment from La Bullana 2B and 3, which was composed to a large extent of limonite, were subjected to a magnetic field to sort the material. For this purpose, a device called magnetic separator, model Frantz Isodynamic L-1, was used. The sediment, moved by the vibration of a motor, goes through a narrow channel, which bifurcates in two separate ways near its end. The magnetic field affects the limonite, directing it in a great proportion to the way closer to the magnetic separator, while the fossils, remains of carbonate, quartz, etc., unaffected by the field, go mostly to the other way. However, this separation is not perfect, and some fossils may end up mixed with the magnetic fraction. To prevent this, the magnetic fraction may be subjected to several rounds of separation, but in the end, it is a matter of finding an acceptable balance between the time involved in the separation and the losses of fossil material.

III.3.4. Fractionation

The separation of the final concentrate into fractions of different grain size eases the handpicking of the fossils. Untreated concentrates in which there has been no fractionation are much more difficult to work with, and many fossils, particularly the smaller ones, may be unnoticed. To discriminate between different grain sizes, we used a set of sieves of different mesh size, ranging from 2.0 to 0.5 mm. Fractionating the final concentrate with all sieves of this range, starting with that of biggest mesh size and then in decreasing order, produces seven concentrates (2.0 – 1.5 – 1.25 – 1.0 – 0.75 – 0.63 – 0.5) with a homogeneous grain size within each category.

III.4. Office techniques

III.4.1. Handpicking

Once the volume of the sample has been reduced by the field and laboratory techniques, and separated in several fractions, it is time to pick the fossils out. The bigger remains, of more than 2.0 mm, can be picked out directly with the naked eye. Smaller remains, however, must be picked out under the binocular lens, using the appropriate magnification for each grain size. I separated complete bones, osteoderms and dental elements of mammals, fishes, reptiles and amphibians, not picking out very fragmented or unidentifiable remains.

III.4.2. Assembling of the collections

The final step before the study of the specimens is the assembling. Because of the diminutive size of the specimens, a holder is needed. In the case of the collections from the Alcoy Basin, we used white LEGO bricks as plastic supporters. Some of the collections from Venta del Moro were assembled using LEGO too, but the bulk of the *Apocricetus* remains are stuck to microscope slides. The adhesive used is Blu-tack in the Alcoy collections, but in the collections from Venta del Moro, which were assembled later, we used the paste Faber-Castell Knetgummi Art Eraser 127020, which is less greasy.

Each specimen has been coded with a field label indicating the locality in which it was extracted and a serial number. All the collections are kept at the Museu de Geologia de la Universitat de València (MGUV).

III.4.3. Measurement method, nomenclature and abbreviations

All measurements (L x W) are in millimetres and were taken on a Leica MZ75 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. The nomenclature used is explained at the beginning of each chapter, in the section “Material and methods”. Roots are described only in the case they are preserved. The abbreviations used in figures and tables are explained in figure and table captions.

Abbreviations: **ABS**, Alcoi Barranc Sud; **AC**, Alcoi Cristian; **AF**, Alcoi Forn; **AGU,** Cerro del Águila; **AL2-C**, Alcoy 2C; **AL2-D**, Alcoy 2D; **AL2D’08**, sample of Alcoy-2D taken in 2008; **ALDH**, Aldehuela; **ALM-M**, Almenara-M; **AR-4**, Arquillo 4; **AW**, anterior width; **BL**, bucal length; **BRA**, Brácana; **c1**, posterior accessory cusp; **CAC**, Cacín; **CEL**, Celadas; **CLC**, Calicasas; **CLR**, Calerico; **CR,** Crevillente; **D4**, deciduous element; **DEPUG**, Departamento de Estratigrafía y Paleontología of the University of Granada, Spain; **DHS**, Dehesa; **FAD,** First Appearance Datum; **GOR**, Gorafe; **H**, height; **I**, upper incisor; **L,** length; **L1**, length of the occlusal surface; **L2**, total length (base of the crown); **LAD,** Last Appearance Datum; **LB**, La Bullana; **LG**, La Gloria-4; **LL**, labial length; **LPE**, length posterior emargination; **m1**, first lower molar; **m2**, second lower molar; **m3**, third lower molar; **M1**, first upper molar; **M2**, second upper molar; **M3**, third upper molar**;** **MGUV**, Museu de Geologia de la Universitat de València, Spain; **MN**, European Neogene land mammal units; **MNA**, Mina; **NGR**, Negratín; **p4**, lower premolar; **P4**, upper premolar; **PER**, Peralejos; **PUR**, Purcal; **PW**, posterior width; **RCH-3**, Rambla Chimeneas 3; **SCSIE (UV)**, Servei Central de support a la Investigació Experimental de la Universitat de Valéncia; **TCH**, Tollo de Chiclana; **TLW**, talonid width; **tma**, antero-central cusp; **TRW**, trigonid width; **UCM**, Universidad Complutense de Madrid; **VAR**, Villalba Alta Río; **VM**, Venta del Moro; **VVm**, fossil collection from Venta del Moro housed at the Universitat de València; **W**, width, **YEG**, Yeguas; **ZOR**, Zorreras.

III.4.4. Photographs and drawings

The specimens were photographed using a HITACHI 4100 or HITACHI 4800 scanning microscope (SEM) at the Servei Central de Suport de la Investigació Experimental (SCSIE) of the *Universitat de València*. The illustrations were hand drawn using a Leica binocular lens with an attached camera lucida, and then scanned and retouched using Photoshop CS6 and Adobe Illustrator CS6.

CHAPTER IV. THE FOSSIL RODENT FAUNAS OF THE LOCALITIES ALCOY 2C AND 2D (ALCOY BASIN, SPAIN). IMPLICATIONS FOR DATING THE CLASSICAL LOCALITY OF ALCOY-MINA.

IV.1. Material and methods

Since 2005, nearly 1 Tm of sediment has been extracted from AL2-C and AL2-D. The recovered fossils are kept at the *Museu de Geologia de la Universitat de València* (MGUV) with the acronyms AL2C- and AL2D-, respectively. The nomenclature and measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, Adrover (1986) for the Trilophomyidae and Cuenca-Bescós (1988) and Reumer and Hoek Ostende (2003) for the Sciuridae.

IV.2. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1826

Apodemus atavus Heller, 1936 (Fig. IV.1, 1-5)

Localities: AL2-C, AL2-D.

Material: **3 m1** (AL2D-25, AL2D-26, AL2D-41), **3 m2** (AL2D-68, AL2D-69, AL2D-360), **6 m3** (AL2C-51, AL2C-53, AL2C-61, AL2D-74, AL2D-92, AL2D-96), **4 M2** (AL2C-30, AL2D-182 to AL2D-184), **3 M3** (AL2C- 40, AL2D-217, AL2D-218).

Measurements: see Table IV.1.

Description:

m1: The tma is large, round and central. Symmetrical anteroconid, connected to the metaconid-protoconid pair by a narrow crest in one of the specimens. Large labial cingulum, interrupted between the hypoconid and protoconid. The c1 is larger than both the tma and the posterior heel. In one of the specimens this cusp seems to have a very small c0 attached to its posterior side. There is an accessory cusp equivalent in size to the c1 in contact with the protoconid. The posterior heel is big, round and shifted towards the lingual side of the tooth.

m2: The anterolabial cusp is large and comma-shaped; in advanced stages of wear the connection to the protoconid is very evident. Well-developed labial cingulum, separated from the protoconid and hypoconid. There is a large c1 and an accessory cusp, which is highly reduced in one of the specimens. Round or oval posterior heel.

m3: The anterolabial cusp is absent. No longitudinal crest. One of the teeth has a small c1, absent in the others.

M2: The t1 is large. The t3 is small and round. The t7 is oval or round and separated from t4. The t6 is connected to t9. The t12 is connected to t8 and separated from t9.

Discussion:

Apodemus dominans Kretzoi, 1959, and *A. atavus* have been considered synonyms by several authors (Minwer-Barakat 2005, Minwer-Barakat *et al*. 2005, García-Alix 2006, García-Alix *et al*. 2008a). The specimens from AL2-C and AL2-D present some typical features of *A. atavus*, such as the metaconid linked to the lingual lobe of the anteroconid by a low crest (Fig. IV.1, 1), the large posterior heel of the m2 that usually protrudes over the outline of the tooth (Fig. IV.1, 2), and the t7-t4 separation which is deep (at the base of the crown) or of medium height in M2 (Fig. IV.1, 4). We have discarded these molars as belonging to *A. gudrunae* van de Weerd, 1976, because of the individualized t7 (Fig. IV.1, 4) and smaller size.

The measurements of our specimens (Table IV.1) match a small sized *Apodemus*, being similar to those of *A. dominans* from Sarrión, Orrios 3, Arquillo 3, Villalba Alta and Aldehuela (Adrover 1986), Escorihuela, Orrios, Csarnóta 2 (Weerd 1976), Moreda-1A, Belmez-1 and Moreda-1B (Castillo 1990), Alozaina (Aguilar *et al*. 1993) Mont-Hélène (Aguilar *et al*. 1986), Concud Estación 1 and 3, and Concud Pueblo 3 (Adrover *et al*. 1988). These measurements also fall within the range of variation of *A. atavus* from the localities of TCH-1, 1B, 3 and 13 (Minwer-Barakar *et al*. 2005), being slightly smaller than those from PUR-7, PUR-13, CLC-3, CLC-3B, CLC- 4B, AGU-1C and DHS-1 (García-Alix *et al*. 2008a).

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L	2	1.56	1.61	1.66
		W	2	0.89	0.92	0.96
m2	AL2-D	L	3	1.14	1.17	1.20
		W	3	0.92	1.00	1.06
m3	AL2-D	L	3	1.11	1.16	1.19
		W	3	0.91	1.02	1.16
	AL2-C	L	2	1.06	1.10	1.15
		W	2	1.00	1.03	1.06
M2	AL2-D	L	3	1.21	1.23	1.26
		W	3	1.07	1.11	1.19
	AL2-C	L	1	-	1.27	-
		W	1	-	1.09	-
M3	AL2-D	L	2	0.94	0.95	0.95
		W	2	0.95	0.96	0.98
	AL2-C	L	1	-	1.10	-

Table IV.1. Measurements in millimetres of the teeth of *Apodemus atavus* from the localities AL2-C and AL2-D. n= number of measurable specimens.

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. IV.1, 6-11)

Localities: AL2-C, AL2-D.

Material: **1 m1** (AL2D-17), **5 m2** (AL2D-50, AL2D-51, AL2D-56, AL2D-62, AL2D-64), **6 m3** (AL2C-48, AL2D-72, AL2D-91, AL2D-93, AL2D-136, AL2D-220), **6 M1** (AL2C-20 to AL2C-22, AL2D-131, AL2D-133, AL2D-134), **6 M2** (AL2C-37, AL2D-142, AL2D-176, AL2D-177, AL2D-181, AL2D-351), **4 M3** (AL2D-206, AL2D-212, AL2D-213, AL2D-222).

Measurements: see Table IV.2.

Description:

m1: The tooth is in an advanced stage of wear. There is a large tma. The molar has a large c1 and two accessory cusps. The posterior heel cannot be observed. Two roots.

m2: Isolated anterolabial cusp. Well-developed labial cingulum. There is a large c1, and an accessory cusp may also be present. Round or oval posterior heel.

m3: Highly reduced anterolabial cusp. No longitudinal crest. One of the specimens has a small c1.

M1: The t1 is situated posteriorly with respect to the t3. The connection between t1 and t2 is very low. There is neither t1bis nor t2 bis. All the teeth have a small posterior spur on the t3 directed towards the t6. One specimen has a small distal spur on the t1 directed towards the t5. The valley between t3 and t6 is very deep and wide. The t4, t5, t6, t7 and t9 are connected. The t12 is round and medium-sized, connected to the posterolabial part of the t8. There are four roots.

M2: Oval or round t1. The specimen from AL2-C, which is very worn, and one molar from AL2-D show a spur directed towards the t4-t5 intersection. The t3 is smaller than t1, and highly reduced in one tooth. The t4 and t7 are separated. The t6 and t9 are connected in the molars with an advanced stage of wear. The t12 is small and connected to the posterolabial part of t8 and separated from t9.

M3: The t1 isolated in two specimens**.** The t3 is absent. The t4, t5, t6 and t8 are connected.

Discussion:

During the Early and Middle Pliocene of Western Europe, two different lineages of *Apodemus* can be distinguished, a smaller form and a larger one (Martín-Suárez and Mein 1998). In the Iberian basins there are a number of localities in which this situation occurs, in particular with *A. atavus* or *A.* aff. *atavus* and and *A. gorafensis* or *A.* aff. *gorafensis*. The coexistence of these two lineages has been recorded in the localities of Peralejos E (Adrover *et al*. 1988), Celadas 9 and La Gloria 4 (Adrover *et al*. 1993), from Teruel, PUR-4, PUR-13 and CLC-3B in the Granada Basin (García-Alix *et al.* 2008a) (Fig. VIII.1) and Alcoy-2 (Esteban Aenlle and Lacomba 1988) (Table IV.5). The specimens from AL2-C and AL2-D are larger and with a more developed t7 than *A. gudrunae*, and smaller and with a more developed tma than *A. jeanteti* Michaux, 1967. *Apodemus agustii* Martín Suárez, 1988, differs from our material by its bigger tma, lack of stephanodonty in the upper molars and a funnel delimited by the anteroconid, protoconid and metaconid in the m1.

The populations from AL2-C and AL2-D are consistent with the measurements and morphology of *A. gorafensis* of the collection from Gorafe-A, the type locality of the species (Ruiz Bustos *et al*. 1984), showing a relatively large tma and well-developed labial cingulum and t7. Our specimens are somewhat bigger than *Apodemus* aff. *gorafensis* from Peralejos E (Adrover *et al*. 1988), falling within the range of variation of *A.* aff. *gorafensis* from Celadas 9 and La Gloria 4 (Adrover *et al.* 1993). The mean measurements of the populations from AL2-C and AL2-D are slightly bigger than *A.* aff. *gorafensis* from PUR-23, being also very similar to those of *A. gorafensis* from PUR-4, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al*. 2008a).

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L	1	-	2.25	-
		W	1	-	1.36	-
	AL2-D	L	5	1.60	1.72	1.78
		W	5	1.37	1.54	1.66
	AL2-D	L	3	1.29	1.31	1.33
		W	5	1.13	1.22	1.32
	AL2-C	L	1	-	1.36	-
		W	1	-	1.28	-
M1	AL2-D	L	1	-	2.43	-
		W	3	1.33	1.38	1.43
	AL2-C	L	2	2.24	2.25	2.27
		W	2	1.32	1.33	1.33
M2	AL2-D	L	4	1.46	1.50	1.57
		W	5	1.24	1.30	1.36
	AL2-C	L	1	-	1.49	-
		W	1	-	1.52	-
M3	AL2-D	L	4	1.13	1.16	1.20
		W	4	0.95	1.07	1.15

Table IV.2. Measurements in millimetres of the teeth of *Apodemus gorafensis* from the localities AL2-C and AL2-D. n= number of measurable specimens.

Genus *Paraethomys* Petter, 1968

Paraethomys meini (Michaux, 1969) (Fig. IV.1, 12-17)

Localities: AL2-C, AL2-D.

Material: **15 m1** (AL2C-1, AL2C-3, AL2C-43, AL2C-45, AL2C-46, AL2C-58, AL2C-66, AL2D-15, AL2D-21 to AL2D-24, AL2D-40, AL2D-347), **6 m2** (AL2C-11, AL2C-12, AL2D-45, AL2D-58, AL2D-66, AL2D-67), **5 m3** (AL2C-50, AL2C-63, AL2D-83, AL2D-87, AL2D-88, AL2D-90), **3 M1** (AL2D-126, AL2D-132, AL2D-253) **4 M2** (AL2D-172, AL2D-178, AL2D-179, AL2D-350), **8 M3** (AL2C-41, AL2C-62, AL2C-68, AL2D-210, AL2D-214 to AL2D-216, AL2D-352).

Measurements: see Table IV.3.

Description:

m1: Absent tma. Slightly asymmetrical anteroconid. The connection between anteroconid and protoconid-metaconid pair is very low, and in some teeth a small round funnel can be observed. Medium-sized labial cingulum. One of the molars has an incipient longitudinal spur. There is a medium size round c1. The size and number of the accessory cusps is very variable, ranging from two to four. Reduced posterior heel.

*m*2*:* The anterolabial cusp is in contact with a moderately developed labial cingulum. Three of the specimens show an accessory cusp in contact with the protoconid. One of the specimens presents a poorly developed longitudinal spur. The posterior heel is reduced and lingually displaced. Two roots.

m3: The anterolabial cusp is highly reduced or completely absent. The hypoconid-entoconid complex is separated from the anterior complex. One specimen presents a small c1 attached to the posterior complex.

M1: The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. One of the specimens presents a very small distal spur on the t3 directed towards the t5. There are no connections between t1 and t3 with t5. The connection between t4 and t8 is very low. There is a small t12.

M2: The t1 and t3 are isolated**.** The t3 is highly reduced. In three of the specimens a small distal spur on the posterior part of t1 directed towards the t4-t5 intersection can be observed. The connection between t4 and t8 is very low. The t9 and t12 are absent.

M3: Large and isolated t1. The t3 is absent. The connection between t8 and t4-t5-t6 is very low, and in two of the specimens completely isolated. There are three roots.

Discussion:

Paraethomys meini (Michaux, 1969) from AL2-C and AL2-D is much smaller than *P. abaigari* Adrover, Mein and Moissenet, 1988 and *P. jaegeri* Montenat and Bruijn, 1976. Moreover, despite being similar in size to the molars of *P. belmezi* Castillo, 1990, these teeth differ from our specimens by the presence of a well-developed tma in m1, loss of the t3 and isolation of t8 in M2 and unconnected t6 and t9 in M1. Two of the M2 present a distal spur on the posterior part of the t1 directed towards the t3-t5 intersection, which is absent in the specimens from Alcoy-2 studied by Esteban Aenlle and Lacomba (1988).

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L	6	1.90	1.94	1.99
		W	6	1.16	1.20	1.25
	AL2-C	L	2	1.93	1.94	1.95
		W	4	1.14	1.19	1.24
m2	AL2-D	L	4	1.41	1.47	1.51
		W	4	1.20	1.27	1.32
	AL2-C	L	2	1.36	1.45	1.55
		W	2	1.13	1.14	1.15
m3	AL2-D	L	4	1.24	1.37	1.43
		W	4	1.12	1.21	1.29
	AL2-C	L	1	-	1.32	-
		W	1	-	1.27	-
M1	AL2-D	L	1	-	2.24	-
		W	2	1.53	1.54	1.54
M2	AL2-D	L	2	-	1.74	-
		W	3	1.55	1.61	1.67
M3	AL2-D	L	5	1.04	1.12	1.26
		W	5	0.97	1.06	1.15
	AL2-C	L	3	1.22	1.27	1.33
		W	3	1.07	1.17	1.22

Table IV.3. Measurements in millimetres of the teeth of *Paraethomys meini* from the localities AL2-C and AL2-D. n= number of measurable specimens.

The measurements of the specimens from AL2-C and AL2-D are similar to those of *P. meini* from the localities of Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover 1986), Villalba Alta Río, Peralejos E (Adrover *et al.* 1988), and *P. anomalus* Bruijn, Dawson and Mein, 1970, from Maritsa and *P. miocaenicus* Jaeger, Michaux and Thaler, 1975, from Khendek el Ouaich (Adrover 1986), considered synonyms of *P. meini* by several authors (Weerd 1976, Adrover 1986, Castillo 1990, Minwer-Barakat 2005, García-Alix 2006, García-Alix *et al.* 2008a). The size of our specimens is consistent with the measurements and morphology of *P. meini* from Celadas 9 and La Gloria 4 (Adrover *et al.* 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11, BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (García-Alix *et al.* 2008a).

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. IV.1, 18-23)

Localities: AL2-C, AL2-D.

Material**: 14 m1** (AL2C-4 to AL2C-6, AL2C-8, AL2C-86, AL2D-1, AL2D-2, AL2D-28 to AL2D-30, AL2D-34, AL2D-36, AL2D-38, AL2D'08-2), **10 m2** (AL2C-9, AL2C-13, AL2C-14, AL2C-19, AL2C-44, AL2D-47, AL2D-48, AL2D-61, AL2D-349, AL2D-354), **5 m3** (AL2C-49, AL2D-75, AL2D-76, AL2D-80, AL2D'08-8), **6 M1** (AL2C-54, AL2D-101, AL2D-103, AL2D-104, AL2D-110, AL2D-122), **16 M2** (AL2C-28, AL2C-36, AL2C-38, AL2D-146, AL2D-148, AL2D-150, AL2D-154, AL2D-156 to AL2D-158, AL2D-160, AL2D-162, AL2D-168 to AL2D-170, AL2D-235), **9 M3** (AL2D-192, AL2D-194, AL2D-195, AL2D-197, AL2D-199, AL2D-200, AL2D-203, AL2D-208, AL2D-209).

Measurements: see Table IV.4.

Description:

m1: Slightly asymmetrical anteroconid. In worn specimens the connection between anteroconid and protoconid-metaconid pair is more evident. The labial cingulum is moderately developed. There is a large c1 in contact with the protoconid and an accessory cusp adjacent to the hypoconid. Some specimens have a small longitudinal spur. The posterior heel is small, lingually displaced and oval. Two roots.

m2: The anterolabial cusp is big, isolated from the other cusps but in contact with the labial cingulum. A small c1 can be observed in five of the specimens. The posterior heel is small, laminar or oval-shaped and lingually displaced.

m3: Both the anterolabial cusp and the c1 are absent. The hypoconid-entoconid complex is separated from the anterior complex. Two roots.

M1: The connection between t1 and t2 is very low. The t2 and t3 are very close together. Distal spurs from the t1 and t3 towards the t4-t5 and t5-t6 connections respectively may be present. There is a small t12. There are three roots.

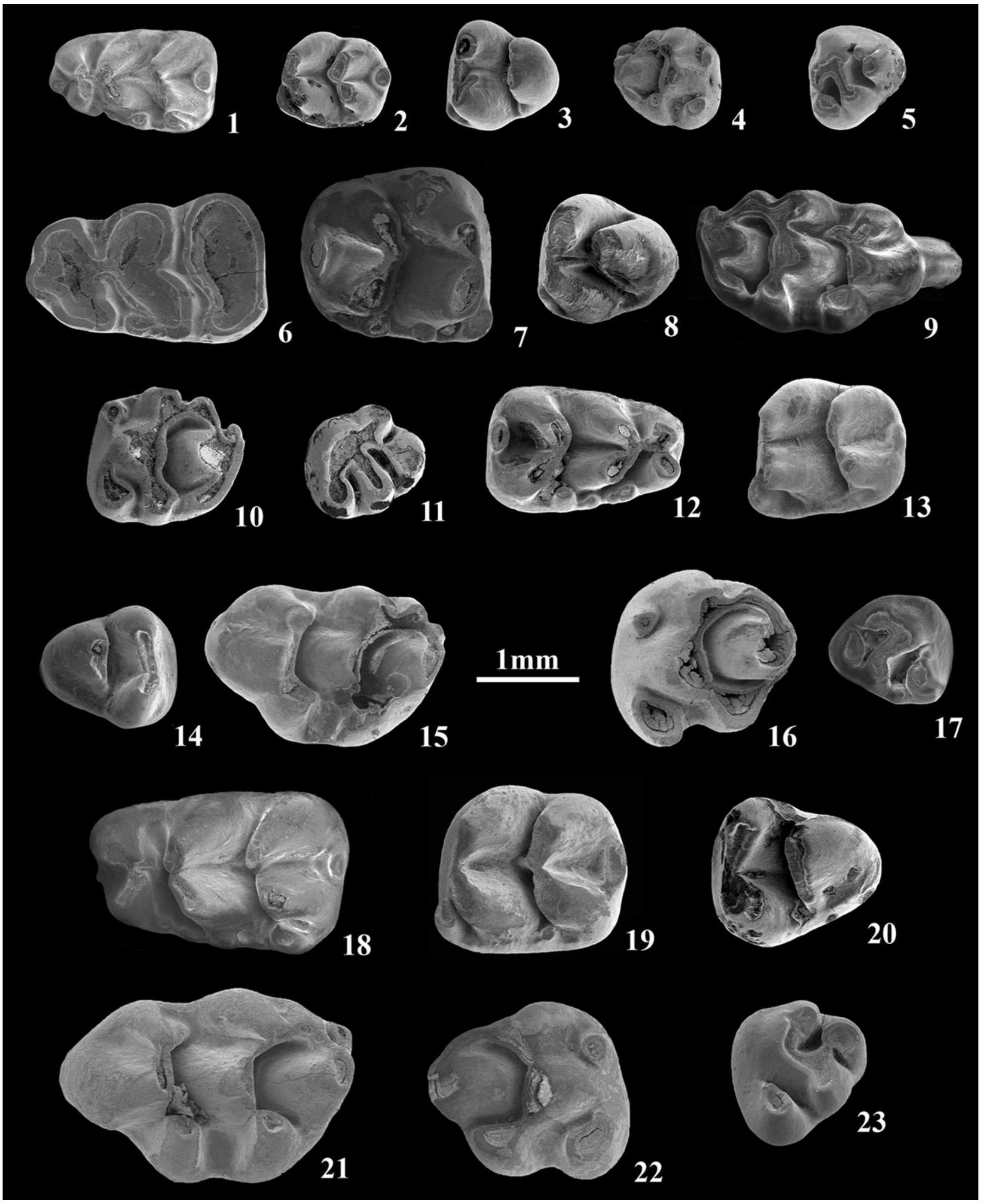


Figure IV.1. Rodent faunas from AL2-C and AL2-D (Alcoy Basin, Spain). *Apodemus atavus* from AL2-C and AL2-D. **1**, left m1, AL2D-25; **2**, left m2, AL2D-68; **3**, left m3, AL2D-74; **4**, right M2, AL2D-184; **5**, left M3, AL2C-40. *Apodemus gorafensis* from AL2-C and AL2-D. **6**, left m1, AL2D-17; **7**, right m2, AL2D-50; **8**, left m3, AL2C-48; **9**, right M1, AL2C-20; **10**, left M2, ALD-176; **11**, left M3, AL2D-212. *Paraethomys meini* from AL2-C and AL2-D. **12**, right m1, AL2D-21; **13**, left m2, AL2D-66; **14**, right m3, ALC-50; **15**, left M1, AL2D-126; **16**, left M2, AL2D-350; **17**, right M3, AL2D-216. *Paraethomys* aff. *abaigari* from AL2-C and AL2-D. **18**, left m1, AL2D-1; **19**, left m2, AL2C-48; **20**, left m3, AL2C-49; **21**, left M1, AL2D-101; **22**, right M2, AL2C-28; **23**, left M3, AL2D-194. Scale=1mm.

M2: The t1 and t3 are isolated**.** The t3 is reduced. Some specimens have a distal spur directed towards the t4-t5 intersection. The t9 is absent. The connection between t4 and t8 is very low. The outline of some of the specimens, the best preserved ones, seems more elongated than the others, and much more than *P. meini*.

M3: The t1 is large and isolated. The t3 is absent. The connection between t8 and t4-t5-t6 is very low, and in some specimens this cusp is almost isolated. Three roots.

Discussion:

The *Paraethomys* from AL2-C and AL2-D can be grouped in two clusters in terms of size. The smaller specimens can be assigned to *Paraethomys meini*, while the larger ones show many of the features of *P. abaigari* from Villalba Alta Río (type locality), such as a reduced longitudinal spur in m1, moderate labial cingulum, large c1 and moderate posterior heel (Adrover *et al*. 1988, García-Alix *et al*. 2008a). Also, these molars differ from *P. meini* in their development of distal spurs on t1 and t3 and persistence of the t12 in the M1. However, our specimens are slightly smaller than *P. abaigari* from Villalba Alta Río, while very similar to those of *Paraethomys* aff. *abaigari* from CLC-5, PUR-13 (García-Alix *et al*. 2008a), La Gloria 4 and Celadas 9 (Adrover *et al*. 1993). These teeth reach some of the lower values of *P. jaegeri*, although the mean values are always bigger in the latter species. For these reasons we ascribe our material to *Paraethomys* aff. *abaigari*.

The coexistence of two *Paraethomys* species of different size has been recorded in a number of Pliocene localities from the Teruel Basin, as Villalba Alta Río, La Judería, Celadas 6 (Adrover *et al*. 1988), Villalba Alta 1, La Gloria 4 (Mein *et al*. 1990), Celadas 14, Celadas 5, Celadas 5A and Celadas 9 (García-Alix *et al*. 2008a) (Fig. VIII.1). Adrover (1986) also described a big-sized form of *Paraethomys* associated to *P. meini* in the localities of Séte and Villalba Alta, where he found *P. jaegeri* and *P*. aff. *jaegeri* respectively. The localities CLC-5A and PUR-13 from the Granada Basin have yielded remains of both *Paraethomys meini* and *Paraethomys* aff. *abaigari* (García-Alix *et al*.

2008a). Also, Adrover *et al*. (1988) recognized individuals of a big-sized phylogenetic lineage of *Paraethomys* in the localities of Gorafe 1 and Gorafe-A, while in the faunal lists given by Ruiz Bustos *et al*. (1984) and Agustí and Martín-Suárez (1984) for Gorafe-A and Gorafe 1 respectively, the only *Paraethomys* species mentioned are *P*. cf. *meini* in Gorafe 1 and *P. meini* in Gorafe A (Fig. VIII.1). Montenat and Bruijn (1976) cited two *Paraethomys* species in the locality of La Juliana (Murcia): the big-sized *P. jaegeri* and the smaller *P. meini*. García-Alix (2006) noted that, when two species of *Paraethomys* coexist, like in the Ruscinian localities of PUR-13 and CLC-5A, the size of *P. meini* is quite reduced, which agrees with *P. meini* from AL2-C and AL2-D, whereas in older localities like PUR-4 the two lineages cannot be distinguished. This author found the same situation in several Lower Pliocene localities of the Teruel Basin, like Celadas 5, 5A, 9 and 14, and La Gloria 4, where *P. meini* appears associated with *P*. aff *abaigari*, and in younger localities like Celadas 6, La Judería and Villalba Alta Río 1 (Adrover *et al*. 1988, Mein *et al.* 1990), where the big-sized *Paraethomys* is identified as *P. abaigari*.

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L	3	2.34	2.42	2.53
		W	6	1.40	1.46	1.54
	AL2-C	L	1	-	2.33	-
		W	3	1.39	1.49	1.60
m2	AL2-D	L	3	1.67	1.81	1.89
		W	3	1.52	1.61	1.72
	AL2-C	L	4	1.73	1.85	1.92
		W	5	1.46	1.58	1.68
m3	AL2-D	L	3	1.56	1.60	1.62
		W	3	1.31	1.38	1.43
	AL2-C	L	1	-	1.62	-
		W	1	-	1.44	-
M1	AL2-D	L	4	2.62	2.69	2.76
		W	4	1.80	1.83	1.87
	AL2-C	L	1	-	2.54	-
		W	1	-	1.84	-
M2	AL2-D	L	12	1.76	1.97	2.16
		W	13	1.57	1.74	1.84
	AL2-C	L	2	1.83	1.94	2.06
		W	3	1.66	1.75	1.80
M3	AL2-D	L	8	1.26	1.36	1.47
		W	8	1.28	1.33	1.47

Table IV.4. Measurements in millimetres of the teeth of *Paraethomys* aff. *abaigari* from the localities AL2-C and AL2-D. n= number of measurable specimens.

In the material from Alcoy-2, Esteban Aenlle and Lacomba (1988) distinguished two *Paraethomys* species, *P. jaegeri* and *P. meini* (Table IV.5). In our revision of the material, we observed that the *Paraethomys* from this locality formed two clusters in terms of size that are almost coincident with the size ranges of the *Paraethomys* in our collections. Therefore, we consider *P. jaegeri* from the Alcoy-2 collection housed at the Universidad Complutense de Madrid (UCM) to be *P.* aff. *abaigari*. Mein *et al.* (1990) noted that the sizes of both lineages of *Paraethomys* tend to increase over time, setting the succession *P.* aff. *abaigari* - *P. abaigari* - *P.*aff. *jaegeri* - *P. jaegeri* for the linage of larger size. Nevertheless, the relationship between the two forms is not clear, being uncertain if *P. abaigari* descends from *P. meini* or is an immigrant taxon (García-Alix *et al*. 2008a).

Alcoy-2 (Esteban Aenlle and Lacomba 1988)	AL2-C	AL2-D
Apodemus dominans	*Apodemus atavus*	*Apodemus atavus*
Apodemus gorafensis	*Apodemus gorafensis*	*Apodemus gorafensis*
Castillomys crusafonti gracilis	-	*Castillomys gracilis*
Paraethomys meini	*Paraethomys meini*	*Paraethomys meini*
Paraethomys jaegeri	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*
-	-	*Occitanomys brailloni*
Stephanomys medius	*Stephanomys cordii*	*Stephanomys cordii*
-	*Apocricetus cf. angustidens*	*Apocricetus* cf. *angustidens*
Ruscinomys aff. *europaeus*	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*
-	-	*Ruscinomys* sp.
Blancomys neglectus	-	*Blancomys* sp.
Trilophomys castroi	*Trilophomys* cf. *castroi*	*Trilophomys* cf. *castroi*
-	*Eliomys intermedius*	*Eliomys intermedius*
-	-	*Glis sp.*
-	-	*Pliopetaurista sp.*

Table IV.5. Faunal list of Alcoy-2 (Esteban Aenlle and Lacomba 1988) compared with the faunal lists of the localities studied in this chapter, AL2-C and AL2-D.

Genus *Stephanomys* Schaub, 1938

Stephanomys cordii Ruiz Bustos, 1986 (Fig. IV.2, 1-7)

Localities: AL2-C, AL2-D.

Material: **26 m1** (AL2C-2, AL2C-7, AL2D-3 to AL2D-14, AL2D-18 to AL2D-20, AL2D-27, AL2D-31 to AL2D-33, AL2D-35, AL2D-37, AL2D-39, AL2D-139, AL2D’08-1) **23 m2** (AL2C-10, AL2C-15 to AL2C-18, AL2D-43, AL2D-44, AL2D-46, AL2D-49, AL2D-52 to AL2D-55, AL2D-57, AL2D-59, AL2D-60, AL2D-63, AL2D-186 to AL2D-189, AL2D-231, AL2D-353), **20 m3** (AL2C-52, AL2C-59, AL2C-60, AL2D-73, AL2D-77 to AL2D-79, AL2D-81, AL2D-82, AL2D-84 to AL2D-86, AL2D-89, AL2D-94, AL2D-95, AL2D-224, AL2D-236, AL2D-357, AL2D-358, AL2D’08-7), **29 M1** (AL2C-23 to AL2C-27, AL2C-56, AL2C-57, AL2D-98, AL2D-100, AL2D-102, AL2D-105 to AL2D-109, AL2D-111, AL2D -112, AL2D-115 to AL2D-121, AL2D-125, AL2D-127 to AL2D-129, AL2D-234), **27 M2** (AL2C-29, AL2C-31 to AL2C-35, AL2C-39, AL2D-143 to AL2D-145, AL2D-147, AL2D-149, AL2D-151 to AL2D-153, AL2D-155, AL2D-159, AL2D-161, AL2D-163, AL2D-164, AL2D-166, AL2D-167, AL2D-171, AL2D, 174, AL2D-175, AL2D-180, AL2D’08-10), **10 M3** (AL2D-74, AL2D-193, AL2D-196, AL2D-198, AL2D-201, AL2D-202, AL2D-204, AL2D-205, AL2D-207, AL2D-211, AL2D-221).

Measurements: see Table IV.6.

Description:

m1: The slightly asymmetrical anteroconid is in contact with the protoconid-metaconid pair. The labial cingulum is low and narrow. A well-developed longitudinal crest connects the posterior cusps to the intersection of the protoconid-metaconid pair. The c1 is well developed, and two of the teeth present an accessory cusp between the labial lobe of the anteroconid and the protoconid, big and round in one case and laminar and slightly smaller in the other one. The posterior heel is smaller than the c1, lingually displaced, and its shape may vary from round to almost laminar. These teeth have two roots.

m2: The anterolabial cusp is high, medium or big sized, and in contact with the protoconid and the reduced labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. A small round or oval c1 is present, and a reduced accessory cusp in contact with the protoconid may also exist. The posterior heel is large, rounded or oval. There are two roots.

m3: Reduced anterolabial cusp, connected to the protoconid. The longitudinal crest seems incomplete in some specimens, being made instead by two contacting spurs. In the junction point, the enamel of each of the spurs may be differentiated from the other one. There are two roots.

M1: The t1 is displaced backwards. There are usually t1 bis and t2 bis, with different stages of development, although in some specimens are reduced to just a fold of enamel. The posterior crests of t1 and t3 are well developed. The t7 is absent. The t12 is highly reduced, just as a thickening of the enamel in some specimens. There are three roots.

M2: There may be a small accessory cusp attached to the posterior side of t1. The posterior crests of t1 and t3 are usually well developed, although two specimens have the t1 and the t3 isolated respectively (Fig. IV.2, 6). The t12 is absent or reduced to a thickening of the t8-t9 crest.

M3: The t1 is connected to the t5. T4, t5 and t6 are connected. The t3 is absent except in one specimen.

Discussion:

The great height of the crown, high longitudinal crests in the lower molars (Fig. IV.2, 1-3) and crests or spurs on t1 and t3 of the upper molars (Fig. IV.2, 4-5) suggest that these specimens belong to the genus *Stephanomys*. These molars are smaller than other *Stephanomys* from the Pliocene such as *S. donnezani* (Déperet, 1890), *S. balcellsi* Gmelig Meyling and Michaux, 1973, *S. vandeweerdi* Adrover, 1986, and *S. thaleri* López-Martínez, Michaux and Hutterer, 1998. Although similar in size, the *Stephanomys* from AL2-C and AL2-D differ from *S. minor* Gmelig-Meyling and Michaux, 1983 in the tubercular shape of the posterior heel.

The *Stephanomys* from AL2-C and AL2-D are larger and with a more pronounced stephanodonty than *S. ramblensis* van de Weerd, 1976, and *S. dubari* Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991. The measurements of these molars match those of *S. margaritae* Adrover, 1986, which are quite close in size to *S. medius* Cordy, 1976, from Alcoy. The specimens from AL2-C and AL2-D show the features used by Cordy (1976) to describe the species *S. medius*: symmetric disposition of t1 and t3 respect the t2 in the M1 (Fig. IV.2, 4), reduced labial cingulum in m1 and m2 (Fig. IV.2, 1-2), tubercular posterior heel (Fig. IV.2, 1-2) and m3 with a poorly-developed anterolabial cusp and longitudinal crest united to the protoconid (Fig. IV.2, 3).

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L	17	2.12	2.24	2.38
		W	21	1.29	1.44	1.55
	AL2-C	L	2	2.22	2.30	2.38
		W	1	-	1.51	-
m2	AL2-D	L	16	1.55	1.65	1.83
		W	16	1.43	1.59	1.72
	AL2-C	L	4	1.60	1.67	1.73
		W	5	1.41	1.48	1.64
m3	AL2-D	L	16	1.26	1.42	1.55
		W	17	1.22	1.28	1.38
	AL2-C	L	3	1.26	1.31	1.36
		W	3	1.24	1.29	1.33
M1	AL2-D	L	15	2.40	2.66	3.01
		W	20	1.71	1.88	2.02
	AL2-C	L	2	2.41	2.42	2.43
		W	5	1.72	1.81	1.93
M2	AL2-D	L	15	1.63	1.85	2.04
		W	14	1.65	1.74	1.84
	AL2-C	L	6	1.52	1.67	1.77
		W	7	1.48	1.64	1.91
M3	AL2-D	L	10	1.21	1.31	1.50
		W	10	1.07	1.19	1.26

Table IV.6. Measurements in millimetres of the teeth of *Stephanomys cordii* from the localities AL2-C and AL2-D. n= number of measurable specimens.

According to López Martínez *et al*. (1998), *S. medius* is a nomen nudum, being the correct name of the species *S. donnezani cordii* Ruiz Bustos, 1986. This is reviewed by García-Alix *et al*. (2008a), elevating *S. donnezani cordii* to species level and renaming it as *Stephanomys cordii*. The size range of our specimens encloses most of the variability of *S. margaritae* and *S. cordii*, except for the maxima for *S. margaritae* and some of the minima for *S. cordii*. In this latter species, the smallest specimens are those from La Gloria 4 (Adrover *et al*. 1993), and Peralejos E (Adrover *et al*. 1988), considered to be *S. dubari* by García-Alix *et al*. (2008a). Minwer-Barakat (2005) proposed an evolutionary frame for the genus *Stephanomys* in which there is a continued increase in size, crown height and stephanodonty during the Pliocene in the anagenetic line *S. ramblensis*- *S. dubari* - *S. cordii* - *S. margaritae.* The populations from AL2-C and AL2-D seem to be close to *S. margaritae,* with some specimens reaching its size or even surpassing it, like one exceptionally large M1, while the mean values are more consistent with *S. cordii*. Those specimens have been directly compared with the collection from Alcoy-2, kept at the Universidad Complutense de Madrid

(UCM), and ascribed by Esteban Aenlle and Lacomba (1988) to *S. medius* (Table IV.5). Both their size and morphology are very similar to our specimens. We ascribe our material to *S. cordii* because of its similarity with the population from the type locality, Alcoy (Cordy 1976).

Genus *Castillomys* Michaux, 1969 (Fig. IV.2, 8-9)

Castillomys gracilis van de Weerd, 1976

Locality: AL2-D.

Material: **2 M1** (AL2D-138, AL2D-233), **1 M2** (AL2D-185).

Description:

M1: (1.58 x 1.12): The t1 is situated much posterior than the t2. The t1 has a hint of longitudinal spur directed towards the t4-t5 intersection. The t3 has a distal spur directed towards the t5-t6 intersection. The t3 is far apart from t6. The t9 is elongated. A small t12 is present. In lateral view, t6 is quite straight, not directed towards t9. This character has been used to distinguish the genus *Castillomys* from the small forms of *Occitanomys* (Martín-Suárez and Mein 1991).

M2: (1.05 x 0.95): Tooth in an advanced stage of wear. The lingual longitudinal crest connects t1 and t5. Isolated t3. The t6 and t9 are equivalent in size. The t12 is small but well formed.

Discussion:

The small size of these specimens, straight t6 in lateral view, absence of a t7 in the upper molars and presence of posterior spurs on the t1 and t3 of the M1 are typical of the genus *Castillomys*. In addition, the lack of longitudinal crests in the upper molars and isolated t3 in M2 (Fig. IV.2, 9) agree with *Castillomys gracilis* van de Weerd, 1976. The size of the specimens recovered from AL2-C and AL2-D lies within the range of variation of *C. gracilis* from Caravaca, Orrios 1 (Weerd 1976), Mont-Hélène (Aguilar *et al*. 1986), Aldehuela and Villalba Alta (Adrover 1986), Moreda 1A and Moreda 1B (Castillo 1990), CLC-3, CLC-3B and PUR-13 (García-Alix *et al*. 2008a), although the width of the single M2 recovered from AL2-D, in a very poor state of preservation, is only comparable to the lower values of the specimens from Caravaca (Weerd 1976). Their size is also consistent with *C. gracilis* from the collection of Alcoy-2 at the Universidad Complutense de Madrid (UCM).

Martín-Suárez and Mein (1991) proposed an evolutionary scenario in which all the Iberian populations from the Pliocene and Pleistocene could be placed in an anagenetic lineage consisting of three consecutive taxa: *C. gracilis*- *C. crusafonti* - *C. rivas*. These authors recognized an increase in size through time, such that the biometrics of the molars can be used as systematic criteria. In the line *C. gracilis* - *C. crusafonti*, only the development of t1 bis and the lingual longitudinal crest (t1-t5) show a positive correlation, whereas the states of the remaining characters are independent from other characters and size. This results in a differential diagnosis for the various species of *Castillomys* based on frequency percentages of the different characters along with size (Martín-Suárez and Mein 1991). The oldest representative of the genus, *C. margaritae* Antunes and Mein 1989, differs from our material by the absence of t12.

Genus *Occitanomys* Michaux, 1969

Occitanomys brailloni Michaux, 1969 (Fig. IV.2, 10-12)

Locality: AL2-D.

Material: **1 m1** (AL2D-16), **3 M1** (AL2D-99, AL2D-113, AL2D-114), **1 M2** (AL2D-173).

Description:

m1: (2.13 x 1.58): Very worn specimen. Slightly asymmetrical anteroconid. The anteroconid and the protoconid-metaconid are connected by a narrow crest. The labial cingulum is very wide and well developed, but no accessory cusps are observed. The c1 is large and elongated anteroposteriorly, which gives this cusp a comma shape. There is no longitudinal spur. Oval posterior heel.

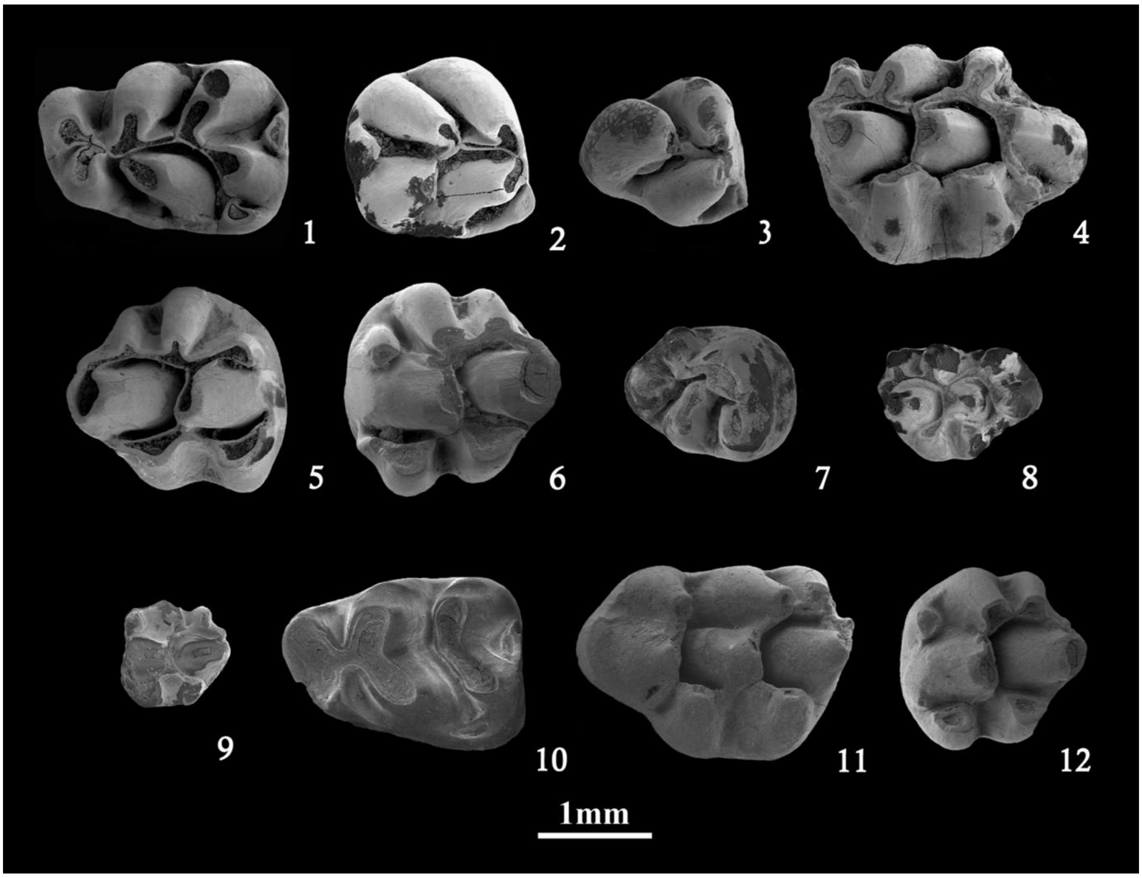


Figure IV.2. Rodent faunas from AL2-D (Alcoy Basin, Spain). *Stephanomys cordii* from AL2-D. **1**, left m1, AL2D-7; **2**, right m2, AL2D-55; **3**, right m3, AL2D-73; **4**, right M1, AL2D-98; **5**, right M2, AL2D-149; **6**, left M2, AL2D-143; **7**, right M3, AL2D-193. *Castillomys gracilis* from AL2-D. **8**, right M1, AL2D-138; **9**, left M2, AL2D-185. *Occitanomys brailloni* from AL2-D. **10**, left m1, AL2D-16; **11**, left M1, AL2D-113; **12**, left M2, AL2D-173. Scale=1mm.

M1: (2.56 x 1.80; 2.54 x 1.81; 2.57 x 1.77): The connection between t1 and t2 is very basal. There is a well developed t1 bis in all specimens, and a smaller t2 bis is present in one of the teeth. The t1 has a distal spur directed to the t4-t5 intersection, but the t3 has no distal spur. The t12 is very small. In labial lateral view, the t6 leans towards the t9, and the apex of the cusp is closer to t9 than to t3.

M2: (1.58 x 1.57): The t1 is much bigger than the t3, and connected basally to t5, while t3 is isolated. The shape of t1 suggests the presence of a small t1 bis. The t9 is well developed. The t12 is very small, barely a fold of the enamel.

Discussion:

The material from AL2-D belongs to a big-sized form of *Occitanomys*. The outline and general morphology of the specimens is consistent with *O. brailloni* Michaux, 1969, having an m1 without tma and a labial cingulum with accessory cusps less developed than *Apodemus*, a t1 bis always present in the M1, reduced t12, reduced t3 and t1 connected to t5 in M2 (Michaux 1969) (Fig. IV.2, 10-12). According to Minwer-Barakat (2005), this taxon is more frequent during the late Ruscinian, although it can be found in some early Ruscinian localities such as Aldehuela (Adrover 1986), Ptolemais 1 and Kardia (Weerd 1979).

The single m1 recovered is consistent with the greatest lengths of *O. brailloni* from the locality of Layna (Michaux 1969), and close to the maxima from Nîmes (Michaux 1969), Arquillo 3 (Adrover 1986), and TCH-1B (Minwer-Barakat *et al*. 2005). The width of this molar, however, clearly surpasses the maxima of the populations from the cited sites. The M1 are bigger than *O. brailloni* from Séte, Nîmes and Layna (Michaux 1969), Arquillo 3 and Aldehuela (Adrover 1986) and TCH-1B (Minwer-Barakat *et al*. 2005). The size of the single M2 lies within the variation observed in the material from Villalba Alta (Adrover 1986). The site of AL2-C has not yielded any remains of *O. brailloni*. This may be due to the scarcity of the material of this taxon, usually rare in the localities where it is found.

In the faunal list published by Esteban Aenlle and Lacomba (1988) for Alcoy-2, these authors did not mention any form of *Occitanomys* (Table IV.5). However, a revision of the material from this locality has shown a few specimens morphologically very similar to the molars described in this chapter, and which in our opinion correspond to a big sized *Occitanomys*.

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Eliomys intermedius Friant, 1953 (Fig. IV.3, 2-5)

Localities: AL2-C, AL2-D.

Material: **2 m1,2** (AL2C-97, AL2D-290), **2 m3** (AL2C-47, AL2D-356), **3 M1,2** (AL2D-291 to AL2D-293).

Description:

m1,2: (1.56 x 1.71; - x 1.61): The anterolophid is continuous and connected to the protoconid. There is no anterotropid. The connection between metalophid and metaconid is very low. The centrolophid is long and not connected to the metalophid. Metaconid and entoconid separated by a deep valley. The mesolophid is connected to the entoconid. The mesoconid is situated on the labial border. Well-developed posterotropid. The hypoconid is very large.

m3: (1.39 x 1.48): Continuous anterolophid, in contact with the metaconid. The labial apex of the metalophid does not reach the metaconid. The accessory crests are absent. The centrolophid is shorter than in m1,2. There is a wide valley between metaconid and entoconid. Continuous posterolophid.

M1,2: (1.38 x 1.74; 1.58 x 1.95): The anteroloph is separated from both the protoloph and the paracone by a deep valley. There are neither anterotrope nor posterotrope. Paracone and metacone are high and separated. The protoloph and metaloph are continuous. In the only complete specimen, there are two centrolophs. Well developed precentroloph, much longer than the postcentroloph. The endoloph and posteroloph are connected and continuous.

Discussion:

The size of our specimens, rounded outline, height of the crests and development of the centrolophs make us assign those teeth to *E. intermedius*. The measurements of the molars from AL2-C and AL2-D fall within the range of variation of the population from the type locality, Sète (Adrover 1986), and are very similar to those of *E. intermedius* from Orrios 3 and *Eliomys* cf. *intermedius* from Arquillo 3, Villalba Alta (Adrover 1986) and Mont Hélène (Aguilar *et al*. 1986).

Their size is bigger than *E. truci,* Mein and Michaux, 1970, and slightly bigger than *E.* aff. *intermedius* from La Gloria 4, La Gloria 5 (Adrover *et al*. 1993) and *Eliomys yevesi* from PUR-4, CLC-3B, AF-1’06, AF-1’07 and ABS-3A (see chapter IX), falling within the ranges of variation of *E. intermedius* from TCH-3, TCH-1B and PUR-13

(García Alix *et al*. 2008a). Both morphology and size in AL2-C and AL2-D are very similar to the specimens from Alcoy-2 deposited at the Universidad Complutense de Madrid (UCM), which lack in the preliminary faunal list published by Esteban Aenlle and Lacomba (1988) (Table IV.5).

Subfamily Glirinae Thomas, 1897

Genus *Glis* Brisson, 1762

Glis sp. (Fig. IV.3, 1)

Locality: AL2-D.

Material: **1 m3** (AL2D-359).

Description:

m3: (1.53 x 1.41): Tooth with four main ridges (anterolophid, metalophid, mesolophid and posterolophid) and three well-developed extra ridges (anterotropid, extra ridge between metalophid and mesolophid and posterotropid). Every ridge, except for the posterolophid, is clearly transverse. Very long anterotropid, connected to the metaconid. The extra ridge between metalophid and mesolophid is very long, of the same length as the anterotropid and not connected to the metalophid or the mesolophid. Mesolophid and posterolophid are not connected to the lingual border. Long posterotropid, connected to the lingual end of the posterolophid. The posterolophid is partially interrupted at the posterolingual corner of the tooth.

Discussion:

The presence of several transverse main and extra ridges allows assigning this material to a form of the genus *Glis*. At the labial border, the main ridges (anterolophid, metalophid, mesolophid and posterolophid) are not connected, and define synclines that are opened on the labial side.

In the Pliocene two species of the genus *Glis* have been described: *Glis minor* Kowalski, 1956 and *Glis sackdillingensis* Heller, 1930 (Kowalski 1956, Aguilar *et al*.

1986), whereas in the Pleistocene several species of the genus have been cited: *G. sackdillingensis*, *G. mihevci* Aguilar and Michaux, 2011, *G. perkoi* Aguilar and Michaux, 2011 and the extant *G. glis* (Linnaeus, 1766) (Kowalski 1963, Aguilar and Michaux 2011). A gradual size increase of the molars is observed in *Glis* between the Pliocene and today. Morphology has evolved in this time span from primitive forms with transversal crests, synclines open on the lingual side in the upper molars and labial side in lower ones and accessory ridges reduced in p4 and m3 (Kowalski 1956, Aguilar and Michaux 2011).

The m3 from AL2-D shows measurements and some of the morphological features that characterize the primitive assemblages of the genus *Glis*. The size is intermediate between *G. minor* and *G. mihevci*-*G. perkoi*-*G. glis*, and maybe more similar to *G. sackdillingensis*. The presence of transversal crests and open synclines on the labial side of the m3 are typical of the primitive forms. Nevertheless, the well-developed anterotropid and posterotropid are different from the Pliocene assemblages of the genus. These extra ridges are very long, exceeding extensively the middle of the tooth, and are connected to the metaconid and the lingual end of the posterolophid, respectively. The size and morphology of these ridges is similar to the Pleistocene species of the genus (*G. mihevci*-*G. perkoi*-*G. glis*) and different from the Pliocene species (*G. minor*-*G. sackdillingensis*).

Castillo (1990) cites *G. sackdillingensis* in Alcoy-2, although in the original list published by Esteban Aenlle and Lacomba (1988) the genus *Glis* is not mentioned. Based on these features and until more material becomes available, we consider the specimen from AL2-D as belonging to *Glis* sp.

Family Cricetidae Fischer, 1817

Subfamily Cricetinae Fischer, 1817

Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998

Apocricetus cf. *angustidens* (Depéret, 1890) (Fig. IV.3, 6-8)

Localities: AL2-C, AL2-D.

Material: **1 m1** (AL2D-260), **1 m2** (AL2D-262), **2 m3** (AL2D-264, AL2D-266), **1 M1** (AL2D-259), **3 M2** (AL2C-93, AL2D-65, AL2D-263).

Description:

m1: (2.72 x 1.58): Smooth, crest-like anteroconid. There are two anterolophulids, well developed and symmetrical, reaching the top of the anterolophid crest, encircling an anterior funnel. The metalophulid is strongly directed forwards. Absent mesolophid. The posterolophid is high and connected to the entoconid, closing the posterosinusid.

m2: (2.26 x 1.79): The lingual anterolophid and the mesolophid are absent. The labial anterolophid is low, reaching the protoconid.

m3: (2.21 x - ; - x 1.59): The lingual anterolophid is absent. Mesolophid very short and low in one specimen, and absent in the other one.

M1: (2.82 x 1.80): There is a cingulum ridge in front of an anterocone formed by two cusps in labial and lingual position. The anterolophule is double and symmetrical. Absent anterior protolophule and posterior metalophule. Absent mesoloph. The anterior metalophule is present.

M2: (2.20 x 1.78; 2.05 x - ; - x 1.81): The lingual anteroloph is short and low. Absent anterior protolophule. Posterior protolophule and anterior metalophule present. The mesoloph is absent.

Discussion:

The cricetid teeth from AL2-D are characterized by the absence of mesolophid in the m1 and of the anterior protolophule in M1 and M2, together with the presence of a crest-like anteroconid and a double anterolophulid in m1, resembling *Apocricetus*. In general, the size of this assemblage overlaps with the minimum values of *A. angustidens* and the maximum of *A. barrierei* (Freudenthal *et al*. 1998). Only the values of the single m1 from AL2-D clearly exceed those of *A. barrierei* (Freudenthal *et al*. 1998).

Although the presence of a cingulum ridge in front of the anterocone and the absence of an anterior protolophule in M1-M2 are morphological features that appear in assemblages of *A. angustidens* and *A. barrierei*, they are more common in the former ones (Freudenthal *et al*. 1998). Based on these features and until more material becomes available, we consider the assemblage from AL2-D as belonging to a form related with *A. angustidens*. An M2 (AL2C-93) from AL2-C shows a poor development of the anterior protolophule and absence of the posterior metalophule, resembling the general morphology of the younger species of the genus *Apocricetus* (Freudenthal *et al*. 1998, chapter XI.4.2.3. and Table XI.5 of this thesis). Nevertheless, a single tooth is not enough to know the variability of this assemblage and, until more material becomes available, we consider it as belonging to a form related with *A. angustidens* too.

Cricetidae Incertae Sedis

Genus *Blancomys* van de Weerd, Adrover, Mein and Soria, 1977

Blancomys sp. (Fig. IV.3, 18)

Locality: AL2-D.

Material: **1 m1** (AL2D-318).

Description:

m1: Tooth broken posteriorly and in an advanced stage of wear. The great lingual fold is very deep, reaching the base of the crown. The fold between anteroconid and metaconid is open and smooth, in contrast with the labial anterior fold, which is very sharp. Nevertheless, both folds reach the base of the crown. The metaconid is well developed, much more than the anteroconid and anterolophid. The anterior labial fold is very smooth, forming a straight line of enamel that connects anterolophid and protoconid. The labial fold is big, reaching the base of the crown and creating an acute vertex of enamel.

Discussion:

Esteban Aenlle and Lacomba (1988) cited the presence of *Blancomys neglectus* van de Weerd, Adrover and Soria, 1977, in Alcoy-2 (Table IV.5). The morphology, size and hypsodonty of the only tooth recovered in AL2-D are consistent with *Blancomys*, but the scarcity of the material impedes a specific adscription.

Subfamily Cricetodontinae Stehlin and Schaub, 1951

Genus *Ruscinomys* Depéret, 1890

Ruscinomys cf. *lasallei* Adrover, 1969 (Fig. IV.3, 14-16)

Localities: AL2-C, AL2-D.

Material: **1 m1** (AL2C-70), **2 m3** (AL2C-69, AL2D-319), **2 M2** (AL2D-308, AL2D-317), **4 M3** (AL2C-71, AL2C-72, AL2D-306, AL2D-307).

Measurements: see Table IV.7.

Description:

m1: The tooth is broken posteriorly, and in an advanced stage of wear. No enamel islet can be observed. Rounded anteroconid. The anterosinusid is open and wide, just a slightly fold of the enamel. The mesosenid is narrow and deep, while the labial sinusid is much wider and smoother. Both folds reach the base of the crown.

m3: The anteroconid is a fold of the enamel. There are two enamel islets. The anterosinusid is smooth and open, almost reaching the base of the crown. The metaconid is round, much smaller than the entoconid. Both cusps are separated by the mesosinusid, which is very deep and steep. The posterosinusid is much narrower, but equally deep. The posterolophid and hypoconid cannot be individualized as separated cusps because of the wear of the molar. The sinusid is very narrow and deep, reaching the base of the crown.

M2: One of the specimens is broken anteriorly, while the other one is complete. In this latter individual two shallow enamel islets can be observed. The mesosinus is deep and narrow, while the sinus is much wider. Both folds reach the base of the enamel.

M3: Bilobed teeth, with the anterior lobe bigger than the posterior one. The lobes are separated by two folds reaching the base of the crown. There are two roots.

Discussion:

The rounded anteroconid (morphotype 3 of García-Alix *et al*. 2008b), flat labial side of the m1, M2 more elongated than *Ruscinomys schaubi* Villalta and Crusafont, 1956 and narrower than *R. europaeus* Depéret, 1890, and M3 with two lobes but more reduced than *R. Schaubi* agree with *Ruscinomys lasallei* Adrover, 1969. Also, these specimens are higher crowned than *R. schaubi*, but less hypsodont than *R. europaeus*. The two unworn M3 (Table IV.7) are higher than *R. schaubi* from Concud 3, Los Mansuetos and Los Mansuetos 2, and similar to *R.* cf. *lasallei* from Caravaca, while shorter than *R. Europaeus* from Layna (data from Weerd 1976).

The size of the *Ruscinomys* present in AL2-C and AL2-D is consistent with *Ruscinomys lasallei* Adrover, 1969 from its type locality, Alcoy, falling within the range of variation of this taxon from the localities of La Gloria 4 (Adrover *et al.* 1993), PUR-13 and PUR-4 (García-Alix *et al*. 2008b), being also similar to *R*. cf. *lasallei* from the localities of Celadas 2, Arquillo1, Arquillo 4, La Gloria 5, Valdecebro 3, Valdecebro 6, and Villastar (Adrover *et al*. 1993). These molars are bigger than *R. gilvosi* Adrover *et al*. 1988, from Peralejos E, and smaller than *R. bravoi* Adrover and Mein, 1996, from Aljezar B, especially in width.

Esteban Aenlle and Lacomba (1988) assigned the material from Alcoy-2 to *Ruscinomys* aff. *europaeus* (Table IV.5) based on its size and morphology. However, the material from AL2-C and AL2-D seems somewhat smaller and more similar to *R. lasallei* than to *R. europaeus*, even falling within the upper range of variation of *R. schaubi* Villalta and Crusafont, 1956, from Aljezar B (Adrover 1986), Los Mansuetos, Los Mansuetos 2, Concud 2 and Concud 3 (Weerd 1976), and *R*. aff. *schaubi* from DHS-4A, 4B and 16, and PUR-23, 24A, 25 and 25A (García-Alix *et al*. 2008b). For these reasons, we ascribe our material to *R*. cf. *lasallei.*

Element	Locality	Parameter	n	min.	mean	max.
m3	AL2-C	L	1	-	2.63	-
		W	1	-	1.81	-
M2	AL2-D	L	1	-	3.01	-
		W	2	2.15	2.18	2.22
M3	AL2-D	L	2	1.97	2.00	2.02
		W	2	1.74	1.76	1.78
		H	1	-	2.49	-
	AL2-C	L	2	1.90	2.01	2.03
		W	2	1.52	1.56	159
		H	1	-	2.44	-

Table IV.7. Measurements in millimetres of the teeth of *Ruscinomys* cf. *lasallei* from the localities AL2-C and AL2-D. n= number of measurable specimens.

Ruscinomys sp. (Fig. IV.3, 17)

Locality: AL2-D.

Material: **1 M3** (AL2D-281).

Description:

M3: (1.40 x 1.39; H: 1.60): Tooth with two lobes delimited by the sinus and mesosinus. The posterior lobe is smaller than the anterior one.

Discussion:

The specimen AL2D-281 is smaller and has a lower crown than *Ruscinomys lasallei* and *R. schaubi*. In addition, the posterior lobe of the M3 is less reduced than *Ruscinomys*, resembling *Hispanomys*. The smallest representative of the genus *Ruscinomys* is *R. gilvosi*, described by Adrover *et al*. (1988) in the Ruscinian locality of Peralejos E. Unfortunately this site has not yielded any M3. The presence of two *Ruscinomys* species in the same locality is rare, although Peralejos E has yielded remains of both *R. gilvosi* and *R.* cf. *europaeus.*

Family Trilophomyidae Kretzoi, 1969

Genus *Trilophomys* Depéret, 1892

Trilophomys cf. *castroi* Adrover, 1983 (Fig. IV.3, 9-13)

Localities: AL2-C, AL2-D.

Material: **7 m1** (AL2C-79 to AL2C-82, AL2D-297, AL2D-298, AL2D-300), **4 m2** (AL2D-301 to AL2D-304), **3 M1** (AL2D-296, AL2D’08-14, AL2’08-15), **2 M2** (AL2C-83, AL2C-85), **2 M3** (AL2D-305, AL2D-316).

Measurements: see Table IV.8.

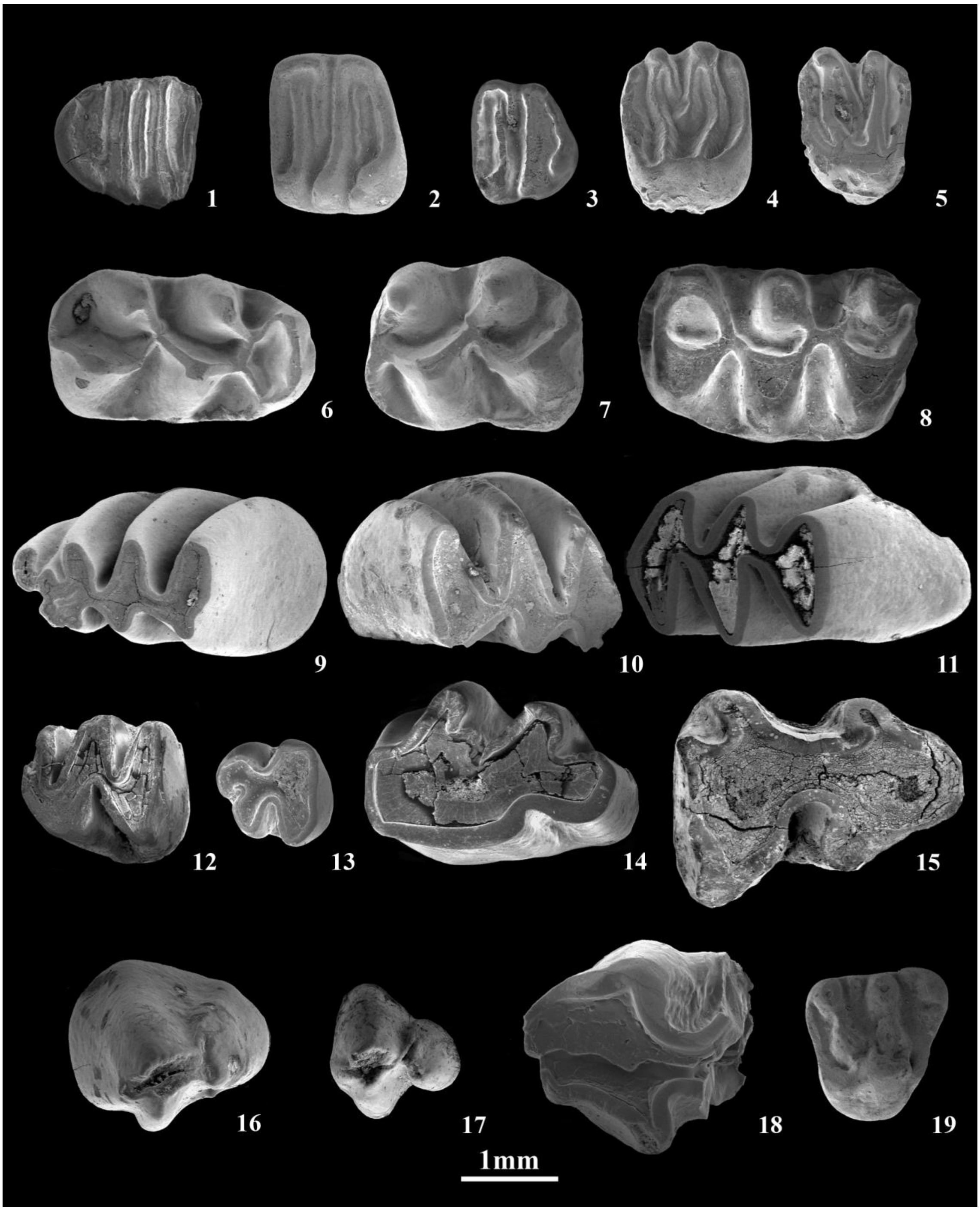


Figure IV.3. Rodent faunas from AL2-C and AL2-D (Alcoy Basin, Spain). *Glis* sp. from AL2-D. **1**, left m3, AL2D-359. *Eliomys intermedius* from AL2-D. **2**, left m1-m2, AL2D-290; **3**, left m3, AL2D-356; **4**, right M1-M2, AL2D-291; **5**, left M1-M2, AL2D-293. *Apocricetus* cf. *angustidens* from AL2-D. **6**, right m1, AL2D-260; **7**, left m2, AL2D-262; **8**, left M1, AL2D-259. *Trilophomys* cf. *castroi* from AL2-C and AL2-D. **9**, left m1, AL2D- 300; **10**, right m2, AL2D-301; **11**, left M1, AL2D'08-14; **12**, right M2, AL2C-83; **13**, right M3, AL2D-316; *Ruscinomys* cf. *lasallei* from AL2-C and AL2-D. **14**, left m3, AL2C-69; **15**, left M2, AL2D-317; **16**, left M3, AL2D-306; **17**, left M3, AL2D-281; *Blancomys* sp. from AL2-D. **18**, left m1, AL2D-318. *Pliopetaurista* sp. from AL2D. **19**, right D4, AL2D-295. Scale=1mm.

Description:

m1: The lingual side of the crown has three reentrant folds, while the labial one presents two. Five specimens have a well-developed anterior fold. This fold reaches near the base of the crown in one specimen, while in another three reaches two thirds of the height of the crown and in another one just the upper third. The lingual folds are deeper than the labial ones. The outward folds have acute apices. The boundary line between enamel and dentine at the base of the crown is quite smooth, rising slightly at the height of the outward folds.

m2: Both the labial and the lingual side have two reentrant folds. The folds of the labial side are much shorter than the lingual ones. The outward folds have acute apices. The labial folds are slightly displaced forwards with respect to the lingual folds. The boundary line between the enamel and dentine at the base of the crown is almost straight and parallel to the occlusal surface of the teeth, rising slightly at the height of the outward folds. The teeth have two roots.

M1: Both the labial and the lingual side have two reentrant folds. The folds of the labial side are deeper than the lingual ones. The enamel boundary is slightly wavy.

M2: Two reentrant folds in the labial side and one in the lingual side. The folds of the labial side are deeper than the lingual ones. Very smooth enamel boundary line. There are two roots.

M3: Two lobes, the anterior one larger than the posterior one. The reentrant lingual fold is deeper than the labial one. The posterior lobe is divided by an inlet of enamel in one of the specimens, displaced to the lingual side of the tooth, while in the other one this character is absent due to the extreme wear of the tooth. The boundary line between the enamel and dentine of the base of the crown is almost straight, rising slightly at the height of the outward folds. There are two roots.

Discussion:

Morphologically, the populations of *Trilophomys* from AL2-C and AL2-D are very similar to *T. castroi* Adrover, 1986. The *Trilophomys* from Alcoy-2 housed at the Universidad Complutense de Madrid (UCM, Spain) were determined as *Trilophomys* cf.

castroi by Esteban Aenlle and Lacomba (1988) (Table IV.5), and seem undistinguishable from our material.

The most significant character is the smooth enamel-dentine boundary. This excludes these molars from belonging to *Trilophomys pyrenaicus* Déperet, 1890. The size of our specimens is somewhat smaller than *T. castroi* from Villalba Alta, its type locality, and Arquillo III, falling within the range of variation of *T.* cf. *castroi* from Aldehuela and Orrios 0 (Adrover 1986) and Villalba Alta Río (Adrover *et al.* 1988).

Element	Locality	Parameter	n	min.	mean	max.
m1	AL2-D	L1	3	1.82	1.87	1.90
		L2	3	2.42	2.58	2.72
		W	3	1.27	1.38	1.54
	AL2-C	L1	3	1.96	2.12	2.23
		L2	3	2.42	2.58	2.75
		W	3	1.31	1.45	1.55
m2	AL2-D	L1	2	1.74	1.83	1.93
		L2	3	2.28	2.45	2.74
		W	4	1.22	1.28	1.42
M1	AL2-D	L1	3	1.99	2.07	2.13
		L2	3	3.11	3.35	3.59
		W	3	1.23	1.28	1.42
M2	AL2-C	L1	1	-	1.50	-
		L2	1	-	1.67	-
		W	2	1.37	1.41	1.46
M3	AL2-D	L1	2	1.08	1.15	1.23
		L2	2	1.15	1.26	1.37
		W	2	1.19	1.20	1.210

Table IV.8. Measurements in millimetres of the teeth of *Trilophomys* cf. *castroi* from the localities AL2-C and AL2-D. n= number of measurable specimens.

Family Sciuridae Fisher, 1817

Subfamily Pteromyinae Brandt, 1855

Genus *Pliopetaurista* Kretzoi, 1962

Pliopetaurista sp. (Fig. IV.3, 19)

Locality: AL2-D.

Material: **1 D4** (AL2D-295).

Description:

D4: (1.46 x 1.46): Triangular outline. The protocone is the highest cusp of the tooth, with the posterior branch higher than the anterior one. The parastyl is strong and of the same height and shape as paracone and metacone. Between the labial border of the parastyl and the paracone a small cusp, attached to the parastyl, nearly closes the valley. Protoloph and metaloph present protoconule and metaconule respectively. Both ridges are connected to the protocone. The protocone bears a small mesoloph. In the labial border, a mesostyl is present between paracone and metacone. The metaconule and the posteroloph are connected by a low lophule.

Discussion:

The genus *Pliopetaurista* was first described from the French locality of Perpignan (Depéret 1897) for Sciuridae of large size, in which the convergence of the lophs and the well developed metaconule in the upper teeth are typical features (Mein 1970). Since the description of *Pliopetaurista* by Depéret (1897), new data have contributed to a better knowledge of the systematics, biostratigraphy and palaeogeography of this genus in Europe (see Dahlmann 2001). Nevertheless, many questions remain open, and the record of this genus in the Iberian basins is one of these issues. So far, the Iberian record of *Pliopetaurista* is restricted to *P. pliocaenica* from the localities of the Granada Basin, PUR-25, PUR-24A and PUR-4 (García-Alix *et al*. 2007) and the localities of the Teruel Basin, La Gloria-2 and Arquillo-3 (Adrover *et al*. 1993). *Pliopetaurista* sp. has also been cited in the Upper Turolian of Venta del Moro, in the Cabriel Basin (Montoya *et al*. 2006a).

The locality AL2-D has yielded only one D4, of a small-sized species. The size of this specimen and the presence of a small mesoloph on the protocone and of a mesostyl in the labial border allow distinguishing it from the large-sized species of the genus. The specimen from AL2-D differs from *P. kollmanni* in size, greater in AL2-D, and by the presence in the material from Alcoy of a more pronounced protoconule and metaconule. With respect to *P. meini*, it differs in the presence of a short mesoloph. Despite the presence in AL2-D of a short mesoloph, similar to that of *P. meini*, the size and general morphology of this tooth resemble those of *P. raui* from Wölfersheim (Dahlmann 2001). Based on these features and until more material becomes available, we consider this specimen as belonging to *Pliopetaurista* sp.

IV.3. Discussion

IV.3.1. Faunal lists

The faunal lists of AL2-C and AL2-D are given in Table IV.5, and compared with Alcoy-2. The differences between AL2-C and AL2-D, with the presence in AL2-D of *Castillomys gracilis*, *Occitanomys brailloni*, *Pliopetaurista* sp., *Glis* sp. and *Blancomys* sp., all of them very scarce, are attributed to the sampling effort. Both faunal assemblages are very similar to the one published by Esteban Aenlle and Lacomba for Alcoy-2 (1988).

IV.3.2. Biostratigraphy

The presence of the genus *Trilophomys* (*T.* cf. *castroi*), accompanied by *Blancomys*, two species of *Paraethomys*, a small-sized form identified as *P. meini* and a bigger form classified as *P. abaigari*, and the presence of *Eliomys intermedius*, are typical features of the Ruscinian (Mein *et al*. 1990, Minwer-Barakat 2005, Sesé 2006a). Moreover, the coexistence of *Stephanomys cordii*, *Apodemus gorafensis*, *Apodemus atavus*, *Castillomys gracilis* and *Paraethomys meini* in the same assemblage is typical of the early Ruscinian, MN14 (García-Alix *et al.* 2008a, Minwer-Barakat 2005, Minwer-Barakat *et al*. 2012) (see Fig. VIII.1).

The *Ruscinomys* from the studied localities has been determined as *R.* cf. *lasallei*, a taxon found in latest Turolian and Early Ruscinian (García-Alix *et al.* 2008b). Adrover *et al*. (1993) noted that *Ruscinomys* was very abundant in the middle Turolian, becoming very scarce from MN13 onwards, which seems to be the situation of AL2-C and AL2-D. Regarding *Apocricetus, A. barrierei* is typical of MN14 and replaced by *A. angustidens, which* is present in both MN14 and MN15. The material from AL2-D has been ascribed to *A.* cf. *angustidens* on biometric criteria; morphologically both species can only be distinghised on a statistical basis (Freudenthal *et al*. 1998).

Esteban Aenlle and Lacomba (1988) proposed a late Ruscinian age for Alcoy-2. Nevertheless, the faunal assemblage, with the presence of *Castillomys gracilis* and *Paraethomys* aff. *abaigari*, initially ascribed to *P. jaegeri*, suggests an older age

(MN14) for this locality, which agrees with the inferred age for Alcoi-Mina on the basis of its macromammal assemblage (Montoya *et al.* 2006b).

VI.3.3. Palaeoecology

Micromammals have been extensively used as palaeoclimatical indicators (Weerd 1976, Daams *et al*. 1988, Montuire *et al*. 2006, García-Alix *et al*. 2008c). The ecological requirements of a number of taxa of Miocene and Pliocene age have been determined using phylogenetic affinities, dental-corporal modifications and association with other taxa of known ecological preferences (García-Alix *et al*. 2008c).

The rodent assemblages from AL2-C and AL2-D are clearly dominated by the Muridae family, with a prevalence of 81 % in the former and 84 % in the latter. The collection from Alcoy-2 also shows a predominance of this family, although not so pronounced as in the localities here studied. The most abundant genus is *Stephanomys*, followed by *Paraethomys* (Table IV.9), which comprise two species, *P. meini* and *P*. aff. *abaigari*. In AL2-C, these two taxa represent 37.98 % of the assemblage, with the same number of specimens ascribed to each of the species, whereas in AL2-D and Alcoy-2 there is a clear predominance of *P*. aff. *abaigari* over *P. meini*. The percentages of the remaining species found in the mentioned localities are evenly matched, apart from the cricetids and insectivores in Alcoy-2 (Table IV.9).

The faunal list published by Esteban Aenlle and Lacomba (1988) does not mention the genus *Apocricetus* (Table IV.5), although in the collection housed at the UCM this taxon represents 5.72 % of the assemblage, compared with 1.26 % in AL2-C and 2.18 % in AL2-D. Regarding the insectivores, they comprise the 7.04 % of all the specimens from Alcoy-2, showing a remarkable contrast with AL2-C, which has yielded a single specimen, and AL2-D, where just a few fragmentary remains have been found.

Regarding the palaeoecological requirements, we have used the climatical and habitat preferences proposed by García Alix *et al.* (2008c) for the studied taxa. Therefore, in the faunal assemblages of AL2-C and AL2-D, several taxa are interpreted as warm climate indicators such as *Apodemus atavus*, *Paraethomys meini* and *Apocricetus*, whereas *Ruscinomys* and *Trilophomys* are associated with cold temperatures. In addition, both *Paraethomys meini* and *Ruscinomys* are thought to indicate dry environmental conditions, whereas *Apodemus gorafensis*, *Apodemus atavus, Eliomys, Pliopetaurista* and *Glis* would point to moist palaeoenvironments. However, Freudenthal *et al*. (2014) consider *Eliomys* a habitat generalist based in its actual distribution, and therefore we refer to this taxon as eurytopic.

	AL2-C	AL2-D	Alcoy-2
Apodemus	12.66	15.54	9.25
Castillomys	0.00	1.09	1.76
Paraethomys	39.78	26.18	18.07
Occitanomys	0.00	2.18	1.76
Stephanomys	30.38	40.00	37.00
Apocricetus	1.26	2.18	5.72
Blancomys	0.00	0.36	3.96
Ruscinomys	6.33	4.00	2.20
Trilophomys	7.59	4.36	7.49
Eliomys	2.53	1.82	3.96
Glis	0.00	0.36	1.76
Pliopetaurista	0.00	0.36	0.00
Soricidae Indet.	1.26	0.36	1.76
Parasorex	0.00	1.82	0.88
Asoriculus	0.00	0.00	4.40

Table IV.9. Relative abundance of the genera present in the localities of AL2-C, AL2-D and Alcoy-2.

In the same way, a number of the taxa present in AL2-C and AL2-D are considered indicators of open and herbaceous habitats, like *Apocricetus*, *Blancomys*, *Ruscinomys* and *Trilophomys*, whereas *Apodemus atavus*, *Pliopetaurista* and *Glis* are considered indicators of forested habitats. There are also several taxa which have no particular environmental requirements (eurytopic) regarding temperature, like *A. atavus*, *Castillomys*, *Stephanomys*, *Blancomys*, *Eliomy*s and *Pliopetaurista*; *Castillomys*, *Apocricetus*, *Blancomys*, *Trilophomys*, *Eliomys* and *Stephanomys* are thought to be indifferent with respect to the humidity. Some taxa cannot be associated with a concrete habitat, like *Castillomys*, *Paraethomys meini*, *Eliomys* and *Stephanomys.*

Because of their scarcity in the Iberian Peninsula and palaeoecological implications, the presence of *Pliopetaurista* and *Glis* in AL2-D is remarkable. *Pliopetaurista* is recognized as a member of the flying squirrels, one of the three adaptive types found among the sciurids (Bruijn 1999). This group is considered arboreal and nocturnal by several authors (Cuenca-Bescós 1988, Bruijn 1999, García-Alix 2006, García-Alix *et al*.

2008c). In addition, Dam and Weltje (1999) assumed a preference for close, humid biotopes in accordance with the lifestyle of their extant relatives and the fossil faunal assemblages in which they are found.

The glirids underwent a dramatic reduction in diversity during the late Vallesian in the coastal basins of Eastern Spain, being reduced to just two genera, *Muscardinus* and *Glis* in the Catalonian basins (Agustí 1990, Sesé 2006a). This reduction is also found in the other basins of the Iberian Peninsula during the Turolian, where the surviving genera were *Muscardinus* and *Eliomys* (Sesé 2006a). In AL2-D, we have a quite unusual glirid assemblage, with the presence of *Eliomys* and *Glis* in the same locality, an association that, as far as we know, has only been cited in the karstic localities of Moreda-1A and Moreda-1B (Castillo 1990). At present times, *Glis* is restricted to the wet northern part of the Iberian Peninsula (Castién 2002), whereas *Eliomys* spreads through the entire peninsula (Moreno 2002). Agustí (1990) considers a wet and cold climatic affinity for the genus *Glis*, which according to this author would explain the particular distribution of fossil species.

The assemblages from AL2-D and Alcoy-2 suggest a relatively wet environment (Table IV.10), whereas AL2-C shows a higher abundance of taxa with dry ecological affinities, like *P. meini* and *Ruscinomys*. In addition, the analysis of the faunas of the studied localities is consistent with warm temperatures (Table IV.10). Regarding the habitat, the taxa considered as open environment indicators are slightly more abundant that those of forested environments (Table IV.10), which agrees with a forest mosaic scenario.

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	Wet	Dry	Eurytopic	Cold	Warm	Eurytopic	Open	Forested	Eurytopic
AL2-C	13.57	25.61	41.61	14.09	26.89	39.82	15.36	6.40	59.03
AL2-D	15.88	14.13	51.02	8.83	20.83	51.37	11.16	6.88	63.00
Alcoy-2	12.18	8.76	61.98	11.54	23.07	51.09	20.30	6.00	59.40

Table IV.10. Relative abundance of the taxa from the studied localities according to their ecological preferences. These percentages have been obtained by dividing each taxon by its number of diagnostic elements, as proposed by Martín-Suárez (1988). The taxa with unknown preferences are not shown.

VI.3.4. Conclusions

According to the geologic context, we consider a probable equivalent stratigraphic position for the classic locality of Alcoy-Mina with Alcoy-2, AL2-C and AL2-D. The age assigned to AL2-C and AL2-D matches the age of Alcoy-Mina proposed by Montoya *et al*. (2006b), who placed this locality in the Early Ruscinian (MN14).

The presence of a small form of the genus *Pliopetaurista* in AL2-D constitutes the southernmost record of this group of squirrels, which only has been described from central Europe (*Pliopetaurista raui* - Dahlmann 2001).

The presence of a form of the genus *Glis* in AL2-D confirms the record of this taxon in the locality Alcoy-2 (Castillo 1990).

From the fossil material yielded by the localities of AL2-C and AL2-D, our age interpretation agrees with the end of the Early Ruscinian (MN14) or the early-late Ruscinian boundary (MN14-MN15), by the presence of *Apocricetus* cf. *angustidens*. Assuming that Alcoy-2 and AL2-C/AL2-D are probably equivalent levels, our age interpretation is clearly older than that of Esteban Aenlle and Lacomba (1988), since these authors proposed an Upper Ruscinian age (MN15) for the locality of Alcoy-2.

The mixture of inhabitants of open and herbaceous habitats, like *Apocricetus*, *Blancomys*, *Ruscinomys* and *Trilophomys*, and others of forested environments like *Apodemus atavus*, *Glis* and *Pliopetaurista* is consistent with a forest mosaic scenario. In addition, the presence in AL2-D of a flying squirrel, *Pliopetaurista* sp., and a glirid with humid ecological affinities like *Glis* sp. suggest a wet environment. The macrofauna from Alcoy is very singular, differing from the faunal assemblages of other contemporaneous Iberian localities (Montoya *et al*. 2006b). These authors suggested that the differences may be due to a relatively wetter environment, which agrees with the palaeoenvironmental inferences made in this chapter.

Regarding the temperature, both AL2-C and AL2-D present cold weather indicators (*Trilophomys*, *Ruscinomys*) and taxa with warm preferences (*Apodemus atavus*, *Paraethomys meini*, *Apocricetus*). However, the much higher relative abundance of warm climate indicators makes us consider a mild climate at the moment of the deposition of the studied sites.

CHAPTER V. MICROMAMMAL FAUNAS FROM THE MIO-PLIOCENE BOUNDARY IN THE ALCOY BASIN (SE SPAIN): BIOSTRATIGRAPHICAL AND PALAEOLOGICAL INFERENCES.

V.1. Material and methods

Since 2005, about 3,000 kg of sediment were extracted from the localities of Alcoi Barranc Sud and Alcoi Cristian in several field campaigns. The resulting fossil collections are stored at the *Museu de Geologia de la Universitat de València* (MGUV) with the acronyms ABS1’05-, ABS2-, ABS2’05-, ABS3’05-, ABS3’08-, ABS3A-, ABS7’05-, ABS8-, ABS9-, ABS10-, AC0-, AC0B- and AC0C-. ABS1’05, ABS2’05, ABS3’05 and ABS7’05, corresponding all of them to the samplings of the year 2005, and ABS3’08 to a sampling in 2008.

The nomenclature and measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, and Reumer (1984) for the insectivores.

V.2. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1826

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial 1984 (Fig. V.1, 1)

Localities: ABS-3, AC-0, AC-0C.

Material: **1 m1** (ABS3’08-3), **1 m2** (AC0-46), **2 M1** (AC0-20, AC0-119), **1 M3** (ABS3’08-34).

Description:

m1: (2.35 x –): The lingual side of the molar is missing. The tma and labial cingulum are well developed. There is a large oval c1.

m2: (1.53 x 1.32): The anterolabial cusp is large and connected basally to the protoconid and a well-developed labial cingulum. There is a medium-sized round c1 and a slightly smaller accessory cusp, connected basally to the posterior side of the protoconid (Fig. V.1, 1). The posterior heel is large, oval and lingually displaced.

M1: (– x 1.50): The specimens are poorly preserved. The t1 and t3 have small distal spurs. There is a well-developed t7.

M3: The labial side of the molar is absent. The t1 is connected to t4-t5-t6. There is a t9 attached to the posterior side of the t8.

Discussion:

The presence of a big tma, well-developed labial cingulum in the lower molars and t7 in M1 and M2 are typical traits of *Apodemus*. In addition, some Late Miocene and Early Pliocene populations of *A. atavus* and *A. gorafensis* have a t9 in M3 (García-Alix *et al.* 2008a). The studied molars differ from *A. gudrunae* by their bigger size and presence of a well-developed t7, and from *A. agustii* by the connection of the t6-t9 in M1 and a smaller tma. The length of the single m1 is consistent with the highest values of *A. gorafensis*, such as the biggest specimens from MNA-2, MNA-4 and CLR-1 (García-Alix *et al*. 2008a). Its size is also close to the values of *A. jeanteti* from Villalba Alta and Arquillo 3. However, this latter species shows a reduced or absent tma, which is well developed in specimen ABS3’08-3.

The size of the molars from AC-0 and AC-0C are consistent with those of *A. gorafensis* from Botardo C (Martín-Suárez 1988), DHS-16, PUR-4, PUR-24A, PUR 25 and PUR-25A, (García-Alix *et al.* 2008a), being slightly smaller than the teeth from Gorafe A (type locality, Ruiz Bustos *et al*. 1984), Gorafe 3, 4 and 5 (Martín-Suárez 1988) MNA-2 and MNA-4 (García-Alix *et al.* 2008a) and AL2-D (Mansino *et al*. 2013, chapter IV). Their size is similar to those of *A.* aff. *gorafensis* from Peralejos E (Adrover *et al.* 1988), Celadas 9 and La Gloria 4 (Adrover *et al.* 1993), and to the highest values of *A.* aff. *gorafensis* from PUR-23 (García-Alix *et al.* 2008a).

Genus *Micromys* Dehne, 1841

Micromys sp. (Fig. V.1, 2)

Localities: ABS-2, ABS-9.

Material: **1 m2** (ABS9-1), **1 M3** (ABS2’05-5).

Description:

m2: (1.05 x 0.95): The anterolabial cusp is big and isolated. The labial cingulum is low and wide. There is a large round c1. There are no accessory cusps. The posterior heel is big and oval.

M3: Molar broken anteriorly. The t4, t5 and t6 are connected. The t8 is very big and connects labially to a much smaller t9.

Discussion:

The diminutive size of the specimens, brachyodonty of the molars and distinct labial cingulum agree with the genus *Micromys* (Fig. V.1, 2). The m2 is smaller than in *M. steffensi* van de Weerd, 1979, from Kardia, and *M. cingulatus* Storch and Dahlmann, 1995 from Maramena, being consistent with the smallest specimens of *M. bendai* van de Weerd, 1979 and *M. kozaniensis* van de Weerd, 1979 from Ptolemais 1 and Ptolemais 3, respectively. Its size agrees with the biggest molars of *M. praeminutus*, such as the m2 from Sète (Michaux 1969), and *M. tedfordi* Wu and Flynn, 1992, being bigger than *M. caesaris* Minwer-Barakat, García-Alix, Martín-Suárez and Freudenthal, 2008, which is considered a junior synonym of *M. praeminutus* by Horáček *et al*. (2013), *M. minutus* (Pallas, 1771), *M. chalceus* Storch, 1987 and *M. paricioi* Mein, Moissenet and Adrover, 1983.

The absence of accessory cusps differs from *M. cingulatus*, *M. steffensi*, *M. bendai* and *M. kozaniensis*. The m2 has a wider labial cingulum than *M. paricioi*, *M. caesaris* and *M. minutus*. According to Minwer-Barakat *et al*. (2008), the m2 of *M. praeminutus* from Sète has a large anterolabial cup, more separated from the protoconid than in *M. caesaris*, a well-developed labial cingulum, and it is wider anteriorly than posteriorly. The specimen ABS9-1 agrees with this morphology (Fig. V.1, 2), but because of the scarcity of the material and lack of diagnostic features, we ascribe the studied material to *Micromys* sp.

Genus *Occitanomys* Michaux, 1969

Occitanomys alcalai Adrover, Mein and Moissenet, 1988 (Fig. V.1, 3–4)

Localities: ABS-2, ABS-3, ABS-3A, AC-0, AC-0B, AC-0C.

Material: **5 m1** (ABS3’08-45, AC0-66, AC0-107, AC0-109, AC0C-3), **3 m2** (ABS3A-17, AC0-5, AC0C-12), **2 m3** (ABS3’08-43, AC0-106) **3 M1** (ABS2-36, AC0C-5, AC0-114), **1 M2** (AC0B-12).

Description:

m1: (– x 1.30; – x 1.32; – x 1.24): The metaconid and the lingual lobe of the anteroconid are connected by a narrow crest. The labial cingulum is wide. There is a well-developed round c1. One specimen has a large accessory cusp connected to the protoconid. There is a hint of distal spur. The posterior heel is moderate, oval and lingually displaced.

m2: (1.38 x 1.24; – x 1.25): The anterolabial cusp is large, round and connected basally to the protoconid and a reduced labial cingulum. The c1 is much reduced, and there are no accessory cusps. There is a hint of longitudinal spur. The posterior heel is well developed and round.

m3: (– x 0.91): One molar is broken anteriorly and the other one posteriorly. There is no anterolabial cusp. The protoconid and metaconid are separated from the hypoconid-entoconid by a deep valley. There is no c1.

M1: The t1 is displaced backwards and connects basally to the lingual side of t5. There are a well-developed t1 bis and a weak t2 bis. The t6 and t9 are connected. The t12 is small but distinct.

M2: The specimen is broken anterolabially. The t1 is connected to t5 by a low crest. There is a t1bis. The t3 is reduced and isolated. There is no t7.

Discussion:

Occitanomys alcalai ranges in age from the Late Turolian to the Ruscinian. Several authors considered this taxon an immigrant in the Iberian Peninsula (Adrover *et al.* 1988, Freudenthal and Martín-Suárez 1999), and the phylogenetic relationship with other species of the genus is not clear. The molars from ABS-2, ABS-3, ABS-3A, AC-0, AC-0B and AC-0C show a symmetric anteroconid, relative high crown, well-developed t1 bis, absence of isolated cusps in the upper molars, and lack of complete longitudinal crests in the lower molars, which are typical traits of *O. alcalai*.

The size of the measurable specimens from AC-0 and AC-0C is similar to the maxima of *O. alcalai* from the Ruscinian localities of Peralejos E (Adrover *et al.* 1988), La Gloria 4 and 5, Celadas 9 and the Late Turolian sites of Villastar and Valdecebro 3 and 6 (Adrover *et al.* 1993), and slightly bigger than *O. alcalai* from the localities of the Granada Basin (García-Alix *et al.* 2008a). Their size is also close to the lower measurements of *O. adroveri* (Thaler, 1966), but this species has more developed longitudinal connections in m1 and m2, an asymmetrical anteroconid and less developed longitudinal crests in the upper molars.

In addition, the absence of anterolabial cusp in m3 and the t1-t5 connection in M2 are more frequent in *O. alcalai* (Minwer-Barakat *et al*. 2009a). The specimens studied differ from *O. sondaari* by its bigger size, greater development of t1 bis, less developed longitudinal crests in the lower molars, higher t6-t9 connection and more developed labial cingulum, and from *O. brailloni* by their smaller size and less-developed spurs and crests in the upper molars.

Genus *Paraethomys* Petter, 1968

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. V.1, 5–9)

Localities: ABS-2, ABS-3, ABS-3A, AC-0, AC-0B.

Material: **7 m1** (ABS3’08-1, ABS3’08-5, ABS3A-36, AC0-19, AC0-35, AC0-41, AC0-51), **11 m2** (ABS3’05-2, ABS3’05-3, ABS3’08-6, ABS3’08-11, ABS3A-12, ABS3A-15, AC0-3, AC0-4, AC0-18, AC0-47, AC0-110), **2 m3** (ABS2-20, ABS3’05-4), **8 M1** (ABS3’08-18, ABS3’08-19, ABS3’08-27, ABS3A-19, AC0-28, AC0-43, AC0-44, AC0-113), **15 M2** (ABS2’05-4, ABS2-35, ABS3’08-28, ABS3’08-29, ABS3A-2, ABS3A-21 to ABS3A-24, AC0-7, AC0-26, AC0C-49, AC0-117, AC0B-5, AC0B-6), **7 M3** (ABS3’08-31, ABS3A-25 to ABS3A-27, AC0-9, AC0-16, AC0C-10).

Measurements: see Table V.1.

Description:

m1: Slightly asymmetrical anteroconid. The two anterior pairs of cusps are connected by a narrow crest. Two specimens have a reduced longitudinal spur. Moderate labial cingulum, which bears one or two small accessory cusps. The posterior heel is big, round or oval and lingually displaced.

m2: The anterolabial cusp is big and connected basally to the protoconid and the labial cingulum. The c1 is well developed, and a small accessory cusp attached to the labial side of the protoconid may be present. There is a longitudinal spur in 8 out of 11 specimens. The posterior heel is laminar in three specimens, oval in the others.

m3: The specimens are broken anteriorly. There is no longitudinal connection. There is neither c1 nor accessory cusps.

M1: The t1 is displaced backwards. The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. There are distal spurs on t1 and t3, although much reduced in some specimens (Fig. V.1, 7). The connection between t4 and t8 is very low. There is a small t12. There are three roots.

M2: The t1 and t3 are isolated. The t3 is reduced. In 7 out of 13 specimens there is a reduced spur on t1. One molar has a slightly swollen t9 (Fig. V.1, 8), which is reduced in the others (Fig. V.1, 9). There is no t12. There are four roots.

M3: The t1 is large and isolated. The t3 is absent. The t8 is connected to the t4-t5-t6 junction. There are three roots.

Discussion:

Two different lineages of *Paraethomys* can be distinguished in the Early Pliocene: the small sized *P. meini*, and the bigger forms of the anagenetic lineage *P.* aff. *abaigari*-*P. abaigari*-*P. jaegeri*. Besides the difference in size, Adrover *et al*. (1988) noted a greater development of the distal spurs on t1 and t3 in the upper molars of the bigger species. These differences are clear in *P. jaegeri* and *P. abaigari*, but the older *P.* aff *abaigari* is more similar to *P. meini* and the size of both species can overlap, making specific adscription complicated (García-Alix *et al*. 2008a). That is the case in some localities such as PUR-4 in the Granada Basin (García-Alix *et al.* 2008a) and AF-1’06 (chapter VI), where *Paraethomys* has a great variability in size but two species cannot be discriminated (García-Alix *et al.* 2008a).

This situation is the same as in the assemblages studied in this paper from the Alcoi Barranc Sud and Alcoi Cristian sections, where a reduced number of *Paraethomys* remains have been located. We cannot assess if there is a continuous distribution ranging from the smallest to the biggest specimens as in PUR-4 and AF-1’06. However, the size of the molars ascribed to *P.* aff. *abaigari* matches the biggest specimens from these localities, with some specimens being clearly bigger, falling within the range of variation of *P.* aff. *abaigari* from CLC-5A and PUR-13 (García-Alix *et al*. 2008a), Celadas 9 and La Gloria 4 (Adrover *et al.* 1993) and AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV).

Adrover *et al.* (1988) noted that *P. abaigari* and *P. jaegeri* have more developed distal spurs on t1 and t3 in M1, and that the molars are relatively wider. However, these differences are not as conspicuous between *P.* aff. *abaigari* and *P. meini*, since the shape of the molars of both species is similar and some specimens of *P. meini* have moderately developed spurs, which are absent in some molars of *P.* aff. *abaigari*. Since more data are needed to clarify the morphological differences between both taxa, we ascribe the biggest specimens from these localities to *P.* aff. *abaigari*.

Paraethomys meini (Michaux, 1969) (Fig. V.1, 10–13)

Localities: ABS-2, ABS-3, ABS-3A, AC-0, AC-0B.

Material: **2 m1** (AC0-102, AC0B-8), **6 m2** (ABS3’08-10, ABS3’08-11, ABS3A-13, ABS3A-14, ABS3A-42, AC0-53), **6 m3** (ABS3’08-15 to ABS3’08-17, ABS3A-28, AC0-111, AC0B-9), **3 M1** (ABS3’08-21, ABS3A-20, AC0B-7), **1 M3** (ABS2’05-2).

Measurements: see Table V.1.

Description:

m1: Slightly asymmetrical anteroconid. The two anterior pairs of cusps are connected by a narrow crest. One specimen has a reduced longitudinal spur. Moderate labial cingulum, which bears a large accessory cusp in one specimen. The posterior heel is big, oval and central.

m2: Moderate anterolabial cusp, in contact with the labial cingulum and the anterior side of the metaconid. There is a much reduced longitudinal spur. One specimen has a very small c1, absent in the others. The posterior heel is much reduced.

m3: The anterolabial cusp is absent or reduced. There is neither c1 nor accessory cusps

M1: The t1 is displaced backwards. The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. One specimen has low longitudinal connections between t1-t5 and t3-t6 (Fig. V.1, 12). The other two molars have a spur on t1, and one of them also on t3. There is a small t12.

M3: The t1 is large and isolated. The t3 is absent. The t8 is connected to the t4-t5-t6 junction.

Discussion:

The morphology of this group of specimens is consistent with *P. meini,* although the presence of distal spurs in M1, especially on t3, is more frequent in *P. abaigari* (Adrover *et al.* 1998). However, some specimens of *P. meini* can also develop this feature (García-Alix *et al.* 2008a, Mansino *et al.* 2013, chapter IV of this thesis) and the size of the molars described is similar to that of *P. meini* from CLC-5A, PUR-13 (García-Alix *et al.* 2008a), Peralejos E (Adrover *et al.* 1988), Celadas 9, La Gloria 4 (Adrover *et al.* 1993), AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV), and LB2B (chapter VII). Because of this, we ascribe the specimens from Alcoi Barranc Sud and Alcoi Cristian to *P. meini*.

Element	Locality	Sp.	Parameter	n	min.	mean	max.
m1	ABS-3	aff. *abaigari*	L	1	-	2.29	-
			W	2	1.42	1.45	1.48
	AC-0	aff. *abaigari*	L	1	-	2.22	-
			W	2	1.44	1.46	1.48
m2	ABS-3	aff. *abaigari*	L	1	-	1.63	-
			W	1	-	1.40	-
		meini	L	2	1.47	1.52	1.57
			W	1	-	1.38	-
	ABS-3A	aff. *abaigari*	L	1	-	1.71	-
			W	2	1.43	1.46	1.49
		meini	L	3	1.42	1.46	1.52
			W	3	1.29	1.33	1.40
	AC-0	aff. *abaigari*	L	3	1.63	1.67	1.69
			W	5	1.46	1.53	1.61
m3	ABS-2	aff. *abaigari*	W	1	-	1.28	-
	ABS-3	*meini*	L	1	-	1.12	-
			W	2	1.16	1.19	1.23
	AC0	*meini*	W	2	1.16	1.19	1.22
M1	ABS-3	aff. *abaigari*	W	1	-	1.73	-
	ABS3-A	*meini*	L	1	-	2.31	-
			W	1	-	1.46	-
	AC-0	aff. *abaigari*	L	2	2.55	2.62	2.69
			W	3	1.58	1.63	1.68
	AC-0B	*meini*	L	1	-	2.30	-
M2	ABS-2	aff. *abaigari*	L	1	1.74	1.83	1.91
	ABS-3A	aff. *abaigari*	L	3	1.80	1.84	1.91
			W	3	1.59	1.66	1.70
	AC-0	aff. *abaigari*	L	2	1.78	1.82	1.85
			W	3	1.52	1.59	1.69
	AC-0B	aff. *abaigari*	W	1	-	1.69	-
M3	ABS-2	*meini*	L	1	-	1.00	-
			W	1	-	1.10	-
	ABS-3	aff. *abaigari*	L	1	-	1.23	-
			W	1	-	1.17	-
	ABS-3A	aff. *abaigari*	L	2	1.23	1.26	1.30
			W	3	1.18	1.20	1.23
	AC-0	aff. *abaigari*	L	2	-	1.23	-
			W	2	1.23	1.24	1.25

Table V.1. Measurements in millimetres of the teeth of *Paraethomys* from ABS-2, ABS-3, ABS-3A, AC-0 and AC-0B. n= number of measurable specimens.

Genus *Stephanomys* Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Fig. V.1, 14–19)

Localities: ABS-1, ABS-2, ABS-3, ABS-3A.

Material: **8 m1** (ABS2-33, ABS2-38, ABS3'05-1, ABS3'08-2, ABS3'08-37, ABS3A-8 to ABS3A-10), **9 m2** (ABS2-1, ABS3'08-7 to ABS3'08-9, ABS3'08-12, ABS3'08-13, ABS3'08-22, ABS3A-1, ABSA-16), **3 m3** (ABS3'08-14, ABS3'08-39, ABS3A-18); **3 M1** (ABS2-2, ABS2-34, ABS2-37), **4 M2** (ABS3'08-23 to ABS3'08-26), **4 M3** (ABS1-1, ABS2-3, ABS3'08-32, ABS3'08-33).

Measurements: see Table V.2.

Description:

m1: The anteroconid is slightly asymmetrical, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is low and narrow. There is a well-developed longitudinal crest that connects the posterior cusps to the metaconid. The c1 is big and subtriangular. The posterior heel is big and oval.

m2: The anterolabial cusp is high and big, connected to the protoconid and a moderately developed labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. The c1 may be absent, small or well-developed. The c1 ranges from very small to well-developed. There are no accessory cusps. The posterior heel is large and oval. There are two roots.

m3: The anterolabial cusp is absent in the specimen from ABS-3A (Fig. V.1, 16), and reduced in ABS-3 and reduced in ABS-3. There is a longitudinal crest that reaches the protoconid-metaconid junction. There are two roots.

M1: The t1 is displaced backwards. The t1 bis and t2 bis are well developed. The posterior crest of t1 and the labial longitudinal crest of t3 are complete, but the crest on t1 is usually lower (Fig. V.1, 18). The t12 is reduced.

M2: The t1 has a small t1bis attached to its anterior side. The longitudinal crest of t1 is low in two specimens, and the t3 is isolated in another two. The t12 is well developed. These molars have three roots.

M3: The t1 and t8 are connected to the t4-t5-t6 junction. The t3 is absent. There are three roots.

Discussion:

The height of the crown, development of longitudinal crests in the lower molars and distal crests or spurs on t1 and t3 of the upper molars suggest that the specimens studied belong to the genus *Stephanomys*. These molars are smaller, less hypsodont and with a less pronounced stephanodonty than younger *Stephanomy*s such as *S. donnezani* (Déperet, 1890), *S. balcellsi* Gmelig-Meyling and Michaux, 1973, *S. vandeweerdi* Adrover, 1986, *S. thaleri* López-Martínez, Michaux and Hutterer, 1998, *Stephanomys progressus* Minwer-Barakat, García-Alix and Martín-Suárez, 2011, and *S. minor* Gmelig-Meyling and Michaux, 1983. In addition, *S. balcellsi, S. progressus* and *S. minor* differ from other species of the genus by having a tubercular posterior heel. *Stephanomys debruijni* de Giuli, 1989 differs from our specimens by having a small tma in some m1, a reduced and rounded posterior heel and a t1 situated extremely backwards in the M1. *Stephanomys dubari* is bigger, more hypsodont and with a more pronounced stephanodonty than *S. ramblensis* van de Weerd, 1976. This latter species presents sometimes the longitudinal crest of the m1 directed to the protoconid, and the t1 and t3 of the M1 and M2 rarely develop full longitudinal crests (García-Alix 2006).

The studied specimens fall within the range of variation of *S. dubari* from Castelnou 3, its type locality (Aguilar *et al.* 1991), being slightly smaller than *S. cordii* from Alcoy (Cordy 1976) and AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV). One m1 from ABS-2, much worn and broken posteriorly, seems much smaller than the other molars of *S. dubari* (Fig. V.1, 14), even the specimens from the same locality (compare with Fig. V.1, 15), but because of the great development of the longitudinal crest, which reaches the metaconid-protoconid connection, reduced labial cingulum and height of the crown, we ascribe this molar to *Stephanomys*. These molars also differ from *S. cordii* by the t1 displaced backwards (Fig. V.1, 18), the longitudinal crest of the m3 reaching the protoconid-metaconid junction instead of the protoconid and the less developed distal crests in M1 and M2.

Stephanomys aff. *cordii* Ruiz Bustos, 1986 (Fig. V.1, 20–26)

Localities: ABS-8, AC-0, AC-0B, AC-0C.

Material: **8 m1** (AC0-1, AC0-2, AC0-98 to AC0-101, AC0-108, AC0C-6), **4 m2** (AC0-8, AC0B-2, AC0C-4, AC0C-11), **7 m3** (AC0-11, AC0-42, AC0-56, AC0-103 to AC0-105, AC0B-1), **7 M1** (AC0-12 to AC0-14, AC0-45, AC0-133, AC0B-10, AC0C-1), **10 M2** (ABS8-1, AC0-6, AC0-15, AC0-48, AC0-50, AC0-115, AC0-116, AC0-118, AC0-134, AC0C-7), **6 M3** (AC0-10, AC0-17, AC0-58, AC0-59, AC0-121, AC0C-8).

Measurements: see Table V.2.

Description:

m1: The anteroconid is slightly asymmetrical, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is moderately developed. There is a well-developed longitudinal crest that connects the posterior cusps with the metaconid or the protoconid-metaconid junction. The c1 is moderate in size and subtriangular. The posterior heel is big, oval or subtriangular. There are two roots.

m2: The anterolabial cusp is high and big, connected to the protoconid and a moderately developed labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. The c1 is reduced. There are no accessory cusps. The posterior heel is large, ranging from round to laminar.

m3: The anterolabial cusp is low and reduced. The longitudinal crest can reach the metaconid (1) the protoconid-metaconid junction (3) or the protoconid (3).

M1: The position of t1 and t3 is almost symmetrical (Fig. V.1, 23). The t1 bis and t2 bis are well developed. The posterior crest on t1 and the labial longitudinal crest on t3 are high and complete except in one specimen, which has a lower distal crest on t1. The t12 is reduced.

M2: The t1 has a small t1bis attached to its anterior side. The longitudinal crest on t1 is absent in 1 out of 9 specimens and low in three. The longitudinal crest on t3 is absent in 2 out of 9 specimens and low in another one (Fig. V.1, 25). The t12 is well developed.

M3: The t1 and t8 are connected to the t4-t5-t6. The t3 is absent.

Discussion:

The material from ABS-8, AC-0, AC-0B and AC-0C has been directly compared with the collection of *S. cordii* from AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV) housed at the *Museu de Geologia de la Universitat de València*. In general, the morphology of the specimens is similar to *S. cordii*, which has as a reduced labial cingulum and tubercular posterior heel in m1 and m2, a poorly-developed anterolabial cusp in m3, a longitudinal crest of m3 usually united to the protoconid and a symmetrical position of t1 and t2 in M1. In the m3 from AL2-C and AL2-D, the longitudinal crest reaches the protoconid in eight specimens, the protoconid-metaconid junction in five and cannot be observed properly in another six. This proportion is slightly higher than in the specimens from AC-0 and AC-0B (3 out of 7). The relative positions of t1 and t3 in the M1 are also similar, but the longitudinal crests are higher in M1 and M2 from AL2-C/AL2-D.

Stephanomys dubari is considered the likely descendant of *S. ramblensis* and the ancestor of *S. cordii* by several authors (Minwer-Barakat 2005, García-Alix *et al.* 2008a among others). There is an increase in size, stephanodonty and hypsodonty in the lineage *Occitanomys adroveri*-*S. ramblensis*-*S. dubari*-*S. cordii* (García-Alix *et al.* 2008a), which will continue in some of their Middle and Late Pliocene descendants (for a complete phylogeny of the genus see García-Alix 2006). The size of the specimens studied falls within the range of variation of *S. cordii* from Alcoy (Cordy 1976) and AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV). Its average sizes are also similar to *S. dubari* described in this paper, but some of the smaller specimens of this latter taxon cannot be measured properly (see Fig. V.1, 14) and the highest values usually correspond to *S.* aff. *cordii* (see Table V.2). For these reasons, we ascribe the material from ABS-8, AC-0, AC-0B and AC-0C to *S.* aff. *cordii*, which has a similar size but lower longitudinal connections than *S. cordii*.

Element	Locality	Sp.	Parameter	n	min.	mean	max.
m1	ABS-3	*dubari*	L	1	-	2.29	-
			W	1	-	1.38	-
	AC-0	aff. *cordii*	L	4	2.11	2.21	2.33
			W	4	1.33	1.43	1.52
m2	ABS-2	*dubari*	W	1	-	1.47	-
	ABS-3	*dubari*	L	3	1.53	1.63	1.69
			W	5	1.46	1.50	1.55
	ABS-3A	*dubari*	L	1	-	1.62	-
	AC-0	aff. *cordii*	L	1	-	1.63	-
			W	1	-	1.59	-
	AC-0C	aff. *cordii*	W	1	-	1.58	-
m3	ABS-3	*dubari*	L	1	-	1.48	-
			W	1	-	1.35	-
	ABS-3A	*dubari*	L	1	-	1.27	-
			W	1	-	1.22	-
	AC-0	aff. *cordii*	L	4	1.31	1.34	1.36
			W	6	1.19	1.23	1.28
	AC-0B	aff. *cordii*	W	1	-	1.34	-
M1	ABS-2	*dubari*	L	1	-	2.43	-
			W	3	1.59	1.73	1.88
	AC-0	aff. *cordii*	L	2	2.59	2.63	2.67
			W	5	1.77	1.84	1.96
M2	ABS-3	*dubari*	L	4	1.66	1.74	1.86
			W	4	1.62	1.71	1.83
	ABS-8	aff. *cordii*	L	1	-	1.92	-
			W	1	-	1.66	-
	AC-0	aff. *cordii*	L	5	1.50	1.75	1.96
			W	7	1.56	1.71	1.82
	AC-0C	aff. *cordii*	L	1	-	1.95	-
			W	1	-	1.83	-
M3	ABS-1	*dubari*	L	1	-	1.16	-
			W	1	-	1.13	-
	ABS-3	dubari	L	2	1.18	1.23	1.28
			W	2	1.03	1.13	1.23
	AC-0	aff. *cordii*	L	2	1.20	1.24	1.29
			W	5	1.13	1.19	1.25
	AC-0C	aff. *cordii*	L	1	-	1.19	-
			W	1	-	1.29	-

Table V.2. Measurements in millimetres of the teeth of *Stephanomys dubari* from ABS-1, ABS-2, ABS-3, ABS-3A and *Stephanomys* aff. *cordii* from ABS-8, AC-0, AC-0B and AC-0C. n= number of measurable specimens.

Stephanomys sp.

Localities: ABS-7, ABS-9.

Material: **1 m2** (ABS7’05-3), **1 M1** (ABS9-3).

Description:

m2: The molar is broken anteriorly and much worn. Most of the enamel has been lost. There is a full longitudinal crest that reaches the metaconid. The posterior heel is big and subtriangular.

M1: The specimen is broken, only the t3, t5 and t6 can be observed. The t3 has a high and full distal crest that reaches the t5-t6 connection.

Discussion:

The full longitudinal crests and great height of the crown agree with *Stephanomys*. However, the scarcity of the material and poor state of preservation prevent us from reaching a specific ascription, since we cannot discriminate if they belong to *S. dubari* or *S. cordii*.

Family Cricetidae Fischer, 1817

Subfamily Cricetinae Murray, 1886

Genus *Apocricetus* Freudenthal, Mein and Martín Suárez, 1998

Apocricetus cf. *barrierei* (Mein and Michaux, 1970) (Fig. V.2, 1)

Localitiy: ABS-3A

Material: **1 M1** (ABS3A-37).

Description:

M1: (2.67 x 1.72): Weak cingulum ridge. Double anterolophule, arising from a short preloph. Absent anterior protolophule, mesoloph and ectomesoloph. Present anterior metalophule. Absent posterior metalophule. The posterior part of the posterosinus is shallow, whereas the anterior part is much deeper. The posteroloph, and not the metacone, constitutes the posterior side of the tooth. There are four roots.

Discussion:

Usually, size has been the main criterion used to distinguish between species of the genus *Apocricetus*, especially in the youngest part of the phylogenetic lineage defined by Freudenthal *et al.* (1998). The size of the M1 of *A.* cf. *barrierei* from ABS-3A coincides approximately with the mean length and width values of *A. barrierei* (see data from Ruiz-Sánchez *et al.* 2014; Fig. V.2, 1-3). The length of this tooth is clearly smaller than *A. angustidens* (Depéret, 1890) and longer than those of *A.* aff. *plinii*, *A. plinii* (Freudenthal, Lacomba and Martín-Suárez, 1991) and *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998

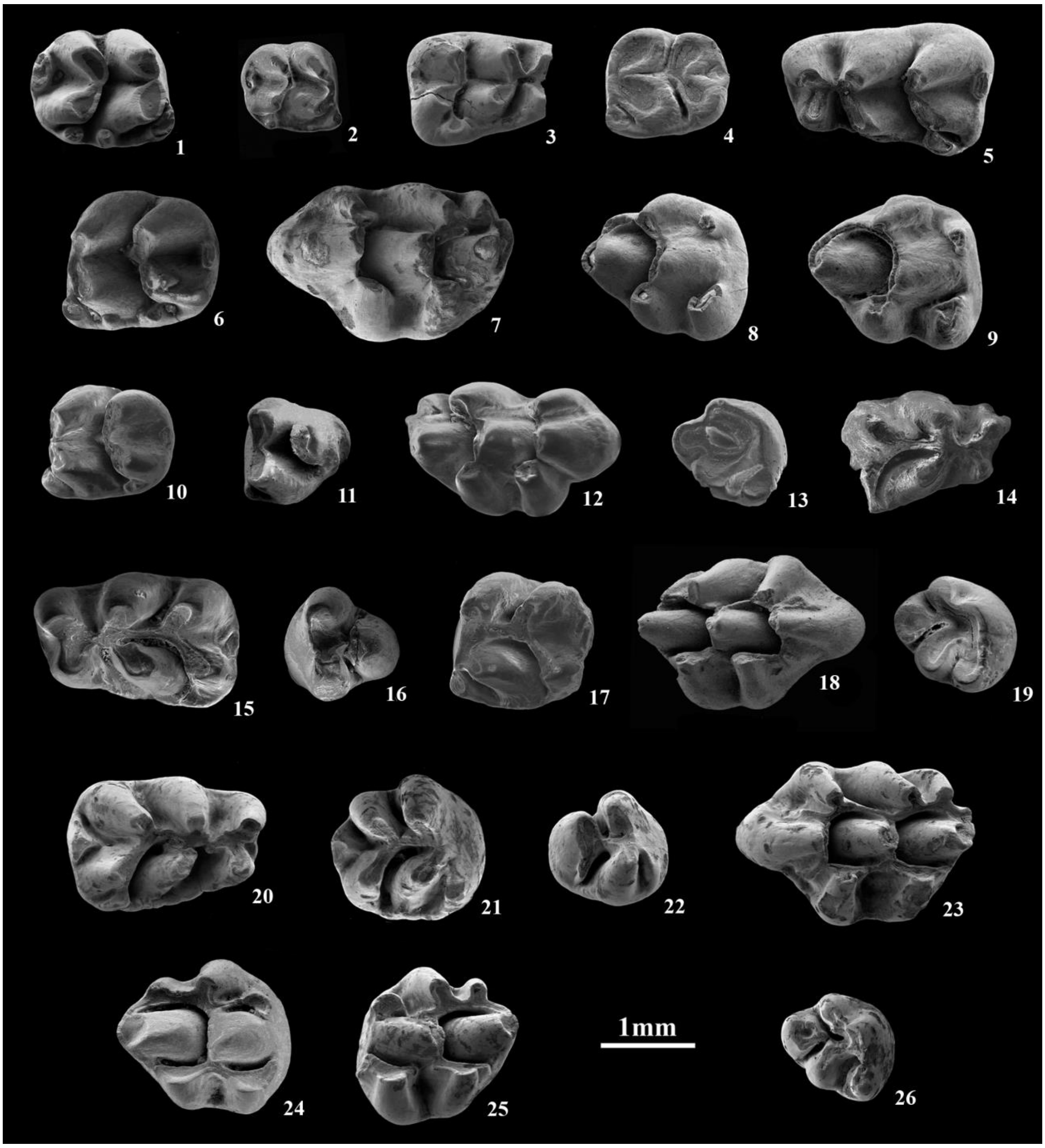


Figure V.1. Fossil rodents from ABS-2, ABS-3, ABS-3A, ABS-9, AC-0 and AC-0C. *Apodemus* cf. *gorafensis* from AC-0. **1**, right m2, AC0-46. *Micromys* cf. *praeminutus* from ABS-9. **2**, right m2, ABS9-1. *Occitanomys* cf. *alcalai* from AC-0. **3**, right m1, AC0C-3; **4**, left m2, AC0C-5. *Paraethomys* aff. *abaigari* from ABS-3, ABS-3A and AC-0. **5**, left m1, ABS3’08-1; **6**, left m2, AC0-110; **7**, left M1, AC0-43; **8**, right M2, ABS3A-2; **9**, right M2, ABS3A-21. *Paraethomys meini* from ABS-3 and ABS-3A. **10**, left m2, ABS3A; **11**, left m3, ABS3’08-15; **12**, right M1, ABS3A-20; **13**, right M3, ABS3’08-31. *Stephanomys dubari* from ABS-2, ABS-3 and ABS-3A. **14**, right m1, ABS2-33. **15**, left m1, ABS3’08-2; **16**, left m3, ABS3A-18; **17**, left m2, ABS3’08-8; **18**, right M1, ABS2-34. **19**, right M3, ABS3’08-33. *Stephanomys* aff. *cordii* from AC-0. **20**, right m1, AC0-1; **21**, right m2, AC0-8; **22**, right m3, AC0-11; **23**, left M1, AC0-12; **24**, right M2, AC0-15; **25**, left M2, AC0-15; **26**, right M3, AC0-10. Scale: 1 mm.

A weak cingulum ridge is present in some specimens of *A. alberti* (Mansino *et al.* 2014, chapter XI) and *A. barrierei* (Ruiz-Sánchez *et al.* 2014), being more developed in *A. angustidens* (Freudenthal *et al.* 1998). The double anterolophule and the absence of mesoloph in M1 distinguish *A.* cf. *barrierei* from ABS-3A from *A. plinii* from Crevillente 15 (type locality) and *A.* aff. *plinii* from Crevillente 23. The development of the preloph of the specimen from ABS-3A is similar to that of *A. barrierei* from La Bullana 2B (Fig. V.2, 1-3; Ruiz-Sánchez *et al.* 2014). This crest is absent in *A.* aff. *plinii* and *A. plinii*, and much rarer and less developed in *A. alberti*, while it has not been described in the populations of *A. angustidens* (chapter XI). The anterior protolophule is more frequent in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and less frequent in *A. barrierei* and *A. angustidens* (chapter XI, Ruiz-Sánchez *et al.* 2014). The proportion of specimens with posterior metalophule in M1 decreases from the older to the younger species of the genus, being absent in *A. barrierei* and *A. angustidens* (chapter XI). Hence, on the base on metric and morphological features, the material of the genus *Apocricetus* from ABS-3A may be assigned to *A. barrierei*. Nonetheless, due to the scarcity of material we ascribe this molar to *A.* cf. *barrierei*.

Genus *Neocricetodon* Schaub, 1934

Neocricetodon sp. (Fig. V.3, 1)

Locality: AC-0C.

Material: **1 m3** (AC0C-9).

Description:

m3: (1.12 x 0.86): Subtriangular outline, the posterior part is narrower than the anterior part (Fig. V.3, 1). The anterosinusid is very small. A very short lingual anterolophulid is present. The metalophulid is very short and transversal. The labial anterolophulid reaches the base of protoconid, enclosing a narrower protosinusid. The mesosinusid and sinusid are closed by a cingulum ridge. A trace of mesolophid, low and connected to the metaconid, is present. The ectomesolophid is absent. The posterolophid is connected to the entoconid. Roots are not preserved.

Discussion:

Size has been the criterion used to distinguish the species *N. lavocati* (Hugueney and Mein 1965) from another bigger species in its type locality (Lissieu). In this latter locality, Freudenthal *et al.* (1998) mentioned two very small m3: one of the size of the small specimens from Crevillente 2 (*Neocricetodon occidentalis* Aguilar, 1982) and another one even smaller (1.14 × 0.96). This latter specimen is much worn (Hugueney and Mein 1965, pl. 2, fig. 55) and the morphology cannot be clearly observed, but the outline is very similar to the m3 from AC-0C. According to Freudenthal *et al.* (1998) the mesolophid is very developed in the m1 from Lissieu, nearly always reaching the margin of the molar, but this trait cannot be observed in the much worn m3. The small size of the specimen resembles *N. lavocati*, but because of the scarcity of the material and lack of any unworn m3, we ascribe this molar to *Neocricetodon* sp. until more material becomes available.

Cricetinae indet.

Locality: AC-0B.

Material: **1 m3** (AC0B-11).

Description:

m3: The specimen is broken anteriorly, posteriorly and labially. The only cusps that can be observed are the entoconid, the metaconid and the lingual portion of the hypoconid. There is no mesolophid.

Discussion:

This molar is clearly bigger and more hypsodont than the m3 ascribed to *Neocricetodon* sp. from AC-0C. Because of the poor state of preservation of the specimen, we cannot reach a generic ascription, and therefore we assign this molar to Cricetinae indet.

Subfamily Cricetodontinae Stehlin and Schaub, 1951

Genus *Ruscinomys* Depéret, 1890

Ruscinomys cf. *lasallei* Adrover, 1969 (Fig. V.2, 4–6)

Localities: ABS-3A, AC-0, AC-0B, AC-0C.

Material: **2 m1** (AC0-30, AC0-68), **1 m2** (AC0-69), **3 m3** (ABS3A-41, AC0-31, AC0-129), **1 M1** (AC0-72), **1 M2** (AC0-70), **4 M3** (AC0-71), (AC0-73, AC0B-14, AC0C-15), **3 Frag. Indet.** (AC0-74, AC0-128, AC0-130).

Description:

m1: Both molars are much worn. The specimens are broken posteriorly, and one of them is also broken anteriorly. The anteroconid is rounded (Morphotype 3, García-Alix *et al.* 2008b). The anterolophid is absent. The mesolophid cannot be observed. The sinusoid is deep and narrow.

m2: This molar is broken anteriorly and extremely worn. The anteroconid is shorter than in m1. The posterolophid cannot be observed. The sinusoid is deep and narrow.

m3: All specimens are broken anteriorly and much worn. The posterolophid cannot be observed. The sinusoid is deep and narrow.

M1: (– x 2.68): The molar is broken posteriorly and extremely worn.

M2: (– x 2.22): The specimen is poorly preserved and broken anteriorly. The ectolophs cannot be observed.

M3: (1.95 x 1.57; 1.83 x 1.62; 1.98 x 1.63): The specimens are much worn. These teeth are bilobed, the anterior lobe being much bigger than the posterior one.

Discussion:

Several authors have proposed the phyletic lineage *R. schaubi-R. lasallei-R. europaeus* (Adrover 1969, Weerd 1976, García-Alix *et al.* 2008b, among others) in which there is a continuous increase in size and hypsodonty, as well as changes in some morphological features such as the shape of anterocone and anteroconid, along time. The specimens studied are smaller than *R. europaeus*, and agree in size with *R. lasallei* Adrover, 1969, from the localities of Alcoy (Adrover 1969), BRA-5B, PUR-4 and PUR-13 (García-Alix *et al*. 2008b), being similar to *R.* cf. *lasallei* from, Arquillo1, Arquillo 4, La Gloria 5, (Adrover *et al*. 1993) and Caravaca (Weerd 1976) and slightly bigger than *R.* cf. *lasallei* from Valdecebro 3, Valdecebro 6 and Villastar (Adrover *et al.* 1993). Because of the advanced wear of the specimens it is impossible estimating hypsodonty of these molars, as well as the observation of the diagnostic features of the occlusal surface. However, the relatively flat surfaces of the labial sides of the m1 and m2 and the reduction of the M3 agree better with *R. lasallei* than with *Ruscinomys schaubi* Villalta and Crusafont Pairó, 1956. For these reasons, we ascribe the molars from ABS-3A, AC-0, AC-0B and AC-0C to *R.* cf. *lasallei.*

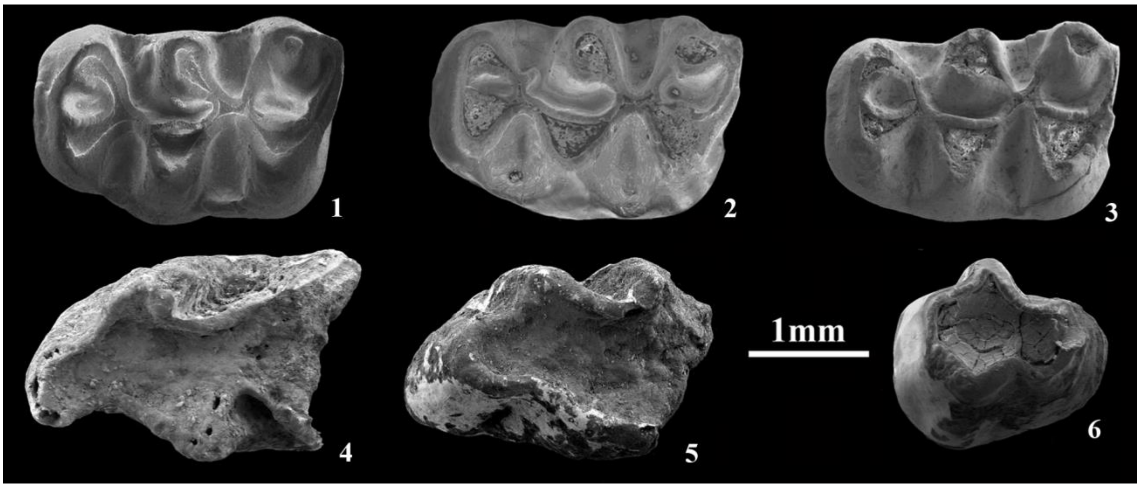


Figure V.2. Fossil rodents from ABS-3A, AC-0, AC-0B and La Bullana 2B (LB2B). *Apocricetus* cf. *barrierei* from ABS-3A and LB2B. **1**, left M1, ABS3A-37; **2**, left M1, LB2B-261; **3**, left M1, LB2B-223. *Ruscinomys* cf. *lasallei* from AC-0 and AC-0B. **4**, left m1, AC0-68; **5**, left m2, AC0-69; **6**, left m3, AC0B-14. Scale: 1 mm.

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Eliomys yevesi Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014 (Fig. V.3, 7)

Locality: ABS-3A.

Material: **1 m1,2** (ABS3A-38).

Description:

m1,2: (1.30 x 1.45): Trapezoidal outline. The anterolophid is connected to the protoconid basally. No anterotropid. The metalophid does not reach the metaconid. The centrolophid is not continuous, and its labial end is separated from the metalophid by a wide furrow. The metaconid and entoconid are separated. Well-developed posterotropid. Large hypoconid.

Discussion:

The presence of a mixture of characters typical of *E. truci* and *E. intermedius* in some populations of *Eliomys* from the Granada and Alcoy basins and the locality of Venta del Moro led Mansino *et al.* (in press, chapter X), to create a new species, *E. yevesi.* The single specimen from ABS-3A share some characters with the populations of *E. truci*, like the absence of connections between metalophid-metaconid as well as the presence of a large posterotropid, usually absent or reduced in *E. intermedius*. This molar is bigger and has higher cusps than *E. truci*, and is smaller and relatively narrower, with a more quadrangular shape than *E. intermedius*.

Eliomys intermedius Friant, 1953 (Fig. V.3, 8)

Locality: AC-0.

Material: **1 m3** (AC0-88), **1 M1,2** (AC0-87).

m3: (1.27 x 1.41): Sub-trapezoidal outline. The anterolophid and the protoconid are separated. No anterotropid. The metalophid is connected to the metaconid. There is a short centrolophid, not connected to the metalophid (Fig. V.3, 8). The metaconid and entoconid are separated. No posterotropid.

M1,2: Subrectangular outline. The anteroloph and paracone are connected basally. The protoloph and metaloph are distinctly sinuous. Both centrolophs are present. The posteroloph is connected to the endoloph. There are three roots.

Discussion:

The molars from AC-0 are slightly smaller than those of *E. intermedius* from younger localities (Mansino *et al.* in press, chapter X), but they agree in size with the population from Sète, type locality of the species (Adrover 1986) and are clearly bigger, more concave, more rounded and with more developed centrolophs than *E. yevesi* and *E. truci* (Mansino *et al.* in press, chapter X).

Subfamily Glirinae Thomas, 1897

Genus *Muscardinu*s Kaup, 1829

Muscardinus sp. (Fig. V.3, 9)

Locality: AC-0.

Material: **1 M3** (AC0-89).

Description:

M3: (> 1.10 x -): The specimen lacks the medial part of the labial border, and the posterior border is much worn, thus its length is slightly underestimated. The outline is sub-trapezoidal. The occlusal surface has eight low ridges, the anterior one straight and the others slightly convex towards the posterior side of the molar. The lingual sides of the ridges reach a continuous endoloph. There are four roots.

Discussion:

During the Late Miocene and Pliocene, three lineages have been discerned within the genus *Muscardinus*: the *M. vireti-M. meridionalis-M. helleri* lineage, *M. pliocaenicus* lineage and *M. davidi-M*. aff. *dacius* lineage (García-Alix *et al.* 2008d). The presence of four roots in M3, like in the specimen from AC-0, has been observed in *M. avellanarius* (Linnaeus, 1758), *M. dacicus* Kormos, 1930, *M. cyclopeus* Agustí, Moyà Solà and Pons-Moyà, 1982, *M. pliocaenicus* Kowalski, 1963 and *M. vireti* Hugueney and Mein, 1965. Of these taxa, only *M. cyclopeus* and *M. vireti* have eight ridges in their M3. *M. meridionalis* García-Alix, Minwer-Barakat, Martín-Suárez and Freudenthal, 2008, have also eight ridges in the M3, but the number of roots is unknown (García-Alix *et al*. 2008d).

The specimen studied is smaller than *M. cyclopeus*, being close to the maxima of *M. vireti* from Lissieu and *M. meridionalis* from PUR-4 (García-Alix *et al*. 2008d). Because of the size of the specimen and high number of ridges in M3, we consider the molar from AC-0 a form related to the line *M. vireti-M. meridionalis-M. helleri*, which maintains a medium-large size and a high number of ridges in the upper teeth (García-Alix *et al.* 2008d). No M3 of *M. helleri* have been recovered. For these reasons, we assign the M3 from AC-0 to *Muscardinus* sp.

Order Soricomorpha Gregory, 1910

Family Soricidae Fischer von Waldheim, 1817

Subfamily Soricinae Fischer von Waldheim, 1817

Tribe Nectogalini Anderson, 1879

Genus *Asoriculus* Kretzoi, 1959

Asoriculus gibberodon (Petényi, 1864) (Fig. V.3, 2–6)

Localities: ABS-3, ABS-10, AC-0.

Material: **3 m1,2** (ABS10-2, AC0-57, AC0-94), **1 m3** (ABS10-1), **1 I1** (ABS3’08-35), **1 M1** (AC0-90), **6 M2** (ABS3A-39, AC0-22, AC0-91, AC0-92, AC0-93, AC0-95).

Description:

m1,2: (TRW: 0.81; L: 1.33 x TRW: 0.90 x TLW: 0.93; L: 1.34): The talonid and the trigonid width are very similar. The difference between both values is usually bigger in m1 than in m2. The entoconid is large, high and very close to the entostylid. The entoconid crest is slightly lower, and connects basally to the metaconid. There is no mesoconid. The labial cingulum is low and narrow. The lingual cingulum is broken in two specimens and well-developed in the other one.

m3: (L: 1.03 x W: 0.57): The hypoconid and entoconid are distinct, and the talonid basin is long and narrow. The labial cingulum is more developed than in m1,2, and higher than the lingual cingulum. The protoconid is the highest cusp.

I1: (L: 1.29 x W: 1.05; LT: 0.61): Bifid and moderately fissident tooth. Well developed labial cingulum, wider ventrally than dorsally. The posterior margin is very straight. A narrow cingulum is also present along the lingual posterior border.

M1: (LPE: 1.11; LL: 1.44; BL: 1.42; AW: 1.48; PW: 1.74): The metacone is bigger and much higher than the paracone. The metastyle protrudes markedly over the labial border. The protocone is connected to the paracone by a high crest and to the hypocone by a lower crest. The hypocone is smaller and lower than the protocone, and connected to the posteroloph (Morphotype B, Reumer 1984). The hypoconal flange is wide. The posterior emargination is smooth. The posteroloph extends in a continuous posterior cingulum, which reaches the base of the metastyle.

M2: (LPE: 1.20 x LL: 1.51 x BL: 1.44 x AW: 1.60 x PW: 1.93): The metacone is much higher than the paracone. The metastyle protrudes over the labial border. The protocone is connected to the paracone by a high crest. The hypocone and the protocone are separated by a narrow valley. The hypocone is the lowest and smallest cusp, and reaches the posteroloph (Morphotype B, Reumer 1984). The hypoconal flange is narrower than in the m1. The posterior emargination is smooth. The posteroloph extends in a continuous posterior cingulum, which reaches the base of the metastyle.

Discussion:

Asoriculus gibberodon (Petényi, 1864) is a very common soricid in the Pliocene and Early Pleistocene of Europe, also present in the latest Miocene from Maramena (Doukas *et al*. 1995). In the studied material, the presence of a high entoconid crest in the lower molars, a talonid basin in m3, fissident upper incisors and a moderate posterior emargination agree with this species (Reumer 1984). The presence of a small hypocone connected to the posteroloph is consistent with the Morphotype B of Reumer (1984).

