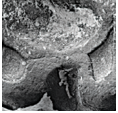


# Diggers, gliders and runners: The squirrels from the Ribesalbes-Alcora Basin (East of Spain)

VICENTE D. CRESPO, ANA FAGOAGA, FRANCISCO J. RUIZ-SÁNCHEZ & PLINI MONTOYA



The Campisano Ravine in the Ribesalbes-Alcora Basin (Spain, early Miocene, biozone C, MN 4) yielded a relatively diverse assemblage of squirrels, composed by the ground squirrels *Heteroxerus rubricati*, *Atlantoxerus blacki* and *Aragoxerus* sp. the marmotines *Palaeosciurus* cf. *sutteri*, *Spermophilinus* sp., Marmotini indet. and the flying squirrel *Aliveria* cf. *luteyni*. *Heteroxerus rubricati*, *Atlantoxerus blacki* and *Spermophilinus* are typical early Miocene species from the Iberian Peninsula, and in this work we increase the knowledge of the variability of them. In MN4, the genus *Aragoxerus* is reported for the first time in the Iberian Peninsula, and, apart from France, it is its only record in Europe. We report here the first record of the species *Palaeosciurus* cf. *sutteri* in the Iberian Peninsula, and one of the oldest in Europe. The occurrence of *Aliveria* cf. *luteyni* marks the first record of the genus *Aliveria* in Western Europe. Additionally, the palaeoecological significance of this assemblage is discussed. • Key words: Sciuridae, Miocene, Aragonian, Iberian Peninsula, paleoecology, biostratigraphy.

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The family Sciuridae currently comprises more than 273 species and 50 genera, distributed in all continents except Australia and Antarctica. This group, together with the mountain beavers (Aplodontiidae) constitute the Suborder Sciurida in the order Rodentia (McKenna & Bell 1997, Churakov *et al.* 2010).

In the Miocene the sciurids experienced a big ecomorphologic diversification (with terrestrial, arboreal and gliding forms) as well as a substantial increase in diversity, with up to six species coexisting in some sites. In the Plio-Pleistocene transition, this family underwent a crisis, with less genera surviving in Europe than before, reflecting the deterioration of the climate (de Bruijn 1999). In the Iberian Peninsula, the dominant ecomorphological type during the early Miocene are the ground squirrels, with a combined representation of the genera *Heteroxerus* and *Atlantoxerus* at many sites, accompanied to a lesser degree by *Aragoxerus*, *Spermophilinus* and *Palaeosciurus* (Cuenca-Bescós 1988, Aldana-Carrasco 1992, Ruiz-Sánchez *et al.* 2003, Van der Meulen *et al.* 2012, Casanovas-Vilar *et al.* 2016,

García-Paredes *et al.* 2016, Hernández-Ballarín & Peláez-Campomanes 2018).

The fossil flying squirrels along the early Miocene of the Iberian Peninsula are restricted to a few records, assigned to different genera (Casanovas-Vilar *et al.* 2015). The oldest record corresponds to *Blackia miocaenica* Mein, 1970 from the Ramblan of Rubielos de Mora 2 (MN3, Rubielos de Mora Basin; de Bruijn & Moltzer 1974) and Buñol (MN4, Magro Basin; Robles *et al.* 1991); in the latter locality it occurs together with another flying squirrel, *Miopetaurista diescalidus* Daams, 1977. Finally, the genus *Albanensia* is recorded in the sites of Barranco de Candel (MN4, Margo Basin; Adrover *et al.* 1987) and Montalvos 2, as *Albanensia* cf. *sansaniensis* (Lartet, 1851) in this site (Hordijk *et al.* 2015).