Asoriculus gibberodon shows a wide biometrical variability, differing greatly from one locality to another (Reumer 1984, Minwer-Barakat *et al.* 2010). The lower molars from the studied localities are consistent with the smaller sizes of the specimens from Villány 3, Csarnóta 2, Osztramos 1 and 9 (Reumer 1984), Varshets (Popov 2003), Venta Micena 1 (Martín-Suárez 1988) and TCH-1, TCH-1B and TCH-3 (Minwer-Barakat *et al.* 2010), Fuente Nueva 3 and Barranco León (Furió 2007), while the upper molars are relatively bigger.

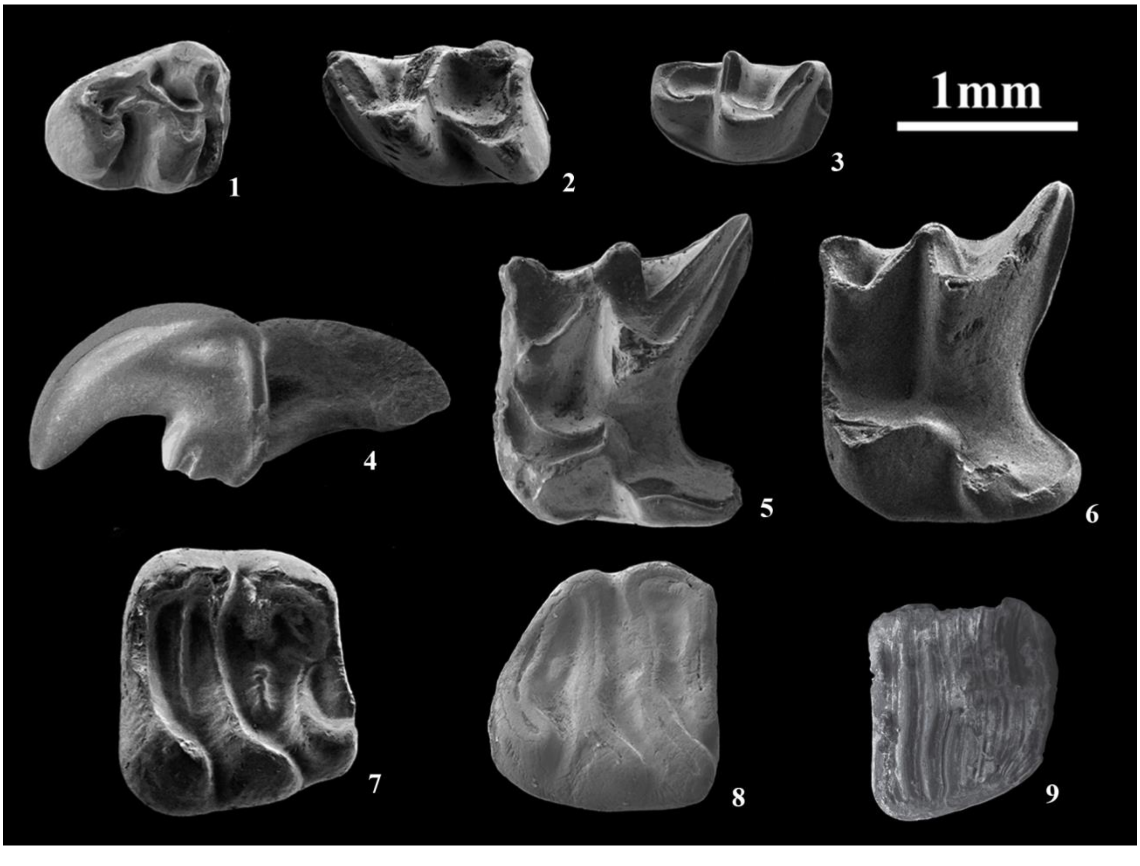


Figure V.3. Fossil rodents from ABS-3, ABS-3A, ABS-10 and AC-0. *Neocricetodon* sp. from AC-0C. **1**, right m3, AC0-9. *Asoriculus gibberodon* from ABS-3, ABS-10 and AC-0. **2**, left m1,2, AC0-57; **3**, right m3, ABS10-1; **4**, left I1, ABS3’08-35; **5**, left M1, AC0-90; **6**, left M2, ABS3A-39. *Eliomys yevesi* from ABS-3A. **7**, right m1,2, ABS3A-38. *Eliomys intermedius* from AC-0. **8**, right m3, AC0-88. *Muscardinus* sp. from AC-0. **9**, left M3, AC0-89. Scale: 1 mm.

Soricidae indet.

Locality: AC-0.

Material: **1 m3** (AC0-97).

Description:

m3: The anterior part of the molar is missing. The talonid basin is not reduced.

Discussion:

The shape of the m3 resembles *Asoriculus*. Nevertheless, its size is much bigger and clearly out of the measure range than those of *Asoriculus gibberodon* described above.

Order Erinaceidomorpha Gregory, 1910

Family Erinaceidae Bonaparte, 1838

Erinaceidae indet.

Localities: AC-0, AC-0B.

Material: **1 p4** (AC0B-19), **1 P1,2** (AC0-63), **1 P4** (AC0-131), **1 M2** (ABS3-10).

Description:

p4: The posterior side is missing. The protoconid is very large. There is no metaconid. The paraconid is connected to the protoconid by a low paralophid.

P1,2: (1.60 x 0.87): The low and small paraconid is connected to the protoconid by a low paralophid. There is no metaconid. There is no posterior cingulum.

P4: The labial side of the specimen is missing. The protocone and hypocone are well developed, but the former is higher. There is a well-developed posterior cingulum.

M2: The specimen is broken anteriorly and lingually. The parastyle is small and protrudes from the anterolabial part of the molar. The labial cingulum is low and wide. There is a low mesostyle. The metacone is big and high. The metastyle is well developed.

Discussion:

The scarcity and poor state of preservation of the material prevent us from reaching a generic ascription.

V.3. Discussion

V.3.1. Biostratigraphy

The faunal lists of the localities Alcoy-Barranco, ABS-3, ABS-3A and AC-0 are given in Table V.3. Considering subsequent synonymies, the faunal list of Alcoy-Barranco (Thaler *et al*. 1965, Adrover 1969) is very similar to the new faunas from AC-0. In particular, *Stephanomys* aff. *donnezani* from Alcoy-Barranco was renamed as *Stephanomys medius* by Cordy (1976), which is considered a synonym of *S. cordii* (García-Alix *et al.* 2008a), *Anthracomys ellenbergeri* was considered as *Anthracomys meini* by Michaux (1969), and included later within the genus *Paraethomys* by Jaeger *et al.* (1975), and finally, *Cricetus* aff. *angustidens* is considered *Apocricetus barrierei* by Freudenthal *et al.* (1998).

Based on the faunal list of Alcoy-N, López-Martínez (1989) gives a Late Miocene age for this locality. This site has yielded remains of *Prolagus michauxi*, *Trischizolagus* cf. *maritsae*, *Eliomys* sp., *Ruscinomys lasallei*, *Cricetus* cf. *kormosi* (synonym of *Apocricetus alberti* according to Freudenthal *et al.* 1998), Gerbilidae indet., *Occitanomys* sp., *Stephanomys* sp., *Apodemus primaevus* (synonymized as *Rhagapodemus primaevus* in Martín-Suárez and Mein 1998), *Paraethomys miocaenicus* and *Paraethomys* cf. *anomalus* (both considered synonyms of *Paraethomys meini* by several authors, see García-Alix *et al.* 2008a for a complete list). *Cricetus* cf. *kormosi* (*Apocricetus alberti* in synonymy) is a biostratigraphic marker from the Late Miocene (MN13). The presence of an unclassified gerbillid in Alcoy-N does not allow to determine the exact age because this group arrives to the Iberian Peninsula during MN13 (*Debruijnimys almenarensis* Agustí, 1990), surviving until MN15 (*Debruijnimys julii* Castillo and Agustí, 1996). Both *Debruijnimys* sp. (Agustí and Casanovas-Vilar 2003) and *D. julii* are present in early MN14 (chapter VII), being uncertain if the form present in Alcoy-N is related to *D. almenarensis* or to these other taxa. In the northern side of the Gormaget ravine, a locality containing gerbil remains, Alcoy-4B (Freudenthal pers. comm.), is present. Probably, Alcoy-4B represents a Ruscinian (Early Pliocene) level, younger than Alcoy-N. The presence of *Cricetus* cf. *kormosi* (*Apocricetus alberti*) in Alcoy-N (López-Martínez 1989) would be the main argument to assign this locality to the MN13.

On the other hand, an equivalent stratigraphic position for the classic locality of Alcoy-Mina and AL2-C and AL2-D is probable (Mansino *et al.* 2013, chapter IV), placing these localities in Early Ruscinian (MN14). The faunal content of AL2-C and AL2-D shows that they are younger than the localities from the ABS and AC sections, having yielded *Stephanomys cordii* and *Apocricetus* cf. *angustidens*, being their age probably close to the Early-Late Ruscinian boundary (MN14-MN15, Mansino *et al.* 2013, chapter IV).

In ABS-3 and ABS-3A, the occurrence of *Stephanomys dubari*, *Apodemus gorafensis* and *Paraethomys meini* is typical of the latest Turolian-earliest Ruscinian (García-Alix *et al.* 2008a). The presence of *Ruscinomys lasallei* is common in the Early Ruscinian, although it is also present in the Late Turolian of Granada (García-Alix *et al.* 2008b) and *R.* aff. *lasallei* is found in the Late Turolian of Teruel (Adrover *et al.* 1993, García-Alix *et al.* 2008b). *Stephanomys cordii* appears in MN14 (Mein *et al.* 1990, Sesé 2006a, Minwer-Barakat 2005, Minwer-Barakat *et al.* 2012), and the presence in AC-0 of a very close form, *S.* aff. *cordii*, suggest an Early Ruscinian age for this locality.

Eliomys yevesi has been described with material from the Late Turolian locality of Venta del Moro, being present also in some Early Ruscinian localities like PUR-4, CLC-3B in the Granada Basin, and AF-1’06 and AF-1’07 in the Alcoy Basin (chapter VI). This taxon is the ancestor of *E. intermedius* (Mansino *et al.* in press, chapter X), which is present in AC-0.

Alcoy-Barranco (Thaler *et al*. 1965, Adrover 1969)	ABS-2 (This thesis)	ABS-3 (This thesis)	ABS-3A (This thesis)	ABS-7 (This thesis)	ABS-8 (This thesis)	ABS-9 (This thesis)	AC-0B (This thesis)	AC-0C (This thesis)	AC-0 (This thesis)
Apodemus sp.	-	*Apodemus gorafensis*	-	-	-	-	-	*Apodemus gorafensis*	*Apodemus gorafensis*
Anthracomys ellenbergeri	*Paraethomys meini*	*Paraethomys meini*	*Paraethomys meini*	-	-	-	*Paraethomys meini*	-	*Paraethomys meini*
-	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*	-	-	-	*Paraethomys* aff. *abaigari*	-	*Paraethomys* aff. *abaigari*
-	*Micromys* sp.	-	-	-	-	*Micromys* sp.	-	-	-
Parapodemus sp.	-	-	-	-	-	-	-	-	-
-	-	*Occitanomys alcalai*	*Occitanomys alcalai*	-	-	-	*Occitanomys alcalai*	*Occitanomys alcalai*	*Occitanomys alcalai*
Stephanomys aff. *donnezani*	*Stephanomys dubari*	*Stephanomys dubari*	*Stephanomys dubari*	*Stephanomys* sp.	*Stephanomys* aff. *cordii*	*Stephanomys* sp.	*Stephanomys* aff. *cordii*	*Stephanomys* aff. *cordii*	*Stephanomys* aff. *cordii*
Cricetus aff. *angustidens*	-	-	*Apocricetus* cf. *barrierei*	-	-	-	-	-	-
-	-	-	-	-	-	-	-	*Neocricetodon* sp.	-
-	-	-	-	-	-	-	*Cricetinae indet.*	-	-
Ruscinomys lasallei	-	-	*Ruscinomys* cf. *lasallei*	-	-	-	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*
Eliomys aff. *intermedius*	-	-	*Eliomys yevesi*	-	-	-	-	-	*Eliomys intermedius*
Muscardinus sp.	-	-	-	-	-	-	-	-	*Muscardinus* sp.
-	-	*Asoriculus gibberodon*	-	-	-	-	-	-	*Asoriculus gibberodon*
Galerix sp.	-	-	-	-	-	-	-	-	Erinaceidae indet.
Sorex sp.	-	-	-	-	-	-	-	-	Soricidae indet.

Table V.3. Faunal lists of the localities Alcoy-Barranco, ABS-3, ABS-3A and AC-0.

The presence of *Muscardinus* sp. in AC-0 is consistent with the Turolian and Ruscinian populations of the lineage *M. vireti-M. meridionalis-M. helleri* (García-Alix *et al.* 2008d). Thaler *et al.* (1965) mentioned the presence of two M1 of *Muscardinus* in Alcoy-Barranco, with six transversal ridges each. Despite the scarcity of material of this glirid in AC-0, the morphology described in this locality is clearly consistent with a form of the previously cited lineage.

The presence of *Stephanomys* aff. *cordii* in ABS-8, AC-0, AC-0C and AC-0B supports an Early Ruscinian age for these localities (Minwer-Barakat 2005, Minwer-Barakat *et al.* 2012), slightly younger than ABS-1, ABS-2, ABS-3 and ABS-3A (Fig. II.2), in which *S. dubari*, ancestor of *S. cordii*, is present. The cricetid *Apocricetus barrierei* is considered a guide taxon for the Early Ruscinian in the Iberian Peninsula (Freudenthal *et al*. 1998, García-Alix *et al.* 2008b), and its presence supports an Early Ruscinian age for ABS-3A. In the same way, the presence of a big sized *Paraethomys*, *P*. aff. *abaigari*, in ABS-2, ABS-3, ABS-3A, AC-0 and AC-0B supports an Early Ruscinian age for these sites (Mein *et al.* 1990, García-Alix *et al.* 2008a) also. Therefore, all taxa yielded by this section confirm an Early Ruscinian age for the new micromammal localities represented in the sections of Alcoi Barranc Sud (ABS) and Alcoi Cristian (AC).

V.3.2. Palaeoecology

The species spectrum of micromammal assemblages has been widely used as a palaeoclimatical indicator. For these analysis, some authors have proposed a minimum sample size of at least 100 specimens (Daams *et al*. 1999, García-Alix *et al*. 2008c), while others used a minimum of 50 specimens (Casanovas-Vilar and Agustí 2007), arguing that in most cases the bigger samples only add one or two new species to the assemblage, and the abundance of these new species is less than 1 %. The locality of AC-0 has yielded 91 identifiable specimens, whereas in the other localities the sample is too scarce to perform a proper analysis.

Following García-Alix *et al.* (2008c), we have considered the taxa *Apodemus gorafensis*, *Micromys*, *Paraethomys meini*, *Occitanomys alcalai* and *Asoriculus gibberodon* as warm weather indicators, and *Ruscinomys* as a cold indicator. Also, *Apodemus gorafensis*, *Occitanomys alcalai*, *Asoriculus gibberodon* and Soricidae indet. are regarded as wet environment indicators, whereas *Ruscinomys* and *Paraethomys meini* are associated with dry conditions. Traditionally the genera *Eliomys* and *Muscardinus* have been considered wet environment indicators (see García-Alix *et al.* 2008c, and references therein), but Freudenthal *et al.* (2014) state that these taxa cannot be considered as indicators of humidity based on their current distribution.

Regarding the habitat, most of the taxa from AC-0 are eurytopic (Table V.4) except *Ruscinomys*, which indicate open environments, and *A. gibberodon* and *Muscardinus*, which are associated with forested habitats (García-Alix *et al.* 2008d, Freudenthal *et al*. 2014). The genus *Eliomys* is a habitat generalist, with extant representatives ranging from environments with a moderate forest cover and a high annual precipitation to open semi-desertic environments (Freudenthal *et al.* 2014).

According to Agustí (1990), the presence of *Eliomys* instead of *Glis* in the western basins of the Iberian Peninsula suggests dryer and warmer conditions than in the Catalonian basins (NE Spain). The analysis of the faunal assemblage of AC-0, in which both *Eliomys* and *Muscardinus* are present, agrees with this interpretation, suggesting warm and relatively dry conditions (see Table V.4).

As discussed before, the scarcity of the remains from the other localities prevents a proper palaeoenvironmental interpretation, although the relative percentages of the taxa present in ABS-3 and ABS-3A indicate similar conditions to those of AC-0. However, the localities ABS-9, ABS-10 and AC-0C have yielded mostly taxa considered as humid indicators. ABS-9 has yielded *Micromys* sp. and *Asoriculus gibberodon*, both wet environments indicators, and the only micromammal fossils recovered from ABS-10 belong to *A. gibberodon*. In the assemblage from AC-0C *Apodemus* cf. *gorafensis* and *O. alcalai* are considered indicators of humidity. Therefore, ABS-9, ABS-10 and AC-0C may represent a wetter environment hiatus in the series, although these changes could also be explained by local or regional environments rather than general trends (García-Alix *et al.* 2013, Freudenthal *et al.* 2014).

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	Wet	Dry	Eurytopic	Cold	Warm	Eurytopic	Open	Forested	Eurytopic
AC-0	17.06	41.42	40.54	14.21	43.57	41.25	14.21	6.57	78.25

Table V.4. Percentages of species according to humidity, temperature and habitat parameters in the locality AC-0. These percentages have been obtained by dividing each taxon by its number of diagnostic elements, as proposed by Martín-Suárez (1988). The taxa with unknown preferences are not shown.

V.4. Conclusions

In the lower deposits from the ABS section (Gormaget area, Alcoy Basin), two new localities (ABS-3 and ABS-3A) have yielded abundant mammal fossil remains. The presence in ABS-3 of *Apodemus gorafensis, Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai*, *Stephanomys dubari* and *Asoriculus gibberodon* and in ABS-3A of *Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai, Stephanomys dubari, Apocricetus* cf. *barrierei*, *Ruscinomys* cf. *lasallei* and *Eliomys* cf. *yevesi* allow us to assign an Early Ruscinian age, close to the Mio-Pliocene boundary, for these sites.

Near the top of the youngest stratigraphic sequence here studied, a new locality (AC-0) has yielded also a rich fossil mammal assemblage, comprising to *Apodemus gorafensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Paraethomys* aff. *abaigari, Stephanomys cordii*, *Asoriculus gibberodon*, *Ruscinomys* cf. *lasallei*, *Muscardinus* sp., *Eliomys intermedius*, Erinaceidae indet. and Soricidae indet. This faunal assemblage suggests an Early Ruscinian age for this locality.

The palaeoecological context of the studied deposits shows, from the bottom to the top of the stratigraphic sequence, a changing palaeoenvironment. While the scarce data from some of the lower deposits (localities ABS-9, ABS-10 and AC-0C) suggest wetter conditions for these sites, the taxa present in AC-0 indicate warm and relatively dry conditions. According to the stratigraphical position and the environment requirements of the small mammal fauna located in these localities, a progressive aridification process may occur along the lower part of the Early Pliocene in the Alcoy Basin.

The presence of *Micromys* and *Muscardinus* in several localities from the new sections of the Alcoy Basin represent the first record of these genera in the area.

Finally, and based on the faunal content of AC-0, characterized by the presence of *R. lasallei* and *Stephanomys cordii*, its relative stratigraphic position, deduced age and geographic proximity, we consider AC-0 as a probable coetaneous level to that of the classical site described by Adrover (1969), Alcoy-Barranco.

CHAPTER VI. MIO-PLIOCENE RODENT ASSEMBLAGES FROM ALCOI FORN (ALCOY BASIN, EASTERN SPAIN). BIOSTRATIGRAPHICAL AND PALAEOCLIMATICAL INFERENCES.

VI.1. Material and methods

During the summer of the years 2006 and 2007, approximately 3,200 kg. of sediment were extracted from the levels AF-1’06, AF-1’07, AF-1A and AF-2. The resulting fossils are kept in the *Museu de Geologia of the Universitat de València* (MGUV) with the field labels AF1’06-, AF1’07-, AF1A- and AF2-.

The nomenclature and measurement methods are those of Martín-Suárez and Freudenthal (1993) for the Muridae family, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, and Cuenca-Bescós (1988) and Reumer and Hoek Ostende (2003) for the Sciuridae. We use the term neoenterostyle (Lazzari *et al*. 2010) for the cusp situated lingually between t1 and t4 in the nomenclature of murids.

VI.2. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1826

Type species: *Mus agrarius* Pallas, 1778

Apodemus cf. *gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. VI.1, 1)

Locality: AF-1’06.

Material: **1 m2** (AF1’06-38), **1 M2** (AF1’06-104).

Description:

m2: Large oval anterolabial cusp, connected to the well-developed labial cingulum. There is a hint of distal spur. There is a large round c1 attached to the labial side of the hypoconid, and an even larger accessory cusp connected to the labial side of the protoconid. The posterior heel is large, oval and in central position. Roots are not preserved.

M2: (1.67 x 1.43): Large t1, connected basally to the lingual side of the t5. The t3 is small and isolated. The t6 and t9 are very close. There is a large oval t7, separated from the t4, and a reduced t12.

Discussion:

The morphology of the specimens, with a well-developed labial cingulum, large c1 and accessory cusps in m2 and a well-developed t7 in M2, is consistent with the genus *Apodemus*. The single M2 (1.67 x 1.43) is smaller than *Apodemus jeanteti* and *Apodemus agustii*, and larger than *Apodemus gudrunae*. It differs from *Apodemus agustii* by the close position of t6 and t9, and from *Apodemus gudrunae* in the greater development of the t7. This molar agrees in size with *Apodemus gorafensis* from its type locality, Gorafe-A (Ruiz Bustos *et al.* 1984), PUR-4, PUR-13, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al.* 2008a), AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV), LB2B and LB3 (chapter VII).

Genus *Paraethomys* Petter, 1968

Type species: *Paraethomys filfilae* Petter, 1968.

Paraethomys meini Michaux, 1969 (Fig. VI.1, 2–8)

Localities: AF-1’06, AF-1’07, AF-1A, AF-2.

Material: **14 m1** (AF1’06-1 to AF1’06-3, AF1’06-5, AF1’06-7 to AF1’06-11, AF1’06-15, AF1’06-17, AF1’06-18, AF1’06-24, AF1A-1), **19 m2** (AF1’06-30 to AF1’06-34, AF1’06-36 to AF1’06-41, AF1’06-43 to AF1’06-45, AF1’06-163, AF1’07-

6, AF1’07-7, AF1’07-11, AF2-1), **11 m3** (AF1’06-50 to AF1’06-53, AF1’06-55 to AF1’06-57, AF1’06-59, AF1’07-14, AF1’07-38, AF1A-6), **22 M1** (AF1’06-64 to AF1’06-66, AF1’06-68, AF1’06-69, AF1’06-71 to AF1’06-79, AF1’06-82, AF1’06-84, AF1’06-85, AF1’06-89, AF1’06-122, AF1A-8, AF1A-11, AF2-2), **26 M2** (AF1’06-90 to AF1’06-92, AF1’06-94, AF1’06-96 to AF1’06-98, AF1’06-100 to AF1’06-103, AF1’06-105 to AF1’06-109, AF1’06-111, AF1’06-114, AF1’06-116, AF1’06-121, AF1’07-23, AF1’07-24, AF1’07-26, AF1’07-31, AF1A-12, AF1A-13), **4 M3** (AF1’06-123, AF1’06-125, to AF1’06-127).

Measurements: Table VI.1.

Description:

m1: The anteroconid is clearly asymmetrical in two molars, symmetrical or slightly asymmetrical in the others. There is a small and low tma in 6 out of 14 specimens (Fig. VI.1, 2), and an enamel funnel in the connection between the anteroconid and the protoconid-metaconid in 6 out of 13 specimens. The labial cingulum may be narrow (2) or well developed (11) (Fig. VI.1, 2). There is a hint of distal spur but in one specimen. There are one or two accessory cusps, variable in size. The posterior heel may be reduced, laminar (Fig. VI.1, 2) or oval.

m2: The anterolabial cusp is large, round or oval. The labial cingulum is well developed in 9 out of 17 specimens. In 9 out of 17 molars there is a much reduced distal spur. There is great variability in the size of the c1, and a small accessory cusp connected basally to the protoconid is present in half of the specimens. The posterior heel is variable in size, laminar in one specimen and tubercular in the others, lingually displaced (5) or central (10). There are two roots.

m3: The anterolabial cusp is absent or much reduced. The hypoconid-entoconid complex is separated from the protoconid-metaconid pair. One specimen has a small round accessory cusp.

M1: The t2 and t3 are closer than t1 and t2. Four specimens have a distal spur on the t1. Half of the molars have a distal spur on the t3. One specimen has a well-developed neoenterostyle (Fig. VI.1, 6), isolated from the other cusps. The connection between t4 and t8 is very low. The t12 is well developed.

M2: T The t1 is large, and 12 out of 25 specimens have a distal spur on the t1. The t3 is reduced and isolated. Three specimens have a slightly swollen t9, which is reduced or absent in the others (Fig. VI.1, 7). Four molars have a very low and small t12.

M3: The t1 is large and isolated. The t3 is absent. The t8 is connected to the t4-t5-t6 junction.

Discussion:

The presence of a funnel of enamel in some m1, moderate or reduced labial cingulum in the lower molars, reduced or absent anterolabial cusp in m3 and reduced or absent t9 in M2 are typical traits of *Paraethomys*. *Paraethomys meini* Michaux, 1969 from AF-1'06, AF1-'07, AF-1A and AF-2 is smaller than *P. abaigari* Adrover, Mein and Moissenet, 1988 and *P. jaegeri* Montenat and Bruijn, 1976.

The measurements of *P. belmezi* Castillo Ruiz, 1990, fall within the range of variation of the studied specimens, but this species has a well-developed tma in m1, absent or reduced t3 and isolated t8 in M2 and isolated t6 and t9 in M1. The specimens studied are very similar to *Paraethomys lissasfensis* Geraads, 1998, from the Late Miocene North African locality of Lissasfa, possibly related to the Spanish *Paraethomys* forms (Geraads 1998). This taxon differs from the European *P. meini* by presenting always a deep valley between t2 and t3 and a distal spur on t3 of the M1. The molars from AF-1'06, the richest of the localities studied, show a great variability in size. The remains from the other localities fall within this variability.

The molars from AF-1'06, the richest of the localities studied, show a great variability in size. The remains from AF-1'07, AF-1A and AF-2 fall within this variability. The size of *P. meini* from the localities of Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover 1986), Villalba Alta Río, Peralejos E (Adrover *et al.* 1988), Celadas 9, La Gloria 4 (Adrover *et al.* 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11, BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (García-Alix *et al.* 2008a), and *Paraethomys anomalus* from Maritsa and *Paraethomys miocaenicus* from Khendek el Ouaich (Adrover 1986), considered synonyms of *P. meini* by several authors (Weerd 1976, Adrover 1986, Martín-Suárez 1988, Castillo 1990, Minwer-Barakat 2005, García-Alix 2006, García-Alix *et al.* 2008a), is in general consistent with our specimens.

However, the larger specimens from AF-1’06 agree with the lower values of *P.* aff. *abaigari*. In younger localities from the Alcoy Basin, like AL2-C and AL2-D (Mansino *et al.* 2013) two species of *Paraethomys*, which differ mainly in size, can be discerned. This situation is also found in a number of Pliocene localities from the Teruel and Granada basins (Adrover 1986, Adrover *et al.* 1988, Mein *et al.* 1990, García-Alix *et al.* 2008a). It has been suggested that the morphotypes that led to two discernible *Paraethomys* species during the Pliocene are already present in older assemblages (García-Alix 2006, García-Alix *et al.* 2008a), close to the Mio-Pliocene boundary, like Peralejos-E and PUR-4. These populations show great variability in size and morphology, although it is assumed that they comprise a single species.

Element	Locality	Parameter	n	min.	mean	max.
m1	AF-1’06	L	10	2.00	2.11	2.25
		W	10	1.24	1.34	1.43
	AF-1A	L	2	2.04	2.05	2.05
		W	2	1.22	1.25	1.27
m2	AF-1’06	L	9	1.42	1.55	1.69
		W	11	1.33	1.44	1.57
	AF-1’07	L	2	1.46	1.52	1.58
		W	3	1.40	1.42	1.44
m3	AF-1’06	L	7	1.30	1.35	1.40
		W	7	1.17	1.24	1.32
	AF-1’07	L	2	1.24	1.36	1.47
M1	AF-1’06	L	13	2.14	2.40	2.68
		W	15	1.42	1.57	1.68
	AF-1A	L	1	-	2.28	-
		W	1	-	1.55	-
M2	AF-1’06	L	13	1.53	1.74	1.93
		W	2	1.45	1.53	1.60
M3	AF-1’06	L	3	1.19	1.25	1.32
		W	4	1.19	1.24	1.34

Table VI.1. Measurements in millimetres of the teeth of *Paraethomys meini* from AF-1’06, AF-1’07 and AF-1A. n= number of measurable specimens.

Stephanomys Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Fig. VI.1, 9–15)

Localities: AF-1’06, AF-1’07, AF-1A.

Material: **13 m1** (AF1’06-4, AF1’06-6, AF1’06-12, AF1’06-13, AF1’06-16, AF1’06-19, AF1’06-20, AF1’06-22, AF1’06-23, AF1’06-26, AF1’07-1, AF1’07-2, AF1’07-3), **11 m2** (AF1’06-29, AF1’06-35, AF1’06-46, AF1’07-4, AF1’07-5, AF1’07-8, AF1’07-

9, AF1’07-10, AF1’07-21, AF1’07-33, AF1A’07-3), **8 m3** (AF1’06-48, AF1’06-49, AF1’06-54, AF1’07-13, AF1’07-15, AF1’07-16, AF1’07-39, AF1A-5), **9 M1** (AF1’06-62, AF1’06-63, AF1’06-67, AF1’06-70, AF1’06-95, AF1’06-112, AF1’07-19, AF1A’07-9, AF1’07-18), **5 M2** (AF1’06-93, AF1’06-99, AF1’06-110, AF1’06-113, AF1’07-20), **3 M3** (AF1’07-27, AF1’07-28, AF1’07-29).

Measurements: Table VI.2.

Description:

m1: The anteroconid is slightly asymmetrical, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is narrow in two specimens and well developed in the others. The longitudinal crest is well developed, reaching the protoconid-metaconid junction in 3 out of 10 specimens and the labial side of the metaconid in the others. The c1 is large, and one or two accessory cusps may be present. The posterior heel is similar in size to the c1, oval or triangular, and central or lingually displaced.

m2: The anterolabial cup is high, large and connected to the protoconid and a reduced labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. A small c1 and an accessory cusp may be present. The posterior heel is large, oval or triangular, lingually displaced (3) or in a central position (5). There are two roots.

m3: The anterolabial cusp is reduced and connected basally to the protoconid. The longitudinal crest may reach the metaconid (3), the protoconid-metaconid junction (3), the protoconid (1) or be reduced to a spur (1). Two specimens have a small crest-like c1. There are two roots

M1: The t1 is displaced backwards. There are a small t1 bis and t2 bis, which cannot be observed in worn specimens. The distal crests of t1 and t3 reach the t4-t5 and the t5-t6 junction respectively. The t4-t5-t6-t8 and t9 are connected. The t7 is absent. There is a small t12.

M2: The t1 is large, with a small accessory cusp attached to its posterolabial side. A longitudinal crest connects the t1 and the t4-t5 junction. The longitudinal crest on the t3 may be complete (3) or a spur that does not reach the t5-t6 junction (2). There is no t7. The t9 is well developed. The t12 is absent or reduced.

M3: The t1 is connected to the t5 in one specimen and isolated in the other one. The t3 is absent. The t4, t5 and t6 are connected. There is a small t9 connected to the labial side of the t8 (Fig. VI.1, 15)

Discussion:

The great hypsodonty of the specimens, high longitudinal crests in the lower molars and crests or spurs on the t1 and t3 of the upper molars suggest that the studied material belongs to the genus *Stephanomys.* These molars are smaller, lower crowned and have a less pronounced stephanodonty than the *Stephanomys* from the Pliocene and Pleistocene (see Minwer-Barakat *et al.* 2011a, and references therein).

The molars from AF-1’06, AF1’07 and AF-1A are larger than *Stephanomys ramblensis* van de Weerd, 1976, present in MN13 (Adrover *et al.* 1993, Mein *et al.* 1990, Sesé 2006a, García-Alix *et al.* 2008a), although some specimens like a particularly small m1 from AF-1’06 (see Fig. VI.1, 9), which agree in size with the lower values of *S. dubari* from the localities PUR-4 and PUR-7 (García-Alix *et al.* 2008a), also fall within the range of variation of *S. ramblensis*. The average values fall within the range of variation of *S. dubari* from Castelnou 3, type locality of the species (Aguilar *et al*. 1991) and are similar to *S. dubari* from the Granada Basin (García-Alix *et al.* 2008a).

Stephanomys cordii from Peralejos-E (Adrover *et al.* 1988) and La Gloria-4 (Adrover *et al.* 1993) is considered to be *S. dubari* by García-Alix *et al.* (2008a), being its size similar to the specimens studied in this work.

The development of posterior crests and spurs in M1 and M2 is much more frequent in *S. dubari* (MN13-MN14) than in *S. ramblensis* (MN13). The studied molars show well-developed crests on the t1 and t3 of the M1. In M2, the posterior crest of the t1 is complete in all four specimens, while 3 out of 5 molars have a complete crest on the t3, and another two just a spur. This morphology is consistent with *S. dubari* from the Granada Basin (García-Alix 2006, García-Alix *et al.* 2008a).

The studied specimens have been directly compared with the collection of *S. cordii* from AL2-C and AL2-D (Mansino *et al.* 2013, chapter IV) housed at the Museum of Geology of the University of Valencia. These molars are larger and have higher crowns and more developed crests than the specimens from AF-1’06, AF1’07 and AF-1A. The longitudinal crests are higher in *S. cordii,* being unusual the isolated t1 or t3 in M1 and M2. In addition, the M1 have more developed t1bis and t2bis, and the position of t1 respect t3 is more symmetric in *S. cordii*, being posteriorly displaced in *S. dubari* (Cordy 1976).

Element	Locality	Parameter	n	min.	mean	max.
m1	AF-1’06	L	3	1.97	2.06	2.10
		W	5	1.26	1.39	1.56
	AF-1’07	L	1	-	2.17	-
		W	2	1.42	1.42	1.42
m2	AF-1’06	L	1	-	1.53	-
		W	1	-	1.41	-
	AF-1’07	L	5	1.57	1.62	1.64
		W	5	1.48	1.55	1.64
m3	AF-1’06	L	3	1.23	1.34	1.44
		W	3	1.24	1.21	1.37
	AF-1’07	L	3	1.25	1.31	1.35
		W	3	1.26	1.28	1.30
M1	AF-1’06	L	4	2.39	2.54	2.60
		W	6	1.71	1.75	1.79
M2	AF-1’06	L	3	1.62	1.75	1.89
		W	4	1.65	1.68	1.71
M3	AF-1’06	L	1	-	1.21	-
		W	2	1.05	1.14	1.22

Table VI.2. Measurements in millimetres of the teeth of *Stephanomys dubari* from AF-1’06, AF-1’07, and AF-1A. n= number of measurable specimens.

Genus *Occitanomys* Michaux, 1969

Type species: *Occitanomys brailloni*, Michaux, 1969

Species: *Occitanomys alcalai,* Adrover, Mein and Moissenet, 1988 (Fig. VI.1, 16-19)

Localities: AF-1’06, AF-1’07, AF-1A.

Material: **3 m1** (AF1’06-14, AF1’06-25, AF1’06-37), **3 m2** (AF1’06-21, AF1’06-42, AF1’06-143), **4 m3** (AF1’06-58, AF1’06-61, AF1A’07-4, AF1A’07-7), **3 M1** (AF1’06-80, AF1’06-81, AF1’07-10), **1 M2** (AF1’07-25), **4 M3** (AF1’06-128, AF1’06-129, AF1’06-130, AF1’06-131).

Measurements: Table VI.3.

Description:

m1: Small and low tma. Symmetrical anteroconid. There is a funnel of enamel in the connection between the anteroconid and the protoconid-metaconid in 4 out of 11 specimens. There is a hint of longitudinal spur. Well-developed labial cingulum. There are no accessory cusps. The c1 is large and round, connected basally to the hypoconid. The posterior heel is large, oval, and slightly displaced lingually.

m2: Well-developed oval anterolabial cusp, in contact with a moderate labial cingulum. All the specimens have a longitudinal spur. In one of the molars, extremely worn, this spur reaches the metaconid-protoconid pair. One specimen has a medium-sized c1. There is a medium-sized posterior heel in central position.

m3: Absent or reduced anterolabial cusp. There is neither c1 nor distal spur.

M1: The t1 is displaced backwards respect the t2 and t3. The three specimens show a t1 bis, and two of them have also a reduced t2bis (Fig. VI.1, 18). The connection between the t1 and the t1 bis is low. A posterior crest connects the t1 and the t5. The t3 presents a hint of distal spur directed towards the t5. The t6 and t9 are connected. There is no t7. There is a very small t12, absent in one specimen.

M2: There is a small t1 bis attached to the posterior side of the t1. The t1 has a very low posterior spur. The t3 is small and connected basally to t1. There is no t7. The t9 is well-developed. The t12 is just a small fold of the enamel.

M3: Isolated t1. There is no t3. One specimen has the t4-t5-t6 junction and the t8 connected, forming a funnel of enamel, while in another two the t4-t5-t8 junction is connected to t6 and t9 by a low spur (Fig. VI.1, 19).

Discussion:

The *Occitanomys* from AF-1’06, AF-1’07 and AF-1A are similar in size to the largest specimens of *O. alcalai* from Peralejos E (type locality, Adrover *et al.* 1988), Valdecebro 3 and 6 and La Gloria 4 and 5 (Adrover *et al.* 1988 and 1993) and the Granada Basin (García-Alix *et al.* 2008a). The material from the studied localities has the diagnostic features of *O. alcalai*: symmetric anteroconid, relative high crown, well-developed t1 bis, absence of isolated cusps in the upper molars and lack of complete longitudinal crests in the lower molars. The morphology of *O. alcalai* is quite heterogeneous, with variations in the development of the longitudinal spur of the lower molars, labial cingulum, posterior spurs on t1 and t3, t1 bis in M1 and M2, t2 bis in M1 and number of roots of the M2 (García-Alix *et al.* 2008a).

Occitanomys adroveri (Thaler, 1966) is larger than *O. alcalai*. Our specimens agree with the smallest values of *O. adroveri* from Los Mansuetos (type locality, Adrover 1986), Masada del Valle 3 and 5, Concud 3 (Weerd 1976), Aljezar B (Adrover 1986), Crevillente 7, 8, 15 and 17 (Martín-Suárez and Freudenthal 1993). This latter species has more developed longitudinal connections in m1 and m2, an asymmetrical anteroconid, a less developed labial cingulum, a less posterior t1 and a higher crown in M1 and less developed longitudinal crests in the upper molars (García-Alix *et al.* 2008a, Minwer-Barakat *et al.* 2009a and 2009b). The anterolabial cup is more frequent in *O. adroveri*, whereas the t1-t5 connection in M2 is more common in *O. alcalai* (Minwer-Barakat *et al.* 2009a and 2009b). The studied specimens differ from *Occitanomys sondaari* van de Weerd, 1976 by its larger size, greater development of t1 bis, less developed longitudinal crests in the lower molars, higher t6-t9 connection and more developed labial cingulum. *Occitanomys brailloni* Michaux, 1969 is much larger than our specimens, and has more developed longitudinal connections in both lower and upper molars.

Element	Locality	Parameter	n	min.	mean	max.
m1	AF-1’06	L	2	1.84	1.9.1	1.97
		W	2	1.22	1.24	1.26
m2	AF-1’06	L	1	-	1.35	-
		W	4	1.12	1.23	1.28
m3	AF-1’06	L	1	-	1.10	-
		W	2	1.05	1.06	1.06
M1	AF-1’06	L	2	-	1.95	-
		W	2	1.39	1.40	1.41
M2	AF-1’07	L	1	-	1.29	-
		W	1	-	1.31	-
M3	AF-1’06	L	3	1.04	1.06	1.09
		W	3	0.98	0.99	1.00

Table VI.3. Measurements in millimetres of the teeth of *Occitanomys alcalai* from AF-1’06 and AF-1’07. n= number of measurable specimens.

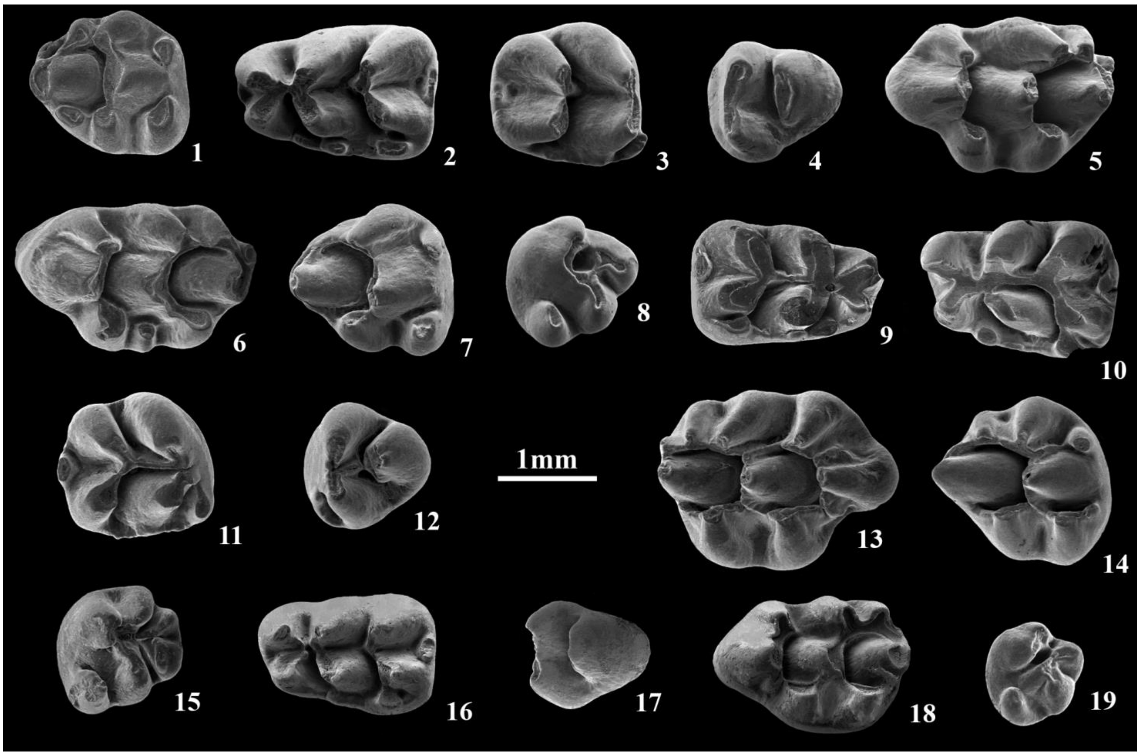


Figure VI.1. Fossil rodents from AF-1’06 and AF-1’07. *Apodemus* cf. *gorafensis* from AF-1’06. **1**, right M2, AF1’06-104. *Paraethomys meini* from AF-1’06. **2**, left m1, AF1’06-10; **3**, right m2, AF1’06-39; **4**, left m3, AF1’06-52; **5**, left M1, AF1’06-72; **6**, left M1, AF1’06-64; **7**, right M2, AF1’06-98; **8**, left M3, AF1’06-123. *Stephanomys dubari* from AF-1’06 and AF-1’07. **9**, right m1, AF1’06-12; **10**, left m1, AF1’06-4; **11**, right m2, AF1’07-5; **12**, left m3, AF1’06-54; **13**, right M1, AF1’06-67; **14**, right M2, AF1’06-93; **15**, left M3, AF1’07-28. *Occitanomys alcalai* from AF-1’06. **16**, left m1, AF1’06-14; **17**, left m3, AF1’06-58; **18**, left M1, AF1’06-80; **19**, left M3, AF1’06-131. Scale: 1 mm.

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Species: *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. (Fig. VI.2, 2–3)

Localities: AF-1’06, AF-1’07.

Material and measurements: **1 m1,2** (AF1’06-190), **1 M1,2** (AF1’07-36), **1 p4** (AF1’06-187).

Description:

m1,2: (1.29 x 1.46): Sub-quadrangular outline. Anterolophid connected basally to the protoconid. No anterotropid. The metaconid and entoconid are separated by a deep valley. The metalophid does not reach the metaconid. Long centrolophid. Large posterotropid. The mesolophid and entoconid are in contact.

M1,2: Anteroloph connected basally to the protocone. Paracone and metacone separated by a deep valley. The precentroloph is long, while the postcentroloph is highly reduced. The endoloph and posteroloph are connected and continuous.

p4: The specimen is extremely worn, and just a small remnant of the enamel can be observed.

Discussion:

The specimens from AF-1’06 and AF-1’07 are smaller than *E.* cf. *intermedius* from Villalba Alta and Arquillo 3 (Adrover 1986), and *E. intermedius* from the localities of Sarrión, Orrios 3, Sète and, Moreda-1A and 1B, Belmez-1 and Rambla Seca-A1 and A2 (Castillo 1990), PUR-13, TCH-1B and TCH-3 (García-Alix *et al.* 2008b). Our material is larger than *E. truci*, being consistent with *E.* aff. *intermedius* from La Gloria 4 (Adrover *et al.* 1993) PUR-4 and CLC-3B (García-Alix *et al.* 2008b).

These latter specimens share some characters with the populations of *E. truci*, like the long centrolophid, absence of connections between anterolophid-protoconid and metalophid-metaconid, and the presence of a large posterotropid, usually absent or reduced in *E. intermedius*. In addition, the presence of a reduced postcentroloph is consistent with the older populations of *E. intermedius*, while this crest is usually absent in the upper molars of *E. truci* (Castillo 1990, García-Alix *et al.* 2008b). This mixture of morphological characters and intermediate size between *E. truci* and *E. intermedius* led Mansino *et al.* (in press, chapter X) to create a new species of *Eliomys*, *E. yevesi*, with material from Venta del Moro and some localities from the Granada and Alcoy basins (see chapter X).

Family Cricetidae Fischer de Waldheim, 1817

Subfamily Cricetinae Fischer von Waldheim, 1817

Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998

Species *Apocricetus barrierei* (Mein and Michaux, 1970) (Fig. VI.2, 4–5)

Locality: AF-1’07.

Material and measurements: **2 m2** (AF1’07-30, AF1’07-35), **1 M1** (AF1’07-34), **1 M3** (AF1’07-12).

Description:

m2: One of the specimens is very poorly preserved, while the other one is broken anteriorly. Both the anterosinusid and the mesolophid are absent.

M1: (2.86 x 1.66): Absent cingulum ridge. Double anterolophule, arising from a short preloph. Both the mesoloph and anterior protolophule are absent. The anterior metalophule is present. No posterior metalophule.

M3: (1.68 x 1.53): Reduced lingual anteroloph. Absent anterior protolophule. Well-developed metalophule. Absent mesoloph.

Discussion:

The studied specimens are clearly larger than *Apocricetus* aff. *plinii*, *A. plinii* (Freudenthal, Lacomba and Martín-Suárez, 1991) and *A. alberti* Freudenthal, Mein and Martín-Suárez, 1998, and smaller than *A. angustidens* (Depéret, 1890). The length of the single M1 from AF-1’07 is consistent with the highest values of *A. barrierei* from La Alberca, Chabrier, Alcoy-4B (Freudenthal *et al*. 1998), Gorafe-A (Ruiz Bustos *et al.* 1984) and LB2B (Ruiz-Sánchez *et al.* 2014), while the width of this specimen and the size of the M3 agree with the mean values of *A. barrierei* from PUR-4 (García-Alix *et al.* 2008b) and Caravaca (Freudenthal, personal comment). These measurements are smaller than *A.* aff. *angustidens* from AL2-C and AL2-D (Mansino *et al.* 2013), except in the case of the length of the M1 recovered, which is narrower and has a weaker cingulum ridge than the specimen from AL2-D.

The absence of cingulum ridge is a common feature in *Apocricetus barrierei* (Mein and Michaux, 1970), while usually is present in *A. angustidens* (Freudenthal *et al.* 1998, Ruiz-Sánchez *et al*. 2014). In addition, the presence of a preloph in M1 is much more common in *A. barrierei* than in *A. alberti* (Ruiz-Sánchez *et al.* 2014, Mansino *et al.* 2014, chapter XI). For these reasons, we ascribe the material from AF-1'07 to *A. barrierei.*

Cricetidae Incertae Subfamiliae

Genus *Blancomys* van de Weerd, Adrover, Mein, and Soria, 1977

Species *Blancomys* cf. *sanzi* Adrover, Mein and Moissenet, 1993 (Fig. VI.2, 1)

Localities: AF-1'06, AF-1'07.

Material: **2 m3** (AF1'06-47, AF1'07-37).

Description:

m3: Bilobed teeth, being the anterior lobe bigger. The sinusoid is wide, while the mesosinus is much narrower. Both folds reach the base of the crown

Discussion:

The morphology, size and hypsodonty of the specimens are consistent with *Blancomys.* Their length agree with the lower values of *Blancomys sanzi* Adrover, Mein and Moissenet, 1993 from La Gloria 5 (type localiy) and Valdecebro, they are smaller than the material from other localities from the Teruel basin (Adrover *et al.* 1993) and PUR-4 (García-Alix *et al.* 2008b). Their width is consistent with *B. sanzi* from Villastar, Valdecebro 3 and La Gloria 5 (Adrover *et al.* 1993).

Family Sciuridae Fisher von Waldheim, 1817

Subfamily Sciurinae Fischer von Waldheim, 1817

Genus *Atlantoxerus* Forsyth Major, 1893

Species *Atlantoxerus* cf. *margaritae* (Fig. VI.2, 6)

Localitiy: AF-1‘06

Material: **1 D4** (AF1’06-192), **3 fragmentary remains** (AF1’06-86, AF1’06-181, AF1’06-196).

Description:

D4: (2.29 x 2.58): Absent anteroconule. The large parastyle is separated from the paracone and protocone by a deep valley. Large protocone, connected to the paracone by the protoloph. Very small mesostyle. Metacone and metaconule are very close together and connected basally. The metacone connects the posteroloph by a narrow crest.

Discussion:

The size of the specimens, presence of a small mesostyle on D4 and the height of the crown and cusps agree with *Atlantoxerus*. The presence of a mesostyle in D4 differs from *A. adroveri* Bruijn and Mein, 1968 and *A. rhodius* Bruijn, Dawson and Mein, 1970. This specimen is larger than *A. martini* Aguilar 2002 and *A. cuencae* Aguilar, Calvet and Michaux, 1995. Its size and morphology are consistent with *A.* cf. *margaritae* Adrover, Mein and Moissenet, 1993 from Aldehuela and PUR-4 (García-Alix *et al.* 2007), being slightly shorter than *A.* cf. *margaritae* from Villalba Alta and smaller than the same taxon from La Gloria 1 (Adrover *et al.* 1993).

Family Erinaceidae Fisher von Waldheim, 1817

Genus *Parasorex* von Mayer, 1865

Species *Parasorex ibericus* Mein and Martín-Suárez, 1993

Localities: AF-1’06, AF-1’07.

Material: **1 p1** (AF1’06-172), **2 m1** (AF1’06-197, AF1’07-41), **1 m2** (AF1’07-42), **1 m3** (AF1’06-195), **1 P3** (AF1’06-158), **1 P4** (AF1’06-83), **1 M1** (AF1’171), **1 M2** (AF1’06-194), **1 M3** (AF1’06-193).

p1: Elliptical teeth. The crown is higher on the anterior side. There is a flange of enamel on the anterior side and another one on the posterior side. One root.

m1: One specimen is broken anteriorly and the other one posteriorly. There is a short labial cingulum connected to the protoconid. The entoconid is higher than the hypoconid. There is a short and low posterior cingulum, not connected to the hypolophid.

m3: Specimen broken posteriorly. There is a well-developed labial cingulum. The metaconid is higher than the protoconid.

P3: Specimen broken labially. Well-developed hypocone and protocone.

P4: Specimen broken labially. Well-developed hypocone and protocone. This molar is more robust than the P3.

M1: Only the posterolabial side has been recovered. There is a very low labial cingulum. The posterior branch of the metaconule borders both metacone and metastyle reaching the posterolabial side of the molar. The metastyle is well developed.

M2: (2.22 x 2.84): This molar is broken anterolabially. There is a short and narrow anterior cingulum. The labial cingulum is narrow and lower than the lingual one. The protocone is the largest and highest cusp. A high preprotocrista, which bears a small protoconule, connects protocone and paracone. The protocone is connected to the hypocone by an entoloph. Protocone and metaconule are not connected. The mesostyle is subdivided. The low anterior branch of the metaconule reaches the base of the metacone, and the posterior branch borders both metacone and metastyle reaching the posterolabial side of the molar. The metastyle is well developed. There is a low and narrow posterior cingulum.

M3: Triangular molars. The paracone, protocone and metacone are of a similar height, and connected by low crests. The anterior cingulum is wide, and the parastyle is well developed. There is neither labial nor posterior cingulum.

Discussion:

Hoek Ostende (2001) included in the genus *Parasorex* those species with a p2 smaller than the p3 and with no connection between protocone and metaconule. On the contrary, those species with p2 larger than p3 and well-developed postprotocrista connecting protocone and metaconule were included in the genus *Galerix*.

The subdivided mesostyle and presence of a reduced posthypocrista differs from *Parasorex socialis* (von Meyer, 1865), which usually has more developed labial and posterior cingula in the lower molars and anterior cingulum in the upper molars (Mein and Martín-Suárez 1993). The presence of labial cingulum in the upper molars differs from *Parasorex depereti* (Crochet, 1896). *Parasorex ibericus* is also clearly smaller than both *P. socialis* and *P. depereti*. The size of the single measurable M2 from AF-1’06 is slightly larger than the specimens from Otura-1 (type locality, Mein and Martín-Suárez 1993), being slightly smaller than the molars from PUR-4 and Negratín (Minwer-Barakat *et al.* 2009a).

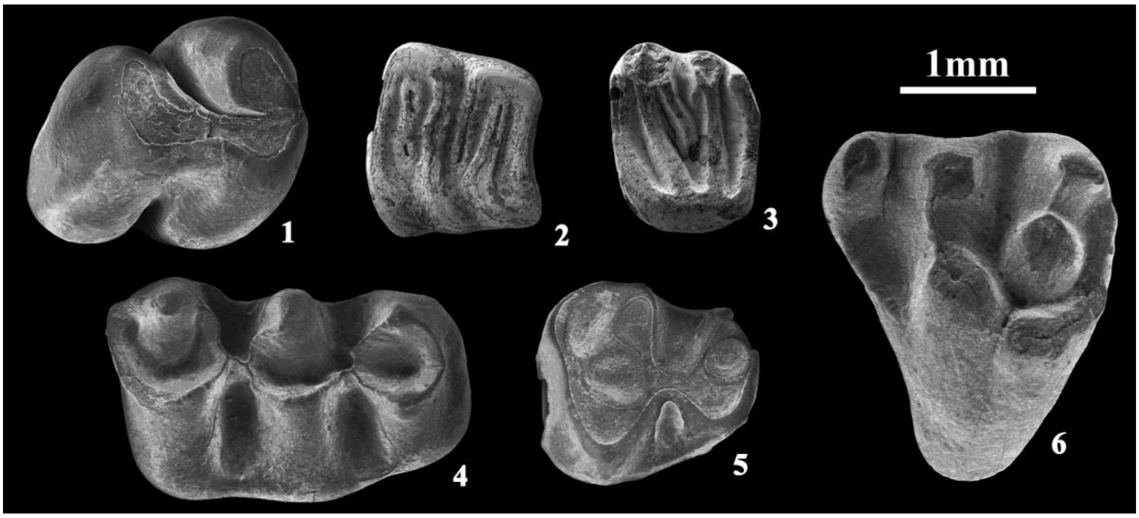


Figure VI.2. Fossil rodents from AF-1’06 and AF-1’07. *Blancomys* sp. from AF-1’06. **1**, right m3, AF1’06-47. *Eliomys yevesi* from AF-1’06 and AF-1’07. **2**, right m1,2, AF1’06-190; **3**, left M1,2, AF1’07-36. *Apocricetus barrierei* from AF-1’07. **4**, right M1, AF1’07-34; **5**, left M3, AF1’07-12. *Atlantoxerus* cf. *margaritae* from AF-1’06. **6**, left D4, AF1’06-192. Scale: 1 mm

Soricidae indet.

Locality: AF-1’06.

Material and measurements: **1 I1** (AF1’06-191).

Description:

I1: (L: 1.44; W: 1.01; LT: 0.67): Bifid and moderately fissident incisor. Straight labial cingulum.

Discussion:

The scarcity of the material and lack of diagnostic elements prevent us from reaching a generic or specific adscription.

VI.3. Discussion

VI.3.1 Biostratigraphy

The faunal list of AF-1'06 comprises *Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai*, *Apodemus* cf. *gorafensis*, *Eliomys yevesi*, *Atlantoxerus* cf. *margaritae*, *Blancomys* cf. *sanzi*, *Parasorex Ibericus* and Soricidae indet. The faunal list of AF-1'07 is very similar, except for the presence of *Apocricetus barrierei* and the absence of *Atlantoxerus* and an undetermined soricid. Regarding AF-1A and AF-2, both localities have yielded scarce fossil remains. Their faunal lists comprises *Paraethomys meini*, *Stephanomys dubari* and *Occitanomys alcalai* the former, and *Paraethomys meini* the latter.

The joint presence of *Stephanomys dubari*, *Paraethomys meini* and *Apodemus gorafensis* is a typical feature of the latest Turolian and earliest Ruscinian (García-Alix *et al.* 2008a). In addition, the presence in AF-1'07 of *Apocricetus barrierei* indicates an early Ruscinian age (Freudenthal *et al.* 1998, García-Alix 2006, García-Alix *et al.* 2008a and 2008b). *Eliomys yevesi* was described in the Late Turolian site of Venta del Moro, being present also in some Lower Ruscinian localities such as PUR-4, and CLC-3B (Mansino *et al.* in press, chapter X). In addition, *Blancomys sanzi* appears in a number of Late Turolian localities like La Gloria 5, Arquillo 1 and 4, Villastar, Valdecebro 3 and 6, and Celadas 2 (Adrover *et al.* 1993) and in Lower Ruscinian sites like Alcoy (Adrover *et al.* 1993) and PUR-4 (García-Alix *et al.* 2008b).

The faunal lists of AF-1'06 and AF-1'07 are very similar, but the presence of *Apocricetus barrierei* in AF-1'07 suggests a slightly younger age with respect to AF-

1’06. For these reasons, we propose a latest Turolian-earliest Ruscinian age for AF-1’06 and AF-1A, and an early Ruscinian age, very close to the MN13-MN14 boundary, for the localities AF-1’07, and AF-2. This dating implies that those are the youngest localities described in the Alcoy Basin, with the exception of Alcoy-N. López-Martínez (1989) proposed a Late Turolian age for this latter locality, in the MN13, its faunal list comprising *Eliomys* sp., *Ruscinomys lasallei*, *Cricetus* cf. *kormos*i, Gerbilidae indet., *Occitanomys* sp., *Apodemus primaevus*, *Paraethomys miocaenicus*, *Paraethomys* cf, *anomalus*, *Prolagus michauxi* and *Trischizolagus* cf. *maritsae*. Of this list, only *Cricetus* cf. *kormos*i, synonymized as *Apocricetus alberti* by Freudenthal *et al*. (1998), and maybe *Apodemus primaevus*, synonymized as *Rhagapodemus primaevus* by Martín-Suárez and Mein (1998), indicate a clear Turolian age. *Rhagapodemus primaevus,* was described in the late Turolian site of Lissieu (Hugueney and Mein 1965). This species is present in the Early Pliocene of Greece (Hordijk and Bruijn 2009), and has sometimes been confounded with *Apodemus gudrunae* (Morales 1984) since Mein *et al.* (1978) put in synonymy both species.

However, it is rare that two *Paraethomys* species are present in a MN13 assemblage, but common in Early Ruscinian sites, where a small sized (*P. meini*) and a large sized (*P. abaigari* or aff. *abaigari*) form can be discriminated. *Paraethomys meini*, *Paraethomys miocaenicus* and *Paraethomys anomalus* have been regarded as synonyms by several authors (see the list in the discussion of *P. meini* of this chapter), but Adrover *et al.* (1993) called the large sized *Paraethomys* from the Ruscinian sites of La Gloria 4 and Celadas 9 *Paraethomys anomalus*, This *Paraethomys* was later considered *P*. aff. *abaigari* by García-Alix *et al.* (2008a). Therefore, a revision of the material from Alcoy-N may be needed.

VI.3.2. Palaeoecology

The faunal assemblages from the Alcoi Forn sites are clearly dominated by the Muridae family. In the localities of AF-1A and AF-2 there is no other family represented, and in AF-1’06 and AF-1’07 murids account for the 87.77 and 78.95 % of the rodent assemblage respectively. The minimal sample size to perform a palaeoecological analysis has been situated in 100 specimens by some authors (Daams *et al.* 1999, García-Alix *et al.* 2008c), while for others a minimum of 50 specimens would be satisfactory (Casanovas-Vilar and Agustí 2007), because usually larger samples only add one or two species to the assemblage, with an abundance of less than 1 %.

Of the studied localities, only AF-1'06 has yielded more than 50 specimens (139). Several of the taxa present in AF-1'06 have been interpreted as warm weather indicators (Table VI.4), such as *Apodemus gorafensis Occitanomys alcalai*, *Paraethomys meini* and *Atlantoxerus* cf. *margaritae* (see García-Alix *et al*. 2008c and references therein). In addition, some of the species from the mentioned localities have been considered typical of wet environments, like *Apodemus gorafensis* and *Occitanomys alcalai*, whereas *P. meini* (Renaud *et al.* 1999) and *Atlantoxerus* would indicate dry climatic conditions (García-Alix *et al*. 2008*c*). The genera *Apocricetus*, *Atlantoxerus* and *Blancomys* suggest an open habitat (García-Alix *et al.* 2008c), while *Eliomys* has usually been related to more forested environments (Daams and Meulen 1984, Dam and Weltje 1999, Meulen and Bruijn 1982, García-Alix *et al.* 2008c). However, Freudenthal *et al.* (2014) consider that the extant representatives of the genus *Eliomys* inhabit in a range of different habitats, from woodlands to semi-desertic environments, and therefore cannot be indicators of humidity. Regarding *Eliomys quercinus* (Linnaeus, 1766), which forms part of the phylogenetic lineage *E. yevesi-E. intermedius-E. quercinus* (Mansino *et al.* in press, chapter X), Freudenthal *et al.* (2014) consider it a generalist form, not restricted to humid and forested environments.

Table VI.4 summarizes the ecological preferences inferred for the taxa from AF-1'06, according to García-Alix *et al.* (2008c) and Freudenthal *et al.* (2014). The percentages of the taxa within each ecological category suggest a warm (74.19 %) and dry (61.32 % environment).

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	Wet	Dry	Eurytopic	Cold	Warm	Eurytopic	Open	Forested	Eurytopic
AF-1'06	12.87	61.32	25.36	0.00	74.19	25.36	3.03	0.00	96.52

Table VI.4. Relative abundance of the taxa from AF-1'06 according to their ecological preferences. These percentages have been obtained by dividing each taxon by its number of diagnostic elements, as proposed by Martín-Suárez (1988). The taxa with unknown preferences are not shown.

VI.3.3. Conclusions

We describe the rodent faunas from four new sites located in the northern side of the Gormaget ravine (Alcoy Basin). Two of them, AF-1A and AF-2, have yielded scarce remains of *Paraethomys meini*, *Stephanomys dubari* and *Occitanomys alcalai* the former and *Paraethomys meini* the latter. On the contrary, the other two localities are richer, comprising the faunal list of AF-1’06 *Paraethomys meini, Stephanomys dubari, Occitanomys alcalai*, *Apodemus* cf. *gorafensis, Eliomys yevesi*, *Atlantoxerus* cf. *margaritae*, *Blancomys* cf. *sanzi*, *Parasorex Ibericus* and Soricidae indet. The faunal list of AF-1’07 is very similar, except for the presence of *Apocricetus barrierei* and the absence of *Atlantoxerus* and soricids.

The faunal assemblage of AF-1’06 suggest a latest Turolian/earliest Ruscinian age, and AF-1A is probably an equivalent level. The presence of *Apocricetus barrierei* in AF-1’07 implies a younger age, and both this site and AF-2 are placed in this work in the earliest Ruscinian. This dating makes the localities from Alcoi Forn the oldest sites described in the Alcoy Basin, with the exception of Alcoy-N.

The only locality in which the assemblage is abundant enough to perform a palaecological analysis is AF-1’06. The relative proportions of the taxa from this site indicate a very warm and dry environment at the moment of its formation.

CHAPTER VII: FIRST EARLY PLIOCENE MICROMAMMAL FAUNAS FROM THE VENTA DEL MORO AREA (CABRIEL BASIN, SPAIN): NEW DATA ON THE MESSINIAN DISPERSAL OF *DEBRUIJNIMYS*.

VII.1. Material and methods

Fieldwork during 2005 and 2007 provided over 1,200 kg of sediment from La Bullana 2B and 1,500 kg from La Bullana 3. After sieving these sediments, the recovered fossils were kept at the *Museu de Geologia de la Universitat de València* (MGUV), with the field labels LB2B- and LB3-, respectively. The nomenclature used in the descriptions of the teeth and the measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, Cuenca-Bescós (1988) and Reumer and Hoek Ostende (2003) for the Sciuridae, and Reumer (1984), modified by Furió (2007), for the insectivores.

VII.2. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1826

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. VII.1, 1-4)

Localities: LB2B, LB3.

Material: **7 m1** (LB2B-25, LB2B-88, LB2B-92, LB2B-183, LB3-2, LB3-3, LB3-30), **9 m2** (LB2B-35, LB2B-36, LB2B-41, LB2B-105, LB2B-142, LB3-10, LB3-11 to LB3-13), **8 m3** (LB2B-44, LB2B-45, LB2B-114, LB2B-115, LB2B-200, LB2B-203, LB3-

17, LB3-18), **8 M1** (LB2B-9, LB2B-13, LB2B-51, LB2B-129, LB2B-250, LB2B-258, LB3-19, LB3-20), **4 M2** (LB2B-20, LB2B-21, LB2B-136, LB3-22), **4 M3** (LB2B-214, LB2B-216, LB2B-219, LB3-24).

Measurements: see Table VII.1.

Description:

m1: The tma is large, round and central. Symmetrical anteroconid, its labial lobe connects to the metaconid. Well-developed labial cingulum, with a big round c1 and two or three accessory cusps. One of the specimens has a hint of longitudinal spur. Big oval posterior heel, shifted towards the lingual side of the tooth.

m2: Big oval anterolabial cusp. Well-developed labial cingulum, separated from the protoconid and hypoconid. There is a large round c1, except for one specimen in which this cusp is much reduced, and one or two accessory cusps. The posterior heel is large, round or oval.

m3: Anterolabial cusp reduced or absent. There is no longitudinal crest. One specimen has a small c1 connected to the labial side of the hypoconid-entoconid complex.

M1: The t1 is displaced backwards. The connection between t1 and t2 is very low. There is neither t1bis nor t2 bis. The valley between t3 and t6 is very deep and wide. The t4, t5, t6 and t9 are connected. The t7 is well developed, and there is a medium-sized t12 connected to the posterolabial side of t8.

M2: The t1 is large, oval or round, and two specimens have a spur directed towards the t4-t5 connection. The t3 is reduced and isolated from the other cusps. The t7 is well developed and separated from t4. The t6 and t9 are connected. The t12 is small, connected to the posterolabial part of t8 and separated from t9.

M3: The t1 is isolated. The t3 is absent. The t4, t5, t6, t8 and t9 are connected.

Discussion:

The presence of a large tma in the m1, well-developed labial cingulum in m1 and m2 and t7 in the upper molars are typical traits of *Apodemus*. The specimens from LB2B and LB3 are larger than *Apodemus atavus* Heller, 1936 from TCH-1, 1B, 3 and 13 (Minwer-Barakar *et al*. 2005), PUR-7, PUR-13, CLC-3, CLC-3B, CLC-4B, AGU-1C and DHS-1 (García-Alix *et al*. 2008a) and smaller than *Apodemus jeanteti* from Arquillo 3 and Villalba Alta (Adrover 1986); this latter species further differs from *A. gorafensis* in the lack of tma in the m1.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	4	2.05	2.08	2.14
		W	4	1.26	1.31	1.35
m2	LB2B	L	5	1.49	1.54	1.57
		W	5	1.27	1.36	1.41
	LB3	L	4	1.49	1.52	1.58
		W	4	1.37	1.42	1.48
m3	LB2B	L	5	1.12	1.17	1.21
		W	5	1.03	1.08	1.12
	LB3	L	1	-	1.22	-
		W	1	-	1.08	-
M1	LB2B	L	1	-	2.22	-
		W	3	1.40	1.46	1.50
	LB3	L	2	-	1.57	-
M2	LB2B	L	3	1.53	1.57	1.63
		W	3	1.37	1.42	1.45
	LB3	L	1	-	1.70	-
		W	1	-	1.50	-
M3	LB2B	L	3	1.00	1.05	1.12
		W	3	0.94	1.02	1.08
	LB3	L	1	-	0.97	-
		W	1	-	1.01	-

Table VII 1. Measurements in millimetres of the teeth of *Apodemus gorafensis* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Apodemus gorafensis differs from its ancestor, *Apodemus gudrunae*, in the presence of a well-developed t7. This latter species is also slightly smaller than our specimens. In addition, *Apodemus agustii* Martín-Suárez, 1988 differs from *A. gorafensis* in the partial stephanodonty of the upper molars, less-developed tma and lack of a pit in m1 between the anteroconid, metaconid and protoconid. The size of the studied molars is consistent with *A. gorafensis* from its type locality, Gorafe A (Ruiz Bustos *et al*. 1984) and PUR-4, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al*. 2008a), Gorafe-3, Gorafe-4, Botardo-C and Huescar-1 (Martín-Suárez 1988) and Alcoy 2C and 2D (Mansino *et al*. 2013, chapter IV), being also similar to *A.* aff *gorafensis* from PUR 23

(García-Alix *et al*. 2008a), Celadas 9, La Gloria 4 (Adrover *et al.* 1993) and Peralejos E (Adrover *et al*. 1988).

The development of the tma, labial cingulum and t7 in the specimens from La Bullana 2B and La Bullana 3 agrees with *A. gorafensis*. There is a t9 (Fig. VII.1, 4) in two M3, while other two are much worn and this cusp cannot be observed. This cusp is absent in the fossil remains of *A. gorafensis* from the mentioned localities, with the exceptions of some specimens from PUR-23 and PUR-24A (García-Alix *et al*. 2008a).

Genus *Castillomys* Michaux, 1969

Castillomys gracilis van de Weerd, 1976 (Fig. VII.1, 5-7)

Locality: LB2B.

Material: **5 m1** (LB2B-90, LB2B-91, LB2B-94, LB2B-95, LB2B-188), **4 m2** (LB2B-106 to LB2B-109), **6 M1** (LB2B-14, LB2B-125, LB2B-126, LB2B-204, LB2B-205, LB2B-210) **1 M2** (LB2B-22), **1 M3** (LB2B-218).

Measurements: see Table VII.2.

Description:

m1: One specimen has a very small and low tma (Fig. VII.1, 5), absent in the rest. The anteroconid is symmetrical and connected to the protoconid-metaconid pair. There is a longitudinal spur and a narrow labial cingulum. The c1 is round or oval and connected basally to the hypoconid. One molar has a small accessory cusp. The posterior heel is small and lingually displaced.

m2: Large anterolabial cusp, connected to the labial cingulum. There is a small round c1. All specimens have a longitudinal spur. The posterior heel is small and oval.

M1: The t1 is displaced backwards. All specimens have a small t1 bis. The t1 is connected to the t4-t5 junction by a longitudinal crest. There is a small distal spur on t3, directed towards the t5-t6 connection, and one specimen has a low labial longitudinal crest. The t9 is large. A small t12 is present.

M2: The only available specimen is broken anterolabially. The t1 is connected to the t4-t5 junction by a low crest. The t3 is small and isolated.

M3: Isolated t1. There is no t3. The connection between t4 and the t5-t6 junction is very low. The t8 is isolated.

Discussion:

Martín-Suárez and Mein (1991) recognized an increase in size from older to younger populations in the anagenetic line *C. gracilis–C. crusafonti–C. rivas,* in which all the Iberian populations from the Pliocene and Pleistocene could be encompassed. This means that the biometrics of the molars could be used as systematic criteria along the frequency percentages of some morphological characters (Martín-Suárez and Mein 1991). The size of *Castillomys* from La Bullana 2B is consistent with *Castillomys gracilis* from its type locality (Caravaca), and Orrios-1 (Weerd 1976), Moreda-1A and 1B, Rambla Seca-AB and Belmez-1 (Castillo,1990), Botardo C and Gorafe 3 and 4 (Martín-Suárez 1988), Mont-Hélène (Aguilar *et al*. 1986), Aldehuela and Villalba Alta (Adrover 1986) and CLC-3, CLC-3B and PUR-13 (García-Alix *et al*. 2008a), but also agrees with some of the smallest measurements of *Castillomys crusafonti* Michaux, 1969 (Martín-Suárez and Mein 1991, Minwer-Barakat *et al*. 2005).

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	1.35	1.40	1.47
		W	5	0.88	0.90	0.93
m2	LB2B	L	4	1.02	1.06	1.12
		W	4	0.93	0.95	0.98
M1	LB2B	L	6	1.44	1.52	1.61
		W	6	1.01	1.05	1.12
M2	LB2B	W	1	-	1.21	-
M3	LB2B	L	1	-	0.76	-
		W	1	-	0.69	-

Table VII.2. Measurements in millimetres of the teeth of *Castillomys gracilis* from the locality La Bullana 2B. n= number of measurable specimens.

The morphology of the studied specimens agrees better with *C. gracilis* than with *C. crusafonti*, showing a longitudinal spur in m1 and a posterior spur on t3 of M1 instead of full longitudinal crests. However, 1 out of 6 M1 does have a low longitudinal crest on t3, and all of them present a complete longitudinal crest connecting the t1 to the t4-t5, which is unusual in *C. gracilis* (Martín-Suárez and Mein 1991). Moreover, the presence of a low crest on the t1 of the M2 is rare in this species. However, based on the size of the specimens and the lack of longitudinal crests in the lower molars, we ascribe the sample from La Bullana 2B to *C. gracilis*.

Genus *Occitanomys* Michaux, 1969

Occitanomys brailloni Michaux, 1969 (Fig. VII.1, 8-13)

Locality: LB2B.

Material: **5 m1** (LB2B-53, LB2B-82, LB2B-93, LB2B-96, LB2B-184), **2 m2** (LB2B-39, LB2B-100), **5 m3** (LB2B-112, LB2B-113, LB2B-116, LB2B-119, LB2B-201), **4 M1** (LB2B-11, LB2B-123, LB2B-124, LB2B-251) **1 M2** (LB2B-135).

Measurements: see Table VII.3.

Description:

m1: Symmetrical anteroconid, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is well developed. The c1 is large and round. Two specimens have a very small accessory cusp. There is a longitudinal spur, which is reduced in two molars (Fig. VII.1, 8), more developed in another two, and developed into a very low longitudinal crest in one specimen (Fig. VII.1, 9). The posterior heel is small and oval. There are two roots.

m2: Trapezoidal outline, with the anterior side wider than the posterior one. Big round anterolabial cup, connected basally to the protoconid. The labial cingulum is reduced. The two available specimens have a longitudinal spur. The posterior heel is round.

m3: There is neither anterolabial cusp nor c1.

M1: The connection between t1 and t2 is very low. The t1 bis is well developed. There is a small t2 bis (Fig. VII.1, 12), absent in one specimen. There is a low connection between t1 and the anterolingual side of t5. One specimen has a hint of distal spur on t3. The t6 and t9 are connected. The t12 is very small, barely a fold of the enamel.

M2: The t1 is well developed, connected to the anterolingual side of t5 in one molar (Fig. VII.1, 13) and isolated in the other one. One specimen has a large t1 bis (Fig. VII.1, 13). Reduced t3, isolated from the other cusps. The t9 is well developed.

Discussion:

The specimens from La Bullana 2B largely agree with the material of *O. brailloni* from Layna (type locality) described by Michaux (1969): m1 without tma and with the accessory cusps less developed than *Apodemus*, M1 with t1 bis, a crest that connects t1 to the posterior crown and a much reduced t12, and M2 with reduced t3 and well-developed t1 connected to the t5 by a crest. Michaux (1969) also considered diagnostic the presence of a low longitudinal crest in m1, lower than in *Stephanomys*. Regarding this character, there seems to be a great variability among populations, and Adrover (1986) suggested an increase of the longitudinal crest in m1 and m2 through time. In the localities of the MN14 the longitudinal crest of m1 is developed in 3 out of 7 molars from Kardia and Ptolemais (Weerd 1979), absent in the single m1 from Gorafe A (Ruiz Bustos *et al*. 1984), and present in 1 out of 5 specimens from La Bullana 2B. In localities assigned to the early MN15, this crest is present in 2 out of 7 specimens from Arquillo 3 (Adrover 1986), and absent in the two m1 from Vorio 3 (Hordijk and Bruijn 2009). In more recent localities, such as Layna, Nîmes (Michaux 1969) and TCH-1B (Minwer-Barakat *et al*. 2005) there is always a low longitudinal crest.

The distal crests of M1 show also a great variability. The specimens from Kardia (Weerd 1979) have a crest on t1, and 1 out of 4 molars have also a crest on t3, while other two have a small spur. The single M1 from Gorafe A has a weak t1-t5 connection, and no trace of t3-t5 connection (Ruiz Bustos *et al*. 1984). In the specimens from La Bullana 2B, the crest on t1 is high in one molar and much lower in the other one, while 2 out of 3 specimens have a much reduced spur on t3 (Fig. VII.1, 12). All specimens from Arquillo 3 have a crest on t1, and 4 out of 6 M1 have a spur on t3 (Adrover 1986). In the Greek locality of Vorio 3 (Hordijk and Bruijn 2009) all M1 have a crest on t1, two molars have a spur on t3 and another one a developed crest. In Layna and Nîmes there is always a crest on t1, but the t3 has a spur (Michaux 1969). The single M1 from TCH-1B has well-developed crests on t1 and t3 (Minwer-Barakat *et al*. 2005). The single specimen from Rambla Seca A1 also has developed crests, but lower than in the molar from TCH-1B (Minwer-Barakat 2005). Each of the localities Cañada del Castaño 1 and Rambla Seca A2 yielded one M1, with a low crest on t3 and an isolated t1, while in the two M1 from Bélmez 1 the t1 has a low crest, and one specimen has a crest on t3, absent in the other one (Castillo 1990, Martín-Suárez 1988). The morphological variability of these connections is difficult to assess because of the scarcity of the remains in the localities where this species is found (Minwer-Barakat 2005), although they seem to be slightly more developed in younger localities.

With respect to the size, the material from La Bullana 2B is similar in size to *O. brailloni* from other MN14 localities such as Ptolemais 1 and 3 and Kardia (Weerd 1979), Gorafe A (Ruiz Bustos *et al*. 1984) and Vorio 1 (Hordijk and Bruijn 2009), and slightly smaller than the same taxon from MN15 localities such as Vorio 3 (Hordijk and Bruijn 2009), Arquillo 3 and Aldehuela (Adrover 1986), Layna, Nîmes and Sête (Michaux 1969), Cañada del Castaño 1 (Martín-Suárez 1988), TCH-1B (Minwer-Barakat *et al*. 2005), Bélmez 1, Rambla Seca A1, A2 and A3, Moreda 1L-4 and the MN16 locality of Moreda 1B (Castillo 1990). The scarce material from AL2-D (Mansino *et al*. 2013, chapter IV) is morphologically consistent with *O. brailloni*, but due to its extremely large size it is not clear if these specimens should be ascribed to this taxon or to a related form.

O. brailloni differs from *O. alcalai* Adrover, Mein and Moissenet, 1988, *O. adroveri* (Thaler 1966), *O. sondaari* van de Weerd, 1976 and *O. debruijni* Sen, Jaeger, Dalfes, Mazin and Bochernes, 1989, by its larger size. It differs from *O. montheleni* Aguilar, Calvet and Michaux, 1984, by its smaller size. Some of the specimens from La Bullana 2B are close to the smallest values of *O. brailloni*, and therefore close to the largest dimensions of *O. alcalai* and within the size range of *O. adroveri*. *O. sondaari* differs from *O. brailloni* by the weak t6-t9 junction, the lesser development of the longitudinal crest in m1, the absence of t1-t5 connection in unworn specimens and by the absence of a crest on the t3 of the M1. *O. alcalai* differs from *O. brailloni* by the lesser development of longitudinal crests in the upper and lower molars. According to Michaux (1969), the longitudinal crest of *O. adroveri* is less developed than in *O. brailloni*, but as we noted before this character shows a great variability. The m1 of *O.*

adroveri may present well-developed accessory cups. In the upper molars, the distal crests on t1 and t3 are usually more developed in *O. brailloni* than in *O. adroveri*, and the t12 is more reduced in *O. brailloni*. *O. debruijni* differs from *O. brailloni* by the reduced or absent t3-t5 connection and absence of c1 in m2, which may be present in *O. brailloni* (see material from Layna and Vorio 3 in Hordijk and Bruijn, 2009, plate 8).

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	3	1.84	1.87	1.90
		W	4	1.25	1.28	1.31
m2	LB2B	L	2	1.45	1.50	1.55
		W	2	1.39	1.40	1.40
m3	LB2B	L	5	1.05	1.09	1.15
		W	5	0.97	1.02	1.06
M1	LB2B	L	3	1.96	2.05	2.11
		W	3	1.42	1.46	1.49
M2	LB2B	L	1	-	1.48	-
		W	1	-	1.40	-

Table VII.3. Measurements in millimetres of the teeth of *Occitanomys brailloni* from the locality La Bullana 2B. n= number of measurable specimens.

Occitanomys sp.

Locality: LB2B.

Material: **1 M2** (LB2B-211).

Description:

M2: (1.38 x 1.32): The t1 is well developed, and connects basally to the t5. The t3 is smaller than the t1 and isolated from the other cusps. The t9 is well developed.

Discussion:

The general morphology of the specimen resembles *Occitanomys*, but it is much smaller than the remains ascribed to *O. brailloni*. In addition, the t1-t5 connection is very low, while in *O. alcalai* it is usually higher. Because of the scarcity of the material that prevents the observation of more diagnostic features, we ascribe this molar to *Occitanomys* sp.

Genus *Paraethomys* Petter, 1968

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. VII.1, 18-22)

Localities: LB2B, LB3.

Material: **5 m1** (LB2B-87, LB2B-99, LB2B-187, LB2B-189, LB3-1), **13 m2** (LB2B-2, LB2B-34, LB2B-38, LB2B-40, LB2B-42, LB2B-86, LB2B-103, LB2B-110, LB2B-191, LB3-7 to LB3-9, LB3-14), **7 m3** (LB2B-3, LB2B-47, LB2B-48, LB2B-118, LB2B-121, LB2B-195, LB2B-197), **6 M1** (LB2B-4, LB2B-15, LB2B-128, LB2B-206, LB2B-208, LB2B-209), **6 M2** (LB2B-17, LB2B-18, LB2B-130, LB2B-134, LB2B-212, LB2B-213), **4 M3** (LB2B-139, LB2B-140, LB2B-215, LB2B-217).

Measurements: see Table VII.4.

Description:

m1: One molar has a very small cingulum ridge between the lobes of the anteroconid (Fig. VII.1, 18) and another one shows a low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pairs are connected by a narrow crest, which has an enamel funnel in one specimen. There is a longitudinal spur. The labial cingulum is moderately developed, with a large oval c1 and one or two accessory cups. The posterior heel is variable in size and shape, and lingually displaced.

m2: Well-developed anterolabial cup, connected basally to the protoconid and the labial cingulum. A c1 variable in size and an accessory cusp may be present. There is a longitudinal spur in 9 out of 11 specimens. The posterior heel is reduced in some molars, while others have a medium sized cusp.

m3: The anterolabial cusp is reduced in two specimens and absent in five. The hypoconid-entoconid complex is separated from the protoconid-metaconid pair. One of the specimens presents a small c1 attached to the labial side of the posterior complex.

M1: The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. Two specimens have a very low crest connecting t1 to the posterolingual side of t5. The spur on t3 is always present, small in two specimens and more developed in other two. The t9 is well developed. The connection between t4 and t8 is low. There is a small t12.

M2: Isolated t1 and t3. The t9 may be absent (2), reduced (2) or developed (1). A much reduced t12 is present in two specimens.

M3: The t1 is large and isolated, while t3 is absent. The t8 is connected to the t4-t5-t6 junction.

Discussion:

Different species of *Paraethomys* are recognized in MN14 localities from the Iberian Peninsula: the small sized *P. meini* (Michaux, 1969), and the larger *P. abaigari* and *P.* aff. *abaigari*, which have more developed distal spurs in the upper molars. Adrover *et al*. (1993) identified two species of *Paraethomys* in La Gloria 4 and Celadas 1 and 9, *P. meini* and *P. anomalus* (Bruijn, Dawson and Mein, 1970). These two species were morphologically very similar, and differed mainly in their size. Later, García-Alix *et al*. (2008a) ascribed the big-sized specimens from PUR-13 and CLC-5A to *P*. aff. *abaigari*, a form related to *P. abaigari* but slightly smaller, and considered the big-sized *Paraethomys* from La Gloria 4 and Celadas 9 to belong to the same taxon. Slightly older assemblages of *Paraethomys*, like the rich population from PUR-4, show a wide size range but, due to the impossibility to discriminate two clusters in this population, García-Alix *et al.* (2008a) ascribed that sample to *P. meini*, considering unlikely the coexistence of two *Paraethomys* species in that locality.

The specimens from La Bullana 2B and La Bullana 3 are similar in size to *P*. aff. *abaigari* from CLC-5A and PUR-13 (García-Alix *et al*. 2008a), Celadas 9 and La Gloria 4 (Adrover *et al*. 1993), slightly smaller than *P*. aff. *abaigari* from AL2-C and AL2-D (Mansino *et al*. 2013), and clearly smaller than *P. abaigari* from Villalba Alta (Adrover *et al*. 1988). These molars are larger than *P. meini* from Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover 1986), Villalba Alta Río, Peralejos E (Adrover *et al*. 1988), Celadas 9 and La Gloria 4 (Adrover *et al*. 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (GarcíaAlix *et al*. 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al*. 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover 1986), considered synonyms of *P.*

meini by several authors (Weerd 1976, Adrover 1986, Castillo 1990, Minwer-Barakat 2005, García-Alix 2006, García-Alixet *et al*. 2008a)

The development of distal spurs on the t1 and t3 of the M1 also agrees with *P. abaigari* rather than with *P. meini*. For these reasons, we ascribe the studied material to *P*. aff. *abaigari*.

Element	Sp.	Locality	Parameter	n	min.	mean	max.
m1	aff. *abaigari*	LB2B	L	1	-	2.36	-
			W	3	1.49	1.52	1.57
	aff. *abaigari*	LB3	L	1	-	2.36	-
			W	1	-	1.54	-
	meini	LB2B	L	8	2.12	2.18	2.26
			W	9	1.38	1.43	1.46
m2	aff. *abaigari*	LB2B	L	7	1.65	1.71	1.76
			W	9	1.45	1.53	1.62
	aff. *abaigari*	LB3	L	3	1.66	1.71	1.76
			W	3	1.51	1.53	1.58
	meini	LB2B	L	2	1.37	1.40	1.42
			W	2	1.25	1.32	1.39
m3	aff. *abaigari*	LB2B	L	7	1.43	1.47	1.51
			W	7	1.25	1.31	1.37
	meini	LB2B	L	5	1.29	1.31	1.35
			W	6	1.15	1.20	1.28
M1	aff. *abaigari*	LB2B	L	4	2.53	2.56	2.61
			W	4	1.67	1.70	1.74
	meini	LB2B	W	1	-	1.50	-
M2	aff. *abaigari*	LB2B	L	5	1.79	1.87	1.96
			W	6	1.60	1.67	1.73
	meini	LB2B	L	1	-	1.56	-
			W	2	1.47	1.48	1.49
M3	aff. *abaigari*	LB2B	L	4	1.23	1.29	1.38
			W	4	1.23	1.27	1.34
	meini	LB2B	L	1	-	1.16	-
			W	1	-	1.18	-

Table VII.4. Measurements in millimetres of the teeth of *Paraethomys* aff. *abaigari* and *P. meini* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Paraethomys meini (Michaux, 1969) (Fig. VII.1, 14-17)

Locality: LB2B.

Material: **12 m1** (LB2B-1, LB2B-26, LB2B-29 to LB2B-33, LB2B-83, LB2B-85, LB2B-89, LB2B-185, LB2B-186), **2 m2** (LB2B-100, LB2B-193), **6 m3** (LB2B-46,

LB2B-50, LB2B-120, LB2B-122, LB2B-194, LB2B-198), **3 M1** (LB2B-16, LB2B-52, LB2B-84), **2 M2** (LB2B-19, LB2B-131), **1 M3** (LB2B-138).

Measurements: see Table VII.4.

Description:

m1: one specimen has a very low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pair are connected by a narrow crest. Three specimens have a funnel of enamel in the connection between the anteroconid and the protoconid-metaconid (Fig. VII.1, 14). In 8 out of 11 teeth there is a weak longitudinal spur. The labial cingulum is moderately developed, with a large oval c1 and one or two accessory cusps, variable in size.

m2: Well-developed anterolabial cusp, connected basally to the protoconid and the labial cingulum. A small c1 is present in one specimen. There are no accessory cusps. In 2 out of 3 specimens there is a longitudinal spur. The posterior heel is large in two molars and more reduced in another one.

m3: One specimen has a small anterolabial cup, absent in the others. The hypoconid-entoconid complex is separated from the anterior protoconid-metaconid pair. A small crest-shaped c1 is present in two molars.

M1: All specimens are broken posteriorly. One specimen has two small cusps attached to the anterior side of t2. The t1 has a distal spur, developed into a very low crest in one of the specimens. There is a spur on the t3.

M2: The dentine is almost completely lost in both molars. Isolated t1 and t3. The t9 is slightly developed, and there is no t12..

M3: The t1 is large and isolated. Absent t3. The t8 is connected to the t4-t5-t6 junction.

Discussion:

Together with the large *P*. aff. *abaigari*, a small form of *Paraethomys* occurs in La Bullana 2B. The coexistence of two species of *Paraethomys* differing mainly in size has been recorded in several Pliocene localities from the Teruel and Granada basins

(Adrover 1986, Adrover *et al*. 1988 and 1993, García-Alix *et al*. 2008a), as well as in the French site of Sète (type locality of *P. meini*, Michaux 1969). When both forms appear together, the size of *P. meini* is usually very small (García-Alix 2006). The size of the specimens from La Bullana 2B is similar to *P. meini* from Sète, Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover 1986), Villalba Alta Río, Peralejos E (Adrover *et al*. 1988), Celadas 9 and La Gloria 4 (Adrover *et al*. 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (GarcíaAlix *et al*. 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al*. 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover 1986).

The only morphological character used to distinguish *P. meini* from *P. abaigari* is the development of distal spurs in the upper molars, more prevalent in the latter species (Adrover *et al*. 1993). The three M1 from La Bullana 2B show spurs on the t1 and t3, which is unusual in *P. meini*, although in some localities like Peralejos E the presence of spurs on t1 and especially t3 is quite common (Adrover *et al*. 1993).

Genus *Stephanomys* Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Fig. VII.1, 23-28)

Localities: LB2B, LB3.

Material: **5 m1** (LB2B-27, LB2B-28, LB2B-97, LB2B-98, LB2B-182), **5 m2** (LB2B-37, LB2B-101, LB2B-102, LB2B-104, LB2B-111), **4 m3** (LB2B-49, LB2B-117, LB2B-196, LB2B-197), **4 M1** (LB2B-10, LB2B-12, LB2B-127, LB2B-207), **5 M2** (LB2B-23, LB2B-132, LB2B-133, LB2B-252, LB3-21), **3 M3** (LB2B-24, LB2B-137, LB2B-249).

Measurements: see Table VII.5.

Description:

m1: Slightly asymmetrical anteroconid, connected to the protoconid and metaconid. The labial cingulum is low and narrow. There is a well-developed longitudinal crest that connects the posterior cups to the connection of the protoconid-metaconid pair. There is a well-developed oval c1. The posterior heel is lingually displaced, ranging from oval to laminar. Two roots.

m2: Large and high anterolabial cup, connected to the protoconid and to a narrow labial cingulid. The longitudinal crest is lingually displaced towards the metaconid. There is neither c1 nor accessory cups. The posterior heel is large and oval.

m3: Small and low anterolabial cup, connected to the protoconid. The longitudinal crest is complete (Fig. VII.1, 24). There are two roots.

M1: The t1 is slightly displaced backwards. There are small t1 bis and t2 bis, more developed in one of the specimens (Fig. VII.1, 25). The posterior crest on the t1 is high and well developed in two specimens (Fig. VII.1, 25), and very low in another two (Fig. VII.1, 26), while the posterior crest on the t3 is high in all specimens. The t12 is highly reduced.

M2: The t1 has a small t1 bis attached to its anterior side (Fig. VII.1, 27). In unworn specimens, the posterior crest of t1 is complete in two molars and low in another two, while the posterior crest on the t3 is complete in two specimens, low in one and absent in another one. The t12 is reduced in one molar and well developed in another one (Fig. VII.1, 27). There are three roots.

M3: The t1 is connected basally to t5. The t3 is absent. The t4, t5 and t6 are connected to t8. One specimen has a t9 (Fig. VII.1, 28).

Discussion:

The great height of the crown, high longitudinal crests in the lower molars (Fig. VII.1, 23–24) and crests or spurs on t1 and t3 of the upper molars (Fig. VII.1, 25–27) indicate that these specimens belong to the genus *Stephanomys*. These molars are smaller, lower crowned and have a less pronounced stephanodonty than the *Stephanomys* identified in the Pliocene and Pleistocene (see Minwer-Barakat *et al*. 2011a, and references therein).

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	2.07	2.16	2.27
		W	5	1.29	1.31	1.44
m2	LB2B	L	5	1.51	1.62	1.70
		W	5	1.46	1.51	1.58
m3	LB2B	L	3	1.25	1.31	1.37
		W	3	1.21	1.24	1.28
M1	LB2B	L	4	2.30	2.46	2.69
		W	4	1.58	1.74	1.83
M2	LB2B	L	3	1.58	1.74	1.88
		W	3	1.70	1.73	1.76
	LB3	L	1	-	1.72	-
		W	1	-	1.63	-
M3	LB2B	L	2	1.15	1.25	1.36
		W	2	1.13	1.22	1.31

Table VII.5. Measurements in millimetres of the teeth of *Stephanomys dubari* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

The studied specimens share some characters with *S. cordii*, like the t1 slightly more posterior than the t3 in M1 (Fig. VII.1, 25–26) and one m3 with the longitudinal crest connected to the protoconid (Fig. VII.1, 24). However, although some molars have the size and morphology of *S. cordii* (Fig. VII.1, 25) most of them agree better with *S. dubari*, with low crests connecting t1 and t5 in M1 (Fig. VII.1, 26), low or absent longitudinal crests in M2 and a smaller size. The presence of specimens similar to *S. cordii* has been reported in some populations of *S. dubari*, such as in the lower Ruscinian sites of PUR-4 and PUR-13 in the Granada Basin (García-Alix *et al*. 2008a). The material from La Bullana 2B and La Bullana 3 has been directly compared with *S. cordii* from AL2-C and AL2-D (Mansino *et al*. 2013, chapter IV). The molars from the two latter localities are slightly larger, having usually higher longitudinal crests and are clearly higher crowned than the teeth from La Bullana 2B and La Bullana 3. For these reasons, we ascribe the material from the studied localities to *S. dubari*.

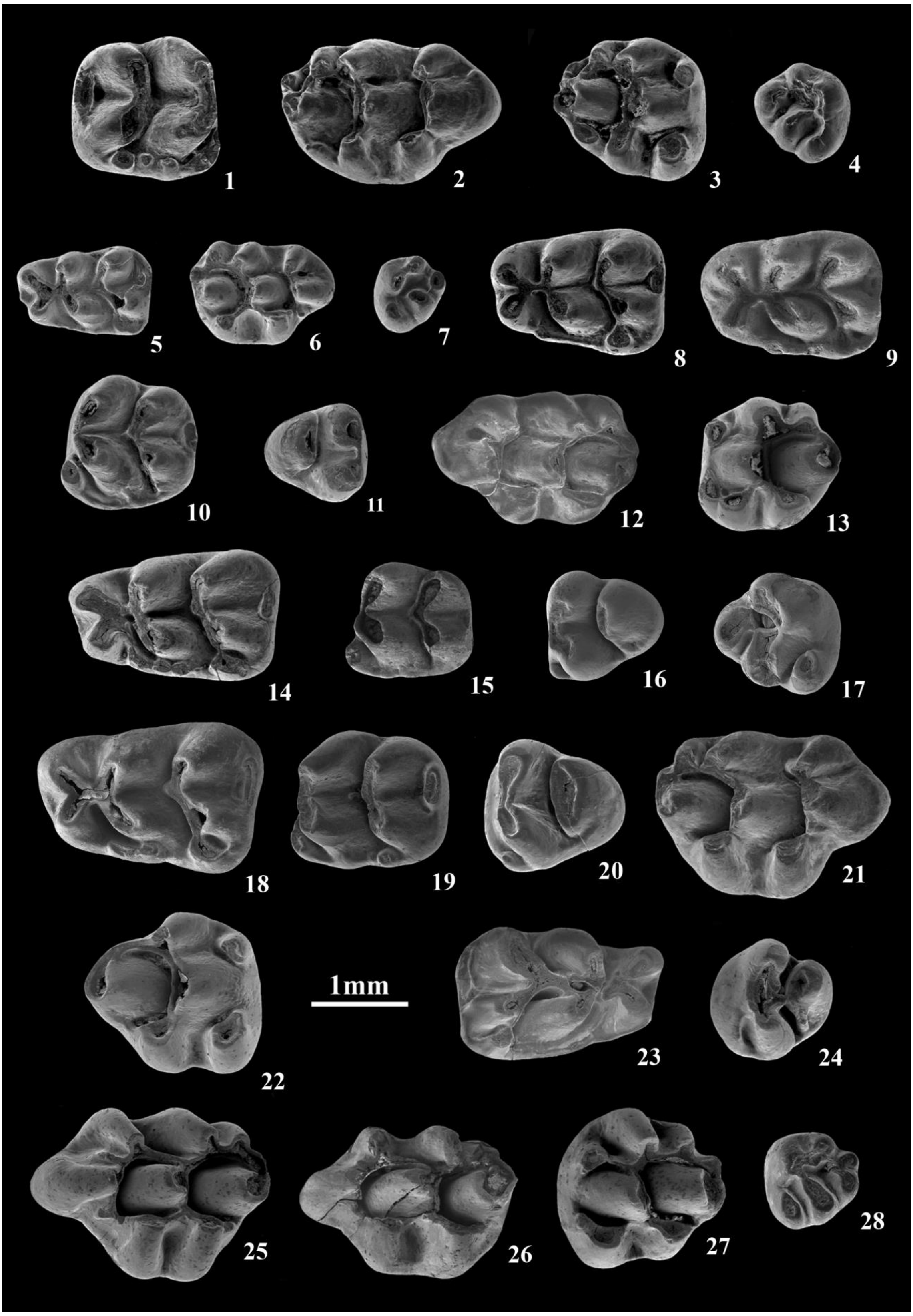


Figure VII.1. Rodents faunas from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Apodemus gorafensis* from LB2B and LB3. **1**, right m2, LB3-10; **2**, right M1, LB2B-9; **3**, right M2, LB2B-21; **4**, right M3, LB2B-219. *Castillomys gracilis* from LB2B. **5**, left m1, LB2B-90; **6**, right M1, LB2B-14; **7**, left M3, LB2B-214. *Occitanomys brailloni* from LB2B. **8**, left m1, LB2B-93; **9**, left m1, LB2B-82; **10**, left m2, LB2B-39

11, right m3, LB2B-112; **12**, left M1, LB2B-123; **13**, left M2, LB2B-135. *Paraethomys meini* from LB2B. **14**, left m1, LB2B-29; **15**, left m2, LB2B-193; **16**, left m3, LB2B-198; **17**, right M3, LB2B-138; *Paraethomys* aff. *abaigari* from LB2B. **18**, left m1, LB2B-187; **19**, left m2, LB2B-191; **20**, left m3, LB2B-3; **21**, right M1, LB2B-128; **22**, right M2, LB2B-134; *Stephanomys dubari* from LB2B and LB3. **23**, right m1, LB2B-182; **24**, left m3, LB2B-199; **25**, left M1, LB2B-127; **26**, left M1, LB2B-12; **27**, left M2, LB2B-132; **28**, left M3, LB3-24. Scale bar: 1 mm.

Family Gerbillidae Alston, 1876

Subfamily Taterillinae Chaline, Mein and Petter, 1977

Genus *Debruijnimys* Castillo and Agustí, 1996

Debruijnimys cf. *julii* Castillo and Agustí, 1996 (Fig. VII.2, 1-2)

Locality: LB2B.

Material: **1 M1** (LB2B-248).

Description:

M1: (2.78 x 2.03): The anterocone is sub-triangular, with a flat anterior face. An indentation on the anterior face of the anterocone subdivides this cusp into two lobes. There is a posterior spur on the lingual lobe of the anterocone, directed towards the protocone-paracone junction. The anterocone and the protocone are linked by a low longitudinal ridge. The protocone and paracone are equivalent in size, and separated from the hypocone-metacone complex by a deep valley. The posterior walls of the protocone and the paracone show low posterior spurs that connect, at medium level, to the hypocone and the metacone, respectively. The hypocone is larger than the metacone, and posteriorly displaced. There is a shallow furrow between hypocone and metacone.

Discussion:

In the Iberian Peninsula several Late Miocene and Early Pliocene localities have yielded remains of *Debruijnimys* Castillo and Agustí, 1996 (see Agustí and Casanovas-Vilar 2003 and Minwer-Barakat *et al*. 2009a). The record of *Debruijnimys* in Spain comprises two species: *D. almenarensis* (Agustí, 1990) from the Late Miocene (MN13) and *D. julii* Castillo and Agustí, 1996 from the middle Pliocene (MN15). *Debruijnimys* *almenarensis* is recorded in Salobreña, Almenara M, Zorreras 2B and 3A, and Negratín-1 (Agustí 1990, Agustí 1991, Martín-Suárez *et al*. 2000, Minwer-Barakat *et al*. 2009b, Agustí *et al*. 2011) and *D. julii* in Asta Regia-3 (Castillo and Agustí 1996).

Other Spanish localities of Early Ruscinian age (MN14) with presence of the genus *Debruijnimys* are Alcoy, Caravaca, Gorafe 1, Botardo, Bacochas 1 and La Gloria 4 (Sesé 1989, Agustí 1991, Castillo and Agustí 1996 and Minwer-Barakat *et al*. 2009a) (Fig. VII.4). The scarcity of material in these localities led the authors to determine these specimens as *Debruijnimys* sp.; Agustí and Casanovas-Vilar (2003) considered that all these samples from the Ruscinian referred to *Debruijnimys* sp. were forms related to *D. julii*.

The phylogenetic relationship of the Spanish forms of *Debruijnimys* is not clear. Thus, the larger size and the presence of derived characters in *D. almenarensis* (MN13), like the very large anteroconid, led Agustí and Casanovas-Vilar (2003) to refuse an ancestor-descendant relationship between *D. almenarensis* and the Spanish material of *Debruijnimys* from the Early Ruscinian (MN14). According to these authors, the forms of *Debruijnimys* of Early Ruscinian age would be an intermediate step in a phylogenetic lineage comprising *D. davidi* from Lissafa (Morocco) (Late Turolian, MN13, 5.5 Ma) (Raynal *et al*. 1999) and *D. julii* from Asta Regia 3 (Late Ruscinian, MN15).

The upper molars of *D. julii* differ from those of *D. almenarensis* by several characters, like the presence of a weak indentation on the anterior face of the anterocone that creates two confluent lobes and the degree of separation between the protocone-paracone and hypocone-metacone pairs. While in *D. almenarensis* there is a wide valley, without posterior spurs (Fig. VII.2, 2), in *D. julii* there is a low connection between the posterior walls of the protocone and paracone and the anterior sides of the hypocone and metacone, respectively (Fig. VII.2, 1) (Castillo and Agustí 1996, Plate 1, Fig. 4-5). Moreover, the shape of the M1, sub-rectangular in the M1 of *D. almenarensis* Minwer-Barakat *et al*. (2009a) observed an increase in size from *D. davidi* from Lissasfa to *D. julii* from Asta Regia. The size of the material of the Early Ruscinian Spanish populations of *Debruijnimys* is similar to that of *D. julii* (Castillo and Agustí 1996) and much larger than that of *D. davidi* from Lissasfa (Geraads 1998). The M1 from La Bullana 2B is much larger than those of *D. davidi* from Lissasfa and very similar in size to those of *D. almenarensis* and *D. julii* (Agustí 1990, Martín Suárez *et al*. 2000, Minwer-Barakat *et al.* 2009a).

Moreover, the M1 from La Bullana 2B clearly differs from those of Lissasfa in the morphology of hypocone-metacone pair. While in Lissasfa the metacone is placed posteriorly with respect to the hypocone, in La Bullana 2B the metacone is placed anteriorly. In the single M1 from La Bullana 2B, the metacone is placed in a more anterior position with respect to the hypocone than in *D. almenarensis* from its type locality, Almenara M (Fig. VII.2, 2), and similar to that of *D. julii* (Castillo and Agustí 1996).

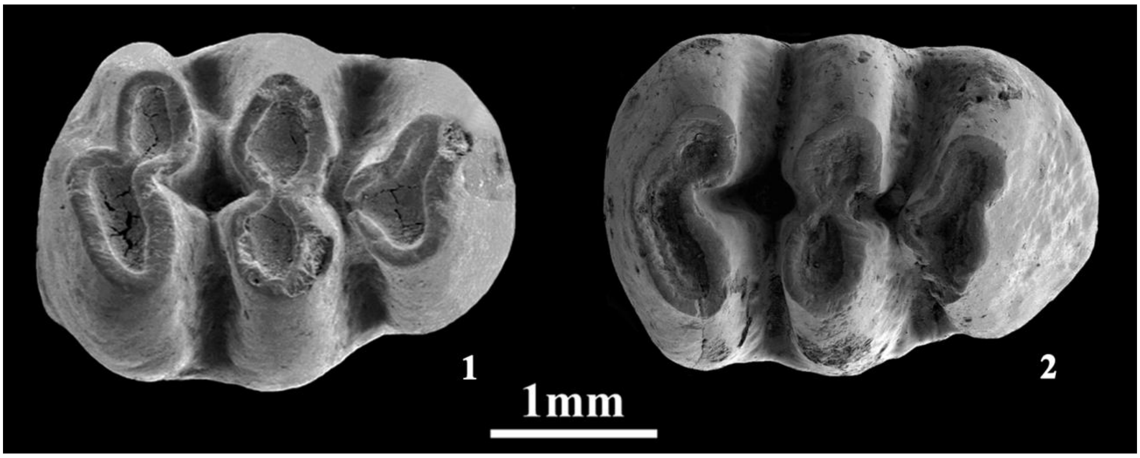


Figure VII.2. *Debruijnimys* cf. *julii* from La Bullana 2B (Cabriel Basin). **1**, right M1, LB2B-248. *Debruijnimys almenarensis* from Almenara-Casablanca M. **2**, right M1, MGUV-27742. Scale bar: 1mm.

The morphology of the anterocone of the M1 from La Bullana 2B is more similar to *D. almenarensis* and *D. julii* than to *D. davidi*. The presence of a weak indentation on the anterior face of the anterocone, that creates two confluent lobes, is present in *D. julii* and, in a lesser degree, also in *D. almenarensis* from Almenara M (Fig. VII.2, 2), and in *Debruijnimys* from La Bullana 2B, being absent in the M1 of *D. davidi* from Lissasfa. The absence of lower dentition and other elements of the upper dentition in La Bullana 2B does not allow going further in the comparison between the African and the Spanish forms of *Debruijnimys* of Late Miocene-Early Pliocene age.

Based on the size, the less elongated shape of this specimen, the presence of low posterior spurs connecting the protocone-hypocone and paracone-metacone pairs and the more accentuated asymmetry in the position of metacone and hypocone in the M1 of *Debruijnimys* from La Bullana 2B, we distinguish this tooth from *D. almenarensis* and assign it to a form related to *D. julii*.

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Eliomys intermedius Friant, 1953 (Fig. VII.3, 8-10)

Locality: LB2B.

Material: **4 m1,2 (**LB2B-6, LB2B-176, LB2B-242, LB2B-243), **1 m3** (LB2B-179), **1 M1,2** (LB2B-241), **1 M3** (LB2B-177), **1 P4** (LB2B-178).

Description:

m1,2: (1.42 x 1.77; 1.51 x -; - x 1.50): The anterolophid is connected to the protoconid in 1 out of 4 specimens. There is no anterotropid. There is a low connection between metalophid and metaconid. The centrolophid is long and not connected to the metalophid but in one specimen. There is no endolophid. The mesolophid is connected to the entoconid. The posterotropids are well developed.

m3: The only available tooth is broken anteriorly. The posterotropid is absent. The centrolophid is shorter than in the m1-2. There is no endolophid. The posterolophid is continuous.

P4: (1.08 x 1.48): Subtriangular outline. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous.

M1,2: (1.25 x 1.79): The anteroloph is separated from both protoloph and paracone by a deep valley. There is neither anterotrope nor posterotrope. Paracone and metacone are high and separated from each other. The protoloph and metaloph are continuous. In the only complete specimen the precentroloph is long, and the postcentroloph is absent (Fig. VII.3, 9). The endoloph and posteroloph are connected and continuous.

M3: (1.27 x 1.52): Trapezoidal outline, with the anterior part notably wider than the posterior side. The anteroloph is separated from protoloph, but closer to paracone than in M1-2. Both anterotrope and posterotrope are absent. The paracone and metacone are high and separated, and attached to a continuous protoloph and metaloph, respectively. Both centrolophs are present and well developed, being the postcentroloph longer and interrupted near its lingual end (Fig. VII.3, 10). The endoloph and posteroloph are connected and continuous.

Discussion:

The specimens from La Bullana 2B are larger, more concave and have a more rounded outline than those of *Eliomys truci* Mein and Michaux 1970 and *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. Their size is similar to *Eliomys intermedius* Friant, 1953 from Sète and Orrios 3 (Adrover 1986), PUR-13, TCH-3, TCH-1B and TCH-13 (García-Alix *et al.* 2008b) and *Eliomys* cf. *intermedius* from Arquillo 3, Villalba Alta (Adrover 1986) and Mont Hélène (Aguilar *et al.* 1986). The presence of two centrolophs, being the postcentroloph well-developed in the single M3 from La Bullana 2B (Fig. VII.3, 10), agree with the species *Eliomys intermedius*.

Family Sciuridae Fisher, 1817

Subfamily Pteromyinae Brandt, 1855

Genus *Atlantoxerus* Forsyth Major, 1893

Atlantoxerus sp. (Fig. VII.3, 1)

Localities: LB2B, LB3.

Material: **1 D4** (LB2B-244), **1 m1,2** (LB3-47).

Description:

D4: (2.36 x -): Tooth broken posterolabially. Sub-triangular outline. The parastyle is connected to the anteroloph, and separated from the protoloph by a wide and deep valley. The protocone is well developed, very high and connected to the paracone by the protoloph. The metacone is partially broken, and connected to the metaconule by a narrow crest. Both cusps are very close to each other and connected basally to the posteroloph. The metaconule is separated from the hypocone and protocone by a deep valley.

m1,2: Molar broken anteriorly. The posterolophid bears a small hypoconulid, and connects the entoconid to the hypoconid.

Discussion:

Heteroxerus and *Atlantoxerus* differ mainly in size, but *Atlantoxerus* has also higher crowns and cusps, more rounded conules and wider crests (Cuenca-Bescós 1988). The studied specimens are larger than those of *Heteroxerus*, *Atlantoxerus cuencae* Aguilar, Calvet and Michaux, 1995, *A. martini* Aguilar, 2002 and *A. idubedensis* Cuenca, 1988, They are clearly smaller than those of *Atlantoxerus tadlae* (Lavocat, 1961), slightly smaller than *A*. cf. *margaritae* from La Gloria-2 and Villalba Alta, and slightly larger than the same taxon from Aldehuela (Adrover *et al*. 1993). The D4 is shorter but wider than that of *A*. cf. *margaritae* from Purcal-4 (García-Alix *et al*. 2007). *Atlantoxerus adroveri* Bruijn and Mein, 1968, from Concud 3 (Weerd 1976), and *A. rhodius* Bruijn, Dawson and Mein, 1970 are slightly smaller than our specimens. Due to the scarcity and bad preservation of the recovered specimens we cannot confirm whether the *Atlantoxerus* from La Bullana 2B is a form related to *A. margaritae* or to *A. adroveri*, so we ascribe these molars to *Atlantoxerus* sp.

Sciuridae indet.?

Locality: LB2B.

Material: **1 m1,2** (LB2B-254).

Description:

m1,2: The molar is broken posterolingually. The protoconid is large, and connected to a well-developed anteroconulid. There is a weak anterior cingulid. The crest that connects the protoconid and the hypoconid is slightly swollen, forming a weak mesoconid.

Discussion:

The specimen from La Bullana 2B certainly corresponds to a sciurid, but it is much smaller than the other remains of sciurids found in this locality ascribed to *Atlantoxerus*.

The presence of an anterior cingulid is characteristic of some species of *Heteroxerus*, although a reduced cingulid may be present in some species of *Atlantoxerus*, like *Atlantoxerus blacki* (Cuenca-Bescós 1988). Therefore, a more precise determination of this tooth is not possible.

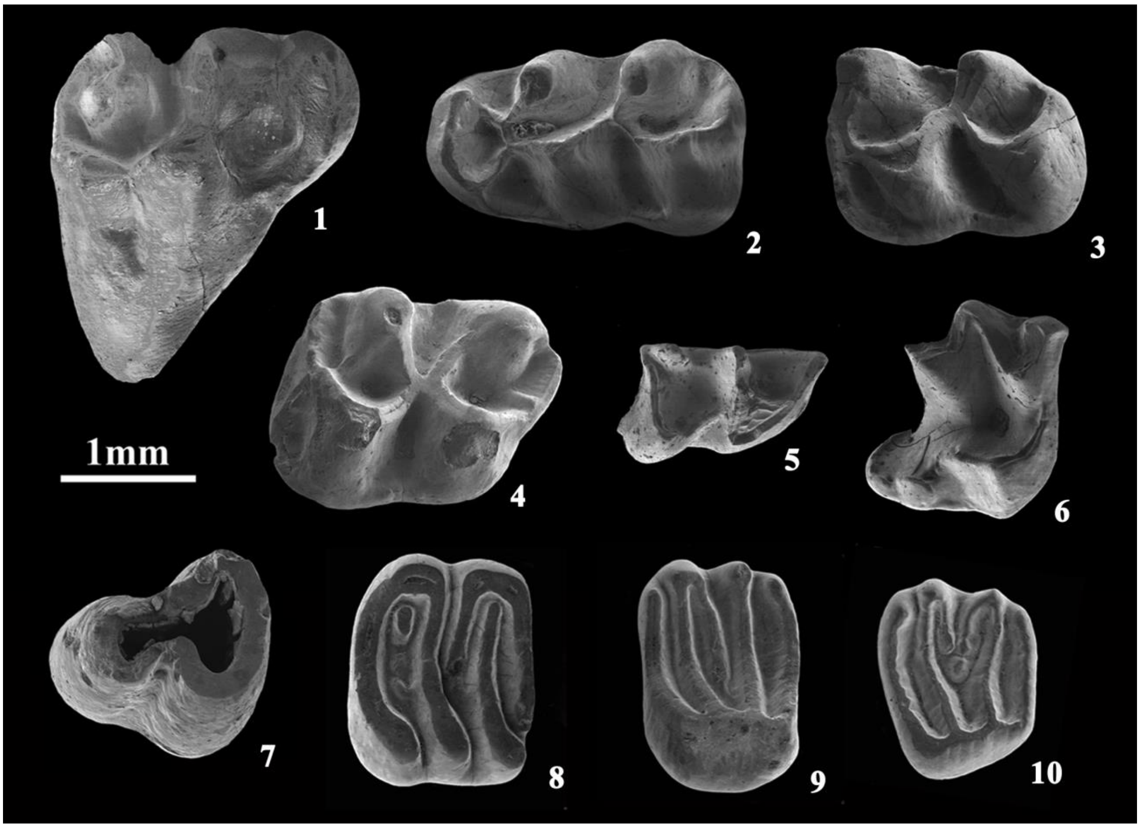


Figure VII.3. Rodents and insectivores from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Atlantoxerus* sp. from LB2B. **1**, right D4, LB2B-244. *Apocricetus barrierei* from LB2B. **2**, left m1, LB2B-141; **3**, left m3, LB2B-232; **4**, left M2, LB2B-220. *Asoriculus* cf. *gibberodon* from LB2B and LB3. **5**, left m1, LB3-31; **6**, right M1, LB2B-245. *Ruscinomys* sp. from LB2B. **7**, right m3, LB2B-175. *Eliomys intermedius* from LB2B. **8**, right m1,2, LB2B-176; **9**, left M1,2, LB2B-241; **10**, left M3, LB2B-177. Scale bar: 1 mm.

Family Cricetidae Fischer, 1817

Subfamily Cricetinae Fischer, 1817

Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998

Apocricetus barrierei (Mein and Michaux, 1970) (Fig. VII.3, 2-4)

Localities: LB2B, LB3.

Material: **16 m1** (LB2B-55 to LB2B-58, LB2B- 141 to LB2B-143, LB2B-145 to LB2B-149, LB2B-221, LB2B-222, LB2B-256, LB2B-259), **19 m2** (LB2B-59 to LB2B 63, LB2B-152, LB2B-156, LB2B-157, LB2B-160, LB2B-169, LB2B-173, LB2B-174, LB2B-227, LB2B-228, LB2B-230, LB2B-231, LB2B-262, LB3-34, LB3-45), **19 m3** (LB2B-7, LB2B-69 to LB2B-71, LB2B-150, LB2B-153, LB2B-154, LB2B-162, LB2B-164, LB2B-232 to LB2B-235, LB2B-239, LB2B-263, LB2B-264, LB3-32, LB3-40, LB3-41), **6 M1** (LB2B-72, LB2B-144, LB2B-224, LB2B-225, LB2B-257, LB2B-261), **24 M2** (LB2B-74 to LB2B-80, LB2B-151, LB2B-155, LB2B-158, LB2B-159, LB2B-163, LB2B-165, LB2B-166, LB2B-168, LB2B-220, LB2B-226, LB2B-229, LB2B-233, LB2B-237, LB3-33, LB3-35, LB3-36, LB3-37), **16 M3** (LB2B-64 to LB2B-68, LB2B-161, LB2B-167, LB2B-170 to LB2B-172, LB2B-236, LB2B-238, LB2B-240, LB2B-260, LB3-38; LB3-39).

Measurements: Table VII.6.

Description:

m1: Crest-like anteroconid, without any trace of subdivision. Anterolophulid usually double. In 2 out of 12 specimens a third crest pointing backwards from the middle of the anteroconid is present. The anterolophulids arise from a prelophid. Metalophulid strongly directed forwards. Mesolophid absent. Three roots.

m2: Anterosinusid absent. Metalophulid very short and strongly directed forwards, forming the anterior wall of the tooth. The labial anterolophulid reaches the base of the protoconid, enclosing a deep protosinusid. Except for 2 out of 16 specimens, the mesosinusid and sinusid are closed by a cingulum ridge. Mesolophid and ectomesolophid absent. Posterolophid low, connected to the base of the entoconid. Two roots.

m3: The shape of these molars is subrectangular in 4 specimens, and slightly subtriangular in 6 (see the explanation of the different shape cattegories in chapter XI.4.2.2). Anterosinusid absent (12) or very small (2). A very short lingual anterolophulid is present in the latter two specimens. Metalophulid very short and strongly directed forwards. The labial anterolophulid reaches the base of protoconid, enclosing a deep protosinusid. The mesosinusid and sinusid are closed by a cingulum ridge. Mesolophid absent (10), low, connected to the metaconid (3) or high (3). Ectomesolophid absent. Posterolophid connected to the entoconid at medium height. Two roots.

M1: Cingulum ridge on the base of the anterocone absent (5) or weak (1). The anterolophules are well developed and arise from a very short preloph. Anterior protolophule absent (4), weak (1) or well-developed (2). Mesoloph and ectomesoloph absent. Anterior metalophule always present. Posterior metalophule absent. The posterior part of the posterosinus is shallow, whereas the anterior part is much deeper.

M2: Medium length-long anteroloph, enclosing a small protosinus. The protocone is not separated from the lingual border. The labial anteroloph is long, enclosing the anterosinus. The anterior protolophule is absent (8) or present (16). One specimen has a second connection between paracone and labial anteroloph. Mesoloph and ectomesoloph are absent. The sinus and mesosinus are closed by a low cingulum ridge. The anterior branch of the metalophule is always present. The posteroloph is strongly curved, forming a L-shaped posterosinus. The posterior metalophule may be complete (2), just a trace of a crest (5) or absent (13). Three roots.

M3: Lingual anteroloph short and low. The protocone is not separated from the lingual border. The labial anteroloph is long, running along the labial border until it connects to the paracone. The anterior protolophule is always present, longitudinal and complete (10) or low and interrupted (5). The sinus and mesosinus are closed by a low cingulum ridge. Mesoloph absent. The posterolingual corner is strongly reduced. The posterior border of the tooth is rounded. Posterosinus strongly reduced. Three roots.

Discussion:

The assemblages from La Bullana 2B and La Bullana 3 have an intermediate size between *A. angustidens* and *A. alberti*. The m1 from La Bullana 2B have a crest-like anteroconid, with a weak subdivision, with two anterolophulids arising from a prelophid. In 2 out of 12 specimens there is a third crest pointing backwards from the middle of the anteroconid. The mesolophids are generally absent in m1 and m2. The m3 is generally longer than the m2, having a complete mesolophid in 3 out of 13 specimens. In the m3 from La Bullana 3 the mesolophid is absent.

In La Bullana 2B, the cingulum ridge on the base of the anterocone of M1 is absent (5) or weak (1). Of the seven M1, two have a complete anterior protolophule, one has a weakly developed crest and four have no crest at all. The posterior metalophule is very scarce in M1. 16 out of 20 M2 from La Bullana 2B have an anterior protolophule, whereas the only complete M2 from La Bullana 3 lacks this ridge. 4 out of 17 M2 from La Bullana 2B and 1 out of 3 from La Bullana 3 have a hint of metalophule. In the M3 an anterior protolophule is always present, being complete in 9 out of 13 specimens from La Bullana 2B and in 1 out of 2 from La Bullana 3.

The size of the *Apocricetus* assemblages from La Bullana 2B and La Bullana 3 agrees with that of *A. barrierei* (Freudenthal *et al*. 1998, Ruiz-Sánchez *et al*. 2014).

The lower molars of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* in the weakly split anteroconid in m1, the more pronounced enlargement of m3 and the absence of mesolophids in most m1-2. The prelophid is present in some specimens of *A. alberti*, but is less developed than in *A. barrierei* (Mansino *et al*. 2014, chapter XI).

The M1-2 of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* by the bifid anterolophule in the M1 and the absence of mesoloph in the M1-2. Some specimens of *A. alberti* and *A. barrierei* develop a weak cingulum ridge on the base of the anterocone of M1 (Mansino *et al*. 2014, chapter XI). This ridge is well-developed in *A. angustidens*.

The anterior protolophule of the upper molars is less developed in *A. barrierei* from La Bullana 2B and La Bullana 3 than in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and higher than in *A. angustidens*. In addition, the presence of posterior metalophule, complete or hinted, in *A. barrierei* from La Bullana 2B and La Bullana 3 differs from those of *A. angustidens*.

Therefore, on the basis of metric and morphological features, the material of the genus *Apocricetus* from La Bullana 2B and La Bullana 3 may be assigned to *A. barrierei*.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	7	2.22	2.34	2.43
		W	8	1.26	1.42	1.64
m2	LB2B	L	13	1.86	2.03	2.13
		W	15	1.49	1.57	1.71
	LB3	W	1	1.47	1.50	1.52
m3	LB2B	L	9	1.89	2.09	2.23
		W	12	1.51	1.53	1.58
	LB3	L	1	-	2.05	-
		W	3	1.53	1.55	1.57
M1	LB2B	L	4	2.45	2.64	2.81
		W	4	1.62	1.73	1.83
M2	LB2B	L	15	1.80	2.05	2.26
		W	18	1.46	1.68	1.81
	LB3	L	1	-	1.92	-
		W	4	1.45	1.60	1.75
M3	LB2B	L	11	1.62	1.79	1.94
		W	12	1.40	1.51	1.67
	LB3	L	4	1.63	1.73	1.83
		W	1	-	1.48	-

Table VII.6. Measurements in millimetres of the teeth of *Apocricetus barrierei* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Subfamily Cricetodontinae Stehlin and Schaub, 1951

Genus *Ruscinomys* Depéret, 1890

Ruscinomys sp. (Fig. VII.3, 7)

Locality: LB2B.

Material: **1 M3** (LB2B-175).

Description:

M3: (1.80 x 1.54): The dentine is completely lost. This molar has two lobes delimited by the sinus and mesosinus. The posterior lobe is smaller than the anterior one.

Discussion:

Because of its general morphology and hypsodonty, we can ascribe the unique cricetodontine tooth from LB2B to the genus *Ruscinomys*, although a specific determination is not possible. The only available molar is an M3, an element which lacks most diagnostic characters. Adrover (1969) noted that the M3 of *Ruscinomys lasallei* Adrover, 1969, and *R. schaubi* Villalta and Crusafont Pairó, 1956, are less reduced than those of *R. europaeus* Déperet, 1890. The M3 from La Bullana 2B differs from the latter species by the presence of two well-developed lobes. However, distinguishing between *R. lasallei* and *R. schaubi* is difficult. The size of the M3 from La Bullana 2B is consistent with the lower measurements of *R. lasallei* and *R. schaubi* and even with smallest values of *R. europaeus*. For all these reasons, we ascribe the specimen from La Bullana 2B to *Ruscinomys* sp.

Order Soricomorpha Gregory, 1910

Family Soricidae Fischer von Waldheim, 1817

Subfamily Soricinae Fischer von Waldheim, 1817

Tribe Nectogalini Anderson, 1879

Genus *Asoriculus* Kretzoi, 1959

Asoriculus cf. *gibberodon* (Petényi, 1864) (Fig. VII.3, 5-6)

Localities: LB2B, LB3.

Material: **1 m1** (LB2B-245), **1 M1** (LB3-31).

Description:

m1: (L: 1.44; TRW: 0.77; TLW: 0.91): The talonid is wider than the trigonid. The hypolophid is well developed and does not reach the entoconid. There is a well-developed oblique crest, which connects the hypoconid with the trigonid. The metaconid is slightly higher than the paraconid. The depression of the trigonid is open and ‘V’ shaped. The protoconid is broken. The lingual cingulid is low and narrow. The labial cingulum is reduced.

M1: (LL: 1.57; AW: 1.68): The metaloph does not reach the hypocone. There is a well-developed hypoconal flange and a pronounced posterior emargination. The basal connection between the hypocone and posteroloph agrees with the morphotype B described by Reumer (1984). The preprotocrista is in contact with the paracone. The parastyle is short. The paracrista is the shortest crest in the ectoloph. The paramesocrista is longer than the postmesocrista. The metastyle is broken. The metacone is higher than the paracone. The ectoloph is asymmetric.

Discussion:

Asoriculus gibberodon is the smallest species of the genus, and very common in the Pliocene of Europe (Minwer-Barakat *et al*. 2010, Furió and Angelone 2010). The presence of a large protoconid and a complete basal cingulum in lower molars are typical features of *A. gibberodon* (Furió 2007). The hypocone attached to the posteroloph in the M1 agree with the morphotype B of Reumer (1984). The size of the m1 is consistent with the minimum values of the molars from Villany 3, Csarnota 2, Ostrazmos 1 and 9 (Reumer 1984), Varshets (Popov 2003), Fuente Nueva 3 (Furió 2007), TCH-1 and TCH-3 (Minwer-Barakat *et al*. 2010) and Capo Mannu D1 (Furió and Angelone 2010). The size of the M1 matches the largest values of the specimens from the mentioned localities. This great biometrical variability is usual in *A. gibberodon* (Reumer 1984, Minwer-Barakat *et al*. 2010).

VII.3. Discussion

VII.3.1. Biostratigraphy

Fig. VII.4 contains information on the stratigraphical distribution of the rodent faunas described in La Bullana 2B and La Bullana 3, besides other of Spanish localities from MN13 to MN15. The locality of La Bullana 2B contains *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys* aff. *abaigari*, *Paraethomys meini*, *Occitanomys brailloni*, *Occitanomys* sp., *Stephanomys dubari*, *Eliomys intermedius*, *Apocricetus barrierei*, *Ruscinomys* sp., *Atlantoxerus* sp., Sciuridae indet., *Debruijnimys* cf. *julii* and *Asoriculus* cf. *gibberodon*. On the other hand, the locality La Bullana 3 contains

Apodemus gorafensis, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, *Atlantoxerus* sp., and *Asoriculus* cf. *gibberodon*. The coexistence of *Apodemus gorafensis*, *Paraethomys meini*, *Castillomys gracilis* and *Stephanomys dubari* is considered typical of the latest Turolian-earliest Ruscinian (García-Alix *et al*. 2008a). The size and morphology of *Stephanomys* present in La Bullana 2B and La Bullana 3, with some specimens close to *S. cordii*, are similar to the molars from the lower Ruscinian (MN14) sites of PUR-4, PUR-7 and PUR-13 (García-Alix *et al*. 2008a).

Other species of biostratigraphic relevance in La Bullana 2B are *Occitanomys brailloni* and *Paraethomys* aff. *abaigari*. *Occitanomys brailloni* appears in MN14, extending its range to MN16 (Weerd 1979, Ruiz Bustos *et al*. 1984, Castillo 1990, Minwer-Barakat 2005). *Paraethomys* aff. *abaigari* is found together with the smaller *P. meini* in some localities of the MN14, like PUR-13, CLC-5A, Celadas-14, Celadas-5, Celadas-5A, La Gloria 4 and Celadas 9 (García-Alix *et al*. 2008e). In older localities, closer to the MN13-MN14 boundary like PUR-4, *P. meini* shows a wide size range, which may indicate that the lineage of *P. abaigari* is already present in those assemblages, and in Peralejos E two specimens are close to *P.* aff. *abaigari* (García-Alix *et al*. 2008a).

Regarding the cricetids, the presence of *Apocricetus barrierei* in La Bullana 2B and La Bullana 3 is a clearly indicates a lower Ruscinian age for these localities (Freudenthal *et al*. 1998, García-Alix *et al*. 2008b).

In La Bullana 2B, glirids are represented by *Eliomys intermedius*. This species appears in MN14 (Sesé 2006a), being La Gloria 4 in the Teruel basin (Mein *et al.* 1990), and PUR-13 in the Granada Basin (García-Alix *et al*. 2008b), the oldest records of this taxon. The faunal assemblage of La Bullana 2B indicates a similar age for the three localities (see Fig. VII.4).

Debruijnimys julii was described in the middle Pliocene (MN15) locality of Asta Regia (Castillo and Agustí 1996), where *Stephanomys donnezani*, *Paraethomys jaegeri* and *Paraethomys* cf. *meini* are also present. This assemblage is clearly younger than that from LB2B.

Debruijnimys sp. has been cited in the lower Ruscinian sites of Gorafe 1, La Gloria 4, Alcoy 4B and Caravaca (Minwer-Barakat *et al*. 2009b). Gorafe 1, from the latest MN14 is included by Minwer-Barakat *et al*. (2012) in the *Trilophomys* Assemblage Zone of the Guadix basin, characterized by the association of *Apocricetus barrierei*, *Stephanomys cordii*, *Castillomys gracilis*, *Apodemus gorafensis*, *Paraethomys meini* and *Trilophomys*.

With respect to La Gloria 4, this locality belongs to the *Promimomys* and *Paraethomys* Assemblage Zone of the Teruel basin, within the MN14, where two species of *Paraethomys*, *P. meini* and *P. abaigari*, coexist (Mein *et al*. 1990). The presence of *Stephanomys dubari*, two *Paraethomys* species and *Apocricetus barrierei* suggest a similar age for La Gloria 4 and La Bullana 2B and La Bullana 3 (Fig. VII.4). In Caravaca, the presence of *S. dubari*, *Apocricetus barrierei*, *Castillomys gracilis* and a big-sized *Apodemus* indicate a similar age to that of La Bullana 2B and La Bullana 3 (Freudenthal *et al*. 1998, Bruijn *et al.* 1975, Weerd 1976, Aguilar *et al.* 1991).

According to these observations, *Debruijnimys* sp. from Gorafe 1 and Alcoy 4B are younger than the form present in La Bullana 2B, and *Debruijnimys* sp. from Caravaca and La Gloria 4 may be of a similar age. The sites where *D. almenarensis* is present, Negratín-1 and Almenara M, correspond to the Late Turolian and are clearly older than La Bullana 2B and La Bullana 3.

VII.3.2 Palaeomagnetism

We collected five samples to produce a preliminary paleomagnetic study around La Bullana sites, which are stratigraphically above the classical site of Venta del Moro, dated at 6.23 Ma (Gibert *et al*. 2013). The samples from La Bullana 3 show normal polarity, like the two lower samples from La Bullana 2B, while the two upper samples from this locality show reverse or ambiguous polarities, indicating a normal-reverse polarity sequence (Fig. II.8). The presence of a basal normal zone, the differences with Venta del Moro fauna and the similarities with sites located in the latest Miocene or earliest Pliocene suggest that the identified normal zone should be correlated with chron C3n.4n in the earliest Pliocene, dated between 5.235 Ma and 4.997 Ma (Lourens *et al*. 2005). Therefore, the fauna of La Bullana 3 can be constrained to the age of this chron

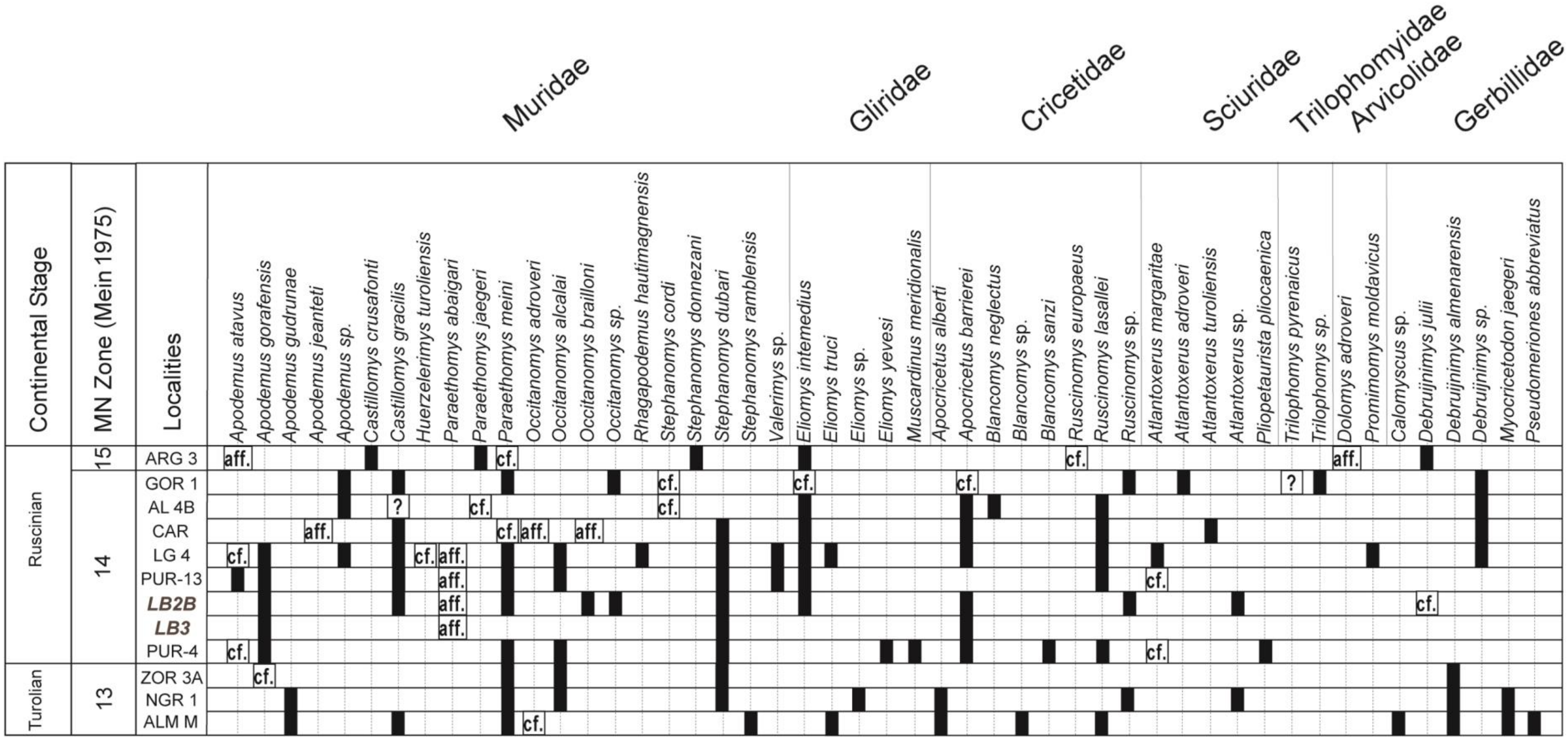


Figure VII.4. Distribution chart of the rodents studied in this chapter and of related species of similar age. Abbreviations: ARG3, Asta Regia 3 (Castillo and Agustí 1996); GOR 1, Gorafe 1 (Bruijn 1974, Martín-Suárez and Mein 1991, Agustí and Martín-Suárez 1984); AL 4B, Alcoy 4B (Agustí personal comment); CAR, Caravaca (Freudenthal *et al*. 1998, Bruijn *et al*. 1975, Weerd 1976, Aguilar *et al.* 1991); LG 4, La Gloria 4 (Mein *et al*. 1990, García-Alix 2006, García-Alix *et al*. 2008a); PUR-13, Purcal 13 (García-Alix 2006); LB3, La Bullana 3 and LB2B, La Bullana 2B; PUR-4, Purcal 4 (García-Alix 2006, Mansino *et al.* in press); ZOR3 A, Zorreras 3A (Martín-Suárez *et al.* 2000); NGR 1, Negratín 1 (Minwer-Barakat *et al.* 2009a); ALM-M, Almenara M (Agustí and Galobart 1986, Agustí *et al*. 2011). For making this figure the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Protatera almenarensis* as *Debruijnimys almenarensis*; *Protatera* sp. as *Debruijnimys* sp.

and the site La Bullana 2B, placed a few meters above its upper boundary, should be constrained between the age of this boundary (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

VII.3.3. Palaeoecology

The analysis of micromammal assemblages has been widely used as a paleoclimatic indicator (Weerd 1976, Daams *et al*. 1988, Casanovas-Vilar and Agustí 2007, García-Alix *et al*. 2008, Furió *et al*. 2011).