This paper continues a serie of works that deal with small mammals from the Ribesalbes-Alcora Basin. Among the published results, some worth mentioning are: the southernmost documented record of the herpetotheriid *Amphiperatherium frequens* (von Meyer, 1846) (Crespo

*et al.* 2020, Furió *et al.* 2012); the new species *Plesiodimylus ilercavonicus* Crespo, Furió, Ruiz-Sánchez & Montoya, 2018 (Crespo *et al.* 2018); the abundant remains of talpids (Crespo *et al.* 2019b); the diversity of soricids (Crespo *et al.* 2019c) and erinaceids (Crespo *et al.* 2020). The rest of groups will be published soon.

## Geographic and geologic setting

The materials studied here have been recovered near the village of Araia d'Alcora (Ribesalbes-Alcora Basin, eastern Iberian Peninsula; Fig. 1; Agustí *et al.* 1988, Crespo *et al.* 2019a). The synthetic stratigraphic column (Fig. 1) is composed of seven sections, which have been named, from oldest to youngest (with some overlap) as: Mas dels Coixos, Mas de Torner, Araia Cantera Sud, Barranc de Campisano, Foieta la Sarra, Mas d'Antolino B and Corral de Brisca. The sediment beds mainly consist of grey and yellow mudstones, limestones and sandstones, about 100 m thick (Crespo *et al.* 2019a), and are included in the "Unit Three" of the Ribesalbes-Alcora Basin *sensu* Anadón (1983).

The sites with mammalian remains from the Ribesalbes-Alcora Basin were first reported by Agustí *et al.* (1988). Until now, up to 45 sites have been described from the seven sections detailed in Crespo *et al.* (2019a). The studied sections represent a stratigraphic range corresponding to the local biozone C from the Calatayud-Daroca Basin (MN4, lower Aragonian, early Miocene), in the chronologic interval 16.5–16 Ma according to Van der Meulen *et al.* (2012) (Crespo *et al.* 2019a).

## Material and methods

The photographic images of the specimens were taken with a Scanning Electron Microscope HITACHI 4800 at the Servei Central de Suport a la Investigació Experimental (SCSIE) and the optical photographic image was taken with a Leica DMS1000 from the Department of Botany and Geology, both in the University of València Estudi General (UVEG). The fossil material is stored at the Museu de la Universitat de València d'Història Natural (MUVHN), Burjassot, Spain.

We have used the nomenclature and the measuring methods of Cuenca-Bescós (1988) for the sciurids. Measurements are given in millimetres and were taken using a Leica MZ75 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. Lower teeth are designated with lower-case letters (lower incisor – i; lower deciduous – dp4; lower premolar – p4; lower molars – m1, m2 and m3) and upper teeth are written in upper case letters (upper incisor – I; upper deciduous – DP4; upper premolar –

P4; upper molars – M1, M2 and M3). Throughout the text, the names of the sections often appear abbreviated as follows: MCX – Mas dels Coixos; MTR – Mas de Torner; BC – Barranc de Campisano; FS – Foieta la Sarra; MAB – Mas d'Antolino B; CBR – Corral de Brisca.

## Results

Class Mammalia Linnaeus, 1758  
Order Rodentia Bowdich, 1821  
Suborder Sciuromorpha Brandt, 1855  
Infraorder Scurida Carus, 1868  
Family Sciuridae Fischer, 1817  
Subfamily Xerinae Osborn, 1910  
Tribe Xerini Murray, 1866