Some authors have proposed a minimum sample size of at least 100 specimens when dealing with fossil assemblages (Daams *et al*. 1999, García-Alix *et al*. 2008c), while others used a minimum of 50 specimens (Casanovas-Vilar and Agustí 2007), arguing that in most cases larger samples only add one or two species to the assemblage, with an abundance of less than 1 %. According to this, the sample from La Bullana 3 is too scarce to carry out any paleoecologic inference, having yielded just 32 specimens. For this reason we only present here the data from La Bullana 2B.

To interpret the paleoecologic requirements of each taxon found in La Bullana 2B, we have used mainly the climatic and habitat preferences proposed by García Alix *et al.* (2008c). According to that work, a number of taxa are considered as warm weather indicators (*Apodemus gorafensis, Paraethomys meini, Apocricetus, Atlantoxerus* and *Asoriculus gibberodon*), whereas *Ruscinomys*, of which a single element has been found, indicates cold conditions. Regarding the humidity, the presence of *P. meini*, *Ruscinomys* and *Atlantoxerus* has been associated with dry conditions, while *A. gorafensis, Eliomys intermedius* and *A. gibberodon* would indicate a wet environment. The presence of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* indicates open habitats, whereas *Eliomys intermedius* and *Asoriculus gibberodon* would suggest the presence of forested zones in the area (García-Alix *et al.* 2008c). However, Freudenthal *et al.* (2014) point out that the genus *Eliomys* cannot be considered a humid environment indicator based on the ecological affinities of extant *E. quercinus,* which is a habitat generalist, and the distribution of *E. munbyanus* and *E. melanurus*, restricted to semi-desert environments. Therefore, we consider *E. intermedius,* probable ancestor of *E. quercinus* (García-Alix *et al*. 2008b), and eurytopic taxon regarding both habitat and humidity.

The presence of the gerbilid *Debruijnimys* suggests a dry and arid environment (Minwer-Barakat *et al*. 2009b), and the affinities of *P*. aff. *abaigari*, *Occitanomys brailloni* and *Occitanomys* sp. are unknown (García-Alix *et al.* 2008c).

The proportions of the taxa within each ecological category are shown in table VII.7. Regarding the humidity, most of the taxa recorded in La Bullana 2B are eurytopic (55.52 %) or with unknown affinities (*P*. aff. *abaigari* and *Occitanomys brailloni* and sp. 21.89 %). Because of that, the relative proportion of humid (10.66 %) and dry (11.93 %) environment indicators does not seem very representative. However, most of the taxa studied in this work are considered as typical to warm environments (57.87 %), and the abundance of *Apocricetus* together with *Ruscinomys* and *Atlantoxerus* and the presence of *Debruijnimys* suggest an open environment (36.78 % of the assemblage). Therefore, we consider that the faunas from La Bullana 2B indicate warm conditions and probably an open environment with some patches of vegetation.

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	Wet	Dry	Eurytopic	Cold	Warm	Eurytopic	Open	Forested	Eurytopic
LB2B	10.66	11.93	55.52	0.40	57.87	19.84	36.78	0.25	41.09

Table VII.7. Relative abundance of the taxa from the studied localities according to their ecological preferences. These percentages have been obtained by dividing each taxon by its number of diagnostic elements, as proposed by Martín-Suárez (1988). The taxa with unknown preferences are not shown.

VII.3.4. Considerations on the details of the gerbil event in Europe according the presence of this taxon in the locality of LB2B

The Messinian Salinity Crisis (MSC) is the main event in the evolution of the Mediterranean during the Neogene. The beginning of the MSC took place about 5.96 Ma ago, with the closure of the Betic and Rifian seaways, which connected the Atlantic and Mediterranean domains. The Mediterranean was reflooded at the base of the Pliocene after the opening of a new seaway, the Gibraltar strait (Hsü *et al*. 1973). The effects of this event on the faunal exchanges between Africa and Europe during this time interval have been widely discussed in the literature, and several authors have accepted the creation of new migration routes for terrestrial organisms (Brandy and

Jaeger 1980, Agustí and Casanovas-Vilar 2003, Aguirre 2003, Made *et al*. 2006, Agustí *et al*. 2006, Minwer-Barakat *et al*. 2009a, Gibert *et al*. 2013, among others).

One of the taxa of African origin that colonised the Iberian Peninsula during the MSC is the gerbil *Debruijnimys*. Until now, only two species of this genus have been recorded in Europe, *D. almenarensis*, identified in some MN13 localities, and *D. julii*, only known from the type locality, Asta Regia (MN15).

The origin of *D. almenarensis* and *D. julii* has been discussed in several papers (Castillo and Agustí 1996, Agustí and Casanovas-Vilar 2003, Minwer-Barakat *et al*. 2009a), which has important paleobiogeographic implications. While *D. almenarensis* (MN13) has a clear African origin, related to the MSC Event, the origin of *D. julii* (MN15) is more difficult to establish. Thus, the dispersion processes which explain the presence of gerbils in Western Europe have proven to be very complicated. According to Agustí and Casanovas-Vilar (2003), there are, at least, two different waves of gerbil colonisation from northern Africa recorded in the Iberian basins. The first wave, of Late Turolian age (Late Miocene), involved *D. almenarensis,* whereas the second one corresponds to the representatives of *Debruijnimys* (*Debruijnimys* sp.) found in the Lower Pliocene (lower Ruscinian, MN14) localities of Alcoy, Gorafe, Caravaca and La Gloria 4. The presence of *A. barrierei* in Botardo, Alcoy 4B, Caravaca, La Gloria 4 (Freudenthal *et al*. 1998) and La Bullana 2B, confirm an Early Pliocene age (early Ruscinian, MN14) for these localities. La Bullana 2B is older than Alcoy 4B, probably slightly older than La Gloria 4 and similar in age to Caravaca and Botardo.

If *D. julii* is not the direct descendant of *D. almenarensis*, the presence of *D. julii* in the MN15 implies, necessarily, a second migration event from Africa to Europe in the span interval between MN13 and MN15 (Agustí and Casanovas-Vilar 2003). Thus, according to Agustí and Casanovas-Vilar (2003), *Debruijnimys* sp. from the lower Ruscinian localities of Alcoy, Gorafe, Caravaca and La Gloria 4 (MN14) would be the descendant of *D. davidi*, and the ancestor of *D. julii*, known from the Late Ruscinian (MN15) site of Asta Regia 3.

However, there is a great similarity between *D. almenarensis* and the subsequent forms of *Debruijnimys* (see Fig. VII.2), and a direct ancestor-descendant relationship cannot be discarded. Still, if the presence of *D. julii* in MN14 is confirmed, it would expand the range of this taxon, until now recorded only in MN15. This would make the phylogeny of *Debruijnimys* even more complex, since the relationship between *Debruijnimys* sp. from MN14 and *D. julii* is not clear, and they may even be the same species. Another option would be a process of cladogenetic speciation along the Early Pliocene, resulting in two different lineages of *Debruijnimys*, and unnamed species and *D. julii*, but the relationship between this latter species and the forms present in MN14 is not clear, and they may be indeed the same taxon.

Nevertheless, any hypothesis on the phylogenetic relationships of *Debruijnimys* is difficult to test because of the scarce material of *Debruijnimys* sp. from the early Pliocene of the Iberian Peninsula. Only Alcoy 4B yielded a rich sample, but nowadays it is a lost locality. Therefore, until new material from Ruscinian sites becomes available, little more can be said in this regard.

The new data from La Bullana 2B contribute to improve the knowledge on the status of this lineage of African rodents in the Iberian Peninsula after the colonisation processes during the Messinian Salinity Crisis, but open new questions around the evolution of this group, too.

VII.4. Conclusions

The faunal list of La Bullana 3 comprises *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon*. In addition to these taxa, La Bullana 2B has yielded remains of *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. Based on these faunal assemblages, we propose a lower Ruscinian age (MN14) for both localities.

The preliminary paleomagnetic analysis indicates an earliest Pliocene age for La Bullana 3 and La Bullana 2B. The age of La Bullana 3 lies probably within the C3n.4n chron, dated between 5.235 Ma and 4.997 Ma. The age of La Bullana 2B should be constrained between the top of this chron (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

The presence of *Eliomys intermedius* in La Bullana 2B constitutes one of the oldest records of this taxon, probably equivalent to la Gloria 4 and PUR-13. The presence in La Bullana 2B of *Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus barrierei*, *Atlantoxerus* and *Asoriculus* cf. *gibberodon* suggest warm conditions, and the relative abundance of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* is consistent with an open environment.

The Early Ruscinian locality of LB2B constitutes the first record of a form related to *Debruijnimys julii* in MN14. However, the scarcity of the available material of *Debruijnimys* from Early Pliocene sites prevents any proper analysis, and its phylogenetic relationships remain controversial.

CHAPTER VIII. MICROMAMMAL BIOSTRATIGRAPHY OF THE LATE MIOCENE-EARLY PLIOCENE OF THE ALCOY BASIN (EASTERN SPAIN).

VIII.1. Biozonation of the Late Turolian-Early Ruscinian of the Alcoy Basin

The study of the taxa present in the localities of the Alcoy Basin has allowed us to distinguish four biozones in the Early Ruscinian and, maybe, the Late Turolian. The faunal lists of all the sites studied in this thesis can be seen in Fig. VIII.1, as well as other important localities of similar age. The locality ABS-1 has yielded a single specimen, and because its stratigraphical position and lack of the species that characterize the biozones defined in this work, its ascription to a certain unit is impossible. Therefore, we do not include this site in any of the biozones defined for the Alcoy Basin.

As recommended by the International Stratigraphic Guide, we have used widespread taxa when defining a biozone. Minwer-Barakat *et al.* (2012) suggest that the preferable definition for a biozone when dealing with fossil mammals is the assemblage zone, arguing that it would be difficult to know the stratigraphical position of a locality in which the first or last occurrence of the taxa that marks the boundaries of a certain biozone are absent. However, because of the relatively short span of time studied, the faunal lists of some localities placed in different biozones greatly overlap, being the main difference the addition or disappearance of a single taxon. For this reason, we have also used the interval and the concurrent-range zones when defining a biozone. Following García-Alix *et al.* (2008e) and Minwer-Barakat *et al.* (2012) we have also included a reference locality as well as a section for each biozone.

					Muridae																					
Series		Continental Stage	MN Zone (Mein, 1975)	Localities	*Apodemus atavus*	*Apodemus gorafensis*	*Apodemus gudrunae*	*Castillomys crusafonti*	*Castillomys gracilis*	*Huerzelerimys turoliensis*	*Micromys* sp.	*Micromys paricioi*	*Occitanomys adroveri*	*Occitanomys alcalai*	*Occitanomys brailloni*	*Occitanomys* sp.	*Parapodemus barbarae*	*Paraethomys abaigari*	*Paraethomys meini*	*Rhagapodemus hautimagnensis*	*Rhagapodemus primaevus*	*Stephanomys cordi*	*Stephanomys dubari*	*Stephanomys margaritae*	*Stephanomys ramblensis*	*Stephanomys* sp.
PLIOCENE	Early	Ruscinian	14	GOR-A		●									cf.				cf.			aff.				
				YEG															●			●				
				VAR-1	●													●	●					●		
				ALDH	●				●						●				●					●		
				AL2-D	●	●			●						●			aff.	●			●				
				AL2-C	●	●												aff.	●			●				
				CEL-9	●	●								●				aff.	●			●				
				LG-4	cf.	aff.			●	cf.				●			●	aff.	●	●			●			
				AC-0		●								●				aff.	●			aff.				
				AC-0B										●				aff.	●			aff.				
				AC-0C		●								●								aff.				
				PUR-13	●	●			●					●				aff.	●				●			
				LB2B		●			●						●	●		aff.	●				●			
				LB3		●												aff.					●			
				CLC-5A										●				aff.	●				●			
				CLC-3B	●	●			●					●					●				●			
				PER-E	●	●						●		●				?	●	●			●			
				ABS-9							●															●
				ABS-8																		aff.				
				ABS-7																						●
				ABS-3A										●				aff.	●				●			
				ABS-3		●								●				aff.	●				●			
				ABS-2							●			●				aff.	●				●			
				ABS-1																			●			
				PUR-7	●									●					●				●			
				PUR-4	cf.	●								●					●				●			
				AF-1'07		cf.								●					●				●			
			13/14	**AF-1A**										●					●				●			
				AF-1'06		cf.								●					●				●			
MIOCENE	Late	Turolian	13	AL-N												●		?	●		●					
				NGR-1			●							●					●				●			
				ALM-M			●	●					cf.						●						●	
				PUR-3										●					●				●			
				ZOR3-A		cf.								●					●				●			
				DHS-16		●			●			●		●					●				●			
				MNA-4		●						●		●					●				●			
				AR-4										●					●						●	
				VM			●							●					●				●			

					Gliridae							Cricetidae													
Series		Continental Stage	MN Zone (Mein, 1975)	Localities	*Eliomys intemedius*	*Eliomys truci*	*Eliomys* sp.	*Eliomys yevesi*	*Glis* sp.	*Muscardinus meridionalis*	*Muscardinus* sp.	*Apocricetus alberti*	*Apocricetus angustidens*	*Apocricetus barrierei*	*Blancomys neglectus*	*Blancomys sanzi*	*Blancomys* sp.	*Celadensia nicolae*	*Neocricetodon* sp.	*Neocricetodon seseae*	*Ruscinomys europaeus*	*Ruscinomys gilothi*	*Ruscinomys lasallei*	*Ruscinomys schaubi*	*Ruscinomys* sp.
PLIOCENE	Early	Ruscinian	14	GOR-A										●									●		
				YEG										●											
				VAR-1	●										●						●				
				ALDH													●				●				
				AL2-D	●				●				cf.				●						cf.		●
				AL2-C	●								cf.										cf.		
				CEL-9																			●		
				LG-4	aff.	●								●									●		
				AC-0	●						●												cf.		
				AC-0B																			cf.		
				AC-0C															●				cf.		
				PUR-13	●																		●		
				LB2B	●									●											●
				LB3										●											
				CLC-5A																					
				CLC-3B				●																	
				PER-E										●				●			●	●			
				ABS-9																					
				ABS-8																					
				ABS-7																					
				ABS-3A				●						cf.									cf.		
				ABS-3																					
				ABS-2																					
				ABS-1																					
				PUR-7			●							●											
				PUR-4				●		●				●		●							●		
				AF-1'07				●						●											
			13/14	**AF-1A**																					
				AF-1'06				●																	
MIOCENE	Late	Turolian	13	AL-N			●					●											●		
				NGR-1			●					●													●
				ALM-M		●						●					●						●		
				PUR-3			●					●											cf.		
				ZOR3-A																					
				DHS-16		●																		aff.	
				MNA-4													●							aff.	
				AR-4												●							cf.		
				VM				●				●								?				●	

					Sciuridae					Trilophomyidae		Arvicolidae	Castoridae		Hystricidae	Gerbillidae						
Series		Continental Stage	MN Zone (Mein, 1975)	Localities	*Atlantoxerus margaritae*	*Atlantoxerus rhodius*	*Atlantoxerus* sp.	*Pliopetaurista plioceanica*	*Pliopetaurista* sp.	*Trilophomys castroi*	*Trilophomys vandeweerdi*	*Polonomys insuliferus*	*Dipoides problematicus*	*Dipoides sigmodus*	*Hystrix depereti*	*Calomyscus* sp.	*Debruijnimys almenarensis*	*Debruijnimys* sp.	*Debruijnimys julii*	Gerbilidae indet.	*Myocricetodon jaegeri*	*Pseudomeriones abbreviatus*
PLIOCENE	Early	Ruscinian	14	GOR-A							●											
				YEG																		
				VAR-1	cf.					cf.												
				ALDH		aff.				cf.												
				AL2-D					●	cf.												
				AL2-C						cf.												
				CEL-9								●										
				LG-4	●							●	●					●				
				AC-0																		
				AC-0B																		
				AC-0C																		
				PUR-13	cf.																	
				LB2B			●												●			
				LB3																		
				CLC-5A																		
				CLC-3B									●									
				PER-E										●								
				ABS-9																		
				ABS-8																		
				ABS-7																		
				ABS-3A																		
				ABS-3																		
				ABS-2																		
				ABS-1																		
				PUR-7																		
				PUR-4	cf.			●														
				AF-1'07																		
			13/14	**AF-1A**																		
				AF-1'06	cf.																	
MIOCENE	Late	Turolian	13	AL-N																●		
				NGR-1			●										●				●	
				ALM-M												●	●				●	●
				PUR-3																		
				ZOR3-A													●					
				DHS-16									●									
				MNA-4																		
				AR-4																		
				VM					●				●		?							

Figure VIII.1. Biostratigraphic context of the localities from the Alcoy Basin and LB2B and LB3 (bold), from the Cabriel Basin, according to their faunal lists. Abbreviations: GOR-A, Gorafe-A (Ruiz Bustos *et al*. 1984); YEG, Yeguas (Minwer-Barakat 2005); PUR-3, PUR-4, PUR-7, PUR-13, Purcal 3, 4, 7 and 13; CLC-3B, CLC-5A, Calicasas 3B and 5A; DHS-16, Dehesa-16; MNA-4, Mina 4 (García-Alix 2006, García-Alix *et al*. 2008a); VAR-1, Villalba Alta Río 1; ALDH, Aldehuela (Adrover 1986); CEL-9, Celadas-9; LG-4, La Gloria-4; AR-4, Arquillo 4 (Adrover *et al.* 1993); PER-E, Peralejos-E (Mein *et al.* 1990); NGR-1, Negratín-1 (Minwer-Barakat *et al*. 2009a); ALM-M, Almenara-M (Agustí *et al.* 2011); ZOR-3A, Zorreras 3A (Martín-Suárez *et al.* 2000); VM, Venta del Moro (Montoya *et al.* 2006a); CR-6, Crevillente 6 (Martín-Suárez and Freudenthal 1998). For the making of this table the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* and *Stephanomys donnezani cordii* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Cricetus kormosi* and *Apocricetus kormosi* as *Apocricetus alberti*; *Protatera almenarensis* as *Debruijnimys almenarensis* and *Protatera* sp. as *Debruijnimys* sp. The locality ABS-10 has not been included since it has yielded no rodent remains.

VIII.1.1. *Paraethomys meini* Interval Zone

Definition:

Interval Zone corresponding to the interval between the FAD of *Paraethomys* below and the FAD of *Apocricetus barrierei* above.

Reference section and locality: Section of Alcoy Forn, locality AF-1’06.

Other localities: AF-1A.

Biostratigraphical correlations:

The FAD of *Paraethomys* in the Iberian Peninsula is recorded in the Late Miocene locality of Venta del Moro, in the Cabriel Basin (SE Spain), with an age of 6.23 Ma (Gibert *et al.* 2013). A similar age has been proposed for Librilla, in the Fortuna Basin (SE Spain, Garcés *et al.* 1998, Agustí *et al.* 2006).

This biozone can be correlated with the upper part of the *Paraethomys meini* zone in the Granada Basin (García-Alix *et al*. 2008e), in which the localities close to the Mio-Pliocene boundary have yielded remains of *Stephanomys dubari* and/or *Apodemus gorafensis*, like MNA-2 and 4, CLR-3, DHS-15B, 14, 16 (reference locality), 1 and 4, BRA-5B, CAC-5 and 11, AGU-1C and PUR-3 (García-Alix *et al.* 2008a and 2008e). Palaeomagnetic data from PUR-3 indicate that this site belongs to chron C3r, which means it is older than 5.23 Ma (Martín-Suárez *et al.* 1998, García-Alix *et al.* 2008e).

The *Paraethomys meini* zone of the Granada Basin has been partly correlated with the *Apodemus gudrunae* zone of the Guadix Basin (Minwer-Barakat *et al.* 2012). However, in the Alcoy Basin the *P. meini* Zone comprises just two localities: AF-1’06 and AF-1A. Both sites are close to the Mio-Pliocene boundary, and the presence of *A. gudrunae* instead of *A. gorafensis* in NGR-1 and RCH-3 in the Guadix Basin (*Apodemus gudrunae* Zone, Minwer-Barakat *et al*. 2012), *Stephanomys ramblensis* instead of *S. dubari* in Celadas-2 and Arquillo-4 in the Teruel Basin (Adrover *et al.* 1993) and *S. ramblensis* and *A. gudrunae* in Crevillente 6 (*Paraethomys* Zone, Martín-Suárez and Freudenthal 1998) suggest an older age for all these latter localities (Fig. VIII.2). In addition, the localities of Zorreras-2B and 3A (Sorbas Basin, Martín-Suárez *et al*. 2000), of latest Turolian age, with the joint presence in Zorreras 3A of *S. dubari*, *P. meini*, *O. alcalai* and *A.* cf. *gorafensis*, may be correlated with this biozone (Fig. VIII.2).

VIII.1.2. *Apocricetus barrierei* Interval Zone

Definition:

Interval Zone corresponding to the interval between the FAD of *A. barrierei* below and the FAD of *Paraethomys* aff. *abaigari* above.

Reference section and locality: Section of Alcoy Forn, locality AF-1’07.

Other localities: AF-2.

Biostratigraphical correlations:

Apocricetus barrierei has been considered an Early Ruscinian indicator (MN14) by a number of authors (Mein *et al.* 1990, Kälin 1999, Freudenthal *et al.* 1998, García-Alix et *al*. 2008a, 2008b and 2008e). The reference locality of the *Apocricetus barrierei* zone of the Granada Basin is PUR-4, which have several taxa in common with AF-1’07, comprising *Apodemus gorafensis*, *Occitanomys alcalai*, *Stephanomys dubari*, *Paraethomys meini*, *Apocricetus barrierei* and *Eliomys yevesi* (García-Alix *et al*. 2008e, chapter VI). Other taxa, like *Stephanomys cordii* and *Trilophomys*, indicators of the end of the Early Ruscinian, are absent.

The *Apocricetus barrierei* biozone from the Alcoy and Granada basins can be correlated with the Celadensia Zone in the Teruel Basin, of which the reference locality is Peralejos-E (Mein *et al.* 1990). This latter biozone is characterized by the presence of the microtoid cricetid *Celadensia nicolae*, very abundant in the localities of the Teruel Basin (Mein *et al*. 1990), which is absent in other Iberian basins such as the Granada Basin (García-Alix *et al*. 2008b), the Guadix Basin (Minwer-Barakat *et al*. 2012) and the Alcoy Basin.

The faunal list of Peralejos-E includes several taxa present in AF-1’07 and PUR-4, like *Cricetus barrieri* (synonymized with *Apocricetus barrierei* by Freudenthal *et al.* 1998), *Occitanomys alcalai*, *Paraethomys anomalus* (synonymized with *P. meini* by several authors, like Weerd (1976), Adrover (1986), Martín-Suárez (1988), Castillo (1990) and García-Alix (2008a), among others) and *Apodemus gorafensis*. It also includes *Stephanomys medius*, synonym of *S. cordii* (García-Alix *et al*. 2008a), which is present in younger localities. Nevertheless, the material of *Stephanomys* from Peralejos-E is reviewed in García-Alix *et al*. (2008a), which consider that is should be ascribed to *S. dubari* rather than to *S. cordii*.

VIII.1.3. *Paraethomys* aff. *abaigari* Interval Zone

Definition:

Interval Zone defined by the interval between the FAD of *Paraethomys* aff. *abaigari* and FAD of *Trilophomys.*

Reference section and locality: Sections of ABS and AC, locality AC-0.

Other localities: ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10, AC-0C, AC-0B.

Biostratigraphical correlations:

The lower part of the section, ranging from ABS-2 to ABS-7, can be correlated with the *Paraethomys* aff. *abaigari* Zone from the Granada Basin, which includes the localities PUR-13 and CLC-5A, in which *Stephanomys dubari* is present (García-Alix *et al*. 2008a). In the upper part of the section, from ABS-8 to AC-0, the *Stephanomys* present is *S. cordii*, which suggest a younger age for these localities respect those of the *Paraethomys* aff. *abaigari* Zone from the Granada Basin.

In the Teruel Basin, the presence of two distinguishable species of *Paraethomy*s is accompanied by the appearance of the arvicolid *Promimomys* (Mein *et al.* 1990), absent in the Granada (García-Alix *et al*. 2008e), Guadix (Minwer-Barakat *et al.* 2012) and Alcoy basins. However, the general resemblance of the faunas from the two *Paraethomys* plus *Promimomys* zone in Teruel makes possible a correlation with the *Paraethomys* aff. *abaigari* Zone from the Alcoy Basin.

The reference locality for the *Promimomys* and *Paraethomys* Zone in Teruel is La Gloria 4 (Mein *et al.* 1990). The faunal list of this locality is similar to those of the sites of the Alcoy Basin in this biozone (see Table VIII.1), with remains of *Episoriculus* (*Assoriculus*) *gibberodon*, *Cricetus* (*Apocricetus*) *barrierei*, *Occitanomys alcalai*, *Paraethomys meini* and *P*. aff. *abaigari*, *Apodemus gorafensis*, *Eliomys intermedius* and *Stephanomys medius* (*cordii*). García-Alix *et al*. (2008a) noted that the *Stephanomys* present in La Gloria 4 and Celadas 9 is *S. dubari*, which agrees with the lower part of the section from Alcoy, but the presence of *Eliomys intermedius* in La Gloria 4 instead of *E. yevesi* like in ABS-3A (see Fig. VIII.1) suggest a slightly younger age.

The locality of LB2B, in the Cabriel Basin (chapter VII) belongs to this latter biozone. Based on palaeomagnetic data, we propose an age between 4.997 Ma and 4.896 Ma for this locality (chapter VII). Neither this biozone nor the next can be correlated with the Rodent Zones of Fejfar *et al*. (1998), which distinguish two zones in the Ruscinian attending to the range of two species of *Promimomys*. This genus is common in eastern Europe, but in the Iberian Peninsula it has only been recorded in the Teruel Basin (Mein *et al.* 1990, Fejfar *et al.* 1998), being absent in the Granada (García-Alix *et al.* 2008a and 2008d), Guadix (Minwer-Barakat *et al.* 2012) and Alcoy basins.

VIII.1.4. *Trilophomys* Assemblage Zone

Definition:

Assemblage zone defined by the association of *Apocricetus barrierei*, *Stephanomys cordii*, *Castillomys gracilis*, *Apodemus gorafensis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari* and *Trilophomys*.

Reference section and locality: Section of AL2, locality AL2-D

Other localities: AL2-C.

Biostratigraphical correlations:

The presence in the Alcoy Basin of several mammal localities recording a relatively short span of time has allowed us to distinguish several biozones in MN14, of which *Trilophomys* assemblage zone is the youngest one. This biozone can be correlated with the *Trilophomys* assemblage zone of the Guadix Basin (Minwer-Barakat *et al*. 2012), in which the joint presence of *Trilophomys, Stephanomys cordii* and *Apocricetus barrierei*, considered MN14 indicators, has been recorded in the localities of Yeguas, Gorafe A and Gorafe 4. However, according to Minwer-Barakat *et al*. (2012), the lower boundary of this biozone coincides with the MN13-MN14 boundary, and the upper one with the MN14-MN15 boundary, calibrated in the Alfambra area with the C3n-C2Ar transition at 4.19 Ma (Opdyke *et al*. 1997, Agustí *et al*. 2001a). Therefore, this correlation is restricted just to the upper part of the *Trilophomys* biozone of the Guadix Basin, close to the MN14-MN15 boundary (see Fig. VIII.2).

The *Trilophomys* Zone of the Teruel Basin, in which usually appears *Blancomys*, can be also correlated with this biozone (Fig. VIII.2). However, the presence of *Stephanomys margaritae* in the reference locality of Villalba Alta Río 1, as well as in Orrios 1, Lomas de Casares 1 and Aldehuela suggest a younger age for these localities.

Epoch	ELMA	MN	Locality	Faunal list
Pliocene	Ruscinian	MN14	AL2-D	*Apodemus atavus*, *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys brailloni*, *Stephanomys cordii*, *Apocricetus* cf. *angustidens*, *Ruscinomys* cf. *lasallei*, *Ruscinomys* sp., *Blancomys* sp., *Trilophomys* cf. *castroi*, *Eliomys intermedius*, *Glis* sp., *Pliopetaurista* sp.
			AL2-C	*Apodemus atavus*, *Apodemus gorafensis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Stephanomys cordii*, *Apocricetus* cf. *angustidens*, *Ruscinomys* cf. *lasallei*, *Blancomys* sp., *Trilophomys* cf. *castroi*, *Eliomys intermedius*
			AC-0	*Apodemus gorafensis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys alcalai*, *Stephanomys* aff. *cordii*, *Ruscinomys* cf. *lasallei*, *Eliomys intermedius*, *Muscardinus* sp., *Asoriculus gibberodon*, Erinaceidae indet., Soricidae indet.
			AC-0B	*Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys alcalai*, *Stephanomys* aff. *cordii*, *Ruscinomys* cf. *lasallei*, Erinaceidae indet.
			AC-0C	*Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys* aff. *cordii*, *Neocricetodon* sp., *Occitanomys alcalai*, *Ruscinomys* cf. *lasallei*
			ABS-10	*Asoriculus gibberodon*
			ABS-9	*Micromys* sp., *Asoriculus gibberodon*, *Stephanomys* sp.
			ABS-8	*Stephanomys* aff. *cordii*
			ABS-7	*Stephanomys* sp.
			ABS-3A	*Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys alcalai*, *Stephanomys dubari*, *Apocricetus* cf. *barrierei*, *Ruscinomys* cf. *lasallei*, *Eliomys yevesi*
			ABS-3	*Apodemus gorafensis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Occitanomys alcalai*, *Stephanomys dubari*, *Asoriculus gibberodon*
			ABS-2	*Micromys* sp., *Paraethomys* aff. *abaigari*, *Occitanomys alcalai*, *Stephanomys dubari*
			ABS-1	*Stephanomys dubari*
			AF-2	*Paraethomys meini*
			AF-1’07	*Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai*, *Apodemus* cf. *gorafensis*, *Eliomys yevesi*, *Apocricetus barrierei*, *Blancomys* cf. *sanzi*, *Parasorex ibericus*
Mio/Plio	Ru/Tu	MN13? MN14?	AF-1A	*Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai*
			AF-1’06	*Apodemus* cf. *gorafensis*, *Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai*, *Eliomys yevesi*, *Atlantoxerus* cf. *margaritae*, *Blancomys* cf. *sanzi*, *Parasorex ibericus*, Soricidae indet.

Table VIII.1. Faunal lists of the localities of the Gormaget ravine (Alcoy Basin). Abbreviations: Mio, Miocene; Plio, Pliocene; Ru, Ruscinian; Tu, Turolian.

VIII.2. Correlation with other European localities

Since the establishment of the MN zonation by Mein (1975), several authors have questioned its validity (Daams and Freudenthal 1981, Fahlbusch 1991, Bruijn *et al.* 1992, Agustí 1999, Dam *et al.* 2001, among others) objecting that MNs are not true biostratigraphic units and that their boundaries are not clear due to their diachronic nature. Despite these problems, and although the MN zonation cannot achieve the resolution of local biozonations, it is a useful tool in order to correlate localities even at a continental level, although the correlations of very distant localities may be not very precise (García-Alix 2006, Minwer-Barakat 2005).

Following the order of biozones proposed in this work, the *Paraethomys meini* biozone of the Granada and Alcoy basins may be correlated with the localities of Casino, Brisighella (Italy) and Castelnou 3 (France, Mein 1990, García-Alix *et al.* 2008a) (Figs. VIII.2 and VIII.3). The locality of Castelnou-3, of the latest Turolian of France, shows a mix of Late Turolian and Ruscinian taxa like *Apodemus gudrunae* and *Apocricetus barrierei*. This could be explained by the fact that Castelnou-3 is a karstic locality, so that fossils from a wide temporal range could be mixed in this site (García-Alix *et al.* 2008b). However, the association *Apodemus gudrunae*-*Apocricetus barrierei* also appears in the post-evaporitic fluvial sediments of Verduno (Italy, Late Turolian, 5.55-5.33 Ma, Colombero *et al*. 2013, CIESM 2008), suggesting that although *A. barrierei* may be considered a MN14 indicator in the Iberian Peninsula, it may not be the case in the rest of Europe.

Following Mein (1990), García-Alix *et al.* (2008e) related the *Paraethomys* aff. *abaigari* zone with the localities of Ptolemais-1 (Greece) and Hautimagne (France), and the *Apocricetus barrieri* zone with the sites of Podlesice (Poland) and Celleneuve (France) (Figs. VIII.2 and VIII.3).

Minwer-Barakat *et al*. (2012) correlate the *Trilophomys* zone of the Guadix Basin, which comprises the whole MN14, with the localities of Podlesice, Osztramos 9 (Hungary), Ptolemais 1 and Kardia (Greece), in which *Promimomys* has been recorded. However, Osztramos 9 is considered a Late Pliocene site by Jánossy (1986). This locality has yielded remains of *Mimomys silasensis* Jánossy 1974 (Jánossy 1986). Chaline (1996) consider *M. silasensis* a synonym of *M. occitanus* Thaler 1955, and Agustí *et al*. (2001a) regard the appereance of this latter taxon as a criterion to define the lower boundary of MN15. On the other hand, Gromov and Polyakov (1992) propose that *M. silasensis* is indeed a subspecies of *Promimomys moldavicus* Kormos, 1932, which Tesakov (2004) situates in MN15. Either way, Osztramos 9 could not be correlated with *Trilophomys* zone of neither the Guadix nor the Alcoy basins. However, younger Osztramos localities with presence of *Promimomys*, but in which *Mimomys* is absent, such as Osztramos 1b, 1c and 1e, could be correlated with these biozones instead.

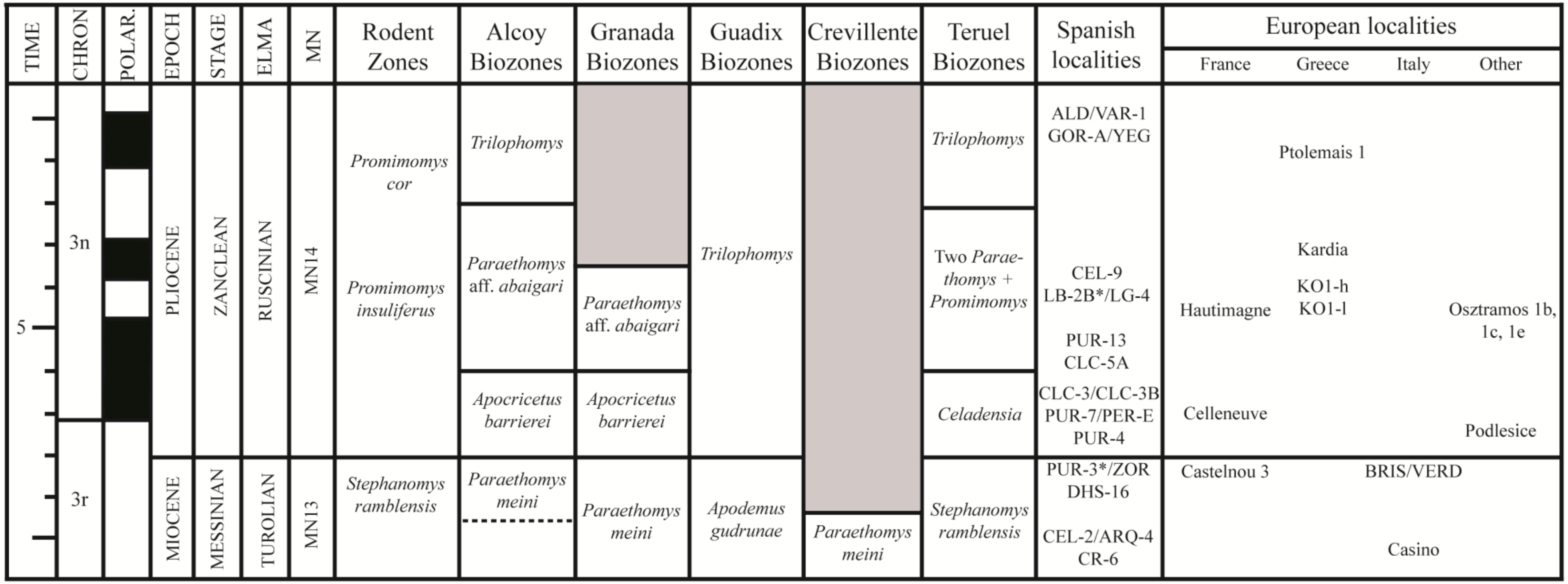


Figure VIII.2. Correlation between the biozones defined in this work for the Alcoy Basin and the local biozonations of other Spanish basins, the Rodent zones of Fejfar *et al.* (1998), and other contemporaneous Spanish and European localities. Abbreviations: ALD, Aldehuela; ARQ, Arquillo; BRIS, Brisighella; CEL, Celadas; CLC, Calicasas; CR, Crevillente; DHS, Dehesas; ELMA, European Land Mammal Age; GOR, Gorafe; KO1-h, Komanos 1 high; KO1-l, Komanos 1 low; LB2B, La Bullana 2B, PER, Peralejos; POLAR, polarity; PUR, Purcal; VAR, Villalba Alta Río; YEG, Yeguas; ZOR, Zorreras. The asterisk indicates the localities from which palaeomagnetic data are available.

The MN14 Greek localities of Komanos 1 high and low and Vorio 1 have yielded remains of *Promimomys*, and in the latter locality also *Occitanomys brailloni* (Hordijk and Bruijn 2009), which appears in MN14 in the Iberian Peninsula. This association of *Promimomys* and *O. brailloni*, which is considered a Ruscinian indicator by Koufos (2006) is also present in the locality of Kardia (see Fig. VIII.2).

VIII.3. Remarks about the Turolian–Ruscinian (MN13-MN14) boundary

The age of the Mio-Pliocene boundary has been estimated at 5.33 Ma (Krijgsman *et al*. 1999, Gradstein *et al*. 2004), and it likely coincides with the Turolian-Ruscinian boundary (Hernández-Fernández *et al*. 2004, García-Alix *et al*. 2008e).

The base of the MN14 was defined by Mein *et al*. (1990) as the entry of the microtid *Celadensia* in the Teruel Basin. However, the occurrence of Celadensia in the MN13 locality of Baccinello (Rook and Torre 1995) led Agustí *et al*. (2001a) to consider the FAD of *Promimomys* the lower boundary of the MN14.

On the other hand, as we have seen *Promimomys* is absent in many Iberian basins of this age, such as Guadix, Granada and Alcoy, which is problematic in order to establish correlations. Agustí *et al*. (2001a) considered that in the absence of arvicolids, the distinction between the MN13 and MN14 is mainly based on the evolutionary stages of the genera *Apodemus*, *Stephanomys*, *Paraethomys*, *Ruscinomys* and *Apocricetus*, which may lead to some uncertainties.

Morales *et al*. (2013) attempt a redefinition of the Ventian Mammal age (Late Miocene) including most of the Spanish faunas of the MN13, but also some localities traditionally placed in the Ruscinian. These authors divide the Ventian in zone M, ranging from the FAD of *Stephanomys ramblensis* to the FAD of *Celadensia*, and zone N, subdivided in N1, corresponding to the range zone of *Celandesia*, and N2, ranging from the appearance of a big sized *Paraethomys* (*P. abaigari* or aff. *abaigari*), and *Promimomys*, which appearance would mark the beginning of the Ruscinian.

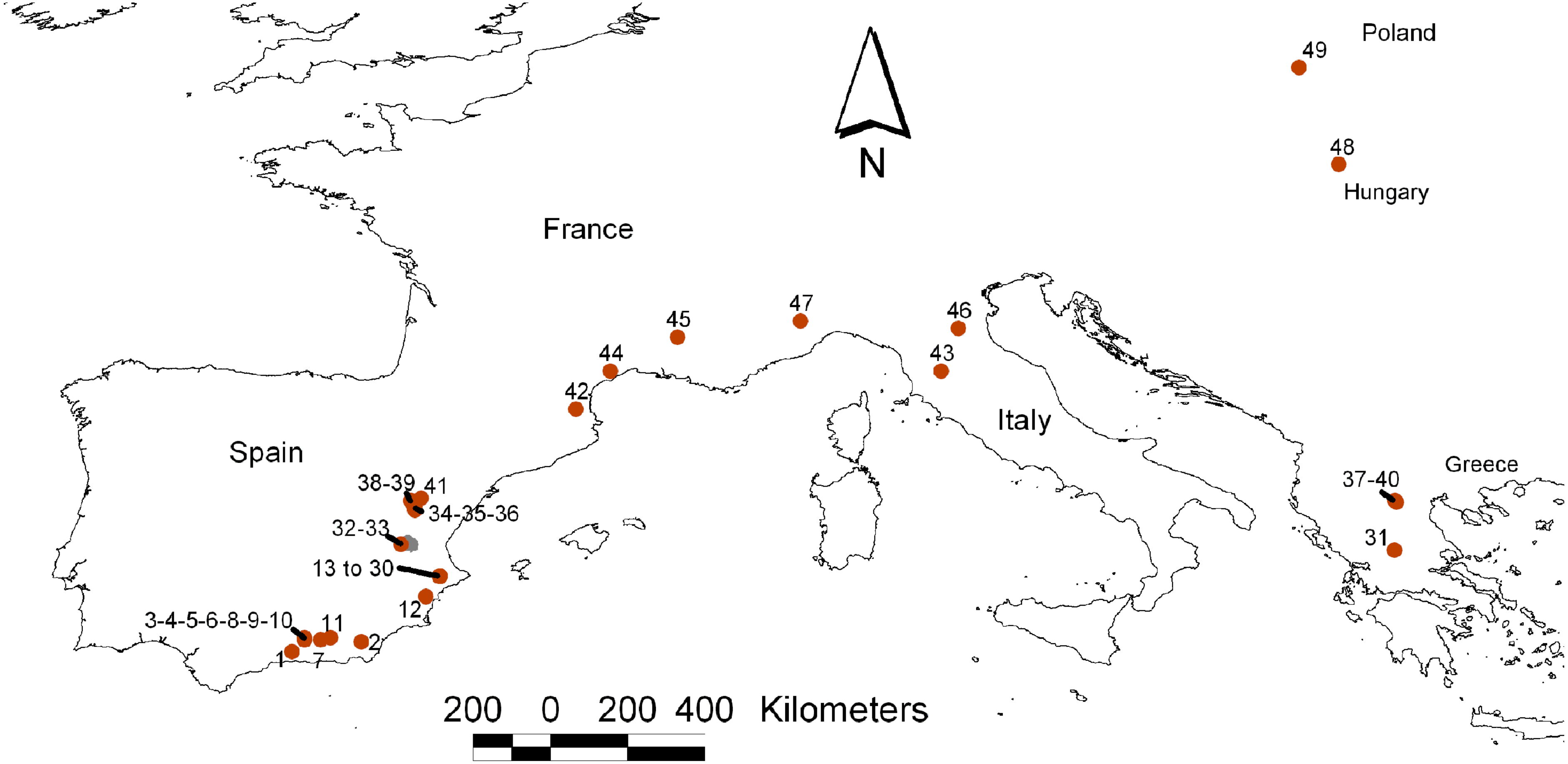


Figure VIII.3. Location of the European sites mentioned in this chapter: **1**, Dehesa 16; **2**, Zorreras 3A; **3**, Purcal 13; **4**, Purcal 3; **5**, Purcal 4; **6**, Purcal 7; **7**, Yeguas; **8**, Calicasas 3; **9**, Calicasas 3B; **10**, Calicasas 5A; **11**, Gorafe A; **12**, Crevillente 6; **13**, AC-0; **14**, AC-0B; **15**, AC-0C; **16**, ABS-1; **17**, ABS-2; **18**, ABS-3; **19**, ABS-3A; **20**, ABS-7; **21**, ABS-8; **22**, ABS-9; **23**, ABS-10; **24**, Alcoy-2; **25**, AL2-C; **26**, AL2-D; **27**, AF-1’06; **28**, AF-1A; **29**, AF-1’07; **30**, AF-2; **31**, Kardia; **32**, LB2B; **33**, LB3; **34**, Aldehuela; **35**, Arquillo 4; **36**, La Gloria 4; **37**, Komanos 1; **38**, Celadas 2; **39**, Celadas 9; **40**, Ptolemais; **41**, Villalba Alta Río 1; **42**, Castelnou 3; **43**, Casino; **44**, Celleneuve; **45**, Hautimagne; **46**, Brisighella; **47**, Verduno; **48**, Osztramos 1; **49**, Podlesice.

However, when Morales *et al*. (2013) correlate with the faunas of the Alcoy and Granada basins, this biozonation presents some problems. First, as we commented above, *Celadensia* and *Promimomys* seem to be absent in some South and Southeastern Iberian basins, which may make difficult to recognize the beginning of the N1 and Ruscinian, respectively. Morales *et al.* (2013) point out to an apparent lack of fossil record above the subzone N2, which may have hindered the inter-basin correlations, since the joint presence of *Promimomys* and two *Paraethomys* has only been described in the Teruel Basin.

In this scenario, the sites from the AC and ABS sections would be included in the N2 (Fig.VIII.4), since they have two distinct *Paraethomys* species. Following this, the position of the localities from the AF section is uncertain. Since AF-1’06 has no *Celadensia* and just one species of *Paraethomys* can be recognized, this locality would belong to the subzone M3 (Fig. VIII.4). However, this is unlikely because of the presence of *Stephanomys dubari* and *Apodemus* cf. *gorafensis* instead of *S. ramblensis* and *A. gudrunae* (see Fig. VIII.4). Furthermore, the locality of AF-1’07, placed just over AF-1’06 (Fig. II.2) has yielded an assemblage similar to AF-1’06 (Table VIII.1), but the presence of *Apocricetus barrierei* and absence of a large sized *Paraethomys* would place this site within the late part of the N1 (Fig. VIII.4). The younger localities of AL2-C and AL2-D, which have *Trilophomys*, would be integrated in the Ruscinian, but they have no *Promimomys*.

Nevertheless, new data from the Cabriel Basin cast doubt on this (chapter VII). *Promimomys* is also absent in the localities of La Bullana 3 (LB3) and La Bullana 2B (LB2B), sites located in the vicinity of Venta del Moro and dated between 5.235-4.997 Ma the former, and 4.997-4.896 Ma the latter using palaeomagnetic data (see chapter VII). LB3 has shown normal polarity, and it has been placed in chron C3n.4n. The closest lower chron with normal polarity is C3An.1n, in which is placed the locality of Venta del Moro, which has much older fauna. LB2B, which is stratigraphically higher, shows reverse polarity, which allows inferring an age between 4.997 and the next magnetic reversal, at 4.896 Ma. These ages imply that both sites are Ruscinian, and indeed their faunal lists are similar to that of the Ruscinian site of La Gloria 4, having in common several species such as *Stephanomys dubari, Apocricetus barrierei, Ruscinomys lasallei,* two species of *Paraethomys, Apodemus gorafensis, Eliomys intermedius, Castillomys gracilis, Occitanomys alcalai* and one representative of the scarce genus *Debruijnimys*, but lacking *Promimomys,* which is thought to enter in Greece around 5.3 Ma (Hordijk and Bruijn 2009) and in Teruel Basin at approximately 5 Ma (Dam *et al.* 2006, Morales *et al*. 2013).

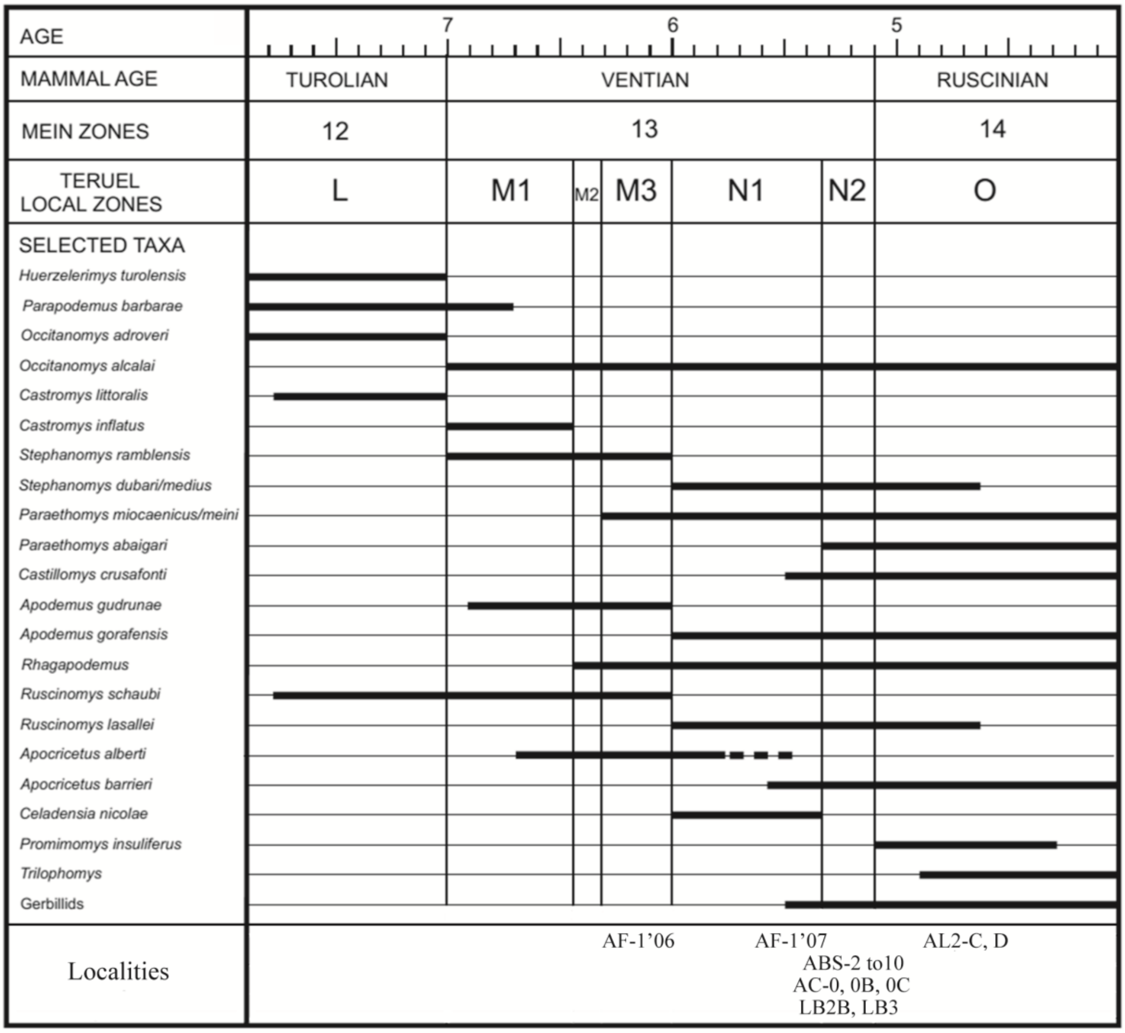


Figure VIII.4. Biostratigraphic position of the localities from the Gormaget ravine, in the Alcoy Basin, as well as LB2B and LB3, according to the biozonation defined by Morales *et al.* 2013.

Besides the absence of *Promimomys,* which marks the upper limit of N2, the lower limit of this subzone shows some problems. According to Morales *et al*. (2013), the appearance of a big sized *Paraethomys* besides the smaller *P. meini* signals the beginning of the N2. However, it is not clear if the big sized *Paraethomys* is an immigrant, or a speciation event has occurred (García-Alix *et al.* 2008a). These latter authors also suggest that two different lineages of *Paraethomys* may be represented in the locality of PUR-4, because the population of *P. meini* shows a great variability in size. The same scenario has been described in AF-1’06 in the Alcoy Basin (see chapter VI), in which two different species of *Paraethomys* cannot be recognized yet, but there is a continuum distribution ranging from small to big specimens. In younger localities, like those of ABS and AC, the difference between both species is greater and two groups of *Paraethomys* may be recognized. Since distinguishing both species of *Paraethomys* is more complicated in older localities, to detect the appearance of a *P.* (aff.) *abaigari* may be difficult beyond a certain point, being troublesome to recognize the lower boundary of the subzone N2. Morales *et al*. (2013) explain that the zone N2, which has two *Paraethomys,* is only supported by stratigraphic criteria, and that it may be Pliocene indeed, but further evidence is needed to solve this question. Based on the data from the Alcoy and Cabriel basins, we consider the zone N2 as belonging to Early Ruscinian.

VIII.4. Conclusions

The study of the faunal content of the localities from the Gormaget ravine (Alcoy Basin, Spain) has allowed us to define four biozones in the earliest Pliocene and possibly the latest Miocene of this area. These biozones comprise:

- The *Paraethomys meini* Interval Zone, corresponding to the interval between the FAD of *Paraethomys* below and the FAD of *Apocricetus barrierei* above, which comprises the localities AF-1’06 and AF-1A.

- The *Apocricetus barrierei* Interval *Zone,* corresponding to the interval between the FAD of *A. barrierei* below and the FAD of *Paraethomys* aff. *abaigari* above, comprising the localities AF-1’07 and AF-2.

- The *Paraethomys* aff. *abaigari* Interval Zone, defined by the interval between the FAD of *Paraethomys* aff. *abaigari* and FAD of *Trilophomys*, comprising the localities ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10, AC-0C and AC-0B.

- The *Trilophomys* Assemblage Zone, defined by the association of *Apocricetus barrierei, Stephanomys cordii, Castillomys gracilis,* *Apodemus gorafensis, Paraethomys meini, Paraethomys* aff. *abaigari* and *Trilophomys,* which comprises the localities AL2-C and AL2-D.

The quality of the register has allowed us to correlate the biozonation of the Alcoy Basin with other local biozonations of the Iberian Peninsula, such as those of the Teruel, Granada, Crevillente and Guadix basins, as well as, tentatively, with other well-known European localities.

In the Alcoy Basin, the *Paraethomys meini* Interval zone can be correlated with localities with the joint presence of *Stephanomys dubari*, *Paraethomys meini*, *Occitanomys alcalai* and *Apodemus gorafensis,* being younger than the sites in which *Apodemus gudrunae* and/or *Stephanomys ramblensis* are present.

The assemblage of *Apodemus gorafensis*, *Occitanomys alcalai, Stephanomys dubari, Paraethomys meini* and *Apocricetus barrierei* is typical of the *Apocricetus barrierei* Interval zone. The presence of these taxa allows a correlation with the *Celadensia* Zone in the Teruel Basin, despite *Celadensia* is absent in the Alcoy Basin.

The *Paraethomys* aff. *abaigari* Interval zone of the Alcoy Basin is defined just by the presence of two *Paraethomys* species, since two forms of anagenetic lineages like *Stephanomys dubari/*aff. *cordii* and *Eliomys yevesi/intermedius* have been described in this interval. This zone can be correlated with local biozonations from other Iberian basins with two *Paraethomys,* although *Promimomys*, which appears together *Paraethomys* in the Teruel Basin, is absent in the Alcoy Basin.

The *Trilophomys* Assemblage Zone of the Alcoy Basin can be correlated with localities from other Iberian basins with the presence of *Trilophomys, Stephanomys cordii* and *Apocricetus barrierei,* while other sites in which *S. margaritae* is present are younger.

As a consequence of this biozonation, we have achieved a great resolution in the earliest Pliocene and Mio-Pliocene boundary of the Alcoy Basin, with several localities concentrated in a relatively short time span. This resolution can be compared to that of the Teruel Basin for the same time span (Mein *et al.* 1990), which is the most studied of the Iberian basins.

In respect to the zonation proposed by Morales *et al*. (2013), we consider the subzone N2 of the Ventian not valid since its lower limit, marked by the presence of two *Paraethomys*, is difficult to recognize in localities close to the Mio-Pliocene boundary, and *Promimomys*, which marks its upper limit, is absent in clearly Ruscinian localities like LB3 and LB2B. Therefore, we consider the subzone N2 (Morales *et al.* 2013) to be Early Ruscinian.

CHAPTER IX: EVOLUTION OF MICROMAMMAL ASSOCIATIONS AND PALAEOCLIMATE IN THE MIO-PLIOCENE AND LOWER PLIOCENE OF THE ALCOY BASIN.

IX.1. Climatic evolution of the Late Miocene-Early Pliocene

The Late Miocene was marked by one of the most dramatic (and most studied) events of the Cenozoic: the Messinian Salinity Crisis (MSC). During the Messinian stage (between 7.25 and 5.33 Ma, Lourens *et al.* 2005) took place a progressive restriction of the Atlantic-Mediterranean connection, which led to the desiccation of the Mediterranean sea and the deposition of thick evaporite deposits on the abyssal part of the basin (Hsü *et al.* 1973).

The onset of the MSC has been dated at 5.96 Ma, with the Mediterranean being completely isolated from the Atlantic Ocean between 5.59 to 5.33 Ma, (Krigjsman *et al.* 1999). The crisis ended with the refilling of the Mediterranean at 5.33 Ma through the Gibraltar strait, marking the beginning of the Pliocene in which has been called the Zanclean flood or post-Messinian flood (Blanc 2002).

During the Messinian, climate underwent a warming at 5.6 Ma, which contrasts with the general cooling trend observed from Mid-Miocene onwards (Shevenell *et al.* 2004, Vautravers 2014). Using palynological data, Fauquette *et al.* (1999 and 2006) find no significant differences in the climate before, during and after the MSC in southwester Spain, being very dry and warm in all cases. Other authors find a slight temperature increase after the MSC using rodents (Montuire *et al.* 2006) or just a limited impact on Mediterranean climate studying cenograms of mammalian communities (Costeur *et al.* 2007).

During the Pliocene occurred a transition from the warm climate of the Miocene to the cooler climate of the Pleistocene. Even though this progressive cooling along the Tertiary, Pliocene was in general warmer than today, with mean annual temperatures in the mid-latitudes often several degrees higher (3 to 5 ºC, Thompson 1991, Dowsett *et* *al.* 1996), and with a MAP 400 to 700 mm higher in Europe (Agustí and Antón 2002). However, major glacial expansions seem to have occurred at least four times (at 4.9-4.8, 4.0, 3.6 and 3.3 Ma, Schepper *et al.* 2014). In southern Spain, there is a marked faunal turnover at about 3.2 Ma related with a dry phase between chrons C2An.2r and C2An.2n (Agustí *et al.* 2001b).

Following the last of these expansions comes the mid-Piacenzian Warm Period (3.29-2.97), with temperatures 2-3 ºC higher than today (Schepper *et al.* 2014) which has been considered a potential analogue of future, warmer climate by several authors (see Sarnthein *et al.* 2009, Haywood *et al*. 2011). After this warm period, climate cooled again, leading to the glaciations at the Pliocene/Pleistocene transition (Funder *et al.* 2001, Bartoli *et al.* 2006, Lawrence *et al.* 2010).

IX.2. Evolution of Late Miocene-Early Pliocene micromammal assemblages

Although it seems logical to assume that the major changes occurred in the Mediterranean during the Messinian would be disastrous for the faunas of peri-Mediterranean regions, there is indeed an increase in diversity of mammalian communities of Messinian localities such as Venta del Moro and Brisighella (Agustí and Antón 2002). This enrichment of the mammalian assemblages in Western Europe is correlated with the creation of land bridges due to the drop of sea level during MSC, with at least three African-Iberian faunal dispersals between 6.3 and 5.3 Ma (Made *et al*. 2006, Gibert *et al.* 2013).

These dispersals tend to be of animals adapted to arid or open environments, such as the gerbils *Debruijnimys, Myocricetodon* and *Calomyscus,* which in some localities such as Salobreña (Granada) and Almenara-M (Castellón) represent more than 50 % of the rodent assemblage (Agustí and Antón 2002). This specialized group of rodents survived in the Iberian Peninsula during the Pliocene (Castillo and Agustí 1996, chapter VII of this thesis), but in more reduced numbers.

In the warm and more humid conditions of Early Pliocene, mammal communities remained similar to those of the Late Miocene, with murids being the most diverse group of rodents together with the cricetids (Agustí *et al.* 2001b). In this period, some taxa usually associated with humid environments, such as flying squirrels and beavers were present in Western Europe for the first time since the Vallesian (Agustí and Antón 2002).

With the cooling at 4 Ma, several genera of northern rodents, such as the microtoid cricetids *Trilophomys*, *Celadensia*, and *Bjornkurtenia*, as well as the arvicolid *Promimomys*, entered Western Europe (Agustí *et al*. 2001b). However, this entry did not affect the diverse communities of rodents and cricetids that were already present, but instead increased small-mammal diversity (Agustí and Antón 2002).

About 3.2 Ma, the climatic shift to cooler and drier conditions provoked a drop in the diversity of small-mammal assemblages, causing the disappearance of some typical Late Miocene and Early Pliocene faunas, such as the murids *Occitanomys* and *Paraethomys*, and the cricetids *Apocricetus* and *Ruscinomys*. The highly diversified faunas of the Ruscinian, in which murids are still dominant, led to the impoverished assemblages of the Villanyian, with the prevalence of one or two arvicolid species (Agustí *et al.* 2001b, Agustí and Antón 2002).

IX.3. Evolution of micromammal assemblages of the Mio-Pliocene boundary and Early Pliocene localities from the Alcoy Basin

The faunal lists of the localities from the Gormaget area are shown in Table VIII.1 and Fig. VIII.1, and that of LB2B, from the Cabriel Basin, of a similar age to AC-0 (see chapter VIII) in Figs. VII.4 and VIII.1. The faunal assemblages from the Alcoy Basin and LB2B are clearly dominated by the family Muridae (see Table IX.1). In contrast, insectivores are poorly represented, except in the locality AC-0, where they constitute 13.19 % of the fossil assemblage.

Paraethomys is the most abundant taxon in the Late Turolian/Early Ruscinian locality of AF-1’06 (60.58 %, see Fig. IX.1), followed by *Stephanomys,* which is dominant in the Early Ruscinian sites of AC-0, AL2-C, AL2-D and Alcoy-2 (Fig. IX.1). This composition is very similar to that of the localities from the Granada Basin (García-Alix *et al.* 2008a and 2008d), in which *Apodemus* is the dominant taxon in Late Turolian sites, being replaced by *Stephanomys* and *Paraethomys* in the Mio-Pliocene boundary and Early Ruscinian.

On the contrary, in the Early Ruscinian site of LB2B (chapter VII), from the Cabriel Basin, *Stephanomys* is not very abundant (9.88 %), being surpassed by *Paraethomys* (24.90 %) and especially by *Apocricetus* (35.18 %). The dominance of *Apocricetus* is rare, since this genus is usually scarce in relation to murids in the Late Miocene and Early Pliocene assemblages.

The localities of the Alcoy Basin belong to a relatively thin and poorly known time slice. Chronologically, in Alcoy Basin the oldest locality is AF-1’06, probably close to the Mio-Pliocene boundary, and the youngest AL2-C and AL2-D, in late MN14 or MN14-MN15 boundary. In the Iberian Peninsula, the most complete record of this age is found in the Teruel Basin, which faunal assemblages show some differences with respect to the Alcoy Basin (see chapter VIII), and as Martín-Suárez *et al*. (2001) noted, there may be climatic differences between the interior basins, such as Teruel, and coastal basins, such as Alcoy. In addition, the orographic features and local environments of the region in study affect the climatic interpretations (García-Alix *et al.* 2013, Freudenthal *et al.* 2014), making comparisons difficult even in nearby regions.

		RODENTIA						INSECTIVORA	
Locality	*N*	*Muridae*	*Cricetidae*	*Gliridae*	*Trilophomyidae*	*Sciuridae*	*Gerbilidae*	*Erinacedae*	*Soricidae*
AF-1’06	139	89.21	0.72	1.44	0.00	2.88	0.00	5.04	0.72
LB2B	253	58.91	35.58	3.95	0.00	0.80	0.40	0.00	0.40
AC-0	91	70.33	13.19	3.30	0.00	0.00	0.00	3.30	9.89
AL2-C	79	81.02	7.59	2.53	7.59	0.72	0.00	0.00	1.26
AL2-D	275	84.09	6.54	2.18	4.36	0.00	0.00	1.82	0.36
Alcoy-2	227	67.77	11.88	5.72	7.49	0.00	0.00	0.88	6.16

Table IX.1. Relative proportions of the families of rodents and insectivores in a sorted, from older (top) to younger (bottom), list of localities from the Alcoy Basin and Cabriel basin (LB2B).

IX.4. Palaeoecological analysis of micromammal assemblages from the Alcoy Basin

With respect to the number of specimens needed to perform a palaeoecological analysis, some authors suggest a minimum sample size of 100 specimens (Daams *et al.* 1999, García-Alix *et al.* 2008c), while Casanovas-Vilar and Agustí (2007) argue that 50 specimens should be enough, since bigger samples only add one or two rare species to the assemblage. Of the localities, in which this analysis has been performed, only AC-0 (91) and AL2-C (79) have yielded less than 100 identifiable remains (Table IX.1).

The palaecological affinities of each taxon present in these sites has been discussed in chapters IV.3.3 (AL2-C and AL2-D), V.3.2 (AC-0) and VI.3.2 (AF-1’06). We have followed mainly the ecological preferences proposed by García-Alix *et al.* 2008c. As commented in these sections, we have followed the methodology proposed by Martín-Suárez (1988), dividing the number of specimens of each taxon between its number of diagnostic elements in order to obtain a percentage of relative abundance. Thus, no taxon is over-represented. The number of diagnostic elements of each family is: Muridae, Cricetidae and Trilophomyidae, 12 (molars); Gliridae and Sciuridae, 16 (P4 and molars); Castoridae and Soricidae, 20 (incisors, P4 and molars); Erinaceidae, 44 (all dental elements), but in *Parasorex ibericus* 42, because it lacks the I3. The relative percentages within each ecological category are summarized in Table IX.2 and Fig. IX.2.

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	Wet	Dry	Eurytopic	Cold	Warm	Eurytopic	Open	Forested	Eurytopic
AF-1’06	12.87	61.32	25.36	0.00	74.19	25.36	3.03	0.00	96.52
AC-0	17.06	41.42	40.54	14.21	43.57	41.25	14.21	6.57	78.25
AL2-C	13.57	25.61	41.61	14.09	26.89	39.82	15.36	6.40	59.03
AL2-D	15.88	14.13	51.02	8.83	20.83	51.37	11.16	6.88	63.00
Alcoy-2	12.18	8.76	61.98	11.54	23.07	51.09	20.30	6.00	59.40

Table IX.2. Relative abundance of the taxa from the studied localities of the Alcoy Basin according to their ecological preferences from older (top) to younger (bottom) localities.

Regarding the humidity, the proportion of wet environment indicators is similar in all the localities of the Alcoy Basin (Table IX.2, Fig. IX.2). However, there is a marked reduction in the proportion of dry environment indicators along time, from AF-1’06 to

AC-0, and from this latter locality to AL2-C, AL2-D and Alcoy 2, as well as a similar increment in the eurytopic taxa (Table IX.2, Fig. IX.2).

There is also a clear gradient concerning the temperature indicators, which are very abundant in AF-1'06, close to the Mio-Pliocene boundary, and progressively less abundant in younger localities.

The abundance of forested indicators is very similar in all sites, with the exception of AF-1'06, which has yielded almost exclusively eurytopic taxa (Table IX.2, Fig. IX.2). Open environment indicators are similar in AC-0, AL2-C and AL2-D, and slightly more abundant in Alcoy 2. These results point out to forest mosaic scenario in all sites but AF-1'06.

Preliminary results from the ABS and AC-0 sections suggest a progressive aridification from the older to the younger sites (chapter V). However, it is the faunal spectrum of AF-1'06, the oldest locality studied in this thesis, which imply more arid conditions, with progressively cooler and more humid environments in AC-0, AL2-C and A2L-D. Since a palaeoecological analysis based on faunal composition cannot be performed in most of the sites discovered in the area because of the scarcity of remains, a finest analysis of the climatical dynamics of earliest Pliocene of the Alcoy Basin must be postponed until more material becomes available.

IX.5. Comparisons with the Late Miocene-Early Pliocene climatic inferences from other Iberian basins

According to García-Alix *et al.* (2008c), there is a decrease in temperature from the Late Turolian, with a tropical to warm-temperate weather, to the Late Ruscinian of the Granada Basin, where only cold indicators are present. There is also a tendency to aridification from Late Turolian onwards, in which the frequency of wet indicators decreases with some oscillations, and an increase of eurytopic taxa at expense of both wet and dry indicators in the Ruscinian. These authors note a correlation between the increase of warm and wet indicators and the decrease of cold and dry indicators from Middle Turolian to the first part of Late Turolian, while near the Mio-Pliocene

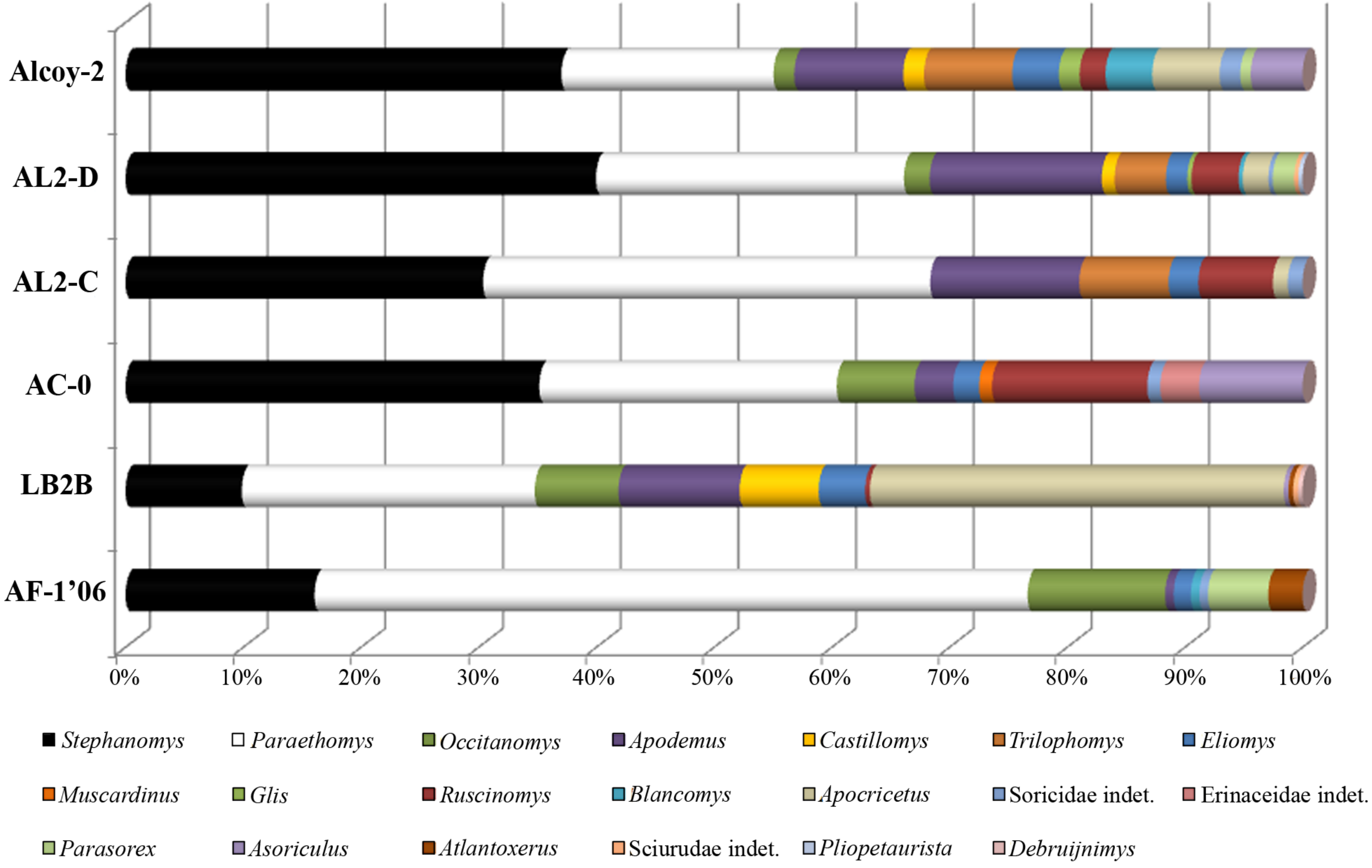
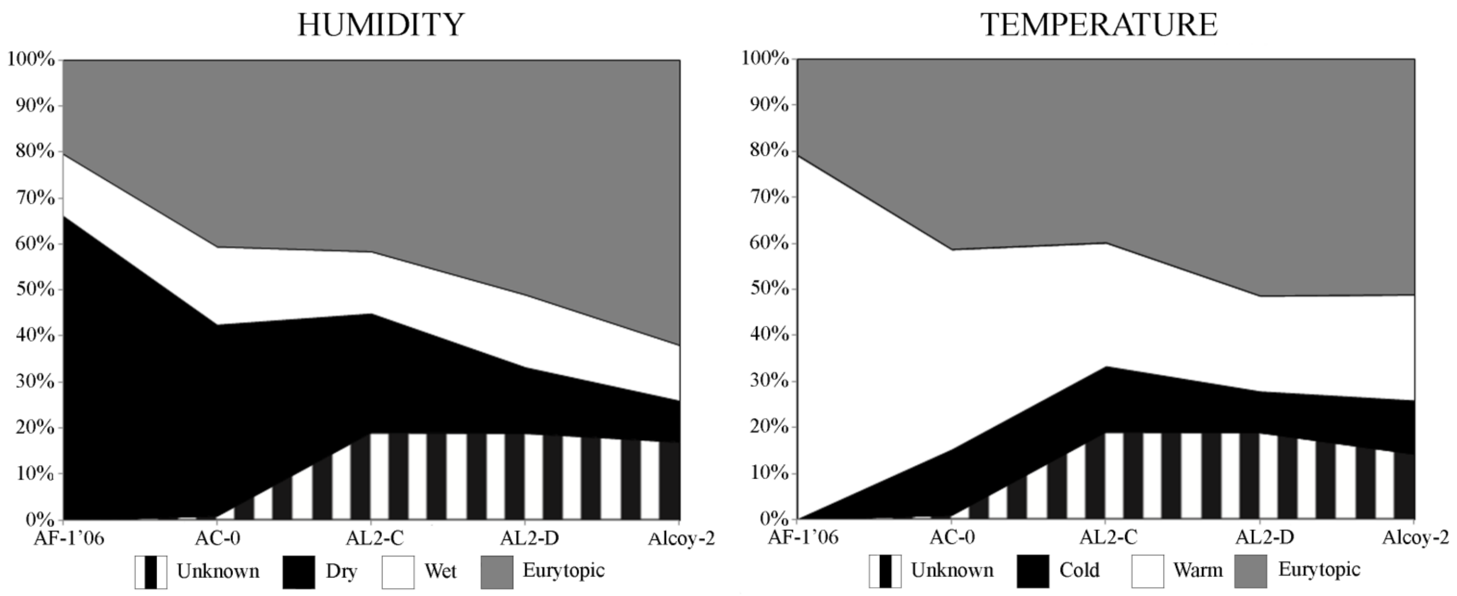


Figure IX.1. Relative proportion of the genera of rodents and insectivores from oldest (bottom) to youngest (top) of the localities from the Alcoy Basin and LB2B.



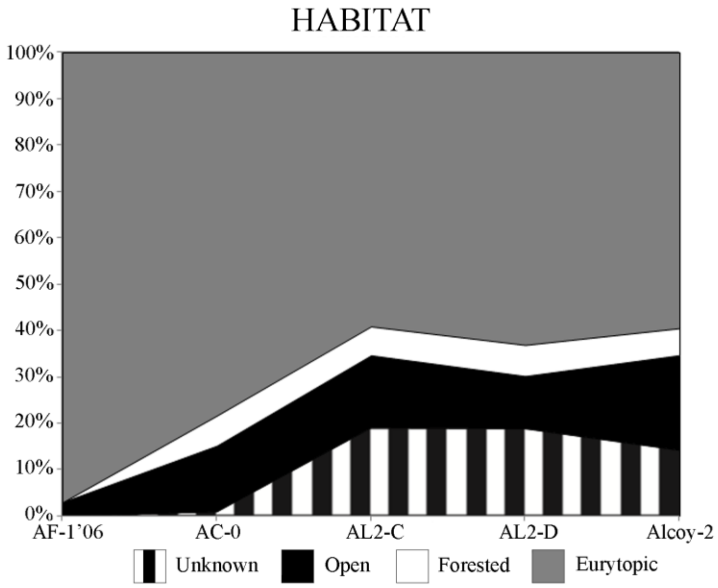


Figure IX.2. Relative abundances of the humidity, temperature and habitat indicators in the localities of the Alcoy Basin, from oldest (left) to youngest (right).

boundary and in the Ruscinian, warm and wet indicators show a positive correlation, which is not observed between cold and dry indicators. This partially agrees with the results of the localities from the Alcoy Basin, in which the faunas from AF-1’06 suggest a warm and dry environment, which becomes colder but slightly more humid in younger localities.

The Calatayud-Teruel Basin has been studied from a palaeoclimatical point of view by Daams *et al.* (1988) and Dam and Weltje (1999). However, none of this works deals with the time span covered by the localities from the Alcoy Basin, since the Ruscinian localities considered by Daams *et al.* (1988) are all of them younger, and the analysis performed by Dam and Weltje (1999) focus in older sites, ranging from 11 to 6 Ma. For this reason, the climatic trends inferred in these works cannot be correlated with the data from the localities studied here, and therefore a comparison is not possible.

Martín-Suárez *et al.* (2001) performed a palaeoecological analysis of the Miocene localities of the Crevillente area. The youngest locality studied in this work is Crevillente 6, of Late Turolian age, which has a fossil assemblage dominated by *Paraethomys* and *Apocricetus*, and in which *Stephanomys* is very scarce. These proportions are similar to that of the Ruscinian locality of LB2B (Fig. IX.1), which may suggest similar palaeoenvironmental conditions for both sites. LB2B has been dated at 4.917 Ma (chapter VII), and its faunal composition suggest a warm environment, close to the conditions inferred for AF-1’06, but more open than any of the sites from the Alcoy Basin.

On the other hand, Hernández-Fernández *et al.* (2007) combining data from several Iberian basins, propose subtropical conditions for the Ruscinian, pointing the existence of two warm and two temperate alternate subphases. The two oldest subphases, D3 and D4, would correspond to the MN14. However, in this work the warm D3 phase would correspond to latest MN14 and the temperate D4 is placed near the Mio-Pliocene boundary, contrary to the data from Alcoy Basin, in which the Late MN14 is cooler than the earliest Ruscinian.

In the Guadix Basin, the only localities that may correspond with the time interval of the sites studied in this thesis are NGR-1, in the Late Turolian, and Yeguas, of Early Ruscinian age. The analysis of the faunal remains from NGR-1 suggests warm and dry conditions, with the predominance of open landscapes (Minwer-Barakat 2005, Minwer-Barakat *et al.* 2009a), while Yeguas has yielded scarce fossil material and a proper analysis cannot be performed, although the data point out to relatively warm conditions (Minwer-Barakat 2005).

Based on the composition of fossil rodent assemblages, Montuire *et al.* (2006) estimated the temperatures of several Late Miocene-Early Pliocene European localities, including those of Teruel and Granada basins, and the locality of Alcoy Barranco studied by Adrover (1969), too. According tho these latter authors, the inferred annual mean temperature for the Alcoy Barranco, considered of a similar age of AC-0 (chapter V), ranges between 11.2 and 20.9 ºC. Montuire *et al.* (2006) noted a slight increase in temperature in Early Ruscinian, but followed by a thermal maximum in MN15, which does not fit the data from the Alcoy Basin.

In addition to the works dealing with fossil rodent faunas, other palaeoclimatical studies have used different approaches to the subject. In this sense, Domingo *et al.* (2013) used the stable carbon and oxygen isotope composition of mammalian tooth enamel to infer the mean annual precipitation (MAP) and mean annual temperature (MAT) of different assemblages from several Iberian basins, ranging in age from the Miocene to Quaternary. The decrease in $\delta^{13}C$ from MN13 to MN14 is interpreted by these authors as a rise in MAP, associated to the Pliocene Warm Period beginning at approximately 5 Ma.

On the other hand, the values of $\delta^{18}O$ obtained by Domingo *et al.* (2013), suggest a decrease in MAT from MN13 to MN14. These results are consistent with the MAT for the same time span obtained by Hernández-Fernández *et al.* (2007) using fossil rodent communities, and the palynological studies by Fauquette *et al.* (1999 and 2006). This also agrees with the data from the Alcoy Basin, in which there is a progressive cooling and more humid conditions from the Mio-Pliocene boundary to the Early Ruscinian.

In similar chronologies, but in other different contexts, the analysis of pollen, dinoflagellate cysts and magnetic susceptibility in marine deposits from the Guadalquivir Basin allowed Jiménez-Moreno *et al.* (2013) to infer climatic oscillations at the end of the Messinian, with cold and arid peaks at 5.95 and 5.6-5.5 Ma and a subsequent warming trend reaching a maximum at 5.3 Ma, which agree with the data from AF-1’06, supposed to be of a similar age.

Therefore, and after all data here presented, the climate in Pliocene is usually regarded as warm and relatively humid (Zachos *et al*. 2001, Agustí and Antón 2002). However, there are still relatively few data of the Mio-Pliocene boundary and earliest Ruscinian when compared with the Late Turolian and Late Pliocene/Plio-Pleistocene boundary.

CHAPTER X: A NEW *ELIOMYS* FROM THE LATE MIOCENE OF SPAIN, AND ITS IMPLICATIONS FOR THE PHYLOGENY OF THE GENUS.

X.1. Introduction

External, genetic and some morphometric characters of the skull distinguish at least three extant species of the genus *Eliomys* (Filipucci *et al.* 1988a and 1988b, Krystufek and Kraft 1997, Holden 2005), including the garden dormouse *Eliomys quercinus* (Linnaeus, 1766), the Asian dormouse *E. melanurus* Wagner, 1839 (type species) and the Maghreb garden dormouse *E. munbyanus* Pomel, 1856. Its biogeographic range comprises Western Europe, where it is widespread, as well as scattered populations across Central, Eastern, and Southeast Europe, Turkey, and the north of Africa. In addition, fossil representatives of the genus include *E. assimilis* Mayr, 1979 and *E. reductus* Mayr, 1979 from Germany, and *E. lafarguei* Aguilar, Michaux, and Lazzari, 2007 from France, all them from the Late Miocene, as well as *E. truci* Mein and Michaux, 1970 from the Late Miocene-Pliocene, and *E. intermedius* Friant, 1953 from the Pliocene and Pleistocene, both of Western Europe.

Eliomys truci, *E. intermedius*, and the extant *E. quercinus* have been proposed to form part of a single phylogenetic lineage, following first a cladogenetic pattern of evolution, based on the coexistence of *E. truci* and *E. intermedius* during the Early–Late Pliocene (Adrover 1986), before culminating in the anagenetic replacement of *E. intermedius* by *E. quercinus* during the Pleistocene (Chaline 1972, Castillo 1990). However, this picture is made more complex by the appearance of an additional, intermediate form (*E.* aff. *intermedius*) sharing features with both *E. truci* and *E. intermedius*, in the Mio-Pliocene of the Granada Basin of southern Spain (García-Alix *et al*. 2008b). Here, we provide new information on the evolutionary history of the genus by describing new Mio-Pliocene material from rich localities with the Cabriel (Venta del Moro and La Bullana) and Alcoy basins of southeastern Spain, which, together with *E.* aff. *intermedius* from the Granada Basin, we refer it to *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014.

X.2. Material and methods

Nomenclature and measurement methods follow Daams (1981) and Freudenthal (2004). The specimens from Venta del Moro, La Bullana and Alcoy are kept at the *Museu de Geologia de la Universitat de València* (MGUV), and labelled according to locality, level and, where applicable, year of collection (Table X.1).

To determine its affinities, we directly compared our material with fossil collections from Huétor Tájar, Tollo de Chiclana, Moreda, Bélmez-1, Cañada Castaños, Gorafe-2 and 5, Botardo-C, Negratín-1, Calicasas-3B, Purcal-4, 23, 24A, and 25, and Otura-1, housed at the DEPUG (see supplementary tables, section X.6.). In addition to these direct comparisons, we took into account published data contained from the localities of Balaruc 2, Layna, Caravaca, Crevillente 1, 3, 5, and 6, Tortajada A and C, and Masada del Valle 2 (all in Weerd 1976), as well as Orrios 3, Sete, Arquillo 3, Villalba Alta, Hautimagne, Los Mansuetos, and Aljezar B (Adrover 1986). Finally, we performed a phylogenetic analysis of the genus using the implicit enumeration option of the phylogenetic software package TNT (Goloboff *et al.* 2003 and 2008). All of the characters included in this analysis are listed in the supplementary tables (section X.6.).

X.3. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Type species: *Eliomys melanurus* Wagner, 1840; extant species.

Eliomys yevesi Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014 (Fig. X.1, 1–21).

Etymology: Dedicated to José María Yeves and his family, owners of the "Hostal Ventamorino", for their friendly hospitality during the many summer campaigns in Venta del Moro.

Holotype: Right M1, VVmA-25.

Type locality: Venta del Moro A, Cabriel Basin, Spain.

Type horizon: Villatoya-Venta del Moro Formation, MN13, late Turolian (Late Miocene, 6.23 Ma).

Localities: VVm-A, VVm-B, VVm-BC, VVm-C, VVm-D, ABS-3A, AF-1’06, AF-1’07, PUR-4, CLC-3B.

Material: **3 p4** (VVmA-42, VVmA-43, PUR-4 871), **29 m1,2** (VVmA-1 to VVmA-11, VVmA-32, VVmB-1, VVmBC-1, VVmBC-2, ABS3A-38, AF1’06-190, PUR-4 872 to PUR-4 883), **13 m3** (VVmA-33 to VVmA-38, VVmBC-5, VVmC-1, AF1’06-187, PUR-4 884 to PUR-4 886, CLC-3B 67), **2 dP4** (VVmA-44, PUR-4 887), **4 P4** (VVmA-39 to VVmA-41, PUR-4 888), **20 M1,2** (VVmA-16, VVmA-21 to VVmA-31, VVmBC-3, AF1’07-36, PUR-4 889, PUR-4 890, CLC-3B 68, CLC-3B 69, VVmD-1, VVmD-2), **13 M3** (VVmA-12 to VVmA-15, VVmA-17 to VVmA-20, VVmBC-4, PUR-4 891 to PUR-4 893, CLC-3B 70).

Diagnosis:

Size intermediate between *E. truci* and the youngest *E. intermedius*; subquadrangular m1,2, usually with a posterotropid and a well-developed centrolophid; no posterotropid on m3; common presence of both centrolophs in the upper molars; posteroloph and endoloph usually connected.

Differential diagnosis:

Eliomys yevesi differs from *E. assimilis* in the more quadrangular shape of m1,2, less reduced m3, and the absence of any accessory crests in the upper molars; from *E. reductus* in its bigger size, more quadrangular shape of the lower molars, discontinuous endolophid, and common presence of posterotropid; and from *E. lafarguei* in its bigger size, long centrolophid on m1,2, discontinuous endolophid, the presence of a centrolophid on many m3, and the common presence of postcentrolophs in the upper molars.

Eliomys yevesi ranges in size from the biggest specimens of *E. truci* to the smallest ones of *E. intermedius*. It differs from *E. truci* in more frequently showing centrolophs in the upper molars, as well as the presence of well-developed postcentrolophs, reaching half the width of the tooth or more, in some specimens (Fig. X.1, 7). *E. yevesi* further differs from *E. intermedius* in the subquadrangular shape (Fig. X.1, 2-3-14-18) and lower and narrower lingual wall of the upper molars (Fig. X.1, 6-7). A long centrolophid connected to the metalophid is present in all but one m1,2 of *E. yevesi*, whereas in *E. intermedius* it is short in 27 out of 106 specimens. In addition, the posterotropid is more frequent and usually longer in *E. yevesi* than in *E. intermedius* (27 out of 29 m1,2 of *E. yevesi*; 80 out of 107 of *E. intermedius*). In the upper molars, the two centrolophs are usually slightly longer and occur somewhat more frequently in *E. intermedius* (97 out of 165, 58.78 %, compared to 17 out of 36, 47.22 %, in *E. yevesi*).

Eliomys yevesi differs from the extant *E. quercinus* in its smaller size, but resembles the latter in the absence of accessory crests in the upper molars and an anteroloph-protoloph connection, as well as the frequent presence of two centrolophs. Two subspecies of *E. quercinus* with distinct m1,2 morphologies occur in the Iberian Peninsula: *E. q. lusitanicus*, which differs from *E. yevesi* in the absence of a centrolophid; and *E. q. quercinus*, which differs from *E. yevesi* in the absence of accessory crests in the lower molars, a continuous endolophid on m1,2 and in having a small centrolophid.

Measurements*:* see Table X.1.

Description:

Material from Venta del Moro:

p4: The occlusal outline of this tooth is subtriangular. The protoconid and the large anterolophid create a high, triangular anterior complex, which is separated from the metaconid by a narrow furrow. One specimen (VVmA-42, Fig. X.1, 1) has a short centrolophid. The mesoconid and entoconid are connected by the mesolophid, and from

Element	Sp.	Locality	Par.	n	min.	mean	max.
p4	Ey	VVm-A	L	2	1.05	1.06	1.06
			W	2	0.95	0.99	1.03
m1/m2	Ey	VVm-A	L	11	1.10	1.16	1.22
			W	11	1.14	1.30	1.47
	Ey	VVm-B	L	1	-	1.06	-
			W	1	-	1.24	-
	Ey	VVm-BC	L	2	1.12	1.16	1.19
			W	2	1.30	1.35	1.40
	Ey	ABS-3A	L	1	-	1.30	-
			W	1	-	1.45	-
	Ey	AF-1	W	1	-	1.46	-
	Ei	AL2-C	W	1	-	1.61	-
	Ei	AL2-D	L	1	-	1.56	-
			W	1	-	1.71	-
	Ei	LB2B	L	2	1.42	1.47	1.51
			W	2	1.50	1.64	1.77
m3	Ey	VVm-A	L	6	0.95	1.03	1.12
			W	6	1.06	1.16	1.23
	Ey	VVm-BC	L	2	-	1.01	-
			W	1	-	1.17	-
	Ei	AC-0	L	1	-	1.31	-
			W	1	-	1.41	-
	Ei	AL2-D	L	1	-	1.34	-
			W	1	-	1.54	-
D4	Ey	VVm-A	L	1	-	0.75	-
			W	1	-	0.78	-
P4	Ey	VVm-A	L	3	0.84	0.86	0.87
			W	3	1.25	1.27	1.29
	Ei	LB2B	L	1	-	1.08	-
			W	1	-	1.48	-
M1/2	Ey	VVm-A	L	12	1.01	1.11	1.22
			W	11	1.33	1.41	1.49
	Ey	VVm-BC	L	1	-	0.99	-
			W	1	-	1.34	-
	Ey	VVm-D	L	2	1.17	1.20	1.22
			W	2	-	1.47	-
	Ey	AF-1	W	1	-	1.38	-
	Ei	AL2-D	L	2	1.38	1.48	1.58
			W	2	1.74	1.85	1.95
	Ei	LB2B	L	1	-	1.25	-
			W	1	-	1.79	-
M3	Ey	VVm-A	L	7	0.85	0.95	1.00
			W	8	1.21	1.28	1.37
	Ey	VVm-C	L	1	-	0.96	-
			W	1	-	1.25	-
	Ei	LB2B	L	1	-	1.27	-
			W	1	-	1.52	-

Table X.1. Measurements (in mm) of the (pre-) molars of *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014, from Venta del Moro and Alcoy Basin, and of *E. intermedius* from Alcoy Basin and LB2B (Crevillente Basin). Abbreviations: Ey, *Eliomys yevesi*; Ei, *Eliomys intermedius*; Par, parameter; Sp., species.

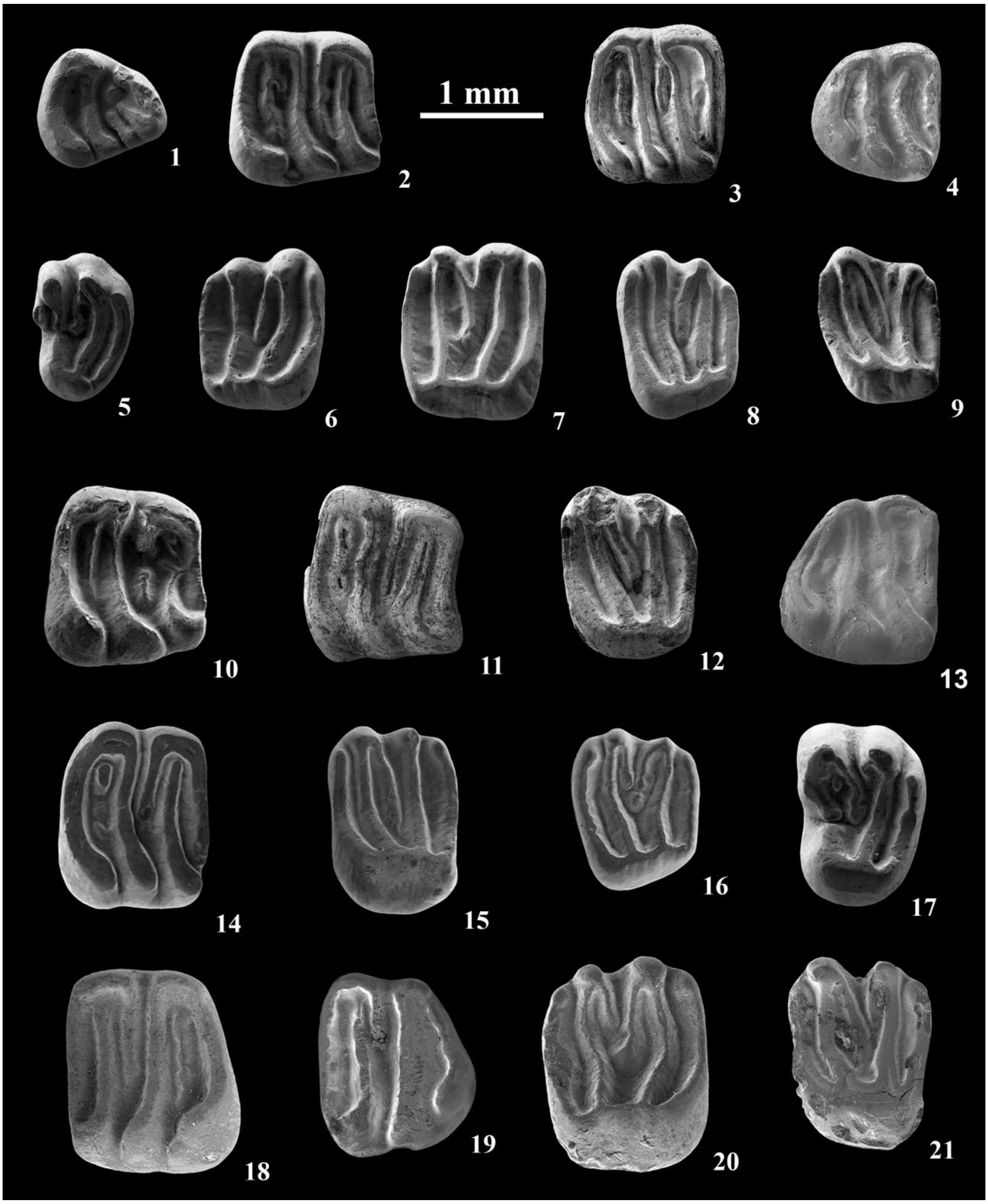


Figure X.1. *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. (**1–12**) from Venta del Moro (VVm-A and VVm-BC), Alcoi Barranc Sud 3A (ABS-3A), Alcoi Forn 1’06 (AF-1’06) and Alcoi Forn 1’07 (AF-1’07). **1**, right p4, VVmA-42; **2**, right m1,2, VVmA-1; **3**, right m1,2, VVmA-6; **4**, right m3, VVmBC-5; **5**, left P4, VVmA-40; **6**, right M1,2, VVmA-16; **7**, right M1,2, VVmA-25; **8**, left M3, VVmA-13; **9**, left M3, VVmA-14; **10**, right m1,2, ABS3A-38; **11**, right m1,2, AF1’06-190; **12**, left M1, AF1’07-36. *E. intermedius* (**13–21**) from Alcoi Cristian 0 (AC-0), La Bullana 2B (LB2B) and Alcoy 2D (AL2-D). **13**, right m3, AC0-88; **14**, right m1,2, LB2B-176; **15**, left M1, LB2B-241; **16**, left M3, LB2B-177; **17**, left P4, LB2B-178; **18**, left m1,2, AL2D-290; **19**, left m3, AL2D-356; **20**, right M1,2, AL2D-291; **21**, left M1,2, AL2D-293.

the anterior complex by a deep valley. The mesoconid and hypoconid are separated. There is no posterotropid. The posterolophid is high and curved. There are two fused roots.

m1,2: The occlusal outlines of these teeth are sub-quadrangular. The anterolophid is connected to the protoconid in 6 out of 14 specimens (4 out of 12 from VVm-A, the only specimen from VVm-B and 1 out of 2 from VVm-BC). One specimen (Fig. X.1, 3) has a vestigial anterotropid. Most molars show a connection between the metalophid and the metaconid, whereas the metaconid and entoconid are separated. The centrolophid is usually long and sometimes connected to the metalophid. The posterotropid is long in 10 specimens (9 out of 12 from VVm-A, 1 out of 2 from VVm-BC), short in three (one specimen from VVmA, the only specimen from VVm-B and 1 of 2 from VVm-BC) and absent in another two (both from VVm-A). The hypoconid is large. There are three roots.

m3: The occlusal outline of this tooth is sub-trapezoidal. The anterolophid is usually separated from the protoconid. The metalophid is sometimes connected to the metaconid. There are no accessory crests. Where present, the centrolophid is not connected to the metalophid. In 1 out of 13 m3, the mesolophid does not reach the entoconid (Fig. X.1, 4). The posterolophid is continuous.

dP4: Known only from a single, extremely worn molar. No features of the occlusal surface can be observed.

P4: The occlusal outline of this tooth is triangular. The paracone and metacone are higher than the protocone. The anteroloph is short, low and connected, at a low level, to the paracone. The protoloph is clearly discontinuous in 1 out of 4 specimens, whereas the remainder shows just a constriction in the central part of this crest. Two specimens present a well-developed precentroloph, and a further one a postcentroloph, which is not connected to the metacone (Fig. X.1, 5). The metaloph is high and continuous. The posteroloph is low and lingually connected to the protocone; discontinuous in two specimens, and not connected to the endoloph in another one (Fig. X.1, 5). The roots are not preserved in any of the specimens.

M1,2: The occlusal outlines of these teeth are trapezoidal or subrectangular. The anteroloph is separated from the paracone and the protoloph. The paracone and metacone are high and separated. The protoloph and metaloph are continuous, and occasionally sinuous. There is a well-developed precentroloph, which is not connected to the paracone in one of the specimens and reaches the metaloph in another one. Where present, the postcentroloph is short, except in VVmA-29, which has a well-developed crest, and VVmA-25, in which both centrolophs are fused into a central crest (Fig. X.1, 7). The posteroloph is connected to the endoloph. There are three roots.

M3: The occlusal outline of this tooth is trapezoidal. The anteroloph is connected to the protocone. In some specimens, the protoloph and metaloph are sinuous. Both centrolophs are present in 5 out of 8 specimens from VVm-A, and the single tooth from VVm-BC. Two of the specimens from VVm-A bear a long postcentroloph (Fig. X.1, 8). Where present, the precentroloph is usually attached to the paracone, whereas the postcentroloph is connected to the metacone. The endoloph is continuous, except for the single specimen from VVm-BC. There are three roots.

Material from Alcoy:

These specimens from the Alcoy Basin resemble the specimens from Venta del Moro, with the exception of having an anterolophid connected basally with the protoconid, and a metalophid that does not reach the metaconid (both on m1,2). In the m1,2 from ABS-3A (Fig. X.1, 10), the centrolophid is not continuous. In the M1,2 from AF-1’07 (Fig. X.1, 12), the anteroloph and the paracone are connected basally.

Discussion:

Eliomys yevesi is a relatively small-sized species, being smaller than Plio-Pleistocene *E. intermedius* and *E. quercinus*, and only slightly larger than the Miocene representatives of the genus (*E. lafarguei*, *E. reductus*, and *E. assimilis*) (Fig. X.2). The molars from Venta del Moro and AF-1’07 fall within the range of variation of *E. truci*. However, the specimens from the Early Ruscinian localities of PUR-4 and CLC-3B (Granada Basin), and AF-1’06 and ABS-3A (Alcoy Basin), are slightly larger, and intermediate between *E. truci* and *E. intermedius* (Fig. X.2).

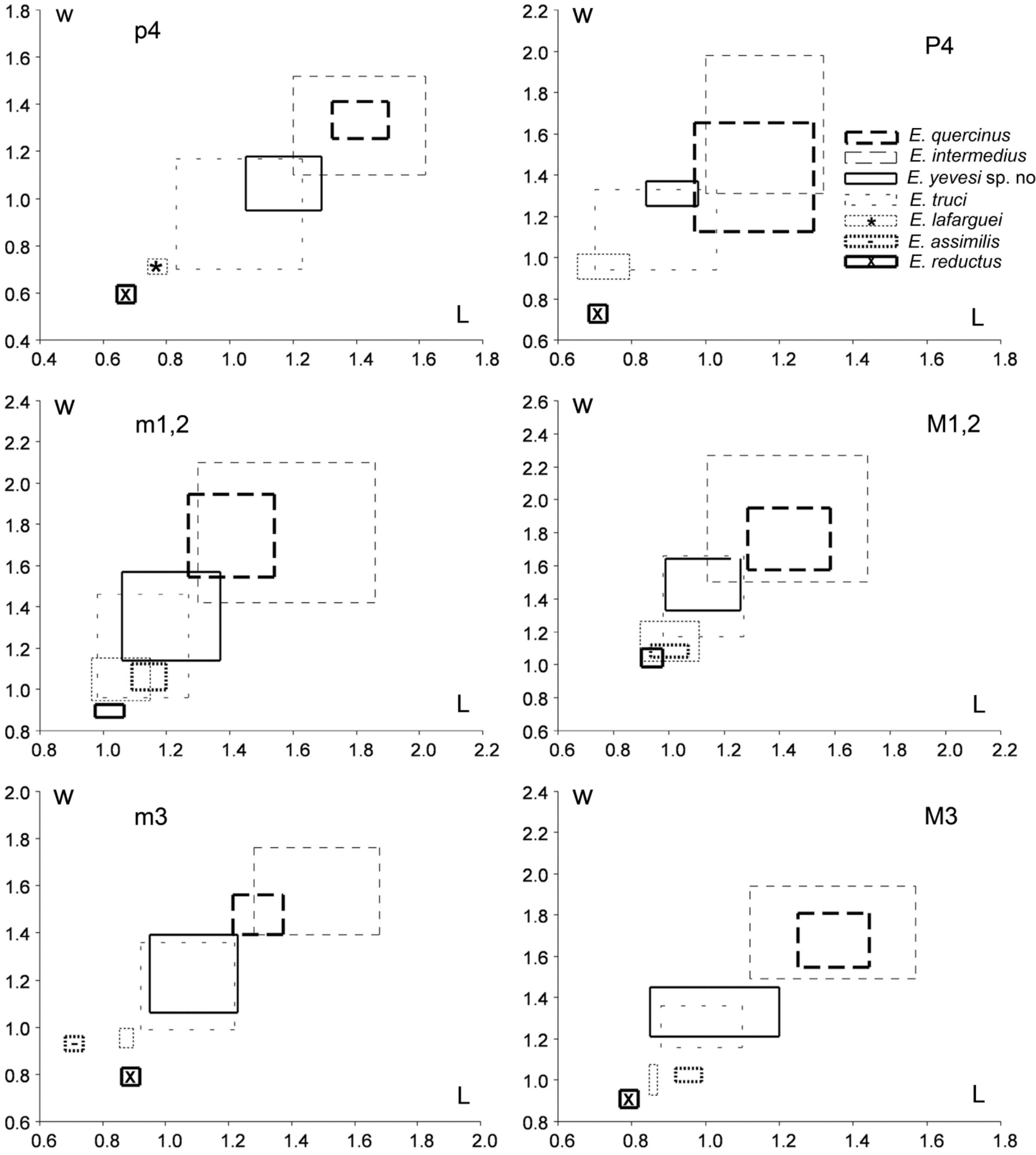


Figure X.2. Comparison of length and width measurements the teeth (p4; P4; m1,2; M1,2; m3; M3) of *E. truci*, from Aljezar B, Hautimagne, Los Mansuetos, Orrios, Sarrión, Sete, Villalba Alta (Adrover 1986), Concud 2 and 3, Concud Barranco de los Calaveros, Los Mansuetos, Masada del Valle 2, 5 and 7, Tortojada A and C (Weerd 1976), DHS-1 and 16, PUR-23, 24, and 25A, OTU-1, TCH-1B and 13 (García- Alix *et al.* 2008b), Negratín-1 (Minwer-Barakat *et al*. 2009a); Moreda 1A, 1B, Rambla Seca 1 (Castillo 1990) and Puente Minero (Alcalá *et al.* 1991); *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014, from VVm-A, B, BC, C and D, ABS-3A, AF-1’06, AF-1’07, CLC-3B and PUR-4; *E. intermedius* from Arquillo 3, Sete, Orrios 3, Villalba Alta (Adrover 1986), Escorihuela, Orrios (Weerd 1976), PUR-13, TCH-1 and 1B, TCH3, TCH-13 (García-Alix *et al.* 2008b), Moreda 1A, 1B, Bélmez 1 and Rambla Seca A1 and A2 (Castillo 1990) and Alozaina (Aguilar *et al.* 1993); *E. quercinus* from Vallparadís and Cal Guardiola (Minwer-Barakat *et al*. 2011b), Baños de Mula (Agustí *et al.* 1990), Peña de Estebanvela (Sesé 2006b), Valdocarros (Sesé *et al*. 2011), Sima de los Huesos (Cuenca-Bescós *et al*. 1997), Bois Roche (Sesé and Villa

2008), Santenay (Chaline 1972); and *E.* aff. *quercinus* from Huétor Tájar 1 and 8 (Martín-Suárez pers. comm.).

Morphologically, the present material resembles *E. truci*, but differs in the development of the centrolophs on M1,2, while the presence of both centrolophs is rare in *E. truci* (5 out of a total of 41 specimens, 12.90 %; two specimens from Concud 3 and one each from OTU-1, PUR-23, and Orrios 3), 4 out of 12 specimens *E. yevesi* from VVm-A and VVm-BC (33.33 %), and all of the M1,2 from VVm-D, AF-1'07, CLC-3B, and PUR-4 (except one) have both centrolophs. Moreover, when present, the postcentroloph is usually reduced in *E. truci*, whereas in some M1,2 of *E. yevesi* from VVm-A it is very well developed, reaching half the width of the molar or more (Fig. X.1, 7). Similarly, *E. truci* never bears two centrolophs on M3, whereas they do occur in 5 out of 8 molars (62.50 %) of *E. yevesi* from VVm-A, as well as the only M3 from VVm-C and CLC-3B.

In the upper molars of *E. intermedius*, 79 out of 130 (60.77 %) M1,2 and 18 out of 35 (51.42 %) M3 have two centrolophs (Weerd 1976, Adrover 1986, Castillo 1990, García-Alix *et al*. 2008b). Specimens from both the extant (Castillo 1990) and relatively young fossil (e.g., Casablanca B; García-Alix *et al*. 2008b) populations of *E. quercinus* generally have two centrolophs, with the anterior one often being longer. Together, these observations support a trend towards better-developed centrolophs within a lineage comprising *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus*.

Besides the change in development of the centrolophs, *Eliomys* also shows a trend towards the reduction of the centrolophid and the accessory crests in the lower molars (Castillo 1990, García-Alix *et al*. 2008b). This observation is borne out by the present data, m1,2 of *E. yevesi* resemble those of *E. truci* in having a long centrolophid and a well-developed posterotropid. In *E. intermedius*, the centrolophid is still present in 104 out of 106 (98.11 %) m1,2, but in 26 of these specimens (24.53 %) it is less than half the width of the molar—with the exception of the material from Sète (n=30), which always displays a long centrolophid. The centrolophid is even more reduced in *E. quercinus*, where it is short in 8 (61.54 %) and absent in 5 (38.46 %) out of the 13 studied specimens. A posterotropid is present in 29 out of 30 m1,2 of *E. truci* (96.67 %), 27 out of 29 m1,2 of *E. yevesi* (93.10 %), 80 out of 107 m1,2 of *E. intermedius* (74.76 %), and 1 out of 11 m1,2 (9.09 %) of *E. quercinus* (2 of the 13 specimens studied here are too damaged or worn to observe this character).

Stratigraphic and geographic range:

MN13–14, Late Miocene–Early Pliocene; Cabriel, Granada, and Alcoy basins of southeastern Spain.

Eliomys intermedius Friant, 1953 (Fig. X.1, 13-21)

Material: **6 m1,2** (AL2C-97, AL2D-290, LB2B-6, LB2B-176, LB2B-242, LB2B-243), **4 m3** (AL2C-47, AL2D-356, AC0-88, LB2B-179), **1 P4** (LB2B-178), **1 M1,2** (AC0-87), **3 M1,2** (AL2D-291-293), **2 M1,2** (LB2B-241, LB2B-253), **1 M3** (LB2B-177).

Measurements*:* see Table X.1.

Description:

m1,2: The occlusal outline of these teeth is trapezoidal or subrectangular. The anterolophid is connected to the protoconid in three specimens, and unconnected in a further three. There is no anterotropid. The metalophid is connected to the metaconid. The centrolophid is long, reaching the metalophid in 3 out of 6 specimens. The metaconid and entoconid are separated. The posterotropid is well developed. The hypoconid is large.

m3: The occlusal outline of this tooth is sub-trapezoidal. The anterolophid and the protoconid are separated. There is no anterotropid. The metalophid is connected to the metaconid. There is a short centrolophid, not connected to the metalophid (Fig. X.1, 19). The metaconid and entoconid are separated. There is no posterotropid.

P4: The occlusal outline of this tooth is subtriangular. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous.

M1,2: The outline of these teeth are subrectangular or trapezoidal. The anteroloph and paracone are connected basally in AC0-87, but not connected in any of the other specimens. In some specimens (especially AC0-97), the protoloph and metaloph are distinctly sinuous. Both centrolophs are usually present. The posteroloph is connected to the endoloph. There are three roots.

M3: The occlusal outline of this molar is trapezoidal. The anteroloph is separated from both protoloph and paracone. There is neither an anterotrope nor a posterotrope. The paracone and metacone are high and separated. The protoloph and metaloph are continuous. Both centrolophs are present and well developed, with the postcentroloph being longer and interrupted (Fig. X.1, 16). The endoloph and posteroloph are connected and continuous.

Discussion:

Eliomys intermedius from the Early Pliocene (Early Ruscinian/Early Zanclean, Mansino *et al*. 2013, chapter IV) localities of AL2-C and AL2-D is slightly bigger than specimens from the slightly older localities of AC-0 (chapter V) and LB2B (chapter VII) (Table X.2), but all of the specimens from these sites fall within the range of *E. intermedius* from Sète, the type locality of the species (Adrover 1986). The specimens of *E. intermedius* from AC-0, AL2-C, AL2-D, and LB2B have higher and thicker lingual walls than *E. truci* and *E. yevesi*, sinuous crests, a rounded occlusal outline, and two well-developed centrolophs in the upper molars (M1,2 from AC-0 and AL2-D, and M3 from LB2B). These features agree with *E. intermedius.*

Stratigraphic and geographic range:

MN 14, Early Pliocene – early Pleistocene (MQ2) of the Alcoy, Cabriel, and Calatayud-Teruel basins of Spain and the Aquitaine, Paris, and Sud-est basins of France. Other reported occurrences (Bruijn *et al.* 1970) are dubious.

X.4. Discussion

X.4.1. Phylogenetic relationships of *Eliomys*

Some previous authors (Nadachowski and Daoud 1995) have suggested a relationship of the extant *Eliomys quercinus* with *E. reductus* and *E. assimilis*, both from the German locality of Hammerschmiede (Late Miocene, early

Vallesian/Tortonian). However, this is seemingly contradicted by the absence of a clear relationship between *E. reductus, E. assimilis* and the likely ancestor of *E. quercinus, E. intermedius* (Daams and Bruijn 1995).

An alternative hypothesis groups *E. reductus* with *E. lafarguei* from Lo Fournas 6C and Lo Fournas 16M (Late Miocene, Vallesian/Tortonian), based on the presence of a continuous endolophid and a trend towards larger size and reduced postcentrolophs, which commonly occurs in glirids (Aguilar *et al*. 2007). This relationship is further supported by m1,2 being longer than wide in these two taxa (albeit only slightly so in *E. lafarguei*) and showing a tendency towards a shortening of the centrolophid. The latter is isolated in the holotype of *E. reductus*, an m2, and shows a low connection with the metaconid in the m1, whereas in *E. lafarguei* the centrolophid is absent or greatly reduced on m2, and variably isolated or connected to the metaconid at a low level on m1. By contrast, in *E. truci*, *E. yevesi*, *E. intermedius*, and *E. quercinus* these teeth are wider than longer, and the centrolophid is usually connected to the metaconid.

Based on these observations, we agree with Aguilar *et al*. (2007) in recognizing two distinct lineages within *Eliomys*, comprising *E. lafarguei-E. reductus*, and *E. truci-E. yevesi-E. intermedius-E. quercinus*, respectively. The former lineage may also include *Eliomys* sp. A from the early Turolian of Tortajada A (Teruel, Spain; Weerd 1976), based on its possible relationship with *E. lafarguei* (Aguilar *et al.* 2007). On the other hand, details of the morphology of *E. assimilis*, which has an accessory crest on M1,2 suggest that this species does not form part of either of the two main lineages. These observations are confirmed by the results of the cladistic analysis (Fig. X.3, Table X.3).

Species	1	2	3	4	5	6	7	8	9	10
E. assimilis	2	0	0	1	1	2	2	1	0	0
E. reductus	2	1	0	0	1	2	0	0	0	0
E. lafarguei	1	1	0	1	0	1	0	0	0	0
E. truci	0	0	0	1	1	1	0	0	0	1
E. yevesi	0	0	0	1	1	2	2	0	0	1
E. intermedius	0	0	0	1	1	2	2	0	0	2
E. q. quercinus	0	1	0	0	0	2	2	0	0	2
E. q. lusitanicus	0	0	0	1	0	2	2	0	0	2
D. nitedula	1	1	1	1	1	2	2	1	1	0

Table X.3. Cladistic data matrix for *Eliomys*, including lower (1 to 4) and upper (5 to 8) molar dental characters. Abbreviations: *E. q.*, *Eliomys quercinus*.

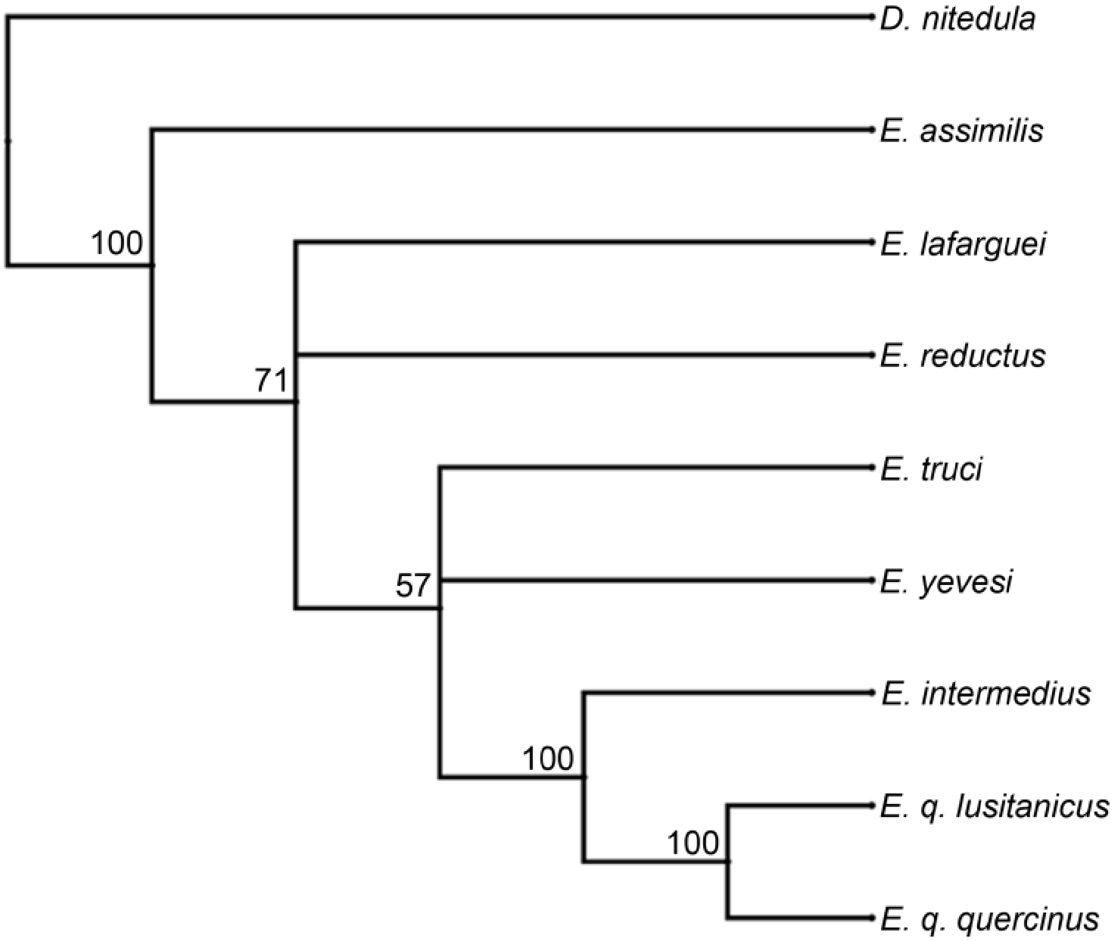


Figure X.3. 50 % majority rule consensus of the seven most parsimonious trees (L = 21, retention index = 0.619, consistency index = 0.619) resulting from the phylogenetic analysis. Numbers next to clades indicate the percentage of most parsimonious trees in which the clade was recovered. The extant glirid *Dryomys nitedula*, a form closely related to *Eliomys*, was chosen as outgroup.

X.4.2. Evolutionary process

The oldest record of *Eliomys* is *E. truci* from the Middle Miocene of Solera (Late Aragonian/Early Tortonian; Daams and Freudenthal 1988). However, the identity of this material has been questioned (García-Alix *et al*. 2008b), thus possibly reducing the earliest occurrence of the genus to *E. truci* from the Late Miocene (early Vallesian/Tortonian) of Pedregueras 2A (Daams and Freudenthal 1988). Several members of the genus co-occur during the Miocene (Fig. X.4), which may imply cladogenetic evolution. Thus, Adrover (1986) suggested *E. truci*, including its ancestor *Eliomys* sp. I from Viveros de Pinos (Teruel Basin, north-central Spain; early Turolian/Tortonian), and *Eliomys* sp. II from Aljezar B (Teruel Basin, middle Turolian, Tortonian), to be descendants of an older, yet unknown species of the same genus. A similar logic applies to *E. truci* on the one hand, and *E. yevesi*–*E. intermedius* on the other. Both of these lineages co-existed during the Ruscinian (Zanclean) and the earliest Villanyan (Piacenzian), as is evident at Orrios-3, Sète, Sarrión, Villalba Alta (Adrover 1986), La Gloria 4, Escorihuela (Mein *et al*. 1990), Moreda-1A, 1B, Rambla Seca 1 (Castillo 1990), TCH-1B and TCH-13 (García-Alix *et al*. 2008b).

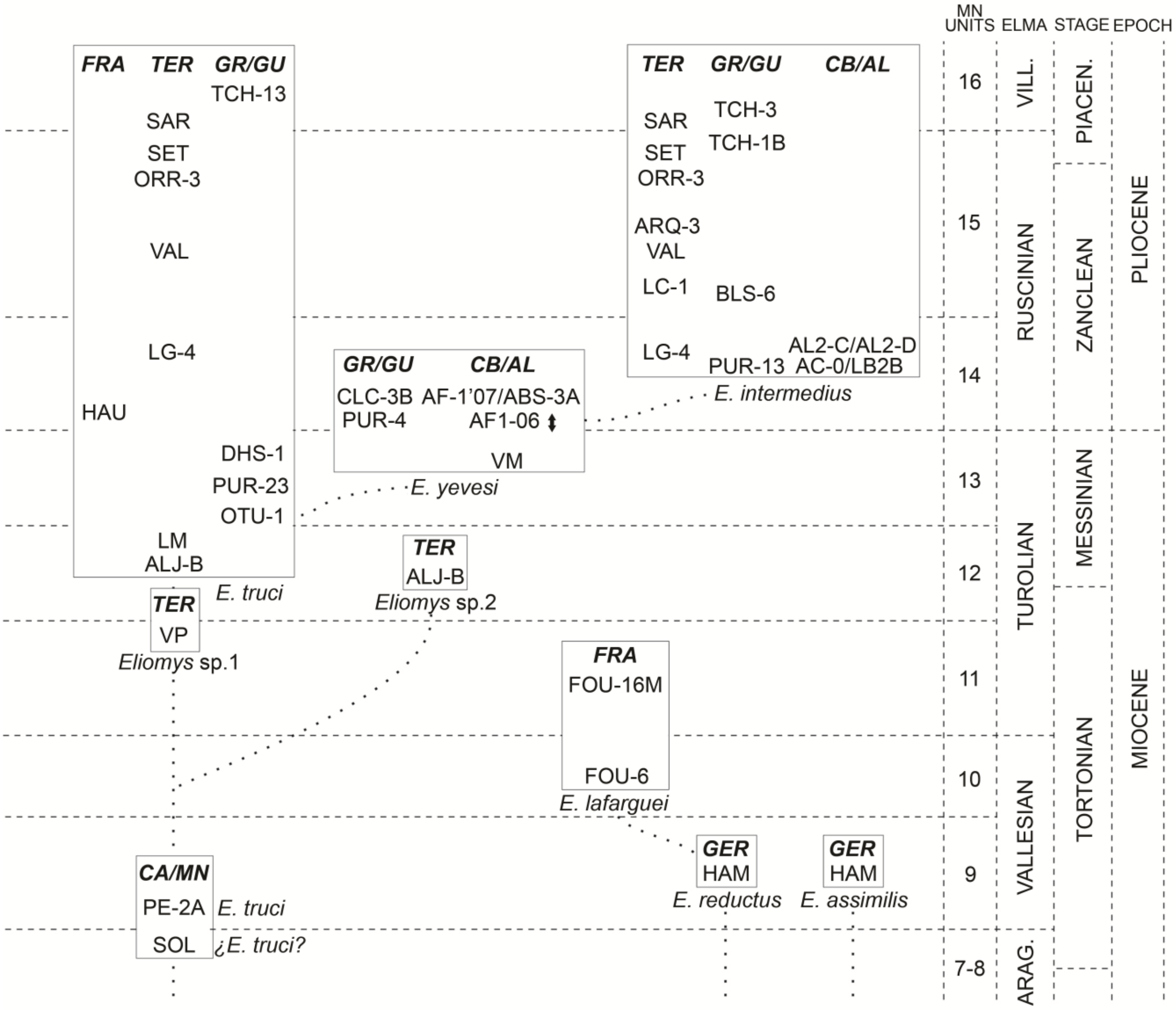


Figure X.4. Early Vallesian (early Tortonian) to early Villanyan (Piacenzian) stratigraphic distribution and proposed phylogenetic relationships of the genus *Eliomys* (modified from García-Alix *et al*. 2008b). Abbreviations: AC, Alcoy Cristian; AF, Alcoi Forn; AL2, Alcoy 2; ALJ, Aljezar; ARAG., Aragonian; BLS, Barranco de Blas; CA/MN, Calatayud-Montalbán Basin; CB/AL, Cabriel and Alcoy basins; CLC, Calicasas; DHS, Dehesa; FOU, Lo Fournas; FRA, France; GR/GU, Granada and Guadix basins; HAU, Hautimagne; Ham, Hammerschmiede; LB2B, La Bullana 2B; LC, Lomas de Casares; LG, La Gloria; LM, Los Mansuelos; ORR, Orrios; OTU, Otura; PE-2A, Pedregueras 2A; PIACEN, Piacencian; PUR, Purcal; SAR, Sarrión; SET, Sète;

SOL, Solera; TCH, Tollo de Chiclana; TER, Teruel Basin; VAL, Villaba Alta; VILL., Villanyan; VM, Venta del Moro; VP, Viveros de Pino.

Until the first occurrence of *E. quercinus* in the earliest Pleistocene locality of Almenara-Casablanca 1 (Agustí *et al*. 2011), the only representative of *Eliomys* during the latest Pliocene and early Pleistocene was *E. intermedius* (García-Alix *et al*. 2008b). In contrast to the earlier process of cladogenesis, several authors have hypothesized that *E. quercinus* may have arisen from *E. intermedius* through a process of anagenetic evolution (Chaline 1972, Castillo 1990, García-Alix *et al*. 2008b), involving a reduction in size and a trend towards an unconnected anteroloph and protoloph (Castillo 1990). Extant *E. quercinus* comprises at least eight subspecies, two of which are found in the Iberian Peninsula (Moreno 1984), the smaller *E. quercinus quercinus*, which inhabits relatively open environments and is characterized by slightly sinuous crests, a continuous endolophid, a small centrolophid, and no accessory crests; and the larger *E. quercinus lusitanicus*, which lives in more closed environments, and is marked by more distinctly sinuous crests, accessory crests, and the absence of both the endolophid and the centrolophids. In the latter two features, *E. quercinus lusitanicus* resembles *E. intermedius*, which even led to the suggestion that the latter should be regarded as a subspecies of *E. quercinus* (Martín-Suárez 1988).

In summary, it therefore seems that the lineage including *E. truci*, *E. yevesi*, and *E. intermedius*, and the extant *E. quercinus* originated and diversified through cladogenesis during the Late Miocene, and Early Pliocene, but then switched to a process of anagenetic evolution during the Late Pliocene and Pleistocene.

X.5. Conclusions

Based on new fossil material from the Alcoy and Cabriel basins of southeastern Spain, as well as material from the Granada Basin previously referred to *E.* aff. *intermedius*, we erect the new species *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014, similar in size or slightly larger than *E. truci*. *E. yevesi* generally resembles *E. truci* in terms of its morphology, but differs in having better and more frequently developed centrolophs in the upper molars, similar to *E. intermedius*.

Based on its size and morphology, we consider the most probable origin of the new species a Late Miocene population of *E. truci* (Fig. X.4), likely an ecomorphotype characterized by well-developed centrolophs in the upper molars, and both a long centrolophid and a well-developed posterotropid in the lower molars. *E. yevesi* thus likely forms part of a lineage comprising *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus* (to the exclusion of other members of the genus, such as *E. assimilis* and *E. reductus*; Fig. X.3), which is characterized by a trend towards the reduction of accessory crests in the lower molars, as well as the development of centrolophs. This arrangement is complemented by a second lineage including *E. reductus* and *E. lafarguei*, marked by an increase in size, a gradual reduction of the postcentroloph and centrolophid, and a trend towards a more quadrangular occlusal outline (lower length-width ratio).

X.6. Supplementary Tables:

Number of specimens which show the morphological characters described in the main text.

Characters of m1,2 and m3

A: Connection anterolophid-protoconid present

B: Connection anterolophid-protoconid absent

C: Connection metalophid-metaconid present

D: Connection metalophid-metaconid absent

E: Centrolophid absent

F: Centrolophid connected to the metaconid

G: Centrolophid not connected to the metaconid

H: Long centrolophid

I: Short centrolophid

J: Presence of posterotropid

K: Absence of posterotropid

Characters of M1,2

A: Presence of precentroloph

B: Presence of postcentroloph

C: Presence of both centrolophs

D: Absence of centrolophs

E: Connection posteroloph-endoloph present

F: Connection posteroloph-endoloph absent

Characters of M3

A: Absence of precentroloph

B: Precentroloph connected to paracone

C: Precentroloph not connected to paracone

D: Absence of postcentroloph

E: Postcentroloph connected to metacone

F: Postcentroloph not connected to metacone

G: Presence of both centrolophs

H: Connection posteroloph-endoloph present

I: Connection posteroloph-endoloph absent

Eliomys species per locality:

E. quercinus: ACB (Almenara Casablanca), El Salt, Huetor Tájar, La Salema,

E. intermedius: AC-0, Arquillo 3, AL2-D, Balaruc 2, Bélmez 1, Caravaca, Cañada Castaños, Gorafe 2 and 5, La Gloria 4, LB2B, Layna , Moreda-1A and 1B, Orrios 3, PUR-13, Séte, TCH-1B and 3, Villalba Alta

E. yevesi: ABS-3A, AF-1’06, AF-1’07, PUR-4, VVm-A, B, BC, C and D

E. truci: Botardo C, Concud 2 and 3, Crevillente 6, DHS-1, Hautimagne, La Gloria 5, Los Mansuetos , Masada del Valle 5, PUR-23, 24-A, 25 and 25A, Orrios 3, Séte, TCH-1B and 13, Tortojada A and C, OTU-1, Valdecebro 6, Villalba Alta, Villastar

Eliomys sp.: Aljezar B, Negratín 1, Crevillente 1, 3 and 5.

When *E. intermedius* and *E. truci* are present in the same locality we use the notation (in.) for *intermedius*, and (tr.) for *truci*.

m1,2

Locality	A	B	C	D	E	F	G	H	I	J	K
La Salema	6	2	4	2	2	0	3	0	5	1	6
El Salt	1	0	2	0	1	0	1	0	1	0	2
ACB 1/5	1	0	0	1	0	0	1	0	1	0	1
Huetor Tájar	0	1	1	0	0	1	0	0	1	0	1
Moreda 1B	5	2	7	0	0	3	4	4	3	5	2
TCH-13	0	2	1	1	1	0	1	0	1	1	1
TCH-3	5	5	6	4	2	3	5	3	5	2	8
TCH-1B (in.)	4	6	7	5	0	2	10	4	8	6	6
TCH-1B (tr.)	1	0	0	1	0	0	1	0	0	1	0
Séte	10	20	14	16	0			30	0	30	0
Orrios 3 (in.)	1	1	0	2	0			1	1	2	0
Orrios 3 (tr.)										1	0
Bélmez 1	7	0	7	0	0	3	4	6	2	3	5
Arquillo 3	5	5	5	5	0			8	2	8	2
Villalba Alta	6	4	6	4	0			10	1	7	4
Moreda-1A	4	0	4	0	0	2	2	4	0	4	0
Gorafe 2	1	0	1	0	0	0	1	0	1	1	0
Gorafe 5	1	0	1	0	0	0	1	0	1	1	0
Hautimagne	4	0	1	3	0			4	0	4	0
PUR-13	0	5	4	1	0	2	3	3	2	5	0
AL2-D	1	1	1	0	0	1	0	1	0	1	0
LB2B	1	3	3	1	0	2	1	3	0	4	0
La Gloria 4			1	0	0			1	0	1	0
ABS-3A	1	0	0	1	0	0	1	1	0	1	0
AF-1’06	1	0	0	1	0	1	0	1	0	1	0
PUR-4	10	2	9	3	0	8	4	12	0	12	0
Botardo C	0	2	2	1	0	1	1	1	0	2	0
Negratín 1	2	0	2	0	0	1	1	2	0	2	0
VVm-A	4	7	11	0	0	10	1	10	1	10	2
VVm-B	1	0	1	0	0	1	0	1	0	1	0
VVm-BC	1	1	1	1	0	2	0	2	0	2	0
PUR-25A	2	0	0	2	0	0	2	2	0	2	0
PUR-25	0	1	1	0	0	0	1	1	0	1	0
PUR-24A	0	1	0	1	0	1	0	1	0	1	0
PUR-23	0	2	0	2	0	1	1	2	0	2	0
OTU-1	0	3	1	2	0	0	2	1	2	3	0
Villastar			1	0	0			3	0	1	0

La Gloria 5			3	0	0			0	3	3	0
Valdecebro 6			2	0	0			2	0	2	0
Los Mansuetos	1	1	0	2	0			1	1	2	0
Aljezar B	0	1	1	0	1			0	0	1	0

m3

Locality	A	B	C	D	E	F	G	H	I	J	K
Salema	1	0	1	0	1	0	0	0	0	0	1
ACB 1/1	0	1	1	0	1	0	0	0	0	0	1
Huétor Tájar	2	0	2	0	0	0	2	0	2	0	2
Moreda-1B	1	1	2	0	0	0	2	0	2	0	2
TCH-13	0	1	0	1	0	0	1	0	1	0	1
TCH-3	2	4	3	3	2	1	3	0	6	0	6
TCH-1B	1	4	2	5	2	0	4	0	6	1	5
Sete (in.)					0			20	0	6	15
Sete (tr.)								1	0		
Bélmez 1	0	2	2	0	0	0	2	0	2	0	2
Arquillo 3					0			1	0	0	1
Villalba Alta (in.)					0			3	0	1	2
Villalba Alta (tr.)	0	1	1	0	0			0	1	0	1
Hautimagne								4	0	0	4
Moreda 1A	0	1	1	0	0	0	1	0	1	0	1
PUR-13	0	1	0	1	0	0	1	0	1	0	1
AL2-D	1	0	1	0	0	0	1	0	1	0	1
AC-0	0	1	1	0	1	0	0	0	0	1	0
LB2B			1	0	0	0	1	0	1	0	1
AF-1’06		?		?	0		?		?		?
CLC-3B	0	1	1	0	0	0	1	0	1	0	1
PUR-4	0	3	3	0	1	0	2	0	2	0	3
Negratín 1	0	1	0	1	1	0	0	0	0	0	1
VVm-A	2	4	3	3	3	0	3	1	2	0	6
VVm-BC	0	2	1	1	1	0	1	0	1	0	2
OTU-1	0	2	0	2	2	0	0	0	0	0	2
La Gloria-5			1	0	1			0	1	1	0
Los Mansuetos								0	1	0	1
Aljezar B			1	1	1			0	1		

M1,2

Locality	A	B	C	D	E	F
Salema	1	0	5	0	0	5
Salt	1	0	0	0	1	0
ACB 1/1	0	0	2	0	1	0
Huétor Tájar	0	0	2	0	1	0
Moreda-1B	1	1	2	0	3	1
TCH-13	1	0	0	0	0	1
TCH-3	7	1	5	1	12	2

TCH-1B	8	1	3	0	10	3
TCH-1B	2	0	0	0	2	0
Balaruc 2			5		5	0
Layna			0		3	0
Sete			25		34	0
Orrios 3 (in.)			1		1	0
Orrios 3 (tr.)			1		1	1
Bélmez 1	3	3	2	0	6	0
Arquillo 3			11	0	18	2
Villalba Alta			8	0	9	0
Moreda-1A (in.)	1	0	1	0	1	0
Moreda-1A (tr.)	1	0	0	0	1	0
Cañada Castaños	0	0	1	0	1	0
Gorafe2	0	0	1	0	1	0
Gorafe5	0	0	1	0	1	0
Hautimagne			0		3	1
AL2-D	0	0	2	0	2	0
PUR-13	0	0	1	0	1	0
AC-0	0	0	1	0	1	0
LB2B	1	0	0	0	1	0
La Gloria-4	1	0	2	0	2	1
Caravaca			7		9	0
AF-1’07	0	0	1	0	1	0
CLC-3B	0	0	2	0	2	0
PUR-4	1	0	1	0	1	0
Negratín 1	0	1	0	0	1	0
VVm-A	7	0	4	0	12	0
VVm-BC	1	0	0	0	1	0
VVm-D	0	0	2	0	2	0
DHS-1	1	0	0	0	1	0
PUR-23	0	0	1	0	1	0
Crevillente 6			0		1	0
OTU-1	0	0	1	0	1	0
Masada del Valle 5			0		2	0
Crevillente 5			0		1	0
Concud 3			2		6	6
Concud 2			0		1	2
Los Mansuetos			0		2	0
Tortajada C			0		0	1
Masada del Valle 2			0		6	0
Tortajada A			0		0	1
Crevillente 1			1		1	0
Crevillente 3			1		1	0

M3

Locality	A	B	C	D	E	F	G	H	I
Salt	0	1	0	0	0	1	1		
ACB 1/2	1	1	0	0	2	0	1	2	0
Huétor Tájar	1	2	0	0	3	0	2	2	1

TCH-13	1	0	0	1	0	0	0	1	0
TCH-3	2	4	0	0	3	3	4	4	2
TCH-1B	3	1	0	0	3	1	1	3	1
TCH-1B	1	0	0	1	0	1	0	1	0
Sete				1			5		
Bélmez 1	4	0	1	0	3	2	1	5	0
Arquillo 3							2		
Villalba Alta							2		
Hautimagne							0		
PUR-13	1	1	0	0	0	1	0	1	0
LB2B	0	1	0	0	1	0	2	1	0
Caravaca							1		
CLC-3B	0	1	0	0	1	0	1	1	0
PUR-4	3	0	0	0	3	0	0	2	1
VVm-A	2	4	2	1	5	1	5	8	0
VVm-C	0	0	1	0	1	0	1	0	1
Los Mansuetos							0		
Viveros de Pinos	1	1	0	2	0	0	0	2	0
Concud 3							0		
Concud 2							0		
Tortajada C							0		

CHAPTER XI. A NEW APPROACH TO THE LATE MIOCENE-EARLY PLIOCENE FORMS OF THE GENUS *APOCRICETUS*. *APOCRICETUS ALBERTI* (RODENTIA, MAMMALIA) FROM VENTA DEL MORO (CABRIEL BASIN, SPAIN).

XI.1. Introduction

The genus *Apocricetus* Freudenthal *et al*. 1998 comprises ‘‘medium to large-sized Cricetinae, practically without mesolophids in m1 and m2, with long third molars; in the younger forms the anterior protolophules and posterior metalophules in the upper molars are reduced or absent’’ (Freudenthal *et al.* 1998). The temporal range of the genus is Late Miocene (Crevillente 15, Early Turolian, MN11)–Late Pliocene (Lo Fournas 13, Early Villanyian, MN16) (Bachelet *et al.* 1990, Freudenthal *et al*. 1998). The genus was erected after *Neocricetodon* and *Cricetulodon* were separated as different genera, because adding the species characterized by the loss of the mesolophids in m1 and m2 and labial or double anterolophulids in m1 to any one of them made impossible to give differential diagnoses (Freudenthal *et al.* 1998).

The genus *Apocricetus* comprises: *Apocricetus angustidens* (Depéret, 1890) (type species), *Apocricetus barrierei* (Mein and Michaux, 1970), *Apocricetus plinii* (Freudenthal, Lacomba and Martín-Suárez 1991) and *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998. In the localities Crevillente 23 (Crevillente Basin, Spain), Masada del Valle 2, Concud Barranco and Los Mansuetos (Teruel Basin, Spain), Freudenthal *et al.* (1998) noted the presence of an unnamed species (or a possible mixture of two species) that they named *Apocricetus* aff. *plinii* and which, according to these authors, may be the ancestor of *A. plinii*. The species of *Apocricetus* constitute a phylogenetic lineage (*Apocricetus* aff. *plinii*–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens*), where the first representative is *Apocricetus* aff. *plinii* from MN11 and the last one is *A. angustidens* from MN16 (Freudenthal *et al*. 1998).

The representatives of the genus *Apocricetus* are key to understanding the biostratigraphic framework in the time span between Late Miocene (Late Turolian) and

Late Pliocene in Southern Europe (Freudenthal *et al*. 1998, García-Alix *et al*. 2008b, Minwer-Barakat *et al*. 2012). Therefore, a reliable taxonomic identification of the species integrating this genus is necessary for dating and correlating continental fossil sites correctly. However, some species of this genus are not well known because they are represented by small samples (Ruiz-Sánchez *et al.* 2014). This is the case of *A. barrierei*, described on the basis of three specimens from the locality of Chabrier (Mein and Michaux 1970). The revision of the fossil remains from La Bullana-2B and La Bullana-3 (Ruiz-Sánchez *et al.* 2014), by far the richest samples of this species with a hundred specimens recovered, allowed a more precise diagnosis on the basis of morphology.

The material of *A. alberti* is not as scarce as that of *A. barrierei*: CR-6, type locality of the species (Freudenthal *et al.* 1998) has yielded 55 measurable teeth, and more material has been extracted from other Late Miocene localities such as Venta del Moro, Librilla, Purcal 23, 24 and 25 (Freudenthal *et al.* 1998), Purcal 3 (García-Alix *et al.* 2008b) and Negratín (Minwer-Barakat *et al*. 2009a). In this chapter we study the remains of *Apocricetus alberti* from the locality of Venta del Moro (levels VM-A, AB, B, BC, C, and D sensu Montoya *et al.* 2006a, here denoted as VVmA-, VVmAB-, VVmB-, VVmBC-, VVmC- and VVmD-), situated in lacustrine and palustrine sediments of the Cabriel Basin in Eastern Spain (Robles 1970, Montoya *et al.* 2006a) (Fig. II.6). These remains constitute the richest collection of this species described to date. Some data about *Apocricetus* from Venta del Moro were already reported in Ruiz-Sánchez *et al*. (2014). These data correspond to a small sample from this locality, kept at the University of Granada. Specimens described in this chapter belong to an unpublished, larger collection from Venta del Moro.

The new data from Venta del Moro allow a better characterization of the species *A. alberti* and a good knowledge of the evolution of the phylogenetic lineage *Apocricetus* aff. *plinii–A. plinii–A. alberti–A. barrierei–A. angustidens*.

XI.2. Material and methods

The new fossils from Venta del Moro are kept in the *Museu de Geologia de la Universitat de València* (MGUV) with the field labels VVmA-, VVmAc-, VVmAB-, VVmB-, VVmBC-, VVmC- and VVmD-. The material of *A.* aff. *plinii* from CR-5A and CR-15 and *A. plinii* from CR-20 and CR-23 is housed at Naturalis Biodiversity Center, Leiden. The material of *A. alberti* from PUR-25A, PUR-25, Librilla and five m3 from Venta del Moro, *A. barrierei* from Caravaca, Chabrier, PUR- 4, YEG and Gorafe 4, casts of *A. angustidens* from Soler and Villeneuve, an m3 from Mont-Hélène, and two specimens with the label Gorafe 4/5, which may be from Gorafe 4 or 5, but were ascribed by the authors to *A. angustidens*, are housed at the University of Granada.

The nomenclature used in the descriptions of the teeth and the measurement method are those of Freudenthal *et al.* (1994). The terms ‘‘preloph’’ and ‘‘prelophid’’ are taken from Freudenthal (1985); a prelophid is a transversal crest, halfway between the anteroconid and the first pair of main cusps, on which the anterolophulids, the protoconid and the protolophulid insert. The preloph is a similar structure in the upper molars, a transversal crest on which the anterolophules insert. The nomenclature of the m1 and M1 of *Apocricetus* is shown in Fig. I.3.

The lower teeth are indicated as **m1**, **m2** and **m3**, and the upper teeth as **M1**, **M2** and **M3**. Fig. XI.7 was made with the program PAST, version 2.17. The box plot was performed assuming 95.0 % intervals of the standard deviation and rounding as the quartile method. 2.1.

XI.3. Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer, 1817

Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998

Type species: *Cricetus angustidens* Depéret, 1890

Other Species: *Cricetus barrierei* Mein and Michaux, 1970; *Neocricetodon plinii* Freudenthal, Lacomba and Martín-Suárez, 1991; *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998. *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998 (Fig. 2).

Holotype: CR6 111, Instituut voor Aardwetenschappen, Utrecht.

Type locality: CR-6, Upper Miocene, Spain.

XI.3.1. Original diagnosis (Freudenthal *et al*. 1998)

Apocricetus with moderately elongated third molars and a simple crest-like anteroconid in m1. Anterior protolophule of M1 frequently absent (3 out of 7 specimens), in M2 nearly always present. M3 without mesoloph. Generally the M1 are banana-shaped, with sinuous borderlines, due to the protruding cusps and indenting valleys.

XI.3.2. Emended diagnosis

Apocricetus similar in size to *A. plinii* and smaller than *A. barrierei* and *A. angustidens*. Anteroconid of m1 superficially divided or crest-like. Absent anterosinusid in m2 and m3. Mesolophid seldom present in m2 and generally present in m3. Shape of m3 similar to *A. plinii*, less triangular than *A.* aff. *plinii* and less subrectangular than *A. barrierei* and *A. angustidens*. The ectomesolophid is absent in all the lower molars. Anterior protolophule present in approximately half of the M1, and all M2 and M3. The mesoloph is absent in the upper molars.

XI.3.3. Differential diagnosis

A. alberti is larger than *A.* aff. *plinii*, similar in size to *A. plinii*, on average smaller than *A. barrierei*, although the maximum lengths and widths of *A. alberti* can overlap the minimum values of *A. barrierei*, and clearly smaller than *A. angustidens* (Figs. XI.1 and XI.2).

A. alberti differs from *A.* aff. *plinii* and *A. plinii* in the shape of the anteroconid, crest-like in some specimens and with a less conspicuous constriction when it is bilobed. It differs from *A. barrierei* and *A. angustidens* by the more conspicuous lobes of the anteroconid, which is crest-like or with a very weak subdivision in these species.

A. alberti differs from *A. plinii*, *A. barrierei* and *A. angustidens* by the presence of a mesolophid in approximately one third of m2. It also differs from *A. plinii* in the complete absence of an ectomesolophid in m2.

A. alberti differs from *A.* aff. *plinii* by the wider posterior side of its m3. It differs from *A. barrierei* and *A. angustidens* by its narrower posterior side of its m3 and from *A. barrierei* also by its less enlarged m3.

A. alberti differs from *A.* aff. *plinii* and *A. plinii* by the presence of a weak cingulum ridge in some M1 (13.51 % in the material from Venta del Moro) and from *A. angustidens* by the lesser development and lesser frequency of this cingulum.

It differs from *A.* aff. *plinii* and *A. plinii* by the presence of a preloph in some specimens, which is less developed than in *A. barrierei*. It differs from *A. angustidens* and *A. barrierei* by the presence of a simple anterolophule.

A. alberti differs from *A. barrierei* and *A. angustidens* in the frequency of the anterior protolophule of the M1: this crest is present in 58.53 % of the specimens from Venta del Moro, 28.57 % of *A. barrierei* from LB2B and 13.33 % of *A. angustidens* from Mont-Hélène. *A. alberti* also differs from the other species of the genus in the frequency of the posterior metalophule in M1. This crest is present in 45.45 % M1 of *A.* aff. *plinii* from CR-23, 23.08 % of *A. plinii* from CR-15, 17.07 % of specimens from Venta del Moro, being absent in *A. barrierei* and *A. angustidens*.

A. alberti differs from *A. barrierei* and *A. angustidens* in the frequency of the anterior protolophule in M2 (this ridge is present in 80 % of the specimens of *A. barrierei* from LB2B and 23.08 % in *A. angustidens* from Mont-Hélène). The frequency of the posterior metalophule in M2 is similar in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and therefore this character only allows a clear distinction between these species and *A. barrierei* and *A. angustidens*. This ridge is complete in 51.72 % M2 of *A.* aff. *plinii* from CR-23, 50 % of *A. plinii* from CR-15, 47.62 % of *A. alberti* from Venta del Moro and 35.29 % of *A. barrierei* from LB2B, being absent in *A. angustidens*. *A. alberti* differs from *A. barrierei* and *A. angustidens* in the development of the anterior protolophule in M3. This crest appears in 100 % of the specimens of *A. alberti*, 25 to 100 % in the samples of *A. barrierei* (Ruiz-Sánchez *et al*. 2014) and 33 % of the M3 of *A. angustidens* from Mont-Hélène.

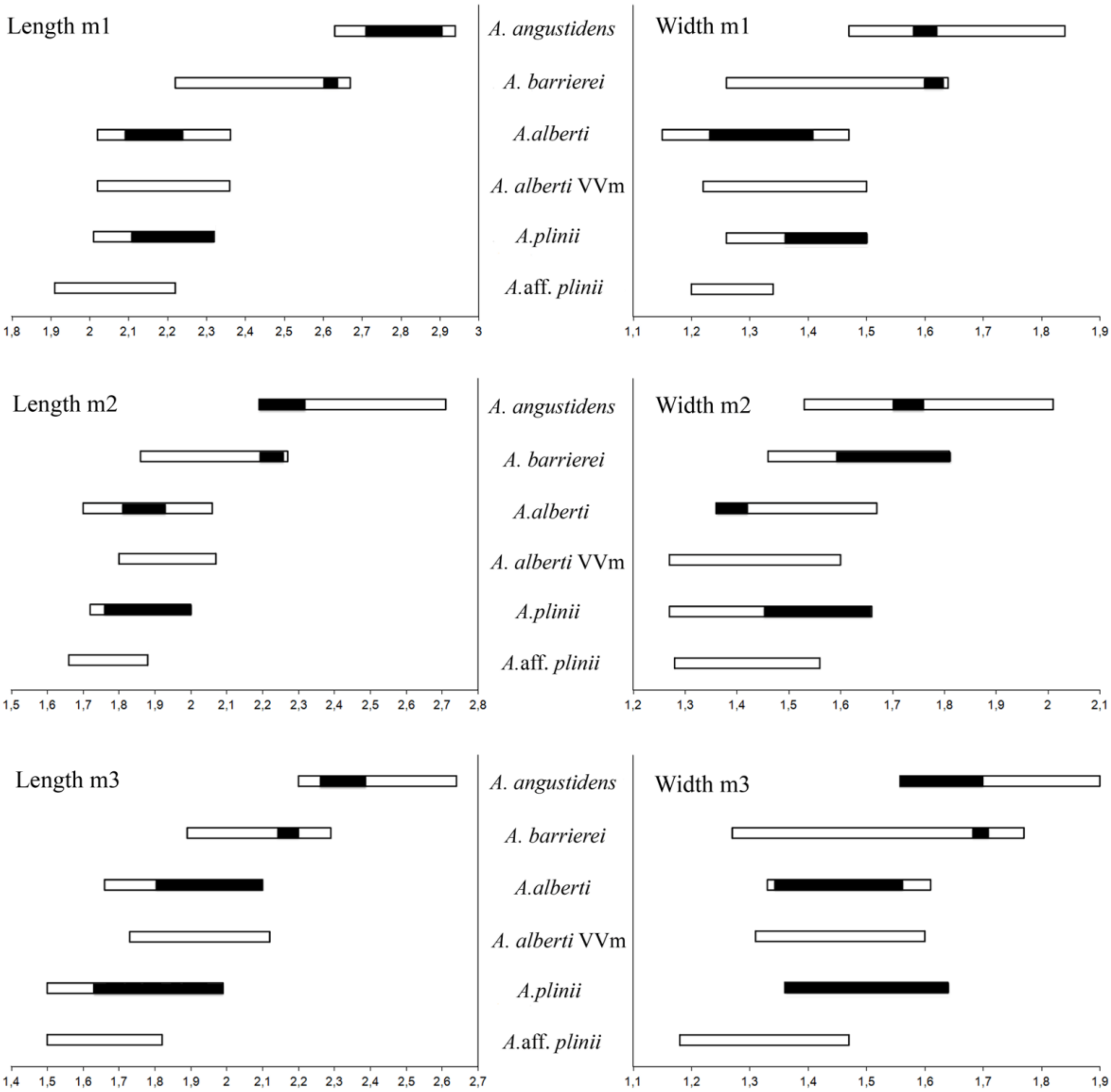


Figure XI.1. Ranges of variation of length and width of the lower molars of *A.* aff. *plinii* from Crevillente 20 and Crevillente 23 (Freudenthal *et al*. 1998), *A. plinii* from Crevillente 15 (type locality), Crevillente 5A, Crevillente 14 and Valdecebro 3 (Weerd 1976, Freudenthal *et al*. 1991, Adrover *et al*. 1993), *A. alberti* from Crevillente 6 (type locality), Negratín, Librilla 1, Librilla 2A, Librilla 2C, Purcal 23, Purcal 24A, Purcal 25, Venta del Moro, La Gloria 5 (Freudenthal *et al*. 1998, García-Alix *et al.* 2008a and 2008b, Minwer-Barakat *et al.* 2009a), *A. barrierei* from Chabrier (type locality), Alcoy, Alcoy 4B, Botardo, La Gloria 4, Gorafe 4, Fuente del Viso, Yeguas, Caravaca, Purcal 4, Loma del Castillo 1, La Tour, La Bullana 2B and La Bullana 3 (Opdyke *et al.* 1997, Freudenthal *et al.* 1998, García-Alix *et al.* 2008a and 2008b, Ruiz-Sánchez *et al.* 2014), *A. angustidens* from Serrat d'en Vacquer (type locality), Mont-Hélène, Sète, Le Soler, Villeneuve de la Raho, Portla-Nouvelle, Gorafe 3 and Gorafe 5 (Freudenthal *et al.* 1998) and *A. alberti* from Venta del Moro (VVm, this chapter). The dark boxes represent the range at the type locality.

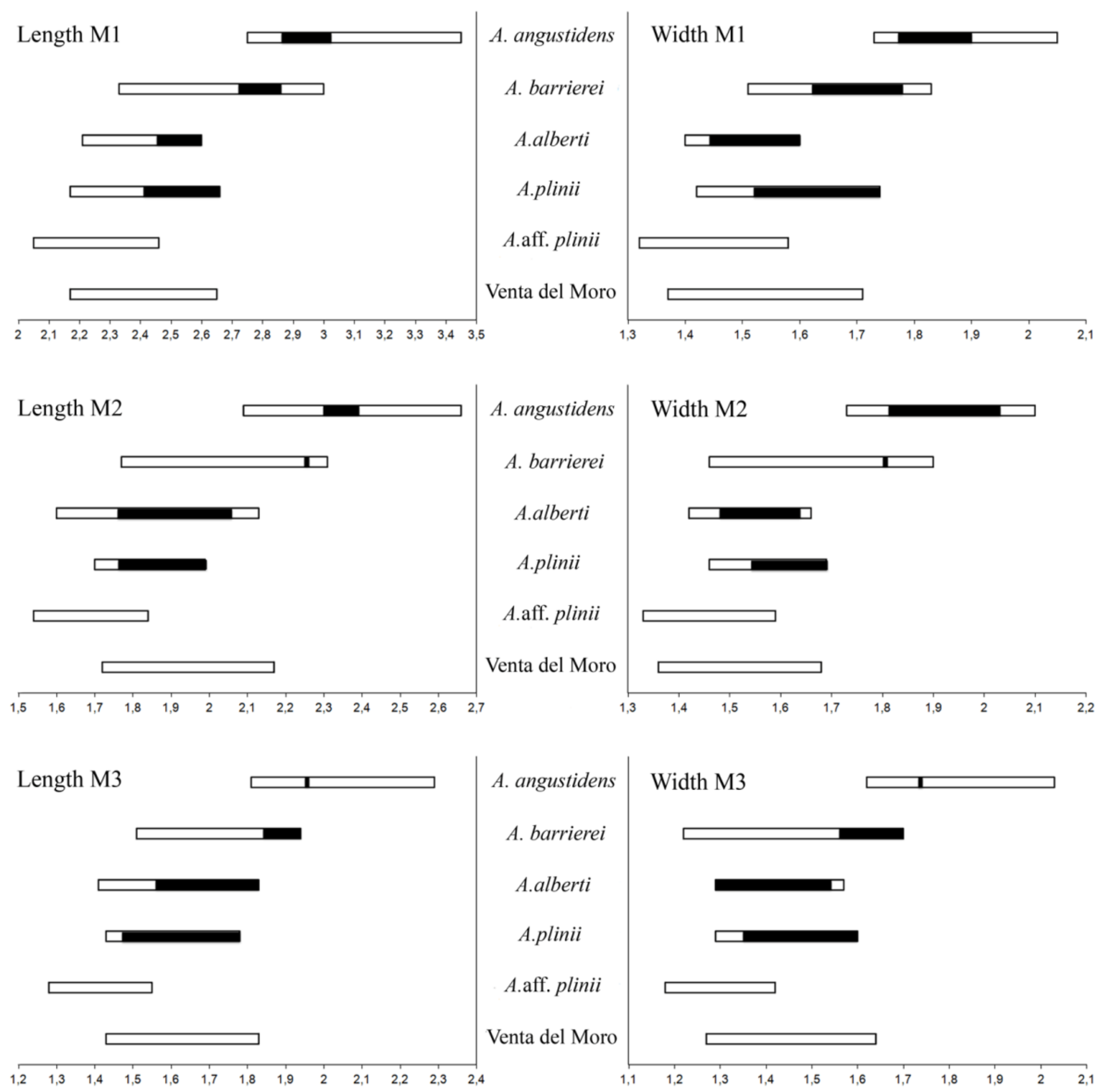


Figure XI.2 .Ranges of variation of length and width of the upper molars of *A.* aff. *plinii* from Crevillente 20 and Crevillente 23 (Freudenthal *et al.* 1998), *A. plinii* from Crevillente 15 (type locality), Crevillente 5A, Crevillente 14 and Valdecebro 3 (Weerd 1976, Freudenthal *et al.* 1991, Adrover *et al*. 1993), *A. alberti* from Crevillente 6 (type locality), Negratín, Librilla 1, Librilla 2A, Librilla 2C, Purcal 23, Purcal 24A, Purcal 25, Venta del Moro (Freudenthal *et al.* 1998, García-Alix *et al.* 2008a and 2008b, Minwer-Barakat *et al.* 2009a) and La Gloria 5 (Freudenthal *et al.* 1998), *A. barrierei* from Chabrier (type locality), Alcoy 1, Alcoy 4B, Botardo, La Gloria 4, Gorafe 4, Fuente del Viso, Yeguas, Caravaca, Purcal 4, Loma del Castillo 1, La Tour, La Bullana 2B and La Bullana 3 (Opdyke *et al.* 1997, Freudenthal *et al*. 1998, García-Alix *et al*. 2008a and 2008b, this chapter), *A. angustidens* from Serrat d'en Vacquer (type locality), Mont-Hélène, Sète, Le Soler, Villeneuve de la Raho, Portla-Nouvelle, Gorafe 3 and Gorafe 5 (Freudenthal *et al*. 1998) and *A. alberti* from Venta del Moro (VVm, this chapter). The dark boxes represent the range from the type locality.

Localities: VVm-A, VVm-Ac, VVm-AB, VVm-B, VVm-BC, VVm-C, and VVm-D.

Material: **47 m1** (VVmA-147 to VVmA-161, VVmA-163 to VVmA-172, VVmA-191 to VVmA-193, VVmAB-1, VVmAB-9, VVmA-10, VVmB- 74 to VVmB-76, VVmB-523, VVmBC-7, VVmBC-15, VVmBC-18, VVmBC-20, VVmBC-25, VVmBC-30, VVmC-29 to VVmC-33, VVmAc-13), **71 m2** (VVmA-45 to VVmA-55, VVmA-173 to VVmA-190, VVmA-194, VVmA-195, VVmAB-2, VVmAB-3, VVmAB-6, VVmAB-8, VVmB-2 to VVmB-15, VVmBC-17, VVmBC- 19, VVmBC-21, VVmBC-26 to VVmBC-28, VVmBC-31, VVmC-2 to VVmC-5, VVmC-19, VVmC-21, VVmC-28, VVmC-34, VVmC-35, VVmD-9, VVmD-11, VVmD-14, VVmD-15, VVmAc-2, VVmAc-3), **53 m3** (VVmA-56 to VVmA-73, VVmA-196, VVmA-197, VVmAB-4, VVmAB-5, VVmAB-11, VVmB-16 to VVmB-21, VVmB-23 to VVmB- 30, VVmB-71, VVmB-77, VVmB-524, VVmBC-6, VVmBC-16, VVmBC-29, VVmC-36 to VVmC-39, VVmD-3, VVmD-4, VVmAc- 4 to VVmAc-7, VVmAc-12), **50 M1** (VVmA-74 to VVmA-100, VVmA-162, VVmA-198, VVmB-31 to VVmB-42, VVmB-525, VVmBC-8 to VVmBC-10, VVmBC-32, VVmBC-33, VVmC-7, VVmC-10, VVmAc-1), **50 M2** (VVmA-101 to VVmA-121, VVmA- 199 to VVmA-201, VVmAB-12, VVmB-43 to VVmB-58, VVmBC- 11, VVmBC-14, VVmC-9, VVmC-40, VVmC-41, VVmD-5, VVmD-6, VVmAc-8, VVmAc-9), **63 M3** (VVmA-70, VVmA-122 to VVmA- 146, VVmA-202 to VVmA-205, VVmB-22, VVmB-59 to VVmB-73, VVmB-78, VVmBC-12, VVmBC-13, VVmC-8, VVmC-12 to VVmC- 15, VVmC-42 to VVmC-44, VVmD-7, VVmD-8, VVmD-10, VVmAc- 10, VVmAc-11, VVmAc-14, VVmAc-18).

Measurements: see Table XI.1.

Description:

m1: Crest-like anteroconid in 16 out of 34 specimens, with a slight subdivision in 17 out of 34 (Figs. XI.3, 1 and XI.3, 3) and trifid in 1. The anterolophulids arise from a prelophid in 18 out of 39 specimens (Fig. XI.3, 3), they are parallel without prelophid in 7 cases (Fig. XI.3, 2), forked with a branch to each one of the anteroconid in 7 (Fig. XI.3, 1), and simple in 7 (central: 2, lingually-displaced: 2 or labially-displaced: 3). Metalophulid strongly directed forwards. Mesolophid absent. Two roots.

m2: Anterosinusid absent. Metalophulid short and strongly directed forwards, forming the anterior part of the tooth. Labial anterolophulid reaching the base of the protoconid, enclosing a deep protosinusid. In one specimen this crest continues backwards bordering the protoconid. The mesosinusid and sinusid are closed by a cingulum ridge. Mesolophid absent in 39 out of 64 specimens (Fig. XI.3, 6), a trace of a mesolophid is present in 20 (Fig. XI.3, 4) and a short one in 5 (Fig. XI.3, 5). Posterolophid very low, connected basally with the posterolingual side of the entoconid, enclosing an L-shaped posterosinusid. Two roots.

m3: Shape subrectangular (1 out of 42 specimens, 2.38 %), slightly triangular (34 specimens, 80.95 %), moderately triangular (5 specimens, 11.90 %, Figs. XI.3, 7 and XI.3, 8) or very triangular (2 teeth, 4.76 %, Fig. XI.3, 9, see section XI.4.2.2). Anterosinusid absent. Metalophulid short and strongly directed forwards. The labial anterolophulid reaches the base of the protoconid. In two specimens this crest continues backwards bordering the protoconid. The mesosinusid and sinusid are closed by a cingulum ridge. The mesolophid is absent in 10 out of 47 molars, there is a trace of a crest in 21 (Fig. XI.3, 7), a short crest in 8 (Fig. XI.3, 9) and a long one in 8 (Fig. XI.3, 8). In one of the latter specimens the mesolophid connects basally with the entoconid, but continues towards the cingulum ridge of the mesosinusid. There are two roots.

M1: Cingulum ridge on the base of the anterocone absent (32 specimens) or weak (5). The anterolophule may be simple (2) (Fig. XI.3, 10), simple with a free labial spur not reaching the anterocone (1), forked (23) (Fig. XI.3, 12) or double and arising from a hint of preloph (10) or from a very short preloph (4) (Fig. XI.3, 11). The anterior protolophule is absent in 17 out of 41 specimens (Fig. XI.3, 12); it is a spur in 3 (Fig. XI.3, 10), a low crest in 8, and a well-developed crest in 13 (Fig. XI.3, 11). Mesoloph and ectomesoloph absent. The anterior metalophule is always present. The posterior metalophule is present in 7 out of 41 molars (Fig. XI.3, 11). In 11 specimens the posteroloph is curved and elongated, separated from the metacone by the transversal posterior part of the L-shaped posterosinus (Fig. XI.3, 10). In other 11 molars the transversal posterior side of the posterosinus is shorter (Fig. XI.3, 12), but the metaconid is still separated from the posterior wall. In 19 specimens, the posterior part of the metacone forms the posterior part of the tooth, while in 22 the posterior part is formed by the posteroloph. Four roots.

M2: The lingual anteroloph is very small in 3 specimens, enclosing a reduced and shallow protosinus, and of medium length or long in the rest, enclosing a protosinus that is highly variable in size and depth. The protocone is not separated from the lingual border. The labial anteroloph is long, enclosing the anterosinus. One specimen (Fig. XI.3, 14) has a short preloph, from which two very short anterolophules arise, reaching the anterolophs. Anterior protolophule well-developed. Mesoloph and ectomesoloph absent. The sinus and mesosinus are closed by a low cingulum ridge. The anterior branch of the metalophule is always present. This crest may be straight (17 specimens, Fig. XI.3, 14), slightly curved, with a hint of a spur (25 specimens, Fig. XI.3, 13, 15 and 16), have a short spur (5 specimens) or even a long crest that connects basally to the border of the molar (1 specimen). In one specimen this branch is transversal instead of oblique, and contacts the metacone anterolingually, resembling a mesoloph. The posterior metalophule is complete (16) (Fig. XI.3, 16), reduced to a spur (4), or absent (22). The posteroloph is strongly curved and elongated, forming an L-shaped posterosinus with deep anterior and posterior parts in 29 out of 45 specimens (Figs. XI.3, 13 and 16), while the posterior part of the posterosinus is much more reduced in the rest (16) (Fig. XI.3, 15). Four roots.

M3: Lingual anteroloph well-developed in 17 out of 60 specimens (Fig. XI.3, 18), reduced in 24 (Fig. XI.3, 19) and absent in 19 (Fig. XI.3, 17). The protocone is not separated from the lingual border. The labial anteroloph is long and connected to the paracone. The anterior protolophule is high and complete (59) or low and interrupted (2). One specimen has two anterior protolophules (Fig. XI.3, 17) and another one has a small enamel button attached to the labial side of the posterior protolophule. The posterolingual corner is rounded. The posterosinus is strongly reduced. In one specimen, the posterolingual corner has the posteroloph displaced to the labial side, forming a strong sinus (Fig. XI.3, 19). Three roots.

Element	Level	Length				Width			
		n	min.	mean	max.	n	min.	mean	max.
m1	VVm-A	21	2.02	2.20	2.36	22	1.22	1.33	1.50
	VVm-AB	2	2.20	2.21	2.21	2	1.32	1.38	1.43
	VVm-B	2	2.16	2.19	2.21	2	1.29	1.31	1.33
	VVm-C	2	2.00	2.13	2.26	4	1.26	1.30	1.36
	VVm-BC	-	-	-	-	2	1.30	1.31	1.31
	VVm-Ac	-	-	-	-	1	-	1.46	-
m2	VVm-A	27	1.80	1.94	2.07	29	1.27	1.46	1.60
	VVm-AB	2	1.80	1.85	1.90	3	1.36	1.41	1.45
	VVm-B	10	1.83	1.92	2.05	11	1.31	1.48	1.59
	VVm-BC	2	1.81	1.88	1.95	5	1.39	1.46	1.54
	VVm-C	4	1.80	1.98	2.15	6	1.37	1.61	1.54
	VVm-D	2	1.81	1.84	1.87	3	1.34	1.39	1.44
	VVm-Ac	2	1.90	1.92	1.94	2	1.39	1.47	1.54
m3	VVm-A	16	1.78	1.92	2.07	16	1.34	1.46	1.57
	VVm-AB	3	1.74	1.83	2.00	2	1.34	1.39	1.45
	VVm-B	13	1.79	1.95	2.12	14	1.32	1.47	1.59
	VVm-BC	2	1.85	1.93	2.00	2	1.38	1.49	1.59
	VVm-C	3	1.88	1.92	1.94	4	1.41	1.44	1.49
	VVm-D	2	1.73	1.92	2.10	2	1.29	1.44	1.58
	VVm-Ac	3	1.80	1.88	1.99	5	1.45	1.51	1.60
M1	VVm-A	21	2.17	2.41	2.65	24	1.37	1.51	1.71
	VVm-B	7	2.18	2.33	2.46	9	1.38	1.49	1.56
	VVm-BC	2	1.97	2.1.	2.27	4	1.44	1.48	1.54
	VVm-C	1	-	2.38	-	2	1.50	1.53	1.55
M2	VVm-A	20	1.79	1.91	2.17	21	1.42	1.54	1.68
	VVm-B	11	1.72	1.90	1.97	13	1.36	1.52	1.64
	VVm-BC	1	-	1.99	-	1	-	1.56	-
	VVm-C	2	1.86	1.93	1.99	3	1.50	1.54	1.58
	VVm-Ac	2	1.73	1.92	2.10	2	1.43	1.53	1.63
M3	VVm-A	25	1.43	1.65	1.83	23	1.26	1.38	1.47
	VVm-B	12	1.49	1.64	1.79	13	1.33	1.40	1.53
	VVm-BC	2	1.44	1.61	1.78	2	1.35	1.42	1.48
	VVm-C	6	1.54	1.63	1.74	7	1.34	1.44	1.64
	VVm-D	1	-	1.60	-	3	1.37	1.44	1.56
	VVm-Ac	3	1.53	1.61	1.72	3	1.34	1.38	1.41

Table XI.1. Measurements (in millimetres) of the teeth of *A. alberti* from Venta del Moro, according to the notation of the fossiliferous levels sensu Montoya *et al*. (2006a) (Venta del Moro A: VVm-A; Venta del Moro AB: VVm-AB; Venta del Moro B: VVm-B; Venta del Moro BC: VVm-BC; Venta del Moro C: VVm-C; Venta del Moro D: VVm-D; Venta del Moro Ac: VVm-Ac).

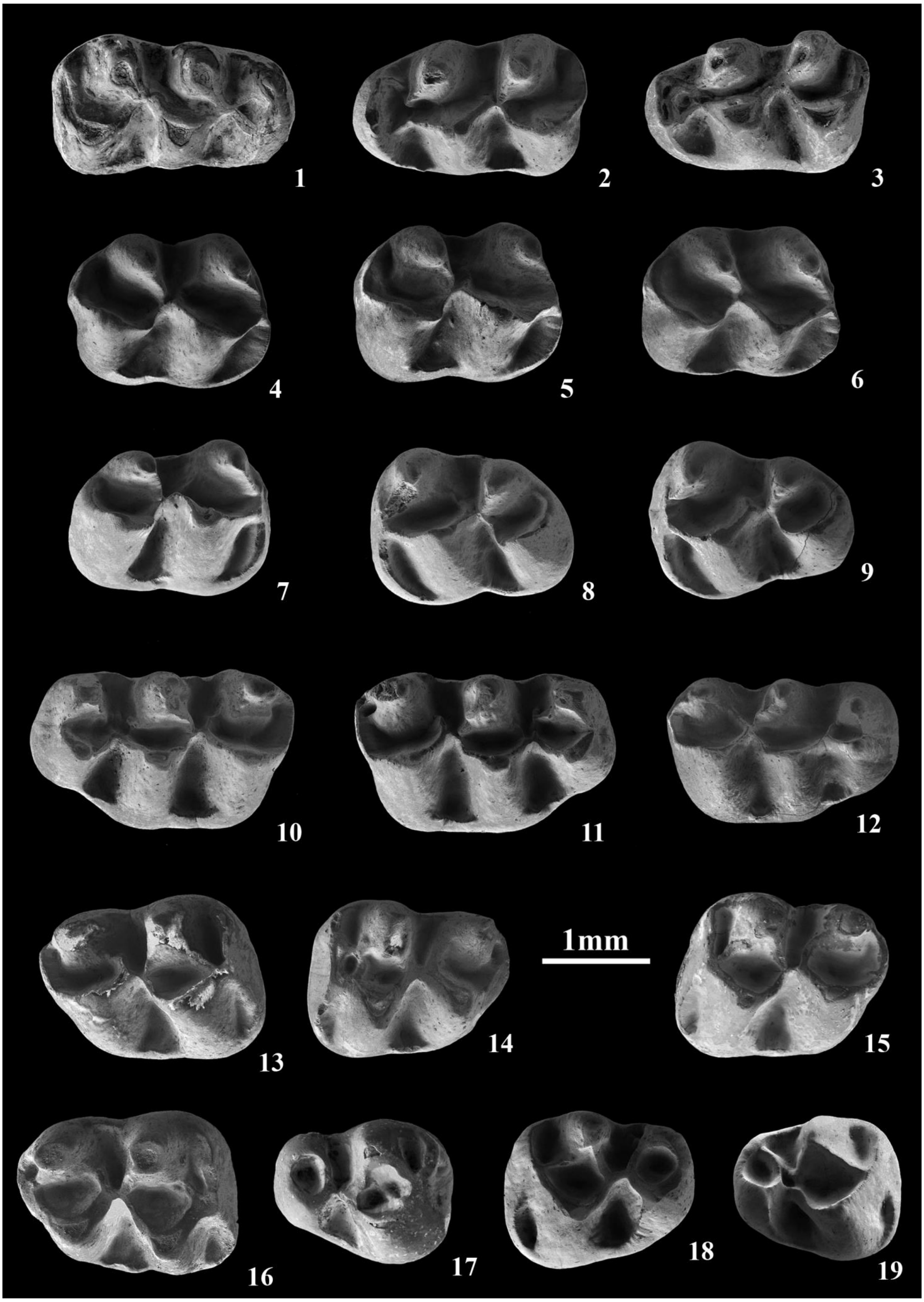


Figure XI.3. *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998 from Venta del Moro, Cabriel Basin. **1**, right m1, VVmA-161; **2**, left m1, VVmA-166; **3**, left m1, VVmA-167; **4**, right m2, VVmA-46; **5**, right m2, VVmA-187; **6**, right m2, VVmB-5; **7**, right m3, VVmA-61; **8**, left m3, VVmA-65; **9**, left m3, VVmB-25; **10**, left M1, VVmA-82; **11**, right M1, VVmA-83; **12**, right M1, VVmB-31; **13**, right M2, VVmA-108; **14**, left M2, VVmA-113; **15**, left M2, VVmBC-11; **16**, right M2, VVmAc-8; **17**, right M3, VVmA-122; **18**, left M3, VVmA-125; **19**, right M3, VVmA-137. Scale = 1 mm.

XI.4. Discussion

Traditionally, size has been the main criterion used to distinguish the species of the genus *Apocricetus* from the Late Miocene to the Early Pliocene (MN11 to MN15) comprising the lineage *Apocricetus* aff. *plinii–A. plinii–A. alberti–A. barrierei–A. angustidens* (Freudenthal *et al.* 1998). The lack of rich collections of some species of the genus prevented a proper morphological characterization (Ruiz-Sánchez *et al.* 2014). The study of the rich material of *Apocricetus* from some new localities such as LB2B and LB3 allows a more reliable differential diagnosis between the species of the genus (Ruiz-Sánchez *et al.* 2014), showing that, in fact, the quantification of these morphologies is the better way to distinguish them.

The new sampling carried out in the last two decades in the Late Miocene locality of Venta del Moro has allowed to recover one of the richest collections of the genus *Apocricetus*, representing also a great opportunity for improving the characterization and diagnosis of the species *A. alberti*, whose type locality is CR-6. *Apocricetus alberti* is restricted to the Late Turolian (Freudenthal *et al.* 1998, García-Alix *et al.* 2008b, Minwer-Barakat *et al.* 2012). This species represent an intermediate form between *A. plinii* (Early Turolian) and *A. barrierei* (Ruscinian). According to Freudenthal *et al.* (1998), *A. alberti* differs from *A. angustidens* and *A. barrierei* by its smaller size and by the presence of an anterior protolophule in M2. It differs from *A. plinii* by its hardly-split anteroconid, more enlarged m3, forked anterolophule with two complete branches in M1, and the absence of a mesoloph, converted into the anterior metalophule. Nevertheless, some of these morphological criteria are not useful to distinguish among these species (Ruiz-Sánchez *et al.* 2014). For example, several populations of *A. barrierei* and *A. angustidens* show an anterior protolophule in M2. As we will explain below, gradual morphological and biometrical changes occurred in this lineage indeed, but they must be previously quantified in each species to know the specific range of variation that will serve to distinguish the different species of the genus.

XI.4.1 Biometry

Apocricetus aff. *plinii*, from the Early Turolian of Spain, is the oldest and smallest form of *Apocricetus*. This taxon is slightly smaller than the Middle and Late Turolian representatives of the genus, *A. plinii* and *A. alberti*, which are similar in size (see Figs. XI.1 and XI.2). In the Early Ruscinian, *A. barrierei* shows a size increase with respect to the Turolian forms, which becomes more evident in the Late Ruscinian and Villanyan *A. angustidens* (Figs. XI.1 and XI.2).

Despite this tendency towards size increase through time in *Apocricetus*, the size range of any given species of the genus overlaps greatly with one or more of the precedent taxa, especially in the group *A.* aff. *plinii*-*A. plinii*-*A. alberti* (Figs. XI.1 and XI.2). The size range of the abundant sample from Venta del Moro is remarkably similar to other previously known populations of *A. alberti* (see Figs. XI.1 and XI.2). Because of the similar size of the populations of *Apocricetus* in the time span Early Turolian-Early Ruscinian and following Freudenthal *et al.* (1998) and Ruiz-Sánchez *et al.* (2014), we consider that this feature is not the best criterion to distinguish between the different forms of *Apocricetus*, with the exception of the youngest species of the genus, *A. angustidens* (Figs. XI.1 and XI.2).

XI.4.2. Morphology

XI.4.2.1. Lower molars

In general, the presence of a crest-like anteroconid and a complete prelophid in almost half of the m1 (47.06 %), and the more rectangular shape in the m3 from Venta del Moro distinguish *A. alberti* from *A.* aff. *plinii.* These morphological features, along with the absence of ectomesolophids in the lower molars, distinguish this latter species from *A. plinii* from its type locality, CR-15.

On the other hand, the presence of simple (17.95 %) or forked (with a branch to each one of the anteroconid cups) (17.95 %) anterolophulids in m1, a small mesolophid in some m2 (39.06 %), and a more triangular m3 in *A. alberti* from Venta del Moro distinguish this latter species from *A. barrierei* and *A. angustidens*.

Several characters in the lower molars of the *A.* aff. *plinii*–*A. angustidens* lineage seem to change from oldest to youngest populations. To summarize all these differences, Table XI.2 shows the variations of these characters in the lower molars of this phylogenetic lineage.

The morphology of the anterolophulids and the presence of a prelophid in m1 are clearly distinctive among the species of the genus *Apocricetus*. In the oldest populations, the anterolophulid is simple or double in *A.* aff. *plinii* from CR-23, and simple or forked in *A. plinii* from CR-15. However, in the youngest populations, *A. barrierei* and *A. angustidens*, the anterolophulids usually arise from a prelophid (Freudenthal *et al*. 1998, Ruiz-Sánchez *et al*. 2014). In *A. alberti* from Venta del Moro, all these morphologies are present, being the most common the one with an anterolophulid arising from a prelophid (Table XI.2). In the specimens studied in this chapter the anterolophulid may be simple (7 out of 39 specimens, 17.95 %), forked, with a branch to each one of the anteroconid cups (7 specimens, 17.95 %), double, arising from a prelophid (18 teeth, 46.15 %) or double and parallel (7 molars, 17.95 %). In the scarce material from Venta del Moro studied by Freudenthal *et al*. (1998), the anterolophulids are parallel, and in CR-6 they may be simple or parallel. In *A.* aff. *plinii* from CR-23, the anterolophulid may be double (2 out of 9 specimens, 22.22 %), or simple (7 out of 9 specimens, 77.77 %), and in this latter case it may be central (2) or labial (5) (Freudenthal *et al*. 1998). In *A. plinii* from CR-15 the anterolophulids may be simple and connected to the labial part of the anteroconid (7 out of 17 specimens, 41.17 %), or forked (10, 58.82 %) (Freudenthal *et al.* 1991). On the contrary, in *A. barrierei* and *A. angustidens* the anterolophulids usually arise from a prelophid (Freudenthal *et al.* 1998, Ruiz-Sánchez *et al.* 2014). The anterosinusid is absent in the m2 and m3 of the new material of *A. alberti* from Venta del Moro and in *A. barrierei*, but present in some m2 of *A.* aff. *plinii* from CR-23. A reduced anterosinusid is present in 64.71 % of the m2 (11 out of 17) and 44.44 % of the m3 (8 out of 18) of *A. plinii* from CR-15 and in some m3 of *A. angustidens* from Serrat d'en Vacquer (Freudenthal *et al.* 1991 and 1998).

In one m2 and two m3 of *A. alberti* from Venta del Moro the labial anterolophid continues bordering the protoconid instead of reaching the base of this cup. This morphology has been observed in 2 out of 18 m2 (11.11 %) and 5 out of 19 m3 (26.31 %) of *A. plinii* from CR-15 (Freudenthal *et al*. 1991).

This character is not present in *A. barrierei* from LB2B and LB3, and has not been described in other populations of the genus. *A. alberti* from Venta del Moro has a short mesolophid in 5 out of 64 m2 (7.81 %), and a hint of a mesolophid is distinct in 20 (31.25 %). Freudenthal *et al.* (1998) described an m2 of *A. alberti* with a short mesolophid in CR-6 and Venta del Moro, and another two specimens with a long mesolophid, reaching the border of the molar, in Venta del Moro and Librilla. However, these authors consider that these latter m2 may belong to another species, since such long mesolophids have not been described in other populations of *A. alberti*. The mesolophid may be absent (17), short (3), of medium length (3), long (2), or reaching the molar border (1) in *A.* aff. *plinii* from CR-23. This crest is absent in *A. plinii*, *A. barrierei* and *A. angustidens*.

There is no ectomesolophid in the m2 of *A.* aff. *plinii*, *A. alberti*, *A. barrierei* and *A. angustidens*, but 10 out of 17 m2 of *A. plinii* from CR- 15 have a weak crest, which is well developed in another specimen (Freudenthal *et al.* 1991).

The frequency of the mesolophid in m3 decreases from the oldest to the youngest populations of *Apocricetus* (see Table XI.2). In the material studied in this chapter, the mesolophid is present in 37 out of 47 m3 (78.72 %), being long in 8 specimens. In 9 out of 35 m3 of *A.* aff. *plinii* from CR-23 (25.71 %) this crest is long, reaching in one of them the border of the molar, while in *A. plinii* from CR-15 it is short or of medium length. The mesolophid is very heterogeneous in the populations of *A. barrierei*. In LB2B this crest reaches the metaconid, and the only m3 from Chabrier, type locality of this species, also shows this morphology. One specimen from La Gloria 4 (Adrover *et al.* 1993) has a long mesolophid, which is absent or short in Gorafe 4, short and reaching the base of the metaconid in Alcoy 4B, of medium length in Loma del Castillo 1, absent or present in Fuente del Viso and absent in Caravaca (Freudenthal et *al.* 1998). In *A. angustidens,* the mesolophid ranges from absent to long in the population from Serrat d'en Vacquer (type locality), and this crest is absent in 16, short in 4 and long, thin and low in 10 m3 from Mont-Hélène (Freudenthal *et al.* 1998).

Species	Locality	m1		m2	m3
		Anteroconid	Anterolophulid	Mesolophid	Mesolophid
A. aff. *plinii*	CR-23	2-3 lobes	simple: 7/9 (77.77 %) double: 2/9 (22.22 %)	Pr: 9/26 (34.61 %)	Pr: 32/35 (91.43 %)
A. plinii	CR-15	2 lobes	simple: 7/17 (41.17 %) forked: 10/17 (58.82 %)	Abs	Pr: 19/22 (86.36 %)
A. alberti	CR-6	crest (1) or 2 lobes	simple or double	Pr: 1/?	Pr: 6/12 (50 %)
A. alberti	VVm	2 lobes: 17/34 (50 %) 3 lobes: 1/34 (2.94 %) crest-like: 16/34 (47.06 %)	simple: 7/39 (17.95 %) double: 7/39 (17.95 %) forked: 7/39 (17.95 %) prelophid: 18/39 (46.15 %)	Pr: 25/64 (39.06 %)	Pr: 37/47 (78.72 %)
A. barrierei	Car	2 weak lobes: 2/3 (66.66 %) crest-like: 1/3 (33.33 %)	prelophid: 100 %	Pr: 2/3 (66.66 %)	Abs
A. barrierei	LB2B	2 weak lobes: 2/12 (16.66 %) crest-like: 10/12 (83.33 %)	prelophid: 12/12 (100 %)	Pr: 0/16 (0 %)	Pr: 6/13 (46.15 %)
A. barrierei	LB3	-	-	Pr: 0/2 (0 %)	Pr: 0/3 (0 %)
A. angustidens	MH	crest like, 2 weak lobes or trifid (1)	prelophid: 100 %	Pr: 0/34 (0 %)	Pr: 14/30 (46.66 %)

Table XI.2. Variation of several characters in the lower molars of *Apocricetus*. Abbreviations: Abs, absent; Car, Caravaca; CR-, Crevillente; LB2B, La Bullana 2B; LB3, La Bullana 3; MH, Mont-Hélène; Pr, present, VVm, Venta del Moro, collection housed at the University of Valencia. After Freudenthal *et al*. (1991 and 1998), Ruiz-Sánchez *et al*. (2014) and this work.

XI.4.2.2. Shape of the m3

The shape of m3 has been regarded as an important character to consider, since a change in the shape of this molar occurs in the lineage of *Apocricetus* (Freudenthal *et al.* 1998, Ruiz-Sánchez *et al.* 2014). Freudenthal *et al.* (1998) noted that in *A. angustidens* from Mont-Hélène, the m2 and m3 are very similar in size and shape, to the extent that it is very difficult to distinguish between them, while in the oldest forms of *Apocricetus*, like *A.* aff. *plinii* and *A. plinii*, the m3 has a posterior side clearly narrower than the anterior one, as other authors have also noted (Ruiz-Sánchez *et al.* 2014).

Following Ruiz-Sánchez *et al.* (2014, Fig. 6), Fig. XI.4 depicts the relative length of m2 with respect to m3 (L m2/L m3). Ratios of m2 to m3 lower than 1 indicate an elongated m3, longer than the m2, while ratios higher than 1 correspond to m2 longer than m3. This ratio decreases from *A.* aff. *plinii* from CR-23 to *A. plinii* from CR-15*, A. alberti* from Venta del Moro and *A. barrierei* from LB2B. However, the m3 of the population of *A. alberti* from CR-6, its type locality, are even more elongated than those of *A. barrierei*. This may be because of the marked discrepancy between the number of m2 (4) and m3 (14) in this locality, with some m3 of great size. This is especially evident for the maximum L m2/maximum L m3, which is far below the value of *A. barrierei* (see Fig. IX.4). On the contrary, *A. angustidens* from Mont-Hélène has an L m2/L m3 ratio similar to that of *A. alberti* from Venta del Moro.

Although the latter calculated ratios may be a first attempt to estimate the shape of the m3, the data shown in Fig. XI.4 are not enough to estimate this feature correctly.

In order to carry out a comparison between the shapes of the m3 of the different species of *Apocricetus,* we propose the use of the ratio W_ant/W_post. Following the measurement method proposed by Daams and Freudenthal (1988) for the cricetids, the anterior width (W_ant) corresponds to the maximum width of the tooth, while the posterior width (W_post), as seen in Fig. XI.5, is measured from the cingulum ridge closing the sinusid to the lingual side of the entoconid.

We consider this ratio a better indicator of the shape of the m3, since higher values indicate a narrower posterior side and therefore a more triangular shape. The W_ant, W_post and the resultant ratios (W_ant/W_post) of the populations of *Apocricetus* measured in this work are summarized in Table XI.4.

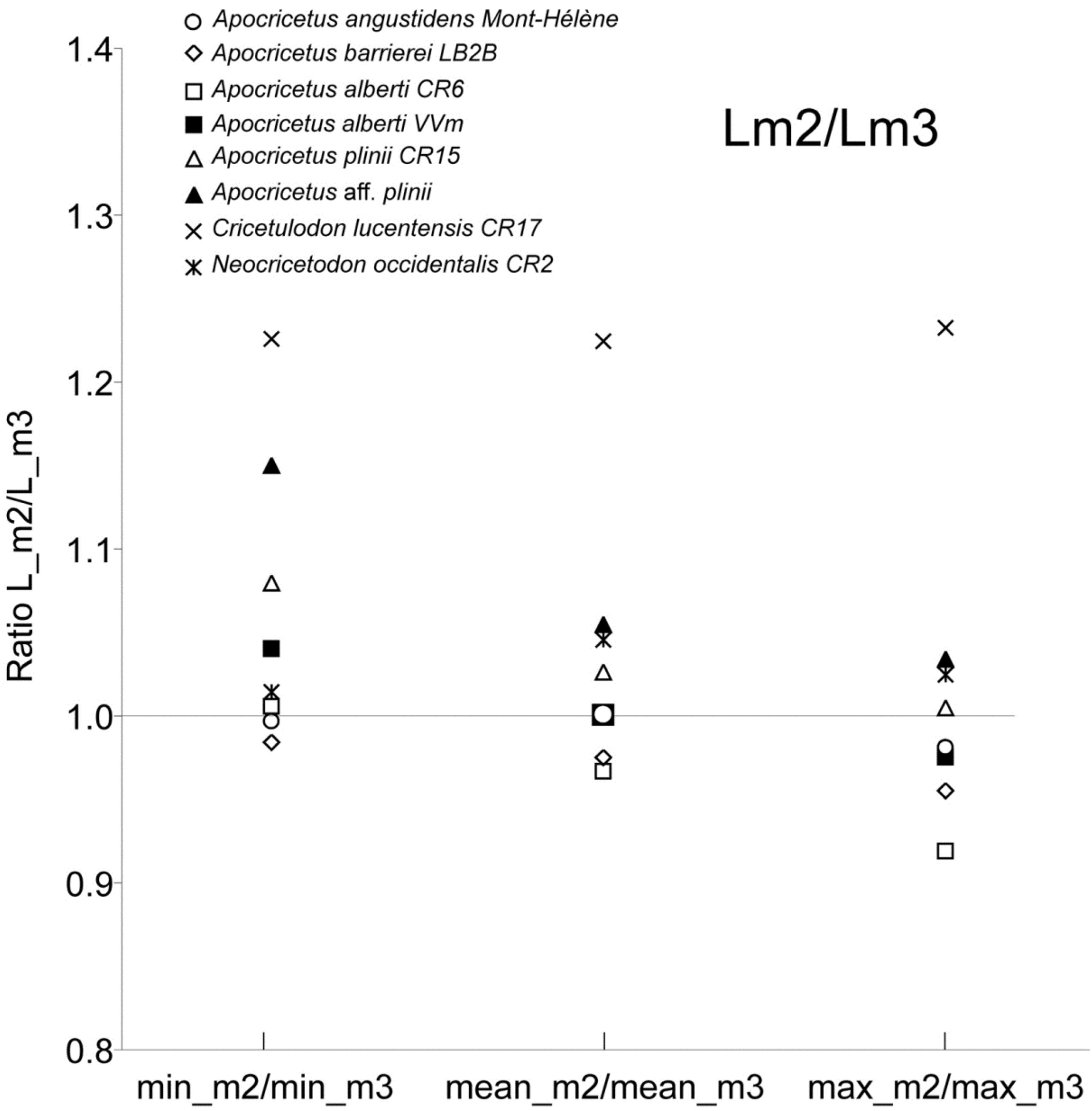


Figure XI.4. Ranges of variation of the ratio Lm2/Lm3 of *Neocricetodon occidentalis* Aguilar, 1982 from Crevillente 2 (CR2), *Cricetulodon lucentensis* Freudenthal *et al*. (1991) from Crevillente 17 (CR17), *A*. aff. *plinii* from CR-20 and CR-23, *Apocricetus plinii* from Crevillente 15 (CR15), *A. alberti* from Crevillente 6 (CR6) and Venta del Moro (VVm), *A. barrierei* from La Bullana 2B (LB2B), and *A. angustidens* from Mont-Hélène. The values of min_m2/min_m3 correspond to (min Lm2)/(min Lm3), mean_m2/mean_m3 to (mean Lm2)/(mean Lm3) and max_m2/max_m3 to (max Lm2)/(max Lm3). The values under 1.0 correspond to: length of m3 larger than length of m2, and above 1.0: length of m2 larger than length of m3 (Modified after Ruiz-Sánchez *et al*. 2014).

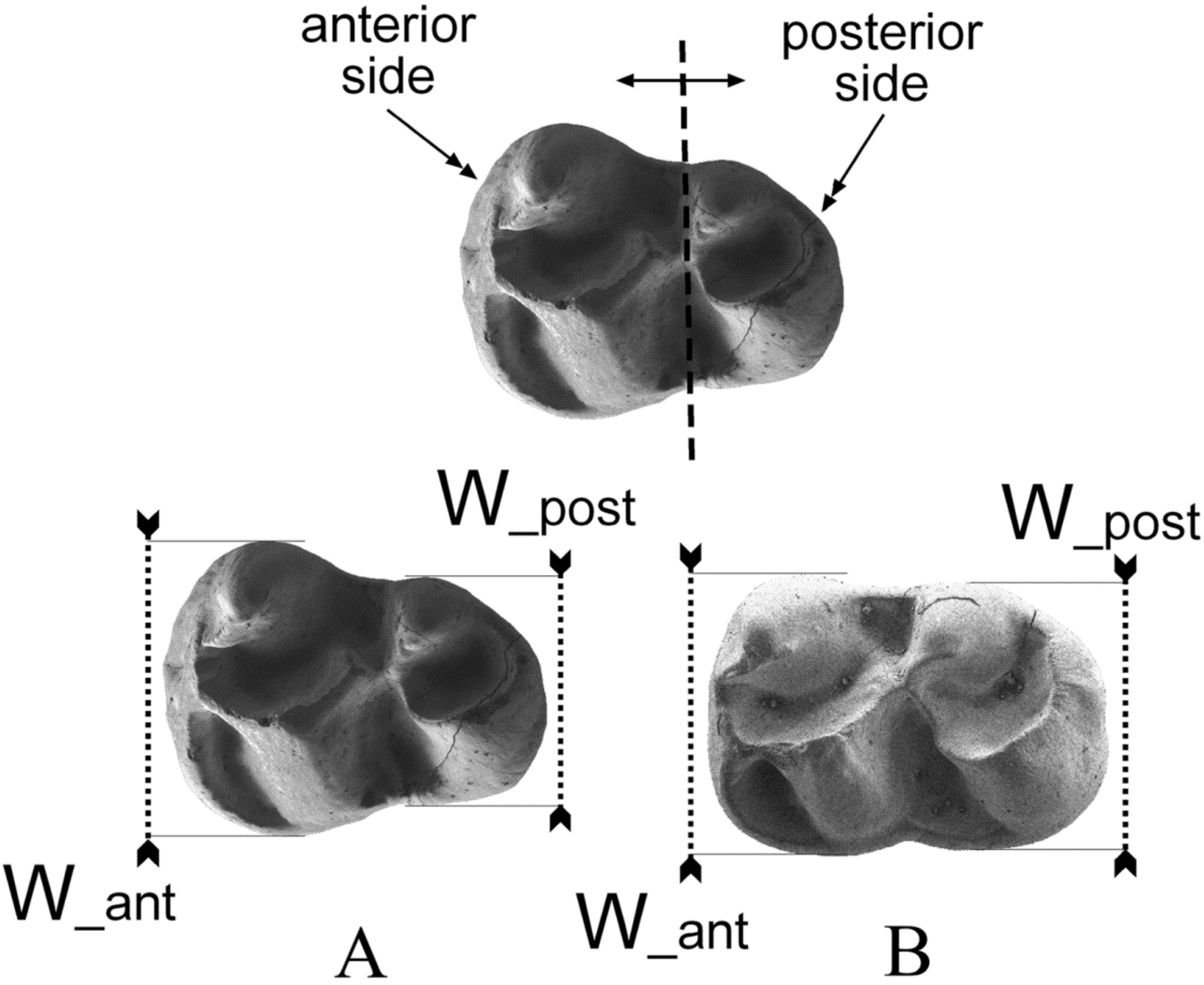


Figure XI.5. Method for taking measurements of the anterior (W_ant) and posterior (W_post) width of the m3 of *Apocricetus*. (A) VVmA-65 (*A. alberti*) and (B) LB2B-154 (*A. barrierei*).

We have defined five categories of W_ant/W_post ratio, as shown in Table XI.3 and Fig. XI.6. Category 1 comprises the values ranging from 1.35 to 1.31: these molars are extremely triangular and only 3 specimens of *A.* aff. *plinii* fall within this range (Table XI.3, Fig. XI.7). Category 2 comprises the values from 1.30 to 1.26 (Fig. XI.6): these m3 are very triangular, and only some specimens of *A.* aff. *plinii* and two molars of *A. alberti* fall within this category. Category 3 comprises the values from 1.25 to 1.21: these molars are moderately triangular (Fig. XI.6), and correspond to some specimens of the Turolian species of the genus, *A.* aff. *plinii*, *A. plinii* and *A. alberti*. The category 4 comprises the specimens with a ratio ranging from 1.20 to 1.11: it includes the m3 which are slightly subtriangular (Fig. XI.6). Most of the specimens studied here belong to this category, and all the *Apocricetus* species are represented within it (Table XI.3, Fig. XI.6), but not in the same proportion. Finally, the specimens with ratios from 1.10 to 1.0 belong to the category 5: These molars are subrectangular with similar W_ant and W_post (see Figs. XI.5 and XI.6), and belong to the species *A. angustidens* and *A. barrierei* and one specimen of *A. alberti* from Venta del Moro, which lies in the upper limit of this category, 1.10 (Tables XI.3 and XI.4, Fig. XI.6).

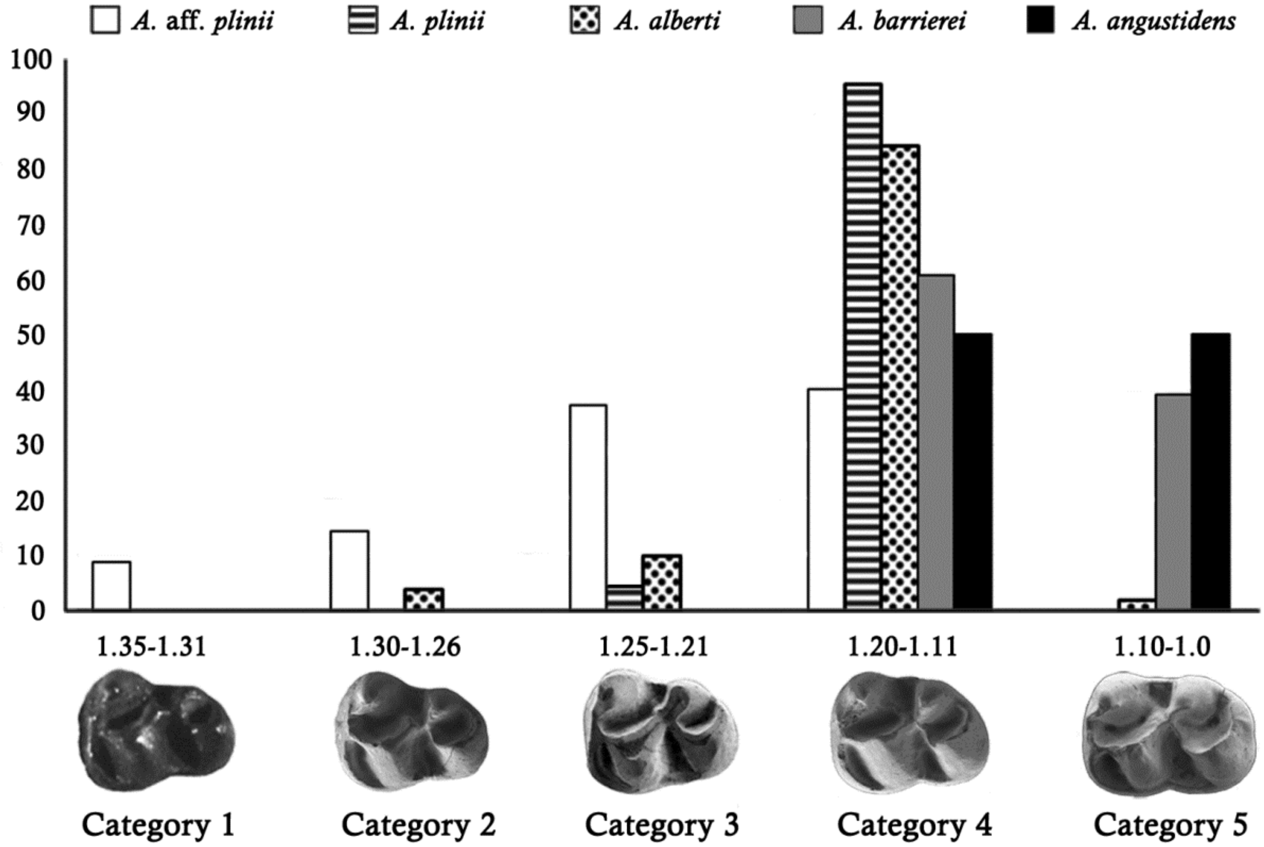


Figure XI.6. Diagram bar with percentage of representation by categories for the W_ant/W_post ratio of m3. Category 1, range 1.35–1.31 (specimen figured RGM 404855, W_ant/ W_post = 1.34), category 2, range 1.30–1.26 (specimen figured VVmB-25, W_ant/W_post = 1.28), category 3, range 1.25–1.21 (specimen figured VVmA-67, W_ant/W_post = 1.23), category 4, range 1.20–1.11 (specimen figured VVmA-65, W_ant/W_post = 1.16) and category 5, range 1.10–1.00 (specimen figured LB2B-154, W_ant/W_post = 1.06).

		Category 1	Category 2	Category 3	Category 4	Category 5
species	n	1.35-1.31	1.30-1.26	1.25-1.21	1.20-1.11	1.10-1.0
A. aff. *plinii*	35	8.6	14.3	37.1	40	0
A. plinii	23	0	0	4.3	95.7	0
A. alberti	51	0	3.9	9.8	84.3	2
A. barrierei	23	0	0	0	60.9	39.1
A. angustidens	6	0	0	0	50	50

Table XI.3. Percentage of specimens by categories defined for the W_ant/W_post ratio of m3. Category 1, range 1.35–1.31 (extremely triangular shape), category 2, range 1.30–1.26 (very triangular shape), category 3, range 1.25–1.21 (moderately triangular shape), category 4, range 1.20–1.11 (slightly triangular shape) and category 5, range 1.10–1.00 (subrectangular shape). Material studied in the making of this table: *A.* aff. *plinii* from Crevillente 20 and 23; *A. plinii* from Crevillente 5A and 15; *A. alberti* from Venta del Moro (Granada and Valencia collections), Librilla, PUR-25 and PUR-25A; *A. barrierei* from La Bullana 2B and 3, Gorafe 4, Yeguas, PUR-4, Chabrier and Caravaca; *A. angustidens* from Mont Hélène, Villeneuve, Soler and two specimens with the label Gorafe 4/5 from the Granada collection.

		Want				Wpost				Want/Wpost			
species	Locality	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.
A. aff. *plinii*	CR-20	2	1.09	1.11	1.13	2	0.94	0.95	0.96	2	1.15	1.16	1.17
A. aff. *plinii*	CR-23	33	0.93	1.10	1.37	33	0.74	0.90	1.19	33	1.12	1.22	1.34
A. plinii	CR-5A	5	1.34	1.42	1.49	5	1.21	1.25	1.32	5	1.10	1.14	1.17
A. plinii	CR-15	18	1.39	1.50	1.63	18	1.13	1.29	1.39	18	1.12	1.16	1.23
A. alberti	PUR-25A	2	-	1.63	-	2	1.40	1.41	1.41	2	1.15	1.16	1.16
A. alberti	PUR-25	2	1.55	1.63	1.71	2	1.42	1.43	1.44	2	1.10	1.14	1.19
A. alberti	LIB	1	-	1.55	-	1	-	1.33	-	1	-	1.16	-
A. alberti	VM*	52	1.29	1.46	1.60	47	1.08	1.25	1.44	46	1.10	1.17	1.28
A. barrierei	CHA	1	-	1.70	-	1	-	1.49	-	1	-	1.14	-
A. barrierei	PUR-4	4	1.48	1.63	1.86	4	1.27	1.44	1.63	4	1.10	1.13	1.16
A. barrierei	LB2B	8	1.47	1.57	1.66	9	1.36	1.43	1.57	8	1.06	1.11	1.15
A. barrierei	LB3	1	-	1.59	-	1	-	1.42	-	1	-	1.20	-
A. barrierei	YEG	1	-	1.62	-	1	-	1.43	-	1	-	1.13	-
A. barrierei	CAR	3	1.56	1.60	1.63	3	1.32	1.45	1.53	3	1.06	1.11	1.18
A. barrierei	GOR-4	4	1.56	1.63	1.70	4	1.39	1.46	1.57	4	1.08	1.12	1.15
A. angustidens	GOR-4/5	2	1.70	1.70	1.71	2	1.47	1.48	1.49	2	1.14	1.15	1.16
A. angustidens	VIL	1	-	1.96	-	1	-	1.78	-	1	-	1.10	-
A. angustidens	SOL	1	-	1.63	-	1	-	1.44	-	1	-	1.14	-
A. angustidens	MH	2	1.72	1.78	1.83	2	1.68	1.69	1.70	2	1.01	1.05	1.09

Table XI.4. Measurements in millimetres of the anterior width (W_ant), posterior width (W_post) and anterior width/posterior width ratio (W_ant/W_post) of m3 of *Apocricetus* aff. *plinii* from Crevillente-20 and Crevillente-23, *A. plinii* from Crevillente-5A and Crevillente-15, *A. alberti* from Purcal-25A, Purcal-25, Librilla and Venta del Moro, *A. barrierei* from Chabrier, Purcal-4, La Bullana-2B, La Bullana-3, Yeguas, Caravaca and Gorafe-4, and *A. angustidens* from Gorafe-4/5, Villeneuve, Solera and Mont-Hélène. Abbreviations: CR-, Crevillente; PUR-, Purcal; LIB, Librilla; VM, Venta del Moro; CHA, Chabrier; LB-, La Bullana; YEG-, Yeguas; CAR-, Caravaca; GOR, Gorafe; VIL, Villeneuve; SOL, Solera; MH, Mont- Hélène. *The measurements of five specimens of *A. alberti* from Venta del Moro housed at the University of Granada were added to the sample housed at the University of Valencia.

The change in shape from the oldest to the youngest species of the genus *Apocricetus* is shown in Figs. XI.6 and XI.7. Fig. XI.6 represents the percentages of m3 of each species of the genus within each of the categories previously described, as given in Table XI.3. Fig. XI.7 includes the ranges of the W_ant/W_post ratio of the *Apocricetus* from the localities studied in this chapter, as well as the median in the populations where more than two specimens have been measured. It is clear that the m3 of *A.* aff. *plinii* are more triangular than those of the other species of the genus, while those of *A. plinii* and *A. alberti* are similar in shape, having W_post closer to W_ant. The great range of variability for W_ant/W_post shown by the population of *A.* aff. *plinii* from CR-23 in Fig. XI.7, which spans four different categories of shape in Fig. XI.6, may be due to the presence of two species in that locality (Freudenthal *et al*. 1998). The range of *A. alberti* from Venta del Moro also covers four categories of shape, but the values are less dispersed, with a single specimen in the categories 2 and 5, while the great majority of the m3 belong to the category 4 (Fig. XI.6). Finally, the molars of the younger species of *Apocricetus*, *A. barrierei* and *A. angustidens*, are subrectangular or just slightly triangular, with values of W_post close to W_ant.

XI.4.2.3. Upper molars

The lack of a cingulum ridge and a preloph in M1, the simple anterolophule in M1, the presence of mesolophs in M1 and M2 and the better-developed posterior metalophule in the upper molars of *A.* aff. *plinii* from CR-23 and *A. plinii* from CR-15, distinguish these latter species from *A. alberti* from Venta del Moro.

The upper molars of *A. alberti*, *A. barrierei*, and *A. angustidens* are morphologically quite similar. Nevertheless, some characters have a different degree of development that allows distinguishing these three species.

The development of the preloph in M1 distinguishes *A. barrierei* and *A. alberti*. The presence of a well-developed cingulum ridge and the absence of a posterior metalophule in M1 and M2 of *A. angustidens* differ from *A. alberti*.

According to Freudenthal *et al*. (1998) and Ruiz-Sánchez *et al*. (2014), the cingulum ridge of M1 is absent in all samples of *A.* aff. *plinii*, *A. plinii* and *A. alberti*, absent or weak (16.66 %) in the populations of *A. barrierei*, and well developed in the populations of *A. angustidens*. In the new material of *A. alberti* from the locality Venta del Moro, a weak cingulum can also be observed in 5 out of 37 specimens (Table XI.5).

The anterolophule is simple in 2 out of 40 M1 from Venta del Moro (5 %), simple with a free labial spur in 1 (2.50 %), forked in 23 (57.50 %), double and arising from a hint of a preloph in 10 (25 %), or with a very short but clear preloph in 4 (10 %). The anterolophule may be simple (10), forked (2) or bear a free labial spur (7) in *A.* aff. *plinii* from CR-23, and simple (2), forked (8) or forked with a free labial branch (6) in *A. plinii* (Freudenthal *et al*. 1991 and 1998). In neither of these two latter species the anterolophules arise from a transversal crest (preloph). In *A. barrierei* from LB2B there is a distinct preloph, longer than in the specimens from Venta del Moro. This morphology has not been described in the populations of *A. angustidens*.

The anterior protolophule is present in approximately 50–60 % of the M1 of the populations of *A.* aff. *plinii*, *A. plinii* and *A. alberti* (see Table XI.5). This crest is less developed in the assemblages of *A. barrierei* and especially in *A. angustidens* (Ruiz-Sánchez *et al*. 2014, Table XI.5).

On the other hand, Freudenthal *et al.* (1998) consider the presence a posterior metalophule in M1 diagnostic. However, Ruiz- Sánchez *et al*. (2014) do not regard the presence of this crest a good criterion to distinguish between species in the lineage *A. alberti*–*A. barrierei*–*A. angustidens*. The rich assemblage of Venta del Moro has allowed to assess the frequency of this character, absent in all populations of *A. angustidens* and *A. barrierei* except for one specimen of this latter species from Caravaca (Freudenthal *et al.* 1998). So, extending this analysis to all species of the genus, it is shown that the posterior metalophule is present in 5 out of 11 (45.45 %) M1 of *A.* aff. *plinii* from CR-23, 3 out of 13 (23.08 %) of *A. plinii* from CR-15, 7 out of 41 (17.07 %) of the new material from Venta del Moro and absent in *A. barrierei* and *A.*

angustidens. Therefore, we consider that the frequency of the posterior metalophule decreases from the oldest to the youngest populations of *Apocricetus*, and consequently it is a useful parameter to distinguish between species of the genus *Apocricetus*.

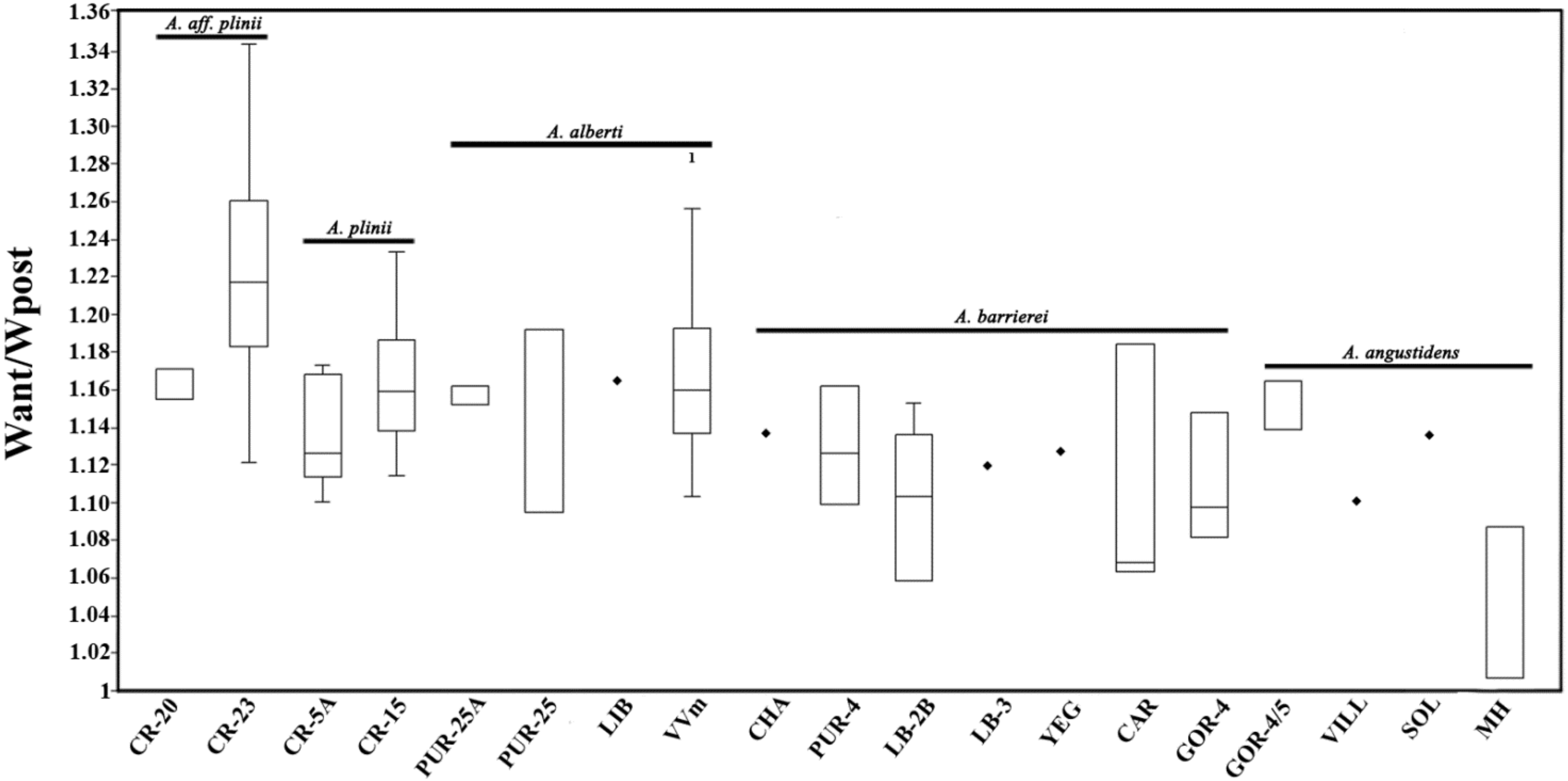


Figure XI.7. Anterior width/posterior width ratio of *Apocricetus* aff. *plinii* from Crevillente-20 and Crevillente-23, *A. plinii* from Crevillente-5A and Crevillente-15, *A. alberti* from Purcal-25A, Purcal-25, Librilla and Venta del Moro, *A. barrierei* from Chabrier, Purcal-4, La Bullana-2B, La Bullana-3, Yeguas, Caravaca and Gorafe-4, and *A. angustidens* from Gorafe-4/5, Villeneuve, Solera and Mont-Hélène. The boxes enclose the percentiles 25 to 75, and the median is represented by a horizontal black line within the box. The blank boxes comprise just two data, and therefore there is no median. In the cases where there is just one datum, this record is indicated by a square. The number ‘‘1’’ in the population from VVm indicates an outlier. Abbreviations: CR-, Crevillente; PUR-, Purcal; LIB, Librilla; VVm, Venta del Moro; CHA, Chabrier; LB-, La Bullana; YEG-, Yeguas; CAR-, Caravaca; GOR, Gorafe; VIL, Villeneuve; SOL, Solera; MH, Mont Hélène.

With respect to the anterior protolophule of M2, this crest is present in almost all specimens of the species *A*. aff. *plinii*, *A. plinii* and *A. alberti*, while its frequency decreases slightly in *A. barrierei* and, more markedly, in *A. angustidens* (Table XI.5).

The posterior metalophule of M2 is reduced gradually from *A*. aff. *plinii* to *A. barrierei* (Table XI.5), becoming absent in all populations of *A. angustidens* (Freudenthal *et al*. 1991 and 1998, Ruiz-Sánchez *et al*. 2014). The decrease in the frequency of the posterior metalophule has been linked to the shortening of the posteroloph in the species *A. alberti*–*A. barrierei*–*A. angustidens* (Ruiz-Sánchez *et al.* 2014). In *A. alberti* from Venta del Moro, the posteroloph is elongated, forming an L-shaped posterosinus in 29 out of 45 (64.44 %) specimens. In the rest of the M2 the posterior part of the posterosinus is much more reduced, so the metacone forms the posterior wall of the tooth. In LB2B and LB3, 9 out of 19 (47.37 %) M2 have a long posteroloph, 7 (36.84 %) have a medium-sized posteroloph and 3 (15.79 %) have a short one. The development of a long posteroloph seems to be related to the presence of a posterior metalophule, since all the specimens from LB2B and Venta del Moro with a complete crest have also a long posteroloph which encloses an L-shaped posterosinus. However, despite the similar development of the posteroloph in the localities of LB2B/LB3 and Venta del Moro, the posterior metalophule is much more frequent in this latter population.

In M3, a well-developed anterior protolophule is present in *A*. aff *plinii*, *A. plinii* and *A. alberti*. In Venta del Moro, 59 out of 61 specimens have a complete crest (96.72 %), and another 2 have a spur. In *A. barrierei* the anterior protolophule is long in LB2B (100 %), being absent in the populations of Gorafe 4, in 3 out of 4 (75 %) molars from Fuente del Viso and 3 out of 8 (37.50 %) from Almudena 1D (Freudenthal *et al*. 1998, Ruiz-Sánchez *et al.* 2014). In *A. angustidens* this crest is well developed in the specimens from Serrat d'en Vacquer, being present in 33 % of the molars from Mont-Hélène and absent in the two specimens from Gorafe 3 (Freudenthal *et al.* 1998, Ruiz-Sánchez *et al.* 2014).

Species	Locality	M1		M2		M3
		Cingulum	Anterior	Anterior	Posterior	Anterior
A. aff. *plinii*	CR-23	Abs	Pr: 6/12 (50 %)	Pr: 30/30 (100 %)	Pr: 15/29 (51.72 %)	Pr: 30/30 (100 %)
A. plinii	CR-15	Abs	Pr: 12/18 (60 %)	Pr: 16/18 (88.88 %)	Pr: 9/18 (50 %)	Pr: 22/22 (100 %)
A. alberti	CR-6	Abs	Pr: 50 %	Pr: 100 %	Pr: 3/11 (27.27 %)	Pr: 100 %
A. alberti	VVm	weak: 5/37 (13.51 %)	Pr: 24/41 (58.54 %)	Pr: 47/47 (100 %)	Pr: 20/42 (47.62 %)	Pr: 61/61 (100 %)
A. barrierei	Car	Abs/weak	Pr: 1/5 (20 %)	Pr: 4/6 (66.66 %)	Pr: 1/6 (16.6 %)	Pr: 3/3 (100 %)
A. barrierei	LB2B	Pr: 1/6 (16.66 %)	Pr: 2/7 (28.57 %)	Pr: 16/20 (80 %)	Pr: 6/17 (35.29 %)	Pr: 13/13 (100 %)
A. angustidens	MH	Well developed	Pr: 4/30 (13.33 %)	Pr: 9/39 (23.08 %)	Abs	Pr: 11/33 (33.33 %)

Table XI.5. Variation of several characters in the upper molars of *Apocricetus*. Abbreviations: Abs, absent; Car, Caravaca; CR-, Crevillente; LB2B, La Bullana 2B; LB3, La Bullana 3; MH, Mont-Hélène; Pr, present, VVm, Venta del Moro, collection housed at the University of Valencia. Data from Freudenthal *et al*. (1991 and 1998), Ruiz-Sánchez *et al*. (2014) and this work.

XI.5. Conclusions

The new sampling carried out in the Late Miocene age (Late Turolian) locality of Venta del Moro has allowed us to recover one of the richest collection of the genus *Apocricetus*, and, without doubt, the most complete of the species *Apocricetus alberti* (over 300 dental remains), which permits a better characterization of this taxon. An emended diagnosis and a more complete differential diagnosis for *A. alberti* are proposed.

To evaluate the change in the shape of the m3 in the different populations of *Apocricetus*, we propose the use of the posterior width of m3, from the cingulum ridge closing the sinusid to the lingual side of the entoconid. The ratio of anterior width to posterior width (W_ant/W_post) is a good indicator of the shape of the m3, since higher values indicate a narrower posterior side and therefore a more triangular shape. Five categories of the ratio W_ant/W_post (extremely triangular to subrectangular) have been defined, showing a clear distinction in the shape of the m3. A change in the shape of the m3 is observed in the phylogenetic lineage of the genus *Apocricetus*, from extreme triangular shapes in *A.* aff. *plinii* (Early Turolian) to subrectangular outlines in *A. barrierei* and *A. angustidens* (Pliocene).

The anteroconid and the anterolophulids in m1 and the anterolophule in M1 present quite heterogeneous morphologies, changing from the older species of the genus to the more recent ones. This morphological variability has not been observed in any other species of *Apocricetus*.

The presence of a crest-like anteroconid and a prelophid in some m1, presence of a weak cingulum ridge and a preloph in some M1, and the absence of mesolophs in the upper molars of *A. alberti* from Venta del Moro differ from *A.* aff. *plinii* and *A. plinii*. The absence of the ectomesolophid in m2 and m3 and the presence of a small mesolophid in some m2 differ from *A. plinii*.

The smaller size, presence of a small mesolophid in some m2, less-developed prelophid in m1, more triangular shape of the m3 and common presence of a posterior metalophule in the M1 of *A. alberti* from Venta del Moro differ from *A. barrierei* and *A. angustidens*. The less-elongated m3 and less-developed preloph in M1 distinguish *A.*

alberti from Venta del Moro from *A. barrierei*. The more-developed cingulum ridge and absent posterior metalophule of *A. angustidens* distinguish this species from *A. alberti*.

CHAPTER XII. SUMMARY AND CONCLUSIONS.

XII.1. Goals

The primary aim of this work was the sampling and study of the rodent faunas from the fossiliferous levels from the Gormaget ravine, in the Alcoy Basin. Once the taxonomy of the abundant micromammal remains recovered was clear, we tried to reach more specific goals, such as:

- Relative dating of the localities inferred from their faunal content.
- Proposal of a local biozonation for the sites from the Gormaget ravine.
- Establishment of a correlation between the proposed faunal units and those described by other authors in several Iberian and European basins.
- Interpretation of the palaeoecology of the studied sites, based on the relative abundance of the taxa found in each one of them.

In addition, we present in this thesis data from the localities La Bullana 2B, La Bullana 3 and Venta del Moro, from the Cabriel Basin. The study of the collections from these sites has allowed to expand these initial goals to include:

- The palaeogeography of rodent African immigrants in Europe in relation with the Messinian Salinity Crisis.
- The taxonomical characterization of relatively scarce taxa, using the extensive collections obtained in the sampling of Venta del Moro.

XII.2. Chapters I, II and III

In this thesis, we have studied fossil material from the localities of the Gormaget ravine area, in the Alcoy Basin, and the sites of Venta del Moro, La Bullana 2B and La Bullana 3, in the Cabriel Basin. The methodologies used are the usual when dealing with fluvio lacustrine localities. These works have produced several research articles, which are included as chapters of the thesis.

The Alcoy Basin has been studied since the 1960s by several authors. However, this is the first time that such a number of mammal localities are described in the area, all of them belonging to a relatively short time span. We have erected two stratigraphic columns, one of them including the ABS, AC and AL2 sections of the southern side of the Gormaget ravine, and another one of the northern side including the AF section. Both columns cannot be correlated directly, although Fig. II.2 shows the supposed stratigraphic relation among deposits of several sections here studied.

The localitity of Venta del Moro has yielded a huge collection of micromammal remains, most of which are under study yet. In this thesis, we have followed the nomenclature proposed by Montoya *et al.* (2006b), who distinguish several fossiliferous levels (VVm-A, VVm-AB, VVm-B, VVm-BC, VVm-C and VVm-D). We have correlated the section of Venta del Moro with the nearby section of La Bullana, which bears the localities LB2B and LB3, in Fig. II.6.

XII.3. Chapter IV

The faunal list of AL2-C comprises *Apodemus atavus*, *Apodemus gorafensis, Paraethomys meini, Paraethomys* aff. *abaigari, Stephanomys medius, Apocricetus* cf. *angustidens*, *Ruscinomys* cf. *lasallei, Trilophomys* cf. *castroi* and *Eliomys intermedius.* In addition of these taxa, AL2-D has yielded remains of *Castillomys gracilis*, *Occitanomys brailloni*, *Pliopetaurista* sp., *Glis* sp. and *Blancomys* sp.

From the fossil material yielded by the localities of AL2-C and AL2-D, our age interpretation agrees with the end of the Early Ruscinian (MN14) or the early-late Ruscinian boundary (MN14-MN15), by the presence of *Apocricetus* cf. *angustidens*. Assuming that Alcoy-2 and AL2-C/AL2-D are probably equivalent levels, our age interpretation is clearly older than that of Esteban Aenlle and Lacomba (1988), since these authors proposed an Upper Ruscinian age (MN15) for the locality of Alcoy-2.

The age assigned to AL2-C and AL2-D matches the age of Alcoy-Mina proposed by Montoya *et al*. (2006b), who placed this locality in the Early Ruscinian (MN14).

According to the geologic context, we consider a probable equivalent stratigraphic position for the classic locality of Alcoy-Mina with Alcoy-2, AL2-C and AL2-D.

The presence of a small form of the genus *Pliopetaurista* in AL2-D constitutes the southernmost record of this group of squirrels, which only has been described from central Europe (*Pliopetaurista raui* - Dahlmann 2001).

The presence of a form of the genus *Glis* in AL2-D confirms the record of this taxon in the locality Alcoy-2 (Castillo 1990).

The mixture of inhabitants of open and herbaceous habitats, like *Apocricetus*, *Blancomys*, *Ruscinomys* and *Trilophomys*, and others of forested environments like *Apodemus atavus, Glis* and *Pliopetaurista* is consistent with a forest mosaic scenario. In addition, the presence in AL2-D of a flying squirrel, *Pliopetaurista* sp., and a glirid with humid ecological affinities like *Glis* sp. suggest a wet environment. The macrofauna from Alcoy is very singular, differing from the faunal assemblages of other contemporaneous Iberian localities (Montoya *et al*. 2006b). These authors suggested that the differences might be due to a relatively wetter environment, which agrees with the palaeoenvironmental inferences made in this chapter.

Regarding the temperature, both AL2-C and AL2-D present cold weather indicators (*Trilophomys*, *Ruscinomys*) and taxa with warm preferences (*Apodemus atavus*, *Paraethomys meini*, *Apocricetus*). However, the much higher relative abundance of warm climate indicators makes us consider a mild climate at the moment of the deposition of the studied sites.

XII.4. Chapter V

In the lower deposits from the ABS section (Gormaget area, Alcoy Basin), two new localities (ABS-3 and ABS-3A) have yielded abundant mammal fossil remains. The presence in ABS-3 of *Apodemus gorafensis, Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai, Stephanomys dubari* and *Asoriculus gibberodon,* and in ABS-3A of *Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai, Stephanomys dubari, Apocricetus* cf. *barrierei, Ruscinomys* cf. *lasallei* and *Eliomys* cf.

yevesi allow us to assign an Early Ruscinian age, close to the Mio-Pliocene boundary, for these sites.

Near the top of the youngest stratigraphic sequence here studied, a new locality (AC-0) has yielded also a rich fossil mammal assemblage, comprising to *Apodemus gorafensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Stephanomys cordii*, *Asoriculus gibberodon*, *Ruscinomys* cf. *lasallei*, *Muscardinus* sp., *Eliomys intermedius*, Erinaceidae indet. and Soricidae indet. This faunal assemblage suggests an Early Ruscinian age for this locality.

The palaeoecological context of the studied deposits shows, from the bottom to the top of the stratigraphic sequence, a changing palaeoenvironment. While the scarce data from some of the lower deposits (localities ABS-9, ABS-10 and AC-0C), suggest wetter conditions for these sites, the taxa present in AC-0 indicate warm and relatively dry conditions. According to the stratigraphical position and the environment requirements of the small mammal fauna located in these localities, a progressive aridification process may occur along the lower part of the Early Pliocene in the Alcoy Basin.

The presence of *Micromys* and *Muscardinus* in several localities from the new sections of the Alcoy Basin represent the first record of these genera in the area.

Finally, and based on the faunal content of AC-0, characterized by the presence of *R. lasallei* and *Stephanomys cordii*, its relative stratigraphic position, deduced age and geographic proximity, we consider AC-0 as a probable coetaneous level to that of the classical site of Alcoy-Barranco (Adrover 1969).

XII.5. Chapter VI

We describe the rodent faunas from four new sites located in the northern side of the Gormaget ravine (Alcoy Basin). Two of them, AF-1A and AF-2, have yielded scarce remains of *Paraethomys meini*, *Stephanomys dubari* and *Occitanomys alcalai* the former and *Paraethomys meini* the latter. On the contrary, the other two localities are richer, comprising the faunal list of AF-1’06 *Paraethomys meini, Stephanomys dubari, Occitanomys alcalai, Apodemus* cf. *gorafensis, Eliomys yevesi, Atlantoxerus* cf.

margaritae, *Blancomys* cf. *sanzi*, *Parasorex Ibericus* and Soricidae indet. The faunal list of AF-1’07 is very similar, except for the presence of *Apocricetus barrierei* and the absence of *Atlantoxerus* and soricids.

The faunal assemblage of AF-1’06 suggest a latest Turolian/earliest Ruscinian age, and AF-1A is probably an equivalent level. The presence of *Apocricetus barrierei* in AF-1’07 implies a younger age, and both this site and AF-2 are placed in the earliest Ruscinian. This dating makes the localities from Alcoi Forn the oldest sites described in the Alcoy Basin, with the exception of Alcoy-N.

Based on the study of the fossil rodent assemblages from the localities of AF-1’06, AF-1’07, AF-1A and AF-2, we propose a Late Turolian-Early Ruscinian age for AF-1’06 and AF-1A, and earliest Ruscinian, at the base of the MN14 and very close to the Mio-Pliocene boundary, for AF-1’07, and AF-2. This makes the sites of the AF section the oldest localities found in the Gormaget ravine, and the one of the oldest in the Alcoy Basin, only a bit younger than that of classic site of Alcoy N. This latter locality has yielded, among others, Gerbilidae indet. and *Apocricetus alberti*, which are not found anywhere else in the Alcoy Basin.

The only locality in which the assemblage is abundant enough to perform a palaecological analysis is AF-1’06. The relative proportions of the taxa from this site indicate a very warm and dry environment at the moment of its formation.

XII.6. Chapter VII

The faunal list of La Bullana 3 comprises *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon*. In addition to these taxa, La Bullana 2B has yielded remains of *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. Based on these faunal assemblages, we propose a lower Ruscinian age (MN14) for both localities.

The preliminary paleomagnetic analysis indicates an earliest Pliocene age for La Bullana 3 and La Bullana 2B. The age of La Bullana 3 lies probably within the C3n.4n chron, dated between 5.235 Ma and 4.997 Ma. The age of La Bullana 2B should be constrained between the top of this chron (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

The presence of *Eliomys intermedius* in La Bullana 2B constitutes one of the oldest records of this taxon, probably equivalent to la Gloria 4 and PUR-13. The presence in La Bullana 2B of *Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus barrierei*, *Atlantoxerus* and *Asoriculus* cf. *gibberodon* suggest warm conditions, and the relative abundance of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* is consistent with an open environment.

The Early Ruscinian locality of LB2B constitutes the first record of a form related to *Debruijnimys julii* in MN14. However, the scarcity of the available material of *Debruijnimys* from Early Pliocene sites prevents any proper analysis, and its phylogenetic relationships remain controversial.

XII.7. Chapter VIII

The study of the faunal content of the localities from the Gormaget ravine (Alcoy Basin, Spain) has allowed us to define four biozones in the earliest Pliocene and possibly the latest Miocene of this area. These biozones comprise:

- The *Paraethomys meini* Interval Zone, corresponding to the interval between the FAD of *Paraethomys* below and the FAD of *Apocricetus barrierei* above, which comprises the localities AF-1’06 and AF-1A.
- The *Apocricetus barrierei* Interval *Zone*, corresponding to the interval between the FAD of *A. barrierei* below and the FAD of *Paraethomys* aff. *abaigari* above, comprising the localities AF-1’07 and AF-2.
- The *Paraethomys* aff. *abaigari* Interval Zone, defined by the interval between the FAD of *Paraethomys* aff. *abaigari* and FAD of *Trilophomys*,

comprising the localities ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10, AC-0C and AC-0B.

- The *Trilophomys* Assemblage Zone, defined by the association of *Apocricetus barrierei*, *Stephanomys cordii*, *Castillomys gracilis*, *Apodemus gorafensis*, *Paraethomys meini*, *Paraethomys* aff. *abaigari* and *Trilophomys*, which comprises the localities AL2-C and AL2-D.

The quality of the register has allowed us to correlate the biozonation of the Alcoy Basin with other local biozonations of the Iberian Peninsula, such as those of the Teruel, Granada, Crevillente and Guadix basins, as well as, tentatively, with other well-known European localities.

In the Alcoy Basin, the *Paraethomys meini* Interval zone can be correlated with localities with the joint presence of *Stephanomys dubari*, *Paraethomys meini*, *Occitanomys alcalai* and *Apodemus gorafensis*, being younger than the sites in which *Apodemus gudrunae* and/or *Stephanomys ramblensis* are present.

The assemblage of *Apodemus gorafensis*, *Occitanomys alcalai*, *Stephanomys dubari*, *Paraethomys meini* and *Apocricetus barrierei* is typical of the *Apocricetus barrierei* Interval zone. The presence of these taxa allows a correlation with the *Celadensia* Zone in the Teruel Basin, despite *Celadensia* is absent in the Alcoy Basin.

The *Paraethomys* aff. *abaigari* Interval zone of the Alcoy Basin is defined just by the presence of two *Paraethomys* species, since two forms of anagenetic lineages like *Stephanomys dubari*/aff. *cordii* and *Eliomys yevesi/intermedius* have been described in this interval. This zone can be correlated with local biozonations from other Iberian basins with two *Paraethomys*, although *Promimomys*, which appears together *Paraethomys* in the Teruel Basin, is absent in the Alcoy Basin.

The *Trilophomys* Assemblage Zone of the Alcoy Basin can be correlated with localities from other Iberian basins with the presence of *Trilophomys*, *Stephanomys cordii* and *Apocricetus barrierei*, while other sites in which *S. margaritae* is present are younger.

As a consequence of this biozonation, we have achieved a great resolution in the earliest Pliocene and Mio-Pliocene boundary of the Alcoy Basin, with several localities concentrated in a relatively short time span. This resolution can be compared to that of the Teruel Basin for the same time span (Mein *et al.* 1990), which is the most studied of the Iberian basins.

In respect to the zonation proposed by Morales *et al*. (2013), we consider the subzone N2 of the Ventian not valid since its lower limit, marked by the presence of two *Paraethomys*, is difficult to recognize in localities close to the Mio-Pliocene boundary, and *Promimomys*, which marks its upper limit, is absent in clearly Ruscinian localities like LB3 and LB2B. Therefore, we consider the subzone N2 (Morales *et al.* 2013) to be Early Ruscinian.

XII.8. Chapter IX

The localities from the Alcoy Basin belong to a relatively thin and poorly known time slice. The analysis of the faunal composition of these sites allows to distinguish a shift from dry and very warm conditions near the Mio-Pliocene boundary to cooler and more humid conditions in Lower Pliocene. These results largely agree with other from previous works, although the time span studied, in the earliest Pliocene, is not as well known as the Messinian or Late Pliocene. Preliminary data from the ABS and AC sections suggest marked oscillations in the environmental conditions in the Early Pliocene of the Alcoy Basin, although more work is needed to check this issue.

XII.9. Chapter X

Based on new fossil material from the Alcoy and Cabriel basins of southeastern Spain, as well as material from the Granada Basin previously referred to *E.* aff. *intermedius*, we erect the new species *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014, similar in size or slightly larger than *E. truci*. *Eliomys yevesi* generally resembles *E. truci* in terms of its morphology, but differs in having better and more frequently developed centrolophs in the upper molars, similar to *E. intermedius*.

Based on its size and morphology, we consider the most probable origin of the new species in a Late Miocene population of *E. truci*, likely an ecomorphotype characterized by well-developed centrolophs in the upper molars, and both a long centrolophid and a well-developed posterotropid in the lower molars.

Eliomys yevesi thus likely forms part of a lineage comprising *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus* (to the exclusion of other members of the genus, such as *E. assimilis* and *E. reductus*), which is characterized by a trend towards the reduction of accessory crests in the lower molars, as well as the development of centrolophs. This arrangement is complemented by a second lineage including *E. reductus* and *E. lafarguei,* marked by an increase in size, a gradual reduction of the postcentroloph and centrolophid, and a trend towards a more quadrangular occlusal outline (lower length-width ratio).

XII.10. Chapter XI

The new sampling carried out in the Late Miocene age (Late Turolian) locality of Venta del Moro has allowed us to recover one of the richest collection of the genus *Apocricetus*, and, without doubt, the most complete of the species *Apocricetus alberti* (over 300 dental remains), which permits a better characterization of this taxon.

An emended diagnosis including the size range and the morphological variability of the material from Venta del Moro is proposed. In addition, we incorporate this variability to the differential diagnosis of *A. alberti*. Based on this, we observe that the smaller size, presence of a small mesolophid in some m2, less-developed prelophid in m1, more triangular shape of the m3 and common presence of a posterior metalophule in the M1 of *A. alberti* from Venta del Moro differ from *A. barrierei* and *A. angustidens*. The less-elongated m3 and less-developed preloph in M1 distinguish *A. alberti* from Venta del Moro from *A. barrierei*. Finally, the more-developed cingulum ridge and absent posterior metalophule of *A. angustidens* distinguish this species from *A. alberti*.

The anteroconid and the anterolophulids in m1 and the anterolophule in M1 of *A. alberti* present quite heterogeneous morphologies, not observed in other species of the genus. These characters change from the older (*A.* aff. *plinii* and *A. plinii*) to the younger (*A. barrierei* and *A. angustidens*) species of *Apocricetus*.

The presence of a crest-like anteroconid and a prelophid in some m1 of *A. alberti* from Venta del Moro, presence of a weak cingulum ridge and a preloph in some M1, and the absence of mesolophs in the upper molars differ from *A.* aff. *plinii* and *A. plinii*. The absence of the ectomesolophid in m2 and m3 and the presence of a small mesolophid in some m2 differ from *A. plinii*.

In addition, we propose the use of the posterior width of m3, from the cingulum ridge closing the sinusid to the lingual side of the entoconid, to evaluate the change in the shape of the m3 in the different populations of *Apocricetus*. The ratio of anterior width to posterior width (W_ant/W_post) is a good indicator of the shape of the m3, since higher values indicate a narrower posterior side and therefore a more triangular shape. Five categories of the ratio W_ant/W_post (extremely triangular to subrectangular) have been defined, showing a clear distinction in the shape of the m3. A change in the shape of the m3 is observed in the phylogenetic lineage of the genus *Apocricetus*, from extreme triangular shapes in *A.* aff. *plinii* (Early Turolian) to subrectangular outlines in *A. barrierei* and *A. angustidens* (Pliocene).

CAPÍTULO XII. RESUMEN Y CONCLUSIONES.

XII.1. Objetivos

El objetivo principal de este trabajo ha sido el muestreo y estudio de los niveles fosilíferos encontrados en el Barranco del Gormaget, en la Cuenca de Alcoy. Una vez estuvo clara la taxonomía de los abundantes restos de micromamíferos procedentes de estos yacimientos, intentamos alcanzar objetivos más específicos, tales como:

- Datación relativa de las distintas localidades en virtud de su contenido faunístico.
- Propuesta de una biozonación local para los yacimientos del Barranco del Gormaget.
- Interpretación de la paleoecología de los yacimientos estudiados, basada en las proporciones relativas de los taxones encontrados en cada uno de ellos.

Además, en esta tesis se presentan datos de las localidades La Bullana 2B, La Bullana 3 y Venta del Moro, de la Cuenca del Cabriel. El estudio de las colecciones de estos yacimientos nos ha permitido expandir los objetivos iniciales, incluyendo:

- Algunas ideas sobre la paleogeografía de los roedores africanos en Europa en relación con la Crisis de Salinidad del Mesiniense.
- La caracterización de taxones de roedores hasta el momento relativamente escasos, usando para ello las grandes colecciones obtenidas del muestreo intensivo del yacimiento de Venta del Moro.

XII.2. Capítulos I, II y III

En esta tesis, se ha estudiado material fósil de los yacimientos del área del Barranc del Gormaget, en la Cuenca de Alcoy, y las localidades de La Bullana 2B, La Bullana 3 y Venta del Moro, en la Cuenca del Cabriel. La metodología usada es la habitual en el estudio de yacimientos fluvio-lacustres. Este trabajo ha dado lugar a varios artículos científicos, que se incluyen como capítulos de esta tesis.

La Cuenca de Alcoy ha sido estudiada desde los años 60 por varios autores. Sin embargo, es la primera vez que se describen un número tan elevado de yacimientos de micromamíferos en esta área, todos ellos pertenecientes a un intervalo de tiempo relativamente corto. El estudio paleontológico se inició después del levantamiento de dos columnas estratigráficas, una de ellas incluyendo las secciones de ABS, AC y AL2 (en la parte sur del Barranco del Gormaget), y otra del lado norte en la que se incluye la sección de AF. Ambas columnas no se pueden correlacionar de forma directa, aunque la figura II.2 muestra la relación estratigráfica supuesta entre los depósitos de las diferentes secciones. Se presenta por vez primera una columna estratigráfica de detalle de los depósitos continentales de esta zona de la Cuenca de Alcoy.

El yacimiento de Venta del Moro ha proporcionado una enorme cantidad de restos de micromamíferos, la mayor parte de los cuales se encuentra todavía en estudio. En esta tesis se ha seguido la nomenclatura propuesta por Montoya *et al*. (2006a), quienes distinguen varios niveles fosilíferos (VVm-A, VVm-AB, VVm-B, VVm-BC, VVm-C y VVm-D). La sección de Venta del Moro se ha correlacionado con la cercana sección de La Bullana, en la que se han identificado los yacimientos LB2B y LB3, en la figura II.4.

XII.3. Capítulo IV

La lista faunística de AL2-C se compone de: *Apodemus atavus, Apodemus gorafensis*, *Paraethomys meini, Paraethomys* aff. *abaigari*, *Stephanomys medius, Apocricetus* cf. *angustidens, Ruscinomys* cf. *lasallei*, *Trilophomys* cf. *castroi* y *Eliomys intermedius.* Además de estos taxones, AL2-D ha proporcionado restos de *Castillomys gracilis*, *Occitanomys brailloni*, *Pliopetaurista* sp., *Glis* sp. y *Blancomys* sp.

A partir del material fósil de AL2-C y AL2-D, y en particular por la presencia de *Apocricetus* cf. *angustidens*, asignamos una edad a estos yacimientos de final de Rusciniense Temprano (MN14), o en el límite Rusciniense temprano-tardío (MN14-MN15). Asumiendo que Alcoy-2 y AL2-C/AL2-D son probablemente niveles equivalentes, la edad aquí propuesta es algo inferior a la considerada por Esteban-Aenlle y Lacomba (1988), quienes sitúan Alcoy-2 en el Rusciniense Superior (MN15).

La edad asignada para AL2-C/AL2-D concuerda con la edad propuesta para Alcoy-Mina por Montoya *et al*. (2006b), quienes situaron esta localidad en el Rusciniense Temprano (MN14). El contexto geológico permite correlacionar Alcoy-Mina con Alcoy-2, AL2-C y AL2-D.

La presencia de una forma pequeña de *Pliopetaurista* en AL2-D constituye el registro más al sur de este grupo de ardillas, que hasta ahora solo se habían descrito en Europa Central (Dahlmann *et al.* 2001).

La presencia de una forma del género *Glis* en AL2-D confirma el registro de este taxón en la localidad de Alcoy-2 (Castillo 1990).

La mezcla de habitantes de ambientes abierto y herbáceos, tales como *Apocricetus*, *Blancomys*, *Ruscinomys* y *Trilophomys*, junto con otros de ambientes arbolados como *Apodemus atavus*, *Glis* y *Pliopetaurista*, permiten suponer un mosaico forestal en este periodo de tiempo en la cuenca de Alcoy. Además, la presencia en AL2-D de *Pliopetaurista* sp., una ardilla voladora, y un glírido como *Glis* sp., sugiere un ambiente húmedo. Estos datos concuerdan con los suministrados por la macrofauna de Alcoy-Mina (Montoya *et al*. 2006b). Según estos autores, las faunas de micromamíferos de Alcoy-Mina se desarrollarían en un ambiente relativamente más húmedo que los de otros yacimientos contemporáneos de la Península Ibérica.

Respecto a la temperatura, tanto AL2-C como AL2-D presentan tanto indicadores de medio frío (*Trilophomys*, *Ruscinomys*) como taxones con preferencias cálidas (*Apodemus atavus, Paraethomys meini, Apocricetus*). Sin embargo, la mayor abundancia relativa de los indicadores de medio húmedo nos hace considerar un clima suave en el momento de depósito de estos yacimientos.

XII.4. Capítulo V

En los depósitos inferiores de la sección de ABS (área del Gormaget, Cuenca de Alcoy), dos nuevos yacimientos (ABS-3 ABS-3A) han cedido abundantes restos fósiles. La presencia en ABS-3 de *Apodemus gorafensis, Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai*, *Stephanomys dubari* y *Asoriculus gibberodon,* y de *Paraethomys* aff. *abaigari, Paraethomys meini, Occitanomys alcalai, Stephanomys dubari, Apocricetus* cf. *barrierei, Ruscinomys* cf. *lasallei* y *Eliomys* cf. *yevesi* en ABS-3A, permiten asignar una edad Rusciniense Temprano a estos yacimientos, en las cercanías del límite Mio-Plioceno.

Cerca del techo de la secuencia estratigráfica aquí estudiada, un nuevo yacimiento (AC-0) ha cedido una rica asociación de micromamíferos, compuesta de *Apodemus gorafensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Stephanomys cordii*, *Asoriculus gibberodon*, *Ruscinomys* cf. *lasallei*, *Muscardinus* sp., *Eliomys intermedius*, Erinaceidae indet. y Soricidae indet. Esta asociación sugiere una edad Rusciniense Temprano.

El contexto paleoecológico de los depósitos estudiados muestra, desde la base hasta el techo de los depósitos estudiados, un paleoambiente cambiante. Mientras que los escasos datos de alguno de los depósitos inferiores (yacimientos ABS-9, ABS-10 y AC-0C) sugieren condiciones húmedas, los taxones presentes en AC-0 indican condiciones cálidas y relativamente secas. En función de la posición estratigráfica y los requerimientos ecológicos de las faunas identificadas en estos yacimientos, parece darse un proceso de aridificación progresiva durante la parte inferior del Plioceno Temprano en la Cuenca de Alcoy.

La presencia de los géneros *Micromys* y *Muscardinus* en algunas localidades de las nuevas secciones descritas en la Cuenca de Alcoy son el primer registro de estos taxones en la zona.

Por último, basándonos en la presencia de *R. lasallei* y *S. cordii* en AC-0, su posición estratigráfica, edad y proximidad geográfica, consideramos AC-0 como un nivel probablemente coetáneo a la localidad clásica de Alcoy Barranco (Adrover 1969).

XII.5. Capítulo VI

En la vertiente norte del Barranco del Gormaget (Cuenca de Alcoy) se han identificado cuatro nuevos niveles fosilíferos (AF-1’06, AF-1’07, AF-1A y AF-2). La lista faunística de AF-1’06, la más rica de estas localidades, consta de *Paraethomys meini*, *Stephanomys dubari*, *Occitanomys alcalai*, *Apodemus* cf. *gorafensis*, *Eliomys yevesi*, *Atlantoxerus* cf. *margaritae*, *Blancomys* cf. *sanzi*, *Parasorex ibericus* y Soricidae indet. La lista faunística de AF-1’07 es muy similar, excepto por la presencia de *Apocricetus barrierei* y la ausencia de *Altlantoxerus* y sorícidos, mientras que AF-1A ha cedido restos de *P. meini*, *S. dubari* y *O. alcalai*, y AF-2 solamente de *P. meini*.

Basándonos en el estudio de las asociaciones de roedores de los yacimientos de AF-1’06, AF-1’07, AF-1A y AF-2, proponemos una edad Turoliense Final-Rusciense

Temprano para AF-1’06 y AF-1A, y Rusciense Temprano, en la base de la MN14 y muy cerca del límite Mio-Plioceno, para AF-1’07 y AF-2. Esto convierte a las localidades de la sección de AF en las más antiguas encontradas en el Barranco del Gormaget, y una de las más antiguas en la Cuenca de Alcoy, algo más recientes que Alcoy N, donde se registran restos de Gerbilidae indet. y *Apocricetus Alberti*, taxones no representados en ningún otro yacimiento de la zona.

Respecto a las consideraciones paleoecológicas, el contenido faunístico de AF-1’06 sugiere un ambiente cálido y seco en el momento de formación de este yacimiento.

XII.6. Capítulo VII

La lista faunística de La Bullana se compone de *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. y *Asoriculus* cf. *gibberodon*. Además de estos taxones, LB2B ha cedido restos de *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* y *Atlantoxerus* sp. Por lo tanto, y basándonos en estas asociaciones, proponemos una edad Pliocena Temprana (MN14) para ambas localidades.

Un análisis paleomagnético preliminar de la sección que contiene ambas localidades indica una edad Plioceno basal para LB3 y LB2B. LB3 se situaría probablemente en el cron C3n.4n, datado entre 5,235 y 4,997 Ma, y LB2B entre el límite de este cron (4,997) y la siguiente inversión magnética, hace 4,896 Ma.

La presencia de *Eliomys intermedius* en La Bullana 2B constituye uno de los registros más antiguos de este taxón, probablemente equivalente a los de La Gloria 4 o PUR-13 en las cuencas de Teruel y Granada, respectivamente. La presencia en La Bullana 2B de *Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus barrierei*, *Atlantoxerus* y *Asoriculus gibberodon* sugiere condiciones cálidas, y la abundancia de *Apocricetus*, *Ruscinomys* and *Atlantoxerus* es coherente con un ambiente abierto.

La localidad Rusciniense de La Bullana 2B supone el primer registro de una forma relacionada con *D. julii* en la MN14. Sin embargo, lo escaso del material recuperado en este yacimiento impide un análisis en profundidad, y las relaciones filogenéticas de este taxón son todavía controvertidas.

XII.7. Capítulo VIII

El estudio del contenido faunístico de los yacimientos del Barranco del Gormaget (Cuenca de Alcoy, España) nos ha permitido definir cuatro biozonas en el Plioceno basal y posiblemente el Mioceno Final en esta área. Estas biozonas constan de:

- Zona de Intervalo de *Paraethomy meini*, correspondiente al intervalo entre el FAD de *Paraethomys* en su zona inferior y el FAD de *Apocricetus barrierei* en su zona superior, y que comprende las localidades de AF-1'06 y AF-1A.

- Zona de Intervalo de *Apocricetus barrierei* correspondiente al intervalo entre el FAD de *Apocricetus barrierei* en su zona inferior y el FAD de *Paraethomys* aff. *abaigari* en su zona superior, y que comprende las localidades de AF-1'07 y AF-2.

- Zona de Intervalo de *Paraethomys* aff. *abaigari*, definida por el intervalo entre el FAD de *Paraethomys* aff. *abaigari* en su zona inferior y el FAD de *Trilophomys* en su zona superior, y que comprende las localidades de ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10, AC-0C y AC-0B.

- Zona de Asociación de *Trilophomys*, definida por la asociación *Apocricetus barrierei, Stephanomys cordii, Castillomys gracilis, Apodemus gorafensis, Paraethomys meini, Paraethomys* aff. *abaigari* y *Trilophomys*, y que comprende las localidades de AL2-C and AL2-D.

La calidad del registro en la Cuenca de Alcoy nos ha permitido correlacionar la biozonación de esta cuenca con otras biozonaciones locales en la Península Ibérica, tales como las de las cuencas de Teruel, Granada, Crevillente y Guadix, así como, de forma provisional, con otras localidades europeas bien conocidas.

En la Cuenca de Alcoy, la Zona de Intervalo de *Paraethomy meini* puede ser correlacionada con localidades en las que aparecen conjuntamente *Stephanomys dubari*, *Paraethomys meini*, *Occitanomys alcalai* y *Apodemus gorafensis*, siendo más reciente que los yacimientos en los que se encuentran *Apodemus gudrunae* y/o *Stephanomys ramblensis*.

La asociación de *Apodemus gorafensis*, *Occitanomys alcalai*, *Stephanomys dubari*, *Paraethomys meini* y *Apocricetus barrierei* es típica de la Zona de Intervalo de *Apocricetus barrierei*. La presencia de estos taxones permite una correlación con la Zona *Celadensia* en la Cuenca de Teruel, a pesar de que *Celadensia* está ausente en la Cuenca de Alcoy.

La Zona de Intervalo de *Paraethomys* aff. *abaigari* se define sólo por la presencia de dos especies de *Paraethomys,* dado que dos formas de los linajes anagenéticos de *Stephanomys dubari/*aff. *cordii* y *Eliomys yevesi/intermedius* han sido descritas dentro de este intervalo. Esta zona se puede correlacionar con las biozonaciones locales de otras cuencas ibéricas con dos *Paraethomys*, aunque *Promimomys,* que aparece junto a *Paraethomys* en la Cuenca de Teruel, está ausente en la Cuenca de Alcoy.

La Zona de Asociación de *Trilophomys* de la Cuenca de Alcoy se puede correlacionar con localidades de otras cuencas ibéricas en las que se da la asociación *Trilophomys, Stephanomys cordii* y *Apocricetus barrierei*, mientras que en yacimientos en los que está presente *S. margaritae* son de edad más moderna.

En la biozonación propuesta en la Cuenca de Alcoy para el intervalo entre el límite Mio-Plioceno y el Plioceno Temprano se concentran varias localidades en un intervalo de tiempo relativamente corto, teniendo por tanto una alta resolución. Esta resolución es comparable, para el mismo intervalo temporal, a la de la Cuenca de Teruel (Mein *et al.* 1990), una de las zonas, en mayor detalle conocidas en Europa.

Respecto a la zonación propuesta por Morales *et al*. (2013) para el Ventiense, consideramos que la subzona N2 del Ventiense debe ser considerada como no válida, dado que su límite inferior, marcado por la presencia de dos especies de *Paraethomys*, es difícil de reconocer en localidades cercanas al límite Mio-Plioceno, y *Promimomys*, que marca su límite superior, está ausente en localidades del Rusciniense tales como

LB3 y LB2B. Por lo tanto, consideramos que la subzona N2 (Morales *et al.* 2013) debería ser incluida dentro del Rusciniense inferior.

XII.8. Capítulo IX

Las localidades de la Cuenca de Alcoy pertenecen a un periodo de tiempo relativamente poco conocido. La diferente composición faunística de estos yacimientos permite distinguir un cambio ambiental, desde condiciones secas y muy cálidas en el límite Mio-Plioceno, a condiciones más frías y húmedas en el Plioceno Inferior. Estos resultados concuerdan en gran medida con los de trabajos previos de otras disciplinas, si bien este lapso temporal no está tan bien caracterizado como los del Mioceno Superior o el Plioceno Superior. Datos preliminares de las secciones de ABS y AC-0 sugieren oscilaciones marcadas en las condiciones ambientales durante el Plioceno Inferior de la Cuenca de Alcoy, aunque se necesitan más datos para verificar esta cuestión.

XII.9. Capítulo X

Basándonos en material fósil de las cuencas de Alcoy y Cabriel del sudoeste de España, así como de material de la Cuenca de Granada, referido previamente como *E.* aff. *intermedius*, erigimos la especie *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014, de tamaño similar o ligeramente superior a *E. truci*. *Eliomys yevesi* se parece a *E. truci* en su morfología general, pero difiere de esta última especie en sus centrolofos más desarrollados, de manera similar a *E. intermedius*.

Eliomys yevesi forma parte, posiblemente, de un linaje que englobaría a *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus* (excluyendo a otras especies del género, tales como *E. assimilis* y *E. reductus*), y que se caracterizaría por una tendencia hacia la reducción de crestas accesorias en los molares inferiores y al desarrollo de los centrolofos. Un segundo linaje, formado por *E. assimilis* y *E. reductus*, muestra una tendencia a un incremento de tamaño, una reducción gradual del postcentrolofo y el centrolófido, y una tendencia hacia formas más cuadrangulares (menores índices longitud-anchura).

XII.10. Capítulo XI

Los nuevos muestreos llevados a cabo en la localidad del Mioceno Terminal (Turoliense Terminal) de Venta del Moro nos han permitido recuperar una de las colecciones más completas del género *Apocricetus*, y, sin lugar a dudas, la más completa de la especie *Apocricetus alberti* (más de 300 restos dentarios), lo que ha permite la correcta caracterización taxonómica de este taxón.

Se ha propuesto una diagnosis enmendada, que incluye el rango de tamaño y la variabilidad morfológica del material de Venta del Moro. Además, incorporamos esta variabilidad morfológica a la diagnosis diferencial de *A. alberti*. Basándonos en esto, observamos que el menor tamaño, presencia de un pequeño mesolófido en algunos m2, prelófido menos desarrollado en el m1, forma más triangular del m3 y presencia común de un metalófulo posterior en los M1 de *A. alberti* de Venta del Moro difieren de *A. barrierei* y *A. angustidens*. El m3 menos alargado y prelofo menos desarrollado en el M1 distinguen *A. alberti* de Venta del Moro de *A. barrierei*. Por último, el cíngulo más desarrollado y la ausencia de metalófulo posterior de *A. angustidens* distinguen a esta especie de *A. alberti*.

El anterocónido y los anterolofúlidos en el m1 y el anterolófulo en los M1 de *A. Alberti* presentan una morfología muy heterogénea, no observada con anterioridad en ninguna especie del género. Estos caracteres cambian desde las más antiguas (*A.* aff. *plinii* y *A. plinii*) a las más modernas (*A. barrierei* y *A. angustidens*) de las especies de *Apocricetus*.

La presencia de un anterocónido en forma de cresta y de un prelófido en algunos m1 de *A. alberti* de Venta del Moro, presencia de un débil cíngulo y un prelofo en algunos M1, así como la ausencia de mesolofos en los molares superiores distinguen a esta especie de *A.* aff. *plinii* y *A. plinii*. La ausencia de ectomesolófido en m2 y m3 y la presencia de un pequeño mesolófido difieren de *A. plinii*.

Además, proponemos el uso de la anchura posterior del m3, medida desde el cíngulo que delimita el sinúsido hasta la cara labial del entocónido, para evaluar el cambio en la forma del m3 en las diferentes poblaciones de *Apocricetus*. El cociente entre la anchura anterior respecto de la anchura posterior (W_ant/W_post) es un buen indicador de la forma de los m3, dado que valores elevados indican una parte posterior más estrecha y por lo tanto una forma más triangular. Se han definido cinco categorías del cociente W_ant/W_post (de extremadamente triangular a subrectangular), que muestran una clara distinción en la forma del m3. Se puede observar un cambio en la forma del m3 en el linaje filogenético de *Apocricetus*, desde formas extremadamente triangulares en *A.* aff. *plinii* (Turoliense Temprano) a subrectangulares en *A. barrierei* y *A. angustidens* (Plioceno).

AGRADECIMIENTOS

Si hubiese sabido desde un principio la cantidad de tiempo y esfuerzo que he tenido que invertir en esta tesis, posiblemente nunca la hubiese empezado. Sin embargo, gracias a ella he podido conocer a mucha gente que me ha ayudado en un momento u otro durante estos años, en los que muchas veces he estado tentado de abandonar, y de los que he aprendido mucho. A todos ellos tengo algo que agradecerles:

A mis directores, los Dres. Fco. Javier Ruiz Sánchez y Plinio Montoya Belló, que se involucraron en este proyecto, prestándome su ayuda y consejo durante todo este tiempo.

A los coaturoes de los artículos que componen esta tesis: Ignacio Fierro, Matthijs Freudenthal, Antonio García-Alix, Luis Gibert, Juan Abellá, Aixa Tossal, Jorge Morales, Luis de Luque, Vicente Daniel Crespo y Gary Scott, cuyo trabajo ha hecho posible esta tesis.

A la Dra. Elvira Martín Suárez, que me acogió en su casa de Granada y me ha prestado su ayuda y consejo en el estudio de los múridos fósiles, contestando a mis innumerables correos.

Al Dr. Matthijs Freudenthal, que me ofreció alojamiento tanto en su casa de Granada como en su piso de Leiden, y que ha formado parte indispensable en el proceso de redacción y corrección de manuscritos, aportando su visión crítica a la hora de discutir nuevas ideas e interpretar los resultados obtenidos.

Al Dr. Antonio García-Alix, que me permitió pasar unos días en su casa y aportó su experiencia y conocimiento de los lirones fósiles al trabajo sobre *Eliomys*, así como sus comentarios en el trabajo de *Apocricetus*.

A Nacho Fierro, cuya ayuda fue indispensable en el trabajo de campo en la siempre complicada zona del Barranc del Gormaget.

Al Dr. Héctor Botella, por sus consejos en la realización del análisis cladístico en el trabajo de *Eliomys*.

A los Dres. Lars van den Hoek Ostende y Reinier van Zelst, que me ayudaron durante mi estancia en Leiden.

A los Dres. María Ángeles Álvarez Sierra y Pablo Peláez Campomanes, por su ayuda y consejos durante mis estancias en el MNCN de Madrid.

Al Dr. Jordi Agustí, que me facilitó la lista faunística de Alcoy 4B, así como por sus comentarios referidos a la redacción del texto del capítulo VII de esta tesis.

A Cesar Laplana, por su ayuda en la discusión del capítulo de bioestratigrafía referida a los arvicólidos de la MN15.

A los miembros de la Asociación Paleontológica Isurus, de Alcoy, que siempre nos han prestado su ayuda y compañía en la realización de las tareas de campo.

A los técnicos del Servicio de Microcopía Electrónica de la UV, por su paciencia y dedicación.

Los trabajos en Venta del Moro han sido sufragados, a partir del año 1995, por la Conselleria de Cultura de la Generalitat Valenciana, y con el permiso del Ministerio de Fomento y la empresa ADIF. Las campañas de excavación fueron parcialmente financiadas por el Ministerio de Economía y Competitividad, a través de la concesión del proyecto CGL2011-25754, así como por la Conselleria d’Empresa, Universitat i Ciència de la Generalitat Valenciana, a través de la financiación del proyecto GV06/304 “Estudio paleoambiental del tránsito Mioceno-Plioceno en facies continentales en la Comunidad Valenciana (Cuencas del Cabriel y de Alcoy)”.

A toda la gente que con la que he coincidido en las camapañas de excavación de Venta del Moro o en las de extracción y lavado de sedimento: Marta, Sandra, Mar, Alba, Feo, Borja, Cristina, Belén y María Lázaro, María Ríos, Efrén, Erica, Lucía, Alex, Paco Gascó, Oscar, Juan…sois muchos y seguro que me dejo a alguien…os agradezco, además de vuestro trabajo, los buenos ratos que me habéis hecho pasar estos años. Un día de trabajo es menos duro si se tiene buena compañía.

A mis compañeros del despacho de doctorandos, con los que tantas horas he compartido. Gracias por todo este tiempo que hemos pasado juntos, los días buenos y los no tan buenos. A Esther, que pone un poco de orden en el despacho (sobre todo a la hora de comer…y a veces nos trae postres); a Rafa por amenizar esas tardes larguísimas con sus chistes (malos…muy malos); a Ana por su optimismo e ilusión (necesitábamos un contrapunto…); a Humberto, que siempre ve el lado bueno de las cosas y nunca pierde la sonrisa…y a Vicent, con el que he compartido no sólo mesa sino una buena parte de mi vida, por aguantar mis momentos de malhumor y frustración, y por aportar siempre una visión distinta (y a menudo polémica) de las cosas.

A mis amigos de toda la vida, Garcés, Álvaro, Toquero, Regui…les agradezco que siempre hayan estado ahí, aunque por cuestiones geográficas ya no nos veamos tanto como antes.

Para acabar, me gustaría dar las gracias a mis padres, que siempre me han apoyado en todo lo que he hecho y que han estado ahí cuando lo he necesitado, a pesar de que su hijo no siempre haya tomado las mejores decisiones. Y por supuesto a Laura, por aguantarme todo este tiempo con mis quejas sobre correcciones, deadlines y demás. Aunque no hubiese sacado nada de todo este trabajo, el haberte conocido habría hecho que mereciese la pena.

REFERENCES

Adrover, R. (1969): Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. I. *Ruscinomys*. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 67, 245–272.

Adrover, R. (1986): *Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico*. PhD. thesis, Instituto de Estudios Turolenses, 423 p.

Adrover, R., Mein, P., Moissenet, E. (1988): Contribución al conocimiento de la fauna de roedores del Plioceno de la región de Teruel. *Teruel* 79 (1), 89–151.

Adrover, R., Mein, P., Moissenet, E. (1993): Roedores de la transición Mio-Plioceno de la región de Teruel. *Paleontologia i Evolució* 26–27, 47–84.

Aguilar, J.P., Michaux, J. (2011): Pleistocene edible dormice (Rodentia, Mammalia) from Slovenia, and their relations to the present day *Glis glis* (Linnaeus 1766). *Acta Carsologica* 40 (2), 369–380.

Aguilar, J.P, Calvet, M., Michaux, J. (1986): Description des rongeurs pliocènes de la faune du Mont-Hélène (Pyrénées-Orientales, France), nouveau jalon entre les faunes de Perpignan (Serrat-D'en-Vacquer) et de Sète. *Paleovertebrata* 16 (3), 127–144.

Aguilar, J.P., Michaux, J., Bachelet, B., Calvet, M., Faillat, J.P. (1991): Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocene en Rousillon. Implications biostratigraphiques et biogeographiques. *Paleovertebrata* 20, 147–174.

Aguilar, J.P., Michaux, J., Delanno, J.J., Guendon, J.L. (1993): A Late Pliocene rodent fauna from Alozaina (Malaga, Spain). *Scripta Geologica* 103, 1–22.

Aguilar, J.P., Legendre, S., Michaux, J. (eds.) (1997): Actes du Congres BiochroM'97. Memoires et travaux École practique de Hautes Études*, lnstitut de Montpellier* 21, 769–805.

Aguilar, J.P., Legendre, S., Michaux, J., Montuire, S. (1999): Pliocene mammals and climatic reconstruction in the western mediterranean area. In: Wrenn, F.H., Suc, J.P., Leroy, S.A.G. (eds). *The Pliocene: Time of Change; American Association of Stratigraphic Palynologists Foundation*, 109–120.

Aguilar, J.P., Michaux, J., Lazzari, V. (2007): Lo Fournas 16-M (Miocène supérieur) et Lo Fournas 16-P (Pliocène moyen), deux nouvelles localités karstiques à Baixas, Sud de la France. Partie II, Nouvelles espèces de rongeurs, listes fauniques et remarque sur l'utilisation biochronologique des faunes karstiques. *Géologie de la France* 1, 63–81.

Aguirre, E. (2003): Messiniense: compleja y grave crisis ecológica. *Estudios Geológicos* 59, 205–212.

Aguirre, E., Robles, F., Thaler, L., López-Martínez, N., Alberdi, M.T., Fuentes, C. (1973): Venta del Moro, nueva fauna finimiocena de moluscos y vertebrados. *Estudios Geológicos* 29, 569–578.

Aguirre E., Hoyos M., Morales J. (1975): Alcoy: observaciones preliminares sobre la secuencia Neógeno-Cuaternaria del Serpis. *Acta Geologica Hispanica* 10 (2), 75–77.

Aguirre, E., López Martínez, N., Morales, J. (1976): Continental faunas in Southeast Spain related to the Messinian. Il significato geodinamico della crisi di salinita' del Miocene terminale nel Mediterraneo. *Messinian seminar 2, Gargano* 62–63.

Agustí, J. (1990): The Miocene rodent succession in Eastern Spain: a zoographical appraisal. In: E.H. Lindsay, E.H., Fahlbusch, V., Mein, P. (eds.). *European Neogene Mammal Chronology,* 375–404.

Agustí, J. (1991): Gerbilidés fossiles d'Europe occidentale. In: Le Berre, M., Guelte, L. (eds.). *Le Rongeur et l'Espace*, 177–182.

Agustí, J. (1999): A critical re-evaluation of the Miocene mammal units in Western Europe: dispersal events and problems of correlation. In: Agustí, J., Rook, L., Andrews, P. (eds.). *Hominoid Evolution and Climatic Change in Europe. Volume 1. The Evolution of Neogene Terrestrial Ecosystems in Europe,* Cambridge University Press, Cambridge, 84–112.

Agustí, J., Antón, M. (2002): *Mammoths, sabertooths and hominids*. New York, Columbia University Press, 313 p.

Agustí, J., Casanovas-Vilar, I. (2003): Neogene gerbils from Europe. *Deinsea* 10, 13–21.

Agustí, J., Galobart, A. (1986): La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. *Paleontologia i Evolució* 20, 57–62

Agustí, J., Martín-Suárez, E. (1984): El Plioceno continental de la depresión Guadix-Baza (Prov. Granada) y su fauna de micromamíferos. Nota preliminar. *Acta Geologica Hispanica* 19 (4), 277–281.

Agustí, J., Martín-Suárez, E. (1986): Un proyecto de análisis ecoestratigráfico en el Plio-Pleistoceno de la Depresión Guadix-Baza. *Memorias I Jornadas de Paleontología*, 21–32.

Agustí, J., Moyà-Solà, S., Pons-Moya, J. (1987): La sucesión de Mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Paleontologia i Evolució Special Issu*e 1, 287–295.

Agustí, J., Freudenthal, M., Lacomba, J.I., Martín-Suárez, E., Nageli, C. (1990): Primeros micromamíferos del Pleistoceno superior de la cuenca de Mula (Murcia, España). *Revista de la Sociedad Geológica de España* 3, 289–343.

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

Agustí, J., Oms, O., Remacha, E. (2001b): Long Plio-Pleistocene Terrestrial Record of Climate Change and Mammal Turnover in Southern Spain. *Quaternary Research* 56, 411–418.

Agustí, J., Garcés, M., Krijgsman, W. (2006): Evidence for African–Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 5–14.

Agustí, J., Santos-Cubedo, A., Furió, M., De Marfá, R., Blain, H.A., Oms, O., Sevilla, P. (2011): The late Neogene-early Quaternary small vertebrate succession from the

Almenara-Casablanca karst complex (Castellón, Eastern Spain): Chronologic and paleoclimatic context. *Quaternary International* 243, 183–191.

Alberdi, M.T. (1974): El género *Hipparion* en España. Nuevas formas de Castilla y Andalucía, revisión e historia evolutiva. *Trabajos sobre Neógeno-Cuaternario* 1, 1–146.

Alberdi, M.T., Bonadonna, F.P. (1988): Is the Ventian a real stratigraphic stage? *Mediterránea Serie de Estudios Geológicos* 7, 65–77.

Alberdi, M.T., López, N., Mazo, A.V., Morales, J. (1977): Venta del Moro y las faunas de vertebrados finimiocenas de España. *Estudios Geológicos* 33: 589–591.

Alberdi, M.T., Arias, C., Bigazzi, G., Bonadonna, F.P., Leone, G., López, N., Michaux, J., Robles, F., Soria, D. (1982): Nuevo yacimiento de moluscos y vertebrados de la cuenca del Júcar (Albacete, España). *Actes Colloque «Le Villafranchien méditerranéen», Lille* 1, 255–271.

Alberdi, M.T., Cerdeño, E., López-Martínez, N., Morales, J., Soria, D. (1997): La fauna Villafranquiense de El Rincón-1 (Albacete, Castilla-La Mancha). *Estudios Geológicos* 1, 255–271.

Alcalá, L., Sesé, C., Herráez, E., Adrover, R. (1991): Mamíferos del Turoliense inferior de Puente Minero (Teruel, España). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geología)* 86 (1–4), 205–251.

Andrews, P. (1990): *Owl, Caves and Fossils*. Natural History Museum Publications, London, 231 p.

Bachelet, B., Aguilar, J.P., Calvet, M., Michaux, J. (1990): Nouvelles faunes de rongeurs du Pliocene des Pyrenees-Orientales: consequences pour le genre *Stephanomys* (Schaub, 1938). *Geobios* 23 (1), 117–120.

Ballesteros Navarro, B.J., Rodríguez Hernández, L., Hernández Bravo, J.A., López Gutiérrez, J.L., Fernández Mejuto, M., García Menéndez, O., Domínguez Sánchez, J.A., Díaz Losada, E., Castillo Pérez, E., Padilla Benítez, A., Vela Mayorga, A., Muñoz Alonso, J., Gómez, Fontalva, J. (2007): Actualización y mejora del conocimiento hidrogeológico y funcionamiento de los acuíferos de Alicante. Caracterización hidrogeológica de la U. H. 08.40 (Sierra Mariola). *Instituto Geológico y Minero de España, Diputación de Alicante*. Tomo I, Memoria, 118 p.

Barciová, L. (2009): Advances in insectivore and rodent systematics due to geometric morphometrics. *Mammal Review* 39 (2), 80–91.

Barciová, L., Macholán, M. (2006): Morphometric study of two species of wood mice *Apodemus sylvaticus* and *A. flavicollis* (Rodentia: Muridae): traditional and geometric morphometric approach. *Acta Theriologica* 51, 15–27.

Bartoli, G., Sarnthein, M., Weinelt, M. (2006): Late Pliocene millenial-scale climate variability in the northern North Atlantic prior to and after the onset of Northern Hemisphere glaciation. *Paleoceanography* 21, PA4205.

Benavent, J.V., Gascó, F., Ruiz-Sánchez, F.J., Montoya, P. (2008): Un Nuevo yacimiento con micromamíferos en el Mioceno Superior del área de Venta del Moro (Cuenca del Cabriel, Valencia). *Stvdia Geologica Salmanticensia* 8, 95–105.

Blainville, H.M. (1826): Sur une nouvelle espèce de rongeur fouisseur du Brésil. *Nouvelle Bulletin des Sciences par la Sociéte Philomatique Paris* 3, 62–64.

Blanc, P.L. (2002): The opening of the Plio-Quaternary Gibraltar Strait: assessing the size of a cataclysm. *Geodinamica Acta* 15, 303–317.

Bolliger, T. (1997): Advantage and disadvantage of the scientific use of karstic faunas. In: Aguilar, J.P., Legendre, S., Michaux, J. (eds.). *Actes du Congrès BiochroM'97. Mémoires et Travaux École practique de Hautes Études, Institut de Montpellier* 21, 39–45.

Boscá, E. (1911): Los Museos de París, Londres, Amsterdam y Bruselas. *Anales de la Junta para Ampliación de Estudios e Investigaciones Científicas* 4, 61 p.

Botella, F. de (1854): Ojeada sobre la geología del Reino de Valencia. *Revista Minera* 5, 15 p.

Bover, P., Alcover, J.A., Michaux, J.J., Hautier, L., Hutterer, R. (2010): Body Shape and Life Style of the Extinct Balearic Dormouse *Hypnomys* (Rodentia, Gliridae): New evidence from the study of associated skeletons. *PLoS ONE* 5 (12), 1–11.

Brandt, J.F. (1855): Beiträge zur nähern Kenntniss der Säugethiere Russlands. *Mémoires de l’Académie Impériale des Sciences de Saint*-*Petersbourg* 6, 1–365.

Brandy, L.D., Jaeger, J.J. (1980): Les échanges de faunes terrestres entre l'Europe et l'Afrique nord-occidentale au Messinien. *Comptes-rendus de l'Académie des Sciences de Paris* 291, 465–468.

Bruijn, H. de (1974): The Ruscinian rodent succession in Southern Spain and its implications for the bioestratigraphic correlation of Europe and North Africa. *Senckerbergiana lethaea* 55, 435–445.

Bruijn, H. de (1999): Superfamily Sciuroidea. In: Rössner, G. E., Heissig, K. (eds.). *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, 271–280.

Bruijn, H. de, Dawson, M.R., Mein, P. (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rodhes (Greece). *I, II y III. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 73, 536–584.

Bruijn, H. de, Mein, P., Montenat, C., Weerd, A. van de (1975): Corrélations entre les Gisements de Rongeurs et les formations marines du Miocéne terminal d’Espagne Meridionale I. (Provinces d’Alicante et de Murcia). *Koninklijke Nederlandse Akademie van Wetenschappen, Series B* 78 (4), 1–36.

Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J. (1992): Report of the RCMNS working group on fossil mammals, Reisensburg, 1990. *Newsletters on Stratigraphy* 26, 65–118.

Butler, P.M. (1972): The problem of insectivore classification. In: Joysey, K.A., Kemp, T.S. (eds.). *Studies in Vertebrate evolution*. New York (Winchester), 253–265.

Calvo, J.P., Elizaga, E., López-Martínez, N., Robles, F., Usera, J. (1978): El Mioceno superior continental del Prebético Externo: Evolución del Estrecho Nordbético. *Boletín Geológico y Minero* 89 (5), 407–426.

Casanovas-Vilar, I. (2007): *The rodent assemblages from the Late Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain)*. PhD. thesis, Universitat Autònoma de Barcelona, 283 p.

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

Castién, E., (2002): *Glis glis* Linnaeus 1766. In: Palomo, J.L., Gisbert, J. (eds.). *Atlas de los Mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza, SECEM-SECEMU, Madrid, 428–431.

Castillo, C. (1990): *Paleocomunidades de Micromamíferos de los yacimientos kársticos del Neógeno Superior de Andalucía Oriental*. PhD. thesis, Universidad de Granada, 225 p.

Castillo, C., Agustí, J., (1996): Early Pliocene rodents (Mammalia) from Asta Regia (Jerez basin, Southwestern Spain). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 991, 25–43.

Chaline, J. (1972): *Les rongeurs du Pléistocène moyen et supérieur de France*. PhD. thesis, Cahiers de Paléontologie, Centre Nationale de la Recherche Scientifique, París, 410 p.