### Genus *Heteroxerus* Stehlin & Schaub, 1951

#### *Heteroxerus rubricati* Crusafont, Villalta & Truyols, 1955

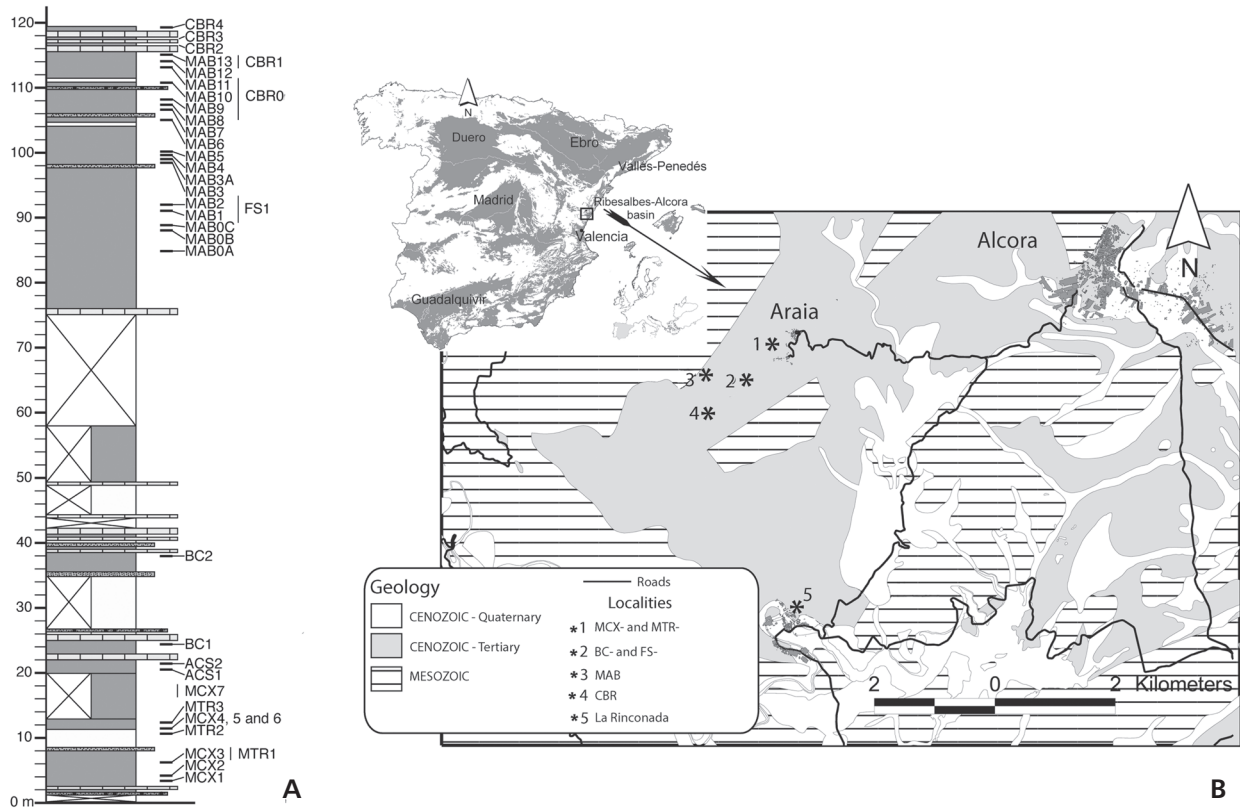
Figure 2

*Material.* – MCX3 – 1 m1, 1 M1; MTR2 – 1 m1; MTR3 – 1 m1; BC1 – 1 dp4, 1p4, 1 m1, 2 m2, 1 DP4; FS1 – 2 m1, 1 DP4, 1 M1; MAB3 – 1 dp4, 2 p4, 1 m1, 2 m2, 3 M1, 4 M2, 2 M1/M2; MAB5 – 1 M1; MAB8 – 1 m3; MAB11 – 1 DP4; CBR0B – 1 m1, 1 DP4, 1 M1/M2; CBR0C – 1 DP4.

*Measurements.* – See Tab. 1.