Chaline, J. (1996): Biostratigraphy and calibrated climatic chronology of the Upper Pliocene and Lower Pleistocene of France. In: Couvering, P. van (ed.). *The Pleistocene Boundary at the Beginning of the Quaternary*. Cambridge University Press, 178–182.

Chaline, J., Mein, P. (1979): *Les Rongeurs et l'Évolution*. Doin Éditeurs, Paris, 235 p.

CIESM (2008): The Messinian Salinity Crisis from mega-deposits to microbiology – A consensus report. *CIESM Workshop Monographs* 33, 168 p.

Colombero, S., Bonelli, E., Kotsakis, T., Pavia, G., Pavia, M., Carnevale, G. (2013): Late Messinian rodents from Verduno (Piedmont, NW Italy): Biochronological, paleoecological and paleobiogeographic implications. *Geobios* 46, 111–125.

Condis Fernández, M.M., Berovides, V. (2002): Valor taxonómico de la morfometría del esqueleto craneal y postcraneal en tres especies de jutías de Cuba (Rodentia: Capromyidae). *Revista Biologia* 16 (2), 150–158.

Cordy, J.M. (1976): *Essai sur la microévolution du genre* Stephanomys *(Rodentia, Muridae).* PhD. thesis, Université de Liège, 351 p.

Costeur, L., Montuire, S., Legendre, S., Maridet, O. (2007): The Messinian event: What happened to the peri-Mediterranean mammalian communities and local climate?. *Geobios* 40, 423–431.

Crusafont, M., Villalta, J. (1955): Sur l'âge des Mammifères d'Alcoy (Espagne). *Compte Rendu Sommaire des Séances de la Société Géologique de France* 148.

Cuenca-Bescós, G. (1988): Revisión de los Sciuridos del Aragoniense y del Rambliense en la fosa de Calatayud-Montalbán. *Scripta Geologica* 87, 1–116.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., Arsuaga, J.L. (1997): Small mammals from Sima de los Huesos. *Journal of Human Evolution* 33, 175–190.

Daams, R. (1981): The dental pattern of the Dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins, special publication* 3, 1–115.

Daams, R. (1990): Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and the Oligocene-Miocene boundary interval of Spain. *Scripta Geologica* 95, 1–63.

Daams, R. (1999): Family Gliridae. In: Rössner, G. E., Heissig, K. (eds.). *The Miocene Land Mammals of Europe.* Verlag Dr. Friedrich Pfeil, Munchen, 301–318.

Daams, R., Bruijn, H. de (1995): A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix* 6, 3–50.

Daams, R., Freudenthal, M. (1981): Aragonian: the Stage concept versus Neogene Mammal Zones. *Scripta Geologica* 62, 1–17.

Daams, R., Freudenthal, M. (1988): Synopsis of the Dutch-Spanish collaboration program in the Aragonian type area, 1975-1986. In: Freudenthal, M. (ed.). Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud-Teruel Basin (Spain). *Scripta Geologica Special Issue* 1, 3–18.

Daams, R., Meulen, A.J. van der (1984): Paleoenvironmental and Paleoclimatic Interpretation of Micromammal faunal succesions in the Upper Oligocene and Miocene of North Central Spain. *Paléobiologie continentale, Montpellier* 14 (2), 241–257.

Daams, R., Freudenthal, M., Meulen, A.J. van der (1988): Ecostratigraphy of micromammal faunas from the Neogene of Spain. *Scripta Geologica Special Issue* 1, 286–302.

Daams, R., Meulen, A.J. van der, Peláez-Campomanes, P., Álvarez-Sierra, M.A. (1999): Trends in rodent assemblages from the Aragonian (early–middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain. In: Agustí, J., Rook, L., Andrews, P. (eds.). *Hominoid evolution and climatic change in Europe. The evolution of Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge, U.K., 1, 127–139.

Dahlmann, T. (2001): Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Courier Forschungsinstitut Senckenberg Series* 227, 1–129.

Dam, J. van, Weltje, G.J. van (1999): Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modeling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 151, 267–305.

Dam, J. van., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W. (2001): The Upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage ⁄ age concepts discussed. *Journal of Vertebrate Paleontology* 21, 367–385.

Dam, J. van, Aziz, H.A., Álvarez-Sierra, M., Hilgen, F.K., Hoek Ostende, L.W. van den, Lourens, L.J., Mein, P., Meulen, A.J. van der, Peláez-Campomanes, P. (2006): Long-period astronomical forcing of mammal turnover. *Nature* 443, 687–691.

Depéret, C. (1890): Les animaux pliocènes du Rousillon. *Mémoires de la Société géologique de France, Paleontologie* 3, 1–194.

Depéret, C. (1897): Étude de quelques gisements nouveaux de vertébrés pléistocènes de l’Île de Corse. *Annales de la Société Linnéenne de Lyon* 44, 113–6.

Domingo, L., Koch, P.L., Hernández-Fernández, M., Fox, D.L., Domingo, M.S., Alberdi, M.A. (2013): Late Neogene and Early Quaternary Paleoenvironmental and Paleoclimatic Conditions in Southwestern Europe: Isotopic Analyses on Mammalian Taxa. *PLoS ONE* 8 (5), e63739.

Doukas, C.S., Hoek Ostende, L.W. van den, Theocharopoulos, C.D., Reumer, J.W.F. (1995): The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia). *Münchner Geowissenschaftliche Abhandlungen (A)* 28, 43–64.

Dowsett, H., Barron, J., Poore, R. (1996): Middle Pliocene sea surface temperatures: A global reconstruction. *Marine Micropaleontology* 27 (1–4), 13–26.

Durand Delga, M., García Rodrigo, B., Magne, J., Polveche, J. (1964): À propos du Miocène de la région d’Alcoy (province d’Alicante, Espagne). *Cursillos y Conferencias* 9, 213–217.

Ellerman, J.R. (1940): *The families and genera of living rodents with a list of named forms (1758-1936)*. British Museum, London, 689 p.

Esteban Aenlle, J., Lacomba, J.I. (1988): El yacimiento de Alcoy-2. Nuevo nivel con micromamíferos del Plioceno inferior (MN15) en el área de Alcoy. *Comunicacions. Col·loqui Homenatge a R. Adrover “Bioeventos y sucesiones faunísticas en el Terciario continental ibérico”*, Sabadell, 17.

Ezquerra, J. (1850): Ensayo de una descripción general de la estructura geológica de España en la Península. *Memorias de la Academia de Ciencias de Madrid* 1, 35–65.

Fahlbusch, V. (1991): The meaning of MN-Zonation: Considerations for a subdivision of the European Continental Tertiary using mammals. *Newsletters on Stratigraphy* 24 (3), 159–173.

Fauquette, S., Suc, J.P., Guiot, J., Diniz, F., Feddi, N., Zheng, Z., Bessais, E., Drivaliari, A. (1999): Climate and biomes in the West Mediterranean area during the Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 152, 15–36.

Fauquette, S., Suc, J.P., Bertini, A., Popescu, S.M., Warny, S., Taoufiq, N.B., Perez-Villa, M.J., Chikhi, H., Feddi. N., Subally, D., Clauzon, G., Ferrier, J. (2006): How much did climate force the Messinian salinity crisis? Quantified climatic conditions from pollen records in the Mediterranean region. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 281–301.

Fejfar, O. (1999): Microtoid cricetids. In: Rössner, G. E., Heissig, K. (eds.). *The Miocene Land Mammals of Europe.* Verlag Dr. Friedrich Pfeil, Munchen, 365–372.

Fejfar, O., Heinrich, W.D., Lindsay, E.H. (1998): Updating the Neogene Rodent biochronology in Europe. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* 60, 533–554.

Filhol, M.H. (1879): Étude des Mammifères fossiles de Saint-Gérand-le-Puy Allier, 1 ère partie. *Annales De la Societé Géologique de Paris* 10, 1252.

Filippucci, M.G., Civitelli, M.V., Capanna, E. (1988a): Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840. 1. Karyotype divergence. *Bolletino di Zoologia* 55, 35–45.

Filippucci, M.G., Rodino, E., Nevo, E., Capanna, E. (1988b): Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840. 2. Allozyme diversity and differentiation of chromosomal races. *Bolletino di Zoologia* 55, 47–57.

Freudenthal, M. (1972): *Deinogalerix koenigswaldi* nov. gen., nov. spec., a giant insectivore from the Neogene of Italy. *Scripta Geologica* 14, 1–19.

Freudenthal, M. (1985): Cricetidae (Rodentia) from the Neogene of Gargano (prov. of Foggia, Italy). *Scripta Geologica* 77, 29–76.

Freudenthal, M. (2004): Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). *Treballs del Museu de Geologia de Barcelona* 12, 97–173.

Freudenthal, M., Martín-Suárez, E. (1999): Family Muridae. In: Rössner, G. E., Heissig, K. (eds.). *The Miocene Land Mammals of Europe.* Verlag Dr. Friedrich Pfeil, Munchen, 401–409.

Freudenthal, M., Martín-Suárez, E. (2013): New ideas on the systematics of Gliridae (Rodentia, Mammalia). *Spanish Journal of Palaeontology* 28 (2), 239–252.

Freudenthal, M., Meijer, M.T., Meulen, A.J. van der (1976): Preliminary report on a field campaign in the continental Pleistocene of Tegelen (The Netherlands), *Scripta Geologica* 34, 1–27.

Freudenthal, M., Lacomba, J.I., Martín-Suárez, E. (1991): The Cricetidae (Mammalia, Rodentia) from the Late Miocene of Crevillente (prov. Alicante, Spain). *Scripta Geologica* 96, 9–46.

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

Freudenthal M., Mein P., Martín-Suárez E. (1998): Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7, 11–93.

Freudenthal, M., García-Alix, A., Rios, M., Ruiz-Sánchez, F.J., Martín-Suárez, E., Delgado Huertas, A. (2014): Review of paleo-humidity parameters in fossil rodents (Mammalia): Isotopic vs. tooth morphology approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 395, 122–130.

Funder, S., Bennike, O., Böcher, J., Israelson, C., Petersen, K.S., Simonarson, L.E. (2001): Late Pliocene Greenland—The Kap København Formation in North Greenland. *Bulletin of the Geological Society of Denmark* 48, 117–134.

Furió, M. (2007): *Los insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno superior del Levante Ibérico*. PhD. thesis, Universitat Autònoma de Barcelona, 341 p.

Furió, M., Angelone, C. (2010): Insectivores (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu D1 (Mandriola, central-western Sardinia, Italy). *Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen* 258, 229–242.

Furió, M., Casanovas-Vilar, I., Hoek Ostende, L.W. van den (2011): Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 219–229.

Garcés, M., Krijgsman, W., Agustí, J. (1998): Chronology of the late Turolian deposits of the Fortuna basin (SE Spain): implications for the Messinian evolution of the eastern Betics. *Earth and Planetary Science Letters* 163, 69–81.

García-Alix, A. (2006): *Bioestratigrafía de los depósitos continentales de la transición Mio-Plioceno de la cuenca de Granada*. PhD. thesis, Universidad de Granada, 429 p.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2007): New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *Comptes Rendus Palevol* 6, 269–279.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008a): Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada basin (southern Spain). Biostratrigraphic and phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlunge*n 248, 183–215.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008b): Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136, 1–37.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., Martín, J.M. (2008c): Late Miocene‑Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265, 214–225.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008d): *Muscardinus meridionalis* sp. nov., a new species of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of *Muscardinus*. *Journal of Vertebrate Paleontology* 28 (2), 568–573.

García-Alix, A., Minwer-Barakat, R., Martín, J.M., Martín-Suárez, E., Freudenthal, M. (2008e): Biostratigraphy and sedimentary evolution of late Miocene and Pliocene continental deposits of the Granada basin (southern Spain). *Lethaia* 41, 431–446.

García-alix, A., Delgado Huertas, A., Martín-Suárez, E., Freudenthal, M. (2013): Environmental conditions vs. landscape. Assessment of the factors that influence small mammal fauna distribution in Southern Iberia during the latest Messinian by mean of stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386, 492–500.

Geraads, D. (1998): Rongeurs du Mio-Pliocène de Lissasfa (Casablanca, Maroc). *Geobios* 31, 229–245.

Gervais, P. (1852): Description des ossements fossiles des mammifères rapportés d'Espagne par MM. De Vernuil, Collomb et De Loriére. *Bulletin de la Société Géologique de la France* 2 (10), 147–168.

Gibert, L., Scott, G.R., Montoya, P., Ruiz-Sánchez, F.J., Morales, J., Luque, L., Abella, J., Lería. M. (2013): Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. *Geology* 41, 691–694.

Gill, P.G., Purnell, M.A., Crumpton, N., Brown, K.R., Gostling, N.J., Stampanoni, M., Rayfield, E.J. (2014): Dietary specializations and diversity in feeding ecology of the earliest stem mammals. *Nature* 512, 303–307.

Goloboff, P.A., Farris, J.S., Nixon, K.C. (2003): T.N.T.: Tree analysis using new technology. Program and documentation. Available from the authors, and from www.zmuc.dk/public/phylogeny

Goloboff, P.A., Farris, J.S., Nixon, K.C. (2008): TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.

Gomes-Rodrigues, H., Merceron, G., Viriot, L. (2009): Dental microwear patterns of extant and extinct Muridae (Rodentia, Mammalia): ecological implications. *Naturwissenschaften* 96: 537–542.

Gomes-Rodrigues, Renaud, S., Charles, C., Poul, Y. Le, Solé, F., Aguilar, J.P., Michaux, J., Tafforeau, P., Headon, D., Jernvall, J., Viriot, L. (2013): Roles of dental development and adaptation in rodent evolution. *Nature Communications* 4, 2504.

Gómez Cano, A.R., García Yelo, B.A., Hernández-Fernández, M. (2006): Cenogramas, análisis bioclimático y muestreo en faunas de mamíferos: implicaciones para la aplicación de métodos de análisis paleoecológico. *Estudios Geológicos* 62 (1), 135–144.

Gradstein, F., Ogg, J., Smith, A. (2004): *A Geologic Time Scale*. Cambridge University Press, Cambridge, UK, 589 p.

Gromolard C. (1980): Révision du type de l'espèce *Parabos? boodon* (Gervais) (Mammalia, Artiodactyla, Bovidae) du gisement Néogène d'Alcoy (Espagne). *Bulletin de la Societé linnéenne de Lyon* 9, 525–533.

Gromov. I., Polyakov, Y. (1992): *Voles (Microtinae). Fauna of the USSR. Mammals, Volume III (8)*. Smithsonian Institution Libraries, 725 p.

Guérin C. (1980): Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 79, 1–1182.

Haywood, A.M., Ridgewell, A., Lunt, D.J., Pound, M.J., Dowsett, H.J., Dolan, A.M., Francis, J.E., Williams, M. (2011): Are there pre Quaternary geological analogues for a future greenhouse warming? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 369, 933–956.

Hernández-Fernández, M., Peláez-Campomanes, P. (2003): Ecomorphological characterization of Murinae and hypsodont "Cricetidae" (Rodentia) from the Iberian Plio-Pleistocene. *Coloquios de Paleontología Special Issue* 1, 237–251.

Hernández-Fernández, M., Azanza, B., Álvarez-Sierra, M.A. (2004): Iberian Plio-Pleistocene biochronology: micromammalian evidence for MNs and ELMAs calibration in southwestern Europe. *Journal of Quaternary Science* 19, 605–616.

Hernández-Fernández, M., Alberdi, M.T., Azanza, B., Montoya, P., Morales, J., Nieto, M., Peláez-Campomanes, P. (2006): Identification problems of arid environments in the Neogene–Quaternary mammal record of Spain. *Journal of Arid Environments* 66, 585–608.

Hernández-Fernández, M., Álvarez-Sierra, M.A., Peláez-Campomanes, P. (2007): Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe during the Plio-Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251, 500–526.

Hernández-Pacheco, E. (1914): Los vertebrados terrestres del Mioceno de la Península Ibérica. *Memorias de la Sociedad Española de Historia Natural* 9, 443–448.

Hoek Ostende, L.W. van den (2001): A revised generic classification of the Galericini (Insectivora, Mammalia) with some remarks on their palaeobiogeography and phylogeny. *Geobios* 34 (6), 681–695.

Hoek Ostende, L.W. van den (2003): Fossils Explained 42. Micromammals. *Geology today* 19 (2), 70–76.

Holden, M.E. (2005): Family Gliridae. In: D.E. Wilson, D.A. Reeder (eds.). *Mammal Species of the World. A Taxonomic and Geographic Reference*. The John Hopkins University Press, Baltimore 4, 819–841.

Horáček, I., Knitlová, M., Wagner, J., Kordos, L., Nadachowski, A. (2013): Late Cenozoic History of the Genus *Micromys* (Mammalia, Rodentia) in Central Europe. *PLoS ONE* 8 (5), 1–19.

Hordijk, K., Bruijn, H. de (2009): The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hellenic Journal of Geosciences* 44, 21–103.

Huchon, D., Madsen, O., Sibbald, M.J.J.B., Ament, K., Stanhope, M.J., Catzeflis, F., de Jong, W.W., Douzery, E.J.P. (2002): Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. *Molecular Biology and Evolution* 19 (7), 1053–1065.

Hugueney, M., Mein, P. (1965): Lagomorphes et rongeurs du Néogène de Lissieu (Rhone). *Travaux Laboratoires de Géologie de la Faculté des Sciences de Lyon, N. S.* 12, 109–123.

Hsü, K.J., Montadert, L., Bernoulli, D., Cita, M.B., Erickson, A., Garrison, R.E., Kidd, R.B, Mèlierés, F., Müller, C., Wright, R. (1973): History of the Mediterranean salinity crisis. *Nature* 267, 399–403.

Jaeger, J.J., Michaux, J., Thaler, L. (1975): Présence d'un rongeur muridé nouveau, *Paraethomys miocaenicus* nov. sp., dans le Turolien supérieur du Maroc et d'Espagne. Implications paléogeógraphiques. *Comptes Rendus de l'Académie des Sciences Paris, série D* 280, 1673–1676.

Jánossy, D. (1986): Pleistocene Vertebrate faunas of Hungary. *Developments in paleontology and stratigraphy* 8, 200 p.

Jiménez-Moreno, G., Fauquette, S., Suc, J.P. (2013): Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology* 162, 403–415.

Kälin, D. (1999): Tribe Cricetini. In: Rössner, G.E., Heissig, K. (eds.). *The Miocene land mammals of Europe*. K. Verlag Dr. Friedrich Pfeil, München, 373–387.

Kaya, F., Kaymakçi, N. (2013): Systematics and dental microwear of the late Miocene Gliridae (Rodentia, Mammalia) from Hayranlı, Anatolia: implications for paleoecology and paleobiodiversity. *Palaeontologia Electronica* 16 (3), 21A.

Klevezal, G.A. (2002): Reconstruction of individual life histories of rodents from their teeth and bone. *Acta Theriologica* 47, 127–138.

Klevezal, G.A., Pucek, M., Sukhovskaya, L.I. (1990): Incisor growth in voles. *Acta Theriologica* 35, 331–344.

Koufos, G.D. (2006): The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hellenic Journal of Geosciences* 4, 183–214.

Kowalski, K. (1956): Insectivores, Bats and Rodents from the early Pleistocene bone breccia of Podlesice, near Kroczyce (Poland). *Acta Palaeontologica Polonica* 1 (4), 331–394.

Kowalski, K. (1963): The Pliocene and Pleistocene Gliridae (Mammalia, Rodentia) from Poland. *Acta Zoologica Cracoviensia* 8 (14), 533–567.

Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J., Wilson D.S. (1999): Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400, 652–655.

Krystufek, B., Kraft, R. (1997): Cranial variation and taxonomy of garden dormice (*Eliomys* Wagner, 1840) in the circum-Mediterranean realm. *Mammalia* 61, 411–429.

Kukal, Z. (1971): *Geology of recent sediments*. Central Geological Survey, Prague, 490 p.

Lacomba, J.I., Morales, J., Robles, F., Santisteban, C. de, Alberdi, M.T. (1986): Sedimentología y paleontología del yacimiento finimioceno de La Portera (Valencia). *Estudios Geológicos* 42, 167–180.

Lawrence, K.T., Sosdian, S., White, H.E., Rosenthal, Y. (2010): North Atlantic climate evolution through the Plio-Pleistocene climate transitions. *Earth and Planetary Science Letters* 300, 329–342.

Lazzari, V., Aguilar, J.P., Michaux, J. (2010): Intraspecific variation and micro-macroevolution connection: illustration with the late Miocene genus *Progonomys* (Rodentia, Muridae). *Paleobiology* 36 (4), 641–657.

Legendre, S. (1986): Analysis of mammalian communities from the late Eocene and Oligocene of Southern France. *Palaeovertebrata* 16, 191–212.

Legendre, S. (1989): Les communautes de mammifères du Paléogène (Éocène supérieur et Oligocene) d'Europe occidentale: structures, milieux et évolution. *Münchner Geowissenscliafrliclie Abhandlungen. (A)* 16, 1– 110.

Lindars, E.S., Grimes, S.T., Mattey, D.P., Collinson, M.E., Hooker, J.J., Jones, T.P. (2001): Phosphate $\delta^{18}O$ determination of modern rodent teeth by direct laser fluorination: an appraisal of methodology and potential application to palaeoclimate reconstruction. *Geochimica et Cosmochimica Acta* 65, 2535–2548.

Linnaeus, C. (1740): *Systema Naturae in quo Naturae Regna tria, secundum. Classes, Ordines, Genera, Species, systematice proponuntur*. Kiesewetter, Stockholm, 80 p.

López-Martínez, N. (1989): Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 3 (3), 1–350.

Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, J. (2005): Chapter 21-The Neogene. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (eds.). *A Geologic Time Scale 2004*, Cambridge University Press, Cambridge, U.K., 409–430.

MacDonald, D. (ed.). (2001): *The new encyclopedia of mammals*. Oxford University Press, Oxford, 961 p.

Made, J. van der, Belinchón, M. (1991): *Korynochoerus palaeochoerus* from the Upermost Miocene of Alcoy. *Revista Española de Paleontología special number* 173–180.

Made, J. van der, Morales, J., Montoya, P. (2006): Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 228–246.

Mansino, S., Ruiz-Sánchez, F.J., Montoya, P. (2009a): Estudio preliminar de las faunas pliocenas de roedores del yacimiento Alcoi Cotes Altes 2 (ACA-2, Alicante, España). *Paleolusitana* 1, 251–256.

Mansino, S., Montoya, P., Luque, L., Ruiz-Sánchez, F.J., Benavent, J.V. (2009b): La Bullana 2B: faunas de micromamíferos del Plioceno en el área de Venta del Moro (Valencia, España). *Resúmenes XXV Jornadas de la Sociedad Española de Paleontología* 1, 204–206.

Mansino, S., Fierro, I., Ruiz-Sánchez, F.J., Montoya, P. (2013): The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of Alcoy-Mina. *Journal of Iberian Geology* 39 (2), 261–284.

Mansino, S., Ruiz-Sánchez, F.J., Freudenthal, M., Montoya, P. (2014): A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain). *Proceedings of the Geologists' Association* 125, 392–405.

Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J., Montoya, P. (in press): A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica*.

Martín-Suárez, E. (1988): *Sucesiones de micromamíferos en la depresión de Guadix Baza*. PhD. thesis, Universidad de Granada, 241 p.

Martín-Suárez, E., Freudenthal, M. (1993): Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica* 103, 65–118.

Martín-Suárez, E., Freudenthal, M. (1998): Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Geobios* 31 (6), 839–847.

Martín-Suárez, E., Mein, P. (1991): Revision of the genus *Castillomys* (Muridae, Rodentia). *Scripta Geologica* 96, 47–81.

Martín-Suárez, E., Mein, P. (1998): Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* 31 (1), 87–97.

Martín Suárez, E., Oms, O., Freudenthal, M., Agustí, J., Parés, J.M. (1998): Continental Mio-Pliocene transition in the Granada Basin. *Lethaia* 31, 161–166.

Martín-Suárez, E., Freudenthal, M., Krijgsman, W., Rutger Fortuin, A. (2000): On the age of continental deposits of the Zorreras member (Sorbas basin, SE Spain). *Geobios* 33 (4), 505–512.

Martín-Suárez, E., Freudenthal, M., Civis, J. (2001): Rodent palaeoecology of the Continental Upper Miocene of Crevillente (Alicante, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 165, 349–356.

Mathisen, M., Morales, J. (1981): Stratigraphy, facies and depositional environments of the Venta del Moro vertebrate locality, Valencia, Spain. *Estudios Geológicos* 37, 199–207.

Mazo, A.V. (1977): *Revisión de los mastodontes de España*. PhD. thesis, Universidad Complutense de Madrid, 440 p.

McKenna, M.C., Bell, S.K. (1997): *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 640 p.

McKenna, A., Bleefeld, R., Mellett, J.S. (1994): Microvertebrate collecting: large-scale wet sieving for fossil microvertebrates in the field. In: Leiggi, P., May, P. (eds). *Vertebrate Paleontological Techniques, Volume I.* Cambridge University Press, Cambridge, 93–111.

Mein, P. (1970): Les Sciuroptères (Mammalia, Rodentia) Neogènes d'Europe Occidentale. *Geobios* 3 (3), 7–77.

Mein, P. (1975): Résultats du Groupe de Travail des Vertébrés. In: Senes, J. (ed.). *Report on Activity on the RCMNS Working Groups (1971-1975),* Bratislava, 78–81.

Mein, P. 1990: Updating of MN zones. In Lindsay, E.H., Fahlbusch, V., Mein, P. (eds): *European Neogene Mammal Chronology,* 73–90. Plenum Press, New York.

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

Mein, P., Martín-Suárez, E. (1993): *Galerix iberica* sp. nov. (Erinaceidae, Insectivora, Mammalia) from the Late Miocene and Early Pliocene of the Iberian Peninsula. *Geobios* 26, 723–730.

Mein, P., Michaux, J. (1970): Un nouveau stade dans l'évolution des rongeurs pliocènes d'Europe sud-occidentale. *Comptes Rendus de l' Académie de Sciences de Paris D* 270, 2780–2783.

Mein, P., Moissenet, E., Truc, G. (1978): Les formations continentales du Néogène Supérieur des Vallées du Júcar et du Cabriel au NE d'Albacete (Espagne). Biostratigraphie et Environment. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 72, 99–147.

Mein, P., Moissenet, E., Adrover, R. (1989-1990): Biostratigraphie du Néogène Supérieur du basin de Teruel. *Paleontologia i Evolució* 23, 121–139.

Meulen, A.J. van der, Bruijn, H. de (1982): The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2: the Gliridae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 85 (4), 485–524.

Michaux, J. (1969): Muridae (Rodentia) du Pliocène supérieur d’Espagne et du Midi de la France. *Palaeovertebrata* 3, 1–25.

Minwer-Barakat, R. (2005): *Roedores e insectívoros del Turoliense superior y el Plioceno del sector central de la cuenca de Guadix*. PhD. thesis, Universidad de Granada, 606 p.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2005): Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, Southern Spain). *Journal of Vertebrate Paleontology* 25 (2), 426–441.

Minwer-Barakat, R., García-Alix, A., Martín Suárez, E., Freudenthal, M. (2008): *Micromys caesaris,* a new murid (Rodentia, Mammalia) from the late Pliocene of the Guadix basin, Southeastern Spain. *Journal of Paleontology* 82 (2), 436–441.

Minwer-Barakat, R., García-Alix, A., Agustí, J., Martín-Suárez, E., Freudenthal, M. (2009a): The micromammal fauna from Negratín-1 (Guadix basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the late Miocene. *Journal of Paleontology* 83 (6), 854–879.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2009b): Late Turolian micromammals from Rambla de Chimeneas-3: considerations on the oldest continental faunas from the Guadix Basin (Southern Spain). *Neues Jahrbuch für Geologie und Paläontologie* 251, 95–108.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2010): Soricidae (Soricomorpha, Mammalia) from the Pliocene of Tollo de Chiclana (Granada, Southeastern Spain). *Journal of Vertebrate Paleontology* 30, 535–546.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2011a): Validation of the Species *Stephanomys progressus*, a Murid (Rodentia) from the Early Pleistocene of Spain. *Journal of Paleontology* 85 (2), 392–394.

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., Esteban Trivigno, S. de, Moyà-Solà, S. (2011b): Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, Northeastern Spain) and biochronological implications. *Journal of Vertebrate Paleontology* 31 (4), 849–865.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M., Viseras, C. (2012): Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. *Lethaia* 45, 594–614.

Montenat, C. (1973): *Les Formations néogènes et Quaternaires du Levant espagnol (Provinces d'Alicante et de Murcia).* PhD. thesis, Université de Orsay-Paris-Sud, 1170 p.

Montenat, C., Bruijn, H. de (1976): The Ruscinian rodent faunule from La Juliana (Murcia); its implication for the correlation of continental and marine biozones. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 79 (4), 245–255.

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J.V., Marín, M.D., Ruiz-Sánchez, F.J. (2006a): Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. *Estudios Geológicos* 62, 313–325.

Montoya, P., Ginsburg, L., Alberdi, M.T., Made, J. van der, Morales, J., Soria, M.D. (2006b): Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28 (1), 137–173.

Montuire, S., Maridet, O., Legendre, S. (2006): Late Miocene‑Early Pliocene temperature estimates in Europe using rodents. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 247–262.

Morales, J. (1984): *Venta del Moro: su macrofauna de mamíferos y bioestratigrafía continental del Mioceno terminal mediterráneo*. PhD. thesis, Editorial Universidad Complutense, 340 p.

Morales, J., Peláez-Campomanes, P., Abella, J., Montoya, P., Ruiz-Sánchez, F.J., Gibert, L., Scott, G., Cantalapiedra, J.L., Sanisidro, O. (2013): The Ventian mammal age (Latest Miocene): present state. *Spanish Journal of Palaeontology* 28 (2), 149–160.

Moreno, S. (1984): *Biometría, Biología y dinámica poblacional del lirón careto,* Eliomys quercinus *(L), en Doñana, sureste de España.* PhD. thesis, Universidad de Granada, 310 p.

Moreno, S. (2002): *Eliomys quercinus* Linnaeus, 1766. In: Palomo, J.L., Gisbert, J. (eds.). *Atlas de los Mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza, SECEM-SECEMU, Madrid, 432–435.

Musser, G., Carleton, M. (2005): Superfamily Muroidea. D. Wilson, D. Reeder (eds.). *Mammal Species of the World*. Baltimore and London: The Johns Hopkins University Press, 894–1531.

Nadachowski, A., Daoud, A. (1995): Patterns of myoxid evolution in the Pliocene and Pleistocene of Europe. *Hystrix* 6, 141–149.

Nehring, A. (1898): Über *Dolomys* nov. gen. foss. *Zoologischer Anzeiger* 21, 13–16.

Nicklés, R. (1893): Investigaciones geológicas sobre los terrenos secundarios y terciarios de la Provincia de Alicante y Sur de la Provincia de Valencia. *Boletín de la comisión del Mapa Geológico de España* 20, 99–312.

Novo, P. (1915): Reseña geológica de la Provincia de Alicante. *Boletín del Instituto Geológico y Minero de España* 36, 57–148.

Nowak, R. (1999): *Walker's Mammals of the World, vol. II*. Baltimore and London, The Johns Hopkins University Press, 2015 p.

Oliver, A., Hernández-Ballarín, V., López-Guerrero, P., García-Paredes, I., Álvarez-Sierra, M.A., Gómez Cano, A.R., García Yelo, B.A., Alcalde, G.M., Peláez-Campomanes, P. (2014): Dental microwear analysis in Gliridae (Rodentia): methodological issues and paleodiet inferences based on *Armantomys* from the Madrid Basin (Spain). *Journal of Iberian Geology* 40 (1), 157–166.

Opdyke, N., Mein, P., Moissenet, E., Pérez-González, A., Lindsay, E., Petko, M. (1990): The magnetic stratigraphy of the late Miocene sediments of the Cabriel Basin, Spain. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (eds.). *European Neogene Mammal Chronology*. Plenum Press, New York, 507–514.

Opdyke, N., Mein, P., Lindsay, E., Pérez-González, A., Moissenet, E., Norton, V.L. (1997): Continental deposits, magnetostratigraphy and vertebrate paleontology, late Neogene of Eastern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 129–148.

Pedraza Gilsanz, J. de (1996): *Geomorfología. Principios, métodos y aplicaciones*. Editorial Rueda, S. L., Madrid, 414 p.

Pierson D'Autrey, L. (1987): *Sédimentation et structuration synsédimentaire dans le bassin néogène d'Alcoy (Cordillères Bétiques externes Orientales Espagne)*. PhD. thesis, Université de Paris, 315 p.

Pomel, M. (1853): Catalogue méthodique et descriptif des Vertébrés Fossiles découverts dans le bassin hydrographique supérieur de la Loire et surtout dans la vallée de son affluent principal, l'Allier. *Annales des sciences littéraires et industrielles d'Auvergne* 1853, 81–229.

Popov, V.V. (2003): Late Pliocene Soricidae (Insectivora, Mammalia) from Varshets (North Bulgaria). *Acta Zoologica Cracoviensia* 46, 43–72.

Quintana, J. (2015): Estudio preliminar del esqueleto postcraneal del *Muscardinus cyclopeus* Agustí, Moyà-Solà & Pons-Moyà, 1982 (Mammalia, Rodentia, Myoxidae). *Estudios Geológicos* 71 (1), e022.

Quintana, J., Köhler, M., Moyà-solà, S. (2011): *Nuralagus rex*, gen. et sp. nov., an endemic insular giant rabbit from the Neogene of Minorca (Balearic Islands, Spain). *Journal of Vertebrate Paleontology* 31 (2), 231–240.

Raynal, J.P., Lefèvre, D., Geraads, D., El Graoui, M. (1999): Contribution du site paléontologique de Lissasfa (Casablanca, Maroc) à une nouvelle interprétation du Mio-Pliocène de la Méseta. *Comptes Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Science* 329 (8), 617–622.

Renaud, S., Dam, J. van (2002): Influence of biotic and abiotic environment on dental size and shape evolution in a Late Miocene lineage of murine rodents (Teruel Basin, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 184, 163–175.

Renaud, S., Benammi, M., Jaeger, J.J. (1999): Morphological Evolution of the Murinae Rodent *Paraethomys* in Response to Climatic Variations (Mio-Pliocene of North Africa). *Paleobiology* 25 (3), 369-382.

Reumer, J.W.F. (1984): Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. *Scripta Geologica* 73, 1–173.

Reumer, J.W.F., Hoek Ostende, L.W. van den (2003): Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). In: Reumer, J.W.F., Wessels, W. (eds.). *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. Deinsea* 10, 455–467.

Rinderknecht, A., Blanco, E.R. (2008): The largest fossil rodent. *Proceedings of Royal Society B* 275, 923–928.

Robles, F. (1970): *Estudio estratigráfico y paleontológico del Neógeno del río Júcar*. PhD. thesis, Universidad de Valencia, 275 p.

Robles, F., Torrens, J., Aguirre, E., Ordóñez, S., Calvo, J.P., Santos-García, J. (1974): Levante. In: E. Aguirre, J. Morales (eds.). *Coloquio Internacional sobre bioestratigrafía continental del Neógeno superior y Cuaternario*. Editorial CSIC, Madrid, 85–135.

Rodriguez, J. (1999): Use of cenograms in mammalian palaeoecology. A critical review. *Lethaia* 32, 331–347.

Rodriguez, J. (2000): Comment on “Mammalian Faunas as Indicators of Environmental and Climatic Changes in Spain during the Pliocene-Quaternary Transition” (Montuire, 1999). *Quaternary Research* 54, 433–435.

Rook, L., Torre, D. (1995): *Celadensia grossetana* n. sp. (Cricetidae, Rodentia.) from the Late Turolian Baccinello–Cinigiano Basin (Italy). *Geobios* 28 (3), 379–382.

Royo-Gómez, J. (1922): El Mioceno Continental Ibérico y su fauna malacológica. *Memorias de la Comisión de Investigaciones Paleontológicas y Prehistóricas, serie Paleontología* 5, 272 p.

Ruiz Bustos, A., Sesé, C., Dabrio, C., Peña, J.A., Padial, J. (1984): Geología y fauna de micromamíferos del nuevo yacimiento del Plioceno inferior de Gorafe-A (depresión de Guadix-Baza, Granada). *Estudios Geológicos* 40, 231–241.

Ruiz-Sánchez, F.J., Santisteban, C. de, Lacomba, J.I. (1994): Edad de los depósitos inferiores de la Cuenca del Cabriel en la localidad Fuen Vich-1. *Resúmenes III Congreso del Grupo Español del Terciario*, Jaca, 197–200.

Ruiz-Sánchez, F.J., Santisteban, C. de, Crespo, V.D., Freudenthal, M. (2011): New rodent faunas from Middle Miocene and Mio-Pliocene in the Cabriel Basin (Valencia, Spain). *Journal of Iberian Geology* 37, 161–172.

Ruiz-Sánchez, F.J., Murelaga, X., Larrasoaña, J.C., Freudenthal, M., Garcés, M. (2012): Hypsodont Myomiminae (Gliridae, Rodentia) from five new localities in the Lower Miocene Tudela Formation (Bardenas Reales, Ebro Basin, Spain) and their bearing on the age of the Agenian-Ramblian boundary. *Geodiversitas* 34 (3), 645–663.

Ruiz-Sánchez, F.J., Freudenthal, M., Mansino, S., Crespo-Roures, V.D., Montoya, P. (2014): *Apocricetus barrierei* (Rodentia, Mammalia) from La Bullana 2B and La Bullana 3 (Cabriel Basin, Valencia, Spain). Revision of the Late Miocene–Early Pliocene forms of the genus *Apocricetus*. *Paläontologische Zeitschrift* 88, 85–98.

Santisteban, C. de, Montoya P., Usera J., Robles F. (1997): El Terciario marino y continental de Alicante. In: Alcalá L., Alonso A. M. (eds.). *Itinerarios Geológicos del Terciario de Centro y Este de la Península Ibérica*. Universidad Complutense de Madrid, Consejo Superior de Investigaciones Científicas, Madrid, 73–107.

Sarnthein, M., Bartoli, G., Prange, M., Schmittner, A., Schneider, B., Weinelt, M., Andersen, N., Garbe-Schönberg, D. (2009): Mid-Pliocene shifts in ocean overturning circulation and the onset of Quaternary-style climates. *Climate of the Past* 5, 269–283.

Schaub, S. (1925): Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. *Abdhalungen der Schweizerischen Paläonologischen Gesellschaft* 45, 1–114.

Schepper, S. de, Gibbard, P.L., Salzmann, U., Ehlers, J. (2014): A global synthesis of the marine and terrestrial evidence for glaciation during the Pliocene Epoch. *Earth-Science Reviews* 135, 83–102.

Schlosser, M. (1884): Die Nager des Europäischen tertiärs nebst Betrachtungen über die organisation und die geschichtliche Entwicklung der Nager überhantp. *Palaeontographica* 31, 223–328.

Schmidt-Kittler, N. (ed.) (1987): International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene – Mainz, February 18th-21st 1987. *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie* 10.

Sesé, C. (1989): Micromamíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada). In: Alberdi, M.T., Bonadonna, F.P. (eds.). *Geología y Paleontología de la Cuenca de Guadix-Baza. Trabajos sobre Neógeno-Cuaternario* 11, 185–213.

Sesé, C. (2006a): Los roedores y lagomorfos del Neógeno de España. *Estudios Geológicos* 62, 429–480.

Sesé, C. (2006b). Micromamíferos (Rodentia, Insectivora, Lagomorpha y Chiroptera) de la Peña de Estebanvela (Segovia). In: Ripoll Cacho, S., Muñoz, F. (eds.). *La Peña de Estebanvela (Estebanvela-Ayllón, Segovia). Grupos Magdalenienses en el Sur del Duero*. Memorias, Junta de Castilla y León. Arqueología en Castilla y León 17, 145–165.

Sesé, C., Villa, P. (2008): Micromammals (rodents and insectivores) from the early Late Pleistocene cave site of Bois Roche (Charente, France): Systematics and paleoclimatology. *Geobios* 41, 399–414.

Sesé, C., Panera, J., Rubio-Jara, S., Pérez-González, A. (2011): Micromamíferos de Pleistoceno Medio y Pleistoceno Superior en el Valle del Jarama: yacimientos de Valdocarros y HAT (Madrid, España). *Estudios Geológicos* 67 (1), 131–151.

Shevenell, A.E., Kennett, J.P., Lea, D.W. (2004): Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science* 305, 1766–1770.

Silcox, M.T., Teaford, M.F. (2002): The diet of worms: an analysis of mole dental microwear. *Journal of Mammalogy* 83 (3), 804–814.

Simpson, G.G. (1945): The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85, 1–350.

Storch, G., Seiffert, C. (2007): Extraordinarily preserved specimen of the oldest known glirid from the Middle Eocene of Messel (Rodentia). *Journal of Vertebrate Paleontology* 27 (1), 189–194.

Storch, G., Engesser, B., Wunke, M. (1996): Oldest fossil record of gliding in rodents. *Nature* 379, 439–441.

Tesakov, A. (2004): Early Pliocene arvicolid faunas from eastern Europe. *18th International Senckenberg Conference in Weimar*.

Thaler, L. (1966) : Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. *Mémoires du Muséum National d'Histoire Naturelle C* 17, 1–295.

Thaler L., Crusafont, M., Adrover R. (1965): Les premiers micromammifères du Pliocène d’Espagne; précisions chronologiques et biogéographiques sur la faune d’Alcoy. *Comptes Rendus de l’Académie des Sciences de Paris* 260, 4024–4027.

Thompson, R.S., (1991): Pliocene environments and climates in the western United States. *Quaternary Science Reviews* 10 (2/3), 115–132.

Thorington, R.W.Jr., Schennum, C.E., Pappas, L.A., Pitassy, D. (2005): The difficulties of identifying flying squirrels (Sciuridae: Pteromyini) in the fossil record. *Journal of Vertebrate Paleontology* 25 (4), 950–961.

Tullberg, T. (1899): Ueber das System der Nagetiere: eine phylogenetische Studie. *Nova Acta Regiæ Societatis Scientiarum Upsaliensis* 18, 1–514.

Ubilla, M. (2008): Postcranial morphology of the extinct caviine rodent *Microcavia criolloensis* (late Pleistocene, South America). *Zoological Journal of the Linnean Society* 154, 795–806.

Vautravers, M.J. (2014): Insight into the latest Messinian (5.7–5.2 Ma) palaeoclimatic events from two deep-sea Atlantic Ocean ODP Sites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 407, 14–24.

Verneuil, E., Collomb, E. (1852): Del terreno cretácico de España. *Revista Minera* 3, 339–471.

Vilanova, J. (1867): Note sur la geólogie de la Province de Valencia. *Bulletin de la Société Géologique de la France* 2, 24.

Visedo, C. (1922): Notas geológicas, paleontológicas y orogénicas. In: Visedo, R. (ed.), *Historia de Alcoy y su región*, 36–64.

Viseras, C., Soria, J.M., Fernández, J. (2004): Cuencas Neógenas Postorogénicas de la Cordillera Bética. In: Vera, J.A. (ed.). *Geología de España*. SGE-IGME, Madrid, 576–581.

Weerd, A. van de (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins, special publication* 2, 1–217.

Weerd, A. van de (1979): Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen ser. B* 82, 127–170.

Wessels, W. (1999): Family Gerbillidae. In: Rössner, G.E., Heissig, K. (eds.). *The Miocene Land Mammals of Europe.* Verlag Dr. Friedrich Pfeil, München, 395–400.

Wilson, D.E., Reeder, D.M. (2011): Class Mammalia Linnaeus, 1758. In: Zhang, Z. Q. (ed.). Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* 3148, 56–60.

Zachos, J., Pagani, M., Thomas, E., Billups, K. (2001): Trends, rhythms, and aberrations in Global climate 65 Ma to present. *Science* 29, 686–693.

Ziegler, R. (1999): Order Insectivora. In: Rössner, G.E., Heissig, K. (eds.). *The Miocene land mammals of Europe*. K. Verlag Dr. Friedrich Pfeil, München, 53–74.

APPENDIXES

Mansino, S., Fierro, I., Ruiz-Sánchez, F.J., Montoya, P. (2013): The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of Alcoy-Mina. *Journal of Iberian Geology* 39 (2), 261–284.

Mansino, S., Fierro, I., Montoya, P., Ruiz-Sánchez, F.J. (in press) Micromammal faunas from the Mio-Pliocene boundary in the Alcoy Basin (SE Spain): biostratigraphical and palaecological inferences. *Bulletin of Geosciences.*

Mansino, S., Ruiz-Sánchez, F.J., Luque, L. de, Montoya, P., Gibert, L., Morales, J., Abella, J., Crespo, V.D., Scott, G. R. (in press): First Early Pliocene micromammal faunas from the Venta del Moro area (Cabriel Basin, Spain): new data on the Messinian dispersal of *Debruijnimys*. *Journal of Iberian Geology*.

Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J., Montoya, P. (in press): A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica*.

Mansino, S., Ruiz-Sánchez, F.J., Freudenthal, M., Montoya, P. (2014): A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain). *Proceedings of the Geologists' Association*. 125, 392–405.

ISSN (print): 1698-6180. ISSN (online): 1886-7995
www.ucm.es/info/estratig/journal.htm

Journal of Iberian Geology 39 (2) 2013: 261-284
http://dx.doi.org/10.5209/rev_JIGE.2013.v39.n2.42501

Journal of
Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of Alcoy-Mina

Las faunas de roedores fósiles de los yacimientos Alcoy 2C y 2D (Cuenca de Alcoy, España). Implicaciones para la datación de la localidad clásica de Alcoy-Mina

S. Mansino[1]*, I. Fierro[2], F.J. Ruiz-Sánchez[1], P. Montoya[1]

[1] Departament de Geologia, Universitat de València, Doctor Moliner 50, 46100 Burjassot, Spain
samuel.mansino@uv.es; francisco.ruiz@uv.es; plinio.montoya@uv.es.

[2] Museo Paleontológico de Elche (MUPE), Plaça de Sant Joan 3, 03203 Elche, Spain
i.fierro@cidarismpe.org.

**Corresponding author*

Received: 29/04/2011 / Accepted: 12/04/2013

Abstract

In the Gormaig area (Alcoy basin, SE Spain) a number of fossil mammal localities are known, of which only the classic site of Alcoy-Mina, known since the mid-19th century, has yielded remains of macrofauna. In the vicinity of this site are the localities of Alcoy-2C (AL2C) and Alcoy-2D (AL2D), probably representing the levels of Alcoy-Mina. The faunal assemblage allows dating the AL2C and AL2D localities as Early Pliocene (end of the Early Ruscinian or early-late Ruscinian boundary, MN14-MN15). Several taxa (*Pliopetaurista* and *Glis*) are thought to have affinities for humid and close biotopes.

Keywords: Rodentia, Pliocene, Ruscinian, Alcoy basin, Spain

Resumen

En el área del Gormaig (cuenca de Alcoy, SE España), se conocen toda una serie de yacimientos de mamíferos fósiles, de los cuáles tan sólo la localidad clásica de Alcoy-Mina, conocida desde mediados del siglo XIX, ha aportado restos de macrofauna. En las proximidades de esta localidad se encuentran los yacimientos de Alcoy-2C (AL2C) y Alcoy-2D (AL2D), probablemente representando los niveles fosilíferos de Alcoy-Mina. La asociación faunística encontrada en AL2C y AL2D permite la datación de estas localidades como pertenecientes al Plioceno inferior (fin del Rusciniense inferior o límite Rusciniense inferior-superior, zona MN14-MN15). Varios taxones (*Pliopetaurista* y *Glis*) se consideran indicadores de biotopos cerrados de carácter húmedo.

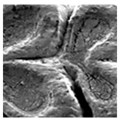
Palabras clave: Rodentia, Plioceno, Rusciniense, Cuenca de Alcoy, España

1. Introduction

In this paper we describe the rodent faunas from the fossil sites Alcoy-2C and Alcoy-2D (AL2C and AL2D), located in the western margin of the lacustrine basin of Alcoy (SE Spain). This basin belongs to the inner Prebetic of the Betic chain, and is surrounded by the mountain ranges of Menejador, Mariola and Benicadell (Fig. 1).

Micromammal faunas from the Mio-Pliocene boundary in the Alcoy Basin (SE Spain): biostratigraphical and palaeoecological inferences

SAMUEL MANSINO, IGNACIO FIERRO, PLINIO MONTOYA & FRANCISCO JAVIER RUIZ-SÁNCHEZ



This paper deals with the fossil rodent and insectivore faunas from the localities of the southern side of the Gormaget ravine (Alcoy Basin, Spain): Alcoi Barranc Sud (ABS-1, ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10), and Alcoi Cristian (AC-0, AC-0B and AC-0C). We infer in this paper an Early Ruscinian age for these sites. Based on the analysis of the fossil micromammal faunas, we consider that the localities ABS-3 and ABS-3A are older than AC-0, which has a similar age as the classic site of Alcoy-Barranco. The palaeoecological interpretation of the fauna recovered from these new sections show dry conditions in the Early Pliocene (MN14) from the Alcoy Basin. • Key words: biostratigraphy, palaeoecology, micromammals, Pliocene, Alcoy Basin, Spain.

MANSINO, S., FIERRO, I., MONTOYA, P. & RUIZ-SÁNCHEZ, F.J. 2015. Micromammal faunas from the Mio-Pliocene boundary in the Alcoy Basin (SE Spain): biostratigraphical and palaeoecological inferences. *Bulletin of Geosciences 90(3)*, xxx–xxx (6 figures, 4 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received October 27, 2014; accepted in revised form March 18, 2015; published online xxxx xx, 2015; issued xxxx xx, 2015.

Samuel Mansino, Francisco Javier Ruiz-Sánchez & Plinio Montoya, Departament de Geologia, Universitat de València, Doctor Moliner 50, 46100 Burjassot, Spain; Samuel Mansino & Francisco Javier Ruiz-Sánchez, Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, 46018 Alginet, Valencia, Spain; samuel.mansino@uv.es, francisco.ruiz@uv.es, plinio.montoya@uv.es • Ignacio Fierro, GeaLand Patrimonio S.L., C/Tibi No. 3, Alicante, Spain; fierro@gealandpatrimonio.com • Francisco Javier Ruiz-Sánchez (corresponding autor), the same addresses as the first author and INCYT-UPSE, Universidad Estatal Península de Santa Elena, 7047, Santa Elena, Ecuador; francisco.ruiz@uv.es

Alcoy Basin in SE Spain is located in the inner Prebetic of the Betic chain, surrounded by the mountain ranges of Menejador, Mariola and Benicadell (Fig. 1). Previously, the geology of this area was studied by Durand Delga *et al.* (1964), Montenat (1973, pp. 1009–1014, fig. 153), Aguirre *et al.* (1975) and Pierson d'Autrey (1987). Despite the Alcoy Basin have been intensively sampled in the past (Thaler *et al.* 1965, Adrover 1969, Esteban Aenlle & Lacomba 1988, López-Martínez 1989, Freudenthal *et al.* 1998, Mansino *et al.* 2013), a relatively scarce number of localities are known. In the Gormaig area, besides the large mammal classic locality of Alcoy-Mina, just a few small mammal localities have been found. Before 2009, four localities containing small mammals were known in the Gormaig area: Alcoy-Barranco (Thaler *et al.* 1965, Adrover 1969), Alcoy-N (López-Martínez 1989), Alcoy-4B (Freudenthal *et al.* 1998), Alcoy-2 (Esteban Aenlle & Lacomba 1988). Of these, Alcoy-4B and Alcoy-2 have been recently relocated, although Alcoy-4B lies now under a dwelling, while the location of the rest (Alcoy-Barranco and Alcoy-N) is uncertain because the intense erosion in the zone has extended the ravine in both margins, changing the references in the terrain. Nevertheless, an intense process of sampling in the west margin of this lacustrine basin (Gormaget ravine) was initiated in 2005 to relocate these two missing localities, resulting in the location of an important number of levels containing micromammal fossil remains: ABS-1, ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9 and ABS-10 in Alcoi Barranc Sud section, and AC-0, AC-0B and AC-0C in Alcoi Cristian section (Figs 1, 2). The three richest localities in the southern side of the Gormaget ravine are: in Alcoi Barranc Sud (lower part of the deposits from the ravine), ABS-3 and ABS-3A, and in Alcoi Cristian section (upper part of the deposits) the locality AC-0 (Fig. 6). The inferred age for these sites ranges from MN 13 to MN 16, from Late Miocene to Late Pliocene, and their approximate location is shown in Fig. 1.

The aim of the paper is the study of the micromammal remains from the oldest mammal localities known in the Alcoi Basin, some of which have yielded a similar fauna to those of Adrover (1969), and their biostratigraphical and palaeoecological implications.

DOI 10.3140/bull.geosci.1541

Material and methods

Since 2005, about 3,200 kg of sediment were extracted from the localities of Alcoi Barranc Sud and Alcoi Cristian in several field campaigns. The resulting fossil collections are stored in the Museu de Geologia de la Universitat de València (MGUV) with the acronyms ABS1'05-, ABS2-, ABS2'05-, ABS3'05-, ABS3'08-, ABS3A-, ABS7'05-, ABS8-, ABS9-, ABS10-, AC0-, AC0B- and AC0C-. ABS1'05, ABS2'05, ABS3'05 and ABS7'05, correspond all of them to the samplings of the year 2005, and ABS3'08 to a sampling in 2008.

The nomenclature and measurement methods are those of Martín-Suárez & Freudenthal (1993) for the family Muridae, Mein & Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, and Reumer (1984) for the insectivores. Measurements are in millimetres and were taken on a Leica MZ7_5 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment.

Abbreviations. – ABS – Alcoi Barranc Sud; AC – Alcoi Cristian; AF – Alcoi Forn; AL2-C – Alcoy 2C; AL2-D – Alcoy 2D; ALDH – Aldehuela; ALM-M – Almenara-M; AR-4 – Arquillo 4; AW – anterior width; BL – bucal length; BRA-5B – Brácana 5B; c1 – posterior accessory cusp; CEL-9 – Celadas-9; CLC – Calicasas; CLR – Calerico; CR-6 – Crevillente 6; GOR-A – Gorafe-A; H – height; I – upper incisor; L – length; LB-2B – La Bullana 2B; LG-4 – La Gloria-4; LL – labial length; LPE – length posterior emargination; MNA – Mina; PER-E – Peralejos-E; PUR-4 – Purcal 4; MN – European Neogene land mammal units; m1 – first lower molar; m2 – second lower molar; m3 – third lower molar; M1 – first upper molar; M2 – second upper molar; M3 – third upper molar; NGR-1 – Negratín-1; PW – posterior width; RCH-3 – Rambla Chimeneas 3; TCH – Tollo de Chiclana; TLW – talonid width; tma – antero-central cusp; TRW – trigonid width; VAR-1 – Villalba Alta Río 1; VM – Venta del Moro; W – width; YEG – Yeguas; ZOR-3A – Zorreras 3A.

Geological setting

The studied outcrops are located in the Barranco del Gormaig area, in the Alcoy Basin (Fig. 1), which exhibits a magnificent series of Neogene deposits, with continental sediments of Upper Miocene and Pliocene age. This basin belongs to the northern side of the inner Prebetic of the Betic chain, surrounded by the mountain ranges of Menejador, Mariola and Benicadell among others (Fig. 1). In the Alcoy area, the Betic context allowed the development of vast synclinal depressions WSW-ENE oriented. Over them were deposited the characteristic marine marls in "Tap" facies during the marine Miocene. The sea isolation of the North Prebetic basins of Alicante occurred very early (Tortonian), and marine sediments are only represented in the Unit I of Viseras *et al.* (2004). In this manner, a marine basal Tortonian with carbonate facies and limited thickness was deposited over "Tap" facies in angular discordance. Over these we find the continental facies, essentially constituted by lacustrine and fluvial sediments. These deposits belong to Unit II of Viseras *et al.* (2004), being represented by alluvial fan facies in the margin and fluvio-lacustrine facies in the centre. In this context, the Miocene-Pliocene transition takes place in a continental environment (Aguirre *et al.* 1975).

The general direction of the Betic mountain range in Alcoy area is interrupted by the Alcoy Basin. This forms a depression that can be subdivided into several quadrangular grabens, being the Almudaina Graben where we find the studied deposits.

Two continental facies associations are present above the marine Lower Tortonian (Pierson d'Autrey 1987): a lacustrine white series and a fluvial red one, which fill all the central part of the Alcoy Basin, covering the ancient sediments.

The measured stratigraphic sequence comprises about 44 meters, of which the last 6 meters are covered (Fig. 2). To obtain the stratigraphic data presented in Fig. 2, we dug some trenches in different places to look for the fresh rock, using the information that the environment of the ravine showed us.

Gormaig ravine series relates to fluvial series that develop without discontinuity above the lacustrine facies of the basin, reaching the foot of the southern slopes of the Benicadell and Mariola ranges and the northern slopes of the Menejador range. The studied series, with alluvial facies included in sandy marls with organic layers, presents lacustrine features and floodplain deposits. Upwards, conglomerates take more importance (greater thickness and grain size), organic marls are not present and reddish colours are predominant.

In the studied area, the sandy-marls deposits with gray to brownish colours, which can be several meters thick, are generally dominant. In marls there are frequent isolated pebbles or sandy to conglomerate linear intercalations. Conglomerate levels are relatively common, reaching a thickness of a meter or more. The presence of organic lev els of intense dark colour is also remarkable. In about 20 meters in the ABS section, we identify up to 10 of these organic levels (fossil levels ABS-1 to ABS-10).

In ABS the conglomeratic intercalations are frequent, with a slightly erosive base and a yellow sandy matrix. Organic levels are always present in the middle or upper part of the sandy marls, which are placed above each conglomeratic intercalation. In this sense, these deposits seem to respond to specific events that are repeated. Some of the con-

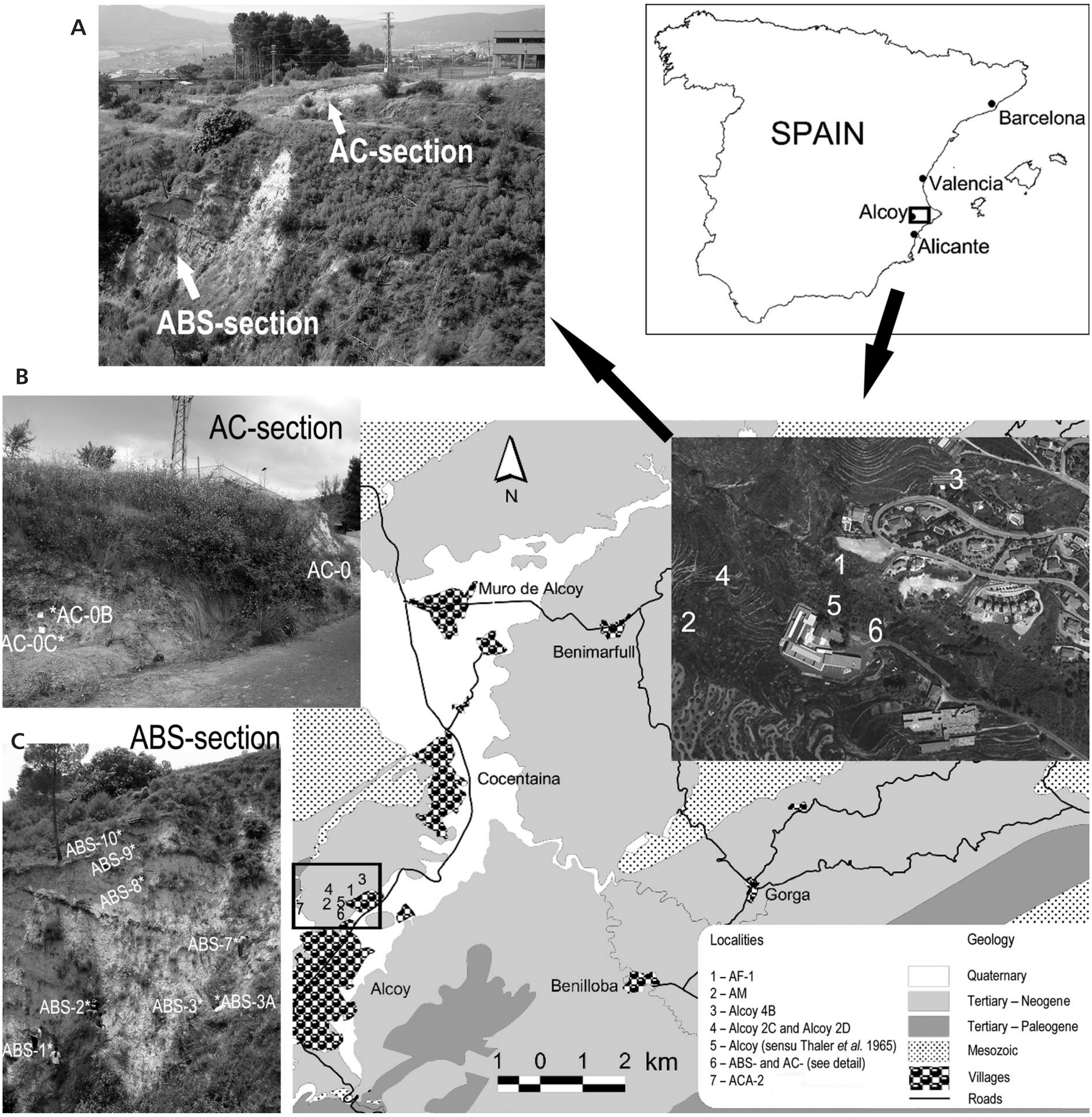


Figure 1. Geographic and geological setting of the Alcoy Basin, showing the location of the outcrops of the Gormaget ravine. A – detail of ABS and AC sections, B – AC-section, C – ABS-section.

glomerates present in ABS are coarsening upward, and some sandy intercalations show the existence of sedimentary structures that indicate the direction of the current. In some organic and sandy-marl levels, the remains of continental gastropods are common. These conglomerates strata are light coloured (often yellow) with a sandy matrix, and often lack internal structure. In some of them we observe coarsening-upward pebbles and minor erosive base. They differ from those at the top of the Gormaig ravine (stratigraphically higher), which have a reddish matrix, a bigger average size of the pebbles and greater thickness of the strata.

Above ABS section, and after a covered stretch of about 7 meters, there is a new section named AC (Alcoi Cristian). The facies association has little differences with that of ABS section, since the organic levels of AC are situated in the middle or upper part of sandy marls, which are arranged above each conglomeratic intercalation or just in contact with the top of conglomerates. AC section shows evidences of paedological structures in marl levels, and of irregular precipitation of carbonates.

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1826

***Apodemus gorafensis* (Ruiz-Bustos, Sesé, Dabrio, Peña & Padial, 1984)**
Figure 3A

Localities. – ABS-3, AC-0, AC-0C.

Material and measurements (L × W). – 1 m1 (ABS3'08-3) (2.35 × –); 1 m2 (AC0-46) (1.53 × 1.32); 2 M1 (AC0-20) (– × 1.50), (AC0-119); 1 M3 (ABS3'08-34).

Description. – m1. The lingual side of the molar is missing. The tma and labial cingulum are well developed. There is a large oval c1. Roots are not preserved.

m2. The anterolabial cusp is large and connected basally to the protoconid and a well-developed labial cingulum. There is a medium-sized round c1 and a slightly smaller accessory cusp, connected basally to the posterior side of the protoconid (Fig. 3A). The posterior heel is large, oval and lingually displaced. Roots are not preserved.

M1. The specimens are poorly preserved. The t1 and t3 have small distal spurs. There is a well-developed t7. Roots are not preserved.

M3. The labial side of the molar is absent. The t1 is connected to t4-t5-t6. There is a t9 attached to the posterior side of the t8. Roots are not preserved.

Discussion. – The presence of a big tma, well-developed labial cingulum in the lower molars and t7 in M1 and M2 are typical traits of *Apodemus.* Also, some Late Miocene and Early Pliocene populations of *A. atavus* Heller, 1936 and *A. gorafensis* have a t9 in M3 (García-Alix *et al.* 2008a). The studied molars differ from *A. gudrunae* van de Weerd, 1976, by their bigger size and presence of a well-developed t7, and from *A. agustii* Martín Suárez, 1988, by the connection of the t6-t9 in M1 and a smaller tma. The length of the single m1 is consistent with the highest values of *A. gorafensis*, such as the biggest specimens from MNA-2, MNA-4 and CLR-1 (García-Alix *et al.* 2008a). Its size is also close to the values of *A. jeanteti* from Villalba Alta and Arquillo 3. However, this latter species shows a reduced or absent tma, which is well developed in specimen ABS3'08-3.

The size of the molars from AC-0 and AC-0C are consistent with those of *A. gorafensis* from Botardo C (Martín-Suárez 1988), DHS-16, PUR-4, PUR-24A, PUR 25 and PUR-25A (García-Alix *et al.* 2008a), being slightly smaller than the teeth from Gorafe A (type locality, Ruiz-Bustos *et al.* 1984), Gorafe 3, 4 and 5 (Martín-Suárez 1988) MNA-2 and MNA-4 (García-Alix *et al.* 2008a) and AL2-D (Mansino *et al.* 2013). Their size is similar to those of *A.* aff. *gorafensis* from Peralejos E (Adrover *et al.* 1988), Celadas 9 and La Gloria 4 (Adrover *et al.* 1993), and to the highest values of *A.* aff. *gorafensis* from PUR-23 (García-Alix *et al.* 2008a).

Genus *Micromys* Dehne, 1841

***Micromys* sp.**
Figure 3B

Localities. – ABS-2, ABS-9.

Material and measurements. – 1 m2 (ABS9-1) (1.05 × 0.95); 1 M3 (ABS2'05-5).

Description. – m2. The anterolabial cusp is big and isolated. The labial cingulum is low and wide. There is a large round c1. There are no accessory cusps. The posterior heel is big and oval. Roots are not preserved.

M3. Molar broken anteriorly. The t4, t5 and t6 are connected. The t8 is very big and connects labially to a much smaller t9. Roots are not preserved.

Discussion. – The diminutive size of the specimens, brachyodonty of the molars and distinct labial cingulum agree with the genus *Micromys* (Fig. 3B). The m2 is smaller than in *M. steffensi* van de Weerd, 1979, from Kardia, and *M. cingulatus* Storch & Dahlmann, 1995 from Maramena, being consistent with the smallest specimens of *M. bendai* van de Weerd, 1979 and *M. kozaniensis* van de Weerd, 1979 from Ptolemais 1 and Ptolemais 3, respectively. Its size agrees with the biggest molars of *M. praeminutus*, such as the m2 from Sète (Michaux 1969), and *M. tedfordi* Wu & Flynn, 1992, being bigger than *M. caesaris* Minwer-Barakat, García-Alix, Martín-Suárez & Freudenthal, 2008, which is considered a junior synonym of *M. praeminutus* by Horáček *et al.* (2013), *M. minutus* (Pallas, 1771), *M. chalceus* Storch, 1987 and *M. paricioi* Mein, Moissenet & Adrover, 1983.

The absence of accessory cusps differs from *M. cingulatus*, *M. steffensi*, *M. bendai* and *M. kozaniensis*. The m2 has a wider labial cingulum than *M. paricioi*, *M. caesaris* and *M. minutus*. According to Minwer-Barakat *et al.* (2008), the m2 of *M. praeminutus* from Sète has a large anterolabial cuspid, more separated from the protoconid

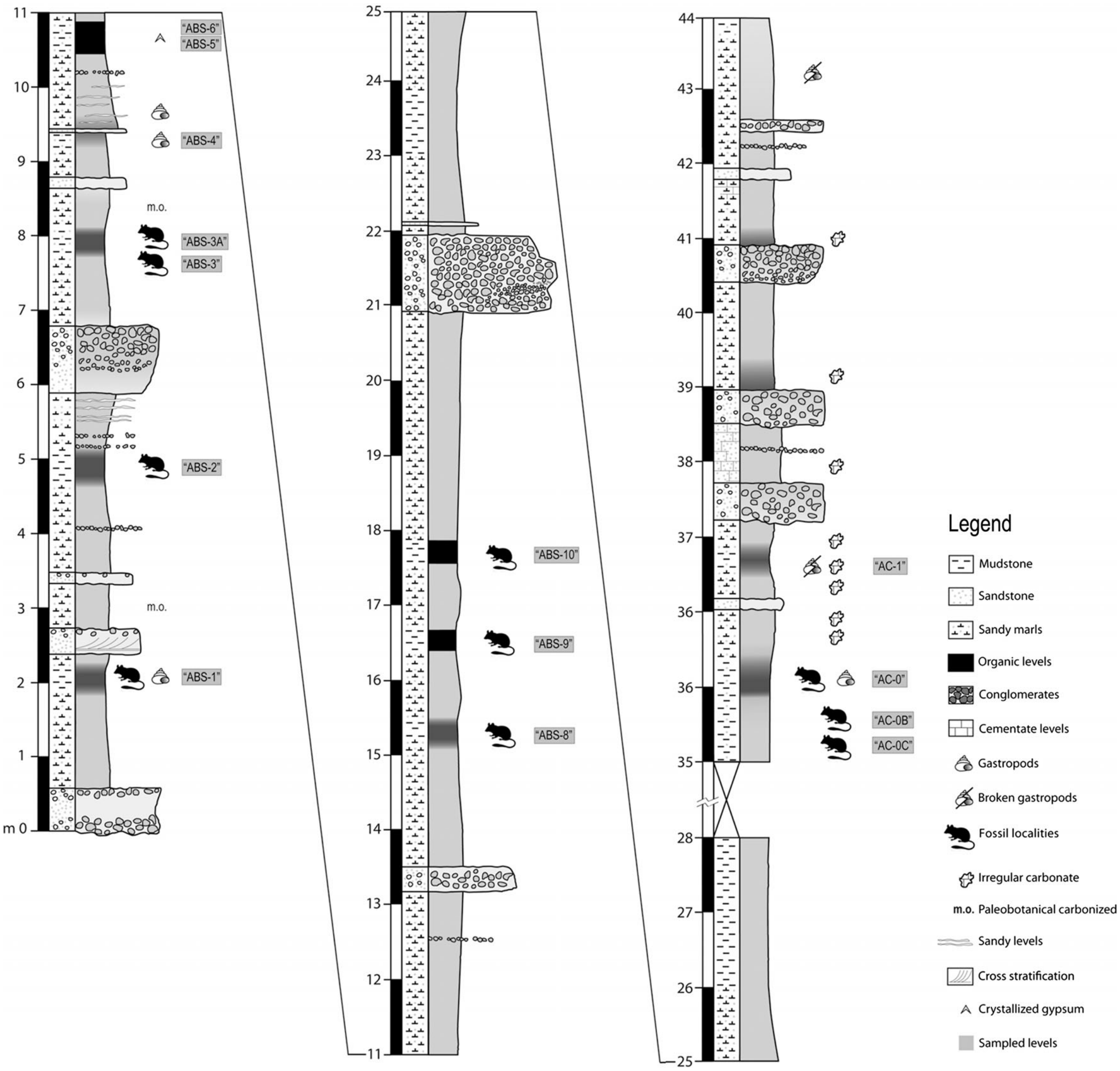


Figure 2. Lithostratigraphic log of the Alcoy-Mina surroundings, with the stratigraphical position of the microvertebrate-bearing localities of ABS-1, ABS-2, ABS-3, ABS-3A, ABS-7, ABS-8, ABS-9, ABS-10, AC-0, AC-0B and AC-0C.

than in *M. caesaris*, a well-developed labial cingulum, and it is wider anteriorly than posteriorly. The specimen ABS9-1 agrees with this morphology (Fig. 3B), but because of the scarcity of the material and lack of diagnostic features, we ascribe the studied material to *Micromys* sp.

Genus *Occitanomys* Michaux, 1969

Occitanomys alcalai **Adrover, Mein & Moissenet, 1988**
Figure 3C, D

Localities. – ABS-2, ABS-3, ABS-3A, AC-0, AC-0B, AC-0C.

Material and measurements. – 5 m1 (ABS3'08-45), (AC0-66) (– × 1.30), (AC0-107) (– × 1.32), (AC0-109), (AC0C-3) (– × 1.24); 3 m2 (ABS3A-17), (AC0-5) (1.38 × 1.24), (AC0C-12) (– × 1.25); 2 m3 (ABS3'08-43) (– × 0.91), (AC0-106); 3 M1 (ABS2-36, AC0C-5, AC0-114), 1 M2 (AC0B-12).

Description. – m1. The metaconid and the lingual lobe of the anteroconid are connected by a narrow crest. The labial cingulum is wide. There is a well-developed round c1. One specimen has a big accessory cusp connected to the protoconid. There is a hint of distal spur. The posterior heel is moderate, oval and lingually displaced. Roots are not preserved.

Table 1. Measurements in millimetres of the teeth of *Paraethomys* from ABS-2, ABS-3, ABS-3A, AC-0 and AC-0B. L = length; W = width; m1 = first lower molar; m2 = second lower molar; m3 = third lower molar; M1 = first upper molar; M2 = second upper molar; M3 = third upper molar.

El.	Loc.	Sp.	Par.	n	Min.	Mean	Max.
m1	ABS-3	*P.* aff. *abaigari*	L	1	–	2.29	–
			W	2	1.42	1.45	1.48
	AC-0	*P.* aff. *abaigari*	L	1	–	2.22	–
			W	2	1.44	1.46	1.48
m2	ABS-3	*P.* aff. *abaigari*	L	1	–	1.63	–
			W	1	–	1.40	–
		P. meini	L	2	1.47	1.52	1.57
			W	1	–	1.38	–
	ABS-3A	*P.* aff. *abaigari*	L	1	–	1.71	–
			W	2	1.43	1.46	1.49
		P. meini	L	3	1.42	1.46	1.52
			W	3	1.29	1.33	1.40
	AC-0	*P.* aff. *abaigari*	L	3	1.63	1.67	1.69
			W	5	1.46	1.53	1.61
m3	ABS-2	*P.* aff. *abaigari*	W	1	–	1.28	–
	ABS-3	*P. meini*	L	1	–	1.12	–
			W	2	1.16	1.19	1.23
	AC-0	*P. meini*	W	2	1.16	1.19	1.22
M1	ABS-3	*P.* aff. *abaigari*	W	1	–	1.73	–
	ABS3-A	*P. meini*	L	1	–	2.31	–
			W	1	–	1.46	–
	AC-0	*P.* aff. *abaigari*	L	2	2.55	2.62	2.69
			W	3	1.58	1.63	1.68
	AC-0B	*P. meini*	L	1	–	2.30	–
M2	ABS-2	*P.* aff. *abaigari*	L	1	1.74	1.83	1.91
	ABS-3A	*P.* aff. *abaigari*	L	3	1.80	1.84	1.91
			W	3	1.59	1.66	1.70
	AC-0	*P.* aff. *abaigari*	L	2	1.78	1.82	1.85
			W	3	1.52	1.59	1.69
	AC-0B	*P.* aff. *abaigari*	W	1	–	1.69	–
M3	ABS-2	*P. meini*	L	1	–	1.00	–
			W	1	–	1.10	–
	ABS-3	*P.* aff. *abaigari*	L	1	–	1.23	–
			W	1	–	1.17	–
	ABS-3A	*P.* aff. *abaigari*	L	2	1.23	1.26	1.30
			W	3	1.18	1.20	1.23
	AC-0	*P.* aff. *abaigari*	L	2	–	1.23	–
			W	2	1.23	1.24	1.25

m2. The anterolabial cusp is big, round and connected basally with the protoconid and a reduced labial cingulum. The c1 is much reduced, and there are no accessory cusps. There is a hint of longitudinal spur. The posterior heel is well developed and round. Roots are not preserved.

m3. One molar is broken anteriorly and the other one posteriorly. There is no anterolabial cusp. The protoconid and metaconid are separated from the hypoconid-entoconid by a deep valley. There is no c1. Roots are not preserved.

M1. The t1 is displaced backwards and connects basally with the lingual side of t5. There are a well-developed t1 bis and a weak t2 bis. The t6 and t9 are connected. The t12 is small but distinct. Roots are not preserved.

M2. The specimen is broken anterolabially. The t1 is connected to t5 by a low crest. There is a t1bis. The t3 is reduced and isolated. There is no t7. Roots are not preserved.

Discussion. – *Occitanomys alcalai* ranges in age from the Late Turolian to the Ruscinian. Several authors considered this taxon an immigrant in the Iberian Peninsula (Adrover *et al.* 1988, Freudenthal & Martín-Suárez 1999), and the phylogenetic relationship with other species of the genus is not clear. The molars from ABS-2, ABS-3, ABS-3A, AC-0, AC-0B and AC-0C show a symmetric anteroconid, relative high crown, well-developed t1 bis, absence of isolated cusps in the upper molars, and lack of complete longitudinal crests in the lower molars, which are typical traits of *O. alcalai*. The size of the measurable specimens from AC-0 and AC-0C is similar to the maxima of *O. alcalai* from the Ruscinian localities of Peralejos E (Adrover *et al.* 1988), La Gloria 4 and 5, Celadas 9 and the Late Turolian sites of Villastar and Valdecebro 3 and 6 (Adrover *et al.* 1993), and slightly bigger than *O. alcalai* from the localities of the Granada Basin (García-Alix *et al.* 2008a). Their size is also close to the lower measurements of *O. adroveri* (Thaler, 1966), but this species has more developed longitudinal connections in m1 and m2, an asymmetrical anteroconid and less developed longitudinal crests in the upper molars. Also, the absence of anterolabial cusp in m3 and the t1-t5 connection in M2 are more frequent in *O. alcalai* (Minwer-Barakat *et al.* 2009a). The specimens studied differ from *O. sondaari* by its bigger size, greater development of t1 bis, less developed longitudinal crests in the lower molars, higher t6-t9 connection and more developed labial cingulum, and from *O. brailloni* by their smaller size and less-developed spurs and crests in the upper molars.

Genus *Paraethomys* Petter, 1968

Paraethomys aff. *abaigari* Adrover, Mein & Moissenet, 1988

Figure 3E–I

Localities. – ABS-2, ABS-3, ABS-3A, AC-0, AC-0B.

Material. – 7 m1 (ABS3'08-1, ABS3'08-5, ABS3A-36, AC0-19, AC0-35, AC0-41, AC0-51); 11 m2, (ABS3'05-2,

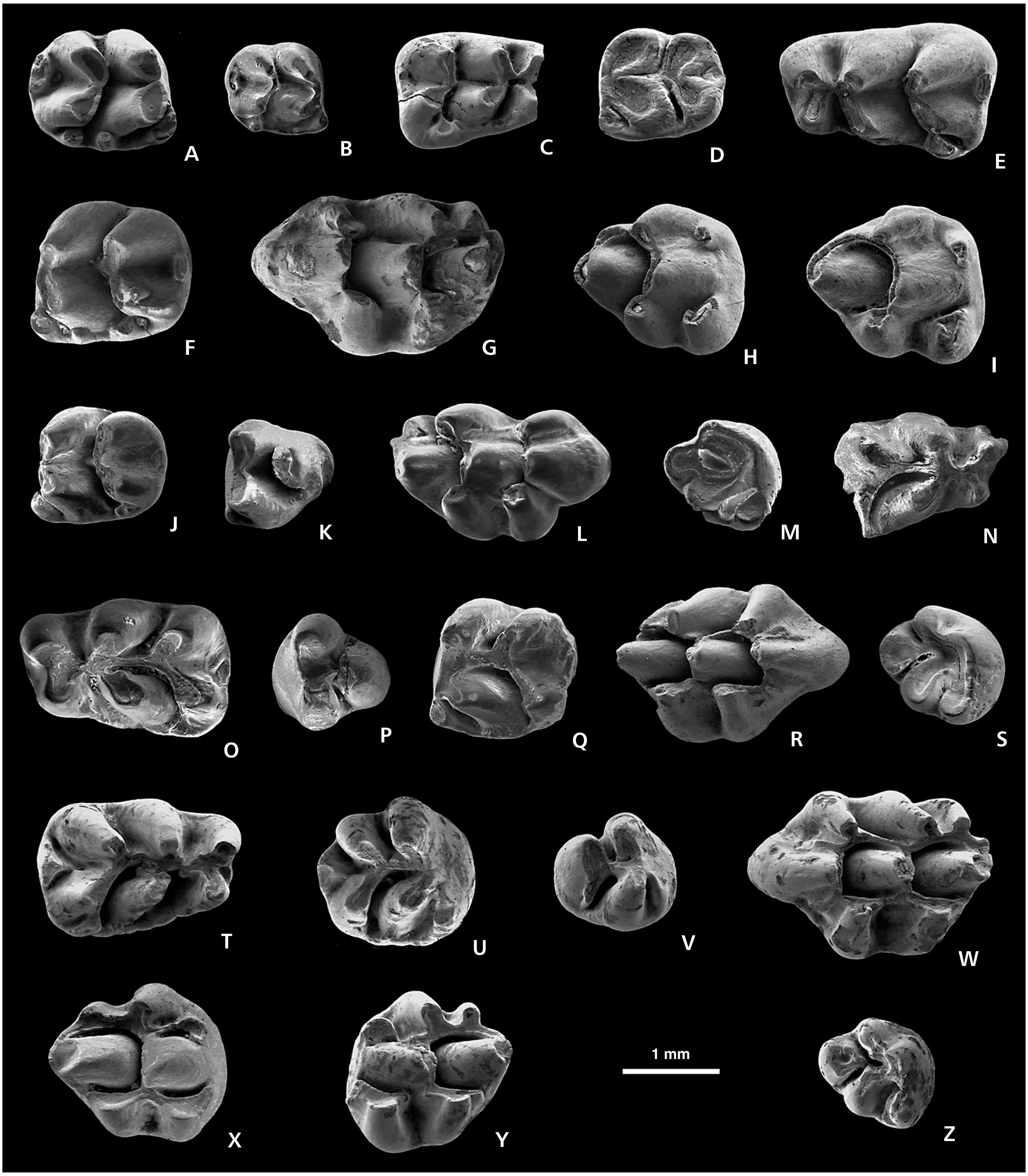


Figure 3. Fossil rodents from ABS-2, ABS-3, ABS-3A, ABS-9, AC-0 and AC-0C. • A – *Apodemus gorafensis*; right m2, AC0-46. • B – *Micromys* sp.; right m2, ABS9-1. • C, D – *Occitanomys alcalai*; C – right m1, AC0C-3; D – left m2, AC0C-5. • E–I – *Paraethomys* aff. *abaigari*; E – left m1, ABS3'08-1; F – left m2, AC0-110; G – right M1, AC0-43; H– right M2, ABS3A-2; I – right M2, ABS3A-21. • J–M – *Paraethomys meini*; J – left m2, ABS3A-42; K – left m3, ABS3'08-15; L – right M1, ABS3A-20; M – right M3, ABS3'08-31. • N–S – *Stephanomys dubari*; N – right m1, ABS2-33; O – left m1, ABS3'08-2; P – left m3, ABS3A-18; Q – left m2, ABS3'08-8; R – right M1, ABS2-34; S – right M3, ABS3'08-33. • T–W – *Stephanomys* aff. *cordii*; T – right m1, AC0-1; U – right m2, AC0-8; V – right m3, AC0-11; W – left M1, AC0-12; X – left M2, AC0-15; Y – right M2, AC0-15; Z – right M3, AC0-10. Scale: 1 mm.

ABS3'05-3, ABS3'08-6, ABS3'08-11, ABS3A-12, ABS3A-15, AC0-3, AC0-4, AC0-18, AC0-47, AC0-110); 2 m3 (ABS2-20, ABS3'05-4); 8 M1 (ABS3'08-18, ABS3'08-19, ABS3'08-27, ABS3A-19, AC0-28, AC0-43, AC0-44, AC0-113); 15 M2 (ABS2'05-4, ABS2-35, ABS3'08-28, ABS3'08-29, ABS3A-2, ABS3A-21 to ABS3A-24, AC0-7, AC0-26, AC0C-49, AC0-117, AC0B-5, AC0B-6); 7 M3 (ABS3'08-31, ABS3A-25 to ABS3A-27, AC0-9, AC0-16, AC0C-10).

Measurements. – See Table 1.

Description. – m1. Slightly asymmetrical anteroconid. The two anterior pairs of cusps are connected by a narrow crest. Two specimens have a reduced longitudinal spur. Moderate labial cingulum, which bears one or two small accessory cusps. The posterior heel is big, round or oval and lingually displaced. Roots are not preserved.

m2. The anterolabial cusp is big and connected basally with the protoconid and the labial cingulum. The c1 is well developed, and a small accessory cusp attached to the labial side of the protoconid may be present. There is a longitudinal spur in 8 out of 11 specimens. The posterior heel is laminar in three specimens, oval in the others. Roots are not preserved.

m3. The specimens are broken anteriorly. There is no longitudinal connection. There is neither c1 nor accessory cusps. Roots are not preserved.

M1. The t1 is displaced backwards. The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. There are distal spurs on t1 and t3, although much reduced in some specimens (Fig. 3G). The connection between t4 and t8 is very low. There is a small t12. There are three roots.

M2. The t1 and t3 are isolated. The t3 is reduced. In 7 out of 13 specimens there is a reduced spur in t1. One molar has a slightly swollen t9 (Fig. 3H), which is reduced in the others (Fig. 3I). There is no t12. There are four roots.

M3. The t1 is large and isolated. The t3 is absent. The t8 is connected to the t4-t5-t6 junction. There are three roots.

Discussion. – Two different lineages of *Paraethomys* can be distinguished in the Early Pliocene: the small sized *P. meini* (Adrover, 1969), and the bigger forms of the anagenetic lineage *P.* aff. *abaigari*-*P. abaigari*-*P. jaegeri* Montenat & de Bruijn, 1976. Besides the difference in size, Adrover *et al.* (1988) noted a greater development of the distal spurs in t1 and t3 in the upper molars of the bigger species. These differences are clear in *P. jaegeri* and *P. abaigari*, but the older *P.* aff *abaigari* is more similar to *P. meini* and the size of both species can overlap, making specific adscription complicated (García-Alix *et al.* 2008a). That is the case in some localities such as PUR-4 in the Granada Basin (García-Alix *et al.* 2008a) and AF-1 (Mansino pers. comm.), where *Paraethomys* has a great variability in size but two species cannot be discriminated (García-Alix *et al.* 2008a). This situation is the same as in the assemblages studied in this paper from the Alcoi Barranc Sud and Alcoi Cristian sections, where a reduced number of *Paraethomys* remains have been located. We cannot assess if there is a continuous distribution ranging from the smallest to the biggest specimens as in PUR-4 and AF-1. However, the size of the molars ascribed to *P.* aff. *abaigari* matches the biggest specimens from these localities, with some specimens being clearly bigger, falling within the range of variation of *P.* aff. *abaigari* from CLC-5A and PUR-13 (García-Alix *et al.* 2008a), Celadas 9 and La Gloria 4 (Adrover *et al.* 1993) and AL2-C and AL2-D (Mansino *et al.* 2013). Adrover *et al.* (1988) noted that *P. abaigari* and *P. jaegeri* have more developed distal spurs in t1 and t3 in M1, and that the molars are relatively wider. However, these differences are not as conspicuous between *P.* aff. *abaigari* and *P. meini*, since the shape of the molars of both species is similar and some specimens of *P. meini* have moderately developed spurs, which are absent in some molars of *P.* aff *abaigari*. Since more data are needed to clarify the morphological differences between both taxa, we ascribe the biggest specimens from these localities to *P.* aff. *abaigari*.

Paraethomys meini (Michaux, 1969)

Figure 3J–M

Localities. – ABS-2, ABS-3, ABS-3A, AC-0, AC-0B.

Material. – 2 m1 (AC0-102, AC0B-8); 6 m2 (ABS3'08-10, ABS3'08-11, ABS3A-13, ABS3A-14, ABS3A-42, AC0-53); 6 m3 (ABS3'08-15 to ABS3'08-17, ABS3A-28, AC0-111, AC0B-9); 3 M1 (ABS3'08-21, ABS3A-20, AC0B-7); 1 M3 (ABS2'05-2).

Measurements. – See Table 1.

Description. – m1. Slightly asymmetrical anteroconid. The two anterior pairs of cusps are connected by a narrow crest. One specimen has a reduced longitudinal spur. Moderate labial cingulum, which bears a big accessory cusp in one specimen. The posterior heel is big, oval and central. Roots are not preserved.

m2. Moderate anterolabial cusp, in contact with the labial cingulum and the anterior side of the metaconid. There is a much reduced longitudinal spur. One specimen has a very small c1, absent in the others. The posterior heel is much reduced. Roots are not preserved.

m3. The anterolabial cusp is absent or reduced. There is neither c1 nor accessory cusps. Roots are not preserved.

M1. The t1 is displaced backwards. The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. One specimen has low longitudinal connections between t1-t5 and t3-t6 (Fig. 3L). The other two molars have a spur in t1, and one of them also in t3. There is a small t12. Roots are not preserved.

M3. The t1 is large and isolated. The t3 is absent. The t8 is connected to the t4-t5-t6 junction. Roots are not preserved.

Discussion. – The morphology of this group of specimens is consistent with *P. meini,* although the presence of distal spurs in M1, especially in t3, is more frequent in *P. abaigari* (Adrover *et al.* 1998). However, some specimens of *P. meini* can also develop this feature (García-Alix *et al.* 2008a, Mansino *et al.* 2013) and the size of the molars described is similar to that of *P. meini* from CLC-5A, PUR-13 (García-Alix *et al.* 2008a), Peralejos E (Adrover *et al.* 1988), Celadas 9, La Gloria 4 (Adrover *et al.* 1993), AL2-C and AL2-D (Mansino *et al.* 2013), and LB-2B (Mansino pers. comm.). Because of this, we ascribe the specimens from Alcoi Barranc Sud and Alcoi Cristian to *P. meini*.

Genus *Stephanomys* Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet & Faillat, 1991

Figure 3N–S

Localities. – ABS-1, ABS-2, ABS-3, ABS-3A.

Material. – 8 m1 (ABS2-33, ABS2-38, ABS3'05-1, ABS3'08-2, ABS3'08-37, ABS3A-8 to ABS3A-10); 9 m2 (ABS2-1, ABS3'08-7 to ABS3'08-9, ABS3'08-12, ABS3'08-13, ABS3'08-22, ABS3A-1, ABSA-16); 3 m3 (ABS3'08-14, ABS3'08-39, ABS3A-18); 3 M1 (ABS2-2, ABS2-34, ABS2-37); 4 M2 (ABS3'08-23 to ABS3'08-26); 4 M3 (ABS1-1, ABS2-3, ABS3'08-32, ABS3'08-33).

Measurements. – See Table 2.

Description. – m1. The anteroconid is slightly asymmetrical, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is low and narrow. There is a well-developed longitudinal crest that connects the posterior cusps with the metaconid. The c1 is big and subtriangular. The posterior heel is big and oval. Roots are not preserved.

m2. The anterolabial cusp is high and big, connected to the protoconid and a moderately developed labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. The c1 may be absent, small or well developed. The c1 ranges from very small to well developed. There are no accessory cusps. The posterior heel is large and oval. There are two roots.

m3. The anterolabial cusp is absent in the specimen from ABS-3A (Fig. 3O), and reduced in ABS-3. There is a longitudinal crest that reaches the protoconid-metaconid junction. There are two roots.

M1. The t1 is displaced backwards. The t1 bis and t2 bis are well developed. The posterior crest of t1 and the labial longitudinal crest of t3 are complete, but the crest in t1 is usually lower (Fig. 3R). The t12 is reduced. Roots are not preserved.

M2. The t1 has a small t1bis attached to its anterior side. The longitudinal crest of t1 is low in two specimens, and the t3 is isolated in another two. The t12 is well developed. These molars have three roots.

M3. The t1 and t8 are connected to the t4-t5-t6 junction. The t3 is absent. There are three roots.

Discussion. – The height of the crown, development of longitudinal crests in the lower molars and distal crests or spurs in t1 and t3 of the upper molars suggest that the specimens studied belong to the genus *Stephanomys*. These molars are smaller, less hypsodont and with a less pronounced stephanodonty than younger *Stephanomy*s such as *S. donnezani* (Déperet, 1890), *S. balcellsi* Gmelig-Meyling & Michaux, 1973, *S. vandeweerdi* Adrover, 1986, *S. thaleri* López-Martínez, Michaux & Hutterer, 1998 and *S. minor* Gmelig-Meyling & Michaux, 1983. In addition, *S. balcellsi* and *S. minor* differ from other species of the genus by having a tubercular posterior heel. *Stephanomys debruijni* de Giuli, 1989 differs from our specimens by having a small tma in some m1, a reduced and rounded posterior heel and a t1 situated extremely backwards in the M1. *Stephanomys dubari* is bigger, more hypsodont and with a more pronounced stephanodonty than *S. ramblensis* van de Weerd, 1976. This latter species presents sometimes the longitudinal crest of the m1 directed to the protoconid, and the t1 and t3 of the M1 and M2 rarely develop full longitudinal crests (García-Alix 2006).

The studied specimens fall within the range of variation of *S. dubari* from Castelnou 3, its type locality (Aguilar *et al.* 1991), being slightly smaller than *S. cordii* Ruiz-Bustos, 1986 from Alcoy (Cordy 1976) and AL2-AL2-C and AL2-AL2-D (Mansino et al. 2013). One m1 from ABS-2, much worn and broken posteriorly, seems much smaller than the other molars of *S. dubari* (Fig. 3N), even the specimens from the same locality (compare with Fig. 3O), but because of the great development of the longitudinal crest, which reaches the metaconid-protoconid connection, reduced labial cingulum and height of the crown, we ascribe this molar to *Stephanomys*. These molars also differ from

S. cordii by the t1 displaced backwards (Fig. 3R), the longitudinal crest of the m3 reaching the protoconid-metaconid junction instead of the protoconid and the less developed distal crests in M1 and M2.

Table 2. Measurements in millimetres of the teeth of *Stephanomys dubari* from ABS-1, ABS-2, ABS-3, ABS-3A and *Stephanomys* aff. *cordii* from ABS-8, AC-0, AC-0B and AC-0C. L = length; W = width; m1 = first lower molar; m2 = second lower molar; m3 = third lower molar; M1 = first upper molar; M2 = second upper molar; M3 = third upper molar.

Element	Locality	Sp.	Parameter	n	Min.	Mean	Max.
m1	ABS-3	*dubari*	L	1	–	2.29	–
			W	1	–	1.38	–
	AC-0	aff. *cordii*	L	4	2.11	2.21	2.33
			W	4	1.33	1.43	1.52
m2	ABS-2	*dubari*	W	1	–	1.47	–
	ABS-3	*dubari*	L	3	1.53	1.63	1.69
			W	5	1.46	1.50	1.55
	ABS-3A	*dubari*	L	1	–	1.62	–
	AC-0	aff. *cordii*	L	1	–	1.63	–
			W	1	–	1.59	–
	AC-0C	aff. *cordii*	W	1	–	1.58	–
m3	ABS-3	*dubari*	L	1	–	1.48	–
			W	1	–	1.35	–
	ABS-3A	*dubari*	L	1	–	1.27	–
			W	1	–	1.22	–
	AC-0	aff. *cordii*	L	4	1.31	1.34	1.36
			W	6	1.19	1.23	1.28
	AC-0B	aff. *cordii*	W	1	–	1.34	–
M1	ABS-2	*dubari*	L	1	–	2.43	–
			W	3	1.59	1.73	1.88
	AC-0	aff. *cordii*	L	2	2.59	2.63	2.67
			W	5	1.77	1.84	1.96
M2	ABS-3	*dubari*	L	4	1.66	1.74	1.86
			W	4	1.62	1.71	1.83
	ABS-8	aff. *cordii*	L	1	–	1.92	–
			W	1	–	1.66	–
	AC-0	aff. *cordii*	L	5	1.50	1.75	1.96
			W	7	1.56	1.71	1.82
	AC-0C	aff. *cordii*	L	1	–	1.95	–
			W	1	–	1.83	–
M3	ABS-1	*dubari*	L	1	–	1.16	–
			W	1	–	1.13	–
	ABS-3	*dubari*	L	2	1.18	1.23	1.28
			W	2	1.03	1.13	1.23
	AC-0	aff. *cordii*	L	2	1.20	1.24	1.29
			W	5	1.13	1.19	1.25
	AC-0C	aff. *cordii*	L	1	–	1.19	–
			W	1	–	1.29	–

Stephanomys aff. _cordii_ Ruiz-Bustos, 1986
Figure 3T–Z

Localities. – ABS-8, AC-0, AC-0B, AC-0C.

Material. – 8 m1 (AC0-1, AC0-2, AC0-98 to AC0-101, AC0-108, AC0C-6); 4 m2 (AC0-8, AC0B-2, AC0C-4, AC0C-11); 7 m3 (AC0-11, AC0-42, AC0-56, AC0-103 to AC0-105, AC0B-1); 7 M1 (AC0-12 to AC0-14, AC0-45, AC0-133, AC0B-10, AC0C-1); 10 M2 (ABS8-1, AC0-6, AC0-15, AC0-48, AC0-50, AC0-115, AC0-116, AC0-118, AC0-134, AC0C-7); 6 M3 (AC0-10, AC0-17, AC0-58, AC0-59, AC0-121, AC0C-8).

Measurements. – See Table 2.

Description. – m1. The anteroconid is slightly asymmetrical, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulum is moderately developed. There is a well-developed longitudinal crest that connects the posterior cusps with the metaconid or the protoconid-metaconid junction. The c1 is moderate in size and subtriangular. The posterior heel is big, oval or subtriangular. There are two roots.

m2. The anterolabial cusp is high and big, connected to the protoconid and a moderately developed labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. The c1 is reduced. There are no accessory cusps. The posterior heel is large, ranging from round to laminar. Roots are not preserved.

m3. The anterolabial cusp is low and reduced. The longitudinal crest can reach the metaconid (1) the protoconid-metaconid junction (3) or the protoconid (3). Roots are not preserved.

M1. The position of t1 and t3 is almost symmetrical (Fig. 3W). The t1 bis and t2 bis are well developed. The posterior crest on t1 and the labial longitudinal crest on t3 are high and complete except in one specimen, which has a lower distal crest on t1. The t12 is reduced. Roots are not preserved.

M2. The t1 has a small t1bis attached to its anterior side. The longitudinal crest on t1 is absent in 1 out of 9 specimens and low in three. The longitudinal crest on t3 is absent in 2 out of 9 specimens and low in another one (Fig. 3Y). The t12 is well developed. Roots are not preserved.

M3. The t1 and t8 are connected to the t4-t5-t6. The t3 is absent. There are three roots.

Discussion. – The material from ABS-8, AC-0, AC-0B and AC-0C has been directly compared with the collection of *S. cordii* from AL2-C and AL2-D (Mansino *et al.* 2013) housed at the Museu de Geologia de la Universitat de València. In general, the morphology of the specimens is similar to *S. cordii*, which has as a reduced labial cingulum and tubercular posterior heel in m1 and m2, a poorly-developed anterolabial cusp in m3, a longitudinal crest of m3 usually united to the protoconid and a symmetrical position of t1 and t2 in M1. In the m3 from AL2-C and AL2-D, the longitudinal crest reaches the protoconid in eight specimens, the protoconid-metaconid junction in five and cannot be observed properly in another six. This proportion is slightly higher than in the specimens from AC-0 and AC-0B (3 out of 7). The relative positions of t1 and t3 in the M1 are also similar, but the longitudinal crests are higher in M1 and M2 from AL2-C/AL2-D.

Stephanomys dubari is considered the likely descendant of *S. ramblensis* and the ancestor of *S. cordii* by several authors (*e.g.* Minwer-Barakat 2005 or García-Alix *et al.* 2008a among others). There is an increase in size, stephanodonty and hypsodonty in the lineage *Occitanomys adroveri-S. ramblensis-S. dubari-S. cordii* (García-Alix *et al.* 2008a), which will continue in some of their Middle and Late Pliocene descendants (for a complete phylogeny of the genus see García-Alix 2006). The size of the specimens studied falls within the range of variation of *S. cordii* from Alcoy (Cordy 1976) and AL2-C and AL2-D (Mansino *et al.* 2013). Its average sizes are also similar to *S. dubari* described in this paper, but some of the smaller specimens of this latter taxon cannot be measured properly (see Fig. 3N) and the highest values usually correspond to *S.* aff. *cordii* (see Table 2). For these reasons, we ascribe the material from ABS-8, AC-0, AC-0B and AC-0C to *S.* aff. *cordii*, which has a similar size but lower longitudinal connections than *S. cordii*.

***Stephanomys* sp.**

Localities. – ABS-7, ABS-9.

Material. – 1 m2 (ABS7'05-3); 1 M1 (ABS9-3).

Description. – m2. The molar is broken anteriorly and much worn. Most of the enamel has been lost. There is a full longitudinal crest that reaches the metaconid. The posterior heel is big and subtriangular.

M1. The specimen is broken, only the t3, t5 and t6 can be observed. The t3 has a high and full distal crest that reaches the t5-t6 connection.

Discussion. – The full longitudinal crests and great height of the crown agree with *Stephanomys*. However, the scarcity of the material and poor state of preservation prevent us from reaching a specific ascription, since we cannot discriminate if they belong to *S. dubari* or *S. cordii*.

Family Cricetidae Fischer, 1817
Subfamily Cricetinae Fischer, 1817

Genus *Apocricetus* Freudenthal, Mein & Martín Suárez, 1998

***Apocricetus* cf. *barrierei* (Mein & Michaux, 1970)**

Figure 4A

Locality. – ABS-3A.

Material. – 1 M1 (ABS3A-37) (2.67 × 1.72).

Description. – M1. Weak cingulum ridge. Double anterolophule, arising from a short preloph. Absent anterior protolophule, mesoloph and ectomesoloph. Present anterior metalophule. Absent posterior metalophule. The posterior part of the posterosinus is shallow, whereas the anterior part is much deeper. The posteroloph, and not the metacone, constitutes the posterior side of the tooth. There are four roots.

Discussion. – Usually, size has been the main criterion used to distinguish between species of the genus *Apocricetus*, especially in the youngest part of the phylogenetic lineage defined by Freudenthal *et al.* (1998). The size of the M1 of *A.* cf. *barrierei* from ABS-3A coincides approximately with the mean length and width values of *A. barrierei* (see data from Ruiz-Sánchez *et al.* 2014; Fig. 4A–C). The length of this tooth is clearly smaller than *A. angustidens* (Depéret, 1890) and longer than those of *A.* aff. *plinii*, *A. plinii* (Freudenthal, Lacomba & Martín-Suárez, 1991) and *Apocricetus alberti* Freudenthal, Mein & Martín-Suárez, 1998. A weak cingulum ridge is present in some specimens of *A. alberti* (Mansino *et al.* 2014) and *A. barrierei* (Ruiz-Sánchez *et al.* 2014), being more developed in *A. angustidens* (Freudenthal *et al.* 1998). The double anterolophule and the absence of mesoloph in M1 distinguish *A.* cf. *barrierei* from ABS-3A from *A. plinii* from Crevillente 15 (type locality) and *A.* aff. *plinii* from Crevillente 23. The development of the preloph of the specimen from ABS-3A is similar to that of *A. barrierei* from La Bullana 2B (Fig. 4C, Ruiz-Sánchez *et al.* 2014). This crest is absent in *A.* aff. *plinii* and *A. plinii*, and much rarer and less developed in *A. alberti*, while it has not been described in the populations of *A. angustidens* (Mansino *et al.* 2014). The anterior protolophule is more frequent in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and less frequent in *A. barrierei* and *A. angustidens* (Mansino *et al.* 2014, Ruiz-Sánchez *et al.* 2014). The proportion of specimens with posterior metalophule in M1 decreases from the older to the younger species of the genus, being absent in *A. barrierei* and *A. angustidens* (Mansino *et al.* 2014). Hence, on the base on metric and morphological features,

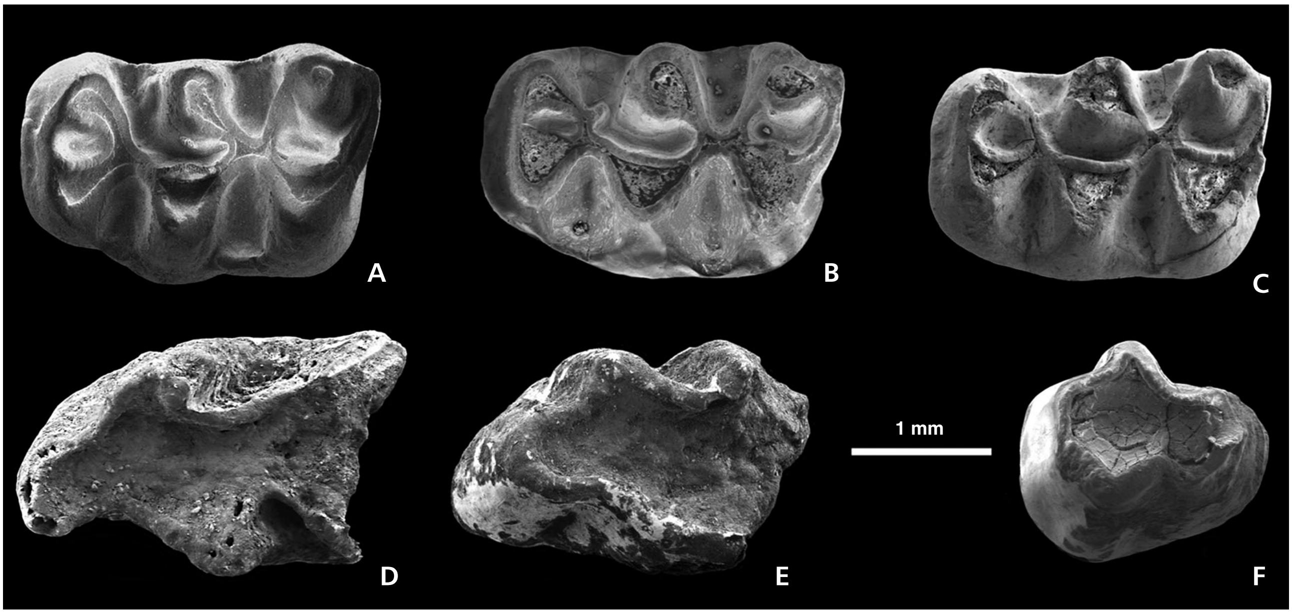


Figure 4. Fossil rodents from ABS-3A, AC-0, AC-0B and La Bullana 2B (LB2B). • A–C – *Apocricetus* cf. *barrierei*; A – left M1, ABS3A-37; B – left M1, LB2B-261; C – left M1, LB2B-223. • D–F – *Ruscinomys* cf. *lasallei*; D – left m1, AC0-68; E – left m2, AC0-69; F – left m3, AC0B-14. Scale: 1 mm.

the material of the genus *Apocricetus* from ABS-3A may be assigned to *A. barrierei*. Nonetheless, due to the scarcity of material we ascribe this molar to *A.* cf. *barrierei*.

Genus *Neocricetodon* Schaub, 1934

***Neocricetodon* sp.**
Figure 5A

Locality. – AC-0C.

Material. – 1 m3 (AC0C-9) (1.12 × 0.86).

Description. – m3. Subtriangular outline, the posterior part is narrower than the anterior part (Fig. 5A). The anterosinusid is very small. A very short lingual anterolophulid is present. The metalophulid is very short and transversal. The labial anterolophulid reaches the base of protoconid, enclosing a narrower protosinusid. The mesosinusid and sinusid are closed by a cingulum ridge. A trace of mesolophid, low and connected to the metaconid, is present. The ectomesolophid is absent. The posterolophid is connected to the entoconid. Roots are not preserved.

Discussion. – Size has been the criterion used to distinguish the species *N. lavocati* (Hugueney & Mein 1965) from another bigger species in its type locality (Lissieu). In this latter locality, Freudenthal *et al.* (1998) mentioned two very small m3: one of the size of the small specimens from Crevillente 2 (*Neocricetodon occidentalis* Aguilar, 1982) and another one even smaller (1.14 × 0.96). This latter specimen is much worn (Hugueney & Mein 1965, pl. 2, fig. 55) and the morphology cannot be clearly observed, but the outline is very similar to the m3 from AC-0C. According to Freudenthal *et al.* (1998) the mesolophid is very developed in the m1 from Lissieu, nearly always reaching the margin of the molar, but this trait cannot be observed in the much worn m3. The small size of the specimen resembles *N. lavocati*, but because of the scarcity of the material and lack of any unworn m3, we ascribe this molar to *Neocricetodon* sp. until more material becomes available.

Cricetinae indet.

Locality. – AC-0B.

Material. – 1 m3 (AC0B-11).

Description. – m3. The specimen is broken anteriorly, posteriorly and labially. The only cusps that can be observed are the entoconid, the metaconid and the lingual portion of the hypoconid. There is no mesolophid. Roots are not preserved.

Discussion. – This molar is clearly bigger and more hypsodont than the m3 ascribed to *Neocricetodon* sp. from AC-0C. Because of the poor state of preservation of the specimen we cannot reach a generic ascription, and therefore we assign this molar to Cricetinae indet.

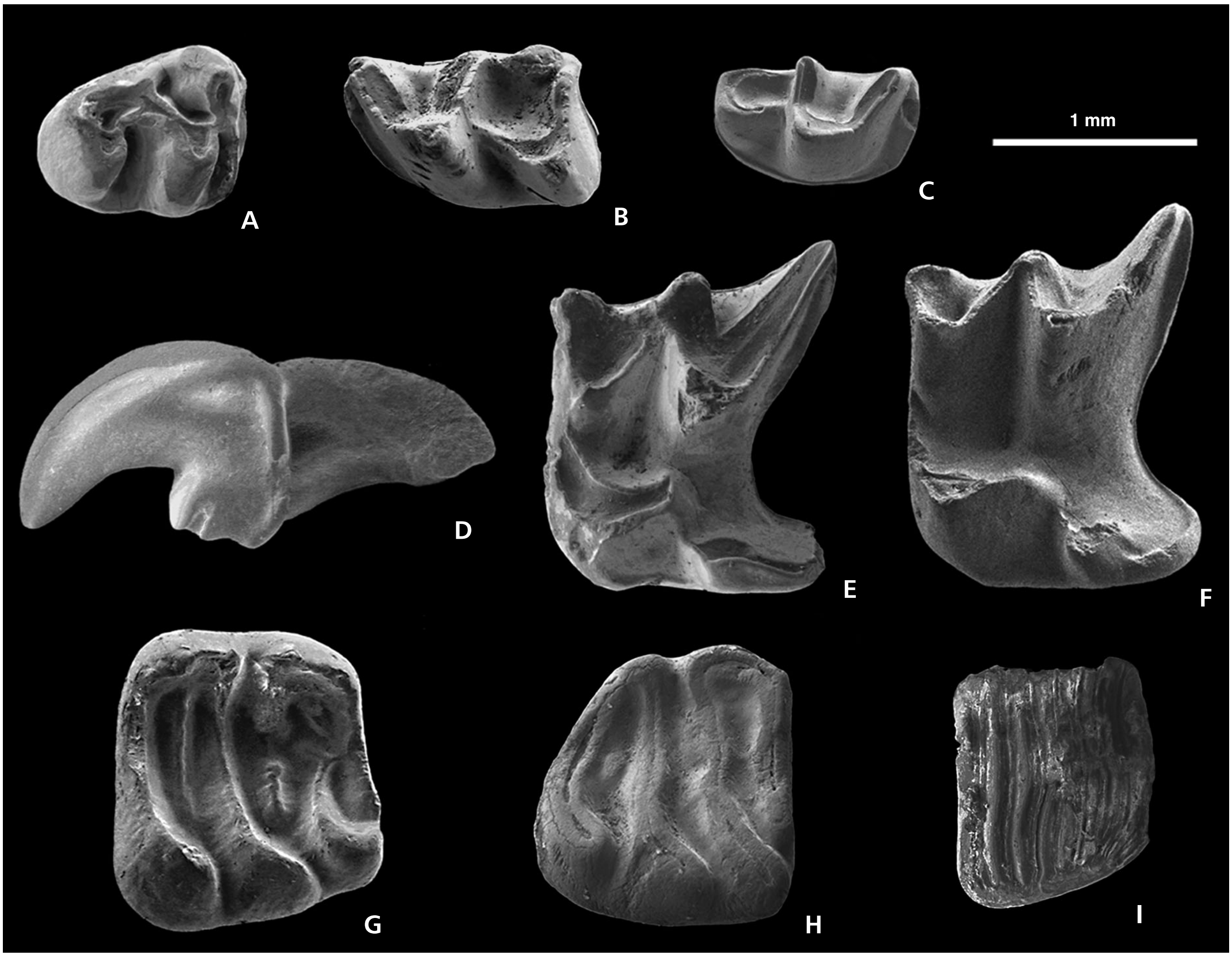


Figure 5. Fossil rodents from ABS-3, ABS-3A, ABS-10 and AC-0. • A – *Neocricetodon* sp.; right m3, AC0-9. • B–F – *Asoriculus gibberodon*; B – left m1,2, AC0-57; C – right m3, ABS10-1; D – left I1, ABS3'08-35; E – left M1, AC0-90; F – left M2, ABS3A-39. • G – *Eliomys yevesi*; right m1,2, ABS3A-38. • H – *Eliomys intermedius*; right m3, AC0-88. • I – *Muscardinus* sp., left M3. Scale: 1 mm.

Subfamily Cricetodontinae Stehlin & Schaub, 1951

Genus *Ruscinomys* Depéret, 1890

***Ruscinomys* cf. *lasallei* Adrover, 1969**
Figure 4D–F

Localities. – ABS-3A, AC-0, AC-0B, AC-0C.

Material. – 2 m1 (AC0-30, AC0-68); 1 m2 (AC0-69); 3 m3 (ABS3A-41, AC0-31, AC0-129); 1 M1 (AC0-72) (– × 2.68); 1 M2 (AC0-70) (– × 2.22); 4 M3 (AC0-71) (1.95 × 1.57), (AC0-73) (1.83 × 1.62), (AC0B-14) (1.98 × 1.63), (AC0C-15); 3 frag. indet. (AC0-74, AC0-128, AC0-130).

Description. – m1. Both molars are much worn. The specimens are broken posteriorly, and one of them is also broken anteriorly. The anteroconid is rounded (Morphotype 3, García-Alix *et al.* 2008b). The anterolophid is absent. The mesolophid cannot be observed. The sinusoid is deep and narrow. Roots are not preserved.

m2. This molar is broken anteriorly and extremely worn. The anteroconid is shorter than in m1. The posterolophid cannot be observed. The sinusoid is deep and narrow. Roots are not preserved.

m3. All specimens are broken anteriorly and much worn. The posterolophid cannot be observed. The sinusoid is deep and narrow. Roots are not preserved.

M1. The molar is broken posteriorly and extremely worn. Roots are not preserved.

M2. The specimen is poorly preserved and broken anteriorly. The ectolophs cannot be observed. Roots are not preserved.

M3. The specimens are much worn. These teeth are bilobed, the anterior lobe being much bigger than the posterior one. Roots are not preserved.

Discussion. – Several authors have proposed the phyletic lineage *R. schaubi-R. lasallei-R. europaeus* (Adrover 1969, van de Weerd 1976, García-Alix *et al.* 2008b, among others) in which there is a continuous increase in size and hypsodonty, as well as changes in some morphological features such as the shape of anterocone and anteroconid, along time. The specimens studied are smaller than *R. europaeus* Déperet, 1890, and agree in size with *R. lasallei* Adrover, 1969, from the localities of Alcoy (Adrover 1969), BRA-5B, PUR-4 and PUR-13 (García-Alix *et al.* 2008b), being similar to *R.* cf. *lasallei* from, Arquillo1, Arquillo 4, La Gloria 5 (Adrover *et al.* 1993) and Caravaca (van de Weerd 1976) and slightly bigger than *R.* cf. *lasallei* from Valdecebro 3, Valdecebro 6 and Villastar (Adrover *et al.* 1993). Because of the advanced wear of the specimens it is impossible estimating hypsodonty of these molars, as well as the observation of the diagnostic features of the occlusal surface. However, the relatively flat surfaces of the labial sides of the m1 and m2 and the reduction of the M3 agree better with *R. lasallei* than with *Ruscinomys schaubi* Villalta & Crusafont Pairó, 1956. For these reasons, we ascribe the molars from ABS-3A, AC-0, AC-0B and AC-0C to *R.* cf. *lasallei*.

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Eliomys yevesi Mansino, García-Alix, Ruiz-Sánchez & Montoya, 2014

Figure 5G

Locality. – ABS-3A.

Material. – 1 m1,2 (ABS3A-38) (1.30 × 1.45).

Description. – m1,2. Trapezoidal outline. The anterolophid is connected to the protoconid basally. No anterotropid. The metalophid does not reach the metaconid. The centrolophid is not continuous, and its labial end is separated from the metalophid by a wide furrow. The metaconid and entoconid are separated. Well-developed posterotropid. Large hypoconid. Roots are not preserved.

Discussion. – The presence of a mixture of characters typical of *E. truci* Mein & Michaux, 1970 and *E. intermedius* Friant, 1953 in some populations of *Eliomys* from the Granada and Alcoy basins and the locality of Venta del Moro led Mansino *et al.* (in press), to create a new species, *E. yevesi.* The single specimen from ABS-3A share some characters with the populations of *E. truci*, like the absence of connections between metalophid-metaconid as well as the presence of a large posterotropid, usually absent or reduced in *E. intermedius*. This molar is bigger and has higher cusps than *E. truci*, and is smaller and relatively narrower, with a more quadrangular shape than *E. intermedius*.

Eliomys intermedius Friant, 1953

Figure 5H

Locality. – AC-0.

Material. – 1 m3 (AC0-88) (1.27 × 1.41); 1 M1,2 (AC0-87).

Description. – m3. Sub-trapezoidal outline. The anterolophid and the protoconid are separated. No anterotropid. The metalophid is connected to the metaconid. There is a short centrolophid, not connected to the metalophid (Fig. 3S). The metaconid and entoconid are separated. No posterotropid. Roots are not preserved.

M1,2. Subrectangular outline. The anteroloph and paracone are connected basally. The protoloph and metaloph are distinctly sinuous. Both centrolophs are present. The posteroloph is connected to the endoloph. There are three roots.

Discussion. – The molars from AC-0 are slightly smaller than those of *E. intermedius* from younger localities (Mansino *et al.* in press.), but they agree in size with the population from Sète, type locality of the species (Adrover 1986) and are clearly bigger, more concave, more rounded and with more developed centrolophs than *E. yevesi* and *E. truci* (Mansino *et al.* in press).

Subfamily Glirinae Muirhead, 1819

Genus *Muscardinus* Kaup, 1829

Muscardinus sp.

Figure 5I

Locality. – AC-0.

Material. – 1 M3 (AC0-89) (> 1.10 × –).

Description. – M3. The specimen lacks the medial part of the labial border, and the posterior border is much worn, thus its length is slightly underestimated. The outline is sub-trapezoidal. The occlusal surface has eight low ridges, the anterior one straight and the others slightly convex towards the posterior side of the molar. The lingual sides of the ridges reach a continuous endoloph. There are four roots.

Table 3. Faunal lists of the localities Alcoy-Barranco, ABS-3, ABS-3A and AC-0.

Alcoy-Barranco (Thaler *et al.* 1965, Adrover 1969)	ABS-2 (This paper)	ABS-3 (This paper)	ABS-3A (This paper)	ABS-7 (This paper)	ABS-8 (This paper)	ABS-9 (This paper)	AC-0B (This paper)	AC-0C (This paper)	AC-0 (This paper)
Apodemus sp.	–	*Apodemus gorafensis*	–	–	–	–	–	*Apodemus gorafensis*	*Apodemus gorafensis*
Anthracomys ellenbergeri	*Paraethomys meini*	*Paraethomys meini*	*Paraethomys meini*	–	–	–	*Paraethomys meini*	–	*Paraethomys meini*
–	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*	–	–	–	*Paraethomys* aff. *abaigari*	–	*Paraethomys* aff. *abaigari*
–	*Micromys* sp.	–	–	–	–	*Micromys* sp.	–	–	–
Parapodemus sp.	–	–	–	–	–	–	–	–	–
–	–	*Occitanomys alcalai*	*Occitanomys alcalai*	–	–	–	*Occitanomys alcalai*	*Occitanomys alcalai*	*Occitanomys alcalai*
Stephanomys aff. *donnezani*	*Stephanomys dubari*	*Stephanomys dubari*	*Stephanomys dubari*	*Stephanomys* sp.	*Stephanomys* aff. *cordii*	*Stephanomys* sp.	*Stephanomys* aff. *cordii*	*Stephanomys* aff. *cordii*	*Stephanomys* aff. *cordii*
Cricetus aff. *angustidens*	–	–	*Apocricetus* cf. *barrierei*	–	–	–	–	–	–
–	–	–	–	–	–	–	–	*Neocricetodon* sp.	–
–	–	–	–	–	–	–	Cricetinae indet.	–	–
Ruscinomys lasallei	–	–	*Ruscinomys* cf. *lasallei*	–	–	–	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*
Eliomys aff. *intermedius*	–	–	*Eliomys yevesi*	–	–	–	–	–	*Eliomys intermedius*
Muscardinus sp.	–	–	–	–	–	–	–	–	*Muscardinus* sp.
–	–	*Asoriculus gibberodon*	–	–	–	–	–	–	*Asoriculus gibberodon*
Galerix sp.	–	–	–	–	–	–	–	–	Erinaceidae indet.
Sorex sp.	–	–	–	–	–	–	–	–	Soricidae indet.

Discussion. – During the Late Miocene and Pliocene, three lineages have been discerned within the genus *Muscardinus*: the *M. vireti-M. meridionalis-M. helleri* lineage, *M. pliocaenicus* lineage and *M. davidi-M.* aff. *dacius* lineage (García-Alix *et al.* 2008c). The presence of four roots in M3, like in the specimen from AC-0, has been observed in *M. avellanarius* (Linnaeus, 1758), *M. dacicus* Kormos, 1930, *M. cyclopeus* Agustí, Moyà Solà & Pons-Moyà, 1982, *M. pliocaenicus* Kowalski, 1963 and *M. vireti* Hugueney & Mein, 1965. Of these taxa, only *M. cyclopeus* and *M. vireti* have eight ridges in their M3. *M. meridionalis* García-Alix, Minwer-Barakat, Martín-Suárez & Freudenthal, 2008, have also eight ridges in the M3, but the number of roots is unknown (García-Alix *et al.* 2008c).

The specimen studied is smaller than *M. cyclopeus*, being close to the maxima of *M. vireti* from Lissieu and *M. meridionalis* from PUR-4 (García-Alix *et al.* 2008c). Because of the size of the specimen and high number of ridges in M3, we consider the molar from AC-0 a form related to the line *M. vireti-M. meridionalis-M. helleri*, which maintains a medium-large size and a high number of ridges in the upper teeth (García-Alix *et al.* 2008c). No M3 of *M. helleri* have been recovered. For these reasons, we assign the M3 from AC-0 to *Muscardinus* sp.

Order Soricomorpha Gregory, 1910
Family Soricidae Fischer, 1814
Subfamily Soricinae Fischer, 1814
Tribe Nectogalini Anderson, 1879

Genus *Asoriculus* Kretzoi, 1959

Asoriculus gibberodon (Petényi, 1864)

Figure 5B–F

Localities. – ABS-3, ABS-10, AC-0.

Material. – 3 m1,2 (ABS10-2) (TRW: 0.81), (AC0-57) (L: 1.33 × TRW: 0.90 × TLW: 0.93), (AC0-94) (L: 1.34); 1 m3 (ABS10-1) (L: 1.03 × W: 0.57); 1 I1 (ABS3’08-35) (L: 1.29 × W: 1.05; LT: 0.61); 1 M1 (AC0-90) (LPE: 1.11;

LL: 1.44; BL: 1.42; AW: 1.48; PW: 1.74); 6 M2 (ABS3A-39) (LPE: 1.20; LL: 1.51; BL: 1.44; AW: 1.60; PW: 1.93), (AC0-22, AC0-91, AC0-92, AC0-93, AC0-95).

Description. – m1,2. The talonid and the trigonid width are very similar. The difference between both values is usually bigger in m1 than in m2. The entoconid is large, high and very close to the entostylid. The entoconid crest is slightly lower, and connects basally with the metaconid. There is no mesoconid. The labial cingulum is low and narrow. The lingual cingulum is broken in two specimens and well-developed in the other one. Roots are not preserved.

m3. The hypoconid and entoconid are distinct, and the talonid basin is long and narrow. The labial cingulum is more developed than in m1,2, and higher than the lingual cingulum. The protoconid is the highest cusp. Roots are not preserved.

I1. Bifid and moderately fissident tooth. Well developed labial cingulum, wider ventrally than dorsally. The posterior margin is very straight. A narrow cingulum is also present along the lingual posterior border. Roots are not preserved.

M1. The metacone is bigger and much higher than the paracone. The metastyle protrudes markedly over the labial border. The protocone is connected to the paracone by a high crest and to the hypocone by a lower crest. The hypocone is smaller and lower than the protocone, and connected to the posteroloph (Morphotype B, Reumer 1984). The hypoconal flange is wide. The posterior emargination is smooth. The posteroloph extends in a continuous posterior cingulum, which reaches the base of the metastyle. Roots are not preserved.

M2. The metacone is much higher than the paracone. The metastyle protrudes over the labial border. The protocone is connected to the paracone by a high crest. The hypocone and the protocone are separated by a narrow valley. The hypocone is the lowest and smallest cusp, and reaches the posteroloph (Morphotype B, Reumer 1984). The hypoconal flange is narrower than in the m1. The posterior emargination is smooth. The posteroloph extends in a continuous posterior cingulum, which reaches the base of the metastyle. Roots are not preserved.

Discussion. – *Asoriculus gibberodon* (Petényi, 1864) is a very common soricid in the Pliocene and Early Pleistocene of Europe, also present in the latest Miocene from Maramena (Doukas *et al.* 1995). In the studied material, the presence of a high entoconid crest in the lower molars, a talonid basin in m3, fissident upper incisors and a moderate posterior emargination agree with this species (Reumer 1984). The presence of a small hypocone connected to the posteroloph is consistent with the Morphotype B of Reumer (1984).

Asoriculus gibberodon shows a wide biometrical variability, differing greatly from one locality to another (Reumer 1984, Minwer-Barakat *et al.* 2010). The lower molars from the studied localities are consistent with the smaller sizes of the specimens from Villány 3, Csarnóta 2, Osztramos 1 and 9 (Reumer 1984), Varshets (Popov 2003), Venta Micena 1 (Martín-Suárez 1988) and TCH-1, TCH-1B and TCH-3 (Minwer-Barakat *et al.* 2010), Fuente Nueva 3 and Barranco León (Furió 2007), while the upper molars are relatively bigger.

Soricidae indet.

Locality. – AC-0.

Material. – 1 m3 (AC0-97).

Description. – m3. The anterior part of the molar is missing. The talonid basin is not reduced. Roots are not preserved.

Discussion. – The shape of the m3 resembles *Asoriculus*. Nevertheless its size is much bigger and clearly out of the measure range than those of *Asoriculus gibberodon* described above.

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer, 1814
Erinaceidae indet.

Localities. – AC-0, AC-0B.

Figure 6. Distribution chart of the rodent species studied in this paper and, according to bibliography of other species of similar age. Abbreviations: GOR-A – Gorafe-A (Ruiz-Bustos *et al.* 1984); YEG – Yeguas (Minwer-Barakat *et al.* 2012); PUR-3, PUR-4, PUR-7, PUR-13 – Purcal 3, 4, 7 and 13; CLC-3B, CLC-5A – Calicasas 3 B and 5A; DHS-16 – Dehesa-16; MNA-4 – Mina 4 (García-Alix 2006, García-Alix *et al.* 2008a); VAR-1 – Villalba Alta Río 1; ALDH – Aldehuela (Adrover 1986); CEL-9 – Celadas-9; LG-4 – La Gloria-4; AR-4 – Arquillo 4 (Adrover *et al.* 1993); PER-E – Peralejos-E (Mein *et al.* 1990); NGR-1 – Negratín-1 (Minwer Barakat *et al.* 2009a; RCH-3 – Rambla Chimeneas 3 (Minwer-Barakat *et al.* 2009b); ALM-M – Almenara-M (Agustí *et al.* 2011); ZOR-3A – Zorreras 3A (Martín-Suárez *et al.* 2000); VM – Venta del Moro (Montoya *et al.* 2006b); CR-6 – Crevillente 6 (Martín-Suárez & Freudenthal 1998). For making of this table the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* and *Stephanomys donnezani cordii* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Cricetus kormosi* and *Apocricetus kormosi* as *Apocricetus alberti*; *Protatera almenarensis* as *Debruijnimys almenarensis* and *Protatera* sp. as *Debruijnimys* sp. The locality ABS-10 has not been included since it has yielded no rodent remains.

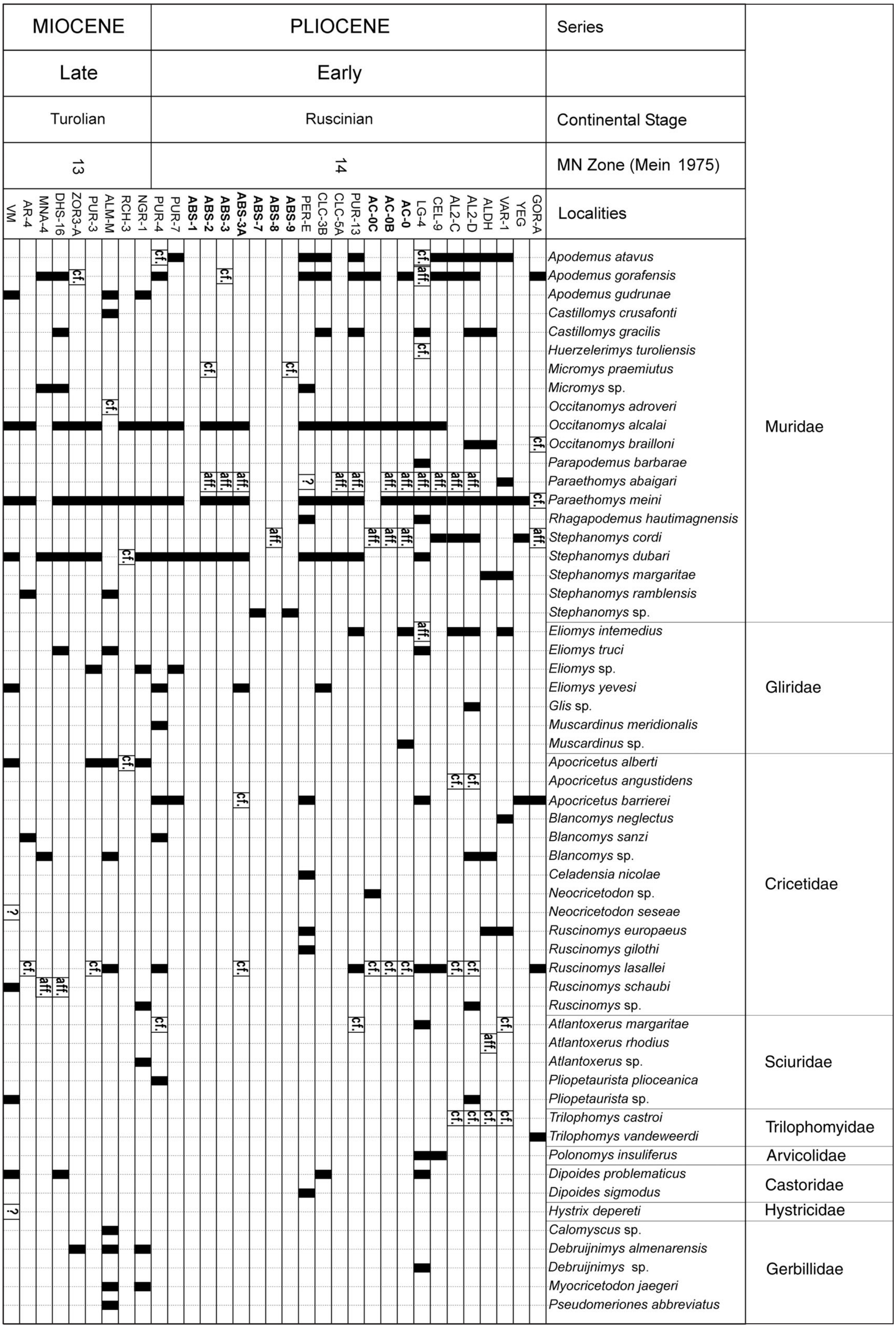

MIOCENE
PLIOCENE
Series
Late
Early
Turolian
Ruscinian
Continental Stage
13
14
MN Zone (Mein 1975)
Localities
VM
AR-4
MNA-4
DHS-16
ZOR3-A
PUR-3
ALM-M
RCH-3
NGR-1
PUR-4
PUR-7
ABS-1
ABS-2
ABS-3
ABS-3A
ABS-7
ABS-8
ABS-9
PER-E
CLC-3B
CLC-5A
PUR-13
AC-0C
AC-0B
AC-0
LG-4
CEL-9
AL2-C
AL2-D
ALDH
VAR-1
YEG
GOR-A
cf.
aff.
?
Apodemus atavus
Apodemus gorafensis
Apodemus gudrunae
Castillomys crusafonti
Castillomys gracilis
Huerzelerimys turoliensis
Micromys praemiutus
Micromys sp.
Occitanomys adroveri
Occitanomys alcalai
Occitanomys brailloni
Parapodemus barbarae
Paraethomys abaigari
Paraethomys meini
Rhagapodemus hautimagnensis
Stephanomys cordi
Stephanomys dubari
Stephanomys margaritae
Stephanomys ramblensis
Stephanomys sp.
Muridae
Eliomys intemedius
Eliomys truci
Eliomys sp.
Eliomys yevesi
Glis sp.
Muscardinus meridionalis
Muscardinus sp.
Gliridae
Apocricetus alberti
Apocricetus angustidens
Apocricetus barrierei
Blancomys neglectus
Blancomys sanzi
Blancomys sp.
Celadensia nicolae
Neocricetodon sp.
Neocricetodon seseae
Ruscinomys europaeus
Ruscinomys gilothi
Ruscinomys lasallei
Ruscinomys schaubi
Ruscinomys sp.
Cricetidae
Atlantoxerus margaritae
Atlantoxerus rhodius
Atlantoxerus sp.
Pliopetaurista plioceanica
Pliopetaurista sp.
Sciuridae
Trilophomys castroi
Trilophomys vandeweerdi
Trilophomyidae
Polonomys insuliferus
Arvicolidae
Dipoides problematicus
Dipoides sigmodus
Castoridae
Hystrix depereti
Hystricidae
Calomyscus sp.
Debruijnimys almenarensis
Debruijnimys sp.
Myocricetodon jaegeri
Pseudomeriones abbreviatus
Gerbillidae

Table 4. Percentages of species according to humidity, temperature and habitat parameters in the locality AC-0. The taxa with unknown preferences are not shown.

	Humidity			Temperature			Habitat		
Locality	*Wet*	*Dry*	*Eurytopic*	*Cold*	*Warm*	*Eurytopic*	*Open*	*Forested*	*Eurytopic*
AC-0	19.79	41.73	35.16	13.19	43.96	39.56	13.19	9.89	73.63

Material. – 1 p4 (AC0B-19); 1 P1,2 (AC0-63) (1.60 × 0.87); 1 P4 (AC0-131); 1 M2 (ABS3-10).

Description. – p4. The posterior side is missing. The protoconid is very large. There is no metaconid. The paraconid is connected to the protoconid by a low paralophid. Roots are not preserved.

P1,2. The low and small paraconid is connected to the protoconid by a low paralophid. There is no metaconid. There is no posterior cingulum. Roots are not preserved.

P4. The labial side of the specimen is missing. The protocone and hypocone are well developed, but the former is higher. There is a well-developed posterior cingulum. Roots are not preserved.

M2. The specimen is broken anteriorly and lingually. The parastyle is small and protrudes from the anterolabial part of the molar. The labial cingulum is low and wide. There is a low mesostyle. The metacone is big and high. The metastyle is well developed. Roots are not preserved.

Discussion. – The scarcity and poor state of preservation of the material prevent us from reaching a generic ascription.

Discussion

Biostratigraphy

The faunal lists of the localities ABS-3, ABS-3A and AC-0 are given in Table 3 and Fig. 6. Considering subsequent synonymies, the faunal list of Alcoy-Barranco (Thaler *et al.* 1965, Adrover *et al.* 1969) is very similar to the new faunas from AC-0. In particular, *Stephanomys* aff. *donnezani* from Alcoy-Barranco was renamed as *Stephanomys medius* by Cordy (1976), which is considered a synonym of *S. cordii* (García-Alix *et al.* 2008a), *Anthracomys ellenbergeri* was considered as *Anthracomys meini* by Michaux (1969), and included later within the genus *Paraethomys* by Jaeger *et al.* (1975), and finally, *Cricetus* aff. *angustidens* is considered *Apocricetus barrierei* by Freudenthal *et al.* (1998).

Based on the faunal list of Alcoy-N, López-Martínez (1989) gives a Late Miocene age for this locality. This site has yielded remains of *Prolagus michauxi*, *Trischizolagus* cf. *maritsae*, *Eliomys* sp., *Ruscinomys lasallei*, *Cricetus* cf. *kormosi* (synonym of *Apocricetus alberti* according to Freudenthal *et al.* 1998), Gerbilidae indet., *Occitanomys* sp., *Stephanomys* sp., *Apodemus primaevus* (synonymized as *Rhagapodemus primaevus* in Martín-Suárez & Mein 1998), *Paraethomys miocaenicus* and *Paraethomys* cf. *anomalus* (both considered synonyms of *Paraethomys meini* by several authors, see García-Alix *et al.* 2008a for a complete list). *Cricetus* cf. *kormosi* (*Apocricetus alberti* in synonymy) is a biostratigraphic marker from the Late Miocene (MN13). The presence of an unclassified gerbillid in Alcoy-N does not allow determining the exact age because this group arrives to the Iberian Peninsula during MN13 (*Debruijnimys almenarensis* Agustí, 1990), surviving until MN15 (*Debruijnimys julii* Castillo & Agustí, 1996). Both *Debruijnimys* sp. (Agustí & Casanovas-Vilar 2003) and *D. julii* are present in early MN14 (Mansino pers. comm.), being uncertain if the form present in Alcoy-N is related to *D. almenarensis* or to these other taxa. In the northern side of the Gormaget ravine, a locality containing gerbil remains, Alcoy-4B (Freudenthal pers. comm.), is present. Probably, Alcoy-4B represents a Ruscinian (Early Pliocene) level, probably younger than Alcoy-N. The presence of *Cricetus* cf. *kormosi* (*Apocricetus alberti*) in Alcoy-N (López-Martínez 1989) would be the main argument to assign this locality to the MN13.

On the other hand, Mansino *et al.* (2013) considered a probable equivalent stratigraphic position for the classic locality of Alcoy-Mina and AL2-C and AL2-D, placing these localities in Early Ruscinian (MN14). The faunal content of AL2-C and AL2-D shows that they are younger than the localities from the ABS and AC sections, having yielded *Stephanomys cordii* and *Apocricetus* cf. *angustidens*, being their age probably close to the Early-Late Ruscinian boundary (MN14-MN15, Mansino *et al.* 2013).

In ABS-3 and ABS-3A, the occurrence of *Stephanomys dubari*, *Apodemus gorafensis* and *Paraethomys meini* is typical of the latest Turolian–earliest Ruscinian (García-Alix *et al.* 2008a). The presence of *Ruscinomys lasallei* is common in the Early Ruscinian, although it is also present in the Late Turolian of Granada (García-Alix *et al.* 2008b) and *R.* aff. *lasallei* is found in the Late Turolian of Teruel (Adrover *et al.* 1993, García-Alix *et al.* 2008b). *Stephanomys cordii* appears in MN14 (Mein *et al.* 1990, Sesé 2006, Minwer-Barakat 2005, Minwer-Barakat *et al.* 2012), and the presence in AC-0 of a very close form, *S.* aff. *cordii*, suggest an Early Ruscinian age for this locality.

Eliomys yevesi has been described with material from the Late Turolian locality of Venta del Moro, being present also in some Early Ruscinian localities like PUR-4, CLC-3B in the Granada Basin, and AF-1'06 and AF-1'07 in the Alcoy Basin (Mansino *et al.* in press). This taxon is the ancestor of *E. intermedius* (Mansino *et al.* in press), which is present in AC-0.

The presence of *Muscardinus* sp. in AC-0 is consistent with the Turolian and Ruscinian populations of the lineage *M. vireti-M. meridionalis-M. helleri* (García-Alix *et al.* 2008c). Thaler *et al.* (1965) mentioned the presence of two M1 of *Muscardinus* in Alcoy-Barranco, with six transversal ridges each. Despite the scarcity of material of this glirid in AC-0, the morphology described in this locality is clearly consistent with a form of the previously cited lineage.

The presence of *Stephanomys* aff. *cordii* in ABS-8, AC-0, AC-0C and AC-0B supports an Early Ruscinian age for these localities (Minwer-Barakat 2005, Minwer-Barakat *et al.* 2012), slightly younger than ABS-1, ABS-2, ABS-3 and ABS-3A (Fig. 2), in which *S. dubari*, ancestor of *S. cordii*, is present. The cricetid *Apocricetus barrierei* is considered a guide taxon for the Early Ruscinian in the Iberian Peninsula (Freudenthal *et al.* 1998, García-Alix *et al.* 2008b), and its presence supports an Early Ruscinian age for ABS-3A. In the same way, the presence of a big sized *Paraethomys*, *P.* aff. *abaigari*, in ABS-2, ABS-3, ABS-3A, AC-0 and AC-0B supports an Early Ruscinian age for these sites (Mein *et al.* 1990, García-Alix *et al.* 2008a) also. Therefore, all taxa yielded by this section confirm an Early Ruscinian age for the new micromammal localities represented in the sections of Alcoi Barranc Sud (ABS) and Alcoi Cristian (AC).

Palaeoecology

The species spectrum of micromammal assemblages has been widely used as a palaeoclimatic indicator. For these analysis, some authors have proposed a minimum sample size of at least 100 specimens (Daams *et al.* 1999, García-Alix *et al.* 2008d), while others used a minimum of 50 specimens (Casanovas-Vilar & Agustí 2007), arguing that in most cases the bigger samples only add one or two new species to the assemblage, and the abundance of these new species is less than 1%. The locality of AC-0 has yielded 91 identifiable specimens, whereas in the other localities the sample is too scarce to perform a proper analysis.

Following García-Alix *et al.* (2008d), we have considered the taxa *Apodemus gorafensis*, *Micromys*, *Paraethomys meini*, *Occitanomys alcalai* and *Asoriculus gibberodon* as warm weather indicators, and *Ruscinomys* as a cold indicator. Also, *Apodemus gorafensis*, *Occitanomys alcalai*, *Asoriculus gibberodon* and Soricidae indet. are regarded as wet environment indicators, whereas *Ruscinomys* and *Paraethomys meini* are associated with dry conditions. Traditionally the genera *Eliomys* and *Muscardinus* have been considered wet environment indicators (see García-Alix *et al.* 2008d, and references therein), but Freudenthal *et al.* (2014) state that these taxa cannot be considered as indicators of humidity based on their current distribution.

Regarding the habitat, most of the taxa from AC-0 are eurytopic (Table 4) except *Ruscinomys*, which indicate open environments, and *A. gibberodon* and *Muscardinus*, which are associated with forested habitats (García-Alix *et al.* 2008d, Freudenthal *et al.* 2014). The genus *Eliomys* is a habitat generalist, with extant representatives ranging from environments with a moderate forest cover and a high annual precipitation to open semi-desertic environments (Freudenthal *et al.* 2014).

According to Agustí (1990), the presence of *Eliomys* instead of *Glis* in the western basins of the Iberian Peninsula suggests dryer and warmer conditions than in the Catalonian basins (NE Spain). The analysis of the faunal assemblage of AC-0 in which both *Eliomys* and *Muscardinus* are present agrees with this interpretation, suggesting warm and relatively dry conditions (see Table 4).

As discussed before, the scarcity of the remains from the other localities prevents a proper palaeoenvironmental interpretation, although the relative percentages of the taxa present in ABS-3 and ABS-3A indicate similar conditions to those of AC-0. However, the localities ABS-9, ABS-10 and AC-0C have yielded mostly taxa considered as humid indicators. ABS-9 has yielded *Micromys* sp. and *Asoriculus gibberodon*, both wet environments indicators, and the only micromammal fossils recovered from ABS-10 belong to *A. gibberodon*. In the assemblage from AC-0C *Apodemus* cf. *gorafensis* and *O. alcalai* are considered indicators of humidity. Therefore, ABS-9, ABS-10 and AC-0C may represent a wetter environment hiatus in the series, although these changes could also be explained by local or regional environments rather than general trends (García-Alix *et al.* 2013, Freudenthal *et al.* 2014).

Conclusions

In the lower deposits from the ABS section (Gormaget area, Alcoy Basin), two new localities (ABS-3 and ABS-3A) have yielded abundant mammal fossil remains. The presence in ABS-3 of *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Paraethomys meini*, *Occitanomys alcalai*, *Stephanomys dubari* and *Asoriculus gibberodon* and in ABS-3A of *Paraethomys* aff. *abaigari*, *Paraethomys meini*, *Occitanomys alcalai*, *Stephanomys dubari*, *Apocricetus* cf. *barrierei*, *Ruscinomys* cf. *lasallei* and *Eliomys* cf. *yevesi* allow us to assign an Early Ruscinian age, close to the Mio-Pliocene boundary, for these sites.

Near the top of the youngest stratigraphic sequence here studied, a new locality (AC-0) has yielded also a rich fossil mammal assemblage, comprising to *Apodemus gorafensis*, *Occitanomys alcalai*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Stephanomys cordii*, *Asoriculus gibberodon*, *Ruscinomys* cf. *lasallei*, *Muscardinus* sp., *Eliomys intermedius*, Erinaceidae indet. and Soricidae indet. This faunal assemblage suggests an Early Ruscinian age for this locality.

The palaeoecological context of the studied deposits shows, from the bottom to the top of the stratigraphic sequence, a changing palaeoenvironment. While the scarce data from some of the lower deposits (localities ABS-9, ABS-10 and AC-0C) suggest wetter conditions for these sites, the taxa present in AC-0 indicate warm and relatively dry conditions. According to the stratigraphic position and the environment requirements from the small mammal fauna located in these localities, a progressive aridification process may occur along the lower part of the Early Pliocene in the Alcoy Basin.

The presence of *Micromys* and *Muscardinus* in several localities from the new sections of the Alcoy Basin represent the first record of these genera in the area.

Finally, and based on the faunal content of AC-0, characterized by the presence of *R. lasallei* and *Stephanomys cordii*, its relative stratigraphic position, deduced age and geographic proximity, we consider AC-0 as a probable coetaneous level to that of the classical site described by Adrover (1969), Alcoy-Barranco.

Acknowledgments

This study was supported by the project CGL2011-25754 of the Spanish Ministry of Economy and Competitiveness and the Conselleria de Cultura of the Valencian Government. This investigation was carried out thanks to the Prometeo Project of the Secretariat for Higher Education, Science, Technology and Innovation from Ecuador. We want to thank the Palaeontological association "Isurus", from Alcoy, as well as all the students from the Universitat de València that have taken part in the fieldwork. We would like to thank Antonio García-Alix, and Jan Wagner, for their help, useful comments and criticism.

References

Adrover, R. 1969. Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. I. *Ruscinomys*. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica) 67*, 245–272.

Adrover, R. 1986. *Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico*. 423 pp. Publicaciones del Instituto de Estudios Turolenses, Teruel.

Adrover, R., Mein, P. & Moissenet, E. 1988. Contribución al conocimiento de la fauna de roedores del Plioceno de la región de Teruel. *Teruel 79(1)*, 89–151.

Adrover, R., Mein, P. & Moissenet, E. 1993. Roedores de la transición Mio-Plioceno de la región de Teruel. *Paleontologia i Evolució 26–27*, 47–84.

Aguilar, J.P., Michaux, J., Bachelet, B., Calvet, M. & Faillat, J.P. 1991. Les nouvelles faunes des rongeurs proches de la limit Mio-Pliocene en Rousillon. Implications bioestratigraphiques et biogeographiques. *Paleovertebrata 20(4)*, 147–174.

Aguirre, E., Hoyos, M. & Morales, J. 1975. Alcoy: observaciones preliminares sobre la secuencia Neógeno-Cuaternaria del Serpis. *Acta Geológica Hispánica 10(2)*, 75–77.

Agustí, J. 1990. The Miocene rodent succession in Eastern Spain: a zoogeographical appraisal, 375–404. *In* Lindsay, E.H., Fahlbusch, V. & Mein, P. (eds) *European Neogene Mammal Chronology.* Plenum Press, New York.

Agustí, J. & Casanovas-Vilar, I. 2003. Neogene gerbils from Europe. *Deinsea 10*, 13–21.

Agustí, J., Santos-Cubedo, A., Furió, M., de Marfá, R., Blain, H.A., Oms, O. & Sevilla, P. 2011. The late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Castellón, Eastern Spain): Chronologic and paleoclimatic context. *Quaternary International 243*, 183–191. DOI 10.1016/j.quaint.2010.11.016

Casanovas-Vilar, I. & Agustí, J. 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology 248*, 169–189.
DOI 10.1016/j.palaeo.2006.12.002

Cordy, J.M. 1976. *Essai sur la microévolution du genre Stephanomys* (*Rodentia, Muridae*). 351 pp. Ph.D. thesis, University of Liège, Liège.

Daams, R. 1981. The dental pattern of the Dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins, Special Publication 3*, 1–115.

Daams, R., Meulen, A.J. van der, Peláez-Campomanes, P. & Álvarez-Sierra, M.A. 1999. Trends in rodent assemblages from the Aragonian (early–middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain, 127–139. *In* Agustí, J., Rook, L. & Andrews, P. (eds) *Hominoid evolution and climatic change in Europe. The evolution of Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge.

Doukas, C.S., Hoek Ostende, L.W. van den, Theocharopoulos, C.D. & Reumer, J.W.F. 1995. The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia). *Münchner Geowissenschaftliche Abhandlungen A 28*, 43–64.

Durand Delga, M., Garcia Rodrigo, B., Magne, J. & Polveche, J. 1964. À propos du Miocène de la région d'Alcoy (province d'Alicante, Espagne). *Cursillos y Conferencias 9*, 213–217.

Esteban-Aenlle, J. & Lacomba, J.I. 1988. El yacimiento de Alcoy-2. Nuevo nivel con micromamíferos del Plioceno inferior (MN15) en el área de Alcoy. *Comunicacions. Col. loqui Homenatge a R. Adrover "Bioeventos y sucesiones faunísticas en el Terciario continental ibérico", Sabadell*, *Abstract Book*, 17.

Freudenthal, M. 2004. Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). *Treballs del Museu de Geologia de Barcelona 12*, 97–173.

Freudenthal, M. & Martín-Suárez, E. 1999. Family Muridae, 401–409. *In* Rössner, G.E. & Heissig, K. (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.

Freudenthal, M., Mein, P. & Martín-Suárez, E. 1998. Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona 7*, 11–93.

Freudenthal, M., García-Alix, A., Ríos, M., Ruiz-Sánchez, F.J., Martín-Suárez, E. & Delgado Huertas, A. 2014. Review of paleo-humidity parameters in fossil rodents (Mammalia): Isotopic vs. tooth morphology approach. *Palaeogeography, Palaeoclimatology, Palaeoecology 395*, 122–130. DOI 10.1016/j.palaeo.2013.12.023

Furió, M. 2007. *Los insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno Superior del Levante Ibérico*. 341 pp. Ph.D. thesis, Autunomous University of Barcelona, Barcelona.

Garcia-Alix, A. 2006. *Bioestratigrafía de los depósitos continentales de la transición Mio-Plioceno de la cuenca de Granada*. 429 pp. Ph.D. thesis, University of Granada, Granada.

García-Alix, A., Delgado Huertas, A., Martín Suárez, E. & Freudenthal, M. 2013. Environmental conditions vs. landscape. Assessment of the factors that influence small mammal fauna distribution in Southern Iberia during the latest Messinian by mean of stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology 386*, 492–500. DOI 10.1016/j.palaeo.2013.06.017

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E. & Freudenthal, M. 2008a. Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada Basin (southern Spain). Biostratigraphic and phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 248(2)*, 183–215. DOI 10.1127/0077-7749/2008/0248-0183

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E. & Freudenthal, M. 2008b. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica 136*, 1–37.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E. & Freudenthal, M. 2008c. *Muscardinus meridionalis* sp. nov., a new species of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of *Muscardinus*. *Journal of Vertebrate Paleontology 28(2)*, 568–573. DOI 10.1671/0272-4634(2008)28[568:MMSNAN]2.0.CO;2

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. & Martín, J.M. 2008d. Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology 265*, 214–225. DOI 10.1016/j.palaeo.2008.04.005

Hugueney, M. & Mein, P. 1965. Les rongeurs pliocénes du Rousillon dans les collections lyonnaises. *Travaux du Laboratoire de Géologie, Faculté des Sciences, Lyon, Nouvelle Série 13*, 243–266.

Horáček, I., Knitlová, M., Wagner, J., Kordos, L. & Nadachowski, A. 2013. Late Cenozoic History of the Genus *Micromys* (Mammalia, Rodentia) in Central Europe. *PLoS ONE 8(5)*, 1–19. e62498. DOI 10.1371/journal.pone.0062498

Jaeger, J.J., Michaux, J. & Thaler, L. 1975. Présence d'un rongeur muridé nouveau, *Paraethomys miocaenicus* nov. sp., dans le Turolien supérieur du Maroc et d'Espagne. Implications paléogéographiques. *Comptes-rendus de l'Académie des Sciences de Paris 280*, 1673–1676.

López-Martínez, N. 1989. Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza 3(3)*, 1–350.

Mansino, S., Fierro, I., Ruiz-Sánchez, F.J. & Montoya, P. 2013. The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of 2 Alcoy-Mina. *Journal of Iberian Geology 39(2)*, 261–284.

Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J. & Montoya, P. in press. A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica.* DOI 10.4202/app.00014.2013

Mansino, S., Ruiz-Sánchez, F.J., Freudenthal, M. & Montoya, P. 2014. A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain). *Proceedings of the Geologists' Association 125*, 392–405. DOI 10.1016/j.pgeola.2014.07.002

Mansino, S., Ruiz-Sánchez, F.J. & Montoya, P. 2009. Estudio preliminar de las faunas pliocenas de roedores del yacimiento Alcoi Cotes Altes 2 (ACA-2, Alicante, España). *Paleolusitana 1*, 251–256.

Martín-Suárez, E. 1988. *Sucesiones de micromamíferos en la Depresión de Guadix-Baza (Granada, España)*. 241 pp. Ph.D. thesis, University of Granada, Granada.

Martín-Suárez, E. & Freudenthal, M. 1993. Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica 103*, 65–118.

Martín-Suárez, E. & Freudenthal, M. 1998. Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Geobios 31(6)*, 839–847. DOI 10.1016/S0016-6995(98)80113-7

Martín-Suárez, E., Freudenthal, M., Krijgsman, W. & Rutger-Fortuin, A. 2000. On the age of continental deposits of the Zorreras member (Sorbas basin, SE Spain). *Geobios 33(4)*, 505–512. DOI 10.1016/S0016-6995(00)80084-4

Martín-Suárez, E. & Mein, P. 1998. Revision of the genera *Parapodemus, Apodemus, Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios 31(1)*, 87–97. DOI 10.1016/S0016-6995(98)80099-5

Mein, P. 1975. Résultats du Groupe de Travail des Vertébrés, 78–81. *In* Senes, J. (ed.) *Report on Activity on the RCMNS Working Groups (1971–1975)*. Bratislava.

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

Mein, P., Moissenet, E. & Adrover, R. 1990. Biostratigraphie du Néogène Supérieur du basin de Teruel. *Paleontologia i Evolució 23*, 121–139.

Michaux, J. 1969. Muridae (Rodentia) du Pliocène supérieur d'Espagne et du Midi de la France. *Paleovertebrata 3*, 1–26.

Minwer-Barakat, R. 2005. *Roedores e insectívoros del Turoliense superior y el Plioceno del sector central de la cuenca de Guadix.* 606 pp. Ph.D. thesis, University of Granada, Granada.

Minwer-Barakat, R., García-Alix, A., Martín-Suarez, E. & Freudenthal, M. 2008. *Micromys caesaris*, a new murid (Rodentia, Mammalia) from the late Pliocene of the Guadix Basin, Southeastern Spain. *Journal of Paleontology 82(2)*, 436–441. DOI 10.1666/06-030.1

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E. & Freudenthal, M. 2009a. The micromammal fauna from Negratín-1 (Guadix Basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the late Miocene. *Journal of Paleontology 83(6)*, 854–879. DOI 10.1666/09-009.1

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E. & Freudenthal, M. 2009b. Late Turolian micromammals from Rambla de Chimeneas-3: considerations on the oldest continental faunas from the Guadix Basin (Southern Spain). *Neues Jahrbuch für Geologie und Paläontologie 251*, 95–108. DOI 10.1127/0077-7749/2009/0251-0095

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E. & Freudenthal, M. 2010. Soricidae (Soricomorpha, Mammalia) from the Pliocene of Tollo de Chiclana (Granada, Southeastern Spain). *Journal of Vertebrate Paleontology 30*, 535–546. DOI 10.1080/02724631003622001

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. & Viseras, C. 2012. Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix Basin, southern Spain. *Lethaia 45*, 594–614. DOI 10.1111/j.1502-3931.2012.00324.x

Montenat, C. 1973. *Les Formations néogènes et Quaternaires du Levant espagnol (Provinces d'Alicante et de Murcia).* 1170 pp. Ph.D. thesis, University of Paris-Sud, Paris.

Montoya, P., Ginsburg, L., Alberdi, M.T., Made, J. van der, Morales, J. & Soria, M.D. 2006a. Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas 28(1)*, 137–173.

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J.V., Marín, M.D. & Ruiz-Sánchez, F.J. 2006b. Las nuevas excavaciones (1995–2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. *Estudios Geológicos 62*, 313–325. DOI 10.3989/egeol.0662128

Morales, J. 1984. *Venta del Moro: Su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo*. 327 pp. Ph.D. thesis, Complutense University of Madrid, Madrid.

Pierson d'Autrey, L. 1987. *Sédimentation et structuration synsédimentaire dans le bassin néogène d'Alcoy (Cordillères Bétiques externes Orientales Espagne)*. 315 pp. Ph.D. thesis, University of Paris, Paris.

Popov, V.V. 2003. Late Pliocene Soricidae (Insectivora, Mammalia) from Varshets (North Bulgaria). *Acta Zoologica Cracoviensia 46(1)*, 43–72.

Reumer, J.W.F. 1984. Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. *Scripta Geologica 73*, 1–173.

Ruiz-Bustos, A., Sesé, C., Dabrio, C., Peña, J.A. & Padial, J. 1984. Geología y fauna de micromamíferos del nuevo yacimiento del Plioceno inferior de Gorafe-A (depresion de Guadix-Baza, Granada). *Estudios Geológicos 40*, 231–241. DOI 10.3989/egeol.84403-4664

Ruiz-Sánchez, F.J., Freudenthal, M., Mansino, S., Crespo, V.D. & Montoya, P. 2014. *Apocricetus barrierei* (Rodentia, Mammalia) from La Bullana 2B and La Bullana 3 (Cabriel Basin, Valencia, Spain). Revision of the Late Miocene–Early Pliocene forms of the genus *Apocricetus*. *Paläontologische Zeitschrift 88*, 85–98. DOI 10.1007/s12542-013-0178-0

Sesé, C. 2006. Los roedores y lagomorfos del Neógeno de España. *Estudios Geológicos 62*, 429–480. DOI 10.3989/egeol.0662138

Thaler, L., Crusafont, M. & Adrover, R. 1965. Les premiers micromammifères du Pliocène d'Espagne; précisions chronologiques et biogéographiques sur la faune d'Alcoy. *Comptes Rendus de l'Académie des Sciences de Paris 260*, 4024–4027.

Viseras, C., Soria, J.M. & Fernández, J. 2004. Cuencas Neógenas Postorogénicas de la Cordillera Bética, 576–581. *In* Vera, J.A. (ed.) *Geología de España.* SGE-IGME, Madrid.

Weerd, A. van de 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins*, *Special Publication 2*, 1–217.

Previous geological studies of this area were carried out by Durand Delga *et al*. (1964), Montenat (1973: 1009-1014, Fig.153) and Aguirre *et al*. (1975). More recently, the Alcoy basin has been studied by Pierson d'Autrey (1987).

In the Gormaget ravine area alluvial deposits are found in a statigraphical sequence made up of red conglomerates with grey marlstones intercalations that contain lenticular lignitic sediments (Santisteban *et al*., 1997). A more modern revision allows to differentiate between a higher set of red conglomerates and a lower one. A number of vertebrate localities are found in this sector (Fig. 1), of which only the historic site of Alcoy-Mina, known since the mid-19th century, has yielded remains of large mammals (Montoya *et al*., 2006a). Hitherto have been cited in this area the micromammal sites of Alcoy-Barranco (Thaler *et al*., 1965; Adrover, 1969), Alcoy-N (López Martínez, 1989), Alcoy-4B (Freudenthal *et al*., 1998), Alcoy-2 (Esteban Aenlle and Lacomba, 1988) and Alcoi Cotes Altes-2 (Mansino *et al*., 2009). The suggested age for these localities ranges between MN13 and MN16, i.e., from terminal Miocene to upper Pliocene. On the other hand, new field work undertaken by the Department of Geology of the Universitat de València has resulted in the discovery of the new micromammal localities which are the subject of this study. They are in the same area where Esteban Aenlle and Lacomba (1988) cited the site of Alcoy-2, in the vicinity of a pithead of the former lignite mine (Alcoy-Mina) that has yielded macromammal remains since the mid-19th century (Gervais, 1853). Four new fossiliferous levels were localized, named AL2A, B, C and D, probably close to Alcoy-2. The resulting sampling of these levels showed that two of them, AL2A and AL2B, were sterile, while AL2C and AL2D yielded a promising richness of micromammal remains. The situation of AL2C and AL2D (Fig. 2), proximity and dip slope of these levels seem to allow correlation with the lignite levels of Alcoy-Mina and to precise the age of the latter classic locality (Montoya *et al*., 2006a). The fossil remains recovered from AL2C and AL2D have been compared with the collection from Alcoy-2 housed at the Universidad Complutense de Madrid (UCM, Spain), of which a preliminary faunal list was published by Esteban Aenlle and Lacomba (1988). In this paper we describe the rodent faunas from AL2C and AL2D, and discuss their bio-chronostratigraphic and paleoecologic implications.

2. Material, methods and abbreviations

Since 2005, nearly 1 Tm of sediment has been extracted from AL2C and AL2D. The recovered fossils are kept in the Museu de Geologia de la Universitat de València (MGUV) with the acronyms AL2C- and AL2D-, respectively. The nomenclature and measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, Weerd (1979), Adrover (1986) for the Trilophomyidae and Cuenca-Bescós (1988) and Reumer and van de Hoek Ostende (2003) for the Sciuridae. Measurements (L x W) are in tenths of millimetres and were taken on a Leica MZ7_5 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. The lower teeth are indicated as **m1**, **m2** and **m3**, the upper teeth as **M1**, **M2** and **M3** and the deciduous elements as **D4**.

Abbreviations.- **AL2C**, Alcoy-2C, **AL2D**, Alcoy-2D and **AL2D'08**, sample of Alcoy-2D taken in 2008 (this paper); **BRA**, Brácana; **CAC**, Cacín; **CLC**, Calicasas; **DHS**, Dehesa; **H**, height; **MNA**, Mina; **PUR**, Purcal; **TCH**, Tollo de Chiclana; **MN**, European Neogene land mammal units; **L**, **W**, length and width, respectively; **L1**, length of the occlusal surface; **L2**, total length (base of the crown); **UCM**, Universidad Complutense de Madrid; **SCSIE (UV)**, Servei Central de support a la Investigació Experimental de la Universitat de Valéncia.

3. Geological setting

In the context of the Betic Range, Neogene postorogenic basins provide an important stratigraphic log. This information is essential to understand the final evolution on the Atlantic-Mediterranean communication. The closure of the seaway and the isolation of the basins are diachronic, so marine to continental transition takes form in different times and depends on its geographical location.

Isolation of the sea in the North Prebetic basins of Alicante was very early (Tortonian), and marine sediments are only represented in the Unit I of Viseras *et al*. (2004). First continental deposits belong to Unit II of the same authors, and are represented by alluvial fan facies in the margin and fluvio-lacustrine facies in the centre. In this context, the Miocene-Pliocene transition takes place in a continental environment (Aguirre *et al*., 1975).

The deposits of Alcoy basin have a very important role to study the paleoenvironmental evolution of this area since they provide interesting fossil sites. According to Ballesteros *et al*. (2007), the continental fossil sites in lignite deposits (like Alcoy Mina) belong to fluvial conglomerates, silts and clays unit, inside sintema V of the same authors. This sintema covers, in angular discordance, different Paleogene and Miocene units, so all the studied deposits are discordant with older material and its direction and dip are related with a normal fault (Ballesteros *et al*., 2007).

From a geomorphologic point of view, the entire studied area (Alcoy Mina environment) is an ancient landslide. The analysis of aerial photography provides enough information to support this hypothesis. This landslide, which occurred prior to mine development and land terracing, allows still recognizing the main escarpment and its right and left flanks. Human activity and the passing of time have contributed to erase part of this natural phenomenon, although part of its vertical activity (Pedraza, 1996) and stratigraphic information can still be deduced.

Fieldwork is really complicated due to the extent of cultivation terraces, soil development and escarpment. It has been possible to obtain synthetic statigraphic information for more than 27 meters in a series of over 50 (Fig. 2). This series includes materials located very close to the outcrop of Alcoy-Mina. Only a few meters of this 27 are in well exposed outcrops. To obtain the stratigraphic data presented in figure 2 we dug some trenches in different

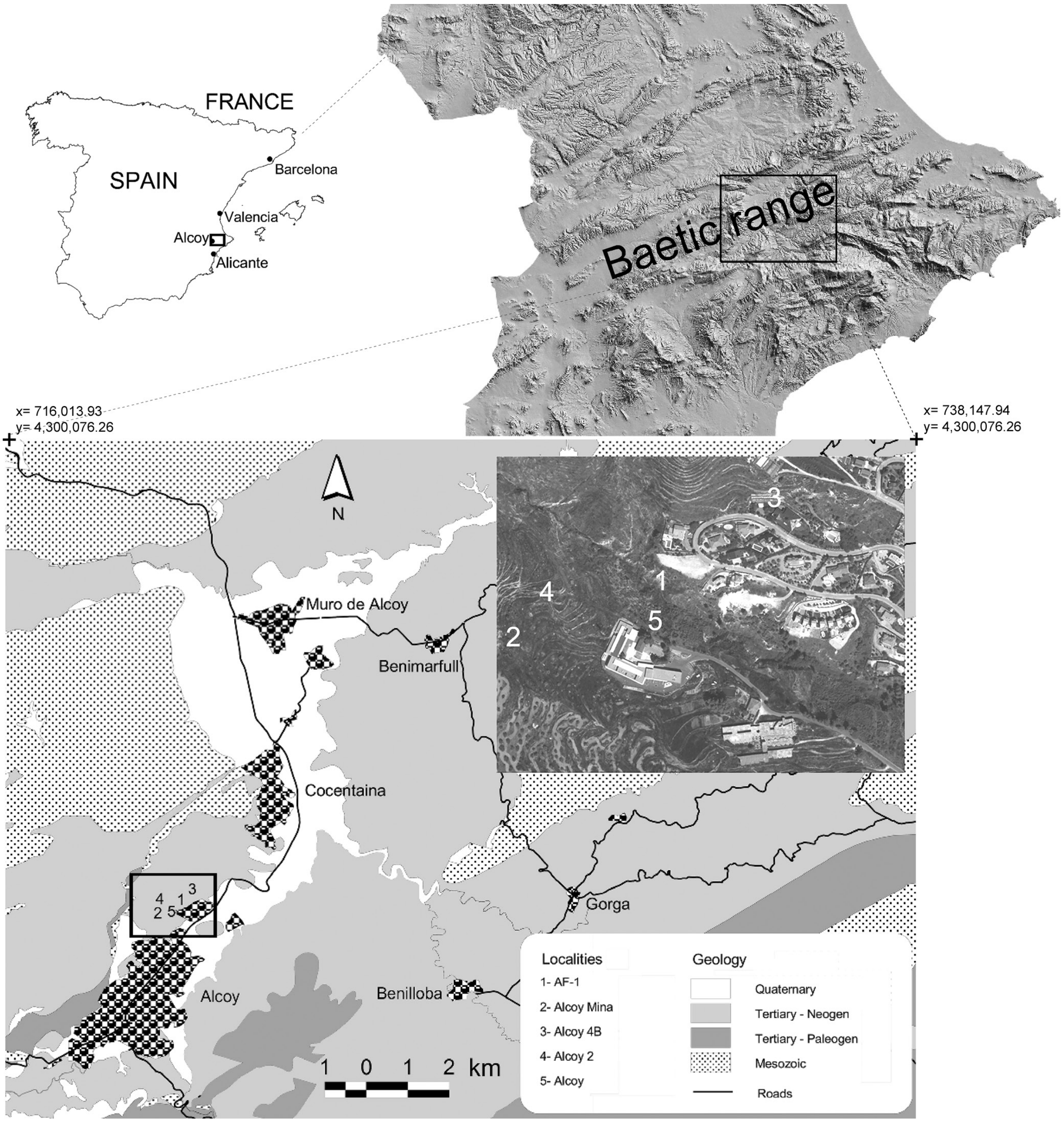
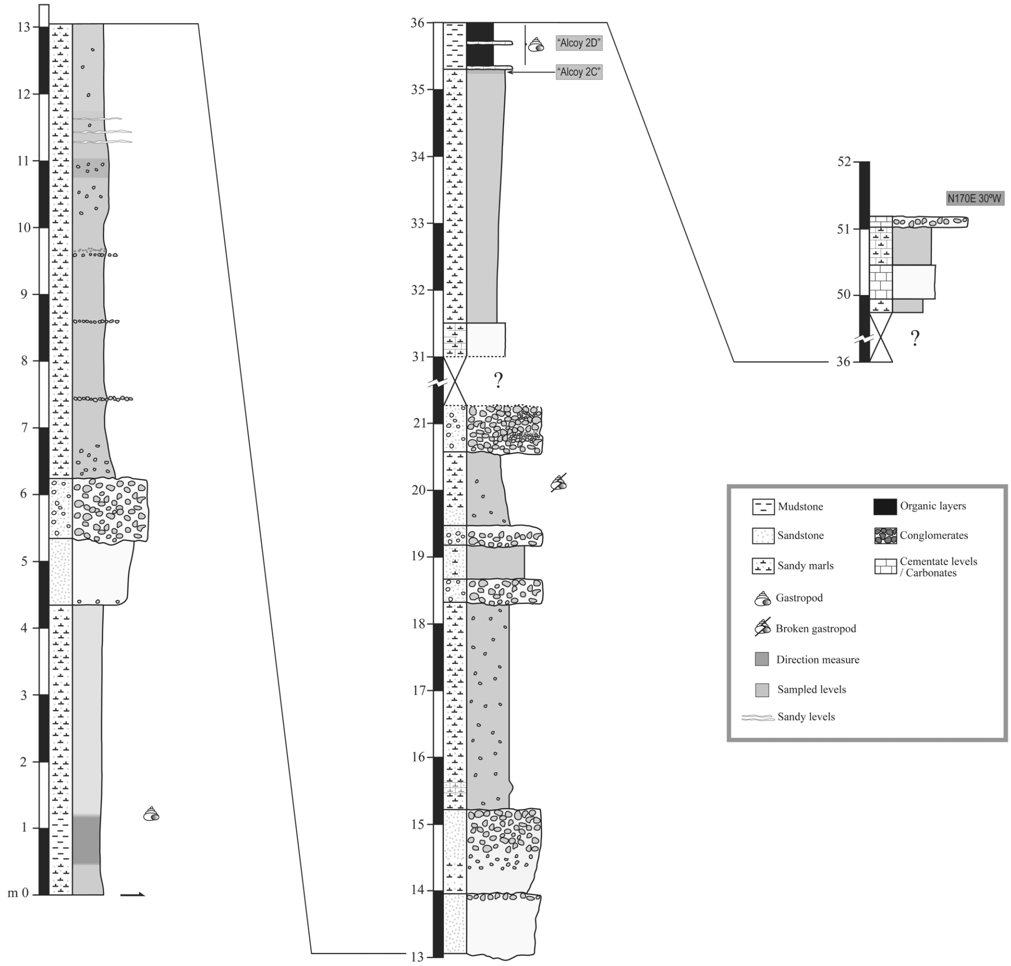


Fig. 1.- Geographic and geological setting of the Alcoy Basin, showing the location of the outcrops of the Gormaget ravine (1 to 5 fossil levels; for acronym, see legend). The location of other fossil localities studied previously is also shown: Alcoy (Adrover,1968), Alcoy-2 (Esteban Aenlle and Lacomba, 1988), Alcoy-4B (Freudenthal *et al*., 1998), Alcoy-Mina (Montoya *et al*., 2006a) and AF-1 (Mansino *et al*., in prep.).

Fig. 1.- Esquema geográfico y geológico de la Cuenca de Alcoy, mostrando la localización de los afloramientos del barranco del Gormaget (niveles fosilíferos del 1 al 5; para acrónimo ver leyenda). Se muestra además, la localización de las localidades previamente estudiadas: Alcoy (Adrover,1968), Alcoy-2 (Esteban Aenlle and Lacomba, 1988), Alcoy-4B (Freudenthal *et al*., 1998), Alcoy-Mina (Montoya *et al*., 2006a) y AF-1 (Mansino *et al*., in prep.).

Fig. 2.- Lithostratigraphic log of the Alcoy-Mina surroundings, with the stratigraphical position of the microvertebrate-bearing localities of the AL2C y AL2D. Scale in meters.

Fig. 2.- Columna litoestratigráfica de los alrededores de Alcoy-Mina, con la posición estratigráfica de los yacimientos de microvertebrados de AL2C y AL2D. Escala en metros.



places to look for the fresh rock, so this is all the stratigraphic information we have of this site. Nevertheless, we know something about the upper and lower materials of the presented series.

Similar marls with conglomerate and sand intercalations are present below the studied materials, where the organic layers increase. Upwards, the conglomerates take more importance (thickness and grain size). Organic marls are not present and reddish colors are predominant.

The alluvial systems present complex landforms in which take part an orographic-dinamic environment and the availability of a solid charge in a fluvial stream (Pedraza, 1996). The stratigraphic sequence described below, in the context of Alcoy-Mina, seems to be the transition between the organic marls with sporadic conglomerates (more distal and in a lower stratigraphic position) and conglomerate units (more proximal and in a higher stratigraphic position). This is the typical context in which subsidence has less importance than contributions.

3.1. Stratigraphy and sedimentology

Studies on the stratigraphy of the Neogene sediments from Alcoy are very scarce. We can mention the revision by Montenat (1973: 1009-1014, fig. 153) of a geological section carried out in the vicinity of Alcoy by Durand Delga *et al*. (1964).

In the studied area, the sandy-marls deposits with gray to brownish colors, which may be several meters thick, are generally dominant. Isolated pebbles in marls or sandy to conglomerate linear intercalations are common. Besides, conglomerate levels are relatively common, and reach a thickness of a meter or even higher.

These conglomerates strata are light colored (often yellow), with a sandy matrix, and often lack internal structure. In some of them we observe coarsening-upward pebbles and minor erosive base. They differ from those in the top of the Gormaget ravine (stratigraphically higher), which have a reddish matrix, a bigger average size of the pebbles and a greater thickness of the strata.

The assembly described has an approximate dip slope of 30º to the West, and it has been possible to identify several faults, although its importance is unknown. Throughout the series there are only two organic layers, AL2D (Fig. 2) and Alcoy-Mina inferior, being the lower one of little importance and without fossil remains (lower part of column presented in figure 2). However, it must be noted that the nature of more than 20 meters of the statigraphic column is not clear because of the great plant and soil development.

AL2D is more than of 60 centimeters thick, only visible in a small outcrop. At first sight we can find abundant gastropod fragments. In the lower part of AL2D there is a fine clay level with intense ochre color (AL2C). In addition, in the middle and lower part of the organic layer we detect two light colored marly limestone levels.

AL2D seems to be a paleosoil of organic nature (histosol) which must have developed in a flooded area of low energy. The lenticular shape of organic levels in the studied area probably is related to the existence of depressions of limited extension in which some drainage occurred.

Alluvial facies like the ones present in the context of Alcoy-Mina are located in the margins of the basin. Massive conglomerates have been interpreted as subaerial deposits, formed by gravitational flows in mass (Santisteban *et al*., 1997).

The bulk of sediments from alluvial plains are overbank deposited during the high floods, when the system often inundates extensive areas (Kukal, 1971). We can think that alluvial systems are formed, to a large degree, by fluviatile processes with the influence of mudflows produced by the downslope movement of solid debris. The organic marls represent lacustrine deposits that could be interpreted like expansive periods of a lake or be placed between river branches, at the margins of alluvial plains or in an area between two fans. In this sense, organic deposits collect vertebrate remains representing the different paleoenvironment around them.

4. Systematic paleontology

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Genus: *Apodemus* Kaup, 1826
Apodemus atavus Heller, 1936 (Fig. 3, 1-5)

Localities: AL2C, AL2D

Material: 3 m1 (AL2D-25, AL2D-26, AL2D-41), 3 m2 (AL2D-68, AL2D-69, AL2D-360), 6 m3 (AL2C-51, AL2C-53, AL2C-61, AL2D-74, AL2D-92, AL2D-96), 4 M2 (AL2C-30, AL2D-182 to AL2D-184), 3 M3 (AL2C-40, AL2D-217, AL2D-218)

Measurements: see Table 1

Description:

m1: The tma is large, round and central. Symmetrical anteroconid, connected with the metaconid-protoconid pair by a narrow crest in one of the specimens. Large labial cingulum, interrupted between the hypoconid and protoconid. The c1 is larger than both the tma and the posterior heel. In one of the specimens this cusp seems to have a very small c0 attached to its posterior side. There is an accessory cusp equivalent in size to the c1 in contact with the protoconid. The posterior heel is big, round and shifted towards the lingual side of the tooth.

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L	2	15.60	16.10	16.60
		W	2	08.90	09.20	09.60
m2	AL2D	L	3	11.40	11.70	12.00
		W	3	09.20	10.00	10.60
m3	AL2D	L	3	11.10	11.60	11.90
		W	3	09.10	10.20	11.60
	AL2C	L	2	10.60	11.00	11.50
		W	2	10.00	10.30	10.60
M2	AL2D	L	3	12.10	12.30	12.60
		W	3	10.70	11.10	11.90
	AL2C	L	1	-	12.70	-
		W	1	-	10.90	-
M3	AL2D	L	2	09.40	09.45	09.50
		W	2	09.50	09.60	09.80
	AL2C	L	1	-	11.00	-

Table 1.- Measurements in tenths of a millimeter of the teeth of *Apodemus atavus* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 1.- Medidas en décimas de milímetro de los dientes de *Apodemus atavus* de las localidades AL2C and AL2D. n= número de especímenes medibles.

m2: The anterolabial cusp is large and comma-shaped; in advanced stages of wear the connection to the protoconid is very evident. Well-developed labial cingulum, separated from the protoconid and hypoconid. There is a large c1 and an accessory cusp, which is highly reduced in one of the specimens. Round or oval posterior heel.

m3: The anterolabial cusp is absent. No longitudinal crest. One of the teeth has a small c1, absent in the others.

M2: The t1 is large. The t3 is small and round. The t7 is oval or round and separated from t4. The t6 is connected to t9. The t12 is connected to t8 and separated from t9.

Discussion:

Apodemus dominans Kretzoi, 1959, and *A. atavus* have been considered synonyms by several authors (Minwer-Barakat, 2005; Minwer-Barakat *et al*., 2005; García-Alix, 2006, García-Alix *et al*., 2008b). The specimens from AL2C and AL2D present some typical features of *A. atavus*, such as the metaconid linked to the lingual lobe of the anteroconid by a low crest (Fig. 3, 1), the large posterior heel of the m2 that usually protrudes over the outline of the tooth (Fig. 3, 2), and the t7-t4 separation which is deep (at the base of the crown) or of medium height in M2 (Fig. 3, 4). We have discarded these molars as belonging to *A. gudrunae* van de Weerd, 1976, because of the individualized t7 (Fig. 3, 4) and smaller size. The measurements of our specimens (Table 1) match a small-sized *Apodemus,* being similar to those of *A. dominans* from Sarrión, Orrios 3, Arquillo 3, Villalba Alta and Aldehuela (Adrover, 1986), Escorihuela, Orrios, Csarnóta 2 (van de Weerd, 1976), Moreda-1A, Belmez-1 and Moreda-1B (Castillo, 1990), Alozaina (Aguilar *et al*., 1993) Mont-Hélène (Aguilar *et al*., 1986), Concud Estación 1 and 3, and Concud Pueblo 3 (Adrover *et al*., 1988). These measurements also fall within the range of variation of *A. atavus* from the localities of TCH-1, 1B, 3 and 13 (Minwer-Barakar *et al*., 2005), being slightly smaller than those from PUR-7, PUR-13, CLC-3, CLC-3B, CLC-4B, AGU-1C and DHS-1 (García-Alix *et al*., 2008b).

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. 3, 6-11)

Locality: AL2C, AL2D

Material: 1m1 (AL2D-17), 5 m2 (AL2D-50, AL2D-51, AL2D-56, AL2D-62, AL2D-64), 6 m3 (AL2C-48, AL2D-72, AL2D-91, AL2D-93, AL2D-136, AL2D-220), 6 M1 (AL2C-20 to AL2C-22, AL2D-131, AL2D-133, AL2D-134), 6 M2 (AL2C-37, AL2D-142, AL2D-176, AL2D-177, AL2D-181, AL2D-351), 4 M3 (AL2D-206, AL2D-212, AL2D-213, AL2D-222)

Measurements: see Table 2

Description:

m1: The only specimen recovered is in an advanced stage of wear. There is a large tma. The tooth has a large c1 and two accessory cusps. The posterior heel cannot be observed. Two roots.

m2: Isolated anterolabial cusp. Well-developed labial cingulum. There is a large c1, and an accessory cusp may also be present. Round or oval posterior heel.

m3: Highly reduced anterolabial cusp. No longitudinal crest. One of the specimens has a small c1.

M1: The t1 is situated posteriorly with respect to the t3. The connection between t1 and t2 is very low. There is neither t1bis nor t2 bis. All the teeth have a small posterior spur in the t3 directed towards the t6. One specimen has a small distal spur in the t1 directed towards the t5. The valley between t3 and t6 is very deep and wide. The t4, t5, t6, t7 and t9 are connected. The t12 is round and medium-sized, connected to the posterolabial part of the t8. There are four roots.

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L	1	-	22.50	-
		W	1	-	13.60	-
m2	AL2D	L	5	16.00	17.20	17.80
		W	5	13.70	15.40	16.60
m3	AL2D	L	3	12.90	13.10	13.30
		W	5	11.30	12.20	13.20
	AL2C	L	1	-	13.60	-
		W	1	-	12.80	-
M1	AL2D	L	1	-	24.30	-
		W	3	13.30	13.80	14.30
	AL2C	L	2	22.40	22.50	22.70
		W	2	13.20	13.25	13.30
M2	AL2D	L	4	14.60	15.00	15.70
		W	5	12.40	13.00	13.60
	AL2C	L	1	-	14.90	-
		W	1	-	15.20	-
M3	AL2D	L	4	11.30	11.60	12.00
		W	4	09.50	10.70	11.50

Table 2.- Measurements in tenths of a millimeter of the teeth of *Apodemus gorafensis* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 2.- Medidas en décimas de milímetro de los dientes de *Apodemus gorafensis* de las localidades AL2C and AL2D. n= número de especímenes medibles.

M2: Oval or round t1. The specimen from AL2C, which is very worn, and one molar from AL2D show a spur directed towards the t4-t5 intersection. The t3 is smaller than t1, and highly reduced in one tooth. The t4 and t7 are separated. The t6 and t9 are connected in the molars with an advanced stage of wear. The t12 is small and connected to the posterolabial part of t8 and separated from t9.

M3: The t1 isolated in two specimens**.** The t3 is absent. The t4, t5, t6 and t8 are connected.

Discussion:

During the Early and Middle Pliocene of Western Europe, two different lineages of *Apodemus* can be distinguished, a smaller form and a larger one (Martín-Suárez and Mein, 1998). In the Iberian basins there are a number of localities in which this situation occurs, in particular with *A. atavus* or *A.* aff. *atavus* and and *A. gorafensis* or *A.* aff. *gorafensis*. The coexistence of these two lineages has been recorded in the localities of Peralejos E (Adrover *et al*., 1988), Celadas 9 and La Gloria 4 (Adrover *et al*., 1993), from Teruel, PUR-4, PUR-13 and CLC-3B in the Granada basin (García-Alix *et al*., 2008b) (Fig. 4) and Alcoy (Esteban Aenlle and Lacomba, 1988) (Table 3). The specimens from AL2C and AL2D are bigger and

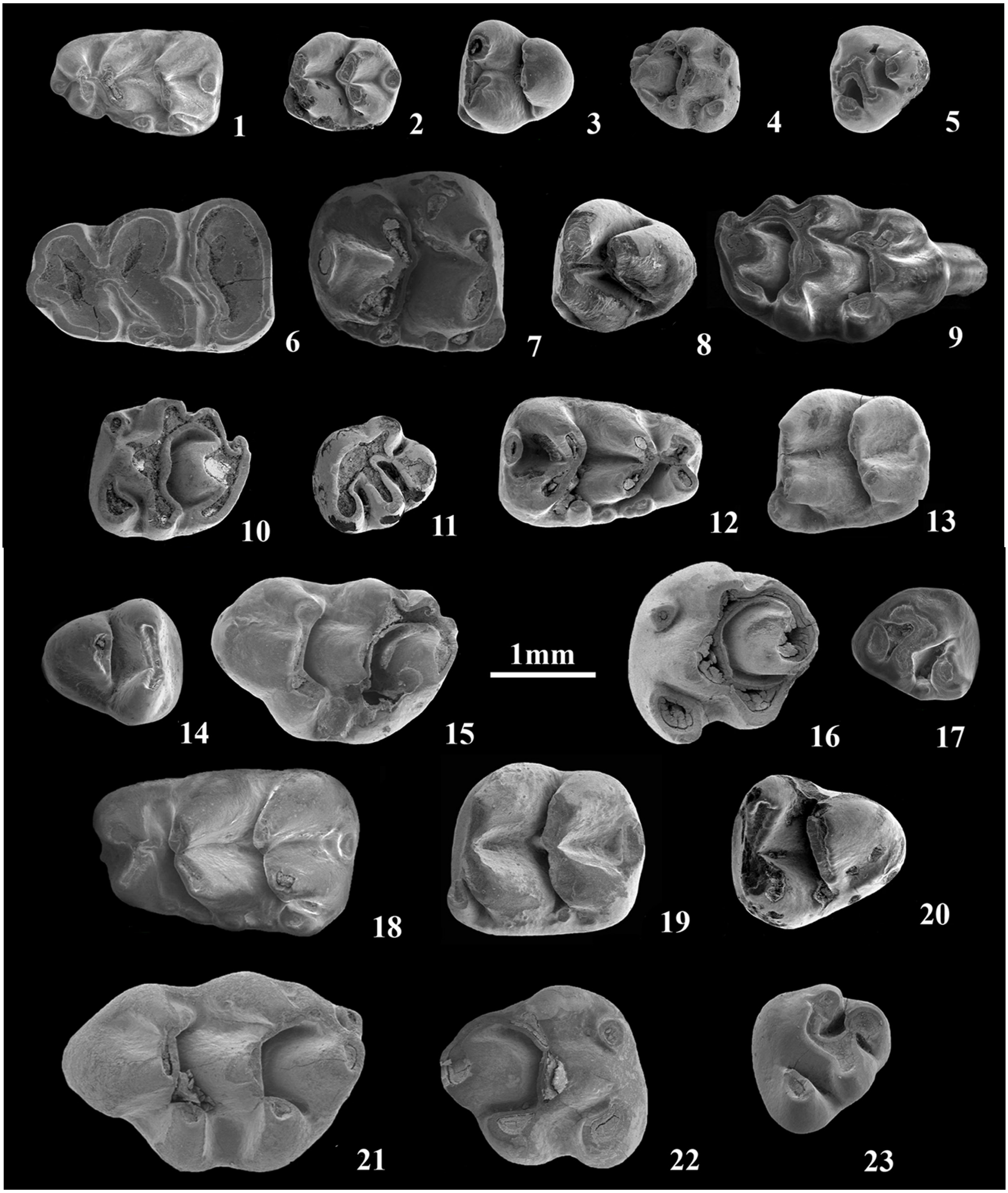


Fig. 3.- Rodent faunas from AL2C and AL2D (Alcoy basin, Spain). *Apodemus atavus* from AL2C and AL2D. 1, left m1, AL2D-25; 2, left m2, AL2D-68; 3, left m3, AL2D-74; 4, right M2, AL2D-184; 5, left M3, AL2C-40. *Apodemus gorafensis* from AL2C and AL2D. 6, left m1, AL2D-17; 7, right m2, AL2D-50; 8, left m3, AL2C-48; 9, right M1, AL2C-20; 10, left M2, ALD-176; 11, left M3, AL2D-212. *Paraethomys meini* from AL2C and AL2D. 12, right m1, AL2D-21; 13, left m2, AL2D-66; 14, right m3, ALC-50; 15, left M1, AL2D-126; 16, left M2, AL2D-350; 17, right M3, AL2D-216. *Paraethomys* aff. *abaigari* from AL2C and AL2D. 18, left m1, AL2D-1; 19, left m2, AL2C-48; 20, left m3, AL2C-49; 21, left M1, AL2D-101; 22, right M2, AL2C-28; 23, left M3, AL2D-194. Scale=1mm.

Fig. 3.- Faunas de roedores de AL2C y AL2D (Cuenca de Alcoy, España). *Apodemus atavus* de AL2C y AL2D. 1, m1 izquierdo, AL2D-25; 2, m2 izquierdo, AL2D-68; 3, m3 derecho, AL2D-74; 4, M2 derecho, AL2D-184; 5, M3 izquierdo, AL2C-40. *Apodemus gorafensis* de AL2C y AL2D. 6, m1 izquierdo, AL2D-17; 7, m2 derecho, AL2D-50; 8, m3 izquierdo, AL2C-48; 9, M1 derecho, AL2C-20; 10, M2 izquierdo, ALD-176; 11, M3 izquierdo, AL2D-212. *Paraethomys meini* de AL2C y AL2D. 12, m1 derecho, AL2D-21; 13, m2 izquierdo, AL2D-66; 14, m3 derecho, ALC-50; 15, M1 izquierdo, AL2D-126; 16, M2 izquierdo, AL2D-350; 17, M3 derecho, AL2D-216. *Paraethomys* aff. *abaigari* de AL2C y AL2D. 18, m1 izquierdo, AL2D-1; 19, m2 izquierdo, AL2C-48; 20, m3 izquierdo, AL2C-49; 21, M1 izquierdo, AL2D-101; 22, M2 derecho, AL2C-28; 23, M3 izquierdo, AL2D-194. Escala=1mm.

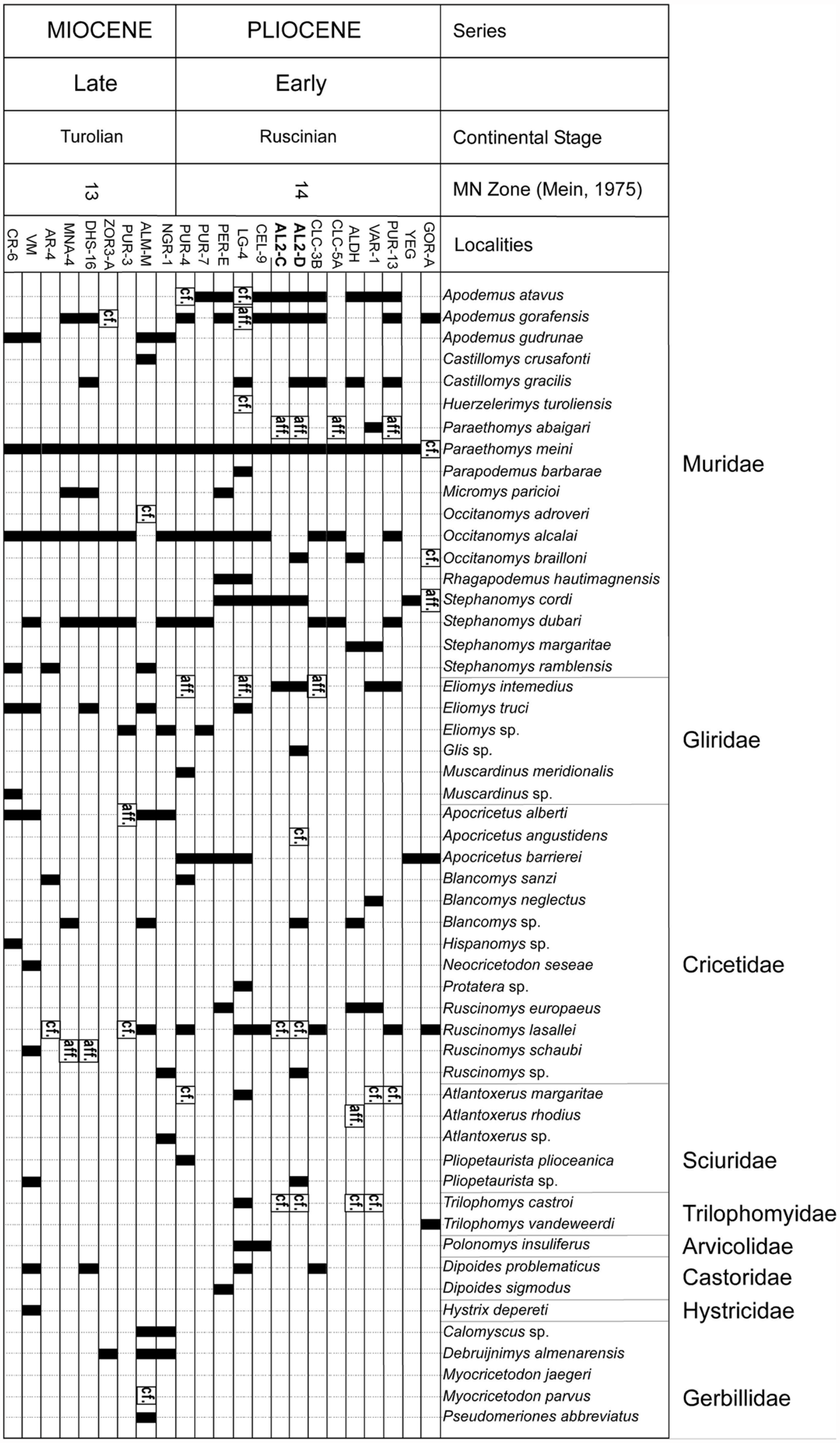


Fig. 4.- Distribution chart of the rodent species studied in this paper and, according to bliblography, of other species of similar age. Abbreviations: GOR-A, Gorafe-A (Ruiz-Bustos *et al*., 1984); YEG, Yeguas (Minwer-Barakat, 2005); PUR-3, PUR-4, PUR-7, PUR-13, Purcal 3, 4, 7 and 13; CLC-3B, CLC-5A, Calicasas 3 B and 5A; DHS-16, Dehesa-16; MNA-4, Mina 4 (García-Alix, 2006); VAR-1, Villalba Alta Río 1; ALDH, Aldehuela (Adrover, 1986); CEL-9, Celadas-9; LG-4, La Gloria-4; AR-4, Arquillo 4 (Adrover *et al*., 1993); PER-E, Peralejos-E (Mein *et al*., 1990); NGR-1, Negratín-1 (Minwer-Barakat *et al.,* 2009); ALM-M, Almenara-M (Furió *et al*., 2005); ZOR-3A, Zorreras 3A (Martín-Suárez *et al*., 2000); VM, Venta del Moro (Montoya *et al*., 2006b); CR-6, Crevillente 6 (Martín-Suárez and Freudenthal, 1998). For the making of this table the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* and *Stephanomys donnezani cordii* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Cricetus kormosi* and *Apocricetus kormosi* as *Apocricetus alberti*; *Protatera almenarensis* as *Debruijnimys almenarensis*.

Fig. 4.- Cuadro de distribución de las especies de roedores estudiados en este trabajo y de otras especies de similar edad según la bibliografía. Abreviaciones: GOR-A, Gorafe-A (Ruiz-Bustos *et al*., 1984); YEG, Yeguas (Minwer-Barakat, 2005); PUR-3, PUR-4, PUR-7, PUR-13, Purcal 3, 4, 7 y 13; CLC-3B, CLC-5A, Calicasas 3 B y 5A; DHS-16, Dehesa-16; MNA-4, Mina 4 (García-Alix, 2006); VAR-1, Villalba Alta Río 1; ALDH, Aldehuela (Adrover, 1986); CEL-9, Celadas-9; LG-4, La Gloria-4; AR-4, Arquillo 4 (Adrover *et al*., 1993); PER-E, Peralejos-E (Mein *et al*., 1990); NGR-1 , Negratín-1 (Minwer-Barakat *et al.,* 2009); ALM-M, Almenara-M (Furió *et al*., 2005); ZOR-3A, Zorreras 3A (Martín-Suárez *et al*., 2000) ; VM, Venta del Moro (Montoya *et al*., 2006b); CR-6, Crevillente 6 (Martín-Suárez and Freudenthal, 1998). Sinonimias tomadas en cuenta para confeccionar esta tabla: *Apodemus dominans* como *A. atavus*; *Castillomys crusafonti gracilis* como *C. gracilis*; *Paraethomys anomalus* como *P. meini*; *Stephanomys medius* y *Stephanomys donnezani cordii* como *S. cordii*; *Cricetus barrierei* como *Apocricetus barrierei*; *Cricetus kormosi* y *Apocricetus kormosi* como *Apocricetus alberti*; *Protatera almenarensis* como *Debruijnimys almenarensis*

with a more developed t7 than *A. gudrunae* van de Weerd 1976, and smaller and with a more developed tma than *A. jeanteti* Michaux, 1967. *Apodemus agustii* Martín Suárez, 1988, differs from our material by its bigger tma, lack of stephanodonty in the upper molars and a funnel delimited by the anteroconid, protoconid and metaconid in the m1. The the populations from AL2C and AL2D are consistent with the measurements and morphology of *A. gorafensis* of the collection from Gorafe-A, the type locality of the species (Ruiz Bustos *et al*., 1984), showing a relatively large tma and well-developed labial cingulum and t7. Our specimens are somewhat bigger than *Apodemus*

Alcoy-2 (Esteban Aenlle and Lacomba, 1988)	AL2C (This paper)	AL2D (This paper)
Apodemus dominans	*Apodemus atavus*	*Apodemus atavus*
Apodemus gorafensis	*Apodemus gorafensis*	*Apodemus gorafensis*
Castillomys crusafonti gracilis	-	*Castillomys gracilis*
Paraethomys meini	*Paraethomys meini*	*Paraethomys meini*
Paraethomys jaegeri	*Paraethomys* aff. *abaigari*	*Paraethomys* aff. *abaigari*
-	-	*Occitanomys brailloni*
Stephanomys medius	*Stephanomys cordii*	*Stephanomys cordii*
-	*Apocricetus* cf. *angustidens*	*Apocricetus* cf. *angustidens*
Ruscinomys aff. *europaeus*	*Ruscinomys* cf. *lasallei*	*Ruscinomys* cf. *lasallei*
Blancomys neglectus	-	*Blancomys* sp.
Trilophomys castroi	*Trilophomys* cf. *castroi*	*Trilophomys* cf. *castroi*
-	*Eliomys intermedius*	*Eliomys intermedius*
-	-	*Glis* sp.
-	-	*Pliopetaurista* sp.

Table 3.- Faunal list of Alcoy-2 (Esteban Aenlle and Lacomba, 1988) compared with the faunal lists of the localities studied in this paper, AL2C and AL2D.

Tabla 3.- Lista faunística de Alcoy-2 (Esteban Aenlle and Lacomba, 1988) comparada con las listas faunísticas de los yacimientos estudiados en este trabajo, AL2C y AL2D.

aff. *gorafensis* from Peralejos E (Adrover *et al*., 1988), falling within the range of variation of *A.* aff. *gorafensis* from Celadas 9 and La Gloria 4 (Adrover *et al.,* 1993). The mean measurements of the populations from AL2C and AL2D are slightly bigger than *A.* aff. *gorafensis* from PUR-23, being also very similar to those of *A. gorafensis* from PUR-4, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al*., 2008b).

Genus *Paraethomys* Petter, 1968
Paraethomys meini (Michaux, 1969) (Fig. 3, 12-17)
Localities: AL2C, AL2D

Material: 15 m1 (AL2C-1, AL2C-3, AL2C-43, AL2C-45, AL2C-46, AL2C-58, AL2C-66, AL2D-15, AL2D-21 to AL2D-24, AL2D-40, AL2D-347), 6 m2 (AL2C-11, AL2C-12, AL2D-45, AL2D-58, AL2D-66, AL2D-67), 5 m3 (AL2C-50, AL2C-63, AL2D-83, AL2D-87, AL2D-88, AL2D-90), 3 M1 (AL2D-126, AL2D-132, AL2D-253) 4 M2 (AL2D-172, AL2D-178, AL2D-179, AL2D-350), 8 M3 (AL2C-41, AL2C-62, AL2C-68, AL2D-210, AL2D-214 to AL2D-216, AL2D-352)

Measurements: see Table 4

Description:

m1: Absent tma. Slightly asymmetrical anteroconid. The connection between anteroconid and protoconid-metaconid pair is very low, and in some teeth a small round funnel can be observed. Medium-sized labial cingulum. One of the molars has an incipient longitudinal spur. There is a medium size round c1. The size and number of the accessory cusps is very variable, ranging from two to four. Reduced posterior heel.

m2: The anterolabial cusp is in contact with a moderately developed labial cingulum. Three of the specimens

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L	6	19.00	19.40	19.90
		W	6	11.60	12.00	12.50
	AL2C	L	2	19.30	19.40	19.50
		W	4	11.40	11.90	12.40
m2	AL2D	L	4	14.10	14.70	15.10
		W	4	12.00	12.70	13.20
	AL2C	L	2	13.60	14.50	15.50
		W	2	11.30	11.40	11.50
m3	AL2D	L	4	12.40	13.70	14.30
		W	4	11.20	12.10	12.90
	AL2C	L	1	-	13.20	-
		W	1	-	12.70	-
M1	AL2D	L	1	-	22.40	-
		W	2	15.30	15.35	15.40
M2	AL2D	L	2	-	17.40	-
		W	3	15.50	16.10	16.70
M3	AL2D	L	5	10.40	11.20	12.60
		W	5	09.70	10.60	11.50
	AL2C	L	3	12.20	12.70	13.30
		W	3	10.70	11.70	12.20

Table 4.- Measurements in tenths of a millimeter of the teeth of *Paraethomys meini* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 4.- Medidas en décimas de milímetro de los dientes de *Paraethomys meini* de las localidades AL2C and AL2D. n= número de especímenes medibles.

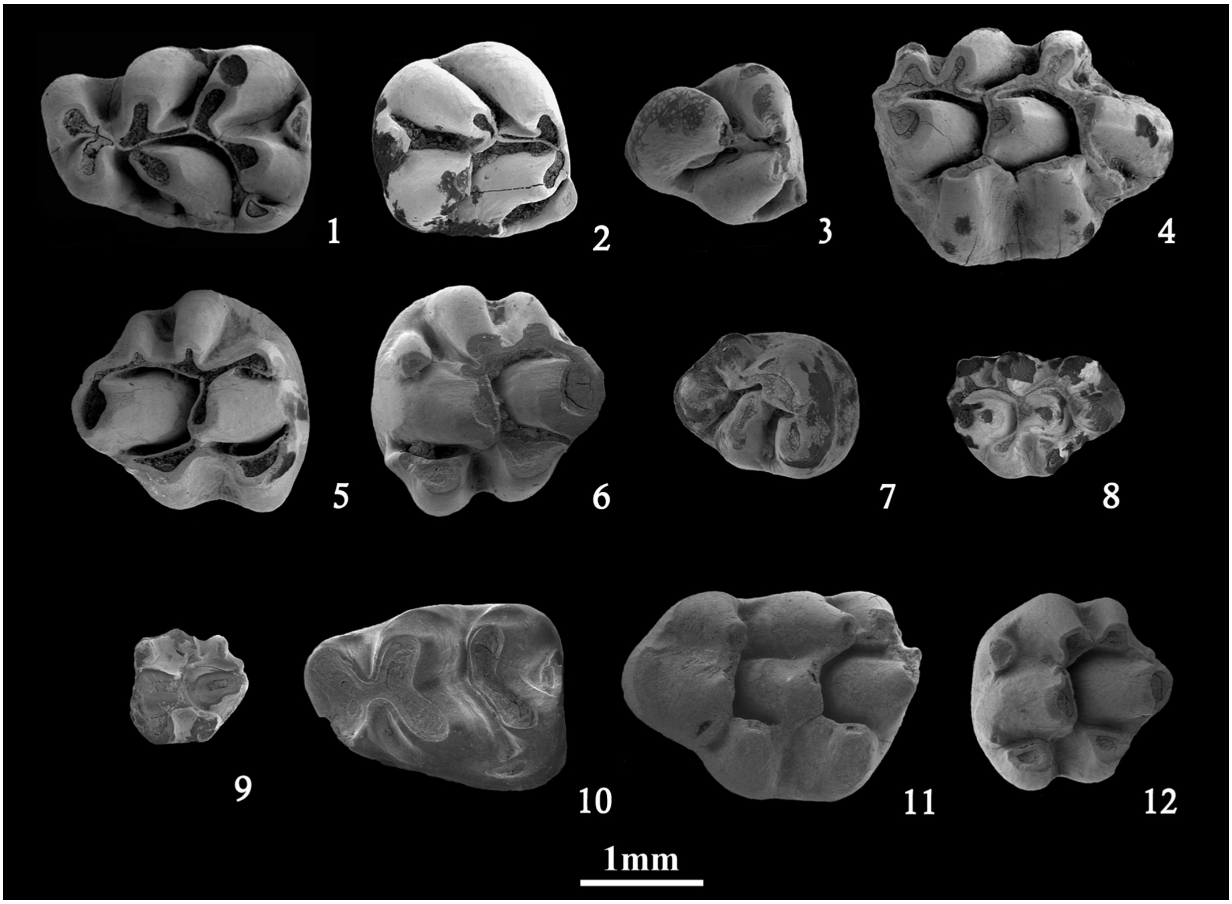


Fig. 5.- Rodent faunas from AL2D (Alcoy basin, Spain). *Stephanomys cordii* from AL2D. 1, left m1, AL2D-7; 2, right m2, AL2D-55; 3, right m3, AL2D-73; 4, right M1, AL2D-98; 5, right M2, AL2D-149; 6, left M2, AL2D-143; 7, right M3, AL2D-193. *Castillomys gracilis* from AL2D. 8, right M1, AL2D-138; 9, left M2, AL2D-185. *Occitanomys brailloni* from AL2D. 10, left m1, AL2D-16; 11, left M1, AL2D-113; 12, left M2, AL2D-173. Scale=1mm.

Fig. 5.- Faunas de roedores AL2D (Alcoy basin, Spain). *Stephanomys cordii* de AL2D. 1, m1 izquierdo, AL2D-7; 2, m2 derecho, AL2D-55; 3, m3 derecho, AL2D-73; 4, M1 derecho, AL2D-98; 5, M2 derecho, AL2D-149; 6, M2 izquierdo, AL2D-143; 7, M3 derecho, AL2D-193. *Castillomys gracilis* de AL2D. 8, M1 derecho, AL2D-138; 9, M2 izquierdo, AL2D-185. *Occitanomys brailloni* de AL2D. 10, m1 izquierdo, AL2D-16; 11, M1 izquierdo, AL2D-113; 12, M2 izquierdo, AL2D-173. Escala=1mm.

show an accessory cusp in contact with the protoconid. One of the specimens presents a poorly developed longitudinal spur. The posterior heel is reduced and lingually displaced. Two roots.

m3: The anterolabial cusp is highly reduced or completely absent. The hypoconid-entoconid complex is separated from the anterior complex. One specimen presents a small c1 attached to the posterior complex.

M1: The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. One of the specimens presents a very small distal spur on the t3 directed towards the t5. There are no connections between t1 and t3 with t5. The connection between t4 and t8 is very low. There is a small t12.

M2: The t1 and t3 are isolated**.** The t3 is highly reduced. In three of the specimens a small distal spur on the posterior part of t1 directed towards the t4-t5 intersection can be observed. The connection between t4 and t8 is very low. The t9 and t12 are absent.

M3: Large and isolated t1. The t3 is absent. The connection between t8 and t4-t5-t6 is very low, and in two of the specimens completely isolated. There are three roots.

Discussion:

Paraethomys meini (Michaux, 1969) from AL2C and AL2D is much smaller than *P. abaigari* Adrover, Mein and Moissenet, 1988 and *P. jaegeri* Montenat and de Brujin, 1976. Moreover, despite being similar in size to the molars of *P. belmezi* Castillo, 1990, these teeth differ from our specimens by the presence of a well-developed tma in the m1, loss of the t3 and isolation of t8 in M2 and unconnected t6 and t9 in the M1. Two of the M2 present a distal spur on the posterior part of the t1 directed towards the t3- t5 intersection, which is absent in the specimens from Alcoy-2 studied by Esteban Aenlle and Lacomba (1988). The measurements of the specimens from AL2C and AL2D are similar to those of *P. meini* from the localities of Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover, 1986), Villalba Alta Río, Peralejos E (Adrover *et al.*, 1988), and *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover, 1986), considered synonyms of *P. meini* by several authors (van de Weerd, 1976; Adrover, 1986; Castillo, 1990; Minwer-Barakat, 2005; García-Alix, 2006, García-Alix *et al.*, 2008b). The size of our specimens is consistent with the measurements and morphology of *P. meini* from Celadas 9 and La Gloria 4 (Adrover *et al.*, 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11, BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (García-Alix *et al.*, 2008b).

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. 3, 18-23)

Localities: AL2C, AL2D

Material**:** 14 m1 (AL2C-4 to AL2C-6, AL2C-8, AL2C-86, AL2D-1, AL2D-2, AL2D-28 to AL2D-30, AL2D-34, AL2D-36, AL2D-38, AL2D'08-2), 10 m2 (AL2C-9, AL2C-13, AL2C-14, AL2C-19, AL2C-44, AL2D-47, AL2D-48, AL2D-61, AL2D-349, AL2D-354), 5 m3 (AL2C-49, AL2D-75, AL2D-76, AL2D-80, AL2D'08-8), 6 M1 (AL2C-54, AL2D-101, AL2D-103, AL2D-104, AL2D-110, AL2D-122), 16 M2 (AL2C-28, AL2C-36, AL2C-38, AL2D-146, AL2D-148, AL2D-150, AL2D-154, AL2D-156 to AL2D-158, AL2D-160, AL2D-162, AL2D-168 to AL2D-170, AL2D-235), 9 M3 (AL2D-192, AL2D-194, AL2D-195, AL2D-197, AL2D-199, AL2D-200, AL2D-203, AL2D-208, AL2D-209)

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L	3	23.40	24.20	25.30
		W	6	14.00	14.60	15.40
	AL2C	L	1	-	23.30	-
		W	3	13.90	14.90	16.00
m2	AL2D	L	3	16.70	18.10	18.90
		W	3	15.20	16.10	17.20
	AL2C	L	4	17.30	18.50	19.20
		W	5	14.60	15.80	16.80
m3	AL2D	L	3	15.60	16.00	16.20
		W	3	13.10	13.80	14.30
	AL2C	L	1	-	16.20	-
		W	1	-	14.40	-
M1	AL2D	L	4	26.20	26.90	27.60
		W	4	18.00	18.30	18.70
	AL2C	L	1	-	25.40	-
		W	1	-	18.40	-
M2	AL2D	L	12	17.60	19.70	21.60
		W	13	15.70	17.40	18.40
	AL2C	L	2	18.30	19.40	20.60
		W	3	16.60	17.50	18.00
M3	AL2D	L	8	12.60	13.60	14.70
		W	8	12.80	13.30	14.70

Table 5.- Measurements in tenths of a millimeter of the teeth of *Paraethomys* aff. *abaigari* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 5.- Medidas en décimas de milímetro de los dientes de *Paraethomys* aff. *abaigari* de las localidades AL2C and AL2D. n= número de especímenes medibles.

Measurements: see Table 5

Description:

m1: Slightly asymmetrical anteroconid. In worn specimens the connection between anteroconid and protoconid-metaconid pair is more evident. The labial cingulum is moderately developed. There is a large c1 in contact with the protoconid and an accessory cusp adjacent to the hypoconid. Some specimens have a small longitudinal spur. The posterior heel is small, lingually displaced and oval. Two roots.

m2: The anterolabial cusp is big, isolated from the other cusps but in contact with the labial cingulum. A small c1 can be observed in five of the specimens. The posterior heel is small, laminar or oval-shaped and lingually displaced.

m3: Both the anterolabial cusp and the c1 are absent. The hypoconid-entoconid complex is separated from the anterior complex. Two roots.

M1: The connection between t1 and t2 is very low. The t2 and t3 are very close together. Distal spurs from the t1 and t3 towards the t4-t5 and t5-t6 connections respectively may be present. There is a small t12. There are three roots.

M2: The t1 and t3 are isolated**.** The t3 is reduced. Some specimens have a distal spur directed towards the t4-t5 intersection. The t9 is absent. The connection between t4 and t8 is very low. The outline of some of the specimens, the best preserved ones, seems more elongated than the others, and much more than *P. meini*.

M3: The t1 is large and isolated. The t3 is absent. The connection between t8 and t4-t5-t6 is very low, and in some specimens this cusp is almost isolated. Three roots.

Discussion:

The *Paraethomys* from AL2C and AL2D can be grouped in two clusters in terms of size. The smaller specimens can be assigned to *Paraethomys meini*, while the larger ones show many of the features of *P. abaigari* from Villalba Alta Río (type locality), such as a reduced longitudinal spur in m1, moderate labial cingulum, large c1 and moderate posterior heel (Adrover *et al.*, 1988; García-Alix *et al.*, 2008b). Also, these molars differ from

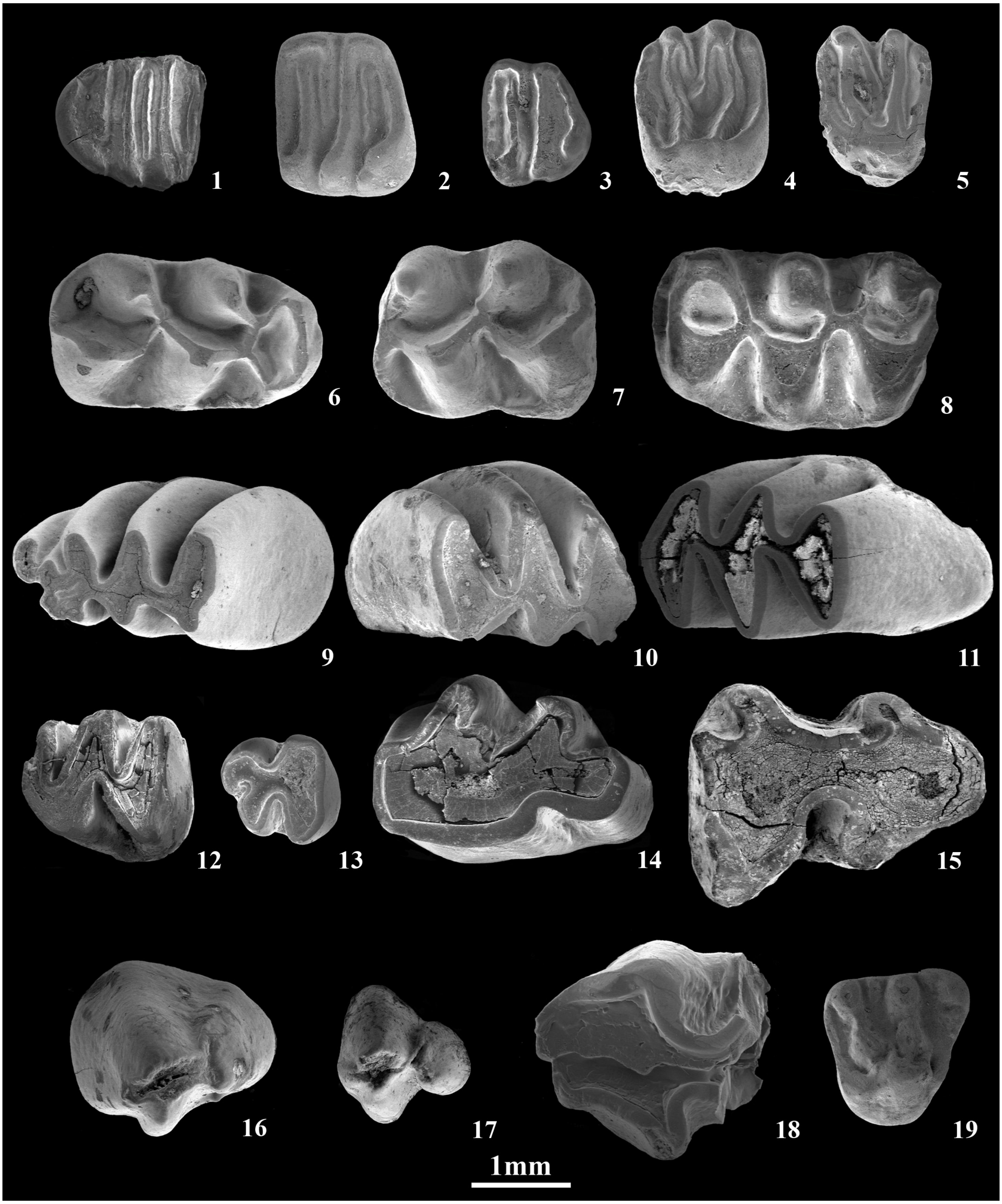


Fig. 6.- Rodent faunas from AL2C and AL2D (Alcoy basin, Spain). *Glis* sp. from AL2D. 1, left m3, AL2D-359. *Eliomys intermedius* from AL2D. 2, left m1-m2, AL2D-290; 3, left m3, AL2D-356; 4, right M1-M2, AL2D-291; 5, left M1-M2, AL2D-293. *Apocricetus* cf. *angustidens* from AL2D. 6, right m1, AL2D-260; 7, left m2, AL2D-262; 8, left M1, AL2D-259. *Trilophomys* cf. *castroi* from AL2C and AL2D. 9, left m1, AL2D-300; 10, right m2, AL2D-301; 11, left M1, AL2D'08-14; 12, right M2, AL2C-83; 13, right M3, AL2D-316; *Ruscinomys* cf. *lasallei* from AL2C and AL2D. 14, left m3, AL2C-69; 15, left M2, AL2D-317; 16, left M3, AL2D-306; 17, left M3, AL2D-281; *Blancomys* aff. *sanzi* from AL2D. 18, left m1, AL2D-318. *Pliopetaurista* sp. from AL2D. 19, right D4, AL2D-295. Scale=1mm.

Fig. 6.- Faunas de roedores de AL2C y AL2D (Cuenca de Alcoy, España). *Glis* sp. de AL2D. 1, m3 izquierdo, AL2D-359. *Eliomys intermedius* de AL2D. 2, m1-m2 izquierdo, AL2D-290; 3, m3 izquierdo, AL2D-356; 4, M1-M2 derecho, AL2D-291; 5, M1-M2 izquierdo, AL2D-293. *Apocricetus* cf. *angustidens* de AL2D. 6, m1 derecho, AL2D-260; 7, m2 izquierdo, AL2D-262; 8, M1 izquierdo, AL2D-259. *Trilophomys* cf. *castroi* de AL2C y AL2D. 9, m1 izquierdo, AL2D-300; 10, m2 derecho, AL2D-301; 11, M1 izquierdo, AL2D'08-14; 12, M2 derecho, AL2C-83; 13, M3 derecho, AL2D-316; *Ruscinomys* cf. *lasallei* de AL2C y AL2D. 14, m3 izquierdo, AL2C-69; 15, M2 izquierdo, AL2D-317; 16, M3 izquierdo, AL2D-306; 17, M3 izquierdo, AL2D-281; *Blancomys* aff. *sanzi* de AL2D. 18, m1 izquierdo, AL2D-318. *Pliopetaurista* sp. de AL2D. 19, D4 derecho, AL2D-295. Escala= 1mm.

P. meini in their development of distal spurs in the t1 and t3 and persistence of the t12 in the M1. However, our specimens are slightly smaller than *P. abaigari* from Villalba Alta Río, while very similar to those of *Paraethomys* aff. *abaigari* from CLC-5, PUR-13 (García-Alix *et al*., 2008b), La Gloria 4 and Celadas 9 (Adrover *et al*., 1993). These teeth reach some of the lower values of *P. jaegeri*, although the mean values are always bigger in the latter species. For these reasons we ascribe our material to *Paraethomys* aff. *abaigari.*

The coexistence of two *Paraethomys* species of different size has been recorded in a number of Pliocene localities from the Teruel basin, as Villalba Alta Río, La Judería, Celadas 6 (Adrover *et al*., 1988), Villalba Alta 1, La Gloria 4 (Mein *et al*., 1990), Celadas 14, Celadas 5, Celadas 5A and Celadas 9 (García-Alix *et al*., 2008b) (Fig. 4). Adrover (1986) also described a big-sized form of *Paraethomys* associated to *P. meini* in the localities of Séte and Villalba Alta, where he found *P. jaegeri* and *P*. aff. *jaegeri* respectively. The localities CLC-5A and PUR-13 from the Granada basin have yielded remains of both *Paraethomys meini* and *Paraethomys* aff. *abaigari* (García-Alix *et al*., 2008b) (Fig. 4). Also, Adrover *et al.* (1988) recognized individuals of a big-sized phylogenetic lineage of *Paraethomys* in the localities of Gorafe 1 and Gorafe-A, while in the faunal lists given by Ruiz Bustos *et al*. (1984) and Agustí and Martín Suárez (1984) for Gorafe-A and Gorafe 1 respectively, the only *Paraethomys* species mentioned are *P*. cf. *meini* in Gorafe 1 and *P. meini* in Gorafe A (Fig. 4). Montenat and de Bruijn (1976) cited two *Paraethomys* species in the locality of La Juliana (Murcia): the big-sized *P. jaegeri* and the smaller *P. meini*. García-Alix (2006) noted that, when two species of *Paraethomys* coexist, like in the Ruscinian localities of PUR-13 and CLC-5A, the size of *P. meini* is quite reduced, which agrees with *P. meini* from AL2C and AL2D, whereas in older localities like PUR-4 the two lineages cannot be distinguished. This author found the same situation in several Lower Pliocene localities of the Teruel basin, like Celadas 5, 5A, 9 and 14, and La Gloria 4, where *P. meini* appears associated with *P.* aff *abaigari*, and in younger localities like Celadas 6, La Judería and Villalba Alta Río 1 (Adrover *et al*., 1988; Mein *et al.,* 1990), where the big-sized *Paraethomys* is identified as *P. abaigari*. In the material from Alcoy-2, Esteban Aenlle and Lacomba (1988) distinguished two *Paraethomys* species, *P. jaegeri* and *P. meini* (Table 3). In our revision of the material, we observed that the *Paraethomys* from this locality formed two clusters in terms of size that are almost coincident with the size ranges of the *Paraethomys* in our collections. Therefore, we consider *P. jaegeri* from the Alcoy-2 collection housed at the Universidad Complutense de Madrid (UCM) to be *P.* aff. *abaigari*. Mein *et al.* (1990) noted that the sizes of both lineages of *Paraethomys* tend to increase over time, setting the succession *P*. aff. *abaigari* - *P. abaigari* - *P*.aff. *jaegeri* - *P*. *jaegeri* for the linage of larger size. Nevertheless, the relationship between the two forms is not clear, being uncertain wether *P. abaigari* descends from *P. meini* or is an immigrant taxon (García-Alix *et al*., 2008b).

Genus: *Stephanomys* Schaub, 1938
Stephanomys cordii Ruiz Bustos, 1986 (Fig. 5, 1-7)

Localities: AL2C, AL2D

Material: 26 m1 (AL2C-2, AL2C-7, AL2D-3 to AL2D-14, AL2D-18 to AL2D-20, AL2D-27, AL2D-31 to AL2D-33, AL2D-35, AL2D-37, AL2D-39, AL2D-139, AL2D'08-1) 23 m2 (AL2C-10, AL2C-15 to AL2C-18, AL2D-43, AL2D-44, AL2D-46, AL2D-49, AL2D-52 to AL2D-55, AL2D-57, AL2D-59, AL2D-60, AL2D-63, AL2D-186 to AL2D-189, AL2D-231, AL2D-353), 20 m3 (AL2C-52, AL2C-59, AL2C-60, AL2D-73, AL2D-77 to AL2D-79, AL2D-81, AL2D-82, AL2D-84 to AL2D-86, AL2D-89, AL2D-94, AL2D-95, AL2D-224, AL2D-236,

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L	17	21.20	22.40	23.80
		W	21	12.90	14.40	15.50
	AL2C	L	2	22.20	23.00	23.80
		W	1	-	15.10	-
m2	AL2D	L	16	15.50	16.50	18.30
		W	16	14.30	15.90	17.20
	AL2C	L	4	16.00	16.70	17.30
		W	5	14.10	14.80	16.40
m3	AL2D	L	16	12.60	14.20	15.50
		W	17	12.20	12.80	13.80
	AL2C	L	3	12.60	13.10	13.60
		W	3	12.40	12.90	13.30
M1	AL2D	L	15	24.00	26.60	30.10
		W	20	17.10	18.80	20.20
	AL2C	L	2	24.10	24.20	24.30
		W	5	17.20	18.10	19.30
M2	AL2D	L	15	16.30	18.50	20.40
		W	14	16.50	17.40	18.40
	AL2C	L	6	15.20	16.70	17.70
		W	7	14.80	16.40	19.10
M3	AL2D	L	10	12.10	13.10	15.00
		W	10	10.70	11.90	12.60

Table 6.- Measurements in tenths of a millimeter of the teeth of *Stephanomys cordii* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 6.- Medidas en décimas de milímetro de los dientes de *Stephanomys cordii* de las localidades AL2C and AL2D. n= número de especímenes medibles.

AL2D-357, AL2D-358, AL2D'08-7), 29 M1 (AL2C-23 to AL2C-27, AL2C-56, AL2C-57, AL2D-98, AL2D-100, AL2D-102, AL2D-105 to AL2D-109, AL2D-111, AL2D-112, AL2D-115 to AL2D-121, AL2D-125, AL2D-127 to AL2D-129, AL2D-234), 27 M2 (AL2C-29, AL2C-31 to AL2C-35, AL2C-39, AL2D-143 to AL2D-145, AL2D-147, AL2D-149, AL2D-151 to AL2D-153, AL2D-155, AL2D-159, AL2D-161, AL2D-163, AL2D-164, AL2D-166, AL2D-167, AL2D-171, AL2D, 174, AL2D-175, AL2D-180, AL2D'08-10), 10 M3 (AL2D-74, AL2D-193, AL2D-196, AL2D-198, AL2D-201, AL2D-202, AL2D-204, AL2D-205, AL2D-207, AL2D-211, AL2D-221)

Measurements: see Table 6

Description:

m1: The slightly asymmetrical anteroconid is in contact with the protoconid-metaconid pair. The labial cingulum is low and narrow. There is a well-developed longitudinal crest that connects the posterior cusps with the intersection of the protoconid-metaconid pair. The c1 is well developed, and two of the teeth present an accessory cusp between the labial lobe of the anteroconid and the protoconid, big and round in one case and laminar and slightly smaller in the other one. The posterior heel is smaller than the c1, lingually displaced, and its shape may vary from round to almost laminar. The teeth have two roots.

m2: The anterolabial cusp is high, medium or big sized, and in contact with the protoconid and the reduced labial cingulum. The longitudinal crest is lingually displaced towards the metaconid. A small round or oval c1 is present, and a reduced accessory cusp in contact with the protoconid may also exist. The posterior heel is large, rounded or oval. There are two roots.

m3: Reduced anterolabial cusp, connected to the protoconid. The longitudinal crest seems incomplete in some specimens, being made instead by two contacting spurs. In the junction point, the enamel of each of the spurs may be differentiated from the other one. There are two roots.

M1: The t1 is displaced backwards. There are usually t1 bis and t2 bis, with different stages of development, although in some specimens are reduced to just a fold of enamel. The posterior crests of t1 and t3 are well developed. The t7 is absent. The t12 is highly reduced, just as a thickening of the enamel in some specimens. There are three roots.

M2: There may be a small accessory cusp attached to the posterior side of t1. The posterior crests of t1 and t3 are usually well developed, although two specimens have the t1 and the t3 isolated respectively (Fig. 5, 6). The t12 is absent or reduced to a thickening of the t8-t9 crest.

M3: The t1 is connected with t5. T4, t5 and t6 are connected. The t3 is absent except in one specimen.

Discussion:

The great height of the crown, high longitudinal crests in the lower molars (Fig. 5, 1-3) and crests or spurs in t1 and t3 of the upper molars (Figs. 5, 4-5) suggest that these specimens belong to the genus *Stephanomys*. These molars are smaller than other *Stephanomys* from the Pliocene such as *S. donnezani* (Déperet, 1890), *S. balcellsi* Gmelig Meyling and Michaux, 1973, *S. vandeweerdi* Adrover, 1986, and *S. thaleri* López-Martínez, Michaux and Hutterer, 1998. Although similar in size, the *Stephanomys* from AL2C and AL2D differ from *S. minor* Gmelig-Meyling and Michaux, 1983 in the tubercular shape of the posterior heel. The *Stephanomys* from AL2C and AL2D are bigger and with a more pronounced stephanodonty than *S. ramblensis* van de Weerd, 1976, and *S. dubari* Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991. The measurements of these molars match those of *S. margaritae* Adrover, 1986, which are quite close in size to *S. medius* Cordy, 1976, from Alcoy. The specimens from AL2C and AL2D show the features used by Cordy (1976) to describe the species *S. medius*: symmetric disposition of t1 and t3 respect the t2 in the M1 (Fig. 5, 4), reduced labial cingulum in m1 and m2 (Fig. 5, 1-2), tubercular posterior heel (Fig. 5, 1-2) and m3 with a poorly-developed anterolabial cusp and longitudinal crest united to the protoconid (Fig. 5, 3).

According to López Martínez *et al*. (1998), *S. medius* is a nomen nudum, being the correct name of the species *S. donnezani cordii* Ruiz Bustos, 1986. This is reviewed by García-Alix *et al*. (2008b), elevating *S. donnezani cordii* to species level and renaming it as *Stephanomys cordii*. The size range of our specimens encloses most of the variability of *S. margaritae* and *S. cordii*, except for the maxima for *S. margaritae* and some of the minima for *S. cordii*. In this latter species, the smallest specimens are those from La Gloria 4 (Adrover *et al*., 1993), and Peralejos E (Adrover *et al*., 1988), considered to be *S. dubari* by García-Alix *et al*. (2008b).

Minwer-Barakat (2005) proposed an evolutionary frame for the genus *Stephanomys* in which there is a continued increase in size, crown height and stephanodonty during the Pliocene in the anagenetic line *S. ramblensis - S. dubari - S. cordii - S. margaritae.* The populations from AL2C and AL2D seem to be close to *S. margaritae,* with some specimens reaching its size or even surpassing it, like one exceptionally large M1, while the mean values are more consistent with *S. cordii*. Those specimens have been directly compared with the collection from Alcoy-2, kept at the Universidad Complutense de Madrid (UCM), and ascribed by Esteban Aenlle and Lacomba (1988) to *S. medius* (Table 3). Both their size and morphology are very similar to our specimens. We ascribe our material to *S. cordii* because of its similarity with the population from the type locality, Alcoy (Cordy, 1976).

Genus *Castillomys* Michaux, 1969 (Fig. 5, 8-9)
Castillomys gracilis van de Weerd, 1976

Locality: AL2D
Material: 2 M1 (AL2D-138, AL2D-233), 1 M2 (AL2D-185)

Description:

M1: (15.80 x 11.20): The t1 is situated much posterior than the t2. The t1 has a hint of longitudinal spur directed towards the t4-t5 intersection. The t3 has a distal spur directed towards the t5-t6 intersection. The t3 is far apart from t6. The t9 is elongated. A small t12 is present. In lateral view, t6 is quite straight, not directed towards t9. This character has been used to distinguish the genus *Castillomys* from the small forms of *Occitanomys* (Martín-Suárez and Mein, 1991).

M2: (10.50 x 09.50): Tooth in an advanced stage of wear. The lingual longitudinal crest connects t1 and t5. Isolated t3. The t6 and t9 are equivalent in size. The t12 is small but well formed.

Discussion:

The small size of these specimens, straight t6 in lateral view, absence of a t7 in the upper molars and presence of posterior spurs in the t1 and t3 of the M1 are typical of the genus *Castillomys*. Also, the lack of longitudinal crests in the upper molars and isolated t3 in M2 (Fig. 5, 8) agree with *Castillomys gracilis* van de Weerd, 1976. The size of the specimens recovered from AL2C and AL2D lies within the range of variation of *C. gracilis* from Caravaca, Orrios 1 (van de Weerd, 1976), Mont-Hélène (Aguilar *et al*. 1986), Aldehuela and Villalba Alta (Adrover, 1986), Moreda 1A and Moreda 1B (Castillo, 1990), CLC-3, CLC-3B and PUR-13 (García-Alix *et al*., 2008b), although the width of the single M2 recovered from AL2D, in a very poor state of preservation, is only comparable to the lower values of the specimens from Caravaca (van de Weerd, 1976). Their size is also consistent with *C. gracilis* from the collection of Alcoy-2 at the Universidad Complutense de Madrid (UCM).

Martín-Suárez and Mein (1991) propose an evolutionary scenario in which all the Iberian populations from the Pliocene and Pleistocene could be placed in an anagenetic lineage consisting of three consecutive taxa: *C. gracilis* - *C. crusafonti* - *C. rivas*. These authors recognized an increase in size through time, such that the biometrics of the molars can be used as systematic criteria. In the line *C. gracilis* - *C. crusafonti*, only the development of t1 bis and the lingual longitudinal crest (t1-t5) show a positive correlation, whereas the states of the remaining characters are independent from other characters and size. This results in a differential diagnosis for the various species of *Castillomys* based on frequency percentages of the different characters along with size (Martín-Suárez and Mein, 1991). The oldest representative of the genus, *C. margaritae* Antunes and Mein, 1989, differs from our material by the absence of t12.

Genus: *Occitanomys* Michaux, 1969
Occitanomys brailloni Michaux, 1969 (Fig. 5, 10-12)

Locality: AL2D
Material: 1 m1 (AL2D-16), 3 M1 (AL2D-99, AL2D-113, AL2D-114), 1 M2 (AL2D-173)

Description:

m1: (21.30 x 15.80): Very worn specimen. Slightly asymmetrical anteroconid. The anteroconid and the protoconid-metaconid are connected by a narrow crest. The labial cingulum is very wide and well developed, but no accessory cusps are observed. The c1 is large and elongated anteroposteriorly, which gives this cusp a comma shape. There is no longitudinal spur. Oval posterior heel.

M1: (25.60 x 18.00; 25.40 x 18.1; 25.70 x 17.70): The connection between t1 and t2 is very basal. There is a well developed t1 bis in all specimens, and a smaller t2 bis is present in one of the teeth. The t1 has a distal spur directed to the t4-t5 intersection, but the t3 has no distal spur. The t12 is very small. In labial lateral view, these teeth show that the t6 leans towards the t9, and the apex of the cusp is closer to t9 than to t3.

M2: (15.80 x 15.70): The t1 is much bigger than t3, and connected basally to t5, while t3 is isolated. The shape of t1 suggests the presence of a small t1 bis. The t9 is well developed. The t12 is very small, barely a fold of the enamel.

Discussion:

The material from AL2D belongs to a big-sized form of *Occitanomys*. The outline and general morphology of the specimens is consistent with *O. brailloni* Michaux, 1969, having an m1 without tma and a labial cingulum with accessory cusps less developed than *Apodemus*, a t1 bis always present in the M1, reduced t12, reduced t3 and t1 connected to t5 in M2 (Michaux, 1969) (Fig. 5, 10-12). According to Minwer-Barakat (2005), this taxon is more frequent during the late Ruscinian, although it can be found in some early Ruscinian localities such as Aldehuela (Adrover, 1986), Ptolemais 1 and Kardia (van de Weerd, 1979).

The single m1 recovered is consistent with the the greatest lengths of *O. brailloni* from the locality of Layna (Michaux, 1969), and close to the maxima from Nîmes (Michaux, 1969), Arquillo 3 (Adrover, 1986), and TCH-1B (Minwer-Barakat *et al*., 2005). The width of this molar, however, clearly surpasses the maxima of the populations from the cited sites. The M1 are bigger than *O. brailloni* from Séte, Nîmes and Layna (Michaux, 1969), Arquillo 3 and Aldehuela (Adrover, 1986) and TCH-1B (Minwer-Barakat *et al*., 2005). The size of the single M2 lies within the variation observed in the material from Villalba Alta (Adrover, 1986). The site of AL2C has not yielded any remains of *O. brailloni*. This may be due to the scarcity of the material of this taxon, usually scarce in the localities where it is found. In the faunal list published by Esteban Aenlle and Lacomba (1988) for Alcoy-2, these authors did not mention any form of *Occitanomys* (Table 3). However, a revision of the material from this locality has shown a few specimens, morphologically very similar to the molars described in this paper, and which in our opinion correspond to a big sized *Occitanomys*.

Family: Gliridae Muirhead, 1819
Subfamily: Dryomyinae de Bruijn, 1967
Genus: *Eliomys* Wagner, 1840
Eliomys intermedius Friant, 1953 (Fig. 6, 2-5)

Localities: AL2C, AL2D
Material: 2 m1,2 (AL2C-97, AL2D-290), 2 m3 (AL2C-47, AL2D-356), 3 M1,2 (AL2D-291 to AL2D-293)

Description:

m1,2: (15.60 x 17.10; - x 16.10): The anterolophid is continuous and connected to the protoconid. There is no anterotropid. The connection between metalophid and metaconid is very low. The centrolophid is long and not connected to the metalophid. Metaconid and entoconid separated by a deep valley. The mesolophid is connected to the entoconid. The mesoconid is situated on the labial border. Well-developed posterotropid. The hypoconid is very large.

m3: (13.90 x 14.80): Continuous anterolophid, in contact with the metaconid. The labial apex of the metalophid does not reach the metaconid. The accessory crests are absent. The centrolophid is shorter than in m1,2. There is a wide valley between metaconid and entoconid. Continuous posterolophid.

M1,2: (13.80 x 17.40; 15.80 x 19.50): The anteroloph is separated from both the protoloph and the paracone by a deep valley. There are neither anterotrope nor posterotrope. Paracone and metacone are high and separated. The protoloph and metaloph are continuous. In the only complete specimen, there are two centrolophs. Well developed precentroloph, much longer than the postcentroloph. The endoloph and posteroloph are connected and continuous.

Discussion:

The size of our specimens, the rounded outline, the height of the crests and the development of the centrolophs make us assign those teeth to *E. intermedius*. The measurements of the molars from AL2C and AL2D fall within the range of variation of the population from the type locality, Sète (Adrover, 1986), and are very similar to those of *E. intermedius* from Orrios 3 and *Eliomys* cf. *intermedius* from Arquillo 3, Villalba Alta (Adrover, 1986) and Mont Hélène (Aguilar *et al*., 1986). Their size is bigger than *E. truci,* Mein and Michaux, 1970, and slightly bigger than *E.* aff. *intermedius* from La Gloria 4, La Gloria 5 (Adrover *et al*., 1993), PUR-4 and CLC-3B (García-Alix *et al*., 2008a), falling within the ranges of variation of *E. intermedius* from TCH-3, TCH-1B and PUR-13 (García Alix *et al*., 2008a). Both morphology and size in AL2C y AL2D are very similar to the specimens from Alcoy-2 deposited at the Universidad Complutense de Madrid (UCM), which lack in the preliminary faunal list published by Esteban Aenlle and Lacomba (1988) (Table 3).

Subfamily: Glirinae Thomas, 1897
Genus: *Glis* Brisson, 1762
Glis sp. (Fig. 6, 1)

Locality: AL2D
Material: 1 m3 (AL2D-359)

Description:

m3: (15.29 x 14.09): Tooth with four main ridges (anterolophid, metalophid, mesolophid and posterolophid) and three well-developed extra ridges (anterotropid, extra ridge between metalophid and mesolophid and posterotropid). Every ridge, except for the posterolophid, is clearly transverse. Very long anterotropid, connected to the metaconid. The extra ridge between metalophid and mesolophid is very long, of the same length as the anterotropid and not connected to the metalophid or the mesolophid. Mesolophid and posterolophid are not connected to the lingual border. Long posterotropid, connected to the lingual end of the posterolophid. The posterolophid is partially interrupted at the postero-lingual corner of the tooth.

Discussion:

The presence of several transverse main and extra ridges allow to assign this material to a form of the genus *Glis*. At the labial border, the main ridges (anterolophid, metalophid, mesolophid and posterolophid) are not connected, and define synclines that are opened on the labial side.

In the Pliocene two species of the genus *Glis* have been described: *Glis minor* Kowalski, 1956 and *Glis sackdillingensis* Heller, 1930 (Kowalski, 1956; Aguilar *et al.*, 1986), whereas in the Pleistocene several species of the genus have been cited: *G. sackdillingensis*, *G. mihevci* Aguilar and Michaux, 2011, *G. perkoi* Aguilar and Michaux, 2011 and the extant *G. glis* (Linnaeus, 1766) (Kowalski, 1963; Aguilar and Michaux, 2011). A gradual size increase of the molars is observed in *Glis* between the Pliocene and today. Morphology has evolved in this time span from primitive forms with transversal crests, synclines open on the lingual side in the upper molars and labial side in lower ones and accessory ridges reduced in p4 and m3 (Kowalski, 1956; Aguilar and Michaux, 2011).

The m3 from AL2D shows measurements and some of the morphological features that characterize the primitive assemblages of the genus *Glis*. The size is intermediate between *G. minor* and *G. mihevci*-*G. perkoi*-*G. glis*, and maybe more similar to *G. sackdillingensis*. The presence of transversal crests and open synclines on the labial side of the m3 are typical of the primitive forms. Nevertheless, the well-developed anterotropid and posterotropid are different from the Pliocene assemblages of the genus. These extra ridges are very long, exceeding extensively the middle of the tooth, and are connected to the metaconid and the lingual end of the posterolophid, respectively. The size and morphology of these ridges is similar to the Pleistocene species of the genus (*G. mihevci*-*G. perkoi*-*G. glis*) and different from the Pliocene species (*G. minor*-*G. sackdillingensis*). Castillo (1990) cites *G. sackdillingensis* in Alcoy-2, although in the original list published by Esteban Aenlle and Lacomba (1988) the genus *Glis* is not mentioned. Based on these features and until more material becomes available, we consider the specimen from AL2D as belonging to *Glis* sp.

Family: Cricetidae Fischer, 1817
Subfamily: Cricetinae Fischer, 1817
Genus: *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998
Apocricetus cf. *angustidens* (Depéret, 1890) (Fig. 6, 6-8)
Localities: AL2C, AL2D

Material: 1 m1 (AL2D-260), 1 m2 (AL2D-262), 2 m3 (AL2D-264, AL2D-266), 1 M1 (AL2D-259), 3 M2 (AL2C-93, AL2D-65, AL2D-263)

Description:

m1: (27.20 x 15.80): Smooth, crest-like anteroconid. There are two anterolophulids, well developed and symmetrical, reaching the top of the anterolophid crest, encircling an anterior funnel. The metalophulid is strongly directed forwards. Absent mesolophid. The posterolophid is high and connected to the entoconid, closing the posterosinusid.

m2: (22.60 x 17.90): The lingual anterolophid and the mesolophid are absent. The labial anterolophid is low, reaching the protoconid.

m3: (22.10 x - ; - x 15.90): The lingual anterolophid is absent. Mesolophid very short and low in one specimen, and absent in the other one.

M1: (28.20 x 18.00): There is a cingulum ridge in front of an anterocone formed by two cusps in labial and lingual position. The anterolophule is double and symmetrical. Absent anterior protolophule and posterior metalophule. Absent mesoloph. The anterior metalophule is present.

M2: (21.98 x 17.77; 20.50 x - ; - x 18.10): The lingual anteroloph is short and low. Absent anterior protolophule. Posterior protolophule and anterior metalophule present. The mesoloph is absent.

Discussion:

In the locality AL2D, a set of cricetid teeth, characterized by the absence of mesolophid in the m1 and of the anterior protolophule in M1 and M2, together with the presence of a crest-like anteroconid and a double anterolophulid in m1 resembles *Apocricetus*. In general, the size of this assemblage overlaps with the minimum values of *A. angustidens* and the maximum of *A. barrierei* (Freudenthal *et al.*, 1998). Only the values of m1 from AL2D clearly exceed those of *A. barrierei* (Freudenthal *et al.*, 1998). Although the presence of a cingulum ridge in front of the anterocone and the absence of an anterior protolophule in M1-M2 are morphological features that appear in assemblages of *A. angustidens* and *A. barrierei*, they are more common in the former ones (Freudenthal *et al.*, 1998). Based on these features and until more material become available, we consider the assemblage from AL2D as belonging to a form related with *A. angustidens*.

A M2 (AL2C-93) from AL2C shows a poor development of the anterior protolophule and absence of the posterior metalophule, resembling the general morphology of the younger species of the genus *Apocricetus* (Freudenthal *et al.*, 1998). Nevertheless, a single tooth is not enough to know the variability of this assemblage and, until more material becomes available, we consider it as belonging to a form related with *A. angustidens* too.

Cricetidae Incertae Sedis
Genus: *Blancomys* van de Weerd, Adrover, Mein & Soria, 1977
Blancomys sp. (Fig. 6, 18)

Locality: AL2D
Material: 1 m1 (AL2D-318)

Description:

m1: Tooth broken posteriorly and in an advanced stage of wear. The great lingual fold is very deep, reaching the base of the crown. The fold between anteroconid and metaconid is open and smooth, in contrast with the labial anterior fold, which is very sharp. Nevertheless, both folds reach the base of the crown. The metaconid is well developed, much more than the anteroconid and anterolophid. The anterior labial fold is very smooth, forming a straight line of enamel that connects anterolophid and protoconid. The labial fold is big, reaching the base of the crown and creating an acute vertex of enamel.

Discussion:

Esteban Aenlle and Lacomba (1988) cited the presence of *Blancomys neglectus* van de Weerd, Adrover and Soria, 1977, in Alcoy-2 (Table 3). The morphology, size and hypsodonty of the only tooth recovered in AL2D are consistent with *Blancomys*, but the scarcity of the material impedes a specific adscription.

Element	Locality	Parameter	n	min.	mean	Max.
m3	AL2C	L	1	-	26.30	-
		W	1	-	18.10	-
M2	AL2D	L	1	-	30.10	-
		W	2	21.50	21.75	22.20
M3	AL2D	L	2	19.70	20.00	20.20
		W	2	17.40	17.60	17.80
		H	1	-	24.90	-
	AL2C	L	2	19.00	20.10	20.30
		W	2	15.20	15.55	15.90
		H	1	-	24.40	-

Table 7.- Measurements in tenths of a millimeter of the teeth of *Ruscinomys* cf. *lasallei* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 7.- Medidas en décimas de milímetro de los dientes de *Ruscinomys* cf. *lasallei* de las localidades AL2C and AL2D. n= número de especímenes medibles.

Subfamily: Cricetodontinae Stehlin and Schaub, 1951
Genus: *Ruscinomys* Depéret, 1890
Ruscinomys cf. *lasallei* Adrover, 1969 (Fig. 6, 14-16)

Localities: AL2C, AL2D
Material: 1 m1 (AL2C-70), 2 m3 (AL2C-69, AL2D-319), 2 M2 (AL2D-308, AL2D-317), 4 M3 (AL2C-71, AL2C-72, AL2D-306, AL2D-307)
Measurements: see Table 7

Description:

m1: The tooth is broken posteriorly, and in an advanced stage of wear. No enamel islet can be observed. Rounded anteroconid. The anterosinusid is open and wide, just a slightly fold of the enamel. The mesosenid is narrow and deep, while the labial sinusid is much wider and smoother. Both folds reach the base of the crown.

m3: The anteroconid is a fold of the enamel. There are two enamel islets. The anterosinusid is smooth and open, almost reaching the base of the crown. The metaconid is round, much smaller than the entoconid. Both cusps are separated by the mesosinusid, which is very deep and steep. The posterosinusid is much narrower, but equally deep. The posterolophid and hypoconid cannot be individualized as separated cusps because of the wear of the molar. The sinusid is very narrow and deep, reaching the base of the crown.

M2: One of the specimens is broken anteriorly, while the other one is complete. In this latter individual two shallow enamel islets can be observed. The mesosinus is deep and narrow, while the sinus is much wider. Both folds reach the base of the enamel.

M3: Bilobed teeth, with the anterior lobe bigger than the posterior one. The lobes are separated by two folds reaching the base of the crown. There are two roots.

Discussion:

The rounded anteroconid (morphotype 3 of García-Alix *et al*., 2008a), flat labial side of the m1, M2 more elongated than *Ruscinomys schaubi* Villalta and Crusafont, 1956 and narrower than *R. europaeus* Depéret, 1890, and M3 with two lobes but more reduced than *R. schaubi* agree with *Ruscinomys lasallei* Adrover, 1969. Also, these specimens are higher crowned than *R. schaubi*, but less hypsodont than *R. europaeus*. The two unworn M3 (Table 7) are higher than *R. schaubi* from Concud 3, Los Mansuetos and Los Mansuetos 2, and similar to *R.* cf. *lasallei* from Caravaca, while shorter than *R. europaeus* from Layna (data from van de Weerd, 1976). The size of the *Ruscinomys* present in AL2C and AL2D is consistent with *Ruscinomys lasallei* Adrover, 1969 from its type locality, Alcoy, falling within the range of variation of this taxon from the localities of La Gloria 4 (Adrover *et al.,* 1993), PUR-13 and PUR-4 (García-Alix *et al*., 2008a), being also similar to *R*. cf. *lasallei* from the localities of Celadas 2, Arquillo1, Arquillo 4, La Gloria 5, Valdecebro 3, Valdecebro 6, and Villastar (Adrover *et al*., 1993). These molars are bigger than *R. gilvosi* Adrover *et al*., 1988, from Peralejos E, and smaller than *R. bravoi* Adrover and Mein, 1996, from Aljezar B, especially in width. Esteban Aenlle and Lacomba (1988) assigned the material from Alcoy-2 to *Ruscinomys* aff. *europaeus* (Table 3) based on its size and morphology. However, the material from AL2C and AL2D seems somewhat smaller and more similar to *R. lasallei* than to *R. europaeus*, even falling within the upper range of variation of *R. schaubi* Villalta and Crusafont, 1956, from Aljezar B (Adrover, 1986), Los Mansuetos, Los Mansuetos 2, Concud 2 and Concud 3 (van de Weerd, 1976), and *R*. aff. *schaubi* from DHS-4A, 4B and 16, and PUR-23, 24A, 25 and 25A (García-Alix *et al*., 2008a). For these reasons we ascribe our material to *R*. cf. *lasallei*.

Ruscinomys sp. (Fig. 6, 17)
Locality: AL2D
Material: 1 M3 (AL2D-281)
Description:
M3: (14.00 x 13.90; H: 16.00): Tooth with two lobes delimited by the sinus and mesosinus. The posterior lobe is smaller than the anterior one.

Discussion:

The specimen AL2D-281 is smaller and has a lower crown than *Ruscinomys lasallei* and *R. schaubi*. Also, the posterior lobe of the M3 is less reduced than *Ruscinomys*, resembling *Hispanomys*. The smallest representative of the genus *Ruscinomys* is *R. gilvosi*, described by Adrover *et al*. (1988) in the Ruscinian locality of Peralejos E. Unfortunately, this site has not yielded any M3. The presence of two *Ruscinomys* species in the same locality is rare, although Peralejos E has yielded remains of both *R. gilvosi* and *R*. cf. *europaeus*.

Family: Trilophomyidae Kretzoi, 1969
Genus: *Trilophomys* Depéret, 1892
Trilophomys cf. *castroi* Adrover, 1983 (Fig. 6, 9-13)

Localities: AL2C, AL2D
Material: 7 m1 (AL2C-79 to AL2C-82, AL2D-297, AL2D-298, AL2D-300), 4 m2 (AL2D-301 to AL2D-304), 3 M1 (AL2D-296, AL2D'08-14, AL2D'08-15), 2 M2 (AL2C-83, AL2C-85), 2 M3 (AL2D-305, AL2D-316)
Measurements: see Table 8

Description:

m1: The lingual side of the crown has three reentrant folds, while the labial one presents two. Five specimens have a well-developed anterior fold. This fold reaches near the base of the crown in one specimen, while in another three reaches two thirds of the height of the crown and in another one just the upper third. The lingual folds are deeper than the labial ones. The outward folds have acute apices. The boundary line between enamel and dentine at the base of the crown is quite smooth, rising slightly at the height of the outward folds.

m2: Both the labial and the lingual side have two reentrant folds. The folds of the labial side are much shorter than the lingual ones. The outward folds have acute apices. The labial folds are slightly displaced forwards with respect to the lingual folds. The boundary line between the enamel and dentine at the base of the crown is almost straight and parallel to the oclusal surface of the teeth, rising slightly at the height of the outward folds. The teeth have two roots.

M1: Both the labial and the lingual side have two reentrant folds. The folds of the labial side are deeper than the lingual ones. The enamel boundary is slightly wavy.

M2: Two reentrant folds in the labial side and one in the lingual side. The folds of the labial side are deeper than the lingual ones. Very smooth enamel boundary line. There are two roots.

Element	Locality	Parameter	n	min.	mean	Max.
m1	AL2D	L1	3	18.20	18.70	19.00
		L2	3	24.20	25.80	27.20
		W	3	12.70	13.80	15.40
	AL2C	L1	3	19.60	21.20	22.30
		L2	3	24.20	25.80	27.50
		W	3	13.10	14.50	15.50
m2	AL2D	L1	2	17.40	18.30	19.30
		L2	3	22.80	24.50	27.40
		W	4	12.20	12.80	14.20
M1	AL2D	L1	3	19.90	20.70	21.30
		L2	3	31.10	33.50	35.90
		W	3	12.30	12.80	14.20
M2	AL2C	L1	1	-	15.00	-
		L2	1	-	16.70	-
		W	2	13.70	14.10	14.60
M3	AL2D	L1	2	10.80	11.50	12.30
		L2	2	11.50	12.60	13.70
		W	2	11.90	12.00	12.10

Table 8.- Measurements in tenths of a millimeter of the teeth of *Trilophomys* cf. *castroi* from the localities AL2C and AL2D. n= number of measurable specimens.

Tabla 8.- Medidas en décimas de milímetro de los dientes de *Trilophomys* cf. *castroi* de las localidades AL2C and AL2D. n= número de especímenes medibles.

M3: Two lobes, the anterior one larger than the posterior one. The reentrant lingual fold is deeper than the labial one. The posterior lobe is divided by an inlet of enamel in one of the specimens, displaced to the lingual side of the tooth, while in the other one this character is absent due to the extreme wear of the tooth. The boundary line between the enamel and dentine of the base of the crown is almost straight, rising slightly at the height of the outward folds. There are two roots.

Discussion:

Morphologically, the populations of *Trilophomys* from AL2C and AL2D are very similar to *T. castroi* Adrover, 1986. The *Trilophomys* from Alcoy-2 housed at the Universidad Complutense de Madrid (UCM, Spain) were determined as *Trilophomys* cf. *castroi* by Esteban Aenlle and Lacomba (1988) (Table 3), and seem undistinguishable from our material. The most significant character is the smooth enamel-dentine boundary. This excludes these molars from belonging to *Trilophomys pyrenaicus* Déperet, 1890. The size of our specimens is somewhat smaller than *T. castroi* from Villalba Alta, its type locality, and Arquillo III, falling within the range of variation of *T.* cf. *castroi* from Aldehuela and Orrios 0 (Adrover, 1986) and Villalba Alta Río (Adrover *et al.,* 1988).

Family: Sciuridae Fisher, 1817
Subfamily: Pteromyinae Brandt, 1855
Genus: *Pliopetaurista* Kretzoi, 1962
Pliopetaurista sp. (Fig. 6, 19)

Locality: AL2D
Material: 1 D4 (AL2D-295)

Description:

D4: (14.60 x 14.60): Triangular outline. The protocone is the highest cusp of the tooth, with the posterior branch higher than the anterior one. The parastyl is strong and of the same height and shape as paracone and metacone. Between the labial border of the parastyl and the paracone a small cusp, attached to the parastyl, nearly closes the valley. Protoloph and metaloph present protoconule and metaconule respectively. Both ridges are connected to the protocone. The protocone bears a small mesoloph. In the labial border, a mesostyl is present between paracone and metacone. The metaconule and the posteroloph are connected by a low lophule.

Discussion:

The genus *Pliopetaurista* was first described from the French locality of Perpignan (Depéret, 1897) for Sciuridae of large size, in which the convergence of the lophs and the well developed metaconule in the upper teeth are typical features (Mein, 1970).

Since the description of *Pliopetaurista* by Depéret (1897), new data have contributed to a better knowledge of the systematics, biostratigraphy and paleogeography of this genus in Europe (see Dahlmann, 2001). Nevertheless, many questions remain open, and the record of this genus in the Iberian basins is one of these issues. So far, the Iberian record of *Pliopetaurista* is restricted to *P. pliocaenica* from the localities of the Granada basin, PUR-25, PUR-24A and PUR-4 (García-Alix *et al*., 2007) and the localities of the Teruel basin, La Gloria-2 and Arquillo-3 (Adrover *et al*., 1993). *Pliopetaurista* sp. has also been cited in the Upper Turolian of Venta del Moro, in the Cabriel Basin (Montoya *et al*., 2006b). The locality AL2D has yielded only one D4, of a small-sized species. The size of this specimen and the presence of a small mesoloph on the protocone and of a mesostyl in the labial border allow to distinguish it from the large-sized species of the genus. The specimen from AL2D differs from *P. kollmanni* in size, greater in AL2D, and by the presence in the material from Alcoy of a more pronou*nce*d protoconule and metaconule. With respect to *P. meini*, it differs in the presence of a short mesoloph. Despite the presence in AL2D of a short mesoloph, similar to that of *P. meini*, the size and general morphology of this tooth resemble those of *P. raui* from Wölfersheim (Dahlmann, 2001). Based on these features and until more material becomes available, we consider this specimen as belonging to *Pliopetaurista* sp.

5. General discussion

5.1. Faunal lists

The faunal lists of AL2C and AL2D are given in Table 3, and compared with Alcoy-2. The differences between AL2C and AL2D, with the presence in AL2D of *Castillomys gracilis*, *Occitanomys brailloni*, *Pliopetaurista* sp., *Glis* sp. and *Blancomys* sp., all of them very scarce, are attributed to the sampling effort. Both faunal assemblages are very similar to the one published by Esteban Aenlle and Lacomba for Alcoy-2 (1988).

5.2. Biostratigraphy

The presence of the genus *Trilophomys* (*T.* cf. *castroi*), accompanied by *Blancomys*, two species of *Paraethomys*, a small-sized form identified as *P. meini* and a bigger form classified as *P. abaigari*, and the presence of *Eliomys intermedius*, are typical features of the Ruscinian (Mein *et al*., 1990; Minwer-Barakat, 2005; Sesé, 2006). Moreover, the coexistence of *Stephanomys cor-*

dii, *Apodemus gorafensis*, *Apodemus atavus*, *Castillomys gracilis* and *Paraethomys meini* in the same assemblage is typical of the early Ruscinian, MN14 (García-Alix *et al.*, 2008b; Minwer-Barakat, 2005).

The *Ruscinomys* from the studied localities has been determined as *R.* cf. *lasallei*, a taxon found in MN14. Adrover *et al.* (1993) noted that *Ruscinomys* was very abundant in the middle Turolian, becoming very scarce from MN13 onwards, which seems to be the situation of AL2C and AL2D. Regarding *Apocricetus*, *A. barrierei* is typical of MN14 and replaced by *A. angustidens* which is present in both MN14 and MN15. The material from AL2D has been adscribed to *A.* aff. *angustidens* on biometric criteria, morphologically both species can only be distinghised on a statistical basis (Freudenthal *et al.*, 1998).

Esteban Aenlle and Lacomba (1988) proposed a late Ruscinian age for Alcoy-2. Nevertheless, the faunal assemblage, with the presence of *Castillomys gracilis* and *Paraethomys* aff. *abaigari*, initially adscribed to *P. jaegeri*, suggests an older age (MN14) for this locality, which agrees with the inferred age for Alcoi-Mina on the basis of its macromammal assemblage (Montoya *et al.,* 2006a).

5.3. Paleoecology

Micromammals have extensively been used as paleoclimatic indicators (van de Weerd, 1976; Daams *et al.*, 1988; Montuire *et al.*, 2006; García-Alix *et al.*, 2008c). The ecological requirements of a number of taxons of Miocene and Pliocene age have been determined using phylogenetic affinities, dental-corporal modifications and association with other taxons of known ecological preferences (García-Alix *et al.*, 2008c).

The rodent assemblages from AL2C and AL2D are clearly dominated by the Muridae family, with a prevalence of 81% in the former and 84% in the latter. The collection from Alcoy-2 also shows a predominance of this family, although not so pronounced as in the localities here studied. The most abundant genus is *Stephanomys*, followed by *Paraethomys* (Table 9), which comprise two species, *P. meini* and *P.* aff. *abaigari*. In AL2C, these two taxa represent 37.98 % of the assemblage, with the same number of specimens adscribed to each of the species, whereas in AL2D and Alcoy-2 there is a clear predominance of *P.* aff. *abaigari* over *P. meini*. The percentages of the remaining species found in the mentioned localities are evenly matched, apart from the cricetids and insectivores in Alcoy-2 (Table 9). The faunal list published by Esteban Aenlle and Lacomba (1988) does not mention the genus *Apocricetus* (Table 3), although in the collection housed at the UCM this taxon represents 5.72 % of the assemblage, compared with 1.26 % in AL2C and 2.18 % in AL2D. Regarding the insectivores, they comprise the 7.04 % of all the specimens from Alcoy-2, showing a remarkable contrast with AL2C, which has yielded a single specimen, and AL2D, where just a few fragmentary remains have been found.

	AL2C	AL2D	Alcoy-2
Apodemus	12.66	15.54	9.25
Castillomys	0.00	1.09	1.76
Paraethomys	39.78	26.18	18.07
Occitanomys	0.00	2.18	1.76
Stephanomys	30.38	40.00	37.00
Apocricetus	1.26	2.18	5.72
Blancomys	0.00	0.36	3.96
Ruscinomys	6.33	4.00	2.20
Trilophomys	7.59	4.36	7.49
Eliomys	2.53	1.82	3.96
Glis	0.00	0.36	1.76
Pliopetaurista	0.00	0.36	0.00
Soricidae Indet.	1.26	0.36	1.76
Parasorex	0.00	1.82	0.88
Asoriculus	0.00	0.00	4.40

Table 9.- Relative abundance of the genera present in the localities of AL2C, AL2D and Alcoy-2.

Tabla 9.- Abundancia relativa de los generos presentes en los yacimientos de AL2C, AL2D y Alcoy-2.

Regarding the paleoecologic requirements, we have used the climatic and habitat preferences proposed by García Alix *et al.* (2008c) for the studied taxa. So, in the faunal assemblages of AL2C and AL2D, several taxa are interpreted as warm climate indicators such as *Apodemus atavus*, *Paraethomys meini* and *Apocricetus*, whereas *Ruscinomys* and *Trilophomys* are associated with cold temperatures. Also, both *Paraethomys meini* and *Ruscinomys* are thought to indicate dry environmental conditions, whereas *Apodemus gorafensis*, *Apodemus atavus, Eliomys*, *Pliopetaurista* and *Glis* would point to moist paleoenvironments. In the same way, a number of the taxa present in AL2C and AL2D are considered indicators of open and herbaceous habitats, like *Apocricetus*, *Blancomys, Ruscinomys* and *Trilophomys*, whereas *Apodemus atavus*, *Eliomys*, *Pliopetaurista* and *Glis* are considered indicators of forested habitats. There are also several taxa which have no particular environmental requirements (eurytopic) regarding temperature, like *A. atavus*, *Castillomys*, *Stephanomys*, *Blancomys*, *Eliomy*s and *Pliopetaurista*; *Castillomys*, *Apocricetus*, *Blancomys*, *Trilophomys* and *Stephanomys* are thought to be indifferent with respect to the humidity. Some taxa cannot be associated with a concrete habitat, like *Castillomys*, *Paraethomys meini* and *Stephanomys.*

Because of their scarcity in the Iberian Peninsula and palaeoecological implications, the presence of *Pliopetaurista* and *Glis* in AL2D is remarkable. *Pliopetaurista* is

	HUMIDITY			TEMPERATURE			HABITAT		
Locality	*Wet*	*Dry*	*Eurytopic*	*Cold*	*Warm*	*Eurytopic*	*Open*	*Forested*	*Eurytopic*
AL2C	16.45	25.32	39.23	13.92	26.58	40.50	15.18	8.86	59.96
AL2D	17.44	13.82	49.81	8.72	20.36	51.99	10.90	8.72	61.45
Alcoy-2	21.13	8.37	56.81	11.45	23.78	51.08	19.37	11.88	55.06

Table 10.- Relative abundance of the taxa from the studied localities according to their ecological preferences. The taxa with unknown preferences are not shown.

Tabla 10.- Abundancia relativa de los taxones de los yacimientos estudiados según sus preferencias ecológicas. No se muestra los taxones con preferencias desconocidas.

recognized as a member of the flying squirrels, one of the three adaptative types found among the sciurids (de Bruijn, 1999). This group is considered arboreal and nocturnal by several authors (Cuenca-Bescós, 1988; de Bruijn, 1999; García-Alix, 2006; García-Alix *et al*. 2008c). Also, van Dam and Weltje (1999) assumed a preference for close, humid biotopes in accordance with the lifestyle of their extant relatives and the fossil faunal assemblages in which they are found.

The glirids underwent a dramatic reduction in diversity during the late Vallesian in the coastal basins of Eastern Spain, being reduced to just two genera, *Muscardinus* and *Glis* in the Catalonian basins (Agustí, 1990; Sesé, 2006). This reduction is also found in the other basins of the Iberian Peninsula during the Turolian, where the surviving genera were *Muscardinus* and *Eliomys* (Sesé, 2006). In AL2D, we have a quite unusual glirid assemblage, with the presence of *Eliomys* and *Glis* in the same locality, an association that, as far as we know, has only been cited in the karstic localities of Moreda-1A and Moreda-1B (Castillo, 1990). At present times, *Glis* is restricted to the wet northern part of the Iberian Peninsula (Castién, 2002), whereas *Eliomys* spreads through the entire peninsula (Moreno, 2002). Agustí (1990) considers a wet and cold climatic affinity for the genus *Glis*, which according to this author would explain the particular distribution of fossil species.

The assemblages from AL2D and Alcoy-2 suggest a relatively wet environment (Table 10), whereas AL2C shows a higher abundance of taxa with dry ecological affinities, like *P. meini* and *Ruscinomys*. Also, the analysis of the faunas of the studied localities is consistent with warm temperatures (Table 10). Regarding the habitat, the taxa considered as open environment indicators are slightly more abundant that those of forested environments (Table 10), which agrees with a forest mosaic scenario.

6. Conclusions

According to the geologic context, we consider a probable equivalent stratigraphic position for the classic locality of Alcoy-Mina with Alcoy-2, AL2C and AL2D. The age assigned to AL2C and AL2D matches age of Alcoy-Mina proposed by Montoya *et al*. (2006a), who placed this locality in the Early Ruscinian (MN14).

The presence of a small form of the genus *Pliopetaurista* in AL2D constitutes the southernmost record of this group of squirrels, which only has been described from central Europe (*Pliopetaurista raui* - Dahlmann, 2001).

The presence of a form of the genus *Glis* in AL2D confirms the record of this taxon in the locality Alcoy-2 (Castillo, 1990).

From the fossil material yielded by the localities of AL2C and AL2D, our age interpretation agrees with the end of the Early Ruscinian (MN14) or the early-late Ruscinian boundary (MN14-MN15), by the presence of *Apocricetus* cf. *angustidens*. Assuming that Alcoy-2 and AL2C/AL2D are probably equivalent levels, our age interpretation is clearly older than that of Esteban Aenlle and Lacomba (1988), since these authors proposed an Upper Ruscinian age (MN15) for the locality of Alcoy-2.

The mixture of inhabitants of open and herbaceous habitats, like *Apocricetus*, *Blancomys, Ruscinomys* and *Trilophomys,* and others of forested environments like *Apodemus atavus* and *Eliomys,* is consistent with a mosaic forest scenario. Also, the presence in AL2D of a flying squirrel, *Pliopetaurista* sp.*,* and a glirid with humid ecological affinities like *Glis* sp. suggest a wet environment. The macrofauna from Alcoy is very singular, differing from the faunal assemblages of other contemporaneous Iberian localities (Montoya *et al*., 2006). These authors suggested that the differences may be due to a relatively wetter environment, which agrees with the paleoenvironmental inferences made in this paper.

Regarding the temperature, both AL2C and AL2D present cold weather indicators (*Trilophomys*, *Ruscinomys*) and taxa with warm preferences (*Apodemus atavus*, *Paraethomys meini*, *Apocricetus*). However, the much higher relative abundance of warm climate indicators makes us consider a mild climate at the moment of the deposition of the studied sites.

Acknowledgements

We would like to thank the Valencian government for supporting this study, encompassed by the project GV06/304. We also acknowledge the funding support by project CGL2011-25754 of the Spanish Ministry of Science and Innovation. We thank the IGN (Instituto Geográfico Nacional), "SIOSE ©Instituto Geográfico Nacional de España - <Instituto Cartográfico Valenciano> for the geographic information necessary for Figure 1. We want to thank the Paleontological association "Isurus", from Alcoy, as well as all the students at the Universitat de València that have taken part in the field work. Finally we would like to express our gratitude to the Drs. María Ángeles Álvarez Sierra, Pablo Peláez Campomanes, Carolina Castillo and Elvira Martín-Suárez for their valuable help and comments. The comments and suggestions by the reviewers M. Freudenthal and A. García-Alix have been much appreciated.

References

Adrover, R. (1969): Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. I. *Ruscinomys*. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 67, 245-272.

Adrover, R. (1986): *Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico*. PhD. Thesis, Instituto de Estudios Turolenses: 423 p.

Adrover, R., Mein, P., Moissenet, E. (1988): Contribución al conocimiento de la fauna de roedores del Plioceno de la región de Teruel. *Teruel* 79 (1), 89-151.

Adrover, R., Mein, P., Moissenet, E. (1993): Roedores de la transición Mio-Plioceno de la región de Teruel. *Paleontologia i Evolució* 26-27, 47-84.

Adrover R., Mein P. (1996): Nuevo *Ruscinomys* (Rodentia, Mammalia) en el Mioceno Superior de la región de Teruel (España). *Estudios Geológicos* 52, 361-365.

Aguilar, J.P, Calvet, M., Michaux, J. (1986): Description des rongeurs pliocènes de la faune du Mont-Hélène (Pyrénées-Orientales, France), nouveau jalon entre les faunes de Perpignan (Serrat-D'en-Vacquer) et de Sète. *Paleovertebrata* 16 (3), 127-144.

Aguilar, J.P., Michaux, J., Delannoy, J.J., Guendon, J.L. (1993): A Late Pliocene rodent fauna from Alozaina (Malaga, Spain). *Scripta Geologica* 103, 1-22.

Aguilar, J.P., Michaux, J. (2011): Pleistocene edible dormice (Rodentia Mammalia) from Slovenia, and their relations to the present day *Glis glis* (Linnaeus 1766). *Acta Carsologica* 40 (2), 369-380.

Aguirre E., Hoyos M., Morales J. (1975): Alcoy: observaciones preliminares sobre la secuencia Neógeno- Cuaternaria del Serpis. *Acta Geologica Hispanica* 10 (2), 75-77.

Agustí, J. (1990): The Miocene rodent succession in Eastern Spain: a zoographical appraisal. In: E.H. Lindsay *et al.* (eds.), *European Neogene Mammal Chronology*. Plenium Press, New York: 375-404.

Agustí, J., Martín-Suárez, E. (1984): El Plioceno continental de la depresión Guadix-Baza (Prov. Granada) y su fauna de micromamíferos. Nota preliminar. *Acta Geologica Hispanica* 19 (4), 277-281.

Ballesteros Navarro, B. J., Rodríguez Hernández, L., Hernández Bravo, J. A., López Gutiérrez, J. L., Fernández Mejuto, M., García Menéndez, O., Domínguez Sánchez, J. A., Díaz Losada, E., Castillo Pérez, E., Padilla Benítez, A., Vela Mayorga, A., Muñoz Alonso, J., Gómez Fontalva, J. (2007): Actualización y mejora del conocimiento hidrogeológico y funcionamiento de los acuíferos de Alicante. Caracterización hidrogeológica de la U. H. 08.40 (Sierra Mariola). *Instituto Geológico y Minero de España, Diputación de Alicante*. Tomo I: Memoria, 118 p.

Bruijn, H. de (1999): Superfamily Sciuroidea. In: Rössner, G. E. y Heissig, K. (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München: 271-280.

Castién, E., (2002): *Glis glis* Linnaeus 1766. In: Palomo, J.L. and Gisbert, J. (eds.), *Atlas de los Mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza, SECEM-SECEMU, Madrid: 428-431.

Castillo, C. (1990): *Paleocomunidades de Micromamíferos de los Yacimientos kársticos del Neógeno Superior de Andalucía Oriental*. PhD. Thesis, Universidad de Granada: 225 p.

Cuenca-Bescós, G. (1988): Revisión de los Sciuridos del Aragoniense y del Rambliense en la fosa de Calatayud-Montalbán. *Scripta Geologica* 87, 1-116.

Daams, R. (1981): The dental pattern of the Dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins, special publication* 3, 1-115.

Daams, R., Freudenthal, M., van der Meulen, A.J. (1988): Ecostratigraphy of micromammal faunas from the Neogene of Spain. *Scripta Geologica, Special Issue* 1, 286-302.

Dahlmann, T. (2001): Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Courier Forschungsinstitut Senckenberg Series* 227, 1-129.

Dam, J. van, Weltje, G.J. (1999): Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modeling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 151, 267-305. doi: 10.1016/S0031-0182(99)00015-2

Depéret, C. (1897): Étude de quelques gisements nouveaux de vertébrés pléistocènes de l'Île de Corse. *Annales de la Société Linnéenne de Lyon* 44, 113–6.

Durand Delga, M., García Rodrigo, B., Magne, J., Polveche, J. (1964): À propos du Miocène de la région d'Alcoy (province d'Alicante, Espagne). *Cursillos y Conferencias* 9, 213-217.

Esteban Aenlle, J., Lacomba, J. I. (1988): El yacimiento de Alcoy-2. Nuevo nivel con micromamíferos del Plioceno inferior (MN15) en el área de Alcoy. *Comunicacions. Col·loqui Homenatge a R. Adrover "Bioeventos y sucesiones faunísticas en el Terciario continental ibérico"*, Sabadell, 17.

Freudenthal, M. (2004): Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). *Treballs del Museu de Geologia de Barcelona* 12, 97-173.

Freudenthal M., Mein P., Martín-Suárez E. (1998): Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7, 11-93.

Furió, M., Santos-Cubedo, A., Blain, H. A., Blaya, E., Casanovas-Vilar, I., Madurell, J., Martínez-Alba, D., (2005): Síntesis sobre las faunas fósiles del complejo cárstico Almenara-Casablanca (Castellón). In: G. Melendez, C. Martínez-Pérez, S. Ros, H. Botella, P. Plasencia (eds.), *Miscelánea Paleontológica* 6, 273-286.

García-Alix, A. (2006): *Bioestratigrafía de los depósitos continentales de la transición Mio-Plioceno de la cuenca de Granada*. PhD. Thesis, Universidad de Granada, 429 p.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2007): New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *Comptes Rendus Palevol* 6, 269–279. doi:10.1016/j.crpv.2007.02.001.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008a): Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136, 1-37.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008b): Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada basin (southern Spain). Biostratrigraphic and phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlunge*n 248, 183-215. doi: 10.1127/0077-7749/2008/0248-0183.

García-Alix, A. Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., Martín, J.M., (2008c): Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265, 214-225. doi: 10.1016/j.palaeo.2008.04.005

Gervais, P. (1853). Description des ossements fossiles de mammifères rapports d'Espagne par MM. de Verneuil, Collomb et de Lorière. *Bulletin de la Société géologique de France 2e sér*ie 10: 147-168, pls 3-6.

Kowalski, K. (1956). Insectivores, Bats and Rodents from the early Pleistocene bone breccia of Podlesice, near Kroczyce (Poland). *Acta Palaeontologica Polonica* 1 (4), 331-394.

Kowalski, K. (1963): The Pliocene and Pleistocene Gliridae (Mammalia, Rodentia) from Poland. *Acta Zoologica Cracoviensia* 8 (14), 533-567.

Kukal, Z. (1971): *Geology of recent sediments*. Central Geological Survey, Prague, 490 p.

López Martínez, N. (1989): Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 3 (3), 1-350.

López-Martinez, N., Michaux, J., Hutterer, R. (1998): The skull of *Stephanomys* and a review of *Malpaisomys* relationships (Rodentia: Muridae): taxonomic incongruence in Murids. *Journal of Mammalian Evolution* 5 (3), 185-215. doi: 10.1023/A:1020508428859.

Mansino, S., Ruiz-Sánchez, F.J., Montoya, P. (2009): Estudio preliminar de las faunas pliocenas de roedores del yacimiento Alcoi Cotes Altes 2 (ACA-2, Alicante, España). *Paleolusitana* 1, 251-256.

Martín-Suárez, E., Mein, P. (1991): Revision of the genus *Castillomys* (Muridae, Rodentia). *Scripta Geologica* 96, 47-81.

Martín-Suárez, E., Freudenthal, M. (1993): Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica* 103, 65-118.

Martín-Suárez, E., Freudenthal, M., (1998): Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Geobios* 31 (6), 839-847. doi:10.1016/S0016-6995(98)80113-7

Martín-Suárez, E., Mein, P. (1998): Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* 31 (1), 87-97. doi: 10.1016/S0016-6995(98)80099-5. ISSN: 0016-6995

Martín-Suárez, E., Freudenthal, M., Krijgsman, W., Rutger Fortuin, A., (2000): On the age of continental deposits of the Zorreras member (Sorbas basin, SE Spain). *Geobios* 33 (4), 505-512. doi:10.1016/S0016-6995(00)80084-4

Mein, P. (1970): Les Sciuroptères (Mammalia, Rodentia) Neogènes d'Europe Occidentale. *Geobios* 3 (3), 7-77. doi: 10.1016/S0016-6995(70)80001-8

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

Mein, P., Moissenet, E., Adrover, R. (1989-1990): Biostratigraphie du Néogène Supérieur du basin de Teruel. *Paleontologia y Evolució* 23, 121-139.

Michaux, J. (1969): Muridae (Rodentia) du Pliocène supérieur d'Espagne et du Midi de la France. *Palaeovertebrata* 3, 1-25.

Minwer-Barakat, R. (2005): *Roedores e insectívoros del Turoliense superior y el Plioceno del sector central de la cuenca de Guadix*. PhD. Thesis, Universidad de Granada: 606 p.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2005): Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, Southern Spain). *Journal of Vertebrate Paleontology* 25 (2), 426-441. doi: 10.1671/0272-4634(2005)025[0426:MRFTPO]2.0.CO;2.

Minwer-Barakat, R., García-Alix, A., Agustí, J., Martín-Suárez, E., Freudenthal, M., (2009): The micromammal fauna from Negratín-1 (Guadix basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the late Miocene. *Journal of Paleontology* 83 (6), 854–879. doi: 10.1666/09-009.1.

Montenat C. (1973): *Les Formations néogènes et Quaternaires du Levant espagnol (Provinces d'Alicante et de Murcia)*. PhD. Thesis, Université de Orsay-Paris-Sud, 1170 p.

Montenat, C., Bruijn, H. de (1976): The Ruscinian rodent faunule from La Juliana (Murcia); its implication for the correlation of continental and marine biozones. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B* 79 (4), 245- 255.

Montoya, P., Ginsburg, L., Alberdi, M.T., Made, J. van der, Morales, J., Soria, M.D. (2006a): Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28 (1), 137-173.

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J. V., Marín, M. D., Ruiz-Sánchez, F. J. (2006b): Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. *Estudios Geológicos* 62, 313-325.

Montuire, S., Maridet, O., Legendre, S. (2006): Late Miocene–Early Pliocene temperature estimates in Europe using rodents. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 247–262. doi: 10.1016/j.palaeo.2006.03.026.

Moreno, S., (2002): *Eliomys quercinus* Linnaeus, 1766. In: Palomo, J. L. and Gisbert, J. (eds.), *Atlas de los Mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza, SECEM-SECEMU, Madrid: 432-435.

Pedraza Gilsanz, J. de (1996): *Geomorfología. Principios, métodos y aplicaciones*. Editorial Rueda, S. L., Madrid. 414 p.

Pierson D'Autrey L. (1987): *Sédimentation et structuration synsédimentaire dans le bassin néogène d'Alcoy (Cordillères Bétiques externes Orientales Espagne)*. PhD. Thesis, Université de Paris: 315 p.

Reumer, J.W.F., Hoek Ostende, L.W. van den (2003): Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). In: Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn.* Deinsea 10, 455-467.

Ruiz Bustos, A. (1986): Análisis del proceso evolutivo del género *Stephanomys* (Rodentia, Muridae). *Paleomammalia* 1 (1), 1-22.

Ruiz Bustos, A., Sesé, C., Dabrio, C., Peña, J.A., Padial, J. (1984): Geología y fauna de micromamíferos del nuevo yacimiento del Plioceno inferior de Gorafe-A (depresión de Guadix-Baza, Granada). *Estudios Geológicos* 40, 231-241.

Santisteban C. de, Montoya P., Usera J., Robles F. (1997): El Terciario marino y continental de Alicante. In: Alcalá L., Alonso A. M. (eds.), *Itinerarios Geológicos del Terciario de Centro y Este de la Península Ibérica*. Universidad Complutense de Madrid, Consejo Superior de Investigaciones Científicas, Madrid: 73-107.

Sesé, C. (2006): Los roedores y lagomorfos del Neógeno de España. *Estudios Geológicos* 62, 429-480.

Thaler L., Crusafont, M., Adrover R. (1965): Les premiers micromammifères du Pliocène d'Espagne; précisions chronologiques et biogéographiques sur la faune d'Alcoy. *Comptes Rendus de l'Académie des Sciences de Paris* 260, 4024-4027.

Viseras, C., Soria, J.M., Fernández, J. (2004): Cuencas Neógenas Postorogénicas de la Cordillera Bética. In: J.A. Vera, (Ed.), *Geología de España*, SGE-IGME, Madrid: 576-581.

Weerd, A. van de (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins*, *special publication* 2, 1-217.

Weerd, A. van de (1979): Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen ser. B* 82, 127-170.

Journal of Iberian Geology **41 (2) 2015: XX**-YY
http://dx.doi.org/10.5209/rev_JIGE.2015.v41.n2.46418

www.ucm.es/info/estratig/journal.htm
ISSN (print): 1698-6180. ISSN (online): 1886-7995

Journal of Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

First Early Pliocene micromammal faunas from Venta del Moro (Cabriel Basin, Spain): new data on the Messinian dispersal of *Debruijnimys*

S. Mansino[1], F. J. Ruiz-Sánchez[1,2,3], L. de Luque[4], P. Montoya[1], L. Gibert[5], J. Morales[6], J. Abella[2,6], V.D. Crespo[1], G. R. Scott[7]

[1]Departament de Geologia, Àrea de Paleontologia, Universitat de València, Doctor Moliner 50, 46100 Burjassot, Spain.
[2]INCYT-UPSE, Universidad Estatal Península de Santa Elena, 7047, Santa Elena, Ecuador;
[3]L'Hort de Feliu, P. O. Box 8460, Alginet, Valencia, 46018, Spain.
[4]Fundación Conjunto Paleontológico Teruel-Dinópolis, Edificio Dinópolis. Avda Sagunto s/n, Teruel 44002, Spain.
[5]Departament de Geoquímica, Petrologia i Prospecció Geològica, Universitat de Barcelona, C/Martí i Franqués s/n, 08028 Barcelona, Spain.
[6]Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain.
[7]Berkeley Geochronology Center, 2455 Ridge Road Berkeley, California 94709, USA.

e-mail addresses: samuel.mansino@uv.es (S.M.), francisco.ruiz@uv.es (F.J.R-S.), luque@fundaciondinopolis.org (L. L.), plinio.montoya@uv.es (P. M.), lgibert@ub.edu (L.G.), mcnm166@mncn.csic.es (J. M), (J. A), vicente.crespo@uv.es (V.D.C-R.), gscott@bgc.org (G. S.)

Received: 1 August 2014 / Accepted: 1 June 2015 / Available online: DD July 2015

Abstract

The localities of La Bullana 3 and LA Bullana 2B (Valencia, E Spain) have yielded remains of *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon* the former, and *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet., *Asoriculus* cf. *gibberodon*, *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. the latter. Based on the study of these micromammal assemblages, we propose an Early Pliocene age (MN14) for both sites. The presence a gerbilid related to *Debruijnimys julii* in La Bullana 2B open new questions about the phylogenetic relationship between *Debruijnimys* species from the Miocene and Pliocene of the Iberian Peninsula. Furthermore, preliminary paleomagnetic data indicate an age between 4.997 Ma and 4.896 Ma for La Bullana 2B, and between 5.235 Ma and 4.997 Ma for La Bullana 3.

Keywords: Rodentia, Neogene, Ruscinian, *Debruijnimys*, Iberian Ranges, Iberian Peninsula

Resumen

Las localidades de La Bullana 3 y La Bullana 2B (Valencia, E Spain) han cedido restos de *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. y *Asoriculus* cf. *gibberodon* la primera, y *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet., *Asoriculus* cf. *gibberodon*, *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* y *Atlantoxerus* sp. la segunda. Basándonos en el estudio de estas asociaciones de micromamíferos, proponemos una edad correspondiente al Plioceno inferior (MN14) para ambos yacimientos. La presencia de un gerbílido relacionado con *Debruijnimys julii* en La Bullana 2B plantea nuevas preguntas acerca de la relación filogenética entre las especies de *Debruijnimys* del Mioceno y Plioceno. Además, datos paleomagnéticos preliminares indican una edad entre 4.997 Ma y 4.896 Ma para La Bullana 2B, y entre 5.235 Ma y 4.997 Ma para La Bullana 3.

Palabras clave: Rodentia, Neógeno, Rusciniense, *Debruijnimys*, Cordilleras Ibéricas, Penísula Ibérica

1. Introduction

Near the village of Venta del Moro (Valencia, Spain) part of the youngest sediments of the Cabriel Basin crop out in La Bullana area. In this zone, the lower part of the limestone Unit that forms the uppermost deposits from this basin includes a significant proportion of detrital deposits, containing several levels with remains of freshwater gastropods and vertebrates.

In the sections of La Bullana 2 and La Bullana 3, four new localities have been located: La Bullana 2A (LB2A), La Bullana 2B (LB2B), La Bullana 3 (LB3) and La Bullana 3A (LB3A). Only two of them, La Bullana 2B and La Bullana 3, have yielded a significant number of fossil remains.

The paleontological research of the Júcar-Cabriel area has been fruitful, with two important Late Turolian (or Ventian, sensu Morales *et al*., 2013) macromammal localities, namely Venta del Moro (Morales, 1984; Montoya *et al*., 2006) and La Portera (Lacomba *et al*., 1986), along with a number of micromammal sites (see references in Montoya *et al*., 2006; Benavent *et al*., 2008; Mansino *et al*., 2009; Ruiz-Sánchez *et al*., 2011). Venta del Moro (6.23 Ma) is one of the key localities for understanding the environmental and faunal changes occurred just before the Messinian Salinity Crisis (5.96-5.33 Ma), with more than a hundred identified species, six of which have been described in this site (Montoya *et al*., 2006; Morales *et al*., 2011; Mansino *et al*., in press). The new localities of La Bullana 2B and La Bullana 3 are stratigraphically higher than the eastern localities of Venta del Moro and Los Mingos (Montoya *et al*., 2006; Benavent *et al*., 2008; Mansino *et al*., 2009) (Figs. 1–2).

In this paper we describe the fossil rodent faunas from La Bullana 2B and La Bullana 3, and discuss their chronostratigraphical, biostratigraphical and paleobiogeographical implications.

2. Material, methods and abbreviations

Field work during 2005 and 2007 provided over 1200 kg of sediment from La Bullana 2B and 1,500 kg from La Bullana 3. After sieving these sediments, the recovered fossils were kept at the Museu de Geologia de la Universitat de València (MGUV), with the field labels LB2B- and LB3-, respectively. The nomenclature used in the descriptions of the teeth and the measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, Cuenca-Bescós (1988) and Reumer and Van de Hoek Ostende (2003) for the Sciuridae, and Reumer (1984), modified by Furió (2007), for the insectivores. Measurements (L x W) are in millimetres and were taken on a Leica MZ75 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. The lower teeth are indicated as **m1**, **m2** and **m3**, the upper teeth as **M1**, **M2** and **M3**, the premolars as **p4** and **P4**, and the deciduous elements as **d4** and **D4**.

Abbreviations.- **AL2-C**, Alcoy-2C; **AL2-D**, Alcoy-2D; **CLC**, Calicasas; **L**, Length; **LB2B**, La Bullana 2B; **LB3**, La Bullana 3; **MN**, European Neogene land mammal Units; **MNA**, Mina; **PUR**, Purcal; **SCSIE (UV)**, Servei Central de Suport a la Investigació Experimental de la Universitat de València; **THC**, Tollo de Chiclana; **TLW**, talonid width; **TRW**, trigonid width; **W**, Width.

3. Geological setting

The studied sites are located in the Cabriel Basin, a Neogene basin located between the Iberian platform to the North and Betic Cordillera to the South. The sedimentary infilling of the Cabriel Basin is mostly composed of Cenozoic limestones with detrital sediments (Fig. 1). The sedimentary record of this Basin contains several mammal sites ranging from the Late Aragonian to the Villanyian (MN7/8 to MN17) (see Ruiz- Sánchez *et al*. 2011 and references therein). The sites of La Bullana 2B and La Bullana 3 are located in the upper part of the Detritic Unit of Los Isidros, within the Venta del Moro-Villatoya Formation, according the stratigraphy described by Robles (1970) (Fig. 1). They are located approximately 3 km Southwest from the classic locality of Venta del Moro, about 10 m below La Molata, the top of the stratigraphic sequence (Fig. 2). However, the dip slope of La Bullana 2B and La Bullana 3 suggests that these localities may correspond to the same carbonated unit. The cross section of La Bullana 2, from where micromammal remains have been obtained, is mainly composed of detritic deposits, although it is crowned by a decametric layer of limestone. This outcrop includes several lignite levels and abundant fluvial sands, resting on red clays with intercalations of sandy channels. One kilometer Southeast from La Bullana 2B (30SXJ6394369), La Bullana 3 is located (30SXJ6404368), which probably represents an outcrop of equivalent deposits.

4. Systematic Paleontology

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Genus *Apodemus* Kaup, 1826
Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. 3, 1-4)

Localities: LB2B, LB3.

Material: 7 m1 (LB2B-25, LB2B-88, LB2B-92, LB2B-183, LB3-2, LB3-3, LB3-30), 9 m2 (LB2B-35, LB2B-36, LB2B-41, LB2B-105, LB2B-142, LB3-10, LB3-11 to LB3-13), 8 m3 (LB2B-44, LB2B-45, LB2B-114, LB2B-115, LB2B-200, LB2B-203, LB3-17, LB3-18), 8 M1 (LB2B-9, LB2B-13, LB2B-51, LB2B-129, LB2B-250, LB2B-258, LB3-19, LB3-20), 4 M2 (LB2B-20, LB2B-21, LB2B-136, LB3-22), 4 M3 (LB2B-214, LB2B-216, LB2B-219, LB3-24).

Measurements: see Table 1.

Description:

m1: The tma is large, round and central. Symmetrical anteroconid, its labial lobe connects with the metaconid. Well-developed labial cingulid, with a big round c1 and two or three accessory cuspids. One of the specimens has a hint of longitudinal spur. Big oval posterior heel, shifted towards the lingual side of the tooth. Roots are not preserved.

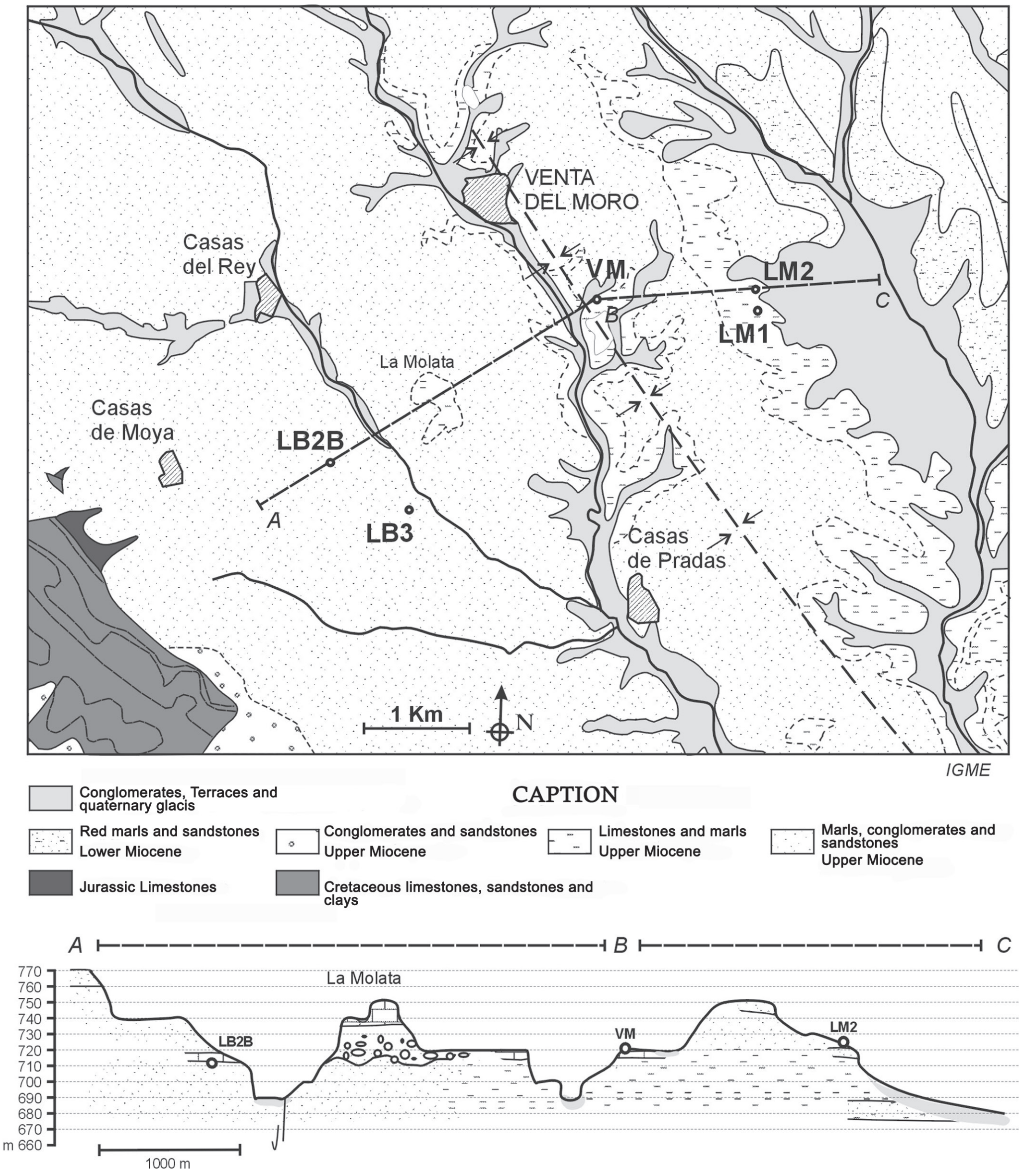


Fig. 1.- Geographic and geological setting of the surroundings of Venta del Moro (VM), showing the location of the sites Los Mingos 1 (LM1) (Benavent *et al*., 2008), Los Mingos 2 (LM2), La Bullana 2B (LB2B) and La Bullana 3 (LB3) (this paper).

m2: Big oval anterolabial cuspid. Well-developed labial cingulid, separated from the protoconid and hypoconid. There is a large round c1, except for one specimen in which this cuspid is much reduced, and one or two accessory cuspids. The posterior heel is large, round or oval. Roots are not preserved.

m3: Anterolabial cuspid reduced or absent. There is no longitudinal crest. One specimen has a small c1 connected to the labial side of the hypoconid-entoconid complex. Roots are not preserved.

M1: The t1 is displaced backwards. The connection between t1 and t2 is very low. There is neither t1 bis nor t2 bis. The valley between t3 and t6 is very deep and wide. The t4, t5, t6 and t9 are connected. The t7 is well developed, and there is a medium-sized t12 connected to the posterolabial side of t8. Roots are not preserved.

M2: The t1 is large, oval or round, and two specimens have a spur directed towards the t4-t5 connection. The t3 is reduced and isolated from the other cusps. The t7 is well developed and separated from t4. The t6 and t9 are connected. The t12 is small, connected to the posterolabial part of t8 and separated from t9. Roots are not preserved.

M3: The t1 is isolated. The t3 is absent. The t4, t5, t6, t8 and t9 are connected. Roots are not preserved.

Discussion:

The presence of a large tma in the m1, well-developed labial cingulid in m1 and m2 and t7 in the upper molars are typical traits of *Apodemus*. The specimens from LB2B and LB3 are larger than *Apodemus atavus* Heller, 1936 from TCH-1, 1B, 3 and 13 (Minwer-Barakar *et al*., 2005), PUR-7, PUR-13, CLC-3, CLC-3B, CLC-4B, AGU-1C and DHS-1 (García-Alix *et al*.,

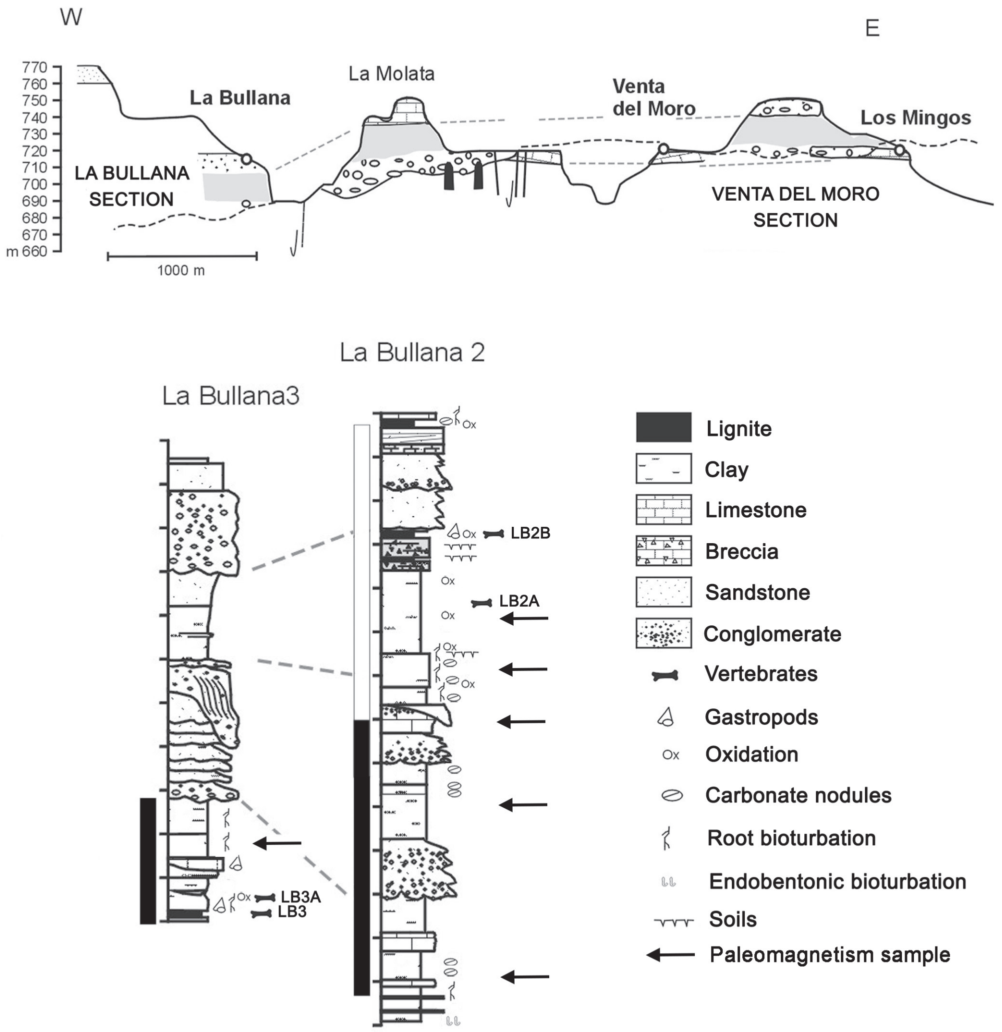


Fig. 2.- Geological sketch in the Venta del Moro area with location of the La Bullana and Venta del Moro sections, their correlation and the available paleomagnetic data: black, normal polarity; white, reversed polarity.

2008a) and smaller than *Apodemus jeanteti* Michaux, 1967 from Arquillo 3 and Villalba Alta (Adrover, 1986); this latter species further differs from *A. gorafensis* in the lack of tma in the m1. *Apodemus gorafensis* differs from its ancestor, *Apodemus gudrunae* van de Weerd, 1976, in the presence of a well-developed t7. This latter species is also slightly smaller than our specimens. In addition, *Apodemus agustii* Martín-Suárez, 1988 differs from *A. gorafensis* in the partial stephanodonty of the upper molars, less-developed tma and lack of a pit in m1 between the anteroconid, metaconid and protoconid. The size of the studied molars is consistent with *A. gorafensis* from its type locality, Gorafe A (Ruiz Bustos *et al*., 1984) and PUR-4, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al*., 2008a), Gorafe-3, Gorafe-4, Botardo-C and Huescar-1 (Martín-Suárez, 1988) and Alcoy 2C and 2D (Mansino *et al*., 2013), being also similar to *A.* aff *gorafensis* from PUR 23 (García-Alix *et al*., 2008a), Celadas 9, La Gloria 4 (Adrover *et al.,* 1993) and Peralejos E (Adrover *et al*., 1988).

The development of the tma, labial cingulid and t7 in the specimens from La Bullana 2B and La Bullana 3 agrees with *A. gorafensis*. There is a t9 (Fig. 3, 4) in two M3, while other two are much worn and this cusp cannot be observed. This cusp is absent in the fossil remains of *A. gorafensis* from the mentioned localities, with the exceptions of some specimens from PUR-23 and PUR-24A (García-Alix *et al*., 2008a).

Genus *Castillomys* Michaux, 1969
Castillomys gracilis van de Weerd, 1976 (Fig. 3, 5-7)

Locality: LB2B.

Material: 5 m1 (LB2B-90, LB2B-91, LB2B-94, LB2B-95, LB2B-188), 4 m2 (LB2B-106 to LB2B-109), 6 M1 (LB2B-14, LB2B-125, LB2B-126, LB2B-204, LB2B-205, LB2B-210) 1 M2 (LB2B-22), 1 M3 (LB2B-218).

Measurements: see Table 2.

Description:

m1: One specimen has a very small and low tma (Fig. 3, 5), absent in the rest. The anteroconid is symmetrical and connected to the protoconid-metaconid pair. There is a longitudinal spur and a narrow labial cingulid. The c1 is round

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	4	2.05	2.08	2.14
		W	4	1.26	1.31	1.35
m2	LB2B	L	5	1.49	1.54	1.57
		W	5	1.27	1.36	1.41
	LB3	L	4	1.49	1.52	1.58
		W	4	1.37	1.42	1.48
m3	LB2B	L	5	1.12	1.17	1.21
		W	5	1.03	1.08	1.12
	LB3	L	1	-	1.22	-
		W	1	-	1.08	-
M1	LB2B	L	1	-	2.22	-
		W	3	1.40	1.46	1.50
	LB3	L	2	-	1.57	-
M2	LB2B	L	3	1.53	1.57	1.63
		W	3	1.37	1.42	1.45
	LB3	L	1	-	1.70	-
		W	1	-	1.50	-
M3	LB2B	L	3	1.00	1.05	1.12
		W	3	0.94	1.02	1.08
	LB3	L	1	-	0.97	-
		W	1	-	1.01	-

Table 1.- Measurements in millimeters of the teeth of *Apodemus gorafensis* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	1.35	1.40	1.47
		W	5	0.88	0.90	0.93
m2	LB2B	L	4	1.02	1.06	1.12
		W	4	0.93	0.95	0.98
M1	LB2B	L	6	1.44	1.52	1.61
		W	6	1.01	1.05	1.12
M2	LB2B	W	1	-	1.21	-
M3	LB2B	L	1	-	0.76	-
		W	1	-	0.69	-

Table 2.- Measurements in millimeters of the teeth of *Castillomys gracilis* from the locality La Bullana 2B. n= number of measurable specimens.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	3	1.84	1.87	1.90
		W	4	1.25	1.28	1.31
m2	LB2B	L	2	1.45	1.50	1.55
		W	2	1.39	1.40	1.40
m3	LB2B	L	5	1.05	1.09	1.15
		W	5	0.97	1.02	1.06
M1	LB2B	L	3	1.96	2.05	2.11
		W	3	1.42	1.46	1.49
M2	LB2B	L	1	-	1.48	-
		W	1	-	1.40	-

Table 3.- Measurements in millimeters of the teeth of *Occitanomys brailloni* from the locality La Bullana 2B. n= number of measurable specimens.

or oval and connected basally to the hypoconid. One molar has a small accessory cuspid. The posterior heel is small and lingually displaced. Roots are not preserved.

m2: Large anterolabial cuspid, connected to the labial cingulid. There is a small round c1. All specimens have a longitudinal spur. The posterior heel is small and oval. Roots are not preserved.

M1: The t1 is displaced backwards. All specimens have a small t1 bis. The t1 is connected to the t4-t5 junction by a longitudinal crest. There is a small distal spur in t3, directed towards the t5-t6 connection, and one specimen has a low labial longitudinal crest. The t9 is large. A small t12 is present. Roots are not preserved.

M2: The only available specimen is broken anterolabially. The t1 is connected with the t4-t5 junction by a low crest. The t3 is small and isolated. Roots are not preserved.

M3: Isolated t1. There is no t3. The connection between t4 and the t5-t6 junction is very low. The t8 is isolated. Roots are not preserved.

Discussion:

Martín-Suárez and Mein (1991) recognized an increase in size from older to younger populations in the anagenetic line *C. gracilis–C. crusafonti–C. rivas,* in which all the Iberian populations from the Pliocene and Pleistocene could be encompassed. This means that the biometrics of the molars could be used as systematic criteria along the frequency percentages of some morphological characters (Martín-Suárez and Mein, 1991). The size of *Castillomys* from La Bullana 2B is consistent with *Castillomys gracilis* van de Weerd, 1976 from its type locality (Caravaca), and Orrios-1 (Weerd, 1976), Moreda-1A and 1B, Rambla Seca-AB and Belmez-1 (Castillo, 1990), Botardo C and Gorafe 3 and 4 (Martín-Suárez, 1988), Mont-Hélène (Aguilar *et al*., 1986), Aldehuela and Villalba Alta (Adrover, 1986) and CLC-3, CLC-3B and PUR-13 (García-Alix *et al*., 2008a), but also agrees with some of the smallest measurements of *Castillomys crusafonti* Michaux, 1969 (Martín-Suárez and Mein, 1991; Minwer-Barakat *et al*., 2005).

The morphology of the studied specimens agrees better with *C. gracilis* than with *C. crusafonti*, showing a longitudinal spur in m1 and a posterior spur in t3 of M1 instead of full longitudinal crests. However, 1 out of 6 M1 does have a low longitudinal crest in t3, and all of them present a complete longitudinal crest connecting the t1 to the t4-t5, which is unusual in *C. gracilis* (Martín-Suárez and Mein, 1991). Moreover, the presence of a low crest in t1 of the M2 is rare in this species. However, based on the size of the specimens and the lack of longitudinal crests in the lower molars, we ascribe the sample from La Bullana 2B to *C. gracilis*.

Genus *Occitanomys* Michaux, 1969
Occitanomys brailloni Michaux, 1969 (Fig. 3, 8-13)

Locality: LB2B.

Material: 5 m1 (LB2B-53, LB2B-82, LB2B-93, LB2B-96, LB2B-184), 2 m2 (LB2B-39, LB2B-100), 5 m3 (LB2B-112, LB2B-113, LB2B-116, LB2B-119, LB2B-201), 4 M1

(LB2B-11, LB2B-123, LB2B-124, LB2B-251) 1 M2 (LB2B-135).

Measurements: see Table 3.

Description:

m1: Symmetrical anteroconid, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulid is well developed. The c1 is large and round. Two specimens have a very small accessory cuspid. There is a longitudinal spur, which is reduced in two molars (Fig. 3, 8), more developed in other two, and developed into a very low longitudinal crest in one specimen (Fig. 3, 9).The posterior heel is small and oval. There are two roots.

m2: Trapezoidal outline, with the anterior side wider than the posterior one. Big round anterolabial cuspid, connected basally to the protoconid. The labial cingulid is reduced. The two available specimens have a longitudinal spur. The posterior heel is round. Roots are not preserved.

m3: There is neither anterolabial cuspid nor c1. Roots are not preserved.

M1: The connection between t1 and t2 is very low. The t1 bis is well developed. There is a small t2 bis (Fig. 3, 12), absent in one specimen. There is a low connection between t1 and the anterolingual side of t5. One specimen has a hint of distal spur in t3. The t6 and t9 are connected. The t12 is very small, barely a fold of the enamel. Roots are not preserved.

M2: The t1 is well developed, connected to the anterolingual side of t5 in one molar (Fig. 3, 13) and isolated in the other one. One specimen has a large t1 bis (Fig. 3, 13). Reduced t3, isolated from the other cusps. The t9 is well developed. Roots are not preserved.

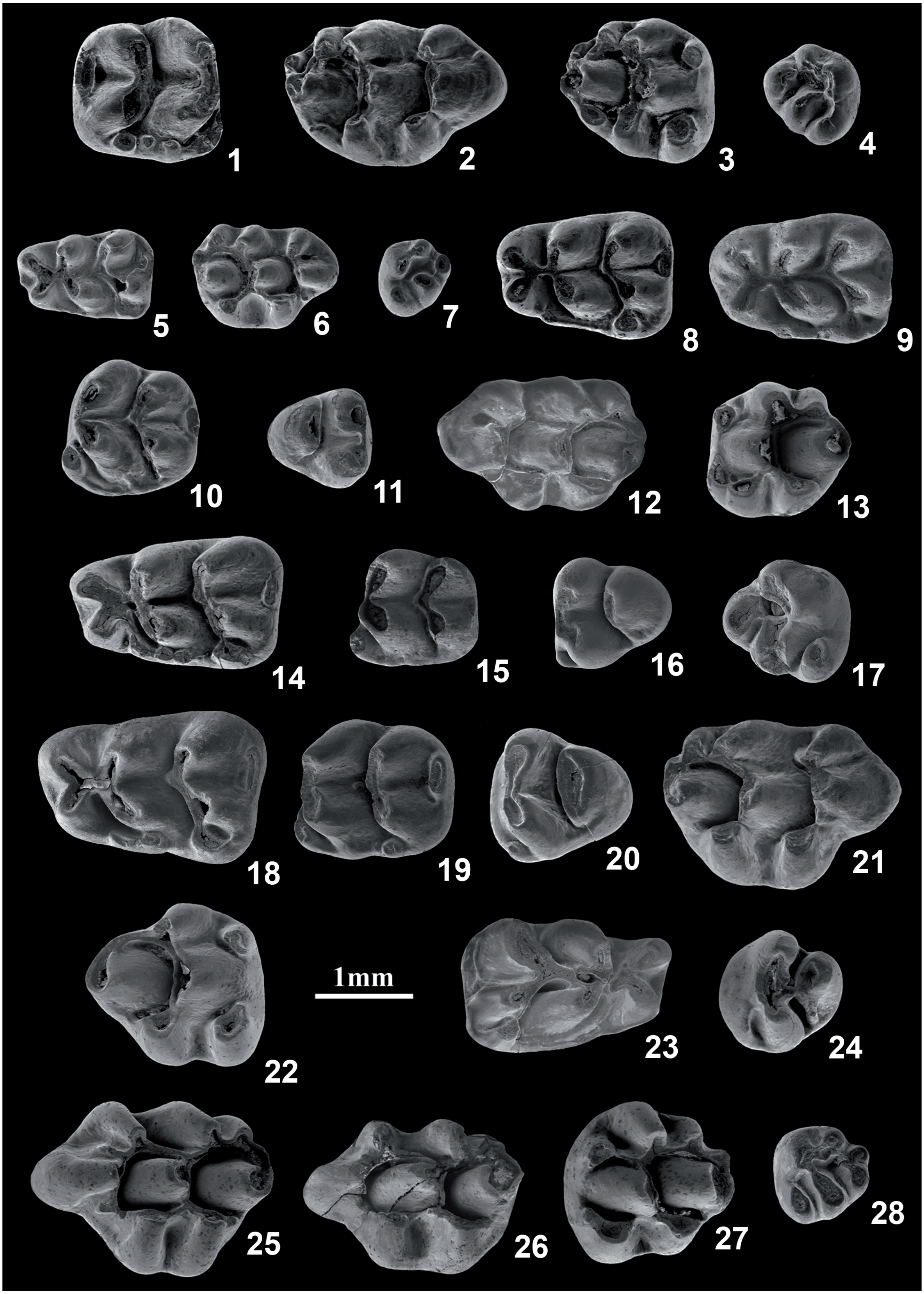
Discussion:

The specimens from La Bullana 2B largely agree with the material of *O. brailloni* from Layna (type locality) described by Michaux (1969): m1 without tma and with the accessory cuspids less developed than *Apodemus*, M1 with t1 bis, a crest that connects t1 with the posterior crown and a much reduced t12, and M2 with reduced t3 and well-developed t1 connected to the t5 by a crest. Michaux (1969) also considered diagnostic the presence of a low longitudinal crest in m1, lower than in *Stephanomys*. Regarding this character, there seems to be a great variability among populations, and Adrover (1986) suggested an increase of the longitudinal crest in m1 and m2 through time. In the localities of the MN14 the longitudinal crest of m1 is developed in 3 out of 7 molars from Kardia and Ptolemais (Weerd, 1979), absent in the single m1 from Gorafe A (Ruiz Bustos *et al*., 1984), and present in 1 out of 5 specimens from La Bullana 2B. In localities assigned to the early MN15, this crest is present in 2 out of 7 specimens from Arquillo 3 (Adrover, 1986), and absent in the two m1 from Vorio 3 (Hordijk and de Bruijn, 2009). In more recent localities, such as Layna, Nîmes (Michaux, 1969) and TCH-1B (Minwer-Barakat *et al*., 2005) there is always a low longitudinal crest.

The distal crests in M1 show also a great variability. The specimens from Kardia (Weerd, 1979) have a crest on t1, and 1 out of 4 molars have also a crest on t3, while other two have a small spur. The single M1 from Gorafe A has a weak t1-t5 connection, and no trace of t3-t5 connection (Ruiz Bustos *et al*., 1984). In the specimens from La Bullana 2B, the crest on t1 is high in one molar and much lower in the other one, while 2 out of 3 specimens have a much reduced spur on t3 (Fig. 3, 11). All specimens from Arquillo 3 have a crest on t1, and 4 out of 6 M1 have a spur on t3 (Adrover, 1986). In the Greek locality of Vorio 3 (Hordijk and de Bruijn, 2009) all M1 have a crest on t1, two molars have a spur on t3 and another one a developed crest. In Layna and Nîmes there is always a crest on t1, but the t3 has a spur (Michaux, 1969). The single M1 from TCH-1B has well-developed crests on t1 and t3 (Minwer-Barakat *et al*., 2005). The single specimen from Rambla Seca A1 also has developed crests, but lower than in the molar from TCH-1B (Minwer-Barakat, 2005). Each of the localities Cañada del Castaño 1 and Rambla Seca A2 yielded one M1, with a low crest on t3 and an isolated t1, while in the two M1 from Bélmez 1 the t1 has a low crest, and one specimen has a crest on t3, absent in the other one (Castillo, 1990; Martín-Suárez, 1988). The morphological variability of these connections is difficult to assess because of the scarcity of the remains in the localities where this species is found (Minwer-Barakat, 2005), although they seem to be slightly more developed in younger localities.

With respect to the size, the material from La Bullana 2B is similar in size to *O. brailloni* from other MN14 localities such as Ptolemais 1 and 3 and Kardia (Weerd, 1979), Gorafe A (Ruiz Bustos *et al*., 1984) and Vorio 1 (Hordijk and de Bruijn, 2009), and slightly smaller than the same taxon from MN15 localities such as Vorio 3 (Hordijk and de Bruijn, 2009), Arquillo 3 and Aldehuela (Adrover, 1986), Layna, Nîmes and Sête (Michaux, 1969), Cañada del Castaño 1 (Martín-Suárez, 1988), TCH-1B (Minwer-Barakat *et al*., 2005), Bélmez 1, Rambla Seca A1, A2 and A3, Moreda 1L-4 and the MN16 locality of Moreda 1B (Castillo, 1990). The scarce material from AL2-D (Mansino *et al*., 2013) is morphologically con-

Fig. 3.- (opposite page). Rodents from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Apodemus gorafensis* from LB2B and LB3. **1**, right m2, LB3-10; **2**, right M1, LB2B-9; **3**, right M2, LB2B-21; **4**, right M3, LB2B-219. *Castillomys gracilis* from LB2B. **5**, left m1, LB2B-90; **6**, right M1, LB2B-14; **7**, left M3, LB2B-214. *Occitanomys brailloni* from LB2B. **8**, left m1, LB2B-93; **9**, left m1, LB2B-82; **10**, left m2, LB2B-39 **11**, right m3, LB2B-112; **12**, left M1, LB2B-123; **13**, left M2, LB2B-135. *Paraethomys meini* from LB2B. **14**, left m1, LB2B-29; **15**, left m2, LB2B-193; **16**, left m3, LB2B-198; **17**, right M3, LB2B-138; *Paraethomys* aff. *abaigari* from LB2B. **18**, left m1, LB2B-187; **19**, left m2, LB2B-191; **20**, left m3, LB2B-3; **21**, right M1, LB2B-128; **22**, right M2, LB2B-134; *Stephanomys dubari* from LB2B and LB3. **23**, right m1, LB2B-182; **24**, left m3, LB2B-199; **25**, left M1, LB2B-127; **26**, left M1, LB2B-12; **27**, left M2, LB2B-132; **28**, left M3, LB3-24. Scale bar equals 1 mm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
1mm
23
24
25
26
27
28

sistent with *O. brailloni*, but due to its extremely large size it is not clear if these specimens should be ascribed to this taxon or to a related form.

O. brailloni differs from *O. alcalai* Adrover, Mein and Moissenet, 1988, *O. adroveri* (Thaler, 1966), *O. sondaari* van de Weerd, 1976 and *O. debruijni* Sen, Jaeger, Dalfes, Mazin and Bochernes, 1989, by its larger size. It differs from *O. montheleni* Aguilar, Calvet and Michaux, 1984, by its smaller size. Some of the specimens from La Bullana 2B are close to the smallest values of *O. brailloni*, and therefore close to the largest dimensions of *O. alcalai* and within the size range of *O. adroveri*. *O. sondaari* differs from *O. brailloni* by the weak t6-t9 junction, the lesser development of the longitudinal crest in m1, the absence of t1-t5 connection in unworn specimens and by the absence of a crest on the t3 of the M1. *O. alcalai* differs from *O. brailloni* by the lesser development of longitudinal crests in the upper and lower molars. According to Michaux (1969), the longitudinal crest of *O. adroveri* is less developed than in *O. brailloni*, but as we noted before this character shows a great variability. The m1 of *O. adroveri* may present well-developed accessory cuspids. In the upper molars, the distal crests on t1 and t3 are usually more developed in *O. brailloni* than in *O. adroveri*, and the t12 is more reduced in *O. brailloni*. *O. debruijni* differs from *O. brailloni* by the reduced or absent t3-t5 connection and absence of c1 in m2, which may be present in *O. brailloni* (see material from Layna and Vorio 3 in Hordijk and de Bruijn, 2009, plate 8).

Occitanomys sp.

Locality: LB2B.

Material: 1 M2 (LB2B-211).

Description:

M2: (1.38 x 1.32): The t1 is well developed, and connects basally with the t5. The t3 is smaller than the t1 and isolated from the other cusps. The t9 is well developed. Roots are not preserved.

Discussion:

The general morphology of the specimen resembles *Occitanomys*, but it is much smaller than the remains ascribed to *O. brailloni*. In addition, the t1-t5 connection is very low, while in *O. alcalai* it is usually higher. Because of the scarcity of the material that prevents the observation of more diagnostic features, we ascribe this molar to *Occitanomys* sp.

Genus *Paraethomys* Petter, 1968

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. 3, 18-22)

Localities: LB2B, LB3.

Material: 5 m1 (LB2B-87, LB2B-99, LB2B-187, LB2B-189, LB3-1), 13 m2 (LB2B-2, LB2B-34, LB2B-38, LB2B-40, LB2B-42, LB2B-86, LB2B-103, LB2B-110, LB2B-191, LB3-7 to LB3-9, LB3-14), 7 m3 (LB2B-3, LB2B-47, LB2B-48, LB2B-118, LB2B-121, LB2B-195, LB2B-197), 6 M1 (LB2B-4, LB2B-15, LB2B-128, LB2B-206, LB2B-208, LB2B-209), 6 M2 (LB2B-17, LB2B-18, LB2B-130, LB2B-134, LB2B-212, LB2B-213), 4 M3 (LB2B-139, LB2B-140, LB2B-215, LB2B-217).

Measurements: see Table 4.

Element	Species	Locality	Parameter	n	min.	mean	max.
m1	*P.* aff *abaigari*	LB2B	L	1	-	2.36	-
			W	3	1.49	1.52	1.57
	P. aff *abaigari*	LB3	L	1	-	2.36	-
			W	1	-	1.54	-
	P. meini	LB2B	L	8	2.12	2.18	2.26
			W	9	1.38	1.43	1.46
m2	*P.* aff *abaigari*	LB2B	L	7	1.65	1.71	1.76
			W	9	1.45	1.53	1.62
	P. aff *abaigari*	LB3	L	3	1.66	1.71	1.76
			W	3	1.51	1.53	1.58
	P. meini	LB2B	L	2	1.37	1.40	1.42
			W	2	1.25	1.32	1.39
m3	*P.* aff *abaigari i*	LB2B	L	7	1.43	1.47	1.51
			W	7	1.25	1.31	1.37
	P. meini	LB2B	L	5	1.29	1.31	1.35
			W	6	1.15	1.20	1.28
M1	*P.* aff *abaigari*	LB2B	L	4	2.53	2.56	2.61
			W	4	1.67	1.70	1.74
	P. meini	LB2B	W	1	-	1.50	-
M2	*P.* aff *abaigari*	LB2B	L	5	1.79	1.87	1.96
			W	6	1.60	1.67	1.73
	P. meini	LB2B	L	1	-	1.56	-
			W	2	1.47	1.48	1.49
M3	*P.* aff *abaigari*	LB2B	L	4	1.23	1.29	1.38
			W	4	1.23	1.27	1.34
	P. meini	LB2B	L	1	-	1.16	-
			W	1	-	1.18	-

Table 4.- Measurements in millimeters of the teeth of *Paraethomys* aff. *abaigari* and *P. meini* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Description:

m1: One molar has a very small cingulid ridge between the lobes of the anteroconid (Fig. 3, 18) and another one shows a low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pairs are connected by a narrow crest, which has an enamel funnel in one specimen. There is a longitudinal spur. The labial cingulid is moderately developed, with a large oval c1 and one or two accessory cuspids. The posterior heel is variable in size and shape, and lingually displaced. Roots are not preserved.

m2: Well-developed anterolabial cuspid, connected basally to the protoconid and the labial cingulid. A c1 variable in size and an accessory cuspid may be present. There is a longitudinal spur in 9 out of 11 specimens. The posterior heel is reduced in some molars, while others have a medium sized cuspid. Roots are not preserved.

m3: The anterolabial cuspid is reduced in two specimens and absent in five. The hypoconid-entoconid complex is separated from the protoconid-metaconid pair. One of the specimens presents a small c1 attached to the labial side of the posterior complex. Roots are not preserved.

M1: The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. Two specimens have a very low crest connecting t1 with the posterolingual side of t5. The spur in t3 is always present, small in two specimens and more developed in other two. The t9 is well developed. The connection between t4 and t8 is low. There is a small t12. Roots are not preserved.

M2: Isolated t1 and t3. The t9 may be absent (2), reduced (2) or developed (1). A much reduced t12 is present in two specimens. Roots are not preserved.

M3: The t1 is large and isolated, while t3 is absent. The t8 is connected with the t4-t5-t6 junction. Roots are not preserved.

Discussion:

Different species of *Paraethomys* are recognized in MN14 localities from the Iberian Peninsula: the small sized *P. meini* (Michaux, 1969), and the larger *P. abaigari* and *P.* aff. *abaigari*, which have more developed distal spurs in the upper molars. Adrover *et al.* (1993) identified two species of *Paraethomys* in La Gloria 4 and Celadas 1 and 9, *P. meini* and *P. anomalus* (Bruijn, Dawson and Mein, 1970). These two species were morphologically very similar, and differed mainly in their size. Later, García-Alix *et al.* (2008a) ascribed the big-sized specimens from PUR-13 and CLC-5A to *P.* aff. *abaigari*, a form related to *P. abaigari* but slightly smaller, and considered the big-sized *Paraethomys* from La Gloria 4 and Celadas 9 to belong to the same taxon. Slightly older assemblages of *Paraethomys*, like the rich population from PUR-4, show a wide size range but, due to the impossibility to discriminate two clusters in this population, García-Alix *et al.* (2008a) ascribed that sample to *P. meini*, considering unlikely the coexistence of two *Paraethomys* species in that locality.

The specimens from La Bullana 2B and La Bullana 3 are similar in size to *P.* aff. *abaigari* from CLC-5A and PUR-13 (García-Alix *et al.*, 2008a), Celadas 9 and La Gloria 4 (Adrover *et al.*, 1993), slightly smaller than *P.* aff. *abaigari* from AL2-C and AL2-D (Mansino *et al.*, 2013), and clearly smaller than *P. abaigari* from Villalba Alta (Adrover *et al.*, 1988). These molars are larger than *P. meini* from Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover, 1986), Villalba Alta Río, Peralejos E (Adrover *et al.*, 1988), Celadas 9 and La Gloria 4 (Adrover *et al.*, 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (GarcíaAlix *et al.*, 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al.*, 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover, 1986), considered synonyms of *P. meini* by several authors (van de Weerd, 1976; Adrover, 1986; Castillo, 1990; Minwer-Barakat, 2005; García-Alix, 2006, García-Alixet *et al.*, 2008a)

The development of distal spurs on the t1 and t3 of the M1 also agrees with *P. abaigari* rather than with *P. meini*. For these reasons, we ascribe the studied material to *P.* aff. *abaigari*.

Paraethomys meini (Michaux, 1969) (Fig. 3, 14-17)

Locality: LB2B.

Material: 12 m1 (LB2B-1, LB2B-26, LB2B-29 to LB2B-33, LB2B-83, LB2B-85, LB2B-89, LB2B-185, LB2B-186), 2 m2 (LB2B-100, LB2B-193), 6 m3 (LB2B-46, LB2B-50, LB2B-120, LB2B-122, LB2B-194, LB2B-198), 3 M1 (LB2B-16, LB2B-52, LB2B-84), 2 M2 (LB2B-19, LB2B-131), 1 M3 (LB2B-138).

Measurements*:* see Table 4.

Description:

m1: one specimen has a very low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pair are connected by a narrow crest. Three specimens have a funnel of enamel in the connection between the anteroconid and the protoconid-metaconid (Fig. 3, 14). In 8 out of 11 teeth there is a weak longitudinal spur. The labial cingulid is moderately developed, with a large oval c1 and one or two accessory cuspids, variable in size. Roots are not preserved.

m2: Well-developed anterolabial cuspid, connected basally to the protoconid and the labial cingulid. A small c1 is present in one specimen. There are no accessory cuspids. In 2 out of 3 specimens there is a longitudinal spur. The posterior heel is large in two molars and more reduced in another one. Roots are not preserved.

m3: One specimen has a small anterolabial cuspid, absent in the others. The hypoconid-entoconid complex is separated from the anterior protoconid-metaconid pair. A small crest-shaped c1 is present in two molars. Roots are not preserved.

M1: All specimens are broken posteriorly. One specimen has two small cusps attached to the anterior side of t2. The t1 has a distal spur, developed into a very low crest in one of the specimens. There is a spur on the t3. Roots are not preserved.

M2: The dentine is almost completely lost in both molars. Isolated t1 and t3. The t9 is slightly developed, and there is no t12. Roots are not preserved.

M3: The t1 is large and isolated. Absent t3. The t8 is connected to the t4-t5-t6 junction. Roots are not preserved.

Discussion:

Together with the large *P.* aff. *abaigari*, a small form of *Paraethomys* occurs in La Bullana 2B. The coexistence of two species of *Paraethomys* differing mainly in size has been recorded in several Pliocene localities from the Teruel and Granada Basins (Adrover, 1986; Adrover *et al.*, 1988, 1993; García-Alix *et al.*, 2008a), as well as in the French site of

Sète (type locality of *P. meini*, Michaux, 1969). When both forms appear together, the size of *P. meini* is usually very small (García-Alix, 2006). The size of the specimens from La Bullana 2B is similar to *P. meini* from Sète, Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover, 1986), Villalba Alta Río, Peralejos E (Adrover *et al*., 1988), Celadas 9 and La Gloria 4 (Adrover *et al*., 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (GarcíaAlix *et al*., 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al*., 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover, 1986).

The only morphological character used to distinguish *P. meini* from *P. abaigari* is the development of distal spurs in the upper molars, more prevalent in the latter species (Adrover *et al*., 1993). The three M1 from La Bullana 2B show spurs on the t1 and t3, which is unusual in *P. meini*, although in some localities like Peralejos E the presence of spurs in t1 and especially t3 is quite common (Adrover *et al*., 1993).

Genus *Stephanomys* Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Fig. 3, 23-28)

Localities: LB2B, LB3.

Material: 5 m1 (LB2B-27, LB2B-28, LB2B-97, LB2B-98, LB2B-182), 5 m2 (LB2B-37, LB2B-101, LB2B-102, LB2B-104, LB2B-111), 4 m3 (LB2B-49, LB2B-117, LB2B-196, LB2B-197), 4 M1 (LB2B-10, LB2B-12, LB2B-127, LB2B-207), 5 M2 (LB2B-23, LB2B-132, LB2B-133, LB2B-252, LB3-21), 3 M3 (LB2B-24, LB2B-137, LB2B-249).

Measurements: see Table 5.

Description:

m1: Slightly asymmetrical anteroconid, connected to the protoconid and metaconid. The labial cingulid is low and narrow. There is a well-developed longitudinal crest that connects the posterior cuspids to the connection of the protoconid-metaconid pair. There is a well-developed oval c1. The posterior heel is lingually displaced, ranging from oval to laminar. Two roots.

m2: Large and high anterolabial cuspid, connected to the protoconid and to a narrow labial cingulid. The longitudinal crest is lingually displaced towards the metaconid. There is neither c1 nor accessory cuspids. The posterior heel is large and oval. Roots are not preserved.

m3: Small and low anterolabial cuspid, connected to the protoconid. The longitudinal crest is complete (Fig. 3, 24). There are two roots.

M1: The t1 is slightly displaced backwards. There are small t1 bis and t2 bis, more developed in one of the specimens (Fig. 3, 25). The posterior crest on the t1 is high and well developed in two specimens (Fig. 3, 25), and very low in other two (Fig. 3, 26), while the posterior crest on the t3 is high in all specimens. The t12 is highly reduced. Roots are not preserved.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	2.07	2.16	2.27
		W	5	1.29	1.31	1.44
m2	LB2B	L	5	1.51	1.62	1.70
		W	5	1.46	1.51	1.58
m3	LB2B	L	3	1.25	1.31	1.37
		W	3	1.21	1.24	1.28
M1	LB2B	L	4	2.30	2.46	2.69
		W	4	1.58	1.74	1.83
M2	LB2B	L	3	1.58	1.74	1.88
		W	3	1.70	1.73	1.76
	LB3	L	1	-	1.72	-
		W	1	-	1.63	-
M3	LB2B	L	2	1.15	1.25	1.36
		W	2	1.13	1.22	1.31

Table 5.- Measurements in millimeters of the teeth of *Stephanomys dubari* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

M2: The t1 has a small t1 bis attached to its anterior side (Fig. 3, 27). In unworn specimens, the posterior crest of t1 is complete in two molars and low in another two, while the posterior crest on the t3 is complete in two specimens, low in one and absent in another one. The t12 is reduced in one molar and well developed in another one (Fig. 3, 27). There are three roots.

M3: The t1 is connected basally to t5. The t3 is absent. The t4, t5 and t6 are connected to t8. One specimen has a t9 (Fig. 3, 28). Roots are not preserved.

Discussion:

The great height of the crown, high longitudinal crests in the lower molars (Fig. 3, 23–24) and crests or spurs in t1 and t3 of the upper molars (Fig. 3, 25–27) indicate that these specimens belong to the genus *Stephanomys*. These molars are smaller, lower crowned and have a less pronounced stephanodonty than the *Stephanomys* identified in the Pliocene and Pleistocene (see Minwer-Barakat *et al*., 2011 and references therein).

The studied specimens share some characters with *S. cordii* Ruiz Bustos, 1986, like the t1 slightly more posterior than the t3 in M1 (Fig. 3, 25–26) and one m3 with the longitudinal crest connected to the protoconid (Fig. 3, 24). However, although some molars have the size and morphology of *S. cordii* (Fig. 3, 25) most of them agree better with *S. dubari* Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, with low crests connecting t1 and t5 in M1 (Fig. 3, 26), low or absent longitudinal crests in M2 and a smaller size. The presence of specimens similar to *S. cordii* has been reported in some populations of *S. dubari*, such as in the lower Ruscinian sites of PUR-4 and PUR-13 in the Granada Basin (García-Alix *et al*., 2008a). The material from La Bullana 2B and La Bullana 3 has been directly compared with *S. cordii* from AL2-C

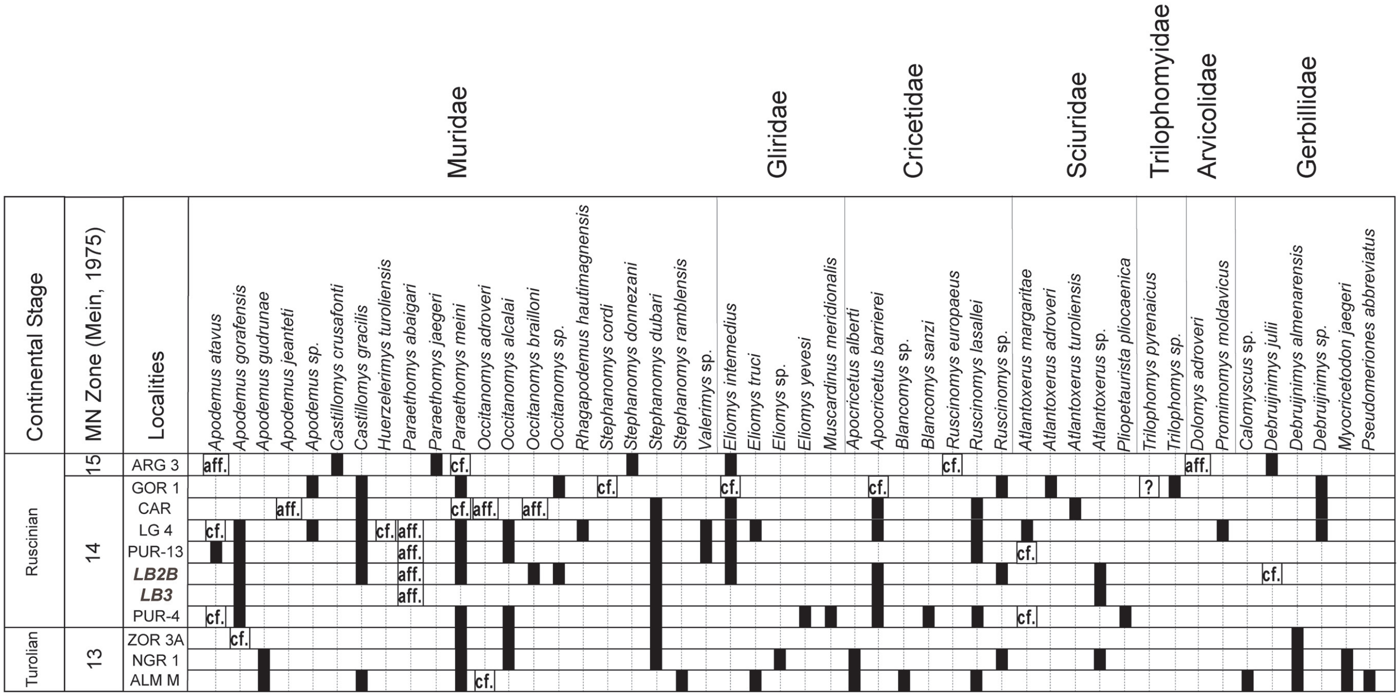


Fig. 4.- Distribution chart of the rodents studied in this paper and of related species of similar age. Abbreviations: **ARG3**, Asta Regia 3 (Castillo and Agustí, 1996); **GOR 1**, Gorafe 1 (Bruijn, 1974; Martín-Suárez and Mein, 1991; Agustí and Martín-Suárez, 1984); **CAR**, Caravaca (Freudenthal *et al*., 1998, Bruijn *et al*., 1975, Weerd 1976, Aguilar *et al*., 1991); **LG 4**, La Gloria 4 (Mein *et al*., 1990); **PUR-13**, Purcal 13 (García-Alix, 2006); **LB3**, La Bullana 3 and **LB2B**, La Bullana 2B (this paper); **PUR-4**, Purcal 4 (García-Alix *et al*., 2008c; Mansino *et al*., in press); **ZOR3 A**, Zorreras 3A (Martín-Suárez *et al*., 2000); **NGR 1**, Negratín 1 (Minwer-Barakat *et al*., 2009 and 2012); **ALM M**, Almenara M (Agustí and Galobart, 1986; Agustí *et al*., 2011). For making this figure the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Protatera almenarensis* as *Debruijnimys almenarensis*; *Protatera* sp. as *Debruijnimys* sp.

and AL2-D (Mansino *et al*., 2013). The molars from the two latter localities are slightly larger, having usually higher longitudinal crests and are clearly higher crowned than the teeth from La Bullana 2B and La Bullana 3. For these reasons, we ascribe the material from the studied localities to *S. dubari*.

Family Gerbillidae Alston, 1876
Subfamily Taterillinae Chaline, Mein and Petter, 1977
Genus *Debruijnimys* Castillo and Agustí, 1996
Debruijnimys cf. *julii* Castillo and Agustí, 1996 (Fig. 5, 1)

Locality: LB2B.
Material: 1 M1 (LB2B-248).

Description:

M1: (2.78 x 2.03): The anterocone is sub-triangular, with a flat anterior face. An indentation on the anterior face of the anterocone subdivides this cusp into two lobes. There is a posterior spur on the lingual lobe of the anterocone, directed towards the protocone-paracone junction. The anterocone and the protocone are linked by a low longitudinal ridge. The protocone and paracone are equivalent in size, and separated from the hypocone-metacone complex by a deep valley. The posterior walls of the protocone and the paracone show low posterior spurs that connect, at medium level, to the hypocone and the metacone, respectively. The hypocone is larger than the metacone, and posteriorly displaced. There is a shallow furrow between hypocone and metacone. Roots are not preserved.

Discussion:

In the Iberian Peninsula several Late Miocene and Early Pliocene localities have yielded remains of *Debruijnimys* Castillo and Agustí, 1996 (see Agustí and Casanovas-Vilar, 2003 and Minwer-Barakat *et al*., 2009b). The record of *Debruijnimys* in Spain comprises two species: *D. almenarensis* (Agustí, 1990) from the Late Miocene (MN13) and *D. julii* Castillo and Agustí, 1996 from the middle Pliocene (MN15). *Debruijnimys almenarensis* is recorded in Salobreña, Almenara M, Zorreras 2B and 3A, and Negratín-1 (Agustí, 1990; Agustí, 1991; Martín-Suárez *et al*., 2000; Minwer-Barakat *et al*., 2009b; Agustí *et al*., 2011) and *D. julii* in Asta Regia-3 (Castillo and Agustí, 1996).

Other Spanish localities of Early Ruscinian age (MN14) with presence of the genus *Debruijnimys* are Alcoy, Caravaca, Gorafe 1, Botardo, Bacochas 1 and La Gloria 4 (Sesé, 1989; Agustí, 1991; Castillo and Agustí, 1996 and Minwer-Barakat *et al*., 2009b) (Fig. 4). The scarcity of material in these localities led the authors to determine these specimens as *Debruijnimys* sp.; Agustí and Casanovas-Vilar (2003) considered that all these samples from the Ruscinian referred to *Debruijnimys* sp. were forms related to *D. julii*.

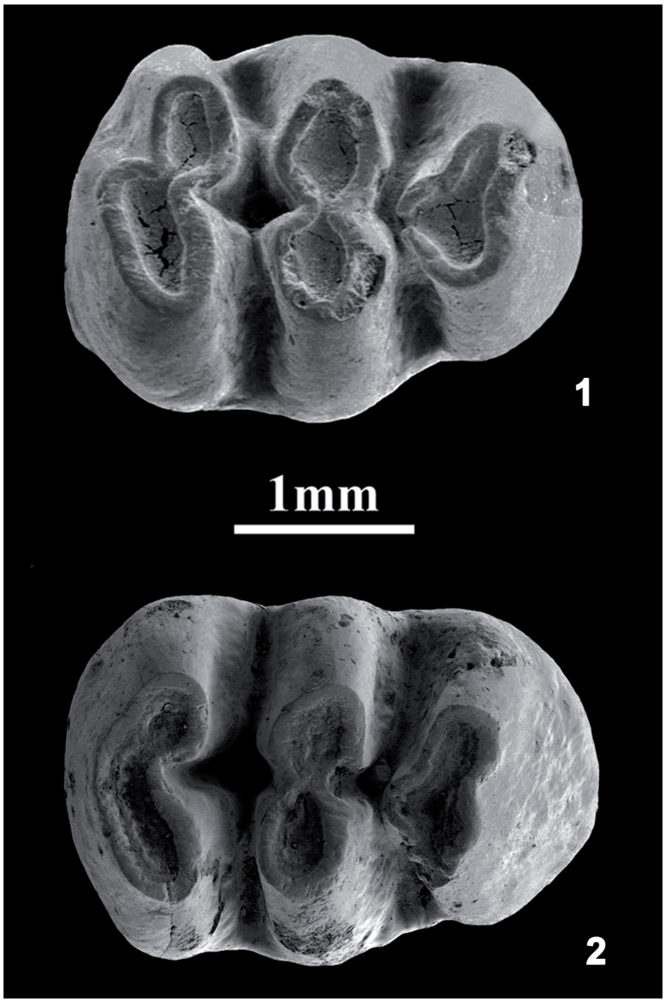


Fig. 5.- *Debruijnimys* cf. *julii* from La Bullana 2B (Cabriel Basin). **1**, right M1, LB2B-248. *Debruijnimys almenarensis* from Almenara M, **2,** right M1, MGUV-27742.

The phylogenetic relationship of the Spanish forms of *Debruijnimys* is not clear. Thus, the larger size and the presence of derived characters in *D. almenarensis* (MN13), like the very large anteroconid, led Agustí and Casanovas-Vilar (2003) to refuse an ancestor-descendant relationship between *D. almenarensis* and the Spanish material of *Debruijnimys* from the Early Ruscinian (MN14). According to these authors, the forms of *Debruijnimys* of Early Ruscinian age would be an intermediate step in a phylogenetic lineage comprising *D. davidi* from Lissafa (Morocco) (Late Turolian, MN13, 5.5 Ma) (Raynal *et al*., 1999) and *D. julii* from Asta Regia 3 (Late Ruscinian, MN15).

The upper molars of *D. julii* differ from those of *D. almenarensis* by several characters, like the presence of a weak indentation on the anterior face of the anterocone that creates two confluent lobes and the degree of separation between the protocone-paracone and hypocone-metacone pairs. While in *D. almenarensis* there is a wide valley, without posterior spurs (Fig. 5, 2), in *D. julii* there is a low connection between the posterior walls of the protocone and paracone and the anterior sides of the hypocone and metacone, respectively (Fig. 5, 1) (Castillo and Agustí, 1996, Plate 1, Fig. 4-5). Moreover, the shape of the M1, sub-rectangular in the M1 of *D. almenarensis* (Fig. 5, 2) and more rounded in *D. julii* (Fig. 5, 1) is another difference between both species.

Minwer-Barakat *et al*. (2009b) observed an increase in size from *D. davidi* from Lissasfa to *D. julii* from Asta Regia. The size of the material of the Early Ruscinian Spanish populations of *Debruijnimys* is similar to that of *D. julii* (Castillo and Agustí, 1996) and much larger than that of *D. davidi* from Lissasfa (Geraads, 1998). The M1 from La Bullana 2B is much larger than those of *D. davidi* from Lissasfa and very similar in size to those of *D. almenarensis* and *D. julii* (Agustí, 1990; Martín Suárez *et al*.; 2000; Minwer-Barakat *et al.* 2009b).

Moreover, the M1 from La Bullana 2B clearly differs from those of Lissasfa in the morphology of hypocone-metacone pair. While in Lissasfa the metacone is placed posteriorly with respect to the hypocone, in La Bullana 2B the metacone is placed anteriorly. In the single M1 from La Bullana 2B, the metacone is placed in a more anterior position with respect to the hypocone than in *D. almenarensis* from its type locality, Almenara M (Fig. 5, 2), and similar to that of *D. julii* (Castillo and Agustí, 1996).

The morphology of the anterocone of the M1 from La Bullana 2B is more similar to *D. almenarensis* and *D. julii* than to *D. davidi*. The presence of a weak indentation on the anterior face of the anterocone, that creates two confluent lobes, is present in *D. julii* and, in a lesser degree, also in *D. almenarensis* from Almenara M (Fig. 5, 2), and in *Debruijnimys* from La Bullana 2B, being absent in the M1 of *D. davidi* from Lissasfa. The absence of lower dentition and other elements of the upper dentition in La Bullana 2B do not allow going further in the comparison between the African and the Spanish forms of *Debruijnimys* of Late Miocene-Early Pliocene age.

Based on the size, the less elongated shape of this specimen, the presence of low posterior spurs connecting the protocone-hypocone and paracone-metacone pairs and the more accentuated asymmetry in the position of metacone and hypocone in the M1 of *Debruijnimys* from La Bullana 2B, we distinguish this tooth from *D. almenarensis* and assign it to a form related with *D. julii*.

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967
Genus *Eliomys* Wagner, 1840
Eliomys intermedius Friant, 1953 (Fig. 6, 8-10)

Locality: LB2B.

Material: 4 m1-2 (LB2B-6, LB2B-176, LB2B-242, LB2B-243), 1 m3 (LB2B-179), 1 P4 (LB2B-178), 1 M1-2 (LB2B-241), 1 M3 (LB2B-177).

Description:

m1-2: (1.42 x 1.77; 1.51 x -; - x 1.50; broken specimen): The anterolophid is connected to the protoconid in 1 out of 4 specimens. There is no anterotropid. There is a low connection between metalophid and metaconid. The centrolophid is

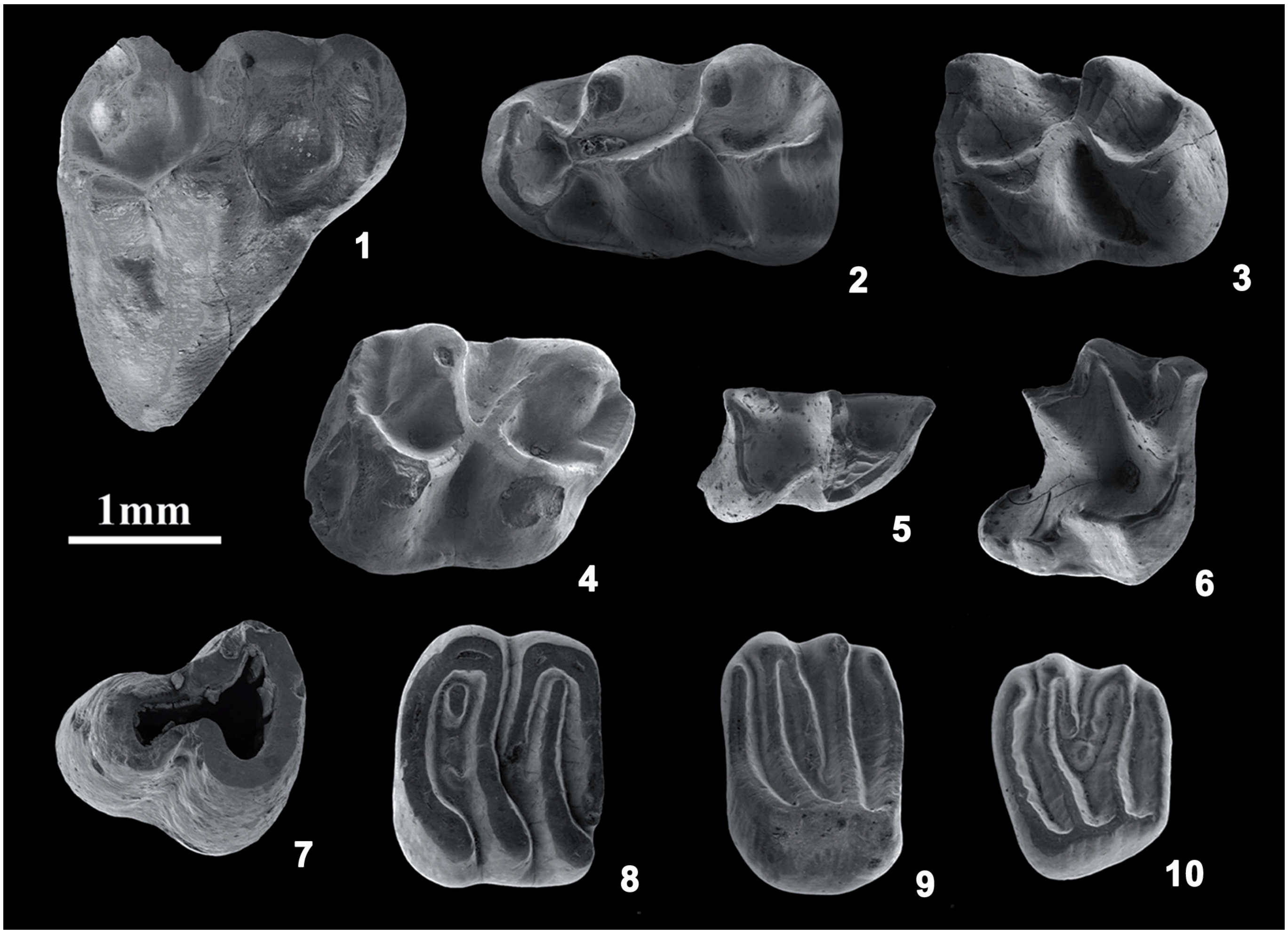


Fig. 6.- Rodents and insectivores from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Atlantoxerus* sp. from LB2B. **1**, right D4, LB2B-244. *Apocricetus barrierei* from LB2B. **2**, left m1, LB2B-141; **3**, left m3, LB2B-232; **4**, left M2, LB2B-220. *Asoriculus* cf. *gibberodon* from LB2B and LB3. **5**, right m1, LB2B-245; **6**, right M1, LB3-31. *Ruscinomys* sp. from LB2B. **7**, right m3, LB2B-175. *Eliomys intermedius* from LB2B. **8**, right m1-2, LB2B-176; **9**, left M1-2, LB2B-241; **10**, left M3, LB2B-177. Scale bar equals 1 mm.

long and not connected to the metalophid but in one specimen. There is no endolophid. The mesolophid is connected to entoconid. The posterotropids are well developed. Roots are not preserved.

m3: The only available tooth is broken anteriorly. The posterotropid is absent. The centrolophid is shorter than in the m1-2. There is no endolophid. The posterolophid is continuous. Roots are not preserved.

P4: (1.08 x 1.48): Subtriangular outline. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous. Roots are not preserved.

M1-2: (1.25 x 1.79): The anteroloph is separated from both protoloph and paracone by a deep valley. There is neither anterotrope nor posterotrope. Paracone and metacone are high and separated from each other. The protoloph and metaloph are continuous. In the only complete specimen the precentroloph is long, and the postcentroloph absent (Fig. 6, 8). The endoloph and posteroloph are connected and continuous. Roots are not preserved.

M3: (1.27 x 1.52): Trapezoidal outline, with the anterior part notably wider than the posterior side. The anteroloph is separated from protoloph, but closer to paracone than in M1-2. Both anterotrope and posterotrope are absent. The paracone and metacone are high and separated, and attached to a continuous protoloph and metaloph, respectively. Both centrolophs are present and well developed, being the postcentroloph longer and interrupted near its lingual end (Fig. 6, 9). The endoloph and posteroloph are connected and continuous. Roots are not preserved.

Discussion:

The specimens from La Bullana 2B are larger, more concave and have a more rounded outline than those of *Eliomys truci* Mein and Michaux 1970 and *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. Their size is similar to *Eliomys intermedius* Friant, 1953 from Sète and Orrios 3 (Adrover, 1986), PUR-13, TCH-3, TCH-1B and TCH-13 (García-Alix *et al.,* 2008b) and *Eliomys* cf. *intermedius* from Arquillo 3, Villalba Alta (Adrover, 1986) and Mont Hélène (Aguilar *et al.*, 1986). The presence of two centrolophs, being the postcentroloph well-developed (Fig. 6, 9), in the single M3 from La Bullana 2B agree with the species *Eliomys intermedius*.

Family Sciuridae Fisher, 1817
Subfamily Pteromyinae Brandt, 1855
Genus *Atlantoxerus* Forsyth Major, 1893
Atlantoxerus sp. (Fig. 6, 1)

Localities: LB2B, LB3
Material: 1 D4 (LB2B-244), 1 m1-2 (LB3-47)

Description:

D4: (2.36 x -): Tooth broken posterolabially. Sub-triangular outline. The parastyle is connected to the anteroloph, and separated from the protoloph by a wide and deep valley. The protocone is well developed, very high and connected to the paracone by the protoloph. The metacone is partially broken, and connected to the metaconule by a narrow crest. Both cusps are very close to each other and connected basally to the posteroloph. The metaconule is separated from the hypocone and protocone by a deep valley. Roots are not preserved.

m1-2: Molar broken anteriorly. The posterolophid bears a small hypoconulid, and connects the entoconid to the hypoconid. Roots are not preserved.

Discussion:

Heteroxerus and *Atlantoxerus* differ mainly in size, but *Atlantoxerus* has also higher crowns and cusps, more rounded conules and wider crests (Cuenca-Bescós, 1988). The studied specimens are larger than those of *Heteroxerus*, *Atlantoxerus cuencae* Aguilar, Calvet and Michaux, 1995, *A. martini* Aguilar, 2002 and *A. idubedensis* Cuenca, 1988, They are clearly smaller than those of *Atlantoxerus tadlae* (Lavocat, 1961), slightly smaller than *A.* cf. *margaritae* from La Gloria-2 and Villalba Alta, and slightly larger than the same taxon from Aldehuela (Adrover *et al*., 1993). The D4 is shorter but wider than that of *A.* cf. *margaritae* from Purcal-4 (García-Alix *et al*., 2007). *Atlantoxerus adroveri* de Bruijn and Mein, 1968, from Concud 3 (Weerd, 1976), and *A. rhodius* De Bruijn, Dawson and Mein, 1970 are slightly smaller than our specimens. Due to the scarcity and bad preservation of the recovered specimens we cannot confirm whether the *Atlantoxerus* from La Bullana 2B is a form related to *A. margaritae* or to *A. adroveri*, so we ascribe these molars to *Atlantoxerus* sp.

Sciuridae indet.?

Locality: LB2B.
Material: 1 m1,2 (LB2B-254).

Description:

m1-2: The molar is broken posterolingually. The protoconid is large, and connected to a well-developed anteroconulid. There is a weak anterior cingulid. The crest that connects the protoconid and the hypoconid is slightly swollen, forming a weak mesoconid. Roots are not preserved.

Discussion:

The specimen from La Bullana 2B certainly corresponds to a sciurid, but it is much smaller than the other remains of sciurids found in this locality ascribed to *Atlantoxerus*. The presence of an anterior cingulid is characteristic of some species of *Heteroxerus*, although a reduced cingulid may be present in some species of *Atlantoxerus*, like *Atlantoxerus blacki* (Cuenca-Bescós, 1988). Therefore, a more precise determination of this tooth is not possible.

Family Cricetidae Fischer, 1817
Subfamily Cricetinae Fischer, 1817
Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998
Apocricetus barrierei (Mein and Michaux, 1970)

Localities: LB2B, LB3.
Material, descriptions and Measurements: in Ruiz-Sánchez *et al*., 2014.

Discussion:

The assemblages from La Bullana 2B and La Bullana 3 have an intermediate size between *A. angustidens* and *A. alberti*. The m1 from La Bullana 2B have a crest-like anteroconid, with a weak subdivision, with two anterolophulids arising from a prelophid. In 2 out of 12 specimens there is a third crest pointing backwards from the middle of the anteroconid. The mesolophids are generally absent in m1 and m2. The m3 is generally longer than the m2, having a complete mesolophid in 3 out of 13 specimens. In the m3 from La Bullana 3 the mesolophid is absent.

In La Bullana 2B, the cingulum ridge on the base of the anterocone of M1 is absent (5) or weak (1). Of the seven M1, two have a complete anterior protolophule, one has a weakly developed crest and four have no crest at all. The posterior metalophule is very scarce in M1. 16 out of 20 M2 from La Bullana 2B have an anterior protolophule, whereas the only complete M2 from La Bullana 3 lacks this ridge. 4 out of 17 M2 from La Bullana 2B and 1 out of 3 from La Bullana 3 have a hint of metalophule. In the M3 an anterior protolophule is always present, being complete in 9 out of 13 specimens from La Bullana 2B and in 1 out of 2 from La Bullana 3.

The size of the *Apocricetus* assemblages from La Bullana 2B and La Bullana 3 agrees with that of *A. barrierei* (Freudenthal *et al*., 1998; Ruiz-Sánchez *et al*., 2014).

The lower molars of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* in the weakly split anteroconid in m1, the more pronounced enlargement of m3 and the absence of mesolophids in most m1-2. The prelophid is present in some specimens of *A. alberti*, but is less developed than in *A. barrierei* (Mansino *et al*., 2014).

The M1-2 of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* by the bifid anterolophule in the M1 and the absence of mesoloph in the M1-2. Some specimens of *A. alberti* and *A. barrierei* develop a weak cingulum ridge on the base of the anterocone of M1 (Mansino *et al*., 2014). This ridge is well-developed in *A. angustidens*.

The anterior protolophule of the upper molars is less developed in *A. barrierei* from La Bullana 2B and La Bullana 3 than in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and higher than in *A. angustidens*. In addition, the presence of posterior metalophule, complete or hinted, in *A. barrierei* from La Bullana 2B and La Bullana 3 differs from those of *A. angustidens*.

Therefore, on the basis of metric and morphological features, the material of the genus *Apocricetus* from La Bullana 2B and La Bullana 3 may be assigned to *A. barrierei*.

Subfamily Cricetodontinae Stehlin and Schaub, 1951
Genus *Ruscinomys* Depéret, 1890
Ruscinomys sp.

Locality: LB2B.
Material: 1 M3 (LB2B-175).

Description:

M3: (1.80 x 1.54): The dentine is completely lost. This molar has two lobes delimited by the sinus and mesosinus. The posterior lobe is smaller than the anterior one. Roots are not preserved.

Discussion:

Because of its general morphology and hypsodonty, we can ascribe the unique cricetodontine tooth from LB2B to the genus *Ruscinomys*, although a specific determination is not possible. The only available is an M3, an element which lacks most diagnostic characters. Adrover (1969) noted that the M3 of *Ruscinomys lasallei* Adrover, 1969, and *R. schaubi* Villalta and Crusafont Pairó, 1956, are less reduced than those of *R. europaeus* Déperet, 1890. The M3 from La Bullana 2B differs from the latter species by the presence of two well-developed lobes. However, distinguishing between *R. lasallei* and *R. schaubi* is difficult. The size of the M3 from La Bullana 2B is consistent with the lower measurements of *R. lasallei* and *R. schaubi* and even with smallest values of *R. europaeus*. For all these reasons, we ascribe the specimen from La Bullana 2B to *Ruscinomys* sp.

Order Soricomorpha Gregory, 1910
Family Soricidae Fischer von Waldheim, 1817
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Nectogalini Anderson, 1879
Genus *Asoriculus* Kretzoi, 1959
Asoriculus cf. *gibberodon* (Petényi, 1864) (Fig. 6, 5-6)

Localities: LB2B, LB3.
Material: 1 m1 (LB2B-245), 1 M1 (LB3-31).

Description:

m1: (L: 1.44; TRW: 0.77; TLW: 0.91): The talonid is wider than the trigonid. The hypolophid is well developed and does not reach the entoconid. There is a well-developed oblique crest, which connects the hypoconid with the trigonid. The metaconid is slightly higher than the paraconid. The depression of the trigonid is open and 'V' shaped. The protoconid is broken. The lingual cingulid is low and narrow. The labial cingulid is reduced. Roots are not preserved.

M1: (LL: 1.57; AW: 1.68): The metaloph does not reach the hypocone. There is a well-developed hypoconal flange and a pronounced posterior emargination. The basal connection between the hypocone and posteroloph agrees with the morphotype B described by Reumer (1984). The preprotocrista is in contact with the paracone. The parastyle is short. The paracrista is the shortest crest in the ectoloph. The paramesocrista is longer than the postmesocrista. The metastyle is broken. The metacone is higher than the paracone. The ectoloph is asymmetric. Roots are not preserved.

Discussion:

Asoriculus gibberodon is the smallest species of the genus, and very common in the Pliocene of Europe (Minwer-Barakat *et al*., 2010; Furió and Angelone, 2010). The presence of a large protoconid and a complete basal cingulid in lower molars are typical features of *A. gibberodon* (Furió, 2007). The hypocone attached to the posteroloph in the M1 agree with the morphotype B of Reumer (1984). The size of the m1 is consistent with the minimum values of the molars from Villany 3, Csarnota 2, Ostrazmos 1 and 9 (Reumer, 1984), Varshets (Popov, 2003), Fuente Nueva 3 (Furió, 2007), TCH-1 and TCH-3 (Minwer-Barakat *et al*., 2010) and Capo Mannu D1 (Furió and Angelone, 2010). The size of the M1 matches the largest values of the specimens from the mentioned localities. This great biometrical variability is usual in *A. gibberodon* (Reumer, 1984; Minwer-Barakat *et al*., 2010).

5. Discussion

5.1. Biostratigraphy

Figure 4 contains information on the stratigraphical distribution of the rodent faunas described in La Bullana 2B and La Bullana 3, besides other of Spanish localities from MN13 to MN15. The locality of La Bullana 2B contains *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys* aff. *abaigari*, *Paraethomys meini*, *Occitanomys brailloni*, *Occitanomys* sp., *Stephanomys dubari*, *Eliomys intermedius*, *Apocricetus barrierei*, *Ruscinomys* sp., *Atlantoxerus* sp., Sciuridae indet., *Debruijnimys* cf. *julii* and *Asoriculus* cf. *gibberodon*. On the other hand, the locality La Bullana 3 contains *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari, Apocricetus barrierei*, *Atlantoxerus* sp., and *Asoriculus* cf. *gibberodon*. The coexistence of *Apodemus gorafensis*, *Paraethomys meini*, *Castillomys gracilis* and *Stephanomys dubari* is considered typical of the latest Turolian-earliest Ruscinian (García-Alix *et al*., 2008a). The size and morphology of *Stephanomys* present in La Bullana 2B and La Bullana 3, with some specimens close to *S. cordii*, are similar to the molars from the lower Ruscinian (MN14) sites of PUR-4, PUR-7 and PUR-13 (García-Alix *et al*., 2008a).

Other species of biostratigraphic relevance in La Bullana 2B are *Occitanomys brailloni* and *Paraethomys* aff. *abaigari*. *Occitanomys brailloni* appears in MN14, extending its range to MN16 (Weerd, 1979; Ruiz Bustos *et al*., 1984; Castillo, 1990; Minwer-Barakat, 2005). *Paraethomys* aff. *abaigari* is found together with the smaller *P. meini* in some localities of the MN14, like PUR-13, CLC-5A, Celadas-14, Celadas-5, Celadas-5A, La Gloria 4 and Celadas 9 (García-Alix *et al*., 2008c). In older localities, closer to the MN13-MN14 boundary like PUR-4, *P. meini* shows a wide size range, which may indicate that the lineage of *P. abaigari* is already present in those assemblages, and in Peralejos E two specimens are close to *P.* aff. *abaigari* (García-Alix *et al*., 2008a).

Regarding the cricetids, the presence of *Apocricetus barrierei* in La Bullana 2B and La Bullana 3 is a clearly indicates a lower Ruscinian age for these localities (Freudenthal *et al*., 1998; García-Alix *et al*., 2008b).

In La Bullana 2B, glirids are represented by *Eliomys intermedius*. This species appears in MN14 (Sesé, 2006), being La Gloria 4 in the Teruel basin (Mein *et al*., 1990), and PUR-13 in the Granada Basin (García-Alix *et al*., 2008b), the oldest records of this taxon. The faunal assemblage of La Bullana 2B indicates a similar age for the three localities (see Fig. 4).

Debruijnimys julii was described in the middle Pliocene (MN15) locality of Asta Regia (Castillo and Agustí, 1996), where *Stephanomys donnezani*, *Paraethomys jaegeri* and *Paraethomys* cf. *meini* are also present. This assemblage is clearly younger than that from LB2B.

Debruijnimys sp. has been cited in the lower Ruscinian sites of Gorafe 1, La Gloria 4, Alcoy 4B and Caravaca (Minwer-Barakat *et al*., 2009b). Gorafe 1, from the latest MN14 is included by Minwer-Barakat *et al*. (2012) in the *Trilophomys* Assemblage Zone of the Guadix basin, characterized by the association of *Apocricetus barrierei*, *Stephanomys cordii*, *Castillomys gracilis*, *Apodemus gorafensis*, *Paraethomys meini* and *Trilophomys*.

With respect to La Gloria 4, this locality belongs to the *Promimomys* and *Paraethomys* Assemblage Zone of the Teruel basin, within the MN14, where two species of *Paraethomys*, *P. meini* and *P. abaigari*, coexist (Mein *et al*., 1990). The presence of *Stephanomys dubari*, two *Paraethomys* species and *Apocricetus barrierei* suggest a similar age for La Gloria 4 and La Bullana 2B and La Bullana 3 (Fig. 4). In Caravaca, the presence of *S. dubari*, *Apocricetus barrierei*, *Castillomys gracilis* and a big-sized *Apodemus* indicate a similar age to that of La Bullana 2B and La Bullana 3 (Freudenthal *et al*., 1998; Bruijn *et al*., 1975; Weerd, 1976; Aguilar *et al*., 1991).

According to these observations, *Debruijnimys* sp. from Gorafe 1 and Alcoy 4B are younger than the form present in La Bullana 2B, and *Debruijnimys* sp. from Caravaca and La Gloria 4 may be of a similar age. The sites where *D. almenarensis* is present, Negratín-1 and Almenara M, correspond to the Late Turolian and are clearly older than La Bullana 2B and La Bullana 3.

5.2. Paleomagnetism

A preliminary paleomagnetic study was carried out in the localities La Bullana 2B and La Bullana 3. We collected five samples to produce a preliminary paleomagnetic study around La Bullana sites, which are stratigraphically above the classical site of Venta del Moro, dated at 6.23 Ma (Gibert *et al*., 2013). The samples from La Bullana 3 show normal polarity, like the two lower samples from La Bullana 2B, while the two upper samples from this locality show reverse or ambiguous polarities, indicating a normal-reverse polarity sequence (Fig. 2). The presence of a basal normal zone, the differences with Venta del Moro fauna and the similarities with sites located in the latest Miocene or earliest Pliocene suggest that the identified normal zone should be correlated with chron C3n.4n in the earliest Pliocene, dated between 5.235 Ma and 4.997 Ma (Lourens *et al*., 2005). Therefore, the fauna of La Bullana 3 can be constrained to the age of this chron and the site La Bullana 2B, placed a few meters above its upper boundary, should be constrained between the age of this boundary (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

5.3. Paleoecology

The analysis of micromammal assemblages has been widely used as a paleoclimatic indicator (Weerd, 1976; Daams *et al*., 1988; Casanovas-Vilar and Agustí, 2007; García-Alix *et al*., 2008; Furió *et al*., 2011).

Some authors have proposed a minimum sample size of at least 100 specimens when dealing with fossil assemblages (Daams *et al*., 1999; García-Alix *et al*., 2008d), while others used a minimum of 50 specimens (Casanovas-Vilar and Agustí, 2007), arguing that in most cases larger samples only add one or two species to the assemblage, with an abundance of less than 1 %. According to this, the sample from La Bullana 3 is too scarce to carry out any paleoecologic inference, having yielded just 32 specimens. For this reason we only present here the data from La Bullana 2B.

To interpret the paleoecologic requirements of each taxon found in La Bullana 2B, we have used mainly the climatic and habitat preferences proposed by García Alix *et al.* (2008d). According to that work, a number of taxa are considered as warm weather indicators (*Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus*, *Atlantoxerus* and *Asoriculus gibberodon*), whereas *Ruscinomys*, of which a single element has been found, indicates cold conditions. Regarding the humidity, the presence of *P. meini*, *Ruscinomys* and *Atlantoxerus* has been associated with dry conditions, while *A.*

	N	DE	N/DE	RA	Temperature	Humidity	Habitat
Apodemus gorafensis	26	12	2.17	10.43	W	H	E
Castillomys gracilis	17	12	1.42	6.81	E	E	E
Occitanomys brailloni	17	12	1.42	6.81	U	U	U
Occitanomys sp.	1	12	0.08	0.40	U	U	U
Paraethomys aff. *abaigari*	36	12	3.00	14.43	U	U	U
Paraethomys meini	27	12	2.25	10.82	W	D	E
Stephanomys dubari	25	12	2.08	10.02	E	E	E
Apocricetus barrierei	89	12	7.42	35.68	W	E	O
Ruscinomys sp.	1	12	0.08	0.40	C	D	O
Debruijnimys cf. julii	1	12	0.63	3.01	U	D	U
Eliomys intermedius	10	16	0.08	0.40	E	E	E
Atlantoxerus sp.	1	16	0.06	0.30	W	D	O
Sciuridae indet.	1	16	0.05	0.24	U	U	U
Asoriculus cf. *gibberodon*	1	20	0.05	0.24	W	H	F
TOTALS					Warm: 57.87 % Cold: 0.40 % Eurytopic: 19.84 % Unknown: 21.89 %	Humid:10.66 % Dry: 11.93 % Eurytopic: 55.52 % Unknown: 21.89 %	Open: 36.78 % Forested: 0.25 % Eurytopic: 41.09 % Unknown: 21.88 %

Table 6.- Paleoecological affinities of the taxa from the studied localities. The relative abundance (RA) of each taxon is calculated following Martín-Suárez (1988), dividing the number of specimens (N) by the number of diagnostic elements (DE) of each group. Abbreviations: **C**, cold; **DE**, diagnostic elements; **D**, dry; **E**, eurytopic; **F**, forested; **H**, humid; **N**, number of specimens; **O**, open; **RA**, relative abundance; **U**, unknown; **W**, warm.

gorafensis, *Eliomys intermedius* and *A. gibberodon* would indicate a wet environment. The presence of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* indicates open habitats, whereas *Eliomys intermedius* and *Asoriculus gibberodon* would suggest the presence of forested zones in the area (García-Alix *et al.*, 2008d). However, Freudenthal *et al.*, (2014) point out that the genus *Eliomys* cannot be considered a humid environment indicator based on the ecological affinities of extant *E. quercinus*, which is a habitat generalist, and the distribution of *E. munbyanus* and *E. melanurus*, restricted to semi-desert environments. Therefore, we consider *E. intermedius*, probable ancestor of *E. quercinus* (García-Alix *et al.*, 2008b), and eurytopic taxon regarding both habitat and humidity. The presence of the gerbilid *Debruijnimys* suggests a dry and arid environment (Minwer-Barakat *et al.*, 2009b), and the affinities of *P.* aff. *abaigari*, *Occitanomys brailloni* and *Occitanomys* sp. are unknown (García-Alix *et al.*, 2008d).

The proportions of the taxa within each ecological category are shown in table 6. Regarding the humidity, most of the taxa recorded in La Bullana 2B are eurytopic (55.52 %) or with unknown affinities (*P.* aff. *abaigari* and *Occitanomys brailloni* and sp. 21.89 %). Because of that, the relative proportion of humid (10.66 %) and dry (11.93 %) environment indicators does not seem very representative. However, most of the taxa studied in this work are considered as typical to warm environments (57.87 %), and the abundance of *Apocricetus* together with *Ruscinomys* and *Atlantoxerus* and the presence of *Debruijnimys* suggest an open environment (36.78 % of the assemblage). Therefore, we consider that the faunas from La Bullana 2B indicate warm conditions and probably an open environment with some patches of vegetation.

5.4. Considerations on the "gerbil event" in Europe according to the presence of Debruijnimys in La Bullana 2B

The Messinian Salinity Crisis (MSC) is the main event in the evolution of the Mediterranean during the Neogene. The beginning of the MSC took place about 5.96 Ma ago, with the closure of the Betic and Rifian seaways, which connected the Atlantic and Mediterranean domains. The Mediterranean was reflooded at the base of the Pliocene after the opening of a new seaway, the Gibraltar strait (Hsü *et al.*, 1973). The effects of this event on the faunal exchanges between Africa and Europe during this time interval have been widely discussed in the literature, and several authors have accepted the creation of new migration routes for terrestrial organisms (Brandy and Jaeger, 1980; Agustí and Casanovas-Vilar, 2003; Aguirre, 2003; Made *et al.*, 2006; Agustí *et al.*, 2006; Minwer-Barakat *et al.*, 2009b; Gibert *et al.*, 2013, among others).

One of the taxa of African origin that colonised the Iberian Peninsula during the MSC is the gerbil *Debruijnimys*. Until now, only two species of this genus have been recorded in Europe, *D. almenarensis*, identified in some MN13 localities, and *D. julii*, only known from the type locality, Asta Regia (MN15).

The origin of *D. almenarensis* and *D. julii* has been discussed in several papers (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003; Minwer-Barakat *et al.*, 2009b), which has important paleobiogeographic implications. While *D. almenarensis* (MN13) has a clear African origin, related to the MSC Event, the origin of *D. julii* (MN15) is more difficult to establish. Thus, the dispersion processes which explain the presence of gerbils in Western Europe have proven to be very complicated. According to Agustí and Casanovas-Vilar (2003), there are, at least, two different waves of gerbil colonisation from northern Africa recorded in the Iberian basins. The first wave, of Late Turolian age (Late Miocene), involved *D. almenarensis*, whereas the second one corresponds to the representatives of *Debruijnimys* (*Debruijnimys* sp.) found in the Lower Pliocene (lower Ruscinian, MN14) localities of Alcoy, Gorafe, Caravaca and La Gloria 4. The presence of *A. barrierei* in Botardo, Alcoy 4B, Caravaca, La Gloria 4 (Freudenthal *et al*., 1998) and La Bullana 2B, confirm an Early Pliocene age (early Ruscinian, MN14) for these localities. La Bullana 2B is older than Alcoy 4B, probably slightly older than La Gloria 4 and similar in age to Caravaca and Botardo.

If *D. julii* is not the direct descendant of *D. almenarensis*, the presence of *D. julii* in the MN15 implies, necessarily, a second migration event from Africa to Europe in the span interval between MN13 and MN15 (Agustí and Casanovas-Vilar, 2003). Thus, according to Agustí and Casanovas-Vilar (2003), *Debruijnimys* sp. from the lower Ruscinian localities of Alcoy, Gorafe, Caravaca and La Gloria 4 (MN14) would be the descendant of *D. davidi*, and the ancestor of *D. julii*, known from the Late Ruscinian (MN15) site of Asta Regia 3.

However, there is a great similarity between *D. almenarensis* and the subsequent forms of *Debruijnimys* (see Fig. 5), and a direct ancestor-descendant relationship cannot be discarded. Still, if the presence of *D. julii* in MN14 is confirmed, it would expand the range of this taxon, until now recorded only in MN15. This would make the phylogeny of *Debruijnimys* even more complex, since the relationship between *Debruijnimys* sp. from MN14 and *D. julii* is not clear, and they may even be the same species. Another option would be a process of cladogenetic speciation along the Early Pliocene, resulting in two different lineages of *Debruijnimys*, and unnamed species and *D. julii*, but the relationship between this latter species and the forms present in MN14 is not clear, and they may be indeed the same taxon.

Nevertheless, any hypothesis on the phylogenetic relationships of *Debruijnimys* is difficult to test because of the scarce material of *Debruijnimys* sp. from the early Pliocene of the Iberian Peninsula. Only Alcoy 4B yielded a rich sample, but nowadays it is a lost locality. Therefore, until new material from Ruscinian sites becomes available, little more can be said in this regard.

The new data from La Bullana 2B contribute to improve the knowledge on the status of this lineage of African rodents in the Iberian Peninsula after the colonisation processes during the Messinian Salinity Crisis, but open new questions around the evolution of this group, too.

6. Conclusions

The faunal list of La Bullana 3 comprises *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon*. In addition to these taxa, La Bullana 2B has yielded remains of *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. Based on these faunal assemblages, we propose a lower Ruscinian age (MN14) for both localities.

The preliminary paleomagnetic analysis indicates an earliest Pliocene age for La Bullana 3 and La Bullana 2B. The age of La Bullana 3 lies probably within the C3n.4n chron, dated between 5.235 Ma and 4.997 Ma. The age of La Bullana 2B should be constrained between the top of this chron (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

The presence of *Eliomys intermedius* in La Bullana 2B constitutes one of the oldest records of this taxon, probably equivalent to la Gloria 4 and PUR-13. The presence in La Bullana 2B of *Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus barrierei*, *Atlantoxerus* and *Asoriculus* cf. *gibberodon* suggest warm conditions, and the relative abundance of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* is consistent with an open environment.

The Early Ruscinian locality of LB2B constitutes the first record of a form related to *Debruijnimys julii* in MN14. However, the scarcity of the available material of *Debruijnimys* from Early Pliocene sites prevents any proper analysis, and its phylogenetic relationships remain controversial.

Acknowledgments

The campaigns of prospection and excavation in the area of Venta del Moro have been funded by the Conselleria de Cultura y Esports of the Valencian government since 1995. We thank the efficient work of the technicians of the SCSIE of the UV, P. Gómez, E. Navarro and A.J. Ibáñez. This investigation was carried out thanks to the Prometeo Project of the Secretariat for Higher Education, Science, Technology and Innovation from Ecuador. We thank Dr. Jordi Agustí for his comments. We thank the Paleomagnetic Laboratory CCiTUB-ICTJA CSIC where the paleomagnetic measurements were conducted and the Ramon y Cajal program of the Spanish Goverment for its help. This investigation has been funded through the project GV06/304 of the Conselleria d’Empresa, Universitat i Ciència “Estudio paleoambiental del tránsito Mioceno-Plioceno en facies continentales en la Comunidad Valenciana (Cuencas del Cabriel y de Alcoy)”. This investigation was supported by project 688 CGL2011-25754 of the Spanish Ministry of Economy and Competitiveness.

References

Adrover, R. (1969): Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. I. *Ruscinomys*. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 67, 245–272.

Adrover, R. (1986): *Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico*. PhD. Thesis, Instituto de Estudios Turolenses, 423 p.

Adrover, R., Mein, P., Moissenet, E. (1988): Contribución al conocimiento de la fauna de roedores del Plioceno de la región de Teruel.

Teruel 79 (1), 89–151.

Adrover, R., Mein, P., Moissenet, E. (1993): Roedores de la transición Mio-Plioceno de la región de Teruel. *Paleontologia i Evolució* 26–27, 47–84.

Aguilar, J.P, Calvet, M., Michaux, J. (1986): Description des rongeurs pliocènes de la faune du Mont-Hélène (Pyrénées-Orientales, France), nouveau jalon entre les faunes de Perpignan (Serrat-Den-Vacquer) et de Sète. *Paleovertebrata* 16 (3), 127–144.

Aguilar, J. P., Michaux, J., Bachelet, B., Calvet, M., Faillat, J. P. (1991): Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocene en Rousillon. Implications biostratigraphiques et biogeographiques. *Paleovertebrata* 20, 147–174.

Aguirre, E. (2003): Messiniense: compleja y grave crisis ecológica. *Estudios Geológicos* 59, 205–212.

Agustí, J. (1990): The Miocene rodent succession in Eastern Spain: a zoogeographical appraisal. In: E. H. Lindsay, V. Fahlbusch, & P. Mein (eds), *European Neogene Mammal Chronology*. Plenum Press, New York, pp. 375–404

Agustí, J. (1991): Gerbilidés fossiles d'Europe occidentale. In: Le Berre, M. & Guelte, L. (eds.), *Le Rongeur et l'Espace*, pp. 177–182.

Agustí, J., Galobart, A. (1986): La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. *Paleontologia y Evolució* 20, 57–62

Agustí, J., Casanovas-Vilar, I. (2003): Neogene gerbils from Europe. *Deinsea* 10, 13–21.

Agustí, J., Martín-Suárez, E. (1984): El Plioceno continental de la depresión Guadix-Baza (Prov. Granada) y su fauna de micromamíferos. Nota preliminar. *Acta Geologica Hispanica* 19 (4), 277–281.

Agustí, J., Oms, O., Furió, M., Pérez-Vila, M. J., Roca, E. (2006): The Messinian terrestrial record in the Pyrenees: The case of Can Vilella (Cerdanya Basin). *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 179–189. doi:10.1016/j.palaeo.2006.03.024

Agustí, J., Santos-Cubedo, A., Furió, M., De Marfá, R., Blain, H. A., Oms, O., Sevilla, P. (2011): The late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Castellón, Eastern Spain): Chronologic and paleoclimatic context. *Quaternary International* 243, 183–191. doi: 10.1016/j.quaint.2010.11.016

Benavent, J. V., Gascó, F., Ruiz-Sánchez, F. J., Montoya, P. (2008): Un Nuevo yacimiento con micromamíferos en el Mioceno Superior del área de Venta del Moro (Cuenca del Cabriel, Valencia). *Stvdia Geologica Salmanticensia* 8, 95–105.

Brandy, L. D., Jaeger, J.J. (1980): Les échanges de faunes terrestres entre l'Europe et l'Afrique nord-occidentale au Messinien. *Comptes-rendus de l'Académie des Sciences de Paris* 291, 465–468.

Bruijn, H. de (1974): The Ruscinian rodent succession in Southern Spain and its implications for the bioestratigraphic correlation of Europe and North Africa. *Senckerbergiana lethaea* 55, 435–445.

Bruijn, H. de, Dawson, M. R., Mein, P. (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rodhes (Greece). *I, II y III. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 73, 536–584.

Bruijn, H. de, Mein, P., Montenat, C., Weerd, A. van de (1975): Corrélations entre les gisements de rongeurs et les formations marines du Miocéne terminal d'Espagne méridional I (Provinces d'Alicante et de Murcia). *Proceedings Koninklijke Akademie van Wetenschappen* 78, 314–338.

Casanovas-Vilar, I., Agustí, J. (2007): Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 248, 169–189. DOI:10.1016/j.palaeo.2006.12.002

Castillo, C. (1990): *Paleocomunidades de Micromamíferos de los Yacimientos kársticos del Neógeno Superior de Andalucía Oriental*. PhD. Thesis, Universidad de Granada, 225 p.

Castillo, C., Agustí, J., (1996): Early Pliocene rodents (Mammalia) from Asta Regia (Jerez basin, Southwestern Spain). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 991, 25–43.

Cuenca-Bescós, G. (1988): Revisión de los Sciuridos del Aragoniense y del Rambliense en la fosa de Calatayud-Montalbán. *Scripta Geologica* 87, 1–116.

Daams, R. (1981): The dental pattern of the Dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. *Utrech Micropaleontological Bulletins special publication* 3, 1–115.

Daams, R., Freudenthal, M., van der Meulen, A. J. (1988): Ecostratigraphy of micromammal faunas from the Neogene of Spain. *Scripta Geologica, Special Issue* 1, 286–302.

Daams, R., van der Meulen, A. J., Peláez-Campomanes, P., Alvarez Sierra, M.A. (1999): Trends in rodent assemblages from the Aragonian (early–middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain. In: Agustí, J., Rook, L., Andrews, P. (eds.), *Hominoid evolution and climatic change in Europe. The evolution of Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge, U. K., vol. 1, pp. 127–139.

Freudenthal, M. (2004): Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). *Treballs del Museu de Geologia de Barcelona* 12, 97–173.

Freudenthal, M., Mein, P., Martín-Suárez, E. (1998): Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7, 11–93.

Freudenthal, M., García-Alix, A., Rios, M., Ruiz-Sánchez, F. J., Martín-Suárez, E., Delgado Huertas, A., 2014: Review of paleo-humidity parameters in fossil rodents (Mammalia): Isotopic vs. tooth morphology approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 395, 122–130. http://dx.doi.org/10.1016/j.palaeo.2013.12.023

Furió, M. (2007): *Los insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno superior del Levante Ibérico*. PhD. Thesis, Universitat Autònoma de Barcelona, 341 p.

Furió, M., Angelone, C., (2010): Insectivores (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu D1 (Mandriola, central-western Sardinia, Italy). *Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen* 258, 229–242.

Furió, M., Casanovas-Vilar, I., van den Hoek Ostende, L. (2011): Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304 (3-4), 219–229. doi:10.1016/j.palaeo.2010.01.039

García-Alix, A. (2006): *Bioestratigrafía de los depósitos continentales de la transición Mio-Plioceno de la cuenca de Granada*. PhD. Thesis, Universidad de Granada, 429 p.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2007): New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *Comptes Rendus Palevol* 6, 269–279. doi:10.1016/j.crpv.2007.02.001.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008a): Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada basin (southern Spain). Biostratrigraphic and phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlunge*n 248, 183–215. doi: 10.1127/0077-7749/2008/0248-0183.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008b): Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136, 1–37.

García-Alix, A., Minwer-Barakat, R., Martín, J. M., Martín Suárez, E. & Freudenthal, M., (2008c): Biostratigraphy and sedimentary evolution of late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). *Lethaia* 41 (4): 431-446. doi: 10.1111/j.1502-3931.2008.00097.x

García-Alix, A. Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., Martín, J. M. (2008d): Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265, 214–225. doi: 10.1016/j.palaeo.2008.04.005

Geraads, D. (1998): Rongeurs du Mio-Pliocène de Lissasfa (Casablanca, Maroc). *Geobios* 31, 229–245.

Gibert, L., Scott, G.R., Montoya, P., Ruiz-Sánchez, F. J., Morales, J., Luque, L., Abella, J., Lería. M. (2013): Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. *Geology* 41, 691–694. doi: 10.1130/G34164.1

Hordijk, K., de Bruijn, H. (2009): The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hellenic Journal of Geosciences* 44, 21–103.

Hsü, K. J., Montadert, L., Bernoulli, D., Cita, M. B., Erickson, A., Garrison, R. E., Kidd, R. B, Mèlierés, F., Müller, C., Wright, R. (1973): History of the Mediterranean salinity crisis. *Nature* 267, 399–403.

Lacomba, J. I., Morales, J., Robles, F., Santisteban, C., Alberdi, M. T. (1986): Sedimentología y paleontología del yacimiento finimioceno de La Portera (Valencia). *Estudios Geológicos* 42, 167–180.

Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, J. (2005): Chapter 21- The Neogene. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, U.K., pp. 409–430.

Made, J. van der, Morales, J., Montoya, P. (2006): Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 228–246. http://dx.doi.org/10.1016/j.palaeo.2006.03.030

Mansino, S., Montoya, P., Luque, L., Ruiz-Sánchez, F. J., Benavent, J. V. (2009): La Bullana 2B: faunas de micromamíferos del Plioceno en el área de Venta del Moro (Valencia, España). *Resúmenes XXV Jornadas de la Sociedad Española de Paleontología* 1, 204–206.

Mansino, S., Fierro, I., Ruiz-Sánchez, F. J., Montoya, P. (2013): The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of 2 Alcoy-Mina. *Journal of Iberian Geology* 39 (2), 261–284. doi: 10.5209/rev_JIGE.2013.v39.n2.42501

Mansino, S., Ruiz-Sánchez, F. J., Freudenthal, M., Montoya, P. (2014): A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain). *Proceedings of the Geologists' Association* 125, 392–405. doi: 10.1016/j.pgeola.2014.07.002

Mansino, S., García-Alix, A., Ruiz-Sánchez, F. J., Montoya, P. (in press): A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica*, http://dx.doi.org/10.4202/app.00014.2013

Martín-Suárez, E. (1988): *Sucesiones de micromamíferos en la depresión de Guadix Baza*. PhD. Thesis, Universidad de Granada, 241 p.

Martín-Suárez, E., Freudenthal, M. (1993): Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica* 103, 65–118.

Martín-Suárez, E., Mein, P. (1991): Revision of the genus *Castillomys* (Muridae, Rodentia). *Scripta Geologica* 96, 47–81.

Martín-Suárez, E., Freudenthal, M., Krijgsman, W., Rutger-Fortuin, A. (2000): On the age of the continental deposits of the Zorreras Member (Sorbas Basin, SE Spain). *Geobios* 33, 505–512.

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

Mein, P., Moissenet, E., Adrover., R. (1990): Biostratigraphie du Néogène Supérieur du basin de Teruel. *Paleontologia i Evolució* 23, 121–139.

Michaux, J. (1969): Muridae (Rodentia) du Pliocène supérieur d'Espagne et du Midi de la France. *Palaeovertebrata* 3, 1–25.

Minwer-Barakat, R. (2005): *Roedores e insectívoros del Turoliense Superior y el Plioceno del sector central de la Cuenca de Guadix*. PhD. Thesis, Universidad de Granada, 606 p.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2005): Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, southeastern Spain). *Journal of Vertebrate Paleontology* 25 (2), 426–441. doi: 10.1671/0272-4634(2005)025[0426:mrftpo]2.0.co;2

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2009a): Late Turolian micromammals from Rambla de Chimeneas-3: considerations on the oldest continental faunas from the Guadix Basin (Southern Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 251 (1), 95–108.

Minwer-Barakat, R., García-Alix, A., Agustí, J., Martín-Suárez, E., Freudenthal, M. (2009b): The micromammal fauna from Negratín-1 (Guadix basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the late Miocene. *Journal of Paleontology* 83 (6), 854–879. doi: 10.1666/09-009.1.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2010): Soricidae (Soricomorpha, Mammalia) from the Pliocene of Tollo de Chiclana (Granada, Southeastern Spain). *Journal of Vertebrate Paleontology* 30, 535–546. doi: http://dx.doi.org/10.1080/02724631003622001

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2011): Validation of the Species *Stephanomys progressus*, a Murid (Rodentia) from the Early Pleistocene of Spain. *Journal of Paleontology* 85 (2), 392–394. doi: http://dx.doi.org/10.1666/10-131.1

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M., Viseras, C. (2012): Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. *Lethaia* 45, 594–614. doi: 10.1111/j.1502-3931.2012.00324.x

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J. V., Marín, M. D., Ruiz-Sánchez, F. J. (2006): Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. *Estudios Geológicos* 62, 313–325.

Morales, J. (1984): *Venta del Moro: su macrofauna de mamíferos y bioestratigrafía continental del Mioceno terminal mediterráneo*. PhD. Thesis. Universidad Complutense de Madrid, 340 p.

Morales, J., Montoya, P., Abellá, J. (2011): Venta del Moro: un yacimiento clave para conocer la historia del límite Mio-Plioceno en el área mediterránea. *Paleoisurus* 4, 60–71.

Morales, J., Peláez-Campomanes, P., Abella, J., Montoya, P., Gibert, L., Scott, G., Cantalapiedra, J.L., Sanisidro, O. (2013): The Ventian mammal age (Latest Miocene): present state. *Spanish Journal of Palaeontology* 28 (2), 149–160.

Popov, V.V. (2003): Late Pliocene Soricidae (Insectivora, Mammalia) from Varshets (North Bulgaria). *Acta Zoologica Cracoviensia* 46, 43–72.

Raynal, J. P., Lefèvre, D., Geraads, D., El Graoui, M. (1999): Contribution du site paléontologique de Lissasfa (Casablanca, Maroc) à une nouvelle interprétation du Mio-Pliocène de la Méseta. C*omptes Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Science* 329 (8), 617–622.

Reumer, J. W. F. (1984): Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. *Scripta Geologica* 73, 1–173.

Reumer, J. W. F., van den Hoek Ostende, L. W. (2003): Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). In: Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn*. Deinsea 10, pp. 455–467.

Robles, F. (1970): *Estudio estratigráfico y paleontológico del Neógeno* *del río Júcar*. PhD. Thesis, Universidad de Valencia, 275 p.

Ruiz Bustos, A., Sesé, C., Dabrio, C., Peña, J.A., Padial, J. (1984): Geología y fauna de micromamíferos del nuevo yacimiento del Plioceno inferior de Gorafe-A (depresión de Guadix-Baza, Granada). *Estudios Geológicos* 40, 231–241.

Ruiz-Sánchez, F. J., Santisteban, C., Crespo-Roures, V. D., Freudenthal, M. (2011): New rodent faunas from Middle Miocene and Mio-Pliocene in the Cabriel Basin (Valencia, Spain). *Journal of Iberian Geology* 37, 161–172. doi: 10.5209/rev_JIGE.2011.v37.n2.5

Ruiz-Sánchez, F. J., Freudenthal, M., Mansino, S., Crespo-Roures, V. D., Montoya, P. (2014): *Apocricetus barrierei* (Rodentia, Mammalia) from La Bullana 2B and La Bullana 3 (Cabriel Basin, Valencia, Spain). Revision of the Late Miocene–Early Pliocene forms of the genus *Apocricetus*. *Paläontologische Zeitschrift* 88, 85–98. doi: 10.1007/s12542-013-0178-0

Sesé, C. (1989): Micromamíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada). In: M. T. Alberdi y F. P. Bonadonna (eds.). *Geología y Paleontología de la Cuenca de Guadix-Baza. Trabajos sobre Neógeno-Cuaternario* 11, pp. 185–213.

Sesé, C. (2006): Los roedores y lagomorfos del Neógeno de España. *Estudios Geológicos* 62, 429–480.

Weerd, A. van de (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrech Micropaleontological Bulletins, special publication* 2, 1–217.

Weerd, A. van de (1979): Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 82, 127–170.

Proceedings of the Geologists' Association 125 (2014) 392–405

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

A new approach to the Late Miocene-Early Pliocene forms of the genus *Apocricetus*. *Apocricetus alberti* (Rodentia, Mammalia) from Venta del Moro (Cabriel Basin, Spain)

Samuel Mansino [a,*], Francisco Javier Ruiz-Sánchez [a,b,c], Matthijs Freudenthal [d,e], Plinio Montoya [a]

[a] *Department of Geology, University of Valencia, Dr. Moliner s/n, 46100 Burjassot, Valencia, Spain*
[b] *Valencian Museum of Natural History, L'Hort de Feliu, P.O. Box 8460, Alginet, 46018, Valencia, Spain*
[c] *INCYT-UPSE, Universidad Estatal Península de Santa Elena, 7047, Santa Elena, Ecuador*
[d] *Departamento de Estratigrafía y Paleontología, University of Granada, 18071 Granada, Spain*
[e] *Netherlands Centre for Biodiversity, Naturalis, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands*

ARTICLE INFO

Article history:
Received 29 April 2014
Received in revised form 2 July 2014
Accepted 11 July 2014
Available online 30 July 2014

Keywords:
Apocricetus
Late Miocene
Spain
Venta del Moro
Shape m3

ABSTRACT

The species of the genus *Apocricetus* are considered to form the phyletic lineage *A.* aff. *plinii* (MN11)–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens* (MN16). Along this lineage, gradual morphological and biometrical changes occur, but not all the species are represented by rich populations. The assemblage of *Apocricetus alberti* from Venta del Moro is by far the most abundant collection of this species. This population shows a great morphological variability in some characters like the morphology of the anteroconid and the anterolophulids in m1 and the shape of the anterolophule in M1, with morphotypes that resemble both older and younger populations of *Apocricetus*. Along the phyletic lineage of *Apocricetus*, a change in the shape of m3 occurs, from predominantly subtriangular forms in the oldest populations to predominantly subrectangular in the youngest. To quantify this feature we use the posterior width of the molar and the anterior width/posterior width ratio, proposing five morphological categories, from extremely triangular to subrectangular.

1. Introduction

The genus *Apocricetus* Freudenthal et al., 1998 comprises "medium to large-sized Cricetinae, practically without mesolophids in m1 and m2, with long third molars; in the younger forms the anterior protolophules and posterior metalophules in the upper molars are reduced or absent" (Freudenthal et al., 1998). The temporal range of the genus is Late Miocene (Crevillente 15, Early Turolian, MN11)–Late Pliocene (Lo Fournas 13, Early Villanyian, MN16) (Bachelet et al., 1990; Freudenthal et al., 1998). The genus was erected after *Neocricetodon* and *Cricetulodon* were separated as different genera, because adding the species characterized by the loss of the mesolophids in m1 and m2 and labial or double anterolophulids in m1 to any one of them made impossible to give differential diagnoses (Freudenthal et al., 1998). The genus *Apocricetus* comprises: *Apocricetus angustidens* (Depéret, 1890) (type species), *Apocricetus barrierei* (Mein and Michaux, 1970), *Apocricetus plinii* (Freudenthal, Lacomba and Martín-Suárez, 1991) and *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998. In the localities Crevillente 23 (Crevillente Basin, Spain), Masada del Valle 2, Concud Barranco and Los Mansuetos (Teruel Basin, Spain), Freudenthal et al. (1998) noted the presence of an unnamed species (or a possible mixture of two species) that they named *Apocricetus* aff. *plinii* and which, according to these authors, may be the ancestor of *A. plinii*. The species of *Apocricetus* constitute a phylogenetic lineage (*Apocricetus* aff. *plinii*–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens*), where the first representative is *Apocricetus* aff. *plinii* from MN11 and the last one is *A. angustidens* from MN16 (Freudenthal et al., 1998).

The representatives of the genus *Apocricetus* are key to understanding the biostratigraphic framework in the time span between Late Miocene (Late Turolian) and Late Pliocene in Southern Europe (Freudenthal et al., 1998; García-Alix et al., 2008a; Minwer-Barakat et al., 2012). So, a reliable taxonomic identification of the species integrating this genus is necessary for

---

* Corresponding author. Tel.: +0034660211526.
E-mail addresses: samuel.mansino@uv.es, samuelmp83@hotmail.com (S. Mansino).

http://dx.doi.org/10.1016/j.pgeola.2014.07.002

dating and correlating continental fossil sites correctly. However, some species of this genus are not well known because they are represented by small samples (Ruiz-Sánchez et al., 2014). This is the case of *A. barrierei*, described on the basis of three specimens from the locality of Chabrier (Mein and Michaux, 1970). The revision of the fossil remains from La Bullana-2B and La Bullana-3 (Ruiz-Sánchez et al., 2014), by far the richest samples of this species with a hundred specimens recovered, allowed a more precise diagnosis on the basis of morphology. The material of *A. alberti* is not as scarce as that of *A. barrierei*: CR-6, type locality of the species (Freudenthal et al., 1998) has yielded 55 measurable teeth, and more material has been extracted from other Late Miocene localities such as Venta del Moro, Librilla, Purcal 23, 24 and 25 (Freudenthal et al., 1998), Purcal 3 (García-Alix et al., 2008b) and Negratín (Minwer-Barakat et al., 2009). In this paper we study the remains of *Apocricetus alberti* from the locality of Venta del Moro (levels VM-A, AB, B, BC, C, and D sensu Montoya et al., 2006; here denoted as VVmA-, VVmAB-, VVmB-, VVmBC-, VVmC- and VVmD-), situated in lacustrine and palustrine sediments of the Cabriel Basin in Eastern Spain (Robles, 1970; Montoya et al., 2006) (Fig. 1). These remains constitute the richest collection of this species described to date. Some data about

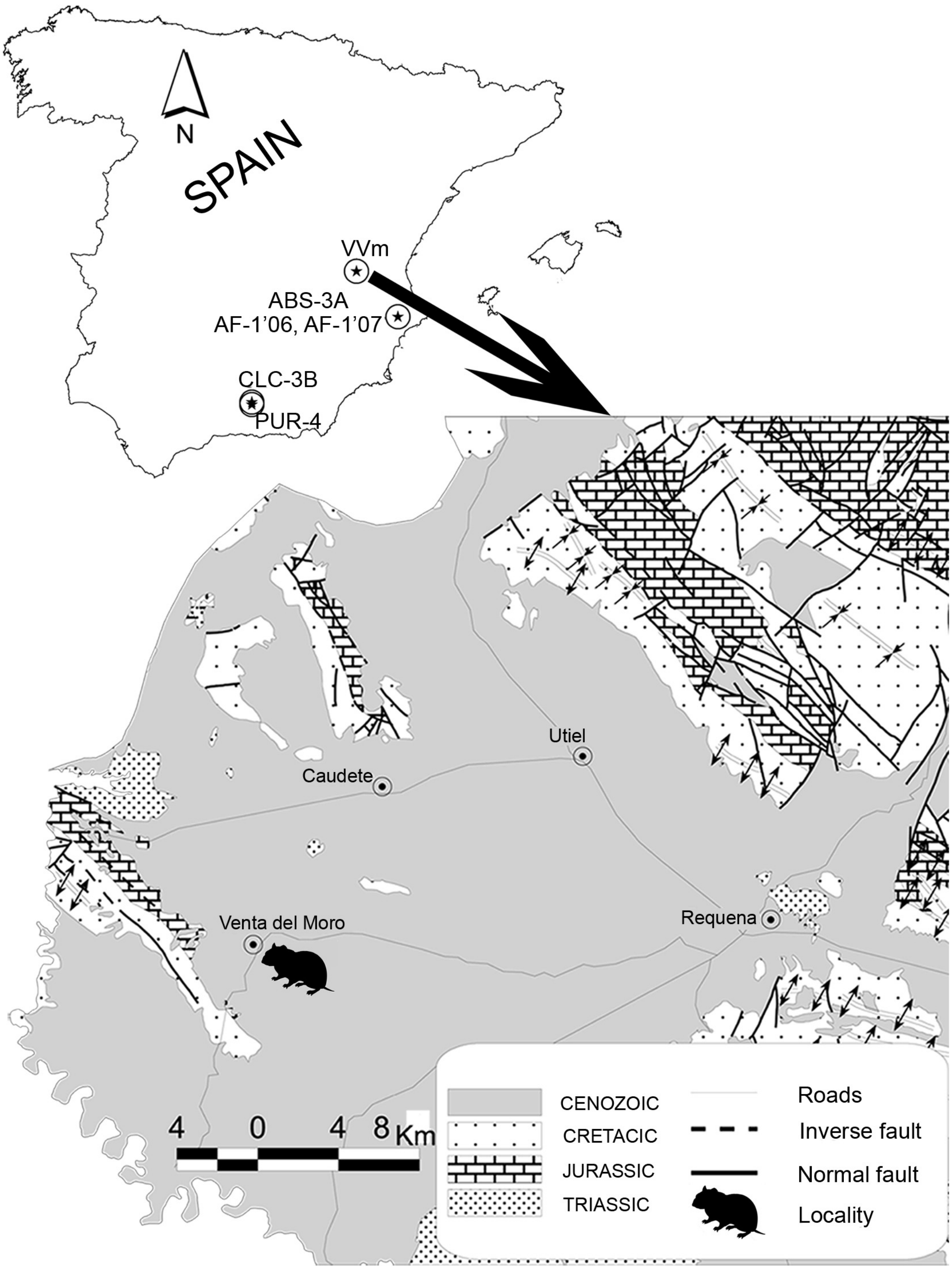


Fig. 1. Geological map of the continental sediments in the Venta del Moro-La Bullana area (Cabriel Basin), with the location of the locality Venta del Moro (VVm) (Modified after Ruiz-Sánchez et al., 2014). *Abbreviations*: ABS, Alcoi Barranc Sud; AF, Alcoi Forn; CLC, Calicasas; VVm, Venta del Moro.

Apocricetus from Venta del Moro were already reported in Ruiz-Sánchez et al. (2014). These data correspond to a small sample from this locality, kept at the University of Granada. Specimens described in this paper belong to an unpublished, larger collection from Venta del Moro.

The new data from Venta del Moro allow a better characterization of the species *A. alberti* and a good knowledge of the evolution of the phylogenetic lineage *Apocricetus* aff. *plinii*–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens.*

2. Material, methods and abbreviations

The new fossils from Venta del Moro are kept in the Museum of Geology of the University of Valencia (MGUV) with the field labels VVmA-, VVmAc-, VVmAB-, VVmB-, VVmBC-, VVmC- and VVmD-. The material of *A.* aff. *plinii* from CR-5A and CR-15 and *A. plinii* from CR-20 and CR-23 is housed at Naturalis Biodiversity Center, Leiden. The material of *A. alberti* from PUR-25A, PUR-25, Librilla and five m3 from Venta del Moro, *A. barrierei* from Caravaca, Chabrier, PUR-4, YEG and Gorafe 4, casts of *A. angustidens* from Soler and Villeneuve, an m3 from Mont-Hélène, and two specimens with the label Gorafe 4/5, which may be from Gorafe 4 or 5, but were ascribed by the authors to *A. angustidens*, are housed at the University of Granada.

The nomenclature used in the descriptions of the teeth and the measurement method are those of Freudenthal et al. (1994). The terms "preloph" and "prelophid" are taken from Freudenthal (1985); a prelophid is a transversal crest, halfway between the anteroconid and the first pair of main cusps, on which the anterolophulids, the protoconid and the protolophulid insert. The preloph is a similar structure in the upper molars, a transversal crest on which the anterolophules insert. The nomenclature of the m1 and M1 of *Apocricetus* is shown in Fig. 2.

The lower teeth are indicated as m1, m2 and m3, and the upper teeth as M1, M2 and M3. Measurements are in millimeters and were taken on a Leica MZ75 binocular microscope. Fig. 9 was made

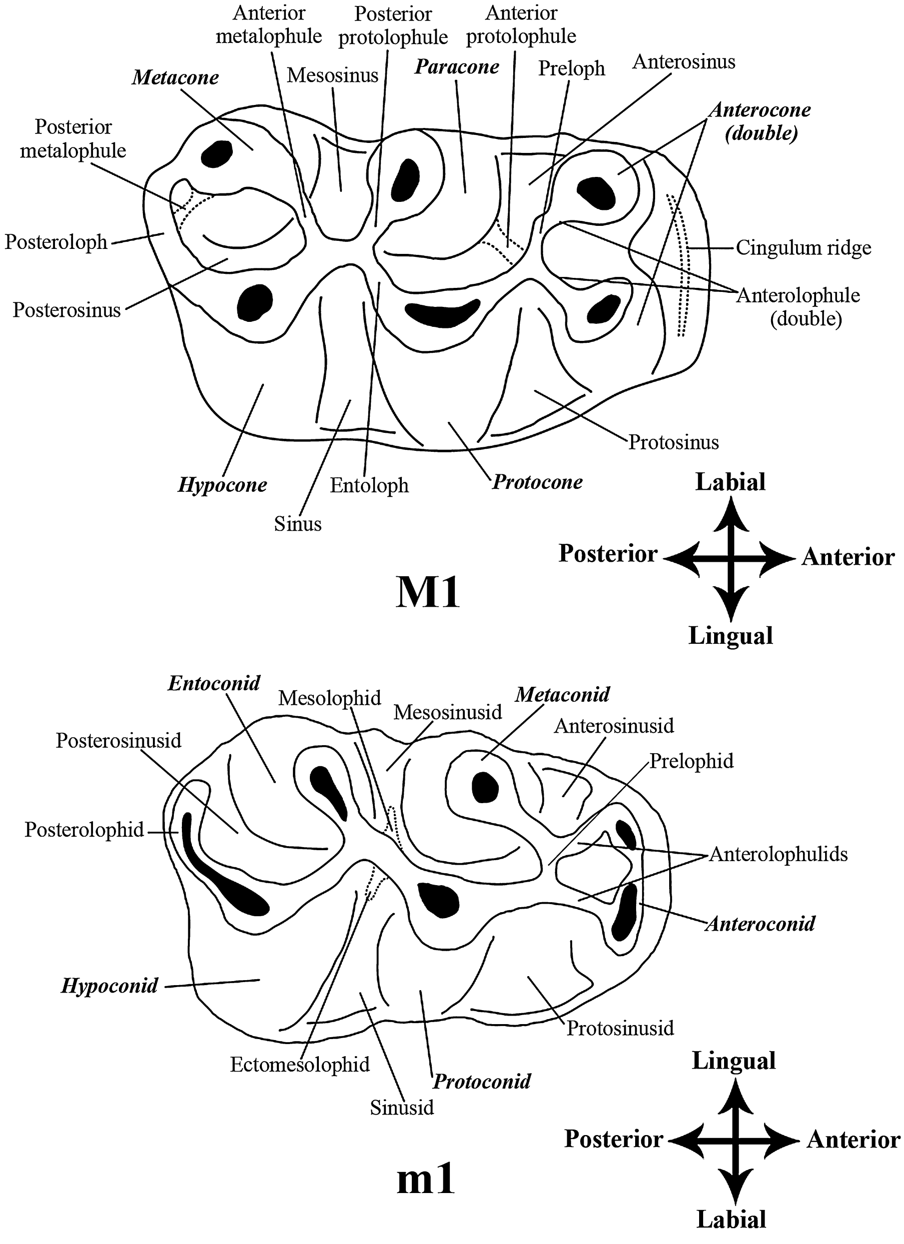


Fig. 2. Nomenclature of the m1 and M1 of *Apocricetus*.

with the program PAST, version 2.17. The box plot was performed assuming 95.0% intervals of the standard deviation and rounding as the quartile method.

2.1. Abbreviations

CR-: Crevillente; L: length; LB-: La Bullana; MN: European Neogene Land Mammal Units; PUR-: Purcal; VVm-: Venta del Moro (collection of micromammals housed at the University of Valencia); W: width; YEG: Yeguas; W_ant: anterior width; W_post: posterior width.

3. Geological setting

The Cabriel Basin, in the East of the Iberian Peninsula, is a mid-sized Neogene basin located between the Iberian platform to the north and the Betic Cordillera to the south. The Cenozoic limestones with detrital sediments of the Cabriel Basin (Fig. 1) contain several mammal sites ranging from Late Aragonian to Villanyian (MN7/8 to MN17) (see references in Ruiz-Sánchez et al., 2011). In the locality of Venta del Moro are represented at least two cycles of carbonated lacustrine facies which intercalate paleosoils and lignitiferous clays. These facies are covered in a discordant way by several meters thick layers of sands and canaliform conglomerates intercalated with floodplain clays (Mathisen and Morales, 1981; Gibert et al., 2013). In the last of these lacustrine cycles are found the rich fossil-bearing levels studied in this paper (Venta del Moro A, AB, B, BC, C and D, sensu Montoya et al., 2006).

4. Systematic paleontology

Order: Rodentia Bowdich, 1821

Family: Cricetidae Fischer, 1817

Genus: *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998

Type species: *Cricetus angustidens* Depéret, 1890

Other Species: *Cricetus barrierei* Mein and Michaux, 1970; *Neocricetodon plinii* Freudenthal, Lacomba and Martín-Suárez, 1991; *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998.

Apocricetus alberti Freudenthal, Mein and Martín-Suárez, 1998 (Fig. 2)

Holotype: CR6 111, Instituut voor Aardwetenschappen, Utrecht.

Type locality: CR-6, Upper Miocene, Spain

Original diagnosis (Freudenthal et al., 1998)

Apocricetus with moderately elongated third molars and a simple crest-like anteroconid in m1. Anterior protolophule of M1 frequently absent (3 out of 7 specimens), in M2 nearly always present. M3 without mesoloph. Generally the M1 are banana-shaped, with sinuous borderlines, due to the protruding cusps and indenting valleys.

Emended diagnosis

Apocricetus similar in size to *A. plinii* and smaller than *A. barrierei* and *A. angustidens*. Anteroconid of m1 superficially divided or crest-like. Absent anterosinusid in m2 and m3. Mesolophid seldom present in m2 and generally present in m3. Shape of m3 similar to *A. plinii*, less triangular than *A.* aff. *plinii* and less subrectangular than *A. barrierei* and *A. angustidens*. The ectomesolophid is absent in all the lower molars. Anterior protolophule present in approximately half of the M1, and all M2 and M3. The mesoloph is absent in the upper molars.

Differential diagnosis

A. alberti is larger than *A.* aff. *plinii*, similar in size to *A. plinii*, on average smaller than *A. barrierei*, although the maximum lengths and widths of *A. alberti* can overlap the minimum values of *A. barrierei*, and clearly smaller than *A. angustidens* (Figs. 3 and 4).

A. alberti differs from *A.* aff. *plinii* and *A. plinii* in the shape of the anteroconid, crest-like in some specimens and with a less conspicuous constriction when it is bilobed. It differs from *A. barrierei* and *A. angustidens* by the more conspicuous lobes of the anteroconid, which is crest-like or with a very weak subdivision in these species.

A. alberti differs from *A. plinii*, *A. barrierei* and *A. angustidens* by the presence of a mesolophid in approximately one third of m2. It also differs from *A. plinii* in the complete absence of an ectomesolophid in m2.

A. alberti differs from *A.* aff. *plinii* by the wider posterior side of its m3. It differs from *A. barrierei* and *A. angustidens* by its narrower posterior side of its m3 and from *A. barrierei* also by its less enlarged m3.

A. alberti differs from *A.* aff. *plinii* and *A. plinii* by the presence of a weak cingulum ridge in some M1 (13.5% in the material from Venta del Moro) and from *A. angustidens* by the lesser development and lesser frequency of this cingulum.

It differs from *A.* aff. *plinii* and *A. plinii* by the presence of a preloph in some specimens, which is less developed than in *A. barrierei*. It differs from *A. angustidens* and *A. barrierei* by the presence of a simple anterolophule.

A. alberti differs from *A. barrierei* and *A. angustidens* in the frequency of the anterior protolophule of the M1: this crest is present in 58.5% of the specimens from Venta del Moro, 28.6% of *A. barrierei* from LB-2B and 13.3% of *A. angustidens* from Mont-Hélène. *A. alberti* also differs from the other species of the genus in the frequency of the posterior metalophule in M1. This crest is present in 45.5% M1 of *A.* aff. *plinii* from CR-23, 23.1% of *A. plinii* from CR-15, 17.1% of specimens from Venta del Moro, being absent in *A. barrierei* and *A. angustidens*.

A. alberti differs from *A. barrierei* and *A. angustidens* in the frequency of the anterior protolophule in M2 (this ridge is present in 80.0% of the specimens of *A. barrierei* from LB-2B and 23.1% in *A. angustidens* from Mont-Hélène). The frequency of the posterior metalophule in M2 is similar in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and therefore this character only allows a clear distinction between these species and *A. barrierei* and *A. angustidens*. This ridge is complete in 51.7% M2 of *A.* aff. *plinii* from CR-23, 50.0% of *A. plinii* from CR-15, 47.6% of *A. alberti* from Venta del Moro and 35.3% of *A. barrierei* from LB-2B, being absent in *A. angustidens*.

A. alberti differs from *A. barrierei* and *A. angustidens* in the development of the anterior protolophule in M3. This crest appears in 100% of the specimens of *A. alberti*, 25 to 100% in the samples of *A. barrierei* (Ruiz-Sánchez et al., 2014) and 33% of the M3 of *A. angustidens* from Mont-Hélène.

Localities

VVmA, VVmAc, VVmAB, VVmB, VVmBC, VVmC, and VVmD.

Referred specimens

47 m1 (VVmA-147 to VVmA-161; VVmA-163 to VVmA-172; VVmA-191 to VVmA-193; VVmAB-1, VVmAB-9, VVmA-10; VVmB-74 to VVmB-76, VVmB-523; VVmBC-7, VVmBC-15, VVmBC-18, VVmBC-20, VVmBC-25, VVmBC-30; VVmC-29 to VVmC-33; VVmAc-13), **71 m2** (VVmA-45 to VVmA-55; VVmA-173 to VVmA-190; VVmA-194, VVmA-195; VVmAB-2; VVmAB-3;

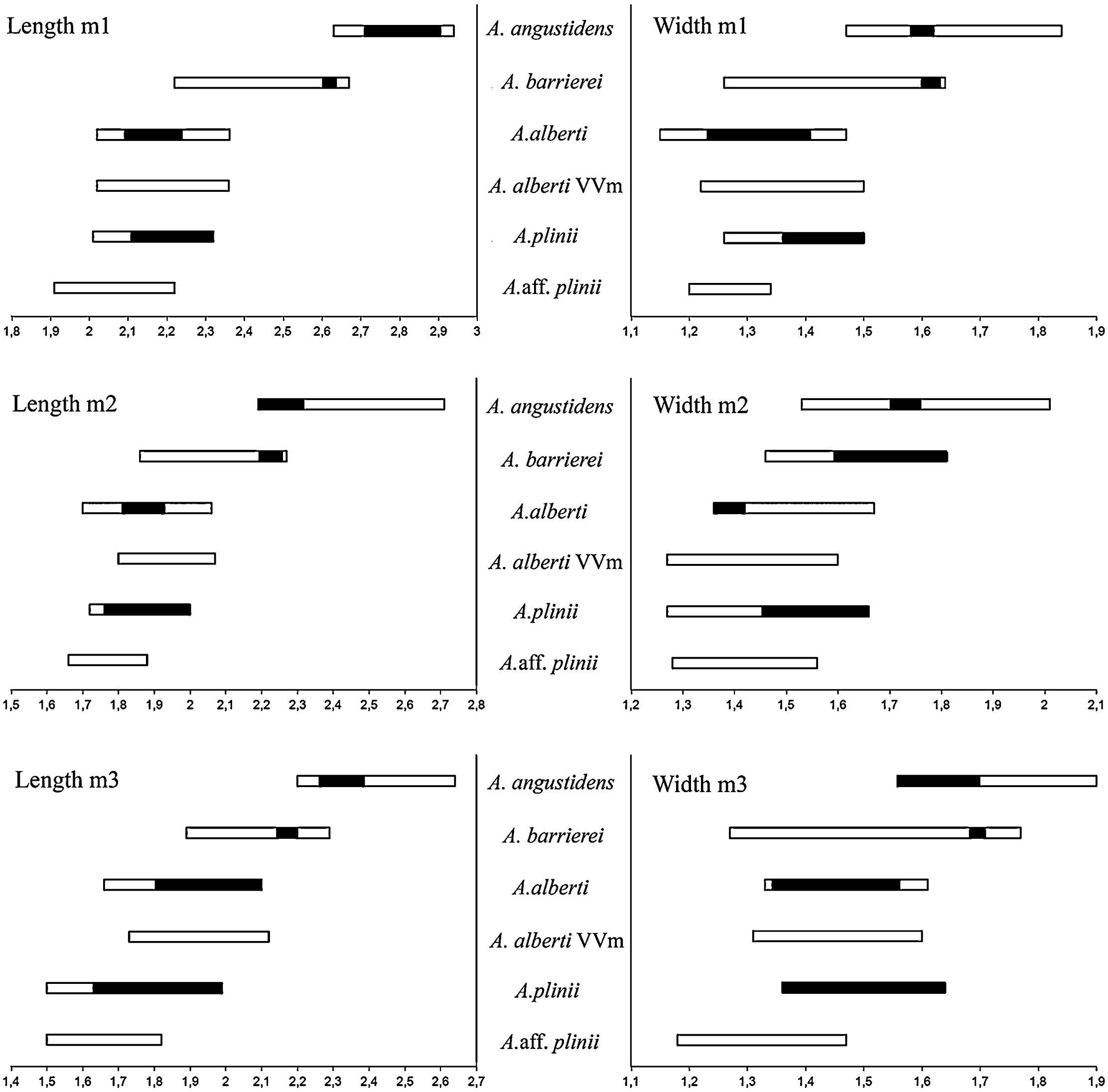


Fig. 3. Ranges of variation of length and width of the lower molars of *A.* aff. *plinii* from Crevillente 20 and Crevillente 23 (Freudenthal et al., 1998), *A. plinii* from Crevillente 15 (type locality), Crevillente 5A, Crevillente 14 and Valdecebro 3 (Weerd, 1976; Freudenthal et al., 1991; Adrover et al., 1993), *A. alberti* from Crevillente 6 (type locality), Negratín, Librilla 1, Librilla 2A, Librilla 2C, Purcal 23, Purcal 24A, Purcal 25, Venta del Moro, La Gloria 5 (Freudenthal et al., 1998; García-Alix et al., 2008a,b; Minwer-Barakat et al., 2009), *A. barrierei* from Chabrier (type locality), Alcoy, Alcoy 4B, Botardo, La Gloria 4, Gorafe 4, Fuente del Viso, Yeguas, Caravaca, Purcal 4, Loma del Castillo 1, La Tour, La Bullana 2B and La Bullana 3 (Opdyke et al., 1997; Freudenthal et al., 1998; García-Alix et al., 2008a,b; Ruiz-Sánchez et al., 2014), *A. angustidens* from Serrat d'en Vacquer (type locality), Mont-Hélène, Sète, Le Soler, Villeneuve de la Raho, Portla-Nouvelle, Gorafe 3 and Gorafe 5 (Freudenthal et al., 1998) and *A. alberti* from Venta del Moro (VVm, this paper). The dark boxes represent the range at the type locality.

VVmAB-6; VVmAB-8; VVmB-2 to VVmB-15; VVmBC-17; VVmBC-19; VVmBC-21; VVmBC-26 to VVmBC-28; VVmBC-31; VVmC-2 to VVmC-5; VVmC-19; VVmC-21; VVmC-28; VVmC-34, VVmC-35; VVmD-9; VVmD-11; VVmD-14; VVmD-15; VVmAc-2; VVmAc-3), **53 m3** (VVmA-56 to VVmA-73; VVmA-196, VVmA-197; VVmAB-4, VVmAB-5, VVmAB-11; VVmB-16 to VVmB-21; VVmB-23 to VVmB-30; VVmB-71, VVmB-77, VVmB-524; VVmBC-6; VVmBC-16; VVmBC-29; VVmC-36 to VVmC-39; VVmD-3; VVmD-4; VVmAc-4 to VVmAc-7; VVmAc-12), **50 M1** (VVmA-74 to VVmA-100; VVmA-162, VVmA-198; VVmB-31 to VVmB-42; VVmB-525; VVmBC-8 to VVmBC-10; VVmBC-32, VVmBC-33; VVmC-7; VVmC-10; VVmAc-1), **50 M2** (VVmA-101 to VVmA-121; VVmA-199 to VVmA-201; VVmAB-12; VVmB-43 to VVmB-58; VVmBC-11; VVmBC-14; VVmC-9; VVmC-40, VVmC-41; VVmD-5; VVmD-6; VVmAc-8; VVmAc-9), **63 M3** (VVmA-70; VVmA-122 to VVmA-146; VVmA-202 to VVmA-205; VVmB-22; VVmB-59 to VVmB-73; VVmB-78; VVmBC-12; VVmBC-13; VVmC-8; VVmC-12 to VVmC-15; VVmC-42 to VVmC-44; VVmD-7; VVmD-8; VVmD-10; VVmAc-10; VVmAc-11; VVmAc-14; VVmAc-18).

Measurements

See Table 1.

Description

m1: Crest-like anteroconid in 16 out of 34 specimens, with a slight subdivision in 17 out of 34 (Figs. 5A and 5C) and trifid in 1. The anterolophulids arise from a prelophid in 18 out of 39 specimens (Fig. 5C), they are parallel without prelophid in 7 cases (Fig. 5B), forked with a branch to each one of the anteroconid in 7 (Fig. 5A), and simple in 7 (central: 2, lingually-displaced: 2 or labially-displaced: 3). Metalophulid strongly directed forwards. Mesolophid absent. Two roots.

m2: Anterosinusid absent. Metalophulid short and strongly directed forwards, forming the anterior part of the tooth. Labial anterolophulid reaching the base of the protoconid, enclosing a deep protosinusid. In one specimen this crest continues backwards bordering the protoconid. The mesosinusid and sinusid are closed by a cingulum ridge. Mesolophid absent in 39 out of 64 specimens

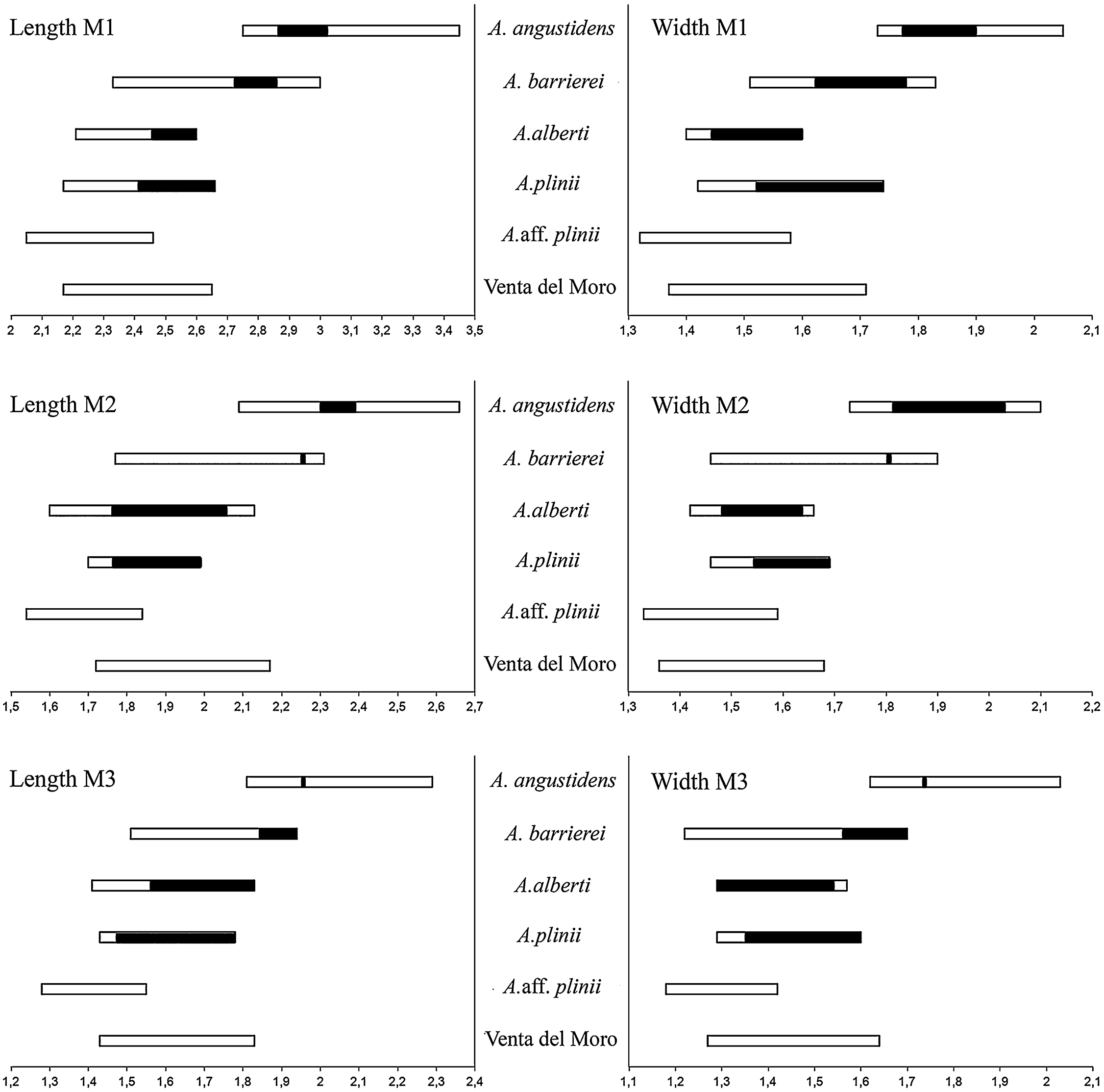


Fig. 4. Ranges of variation of length and width of the upper molars of *A.* aff. *plinii* from Crevillente 20 and Crevillente 23 (Freudenthal et al., 1998), *A. plinii* from Crevillente 15 (type locality), Crevillente 5A, Crevillente 14 and Valdecebro 3 (Weerd, 1976; Freudenthal et al., 1991; Adrover et al., 1993), *A. alberti* from Crevillente 6 (type locality), Negratín, Librilla 1, Librilla 2A, Librilla 2C, Purcal 23, Purcal 24A, Purcal 25, Venta del Moro (Freudenthal et al., 1998; García-Alix et al., 2008a,b; Minwer-Barakat et al., 2009) and La Gloria 5 (Freudenthal et al., 1998), *A. barrierei* from Chabrier (type locality), Alcoy 1, Alcoy 4B, Botardo, La Gloria 4, Gorafe 4, Fuente del Viso, Yeguas, Caravaca, Purcal 4, Loma del Castillo 1, La Tour, La Bullana 2B and La Bullana 3 (Opdyke et al., 1997; Freudenthal et al., 1998; García-Alix et al., 2008a,b; this paper), *A. angustidens* from Serrat d'en Vacquer (type locality), Mont-Hélène, Sète, Le Soler, Villeneuve de la Raho, Portla-Nouvelle, Gorafe 3 and Gorafe 5 (Freudenthal et al., 1998) and *A. alberti* from Venta del Moro (VVm, this paper). The dark boxes represent the range from the type locality.

(Fig. 5F), a trace of a mesolophid is present in 20 (Fig. 5D) and a short one in 5 (Fig. 5E). Posterolophid very low, connected basally with the posterolingual side of the entoconid, enclosing an L-shaped posterosinusid. Two roots.

m3: Shape subrectangular (1 out of 42 specimens, 2.38%), slightly triangular (34 specimens, 80.95%), moderately triangular (5 specimens, 11.9%, Figs. 5G and 5H) or very triangular (2 teeth, 4.76%, Fig. 5I. See Section 5.2.2). Anterosinusid absent. Metalophulid short and strongly directed forwards. The labial anterolophulid reaches the base of the protoconid. In two specimens this crest continues backwards bordering the protoconid. The mesosinusid and sinusid are closed by a cingulum ridge. The mesolophid is absent in 10 out of 47 molars, there is a trace of a crest in 21 (Fig. 5G), a short crest in 8 (Fig. 5I) and a long one in 8 (Fig. 5H). In one of the latter specimens the mesolophid connects basally with the entoconid, but continues towards the cingulum ridge of the mesosinusid. There are two roots.

M1: Cingulum ridge on the base of the anterocone absent (32 specimens) or weak (5). The anterolophule may be simple (2) (Fig. 5J), simple with a free labial spur not reaching the anterocone (1), forked (23) (Fig. 5L) or double and arising from a hint of preloph (10) or from a very short preloph (4) (Fig. 5K). The anterior protolophule is absent in 17 out of 41 specimens (Fig. 5L); it is a spur in 3 (Fig. 5J), a low crest in 8, and a well-developed crest in 13 (Fig. 5K). Mesoloph and ectomesoloph absent. The anterior metalophule is always present. The posterior metalophule is present in 7 out of 41 molars (Fig. 5K). In 11 specimens the posteroloph is curved and elongated, separated from the metacone by the transversal posterior part of the L-shaped posterosinus (Fig. 5J). In other 11 molars the transversal posterior side of the posterosinus is shorter (Fig. 5L), but the metaconid is still separated from the posterior wall. In 19 specimens, the posterior part of the metacone forms the posterior part of the tooth, while in 22 the posterior part is formed by the posteroloph. Four roots.

M2: The lingual anteroloph is very small in 3 specimens, enclosing a reduced and shallow protosinus, and of medium length or long in the rest, enclosing a protosinus that is highly variable in size and depth. The protocone is not separated from the lingual

Table 1
Measurements (in millimeters) of the teeth of *A. alberti* from Venta del Moro, according to the notation of the fossiliferous levels sensu Montoya et al. (2006) (Venta del Moro A: VVmA; Venta del Moro AB: VVmAB; Venta del Moro B: VVmB; Venta del Moro BC: VVmBC; Venta del Moro C: VVmC; Venta del Moro D: VVmD; Venta del Moro Ac: VVmAc).

Element	Level	Length				Width			
		n	Min.	Mean	Max.	*n*	Min.	Mean	Max.
m1	VVmA	21	2.02	2.20	2.36	22	1.22	1.33	1.50
	VVmAB	2	2.20	2.21	2.21	2	1.32	1.38	1.43
	VVmB	2	2.16	2.19	2.21	2	1.29	1.31	1.33
	VVmC	2	2.00	2.13	2.26	4	1.26	1.30	1.36
	VVmBC					2	1.30	1.31	1.31
	VVmAc					1	–	1.46	–
m2	VVmA	27	1.80	1.94	2.07	29	1.27	1.46	1.60
	VVmAB	2	1.80	1.85	1.90	3	1.36	1.41	1.45
	VVmB	10	1.83	1.92	2.05	11	1.31	1.48	1.59
	VVmBC	2	1.81	1.88	1.95	5	1.39	1.46	1.54
	VVmC	4	1.80	1.98	2.15	6	1.37	1.61	1.54
	VVmD	2	1.81	1.84	1.87	3	1.34	1.39	1.44
	VVmAc	2	1.90	1.92	1.94	2	1.39	1.47	1.54
m3	VVmA	16	1.78	1.92	2.07	16	1.34	1.46	1.57
	VVmAB	3	1.74	1.83	2.00	2	1.34	1.39	1.45
	VVmB	13	1.79	1.95	2.12	14	1.32	1.47	1.59
	VVmBC	2	1.85	1.93	2.00	2	1.38	1.49	1.59
	VVmC	3	1.88	1.92	1.94	4	1.41	1.44	1.49
	VVmD	2	1.73	1.92	2.10	2	1.29	1.44	1.58
	VVmAc	3	1.80	1.88	1.99	5	1.45	1.51	1.60
M1	VVmA	21	2.17	2.41	2.65	24	1.37	1.51	1.71
	VVmB	7	2.18	2.33	2.46	9	1.38	1.49	1.56
	VVmBC	2	1.97	2.1.	2.27	4	1.44	1.48	1.54
	VVmC	1	–	2.38	–	2	1.50	1.53	1.55
M2	VVmA	20	1.79	1.91	2.17	21	1.42	1.54	1.68
	VVmB	11	1.72	1.90	1.97	13	1.36	1.52	1.64
	VVmBC	1	–	1.99	–	1	–	1.56	–
	VVmC	2	1.86	1.93	1.99	3	1.50	1.54	1.58
	VVmAc	2	1.73	1.92	2.10	2	1.43	1.53	1.63
M3	VVmA	25	1.43	1.65	1.83	23	1.26	1.38	1.47
	VVmB	12	1.49	1.64	1.79	13	1.33	1.40	1.53
	VVmBC	2	1.44	1.61	1.78	2	1.35	1.42	1.48
	VVmC	6	1.54	1.63	1.74	7	1.34	1.44	1.64
	VVmD	1	–	1.60	–	3	1.37	1.44	1.56
	VVmAc	3	1.53	1.61	1.72	3	1.34	1.38	1.41

border. The labial anteroloph is long, enclosing the anterosinus. One specimen (Fig. 5N) has a short preloph, from which two very short anterolophules arise, reaching the anterolophs. Anterior protolophule well-developed. Mesoloph and ectomesoloph absent. The sinus and mesosinus are closed by a low cingulum ridge. The anterior branch of the metalophule is always present. This crest may be straight (17 specimens, Fig. 5N), slightly curved, with a hint of a spur (25 specimens, Fig. 5M, O and P), have a short spur (5 specimens) or even a long crest that connects basally with the border of the molar (1 specimen). In one specimen this branch is transversal instead of oblique, and contacts the metacone anterolingually, resembling a mesoloph. The posterior metalophule is complete (16) (Fig. 5P), reduced to a spur (4), or absent (22). The posteroloph is strongly curved and elongated, forming an L-shaped posterosinus with deep anterior and posterior parts in 29 out of 45 specimens (Figs. 5M and 5P), while the posterior part of the posterosinus is much more reduced in the rest (16) (Fig. 5O). Four roots.

M3: Lingual anteroloph well-developed in 17 out of 60 specimens (Fig. 5R), reduced in 24 (Fig. 5S) and absent in 19 (Fig. 5Q). The protocone is not separated from the lingual border. The labial anteroloph is long and connected to the paracone. The anterior protolophule is high and complete (59) or low and interrupted (2). One specimen has two anterior protolophules (Fig. 5Q) and another one has a small enamel button attached to the labial side of the posterior protolophule. The posterolingual corner is rounded. The posterosinus is strongly reduced. In one specimen, the postero-lingual corner has the posteroloph displaced to the labial side, forming a strong sinus (Fig. 5S). Three roots.

5. Discussion

Traditionally, size has been the main criterion used to distinguish the species of the genus *Apocricetus* from the Late Miocene to the Early Pliocene (MN11 to MN15) comprising the lineage *Apocricetus* aff. *plinii*–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens* (Freudenthal et al., 1998). The lack of rich collections of some species of the genus prevented a proper morphological characterization (Ruiz-Sánchez et al., 2014). The study of the rich material of *Apocricetus* from some new localities such as LB-2B and LB-3 allows a more reliable differential diagnosis between the species of the genus (Ruiz-Sánchez et al., 2014), showing that, in fact, the quantification of these morphologies is the better way to distinguish them.

The new sampling carried out in the last two decades in the Late Miocene locality of Venta del Moro has allowed to recover one of the richest collections of the genus *Apocricetus*, representing also a great opportunity for improving the characterization and diagnosis of the species *A. alberti*, whose type locality is CR-6. *Apocricetus alberti* is restricted to the Late Turolian (Freudenthal et al., 1998; García-Alix et al., 2008b; Minwer-Barakat et al., 2012). This species represent an intermediate form between *A. plinii* (Early Turolian) and *A. barrierei* (Ruscinian). According to Freudenthal et al. (1998), *A. alberti* differs from *A. angustidens*

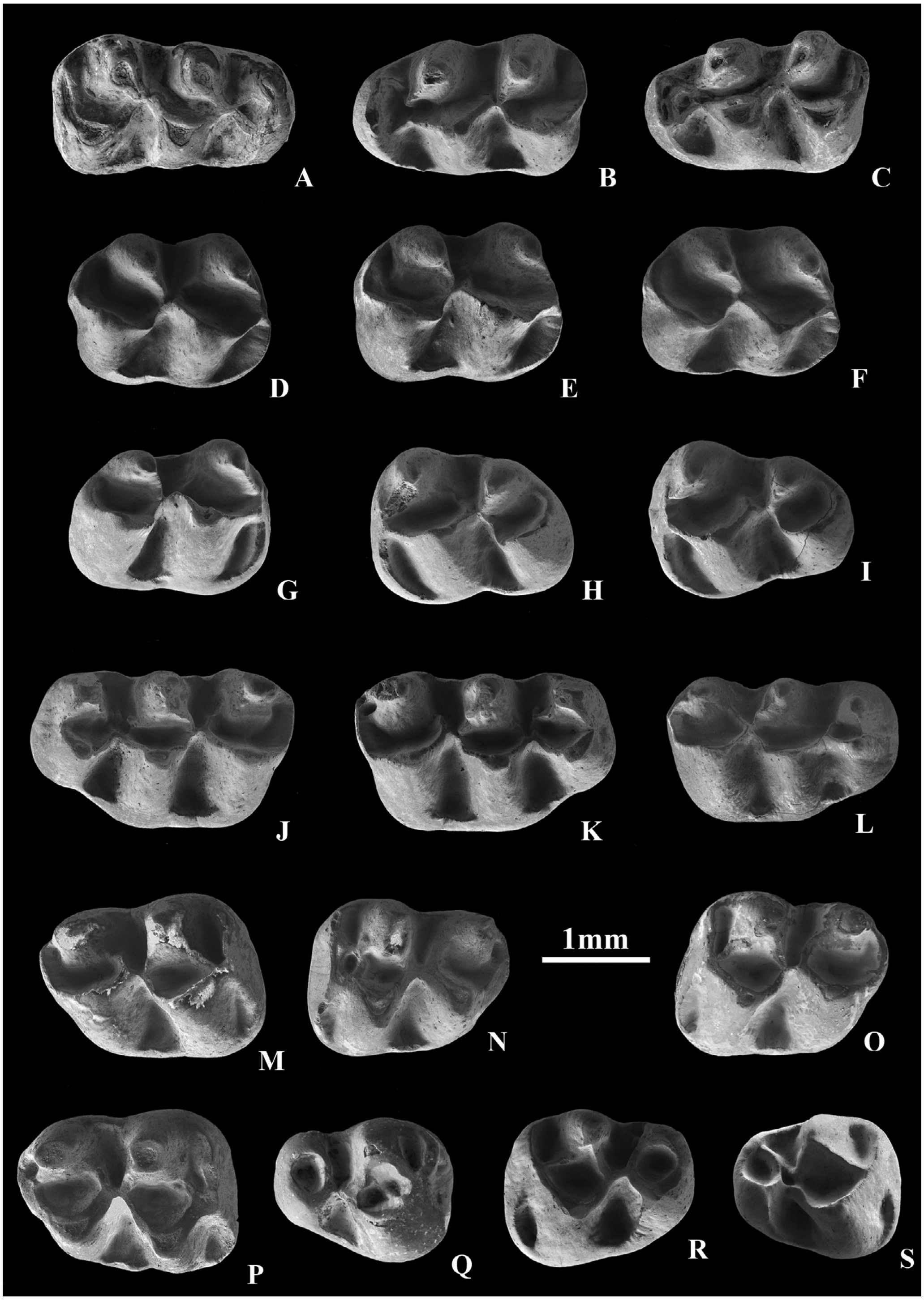


Fig. 5. *Apocricetus alberti* Freudenthal, Mein and Martín-Suárez, 1998 from Venta del Moro, Cabriel Basin. (A) right m1, VVmA-161; (B) left m1, VVmA-166; (C) left m1, VVmA-167; (D) right m2, VVmA-46; (E) right m2, VVmA-187; (F) right m2, VVmB-5; (G) right m3, VVmA-61; (H) left m3, VVmA-65; (I) left m3, VVmB-25; (J) left M1, VVmA-82; (K) right M1, VVmA-83; (L) right M1, VVmB-31; (M) right M2, VVmA-108; (N) left M2, VVmA-113; (O) left M2, VVmBC-11; (P) right M2, VVmAc-8; (Q) right M3, VVmA-122; (R) left M3, VVmA-125; (S) right M3, VVmA-137. Scale = 1 mm.

and *A. barrierei* by its smaller size and by the presence of an anterior protolophule in M2. It differs from *A. plinii* by its hardly-split anteroconid, more enlarged m3, forked anterolophule with two complete branches in M1, and the absence of a mesoloph, converted into the anterior metalophule. Nevertheless, some of these morphological criteria are not useful to distinguish among these species (Ruiz-Sánchez et al., 2014). For example, several populations of *A. barrierei* and *A. angustidens* show an anterior protolophule in M2. As we will explain below, gradual morphological and biometrical changes occurred in this lineage indeed, but they must be previously quantified in each species to know the specific range of variation that will serve to distinguish the different species of the genus.

5.1. Biometry

Apocricetus aff. *plinii*, from the Early Turolian of Spain, is the oldest and smallest form of *Apocricetus*. This taxon is slightly smaller than the Middle and Late Turolian representatives of the genus, *A. plinii* and *A. alberti*, which are similar in size (see Figs. 3 and 4). In the Early Ruscinian, *A. barrierei* shows a size increase with respect to the Turolian forms, which becomes more evident in the Late Ruscinian and Villanyan *A. angustidens* (Figs. 3 and 4).

Despite this tendency towards size increase through time in *Apocricetus*, the size range of any given species of the genus overlaps greatly with one or more of the precedent taxa, especially in the group *A.* aff. *plinii*-*A. plinii*-*A. alberti* (Figs. 3 and 4). The size range of the abundant sample from Venta del Moro is remarkably similar to other previously known populations of *A. alberti* (see Figs. 3 and 4). Because of the similar size of the populations of *Apocricetus* in the time span Early Turolian-Early Ruscinian and following Freudenthal et al. (1998) and Ruiz-Sánchez et al. (2014), we consider that this feature is not the best criterion to distinguish between the different forms of *Apocricetus*, with the exception of the youngest species of the genus, *A. angustidens* (Figs. 3 and 4).

5.2. Morphology

5.2.1. Lower molars

In general, the presence of a crest-like anteroconid and a complete prelophid in almost half of the m1 (47.1%), and the more rectangular shape in the m3 from Venta del Moro distinguish *A. alberti* from *A.* aff. *plinii*. These morphological features, along with the absence of ectomesolophids in the lower molars, distinguish this latter species from *A. plinii* from its type locality, CR-15.

On the other hand, the presence of simple (17.9%) or forked (with a branch to each one of the anteroconid cuspids) (17.9%) anterolophulids in m1, a small mesolophid in some m2 (39.1%), and a more triangular m3 in *A. alberti* from Venta del Moro distinguish this latter species from *A. barrierei* and *A. angustidens*.

Several characters in the lower molars of the *A.* aff. *plinii*–*A. angustidens* lineage seem to change from oldest to youngest populations. To summarize all these differences, Table 2 shows the variations of these characters in the lower molars of this phylogenetic lineage.

The morphology of the anterolophulids and the presence of a prelophid in m1 are clearly distinctive among the species of the genus *Apocricetus*. In the oldest populations the anterolophulid is simple or double in *A.* aff. *plinii* from CR-23, and simple or forked in *A. plinii* from CR-15. However, in the youngest populations, *A. barrierei* and *A. angustidens*, the anterolophulids usually arise from a prelophid (Freudenthal et al., 1998; Ruiz-Sánchez et al., 2014). In *A. alberti* from Venta del Moro, all these morphologies are present, being the most common the one with an anterolophulid arising from a prelophid (Table 2). In the specimens studied in this paper the anterolophulid may be simple (7 out of 39 specimens, 17.9%), forked, with a branch to each one of the anteroconid cuspids (7 specimens, 17.9%), double, arising from a prelophid (18 teeth, 46.2%) or double and parallel (7 molars, 17.9%). In the scarce material from Venta del Moro studied by Freudenthal et al. (1998), the anterolophulids are parallel, and in CR-6 they may be simple or parallel. In *A.* aff. *plinii* from CR-23, the anterolophulid may be double (2 out of 9 specimens, 22.2%), or simple (7 out of 9 specimens, 77.8%), and in this latter case it may be central (2) or labial (5) (Freudenthal et al., 1998). In *A. plinii* from CR-15 the anterolophulids may be simple and connected to the labial part of the anteroconid (7 out of 17 specimens, 41.2%), or forked (10, 58.8%) (Freudenthal et al., 1991). On the contrary, in *A. barrierei* and *A. angustidens* the anterolophulids usually arise from a prelophid (Freudenthal et al., 1998; Ruiz-Sánchez et al., 2014). The anterosinusid is absent in the m2 and m3 of the new material of *A. alberti* from Venta del Moro and in *A. barrierei*, but present in some m2 of *A.* aff. *plinii* from CR-23. A reduced anterosinusid is present in 64.7% of the m2 (11 out of 17) and 44.5% of the m3 (8 out of 18) of *A. plinii* from CR-15 and in some m3 of *A. angustidens* from Serrat d'en Vacquer (Freudenthal et al., 1991, 1998).

In one m2 and two m3 of *A. alberti* from Venta del Moro the labial anterolophid continues bordering the protoconid instead of reaching the base of this cuspid. This morphology has been observed in 2 out of 18 m2 (11.1%) and 5 out of 19 m3 (26.3%) of *A. plinii* from CR-15 (Freudenthal et al., 1991). This character is not present in *A. barrierei* from LB-2B and LB-3, and has not been described in other populations of the genus.

A. alberti from Venta del Moro has a short mesolophid in 5 out of 64 m2 (7.8%), and a hint of a mesolophid is distinct in 20 (31.3%). Freudenthal et al. (1998) described an m2 of *A. alberti* with a short mesolophid in CR-6 and Venta del Moro, and another two specimens with a long mesolophid, reaching the border of the molar, in Venta del Moro and Librilla. However, these authors consider that these latter m2 may belong to another species, since

Table 2
Variation of several characters in the lower molars of *Apocricetus*. *Abbreviations*: Abs, absent; Car, Caravaca; CR-, Crevillente; LB-2B, La Bullana 2B; LB-3, La Bullana 3; MH, Mont-Hélène; Pr, present, VVm, Venta del Moro, collection housed at the University of Valencia. After Freudenthal et al. (1991, 1998), Ruiz-Sánchez et al. (2014) and this work.

Species	Locality	m1		m2	m3
		Anteroconid	Anterolophulid	Mesolophid	Mesolophid
A. aff. *plinii*	CR-23	2–3 lobes	Simple: 7/9 (77.8%) Double: 2/9 (22.2%)	Pr: 9/26 (34.6%)	Pr: 32/35 (91.4%)
A. plinii	CR-15	2 lobes	Simple: 7/17 (41.2%) Forked: 10/17 (58.8%)	Abs	Pr: 19/22 (86.4%)
A. alberti	CR-6	Crest (1) or 2 lobes	Simple or double	Pr: 1/?	Pr: 6/12 (50%)
A. alberti	VVm	2 lobes: 17/34 (50%) 3 lobes: 1/34 (2.9%) Crest-like: 16/34 (47.1%)	Simple: 7/39 (17.9%) Double: 7/39 (17.9%) Forked: 7/39 (17.9%) Prelophid: 18/39 (46.2%)	Pr: 25/64 (39.1%)	Pr: 37/47 (78.7%)
A. barrierei	Car	2 weak lobes: 2/3 (66.7%) Crest-like: 1/3 (33.3%)	Prelophid: 100%	Pr: 2/3 (66.7%)	Abs
A. barrierei	LB-2B	2 weak lobes: 2/12 (16.7%) Crest-like: 10/12 (83.3%) (83.3%)	Prelophid: 12/12 (100%)	Pr: 0/16 (0%)	Pr: 6/13 (46.2%)
A. barrierei	LB3	–	–	Pr: 0/2 (0%)	Pr: 0/3 (0%)
A. angustidens	MH	Crest like, 2 weak Lobes or trifid (1)	Prelophid: 100%	Pr: 0/34 (0%)	Pr: 14/30 (46.7%)

such long mesolophids have not been described in other populations of *A. alberti*. The mesolophid may be absent (17), short (3), of medium length (3), long (2), or reaching the molar border (1) in *A.* aff. *plinii* from CR-23. This crest is absent in *A. plinii*, *A. barrierei* and *A. angustidens*.

There is no ectomesolophid in the m2 of *A.* aff. *plinii*, *A. alberti*, *A. barrierei* and *A. angustidens*, but 10 out of 17 m2 of *A. plinii* from CR-15 have a weak crest, which is well developed in another specimen (Freudenthal et al., 1991).

The frequency of the mesolophid in m3 decreases from the oldest to the youngest populations of *Apocricetus* (see Table 2). In the material studied in this paper, the mesolophid is present in 37 out of 47 m3 (78.7%), being long in 8 specimens. In 9 out of 35 m3 of *A.* aff. *plinii* from CR-23 (25.7%) this crest is long, reaching in one of them the border of the molar, while in *A. plinii* from CR-15 it is short or of medium length. The mesolophid is very heterogeneous in the populations of *A. barrierei*. In LB-2B this crest reaches the metaconid, and the only m3 from Chabrier, type locality of this species, also shows this morphology. One specimen from La Gloria 4 (Adrover et al., 1993) has a long mesolophid, which is absent or short in Gorafe 4, short and reaching the base of the metaconid in Alcoy 4B, of medium length in Loma del Castillo 1, absent or present in Fuente del Viso and absent in Caravaca (Freudenthal et al., 1998). In *A. angustidens*, the mesolophid ranges from absent to long in the population from Serrat d'en Vacquer (type locality), and this crest is absent in 16, short in 4 and long, thin and low in 10 m3 from Mont-Hélène (Freudenthal et al., 1998).

5.2.2. Shape of the m3

The shape of m3 has been regarded as an important character to consider, since a change in the shape of this molar occurs in the lineage of *Apocricetus* (Freudenthal et al., 1998; Ruiz-Sánchez et al., 2014). Freudenthal et al. (1998) noted that in *A. angustidens* from Mont-Hélène, the m2 and m3 are very similar in size and shape, to the extent that it is very difficult to distinguish between them, while in the oldest forms of *Apocricetus*, like *A.* aff. *plinii* and *A. plinii*, the m3 has a posterior side clearly narrower than the anterior one, as other authors have also noted (Ruiz-Sánchez et al., 2014).

Following Ruiz-Sánchez et al. (2014, Fig. 6), Fig. 6 depicts the relative length of m2 with respect to m3 (L m2/L m3). Ratios of m2 to m3 lower than 1 indicate an elongated m3, longer than the m2, while ratios higher than 1 correspond to m2 longer than m3. This ratio decreases from *A.* aff. *plinii* from CR-23 to *A. plinii* from CR-15, *A. alberti* from Venta del Moro and *A. barrierei* from LB-2B. However, the m3 of the population of *A. alberti* from CR-6, its type locality, are even more elongated than those of *A. barrierei*. This may be because of the marked discrepancy between the number of m2 (4) and m3 (14) in this locality, with some m3 of great size. This is especially evident for the maximum L m2/maximum L m3, which is far below the value of *A. barrierei* (see Fig. 6). On the contrary, *A. angustidens* from Mont-Hélène has an L m2/L m3 ratio similar to that of *A. alberti* from Venta del Moro.

Although the latter calculated ratios may be a first attempt to estimate the shape of the m3, the data shown in Fig. 6 are not enough to estimate this feature correctly.

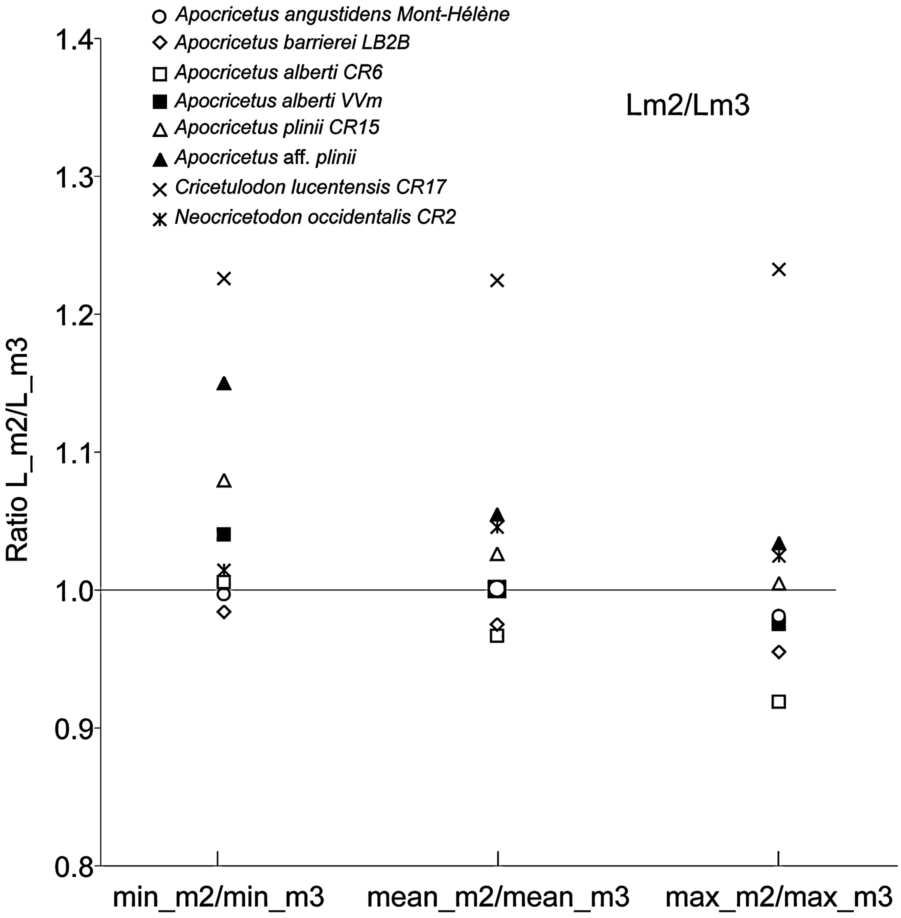


Fig. 6. Ranges of variation of the ratio Lm2/Lm3 of *Neocricetodon occidentalis* Aguilar, 1982 from Crevillente 2 (CR2), *Cricetulodon lucentensis* Freudenthal et al. (1991) from Crevillente 17 (CR17), *A.* aff. *plinii* from CR-20 and CR-23, *Apocricetus plinii* from Crevillente 15 (CR15), *A. alberti* from Crevillente 6 (CR6) and Venta del Moro (VVm), *A. barrierei* from La Bullana 2B (LB-2B), and *A. angustidens* from Mont-Hélène. The values of min_m2/min_m3 correspond to (min Lm2)/(min Lm3), mean_m2/mean_m3 to (mean Lm2)/(mean Lm3) and max_m2/max_m3 to (max Lm2)/(max Lm3). The values under 1.0 correspond to: length of m3 larger than length of m2, and above 1.0: length of m2 larger than length of m3 (Modified after Ruiz-Sánchez et al., 2014).

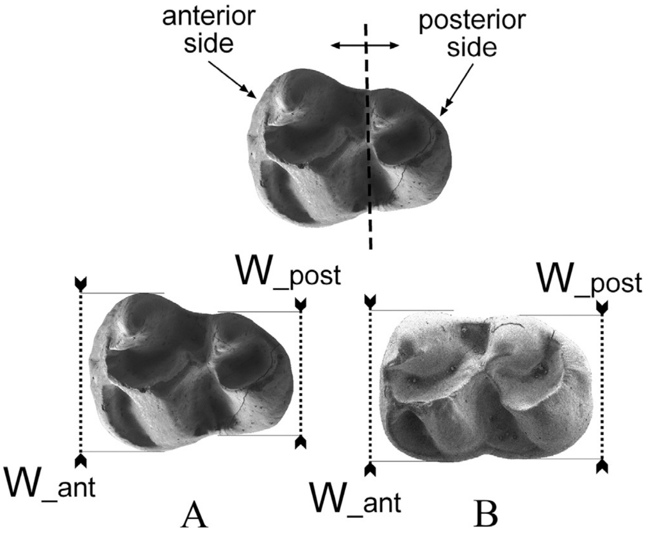


Fig. 7. Method for taking measurements of the anterior (W_ant) and posterior (W_post) width of the m3 of *Apocricetus*. (A) VVmA-65 (*A. alberti*) and (B) LB-2B-154 (*A. barrierei*).

In order to carry out a comparison between the shapes of the m3 of the different species of *Apocricetus*, we propose the use of the ratio W_ant/W_post. Following the measurement method proposed by Daams and Freudenthal (1988) for the cricetids, the anterior width (W_ant) corresponds to the maximum width of the tooth, while the posterior width (W_post), as seen in Fig. 7, is measured from the cingulum ridge closing the sinusid to the lingual side of the entoconid. We consider this ratio a better indicator of the shape of the m3, since higher values indicate a narrower posterior side and therefore a more triangular shape. The W_ant, W_post and the resultant ratios (W_ant/W_post) of the populations of *Apocricetus* measured in this work are summarized in Table 4. We have defined five categories of W_ant/W_post ratio, as shown in Table 3 and Fig. 8. Category 1 comprises the values ranging from 1.35 to 1.31: these molars are extremely triangular and only 3 specimens of *A.* aff. *plinii* fall within this range (Table 3, Fig. 8). Category 2 comprises the values from 1.30 to 1.26 (Fig. 8): these m3 are very triangular, and only some specimens of *A.* aff. *plinii* and two molars of *A. alberti* fall within this category. Category 3 comprises the values from 1.25 to 1.21: these molars are moderately triangular (Fig. 8), and correspond to some specimens of the Turolian species of the genus, *A.* aff. *plinii*, *A. plinii* and

Table 3

Percentage of specimens by categories defined for the W_ant/W_post ratio of m3. Category 1, range 1.35–1.31 (extremely triangular shape), category 2, range 1.30–1.26 (very triangular shape), category 3, range 1.25–1.21 (moderately triangular shape), category 4, range 1.20–1.11 (slightly triangular shape) and category 5, range 1.10–1.00 (subrectangular shape). Material studied in the making of this table: *A.* aff. *plinii* from Crevillente 20 and 23; *A. plinii* from Crevillente 5A and 15; *A. alberti* from Venta del Moro (Granada and Valencia collections), Librilla, PUR-25 and PUR-25A; *A. barrierei* from La Bullana 2B and 3, Gorafe 4, Yeguas, PUR-4, Chabrier and Caravaca; *A. angustidens* from Mont Hélène, Villeneuve, Soler and two specimens with the label Gorafe 4/5 from the Granada collection.

Species	*n*	Category 1	Category 2	Category 3	Category 4	Category 5
		1.35–1.31	1.30–1.26	1.25–1.21	1.20–1.11	1.10–1.0
A. aff. *plinii*	35	8.6	14.3	37.1	40	0
A. plinii	23	0	0	4.3	95.7	0
A. alberti	51	0	3.9	9.8	84.3	2
A. barrierei	23	0	0	0	60.9	39.1
A. angustidens	6	0	0	0	50	50

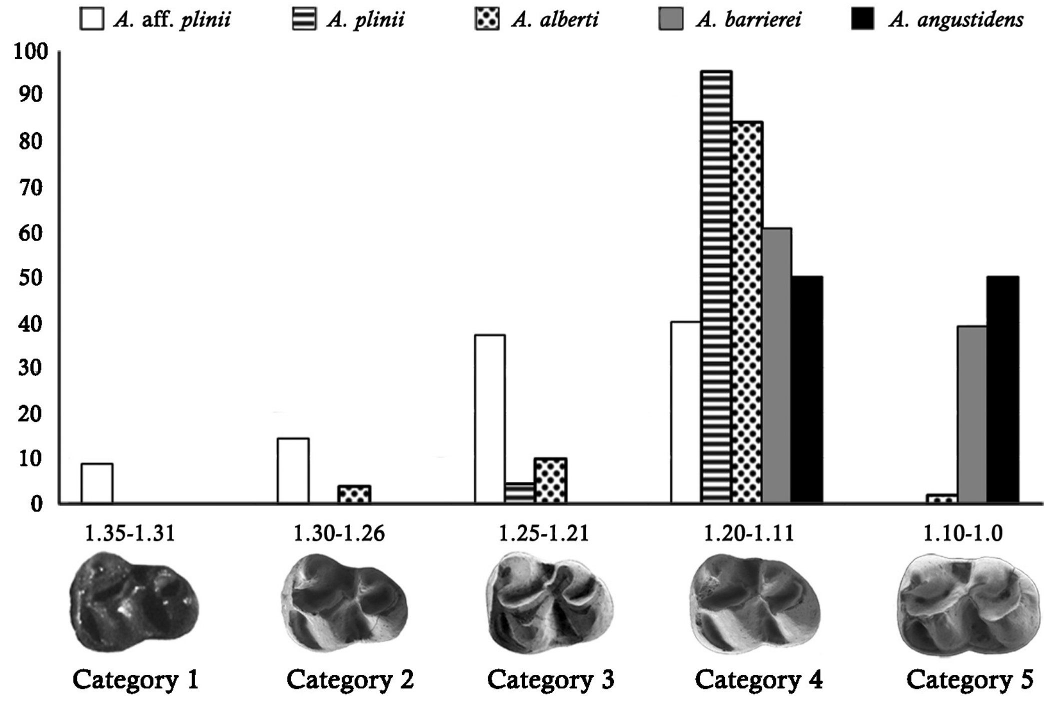


Fig. 8. Diagram bar with percentage of representation by categories for the W_ant/W_post ratio of m3. Category 1, range 1.35–1.31 (specimen figured RGM 404855, W_ant/W_post = 1.34), category 2, range 1.30–1.26 (specimen figured VVmB-25, W_ant/W_post = 1.28), category 3, range 1.25–1.21 (specimen figured VVmA-67, W_ant/W_post = 1.23), category 4, range 1.20–1.11 (specimen figured VVmA-65, W_ant/W_post = 1.16) and category 5, range 1.10–1.00 (specimen figured LB-2B-154, W_ant/W_post = 1.06).

Table 4
Measurements in millimeters of the anterior width (W_ant), posterior width (W_post) and anterior width/posterior width ratio (W_ant/W_post) of m3 of *Apocricetus* aff. *plinii* from Crevillente-20 and Crevillente-23, *A. plinii* from Crevillente-5A and Crevillente-15, *A. alberti* from Purcal-25A, Purcal-25, Librilla and Venta del Moro, *A. barrierei* from Chabrier, Purcal-4, La Bullana-2B, La Bullana-3, Yeguas, Caravaca and Gorafe-4, and *A. angustidens* from Gorafe-4/5, Villeneuve, Solera and Mont-Hélène. *Abbreviations*: CR-, Crevillente; PUR-, Purcal; LIB, Librilla; VM, Venta del Moro; CHA, Chabrier; LB-, La Bullana; YEG-, Yeguas; CAR-, Caravaca; GOR, Gorafe; VIL, Villeneuve; SOL, Solera; MH, Mont-Hélène.

Species	Locality	W_ant				W_post				W_ant/W_post			
		n	Min.	Mean	Max.	*n*	Min.	Mean	Max.	*n*	Min.	Mean	Max.
A. aff. *plinii*	CR-20	2	1.09	1.11	1.13	2	0.94	0.95	0.96	2	1.15	1.16	1.17
A. aff. *plinii*	CR-23	33	0.93	1.10	1.37	33	0.74	0.90	1.19	33	1.12	1.22	1.34
A. plinii	CR-5A	5	1.34	1.42	1.49	5	1.21	1.25	1.32	5	1.10	1.14	1.17
A. plinii	CR-15	18	1.39	1.50	1.63	18	1.13	1.29	1.39	18	1.12	1.16	1.23
A. alberti	PUR-25A	2	–	1.63	–	2	1.40	1.41	1.41	2	1.15	1.16	1.16
A. alberti	PUR-25	2	1.55	1.63	1.71	2	1.42	1.43	1.44	2	1.10	1.14	1.19
A. alberti	LIB	1	–	1.55	–	1	–	1.33	–	1	–	1.16	–
A. alberti	VM[a]	52	1.29	1.46	1.60	47	1.08	1.25	1.44	46	1.10	1.17	1.28
A. barrierei	CHA	1	–	1.70	–	1	–	1.49	–	1	–	1.14	–
A. barrierei	PUR-4	4	1.48	1.63	1.86	4	1.27	1.44	1.63	4	1.10	1.13	1.16
A. barrierei	LB-2B	8	1.47	1.57	1.66	9	1.36	1.43	1.57	8	1.06	1.11	1.15
A. barrierei	LB-3	1	–	1.59	–	1	–	1.42	–	1	–	1.20	–
A. barrierei	YEG	1	–	1.62	–	1	–	1.43	–	1	–	1.13	–
A. barrierei	CAR	3	1.56	1.60	1.63	3	1.32	1.45	1.53	3	1.06	1.11	1.18
A. barrierei	GOR-4	4	1.56	1.63	1.70	4	1.39	1.46	1.57	4	1.08	1.12	1.15
A. angustidens	GOR-4/5	2	1.70	1.70	1.71	2	1.47	1.48	1.49	2	1.14	1.15	1.16
A. angustidens	VIL	1	–	1.96	–	1	–	1.78	–	1	–	1.10	–
A. angustidens	SOL	1	–	1.63	–	1	–	1.44	–	1	–	1.14	–
A. angustidens	MH	2	1.72	1.78	1.83	2	1.68	1.69	1.70	2	1.01	1.05	1.09

[a] The measurements of five specimens of *A. alberti* from Venta del Moro housed at the University of Granada were added to the sample housed at the University of Valencia.

A. alberti. The category 4 comprises the specimens with a ratio ranging from 1.20 to 1.11: it includes the m3 which are slightly subtriangular (Fig. 8). Most of the specimens studied here belong to this category, and all the *Apocricetus* species are represented within it (Table 3, Fig. 8), but not in the same proportion. Finally, the specimens with ratios from 1.10 to 1.0 belong to the category 5: These molars are subrectangular with similar W_ant and W_post (see Figs. 7 and 8), and belong to the species *A. angustidens* and *A. barrierei* and one specimen of *A. alberti* from Venta del Moro, which lies in the upper limit of this category, 1.10 (Tables 3 and 4, Fig. 8).

The change in shape from the oldest to the youngest species of the genus *Apocricetus* is shown in Figs. 8 and 9. Fig. 8 represents the percentages of m3 of each species of the genus within each of the categories previously described, as given in Table 3. Fig. 9 includes the ranges of the W_ant/W_post ratio of the *Apocricetus* from the localities studied in this paper, as well as the median in the populations where more than two specimens have been measured. It is clear that the m3 of *A.* aff. *plinii* are more triangular than those of the other species of the genus, while those of *A. plinii* and *A. alberti* are similar in shape, having W_post closer to W_ant. The great range of variability for W_ant/W_post shown by the population of *A.* aff. *plinii* from CR-23 in Fig. 9, which spans four different categories of shape in Fig. 8, may be due to the presence of two species in that locality (Freudenthal et al., 1998). The range of *A. alberti* from Venta del Moro also covers four categories of shape, but the values are less dispersed, with a single specimen in the

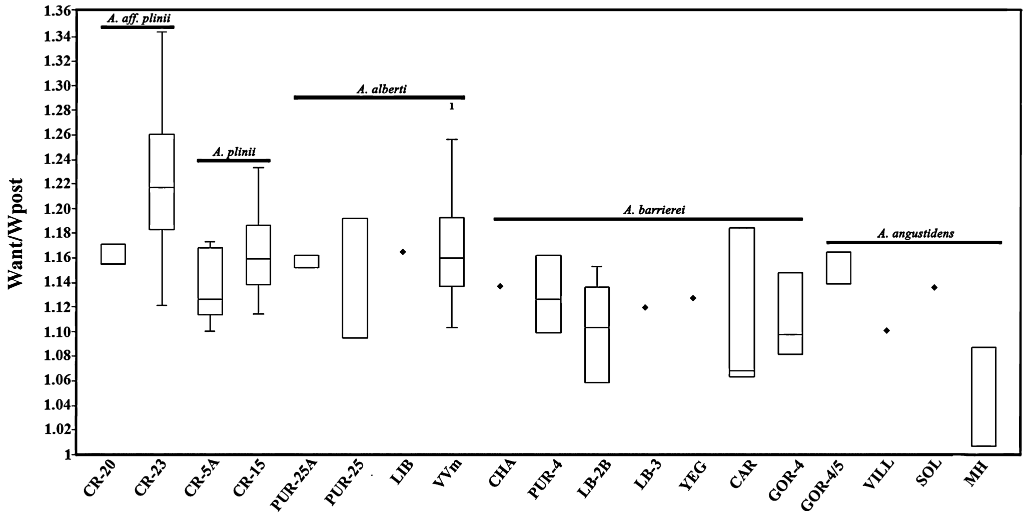


Fig. 9. Anterior width/posterior width ratio of *Apocricetus* aff. *plinii* from Crevillente-20 and Crevillente-23, *A. plinii* from Crevillente-5A and Crevillente-15, *A. alberti* from Purcal-25A, Purcal-25, Librilla and Venta del Moro, *A. barrierei* from Chabrier, Purcal-4, La Bullana-2B, La Bullana-3, Yeguas, Caravaca and Gorafe-4, and *A. angustidens* from Gorafe-4/5, Villeneuve, Solera and Mont-Hélène. The boxes enclose the percentiles 25 to 75, and the median is represented by a horizontal black line within the box. The blank boxes comprise just two data, and therefore there is no median. In the cases where there is just one datum, this record is indicated by a square. The number "1" in the population from VVm indicates an outlier. *Abbreviations*: CR-, Crevillente; PUR-, Purcal; LIB, Librilla; VM, Venta del Moro; CHA, Chabrier; LB-, La Bullana; YEG-, Yeguas; CAR-, Caravaca; GOR, Gorafe; VIL, Villeneuve; SOL, Solera; MH, Mont Hélène.

categories 2 and 5, while the great majority of the m3 belong to the category 4 (Fig. 8). Finally, the molars of the younger species of *Apocricetus*, *A. barrierei* and *A. angustidens*, are subrectangular or just slightly triangular, with values of W_post close to W_ant.

5.2.3. *Upper molars*

The lack of a cingulum ridge and a preloph in M1, the simple anterolophule in M1, the presence of mesolophs in M1 and M2 and the better-developed posterior metalophule in the upper molars of *A.* aff. *plinii* from CR-23 and *A. plinii* from CR-15, distinguish these latter species from *A. alberti* from Venta del Moro.

The upper molars of *A. alberti*, *A. barrierei*, and *A. angustidens* are morphologically quite similar. Nevertheless, some characters have a different degree of development that allows distinguishing these three species.

The development of the preloph in M1 distinguishes *A. barrierei* and *A. alberti*. The presence of a well-developed cingulum ridge and the absence of a posterior metalophule in M1 and M2 of *A. angustidens* differ from *A. alberti*.

According to Freudenthal et al. (1998) and Ruiz-Sánchez et al. (2014), the cingulum ridge of M1 is absent in all samples of *A.* aff. *plinii*, *A. plinii* and *A. alberti*, absent or weak (16.7%) in the populations of *A. barrierei*, and well developed in the populations of *A. angustidens*. In the new material of *A. alberti* from the locality Venta del Moro, a weak cingulum can also be observed in 5 out of 37 specimens (Table 5).

The anterolophule is simple in 2 out of 40 M1 from Venta del Moro (5%), simple with a free labial spur in 1 (2.5%), forked in 23 (57.5%), double and arising from a hint of a preloph in 10 (25%), or with a very short but clear preloph in 4 (10%). The anterolophule may be simple (10), forked (2) or bear a free labial spur (7) in *A.* aff. *plinii* from CR-23, and simple (2), forked (8) or forked with a free labial branch (6) in *A. plinii* (Freudenthal et al., 1991, 1998). In neither of these two latter species the anterolophules arise from a transversal crest (preloph). In *A. barrierei* from LB-2B there is a distinct preloph, longer than in the specimens from Venta del Moro. This morphology has not been described in the populations of *A. angustidens*.

The anterior protolophule is present in approximately 50–60% of the M1 of the populations of *A.* aff. *plinii*, *A. plinii* and *A. alberti* (see Table 5). This crest is less developed in the assemblages of *A. barrierei* and especially in *A. angustidens* (Ruiz-Sánchez et al., 2014; Table 5).

On the other hand, Freudenthal et al. (1998) consider the presence a posterior metalophule in M1 diagnostic. However, Ruiz-Sánchez et al. (2014) do not regard the presence of this crest a good criterion to distinguish between species in the lineage *A. alberti*–*A. barrierei*–*A. angustidens*. The rich assemblage of Venta del Moro has allowed to assess the frequency of this character, absent in all populations of *A. angustidens* and *A. barrierei* except for one specimen of this latter species from Caravaca (Freudenthal et al., 1998). So, extending this analysis to all species of the genus, it is shown that the posterior metalophule is present in 5 out of 11 (45.5%) M1 of *A.* aff. *plinii* from CR-23, 3 out of 13 (23.1%) of *A. plinii* from CR-15, 7 out of 41 (17.1%) of the new material from Venta del Moro and absent in *A. barrierei* and *A. angustidens*. Therefore, we consider that the frequency of the posterior metalophule decreases from the oldest to the youngest populations of *Apocricetus*, and consequently it is a useful parameter to distinguish between species of the genus *Apocricetus*.

With respect to the anterior protolophule of M2, this crest is present in almost all specimens of the species *A.* aff. *plinii*, *A. plinii* and *A. alberti*, while its frequency decreases slightly in *A. barrierei* and, more markedly, in *A. angustidens* (Table 5).

The posterior metalophule of M2 is reduced gradually from *A.* aff. *plinii* to *A. barrierei* (Table 5), becoming absent in all populations of *A. angustidens* (Freudenthal et al., 1991, 1998; Ruiz-Sánchez et al., 2014). The decrease in the frequency of the posterior metalophule has been linked to the shortening of the posteroloph in the species *A. alberti*–*A. barrierei*–*A. angustidens* (Ruiz-Sánchez et al., 2014). In *A. alberti* from Venta del Moro, the posteroloph is elongated, forming an L-shaped posterosinus in 29 out of 45 (64.4%) specimens. In the rest of the M2 the posterior part of the posterosinus is much more reduced, so the metacone forms the posterior wall of the tooth. In LB-2B and LB-3, 9 out of 19 (47.4%) M2 have a long posteroloph, 7 (36.8%) have a medium-sized posteroloph and 3 (15.8%) have a short one. The development of a long posteroloph seems to be related to the presence of a posterior metalophule, since all the specimens from LB-2B and Venta del Moro with a complete crest have also a long posteroloph which encloses an L-shaped posterosinus. However, despite the similar development of the posteroloph in the localities of LB-2B/LB-3 and Venta del Moro, the posterior metalophule is much more frequent in this latter population.

In M3, a well-developed anterior protolophule is present in *A.* aff *plinii*, *A. plinii* and *A. alberti*. In Venta del Moro, 59 out of 61 specimens have a complete crest (96.2%), and another 2 have a spur. In *A. barrierei* the anterior protolophule is long in LB-2B (100%), being absent in the populations of Gorafe 4, in 3 out of 4 (75.0%) molars from Fuente del Viso and 3 out of 8 (37.5%) from Almudena 1D (Freudenthal et al., 1998; Ruiz-Sánchez et al., 2014). In *A. angustidens* this crest is well developed in the specimens from Serrat d'en Vacquer, being present in 33.0% of the molars from Mont-Hélène and absent in the two specimens from Gorafe 3 (Freudenthal et al., 1998; Ruiz-Sánchez et al., 2014).

Table 5

Variation of several characters in the upper molars of *Apocricetus*. *Abbreviations*: Abs, absent; Car, Caravaca; CR-, Crevillente; LB-2B, La Bullana 2B; LB3, La Bullana 3; MH, Mont-Hélène; Pr, present, VVm, Venta del Moro, collection housed at the University of Valencia. Data from Freudenthal et al. (1991, 1998), Ruiz-Sánchez et al. (2014) and this work.

Species	Locality	M1		M2		M3
		Cingulum ridge (anterocone)	Anterior protolophule	Anterior protolophule	Posterior metalophule	Anterior protolophule
A. aff. *plinii*	CR-23	Abs	Pr: 6/12 (50%)	Pr: 30/30 (100%)	Pr: 15/29 (51.7%)	Pr: 30/30 (100%)
A. plinii	CR-15	Abs	Pr: 12/18 (60%)	Pr: 16/18 (88.9%)	Pr: 9/18 (50%)	Pr: 22/22 (100%)
A. alberti	CR-6	Abs	Pr: 50%	Pr: 100%	Pr: 3/11 (27.3%)	Pr: 100%
A. alberti	VVm	Weak: 5/37 (13.5%)	Pr: 24/41 (58.5%)	Pr: 47/47 (100%)	Pr: 20/42 (47.6%)	Pr: 61/61 (100%)
A. barrierei	Car	Abs/weak	Pr: 1/5 (20%)	Pr: 4/6 (66.7%)	Pr: 1/6 (16.6%)	Pr: 3/3 (100%)
A. barrierei	LB2B	Pr: 1/6 (16.7%)	Pr: 2/7 (28.6%)	Pr: 16/20 (80%)	Pr: 6/17 (35.3%)	Pr: 13/13 (100%)
A. angustidens	MH	Well developed	Pr: 4/30 (13.3%)	Pr: 9/39 (23.1%)	Abs	Pr: 11/33 (33.3%)

6. Conclusions

The new sampling carried out in the Late Miocene age (Late Turolian) locality of Venta del Moro has allowed us to recover one of the richest collection of the genus *Apocricetus*, and, without doubt, the most complete of the species *Apocricetus alberti* (over 300 dental remains), which permits a better characterization of this taxon. An emended diagnosis and a more complete differential diagnosis for *A. alberti* are proposed.

To evaluate the change in the shape of the m3 in the different populations of *Apocricetus*, we propose the use of the posterior width of m3, from the cingulum ridge closing the sinusid to the lingual side of the entoconid. The ratio of anterior width to posterior width (W_ant/W_post) is a good indicator of the shape of the m3, since higher values indicate a narrower posterior side and therefore a more triangular shape. Five categories of the ratio W_ant/W_post (extremely triangular to subrectangular) have been defined, showing a clear distinction in the shape of the m3. A change in the shape of the m3 is observed in the phylogenetic lineage of the genus *Apocricetus*, from extreme triangular shapes in *A.* aff. *plinii* (Early Turolian) to subrectangular outlines in *A. barrierei* and *A. angustidens* (Pliocene).

The anteroconid and the anterolophulids in m1 and the anterolophule in M1 present quite heterogeneous morphologies, changing from the older species of the genus to the more recent ones. This morphological variability has not been observed in any other species of *Apocricetus*.

The presence of a crest-like anteroconid and a prelophid in some m1, presence of a weak cingulum ridge and a preloph in some M1, and the absence of mesolophs in the upper molars of *A. alberti* from Venta del Moro differ from *A.* aff. *plinii* and *A. plinii*. The absence of the ectomesolophid in m2 and m3 and the presence of a small mesolophid in some m2 differ from *A. plinii*.

The smaller size, presence of a small mesolophid in some m2, less-developed prelophid in m1, more triangular shape of the m3 and common presence of a posterior metalophule in the M1 of *A. alberti* from Venta del Moro differ from *A. barrierei* and *A. angustidens*. The less-elongated m3 and less-developed preloph in M1 distinguish *A. alberti* from Venta del Moro from *A. barrierei*. The more-developed cingulum ridge and absent posterior metalophule of *A. angustidens* distinguish this species from *A. alberti*.

Acknowledgments

The field work in Venta del Moro was supported, from 1995 on, by the Conselleria de Cultura of the Valencian Government with the permission of the Ministerio de Fomento and the Company ADIF, of the Spanish Government. We thank Dr. Jérôme Prieto for comments about the way to measure the shape of m3, Dr. Lars van de Hoek Ostende for his hospitality during the stay of S.M. in Leiden, and Dr. Reinier van Zelst for granting the access to the collections of this institution. We thank Dr. Elvira Martín-Suárez for granting access to the material kept at the University of Granada, and Dr. A. García-Alix for his comments. We thank the comments and suggestions by the reviewers Dr. Raef Minwer-Barakat and Dr. Jérôme Prieto. This investigation was supported by project CGL2011-25754 of the Spanish Ministry of Economy and Competitiveness.

References

Adrover, R., Mein, P., Moissenet, E., 1993. Roedores de la transición Mio-Plioceno de la región de Teruel. Paleontol. Evol. 26–27, 47–84.

Bachelet, B., Aguilar, J.P., Calvet, M., Michaux, J., 1990. Nouvelles faunes de rongeurs du Pliocene des Pyrenees-Orientales: consequences pour le genre *Stephanomys* (Schaub, 1938). Geobios 23 (1), 117–120.

Daams, R., Freudenthal, M., 1988. Cricetidae (Rodentia) from the type Aragonian; the genus *Megacricetodon*. In: Freudenthal, M. (Ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain) Special Issue, 1. Scripta Geologica, pp. 39–132.

Freudenthal, M., 1985. Cricetidae (Rodentia) from the Neogene of Gargano (prov. of Foggia, Italy). Scripta Geol. 77, 29–76.

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

Freudenthal, M., Lacomba, J.I., Martín-Suárez, E., 1991. The Cricetidae (Mammalia, Rodentia) from the Late Miocene of Crevillente (prov. Alicante, Spain). Scripta Geol. 96, 9–46.

Freudenthal, M., Mein, P., Martín-Suárez, E., 1998. Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. Treballs del Museu de Geologia de Barcelona 7, 11–93.

García-Alix, A., Minwer-Barakat, R., Martín, J.M., Martín-Suárez, E., Freudenthal, M., 2008a. Biostratigraphy and sedimentary evolution of late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). Lethaia 41 (4), 431–446.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008b. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. Scripta Geol. 136, 1–37.

Gibert, L., Scott, G.R., Montoya, P., Ruiz-Sánchez, F.J., Morales, J., Luque, L., Abella, J., Lería, M., 2013. Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. Geology 41, 691–694.

Mathisen, M., Morales, J., 1981. Stratigraphy, facies and depositional environments of the Venta del Moro vertébrate locality, Valencia, Spain. Estudios Geológicos 37, 199–207.

Mein, P., Michaux, J., 1970. Un nouveau stade dans l'évolution des rongeurs pliocènes de Europe sud-occidentale. Compt. Rend. Acad. Sci. Paris D 270, 2780–2783.

Minwer-Barakat, R., García-Alix, A., Agustí, J., Martín-Suárez, E., Freudenthal, M., 2009. The micromammal fauna from Negratín-1 (Guadix basin, Southern Spain): new evidence of African-Iberian mammal exchanges during the late Miocene. J. Paleontol. 83, 854–879.

Minwer-Barakat, R., García-Alix, A., Martín Suárez, E., Freudenthal, M., Viseras, C., 2012. Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. Lethaia 45, 594–614.

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J.V., Marín, M.D., Ruiz-Sánchez, F.J., 2006. Las nuevas excavaciones (1995–2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. Estudios Geológicos 62, 313–326.

Opdyke, N., Mein, P., Lindsay, E., Pérez-González, A., Moissenet, E., Norton, V.L., 1997. Continental deposits, magnetostratigraphy and vertebrate paleontology, late Neogene of Eastern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 133, 129–148.

Robles, F., 1970. Estudio estratigráfico y paleontológico del Neógeno del río Júcar [Ph.D. dissertation] University of Valencia, Valencia 275 pp.

Ruiz-Sánchez, F.J., Santisteban de, C., Crespo-Roures, D., Freudenthal, M., 2011. New rodent faunas from middle Miocene and Mio-Pliocene in the Cabriel Basin (Valencia, Spain). J. Iber. Geol. 37 (2), 161–172.

Ruiz-Sánchez, F.J., Freudenthal, M., Mansino, S., Crespo, V.D., Montoya, P., 2014. *Apocricetus barrierei* (Rodentia, Mammalia) from La Bullana 2B and La Bullana 3 (Cabriel Basin, Valencia, Spain). Revision of the Late Miocene–Early Pliocene forms of the genus *Apocricetus*. Paläontol. Z. 88, 85–98.

Van de Weerd, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. Utrecht Micropaleontol. Bull. 2, 1–217.

A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus

Samuel Mansino, Antonio García-Alix, Francisco J. Ruiz-Sánchez, and Plinio Montoya

Mansino, S., García-Alix, A., Ruiz-Sánchez, F.J., and Montoya, P. 201X. A new *Eliomys* from the Late Miocene of Spain, and its implications for the phylogeny of the genus. *Acta Palaeontologica Polonica* XX (X): xxx-xxx.
http://dx.doi.org/10.4202/app.00014.2013

In this paper, we describe a previously unknown species of the glirid *Eliomys* from the Late Miocene and Early Pliocene Cabriel, Alcoy and Granada basins of southeastern Spain. *Eliomys yevesi* sp. nov. is characterized by its relative small size, narrow lingual wall and common presence of two centrolophs in the upper molars, and well-developed centrolophids in the lower molars. The new species is the probable ancestor of *E. intermedius*, which in turn represents the ancestor of the extant *E. quercinus*. According to its morphologic and biometric features, the origin of *E. yevesi* sp. nov. is likely to be found in some population of *E. truci* from the Late Miocene. Based on these affinities, we propose the lineage *E. truci*-*E. yevesi* sp. nov.-*E. intermedius*-*E. quercinus*, in which there is a trend towards the development of centrolophs, as well as the reduction of accessory crests.

Key words: Mammalia, Rodentia, Gliridae, *Eliomys*, Late Miocene, Spain.

Samuel Mansino [samuel.mansino@uv.es] and Plinio Montoya [plinio.montoya@uv.es], Departament de Geologia, Universitat de València, 46100 Burjassot, Spain;
Antonio García-Alix [agalix@ugr.es], Instituto Andaluz de Ciencias de la Tierra (IACT-CSIC-UGR), Consejo Superior de Investigaciones Científicas, Universidad de Granada, Avenida de las Palmeras nº 4 18100 Armilla, Granada, Spain;
Francisco J. Ruiz-Sánchez [francisco.ruiz@uv.es], Departament de Geologia, Universitat de València, 46100 Burjassot, Spain; and Museu Valencià d'Història Natural, L'Hort de Feliu, P.O. Box 8460, Alginet, Valencia, 46018, Spain.

Received 31 July 2013, accepted 21 February 2014, available online 28 February 2014.

Introduction

External, genetic and some morphometric characters of the skull distinguish at least three extant species of the genus *Eliomys* (Filipucci et al. 1988a, b; Krystufek and Kraft 1997; Holden 2005), including the garden dormouse *Eliomys quercinus* (Linnaeus, 1766), the Asian dormouse *E. melanurus* Wagner, 1839 (type species) and the Maghreb garden dormouse *E. munbyanus* Pomel, 1856. Its biogeographic range comprises Western Europe, where it is widespread, as well as scattered populations across Central, Eastern, and Southeast Europe, Turkey, and the north of Africa. In addition, fossil representatives of the genus include *E. assimilis* Mayr, 1979 and *E. reductus* Mayr, 1979 from Germany, and *E. lafarguei* Aguilar, Michaux, and Lazzari, 2007 from France, all them from the Late Miocene, as well as *E. truci* Mein and Michaux, 1970 from the Late Miocene-Pliocene, and *E. intermedius* Friant, 1953 from the Pliocene and Pleistocene, both of Western Europe.

Eliomys truci, *E. intermedius*, and the extant *E. quercinus* have been proposed to form part of a single phylogenetic lineage, following first a cladogenetic pattern of evolution, based on the coexistence of *E. truci* and *E. intermedius* during the Early–Late Pliocene (Adrover 1986), before culminating in the anagenetic replacement of *E. intermedius* by *E. quercinus* during the Pleistocene (Chaline 1972; Castillo 1990). However, this picture is made more complex by the appearance of an additional, intermediate form (*E*. aff. *intermedius*) sharing features with both *E. truci* and *E. intermedius*, in the Mio-Pliocene of the Granada Basin of southern Spain (García-Alix et al. 2008a). Here, we provide new information on the evolutionary history of the genus by describing new Mio-Pliocene material from rich localities with the Cabriel (Venta del Moro and La Bullana) and Alcoy basins of southeastern Spain, which, together with E. aff. *intermedius* from the Granada Basin, we refer it to the new species *Eliomys yevesi* sp. nov.

Institutional abbreviations.—DEPUG, Departamento de Estratigrafía y Paleontología of the University of Granada, Spain; MGUV, Museum of Geology of the University of Valencia, Spain.

Other abbreviations.—L, length; W, width; see Table 1 for locality name abbreviations.

Material and methods

Nomenclature and measurement methods follow Daams (1981) and Freudenthal (2004). Measurements are in millimetres and were taken on a Leica $MZ7_5$ binocular microscope by means of displacement of a mechanical stage, connected to Sony Magnescale measuring equipment. Photographs were taken with a HITACHI 4800 scanning electron microscope at the Central Support Facility for Experimental Research (SCSIE) of the University of Valencia. The specimens from Venta del Moro, La Bulla and Alcoy are kept at the MGUV, and labelled according to locality, level and, where applicable, year of collection (Table 1).

To determine its affinities, we directly compared our material with fossil collections from Huétor Tájar, Tollo de Chiclana, Moreda, Bélmez-1, Cañada Castaños, Gorafe-2 and 5, Botardo-C, Negratín-1, Calicasas-3B, Purcal-4, 23, 24A, and 25, and Otura-1, housed at the DEPUG (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/appXX-Mansino_etal_SOM.pdf). In addition to these direct comparisons, we took into account published data contained from the localities of Balaruc 2, Layna, Caravaca, Crevillente 1, 3, 5, and 6, Tortajada A and C, and Masada del Valle 2 (all in Weerd 1976), as well as Orrios 3, Sete, Arquillo 3, Villalba Alta, Hautimagne, Los Mansuetos, and Aljezar B (Adrover 1986). Finally, we performed a phylogenetic analysis of the genus using the implicit enumeration option of the phylogenetic analysis of the genus using the implicit enumeration option of the phylogenetic software package TNT (Goloboff et al. 2003, 2008). All of the characters included in this analysis are listed in the Appendix 1.

[Table 1]

Geological setting

The material described here was recovered from lacustrine and palustrine sediments belonging to the Villatoya-Venta del Moro Formation (Robles 1970; Montoya et al. 2006) exposed at Venta del Moro (VVm) and La Bullana 2B (LB-2B), both situated in the Cabriel Basin of southeastern Spain (Robles 1970; Morales 1984; Montoya et al. 2006), as well as the localities of Alcoi Forn 1’06 (AF-1’06), Alcoi Barranc Sud 3A (ABS-3A), Alcoi Cristian 0 (AC-0), and Alcoi 2 (AL2-C and AL2-D), all of them located in the west margin of the lacustrine Basin of Alcoy (southeastern Spain). At Venta del Moro, specimens were collected from several levels, previously referred to as VM-A, B, C, BC, and D by Montoya et al. (2006). The latter are here labeled as VVm-A, VVm-B, VVm-BC, VVm-C, and VVm-D, respectively, to distinguish the specimens housed at the University de Valencia from previously collected material from the same locality housed at the Museo Nacional de Ciencias Naturales, Madrid (Montoya et al. 2006).

[Fig. 1]

The age of the fossiliferous levels of Venta del Moro, has recently been dated to 6.23 Ma, or latest Miocene (late Turolian/late Messinian), based on their faunal assemblage and magnetostratigraphic data (magnetochron C3An; Gibert et al. 2013). This age estimate is confirmed by the presence of *Apocricetus alberti* Freudenthal, Mein, and *meini* (Michaux, 1969) and *Apodemus gudrunae* van de Weerd, 1976 (Freudenthal et al. 1998; Sesé 2006a; García-Alix et al. 2008a). This faunal association is consistent with the *Apodemus gudrunae* Assemblage Zone in the Guadix Basin (Minwer-Barakat et al. 2012). The presence of *Stephanomys dubari* Aguilar, Michaux, Bachelet, Calvet, and Faillat, 1991, in the localities of Venta del Moro (Montoya et al. 2006) differs from late Turolian (late Messinian) sites in the Teruel Basin, such as the locality of Arquillo 4, which instead yields *S. ramblensis* van de Weerd, 1976 (Mein et al. 1990; Adrover et al. 1993).

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, *Apodemus gorafensis* Ruiz-Bustos, Sesé, Dabrio, Peña, and Padial, 1984*, Occitanomys alcalai* Adrover, Mein, and Moissenet, 1988, and *Paraethomys meini* (Michaux, 1969) typically appear together in the latest Turolian-earliest Ruscinian localities of southern Spain (late Messinian-early Zanclean; García-Alix et al. 2008b, c). These taxa are present at PUR-4, CLC-3B, AF-1’06, AF-1’07, and LB-2B, but *Occitanomys alcalai* and *Apodemus gorafensis* are absent in ABS-3A, which has yielded few micromammal remains. By contrast, *Apocricetus barrierei* (Mein and Michaux, 1970), an indicator of early Ruscinian (Zanclean) age (Freudenthal et al. 1998; Sesé 2006a; García-Alix et al. 2008a) is present at ABS-3A, PUR-4, CLC-3B AF-1’07, and LB-2B, yet absent at AF-1’06, which has yielded over a hundred specimens. The localities of PUR-4 and CLC-3B are within the *Apocricetus barrierei* Assemblage Zone (earliest Ruscinian/earliest Zanclean) of the Granada Basin (García-Alix et al. 2008c).

Eliomys intermedius is a typically Ruscinian taxon (Sesé 2006a). The presence of *Apodemus* cf. *gorafensis*, *Occitanomys* cf. *alcalai*, *Paraethomys meini*, and *Stephanomys cordii* at AC-0 place this locality in the Early Ruscinian (MN14). The faunal lists of AL-2C and AL-2D, which include *Trilophomys* cf. *castroi*, *Blancomys* sp., *Stephanomys cordii*, *Paraethomys meini*, *Paraethomys* aff. *abaigari*, *Ruscinomys* cf. *lasallei*, and *Apocricetus* cf. *angustidens* suggest also an early Ruscinian age (Mansino et al. 2013). However, the presence of two species of *Paraethomys*, the more developed crests of *Stephanomys cordii*, and the presence of *Apocricetus* cf. *angustidens* instead of *A. barrierei* indicate a younger age for these localities than for AC-0.

Systematic paleontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Subfamily Dryomyinae de Bruijn, 1967

Genus *Eliomys* Wagner, 1840

Type species: *Eliomys melanurus* Wagner, 1840; extant species.

Eliomys yevesi sp. nov.

Fig. 2A–L.

1953 *Eliomys* aff. *intermedius*; Friant 1953: pl. 4: 9–19.

2008 *Eliomys* aff. *intermedius*; García-Alix et al. 2008a: 24–25.

Etymology: Dedicated to José María Yeves and his family, owners of the "Hostal Ventamorino", for their friendly hospitality during the many summer campaigns in Venta del Moro.

Holotype: Right M1, VVmA-25.

Type locality: Venta del Moro A, Cabriel Basin, Spain.

Type horizon: Villatoya-Venta del Moro Formation, MN13, late Turolian (Late Miocene, 6.23 Ma).

Material.—VVmA: 2 p4 (VVmA-42,43), 12 m1,2 (VVmA-1–11, 32), 6 m3 (VVmA-33–38), 1 dP4 (VVmA-44), 3 P4 (VVmA-39–41), 12 M1,2 (VVmA-16, 21–31), 8 M3 (VVmA-12–15, 17–20). VVmB: 1 m1,2 (VVmB-1). VVmBC: 2 m1,2 (VVmBC-1, 2), 1 m3 (VVmBC-5), 1 M1,2 (VVmBC-3), 1 M3 (VVmBC-4). VM-C: 1 m3 (VVmC-1). VM-D: 2 M1,2 (VVmD-1, 2). ABS-3A (Alcoi Barranc Sud 3A, MN14): 1 m1,2 (ABS3A-38). AF-1’06 (Alcoi Forn 1’06, MN13-MN14): 1 m1,2 (AF1’06-190), 1 m3 (AF1’06-187). AF-1’07 (Alcoi Forn 1’07, MN14): 1 M1,2 (AF1’07-36). PUR-4 (Purcal 4, MN14): 1 p4 (PUR-4 871), 12 m1,2 (PUR-4 872–883), 3 m3 (PUR-4 884–886), 1 dP4 (PUR-4 887), 1 P4 (PUR-4 888), 2 M1,2 (PUR-4 889, 890), 3 M3 (PUR-4 891–893). CLC-3B (Calicasas 3B, MN14): 1 m3 (CLC-3B 67), 2 M1,2 (CLC-3B 68, 69), 1 M3 (CLC-3B 70).

Diagnosis.—Size intermediate between *E. truci* and the youngest *E. intermedius*; sub-quadrangular m1, 2, usually with a posterotropid and a well-developed centrolophid; no posterotropid on m3; common presence of both centrolophs in the upper molars; posteroloph and endoloph usually connected.

Differential diagnosis.—Eliomys yevesi differs from *E. assimilis* in the more quadrangular shape of m1, 2, less reduced m3, and the absence of any accessory crests in the upper molars; from *E. reductus* in its bigger size, more quadrangular shape of the lower molars, discontinuous endolophid, and common presence of posterotropid; and from *E. lafarguei* in its bigger size, long centrolophid on m1,2, discontinuous endolophid, the presence of a centrolophid on many m3, and the common presence of postcentrolophs in the upper molars.

Eliomys yevesi ranges in size from the biggest specimens of *E. truci* to the smallest ones of *E. intermedius*. It differs from *E. truci* in more frequently showing centrolophs in the upper molars, as well as the presence of well-developed postcentrolophs, reaching half the width of the tooth or more, in some specimens (Fig. 2G). *E. yevesi* further differs from *E. intermedius* in the subquadrangular shape (Fig. 2B, C, N, R) and lower and narrower lingual wall of the upper molars (Fig. 2F, G). A long centrolophid connected to the metalophid is present in all but one m1, 2 of *E. yevesi*, whereas in *E. intermedius* it is short in 27 out of 106 specimens. In addition, the posterotropid is more frequent and usually longer in *E. yevesi* than in *E. intermedius* (27 out of 29 m1, 2 of *E. yevesi*; 80 out of 107 of *E. intermedius*). In the upper molars, the two centrolophs are usually slightly longer and occur somewhat more frequently in *E. intermedius* (97 out of 165, 58.78 %, compared to 17 out of 36, 47.22 %, in *E. yevesi*).

Eliomys yevesi differs from the extant *E. quercinus* in its smaller size, but resembles the latter in the absence of accessory crests in the upper molars and an anteroloph-protoloph connection, as well as the frequent presence of two centrolophs. Two subspecies of *E. quercinus* with distinct m1, 2 morphologies occur in the Iberian Peninsula: *E. q. lusitanicus*, which differs from *E. yevesi* in the absence of a centrolophid; and *E. q. quercinus*, which differs from *E. yevesi* in the absence of accessory crests in the lower molars, a continuous endolophid on m1, 2 and in having a small centrolophid.

Measurements.—See Table 2.

[Table 2]

[Fig. 2]

Description

Material from Venta del Moro

p4.—The occlusal outline of this tooth is subtriangular. The protoconid and the large anterolophid create a high, triangular anterior complex, which is separated from the metaconid by a narrow furrow. One specimen (VVmA-42; Fig. 2A) has a short centrolophid. The mesoconid and entoconid are connected by the mesolophid, and separated from the anterior complex by a deep valley. The mesoconid and hypoconid are separated. There is no posterotropid. The posterolophid is high and curved. There are two fused roots.

m1,2.—The occlusal outlines of these teeth are sub-quadrangular. The anterolophid is connected to the protoconid in 6 out of 14 specimens (4 out of 12 from VVm-A, the only specimen from VVm-B and 1 out of 2 from VVm-BC). One specimen (Fig. 2C) has a vestigial anterotropid. Most molars show a connection between the metalophid and the metaconid, whereas the metaconid and entoconid are separated. The centrolophid is usually long and sometimes connected to the metalophid. The posterotropid is long in 10 specimens (9 out of 12 from VVm-A, 1 out of 2 from VVm-BC), short in three (one specimen from VVmA, the only specimen from VVm-B and 1 of 2 from VVm-BC) and absent in another two (both from VVm-A). The hypoconid is large. There are three roots.

m3.—The occlusal outline of this tooth is sub-trapezoidal. The anterolophid is usually separated from the protoconid. The metalophid is sometimes connected to the metaconid. There are no accessory crests. Where present, the centrolophid is not connected to the metalophid. In 1 out of 13 m3, the mesolophid does not reach the entoconid (Fig. 2D). The posterolophid is continuous.

dP4.—Known only from a single, extremely worn molar. No features of the occlusal surface can be observed.

P4.—The occlusal outline of this tooth is triangular. The paracone and metacone are higher than the protocone. The anteroloph is short, low and connected, at a low level, to the paracone. The protoloph is clearly discontinuous in 1 out of 4 specimens, whereas the remainder shows just a constriction in the central part of this crest. Two specimens present a well-developed precentroloph, and a further one a postcentroloph, which is not connected to the metacone (Fig. 2E). The metaloph is high and continuous. The posteroloph is low and lingually connected to the protocone; discontinuous in two specimens, and not connected to the endoloph in another one (Fig. 2E). The roots are not preserved in any of the specimens.

M1, 2.—The occlusal outlines of these teeth are trapezoidal or subrectangular. The anteroloph is separated from the paracone and the protoloph. The paracone and metacone are high and separated. The protoloph and metaloph are continuous, and occasionally sinuous. There is a well-developed precentroloph, which is not connected to the paracone in one of the specimens and reaches the metaloph in another one. Where present, the postcentroloph is short, except in VVmA-29, which has a well-developed crest, and VVmA-25, in which both centrolophs are fused into a central crest (Fig. 2G). The posteroloph is connected to the endoloph. There are three roots.

M3.—The occlusal outline of this tooth is trapezoidal. The anteroloph is connected to the protocone. In some specimens, the protoloph and metaloph are sinuous. Both centrolophs are present in 5 out of 8 specimens from VVm-A, and the single tooth from VVm-BC. Two of the specimens from VVm-A bear a long postcentroloph (Fig. 2H). Where present, the precentroloph is usually attached to the paracone, whereas the postcentroloph is connected to the metacone. The endoloph is continuous, except for the single specimen from VVm-BC. There are three roots.

Material from Alcoy.—These specimens from the Alcoy Basin resemble the specimens from Venta del Moro, with the exception of having an anterolophid connected basally with the protoconid, and a metalophid that does not reach the metaconid (both on m1, 2). In the m1, 2 from ABS-3A (Fig. 2J), the centrolophid is not continuous. In the M1, 2 from AF-1’07 (Fig. 2L), the anteroloph and the paracone are connected basally.

Remarks.—Eliomys yevesi is a relatively small-sized species, being smaller than Plio-Pleistocene *E. intermedius* and *E. quercinus*, and only slightly larger than the Miocene representatives of the genus (*E. lafarguei*, *E. reductus*, and *E. assimilis*) (Fig. 3). The molars from Venta del Moro and AF-1’07 fall within the range of variation of *E. truci*. However, the specimens from the Early Ruscinian localities of PUR-4 and CLC-3B (Granada Basin), and AF-1’06 and ABS-3A (Alcoy Basin), are slightly larger, and intermediate between *E. truci* and *E. intermedius* (Fig. 3).

Morphologically, the present material resembles *E. truci*, but differs in the development of the centrolophs on M1, 2, while the presence of both centrolophs is rare in *E. truci* (5 out of a total of 41 specimens, 12.90 %; two specimens from Concud 3 and one each from OTU-1, PUR-23, and Orrios 3), 4 out of 12 specimens *E. yevesi* from VVm-A and VVm-BC (33.33 %), and all of the M1, 2 from VVm-D, AF-1’07, CLC-3B, and PUR-4 (except one) have both centrolophs. Moreover, when present, the postcentroloph is usually reduced in *E. truci*, whereas in some M1, 2 of *E. yevesi* from VVm-A it is very well developed, reaching half the width of the molar or more (Fig. 2G). Similarly, *E. truci* never bears two centrolophs on M3, whereas they do occur in 5 out of 8 molars (62.50 %) of *E. yevesi* from VVm-A, as well as the only M3 from VVm-C and CLC-3B.

In the upper molars of *E. intermedius*, 79 out of 130 (60.77 %) M1, 2 and 18 out of 35 (51.42 %) M3 have two centrolophs (Weerd 1976; Adrover 1986; Castillo 1990; García-Alix et al. 2008a). Specimens from both the extant (Castillo 1990) and relatively young fossil (e.g., Casablanca B; García-Alix et al. 2008a) populations of *E. quercinus* generally have two centrolophs, with the anterior one often being longer. Together, these observations support a trend towards better-developed centrolophs within a lineage comprising *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus*.

Besides the change in development of the centrolophs, *Eliomys* also shows a trend towards the reduction of the centrolophid and the accessory crests in the lower molars (Castillo 1990; García-Alix et al. 2008a). This observation is borne out by the present data, m1, 2 of *E. yevesi* resemble those of *E. truci* in having a long centrolophid and a well-developed posterotropid. In *E. intermedius*, the centrolophid is still present in 104 out of 106 (98.11 %) m1, 2, but in 26 of these specimens (24.53 %) it is less than half the width of the molar—with the exception of the material from Sète (n=30), which always displays a long centrolophid. The centrolophid is even more reduced in *E. quercinus*, where it is short in 8 (61.54 %) and absent in 5 (38.46 %) out of the 13 studied specimens. A posterotropid is present in 29 out of 30 m1, 2 of *E. truci* (96.67 %), 27 out of 29 m1, 2 of *E. yevesi* (93.10 %), 80 out of 107 m1, 2 of *E. intermedius* (74.76 %), and 1 out of 11 m1, 2 (9.09 %) of *E. quercinus* (2 of the 13 specimens studied here are too damaged or worn to observe this character).

Stratigraphic and geographic range.—MN13–14, Late Miocene–Early Pliocene; Cabriel, Granada, and Alcoy basins of southeastern Spain.

Eliomys intermedius Friant, 1953

Fig. 2M–U.

Material.—AC-0 (Alcoi Cristian 0, MN14): 1 m3 (AC0-88), 1 M1,2 (AC0-87). AL2-C (Alcoi 2C, MN14): 1 m1,2 (AL2C-97), 1 m3 (AL2C-47). AL2-D (Alcoi 2D, MN14): 1 m1,2 (AL2D-290), 1 m3 (AL2D-356), 3 M1,2 (AL2D-291-293). LB-2B (La Bullana 2B, MN14): 4 m1,2 (LB2B-6, LB2B-176, LB2B-242, LB2B-243). 1 m3 (LB2B-179), 1 P4 (LB2B-178), 2 M1,2 (LB2B-241, LB2B-253), 1 M3 (LB2B-177).

Measurements.—See Table 2.

Description

m1, 2.—The occlusal outline of these teeth is trapezoidal or subrectangular. The anterolophid is connected to the protoconid in three specimens, and unconnected in a further three. There is no anterotropid. The metalophid is connected to the metaconid. The centrolophid is long, reaching the metalophid in 3 out of 6 specimens. The metaconid and entoconid are separated. The posterotropid is well developed. The hypoconid is large.

m3.—The occlusal outline of this tooth is sub-trapezoidal. The anterolophid and the protoconid are separated. There is no anterotropid. The metalophid is connected to the metaconid. There is a short centrolophid, not connected to the metalophid (Fig. 2S). The metaconid and entoconid are separated. There is no posterotropid.

P4.—The occlusal outline of this tooth is subtriangular. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous.

M1, 2.—The outline of these teeth are subrectangular or trapezoidal. The anteroloph and paracone are connected basally in AC0-87, but not connected in any of the other specimens. In some specimens (especially AC0-97), the protoloph and metaloph are distinctly sinuous. Both centrolophs are usually present. The posteroloph is connected to the endoloph. There are three roots.

M3.—The occlusal outline of this molar is trapezoidal. The anteroloph is separated from both protoloph and paracone. There is neither an anterotrope nor a posterotrope. The paracone and metacone are high and separated. The protoloph and metaloph are continuous. Both centrolophs are present and well developed, with the postcentroloph being longer and interrupted (Fig. 2P). The endoloph and posteroloph are connected and continuous.

Remarks.—*Eliomys intermedius* from the Early Pliocene (Early Ruscinian/Early Zanclean; Mansino et al. 2013) localities of AL2-C and AL2-D is slightly bigger than specimens from the slightly older localities of AC-0 and LB-2B (Table 2), but all of the specimens from these sites fall within the range of *E. intermedius* from Sète, the type locality of the species (Adrover 1986). The specimens of *E. intermedius* from AC-0, AL2-C, AL2-D, and LB-2B have higher and thicker lingual walls than *E. truci* and *E. yevesi*, sinuous crests, a rounded occlusal outline, and two well-developed centrolophs in the upper molars (M1, 2 from AC-0 and AL2-D, and M3 from LB-2B). These features agree with *E. intermedius.*

Stratigraphic and geographic range.—MN 14, Early Pliocene – early Pleistocene (MQ2) of the Alcoy and Cabriel, and Calatayud-Teruel basins of Spain and the Aquitaine, Paris, and Sud-est basins of France. Other reported occurrences (Bruijn et al. 1970) are dubious.

Discussion

Phylogenetic relationships of Eliomys

Some previous authors (Nadachowski and Daoud 1995) have suggested a relationship of the extant *Eliomys quercinus* with *E. reductus* and *E. assimilis*, both from the German locality of Hammerschmiede (Late Miocene, early Vallesian/Tortonian). However, this is seemingly contradicted by the absence of a clear relationship between *E. reductus*, *E. assimilis* and the likely ancestor of *E. quercinus*, *E. intermedius* (Daams and de Bruijn 1995).

An alternative hypothesis groups *E. reductus* with *E. lafarguei* from Lo Fournas 6C and Lo Fournas 16M (Late Miocene, Vallesian/Tortonian), based on the presence of a continuous endolophid and a trend towards larger size and reduced postcentrolophs, which commonly occurs in glirids (Aguilar et al. 2007). This relationship is further supported by m1,2 being longer than wide in these two taxa (albeit only slightly so in *E. lafarguei*) and showing a tendency towards a shortening of the centrolophid. The latter is isolated in the holotype of *E. reductus*, an m2, and shows a low connection with the metaconid in the m1, whereas in *E. lafarguei* the centrolophid is absent or greatly reduced on m2, and variably isolated or connected to the metaconid at a low level on m1. By contrast, in *E. truci*, *E. yevesi*, *E. intermedius*, and *E. quercinus* these teeth are wider than longer, and the centrolophid is usually connected to the metaconid.

Based on these observations, we agree with Aguilar et al. (2007) in recognizing two distinct lineages within *Eliomys*, comprising *E. lafarguei-E. reductus*, and *E. truci-E. yevesi-E. intermedius-E. quercinus*, respectively. The former lineage may also include *Eliomys* sp. A from the early Turolian of Tortajada A (Teruel, Spain; Weerd 1976), based on its possible relationship with *E. lafarguei* (Aguilar et al. 2007). On the other hand, details of the morphology of *E. assimilis*, which has an accessory crest on M1, 2 suggest that this species does not form part of either of the two main lineages. These observations are confirmed by the results of our cladistic analysis (Fig. 4, Table 3).

[Figs. 4, 5]

Evolutionary process

The oldest record of *Eliomys* is *E. truci* from the Middle Miocene of Solera (Late Aragonian/Early Tortonian; Daams and Freudenthal 1988). However, the identity of this material has been questioned (García-Alix et al. 2008a), thus possibly reducing the earliest occurrence of the genus to *E. truci* from the Late Miocene (early Vallesian/Tortonian) of Pedregueras 2A (Daams and Freudenthal 1988). Several members of the genus co-occur during the Miocene (Fig. 5), which may imply cladogenetic evolution. Thus, Adrover (1986) suggested *E. truci*, including its ancestor *Eliomys* sp. I from Viveros de Pinos (Teruel Basin, north-central Spain; early Turolian/Tortonian), and *Eliomys* sp. II from Aljezar B (Teruel Basin, middle Turolian, Tortonian), to be descendants of an older, yet unknown species of the same genus. A similar logic applies to *E. truci* on the one hand, and *E. yevesi*–*E. intermedius* on the other. Both of these lineages co-existed during the Ruscinian (Zanclean) and the earliest Villanyan (Piacenzian), as is evident at Orrios-3, Sète, Sarrión, Villalba Alta (Adrover 1986), La Gloria 4, Escorihuela (Mein et al. 1990), Moreda-1A, 1B, Rambla Seca 1 (Castillo 1990), TCH-1B and TCH-13 (García-Alix et al 2008a).

Until the first occurrence of *E. quercinus* in the earliest Pleistocene locality of Almenara-Casablanca 1 (Agustí et al. 2011), the only representative of *Eliomys* during the latest Pliocene and early Pleistocene was *E. intermedius* (García-Alix et al. 2008a).

In contrast to the earlier process of cladogenesis, several authors have hypothesized that *E. quercinus* may have arisen from *E. intermedius* through a process of anagenetic evolution (Chaline 1972; Castillo 1990; García-Alix et al. 2008a), involving a reduction in size and a trend towards an unconnected anteroloph and protoloph (Castillo 1990). Extant *E. quercinus* comprises at least eight subspecies, two of which are found in the Iberian Peninsula (Moreno Garrido 1984), the smaller *E. quercinus quercinus*, which inhabits relatively open environments and is characterized by slightly sinuous crests, a continuous endolophid, a small centrolophid, and no accessory crests; and the larger *E. quercinus lusitanicus*, which lives in more closed environments, and is marked by more distinctly sinuous crests, accessory crests, and the absence of both the endolophid and the centrolophids. In the latter two features, *E. quercinus lusitanicus* resembles *E. intermedius*, which even led to the suggestion that the latter should be regarded as a subspecies of *E. quercinus* (Martín-Suárez 1988).

In summary, it therefore seems that the lineage including *E. truci*, *E. yevesi*, and *E. intermedius*, and the extant *E. quercinus* originated and diversified through cladogenesis during the Late Miocene, and Early Pliocene, but then switched to a process of anagenetic evolution during the Late Pliocene and Pleistocene.

[Table 3]

Conclusions

Based on new fossil material from the Alcoy and Cabriel basins of southeastern Spain, as well as material from the Granada Basin previously referred to *E*. aff. *intermedius*, we erect the new species *Eliomys yevesi* sp. nov., similar in size or slightly larger than *E. truci*. *E. yevesi* generally resembles *E. truci* in terms of its morphology, but differs in having better and more frequently developed centrolophs in the upper molars, similar to *E. intermedius*. Based on its size and morphology, we consider the most probable origin of the new species a Late Miocene population of *E. truci* (Fig. 5), likely an ecomorphotype characterized by well-developed centrolophs in the upper molars, and both a long centrolophid and a well-developed posterotropid in the lower molars. *E. yevesi* thus likely forms part of a lineage comprising *E. truci*-*E. yevesi*-*E. intermedius*-*E. quercinus* (to the exclusion of other members of the genus, such as *E. assimilis* and *E. reductus*; Fig. 4), which is characterized by a trend towards the reduction of accessory crests in the lower molars, as well as the development of centrolophs. This arrangement is complemented by a second lineage including *E. reductus* and *E. lafarguei*, marked by an increase in size, a gradual reduction of the postcentroloph and centrolophid, and a trend towards a more quadrangular occlusal outline (lower length-width ratio).

Acknowledgments

We thank Elvira Martín-Suárez (Universidad de Granada, Spain) for her comments, Sacramento Moreno (Doñana Biological Station, Sevilla, Spain) for providing a picture of the occlusal surface of the molars of *Eliomys quercinus quercinus*, Héctor Botella (Universidad de València, Spain) for his help with the cladistic analysis, and Mattijhs Freudenthal (Universidad de Granada, Spain), an anonymous reviewer, and editor Felix G. Marx (University of Otago, New Zealand), for their useful comments and criticism. The field work at Venta del Moro was approved and supported, from 1995 onwards, by the Conselleria de Cultura of the Generalitat Valenciana, with the permission of the Ministerio de Fomento and the Administración de infraestructuras ferroviarias. This investigation was supported by projects GV06/304 and

GVPRE/2008/320 of the Valencian Government, CGL2011-25754 of the Spanish Ministry of Economy and Competitiveness, and RNM 8011 of the Junta de Andalucía.

References

Adrover, R. 1986. Nuevas faunas de roedores en el Mio-Plioceno continental de la regió de Teruel (Espa-a). Interés bioestratigráfico y paleoecológico. 423 pp. Ph.D. thesis Publicaciones del Instituto de Estudios Turolenses, Teruel.

Adrover, R., Mein, P., and Moissenet, E. 1993. Roedores de la transición Mio-Plioceno de l región de Teruel. Paleontologia i Evolució 26–27: 47–84.

Aguilar, J.P., Michaux, J., Delanno, J.J., and Guendon, J.L. 1993. A Late Pliocene roden fauna from Alozaina (Málaga, Spain). Scripta Geologica 103: 1–22.

Aguilar, J.P., Michaux, J., and Lazzari, V. 2007. Lo Fournas 16-M (Miocène supérieur) et L Fournas 16-P (Pliocène moyen), deux nouvelles localités karstiques à Baixas, Sud de la France Partie II – Nouvelles espèces de rongeurs, listes fauniques et remarque sur l'utilisatio biochronologique des faunes karstiques. Géologie de la France 1: 63–81.

Agustí, J., Freudenthal, M., Lacomba, J.I., Martín-Suárez, E., and Nageli, C. 1990. Primero micromamíferos del Pleistoceno superior de la cuenca de Mula (Murcia, Espa-a). Revista de l Sociedad Geológica de Espa-a 3: 289–343.

Agustí, J., Santos-Cubedo, A., Furió, M., Marfá, R. de, Blain, H.A., Oms, O., and Sevilla, P 2011. The late Neogene-early Quaternary small vertebrate succession from the Almenara Casablanca karst complex (Castellón, Eastern Spain): Chronologic and paleoclimatic context Quaternary International 243: 183–191 http://dx.doi.org/10.1016/j.quaint.2010.11.016

Bruijn, H. de, Dawson, M.R., and Mein, P. 1970. Upper Pliocene Rodentia, Lagomorpha an Insectivora (Mammalia) from the isle of Rhodes (Greece). I, II and III. Proceedings van d Koninklijke Nederlandse Akademie van Wetenschappen, Series B 73: 535–584.

Castillo, C. 1990. Paleocomunidades de Micromamíferos de los Yacimientos kársticos de Neógeno Superior de Andalucía Oriental. 255 pp. Unpublished Ph.D. thesis, University o Granada, Granada.

Chaline, J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. 410 pp Unpublished Ph.D. thesis, Cahiers de Paléontologie, Centre Nationale de la Recherch Scientifique, París.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., and Arsuaga, J.L. 1997. Small mammals fro Sima de los Huesos. Journal of Human Evolution 33: 175–190 http://dx.doi.org/10.1006/jhev.1997.0153

Daams, R. 1981. The dental pattern of the Dormice Dryomys, Myomimus, Microdyromys and Peridyromys. Utrech Micropaleontological Bulletins Special Publication 3: 1–115.

Daams, R. and Bruijn, H. de 1995. A classification of the Gliridae (Rodentia) on the basis of dental morphology. Hystrix 6: 3–50.

Daams, R. and Freudenthal, M. 1988. Synopsis of the Dutch-Spanish collaboration program in the Aragonian type area, 1975-1986. In: M. Freudenthal (ed.), Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica Special Issue 1: 3–18.

Filippucci, M.G., Civitelli, M.V., and Capanna, E. 1988a. Evolutionary genetics and systematics of the garden dormouse, Eliomys Wagner, 1840. 1. Karyotype divergence. Bolletino di Zoologia 55: 35–45. http://dx.doi.org/10.1080/11250008809386597

Filippucci, M.G., Rodino, E., Nevo, E., and Capanna, E. 1988b. Evolutionary genetics and systematics of the garden dormouse, Eliomys Wagner, 1840. 2. Allozyme diversity and differentiation of chromosomal races. Bolletino di Zoologia 55: 47–57. http://dx.doi.org/10.1080/11250008809386598

Freudenthal, M. 2004. Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). Treballs del Museu de Geologia de Barcelona 12: 97–173.

Freudenthal, M., Mein, P., and Martín-Suárez, E. 1998. Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. Treballs del Museu de Geologia de Barcelona 7: 11–93.

Friant, M. 1953. Une faune du Quaternaire ancien en France méditerranéenne (Sète, Hérault). Annales de la Société Géologique du Nord 73: 161–170.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., and Freudenthal, M. 2008a. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. Scripta Geologica 136: 1–37.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., and Freudenthal, M. 2008b. Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada basin (southern Spain). Biostratrigraphic and phylogenetic implications. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 248: 183–215. http://dx.doi.org/10.1127/0077-7749/2008/0248-0183

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Martín, J.M., and Freudenthal, M. 2008c. Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continenta deposits of the Granada Basin (southern Spain). Lethaia 41: 431–446. http://dx.doi.org/10.1111/j.1502-3931.2008.00097.x

Gibert, L., Scott, G.R., Montoya, P., Ruiz-Sánchez, F.J., Morales, J., Luque, L., Abella, J., and

Lería, M. 2013. Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. Geology 41: 691–694. http://dx.doi.org/10.1130/G34164.1

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2003. T.N.T.: tree analysis using new technology. Program and documentation. Available from the authors, and from www.zmuc.dk/public/phylogeny

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786. http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x

Holden, M.E. 2005. Family Gliridae. In: D.E. Wilson and D.A. Reeder (eds.), Mammal Species of the World. A Taxonomic and Geographic Reference, 4, 819–841. The John Hopkins University Press, Baltimore.

Krystufek, B. and Kraft, R. 1997. Cranial variation and taxonomy of garden dormice (Eliomys Wagner, 1840) in the circum-Mediterranean realm. Mammalia 61: 411–429.

Mansino, S., Fierro, N., Ruiz-Sánchez, F.J., and Montoya, P. 2013. The fossil rodent faunas of the localities Alcoy 2C and 2D (Alcoy Basin, Spain). Implications for dating the classical locality of Alcoy-Mina. Journal of Iberian Geology 39 (2): 261-284.

Martín-Suárez, E. 1988. Sucesiones de micromamíferos en la depresión de Guadix Baza. 241 pp. Unpublished Ph.D. thesis, University of Granada, Granada.

Mein, P., Moissenet, E., and Adrover, R. 1990. Biostratigraphie du Néogène Supérieur du bassin de Teruel. Paleontologia i Evolució 23: 121–139.

Minwer-Barakat, R., García-Alix, A., Agustí, J., Martín-Suárez, E., and Freudenthal, M. 2009. The micromammal fauna from Negratín-1 (Guadix basin, Southern Spain): new evidence of african-iberian mammal exchanges during the late Miocene. Journal of Paleontology 83: 854–879.
http://dx.doi.org/10.1666/09-009.1

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., Esteban Trivigno, S. de, and Moyà-Solà, S. 2011. Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, Northeastern Spain) and biochronological implications. Journal of Vertebrate Paleontology 31 (4): 849–865. http://dx.doi.org/10.1080/02724634.2011.576730

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M., and Viseras, C. 2012. Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. Lethaia 45: 594–614. http://dx.doi.org/10.1111/j.1502-3931.2012.00324.x

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J.V., Marín, M.D., and Ruiz-Sánchez, F.J. 2006. Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de

Venta del Moro, Valencia. Estudios Geológicos 62: 313–325. http://dx.doi.org/10.3989/egeol.0662128

Morales, J. 1984. Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo. 340 pp. Editorial Universidad Complutense, Madrid.

Moreno Garrido, S. 1984. Biometría, Biología y dinámica poblacional del lirón careto, Eliomys quercinus (L), en Do-ana, sureste de Espa-a. 310 pp. Unpublished Ph.D. thesis, Universidad de Granada, Granada.

Nadachowski, A. and Daoud, A. 1995. Patterns of myoxid evolution in the Pliocene and Pleistocene of Europe. Hystrix 6: 141–149.

Robles, F. 1970. Estudio estratigráfico y paleontológico del Neógeno del río Júcar. 275 pp. Unpublished Ph.D. thesis, Universitat de València, Valencia.

Sesé, C. 2006a. Los roedores y lagomorfos del Neógeno de Espa-a. Estudios Geológicos 62: 429–480.
http://dx.doi.org/10.3989/egeol.0662138

Sesé, C. 2006b. Micromamíferos (Rodentia, Insectivora, Lagomorpha y Chiroptera) de la Pe-a de Estebanvela (Segovia). In: S. Ripoll Cacho and F. Mu-oz (eds.), La Pe-a de Estebanvela (Estebanvela-Ayllón, Segovia). Grupos Magdalenienses en el Sur del Duero, Memorias, Junta de Castilla y León. Arqueología en Castilla y León 17: 145–165.

Sesé, C. and Villa, P. 2008. Micromammals (rodents and insectivores) from the early Late Pleistocene cave site of Bois Roche (Charente, France): Systematics and paleoclimatology. Geobios 41: 399–414. http://dx.doi.org/10.1016/j.geobios.2007.10.005

Sesé, C., Panera, J., Rubio-Jara, S., and Pérez-González, A. 2011. Micromamíferos del Pleistoceno Medio y Pleistoceno Superior en el Valle del Jarama: yacimientos de Valdocarros y HAT (Madrid, Espa-a). Estudios Geológicos 67 (1): 131–151. http://dx.doi.org/10.3989/egeol.40290.127

Weerd, A. van de 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. Utrech Micropaleontological Bulletins, Special Publication 2: 1–217.

Wagner, A. 1840. Beschreibung einiger neuer Nager, welche auf der Reise des Herrn Hofraths v. Schubert gesammelt wurden, mit Bezugnahme auf einige andere verwandte Formen. Abhandlungen der Math.-Phys. Klasse der Bayer. Akademie der Wissenschaften 3: 175–218.

Appendix 1

Dental characters included in the cladistic analysis:

Lower molars: 1, Average value of length/width ratio of m1,2: (0) always less than 1, molars are clearly wider than long; (1) variably above or below 1, molars are sub-quadrangular to sub-rectangular in occlusal outline; (2) always higher than 1, molars are clearly longer than wid ; 2, Endolophid: (0) always discontinuous; (1) continuous in some specimens; 3, Anterotropid: (0) always absent; (1) present in some specimens; 4, Posterotropid: (0) always absent; (1) present in some specimens; 5, Centrolophid: (0) absent or short (less than half the width of the molar); (1) usually long (half the width of the molar or longer).

Upper molars: 6, Presence of both centrolophs on M1,2: (0) absent; (1) rare (less than 30%); (2) common (30% or higher); 7, Presence of both centrolophs on M3: (0) absent; (1) rare (less than 30%); (2) common (30% or higher); 8, Presence of an accessory crest in the upper molars: (0) absent; (1) present in some specimens; 9, Presence of two accessory crests in some upper molars; (0) absent; (1) present in some specimens; 10, Size: (0) clearly smaller on average than *E. truci*, with some dental elements out of the size range of this species (see Fig. 3); (1) equal or largely the same as *E. truci*; (2) clearly bigger on average than *E. truci*, with some dental elements out of the size range of this species.

See Table 3 for the resulting data matrix.

TABLE 1. Locality abbreviations. Square brackets denote modifiers indicating particular levels (e.g. C, D) or years of collection.

Acronym	Name [levels/ year of collection]
MGUV	
ABS-3A	Alcoi Barranc Sud 3A
AC-0	Alcoi Cristian 0
AF-1	Alcoi Forn 1 [2006, 2007]
AL2	Alcoi 2 [C, D]
LB-2B	La Bullana 2B
VVm	Venta del Moro [A–D]
DEPUG	
CLC-3B	Calicasas 3B
OUT-1	Otura 1
PUR	Purcal [4, 23, 23A, 25]
TCH	Tollo de Chiclana [1B, 3, 13]

TABLE 2. Measurements (in mm) of the (pre-)molars of *Eliomys yevesi* sp. nov. from Venta del Moro and Alcoy, and of *E. intermedius* from Alcoy and La Bullana. Abbreviations: Ey, *Eliomys yevesi*; Ei, *Eliomys intermedius*; Par, parameter; Sp., species.

Element	Sp.	Locality	P	n	min.	Mean	Max.
p4	Ey	VVmA	L	2	1.05	1.06	1.06
			W	2	0.95	0.99	1.03
m1/m2	Ey	VVmA	L	11	1.10	1.16	1.22
			W	11	1.14	1.30	1.47
	Ey	VVmB	L	1	-	1.06	-
			W	1	-	1.24	-
	Ey	VVmBC	L	2	1.12	1.16	1.19
			W	2	1.30	1.35	1.40
	Ey	ABS3A	L	1	-	1.30	-
			W	1	-	1.45	-
	Ey	AF1	W	1	-	1.46	-
	Ei	AL2C	W	1	-	1.61	-
	Ei	AL2D	L	1	-	1.56	-
			W	1	-	1.71	-
	Ei	LB2B	L	2	1.42	1.47	1.51
			W	2	1.50	1.64	1.77
m3	Ey	VVmA	L	6	0.95	1.03	1.12
			W	6	1.06	1.16	1.23
	Ey	VVmBC	L	2	-	1.01	-
			W	1	-	1.17	-
	Ei	AC0	L	1	-	1.31	-
			W	1	-	1.41	-
	Ei	AL2D	L	1	-	1.34	-
			W	1	-	1.54	-
D4	Ey	VVmA	L	1	-	0.75	-
			W	1	-	0.78	-
P4	Ey	VVmA	L	3	0.84	0.86	0.87
			W	3	1.25	1.27	1.29
	Ei	LB2B	L	1	-	1.08	-
			W	1	-	1.48	-
M1/2	Ey	VVmA	L	12	1.01	1.11	1.22
			W	11	1.33	1.41	1.49
	Ey	VVmBC	L	1	-	0.99	-
			W	1	-	1.34	-
	Ey	VVmD	L	2	1.17	1.20	1.22
			W	2	-	1.47	-
	Ey	AF1	W	1	-	1.38	-
	Ei	AL2D	L	2	1.38	1.48	1.58
			W	2	1.74	1.85	1.95
	Ei	LB2B	L	1	-	1.25	-
			W	1	-	1.79	-
M3	Ey	VVmA	L	7	0.85	0.95	1.00
			W	8	1.21	1.28	1.37
	Ey	VVmC	L	1	-	0.96	-
			W	1	-	1.25	-
	Ei	LB2B	L	1	-	1.27	-
			W	1	-	1.52	-

TABLE 3. Cladistic data matrix for *Eliomys*, including lower (1 to 4) and upper (5 to 8) molar dental characters. Abbreviations: *E. q.*, *Eliomys quercinus*.

Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
E. assimilis	2	0	0	1	1	2	2	1	0	0
E. reductus	2	1	0	0	1	2	0	0	0	0
E. lafarguei	1	1	0	1	0	1	0	0	0	0
E. truci	0	0	0	1	1	1	0	0	0	1
E. yevesi	0	0	0	1	1	2	2	0	0	1
E. intermedius	0	0	0	1	1	2	2	0	0	2
E. q. quercinus	0	1	0	0	0	2	2	0	0	2
E. q. lusitanicus	0	0	0	1	0	2	2	0	0	2
D. nitedula	1	1	1	1	1	2	2	1	1	0

Figure captions

Fig. 1. Location of the Venta del Moro, Alcoy, Purcal and Calicasas sites that have yielded specimens of *E. yevesi* sp. nov. The dormouse symbol indicates the location of Venta del Moro, the type locality of *Eliomys yevesi* sp. nov. Abbreviations: ABS-3A, Alcoi Barranc Sud 3A; AF-1, Alcoi Forn 1; CLC-3B, Calicasas 3B; PUR-4, Purcal 4; VM, Venta del Moro. [planned for column width]

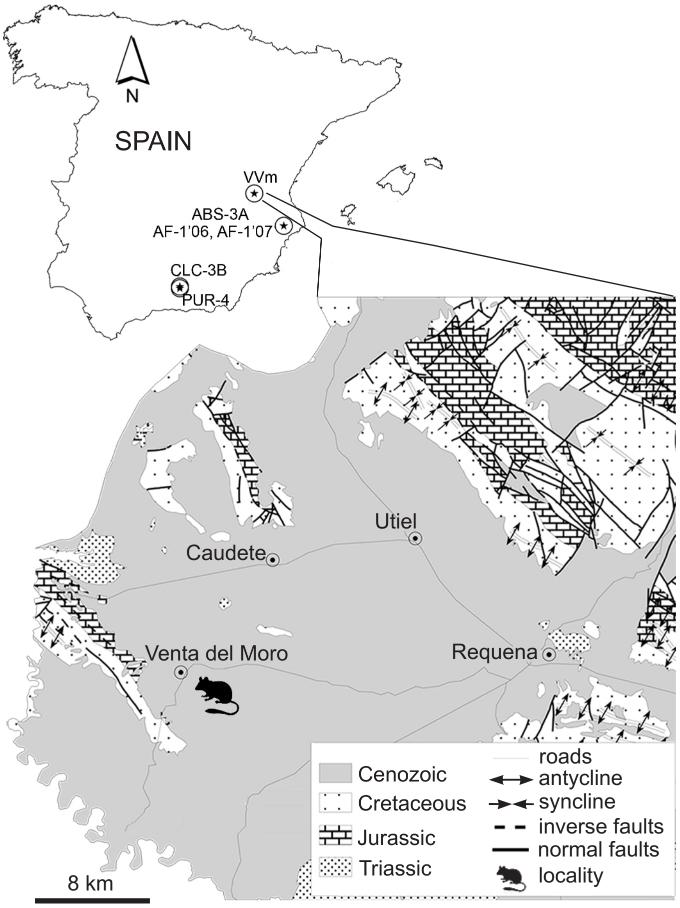
Fig. 2. The glirid mammals *Eliomys yevesi* sp. nov. (A–L) from Venta del Moro (VM-A and BC), Alcoi Barranc Sud 3A (ABS-3A), Alcoi Forn 1’06 (AF-1’06) and Alcoi Forn 1’07 (AF-1’07), and *E. intermedius* Friant, 1953 (M–U) from Alcoi Cristian 0 (AC-0), La Bullana 2B (LB-2B) and Alcoi 2D (AL2-D). **A**. VVmA-42, right p4. **B**. VVmA-1, right m1, 2. **C**. VVmA-6, right m1, 2. **D**. VVmBC-5, right m3. **E**. VVmA-40, left P4. **F**. VVmA-16, right M1, 2. **G**. VVmA-25, right M1,2. **H**. VVmA-13, left M3. **I**. VVmA-14; left M3. **J**. ABS3A-38, right m1, 2. **K**. AF1’06-190, right m1, 2. **L**. AF1’07-36, left M1, 2. **M**. AC0-88, right m3. **N**. LB2B-176, right m1, 2. **O**. LB2B-241, left M1, 2. **P**. LB2B-177, left M3. **Q**. LB2B-178, left P4. **R**. AL2D-290, left m1, 2. **S**. AL2D-356, left m3. **T**. AL2D-291, right M1, 2. **U**. AL2D-293, left M1, 2. [planned for page width]

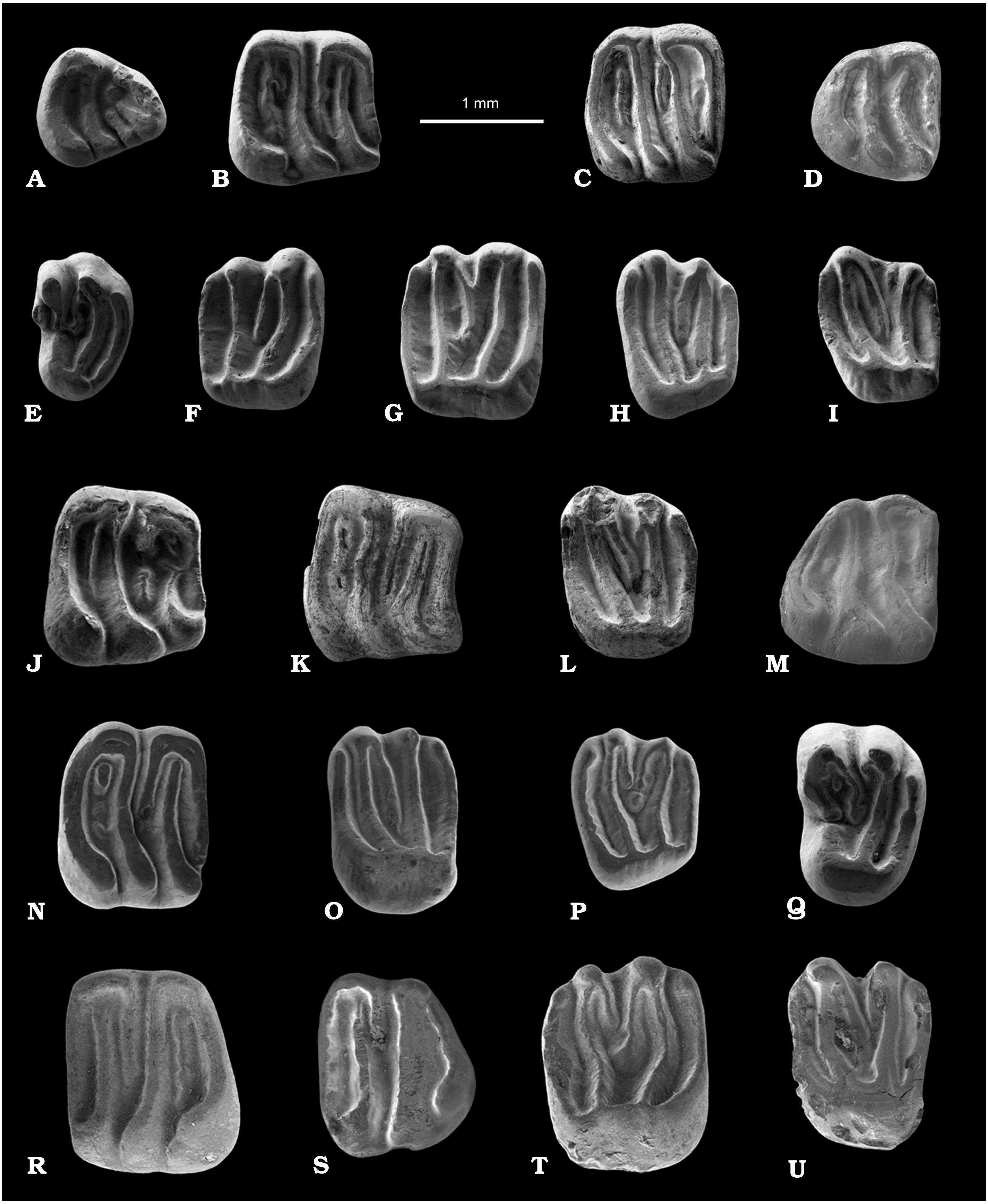
Fig. 3. Comparison of length and width measurements the teeth (**A**, p4; **B**, P4; **C**, m1, 2; **D**, M1, 2; **E**, m3; **F**, M3) of *E. truci*, from Aljezar B, Hautimagne, Los Mansuetos, Orrios, Sarrión, Sete, Villalba Alta (Adrover 1986), Concud 2 and 3, Concud Barranco de los Calaveros, Los Mansuetos, Masada del Valle 2, 5 and 7, Tortojada A and C (Weerd 1976), DHS-1 and 16, PUR-23, 24, and 25A, OTU-1, TCH-1B and 13 (García-Alix et al. 2008a), Negratín-1 (Minwer-Barakat et al. 2009); Moreda 1A, 1B, Rambla Seca 1 (Castillo 1990) and Puente Minero (Alcalá et al. 1991); *E. yevesi* sp. nov. from VM-A, B, BC, C and D, ABS-3A, AF-1’06, AF-1’07, CLC-3B and PUR-4; *E. intermedius* from Arquillo 3, Sete, Orrios 3, Villalba Alta (Adrover 1986), Escorihuela, Orrios (Weerd 1976), PUR-13, TCH-1 and 1B, TCH3, TCH-13 (García-Alix et al. 2008), Moreda 1A, 1B, Bélmez 1 and Rambla Seca A1 and A2 (Castillo 1990) and Alozaina (Aguilar et al. 1993); *E. quercinus* from Vallparadís and Cal Guardiola (Minwer-Barakat et al. 2011, Baños de Mula (Agustí et al. 1990), Peña de Estebanvela (Sesé 2006b), Valdocarros (Sesé et al. 2011), Sima de los Huesos (Cuenca-Bescós et al.

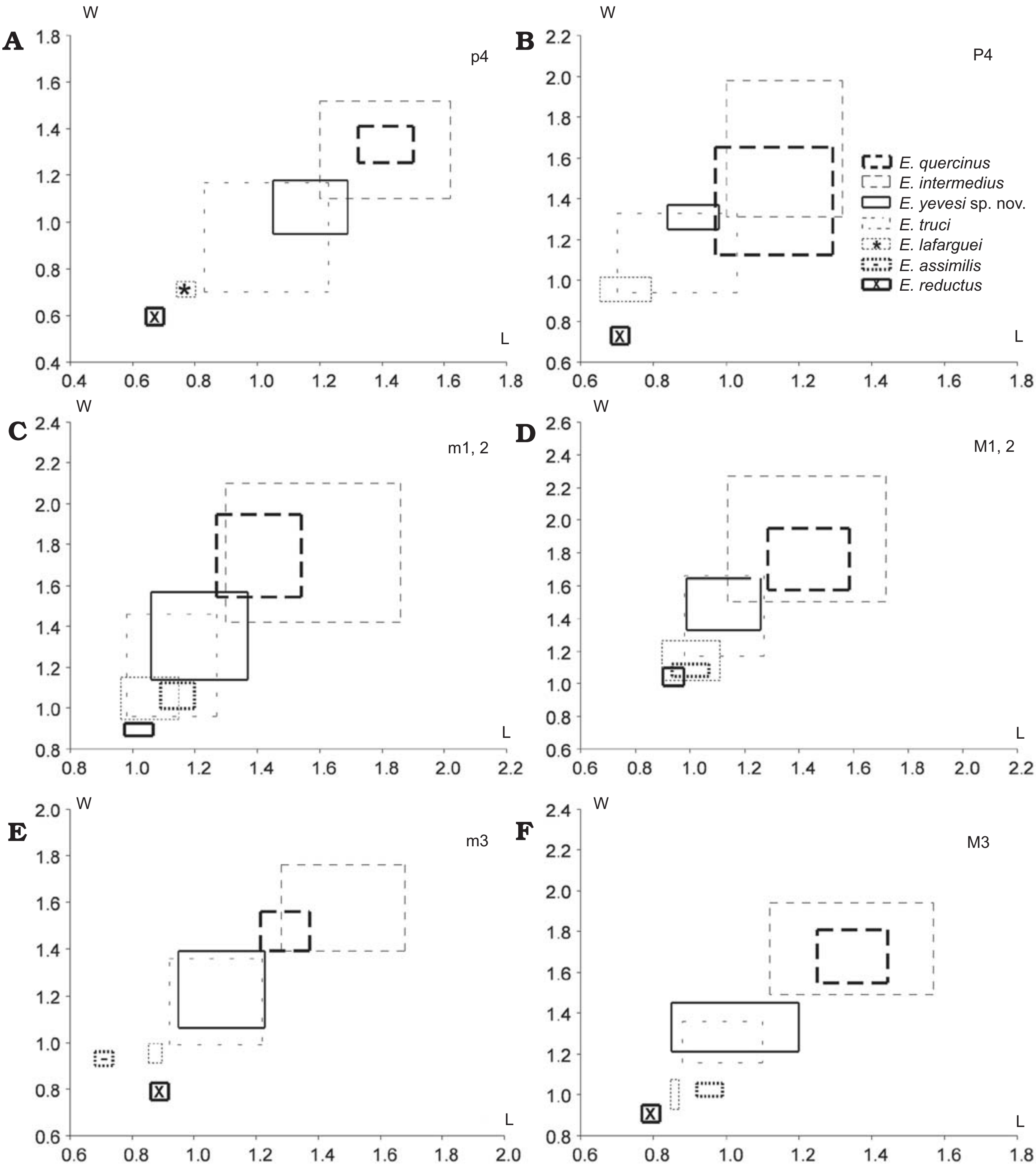
1997), Bois Roche (Sesé and Villa 2008), Santenay (Chaline 1972); and *E.* aff. *quercinus* from Huétor Tájar 1 and 8. [planned for page width]

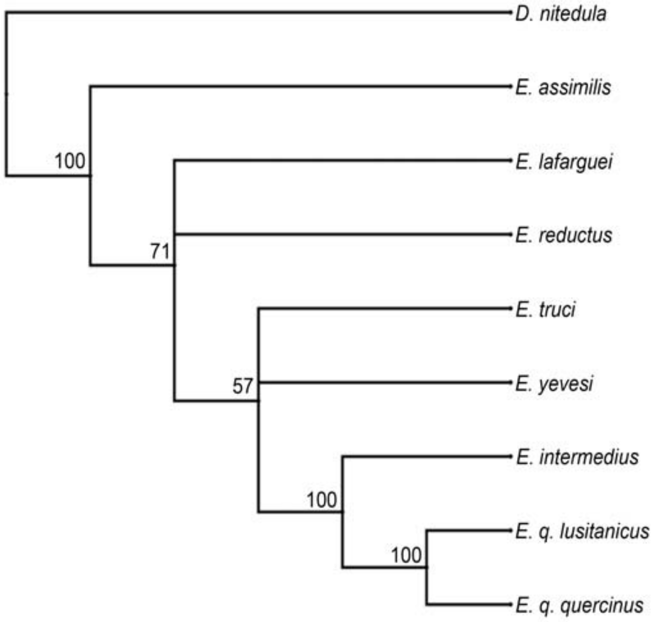
Fig. 4. 50% majority rule consensus of the seven most parsimonious trees (L = 21, retention index = 0.619, consistency index = 0.619) resulting from the phylogenetic analysis. Numbers next to clades indicate the percentage of most parsimonious trees in which the clade was recovered. The extant glirid *Dryomys nitedula*, a form closely related to *Eliomys*, was chosen as outgroup. [planned for column width]

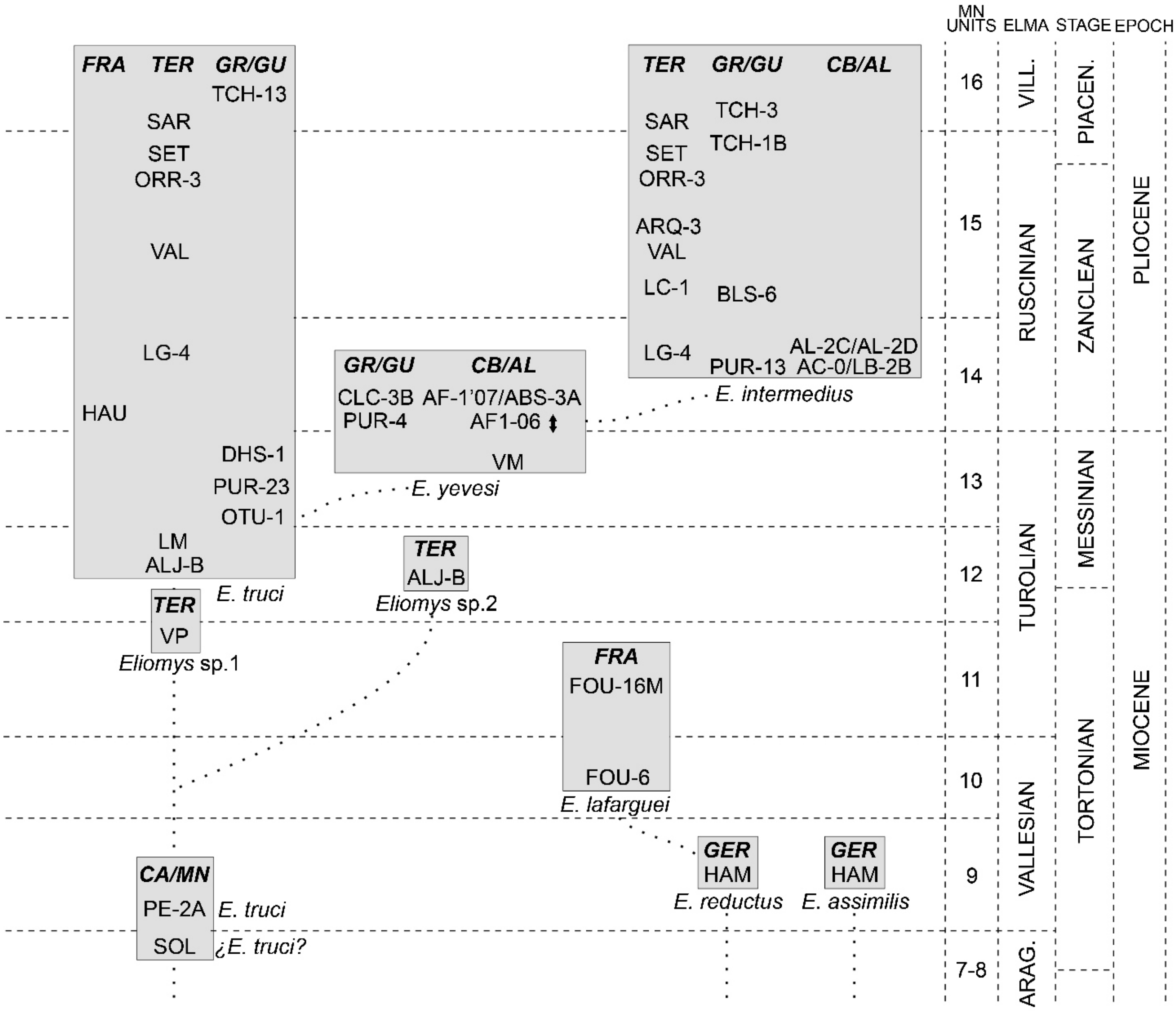
Fig. 5. Early Vallesian (early Tortonian) to early Villanyan (Piacenzian) stratigraphic distribution and proposed phylogenetic relationships of the genus *Eliomys* (modified from García-Alix et al. 2008a). Abbreviations: AC, Alcoy Cristian; AF, Alcoi Forn; AL, Alcoy; ALJ, Aljezar; ARAG., Aragonian; BLS, Barranco de Blas; CA/MN, Calatayud-Montalbán Basin; CB/AL, Cabriel and Alcoy Basins; CLC, Calicasas; DHS, Dehesa; FOU, Lo Fournas; FRA, France; GR/GU, Granada and Guadix Basins; HAU, Hautimagne; Ham, Hammerschmiede; LB, La Bullana; LC, Lomas de Casares; LG, La Gloria; LM, Los Mansuelos; ORR, Orrios; OTU, Otura; PE-2A, Pedregueras 2A; PIACEN, Piacencian; PUR, Purcal; SAR, Sarrión; SET, Sète; SOL, Solera; TCH, Tollo de Chiclana; TER, Teruel Basin; VAL, Villaba Alta; VILL., Villanyan; VM, Venta del Moro; VP, Viveros de Pino. [planned for page width]


N
SPAIN
VVm
ABS-3A
AF-1'06, AF-1'07
CLC-3B
PUR-4
Utiel
Caudete
Venta del Moro
Requena
Cenozoic
Cretaceous
Jurassic
Triassic
roads
antycline
syncline
inverse faults
normal faults
locality
8 km


1 mm
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U


A
W
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
p4
L
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
B
W
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
P4
L
0.6
0.8
1.0
1.2
1.4
1.6
1.8
E. quercinus
E. intermedius
E. yevesi sp. nov.
E. truci
E. lafarguei
E. assimilis
E. reductus
C
W
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
m1, 2
L
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
D
W
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
M1, 2
L
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
E
W
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
m3
L
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
F
W
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
M3
L
0.6
0.8
1.0
1.2
1.4
1.6
1.8


D. nitedula
E. assimilis
E. lafarguei
E. reductus
E. truci
E. yevesi
E. intermedius
E. q. lusitanicus
E. q. quercinus
100
71
57
100
100


MN UNITS
ELMA
STAGE
EPOCH
FRA
TER
GR/GU
TCH-13
SAR
SET
ORR-3
VAL
LG-4
HAU
DHS-1
PUR-23
OTU-1
LM
ALJ-B
E. truci
TER
GR/GU
CB/AL
SAR
SET
ORR-3
TCH-3
TCH-1B
ARQ-3
VAL
LC-1
BLS-6
LG-4
AL-2C/AL-2D
PUR-13
AC-0/LB-2B
E. intermedius
GR/GU
CB/AL
CLC-3B
AF-1'07/ABS-3A
PUR-4
AF1-06
VM
E. yevesi
TER
ALJ-B
Eliomys sp.2
TER
VP
Eliomys sp.1
FRA
FOU-16M
FOU-6
E. lafarguei
GER
HAM
E. reductus
GER
HAM
E. assimilis
CA/MN
PE-2A
E. truci
SOL
¿E. truci?
16
15
14
13
12
11
10
9
7-8
VILL.
RUSCINIAN
TUROLIAN
VALLESIAN
ARAG.
PIACEN.
ZANCLEAN
MESSINIAN
TORTONIAN
PLIOCENE
MIOCENE