*Description.* – dp4 (Fig. 2A, B): The outline is subtriangular. The metaconid and the protoconid are the largest cusps and they are located next to each other. The anteroconulid is small and the metalophid is not present in the specimen from BC1, while in the tooth from MAB3 is small. The metaconid and the entoconid are connected by the mesolophid. The protoconid and the mesoconid are linked by a crestid. The entolophid is complete and connects the hypoconid and the entoconid. In the material from BC1 the entolophid shows a narrowing near the entoconid. The hypoconulid is well developed and incomplete. The roots are divergent.

p4 (Fig. 2C, D): The outline is subtriangular, shorter than the dp4. The metaconid and the protoconid are the largest cusps. In MAB3 the anteroconulid is spur-shaped, while in the other specimens it is reduced. The mesolophid could be a crestid that connected the metaconid and the entoconid (in one tooth) or a spur of the metaconid (in the other tooth). A crestid connects the protoconid and the mesoconid. In MAB3 the entolophid is complete and connects the hypoconulid and the entoconid (in one tooth) or it is incomplete (in the other tooth); in the BC1 specimen it is curved and it does not reach the posterolophid, and the



**Figure 1.** A – synthetic column of the Campisano ravine with the situation of the studied sites. • B – Spanish Cenozoic basins, with location of the Ribesalbes-Alcora Basin and the schematic distribution of sediments and the position of the studied fossil sites. Abbreviations: ACS – Araia Cantera Sud; BC – Barranc de Campisano; CBR – Corral de Brisca; FS – Foietta la Sarra; MAB – Mas d’Antolino B; MCX – Mas dels Coixos; MTR – Mas de Torner. La Rinconada is the classical Fossil-Lagerstätte site with remains of insects, plants and amphibians. Modified from Crespo *et al.* (2018, 2019a). Scale bar is 2 km.

hypoconulid is absent. The posterolophid is incomplete, and in BC1 it is divided.

m1 (Fig. 2E–G): The outline is subrectangular. The four principal cusps are well developed, and the metaconid is the largest one. The anteroconulid is well developed in MAB3 and MCX3; in MTR3 it is isolated, in FS1 it may be well developed (in one tooth) or not (in the other tooth), and in CBR0B it is almost isolated. In MAB3 and MCX3 the anterolophid and the anterior cingulid are short and isolated in their distal parts; in MTR3 the anterolophid is absent and the anterior cingulid is very small; in FS1 it is long and surrounds the protoconid; in CBR0B it is short and connected to the metaconid, and with a short anterior cingulid connected to the protoconid. The metalophid is curved and complete in the material from MAB3 and MCX3; in the teeth from MTR2 and FS1 it is shorter and its ending is isolated; in the tooth from MTR3 it is sigmoidal. The mesolophid in MAB3, MCX3 and FS1 is a spur of the entoconid, while in MTR2 it is absent. The mesoconid and the hypoconulid are not present in MAB3 and MCX3, but there is a crest that joins the hypoconid and the protoconid; in FS1 and CBR0B this crest is narrower

near the hypoconid. The entolophid is complete and sigmoidal in MAB3 and MCX3, while in MTR3 it is curved and connected to a small hypoconulid; in FS1 it is complete and straight and in CBR0B it is curved. The posterolophid is not connected to the entoconid. In FS1 the hypoconulid is an enlargement of a complete posterolophid.

m2 (Fig. 2H–J): The outline is quadrate. The four principal cusps are well developed, and the metaconid is the largest one. The anteroconulid is well developed. The anterolophid is long and connected to the metaconid. The anterior cingulid is short and directed downward, towards the base the crown, in MAB3, while in BC1 it is connected to the protoconid and the metalophid. The metalophid is short and isolated. In MAB3, the mesolophid is absent (in one tooth) or it merely consists in a small enlargement (in the other tooth). The mesoconid is a small enlargement. In MAB3, the crest that connects the protoconid and the metaconid is narrower near the hypoconid (in one tooth) or continuous (in the other tooth). The entolophid is complete and curved; it is connected to the complete posterolophid. The hypoconid is not present. One of the teeth from BC1 is larger in size (Tab. 1).

m3 (Fig. 2K): A fragmented tooth with a rounded posterior side. The anterior cingulid is connected to the protoconid. The metalophid is short and isolated in its ending part. The mesoconid is an enlargement of the crestid that connects the protoconid with the hypoconid, and shows a narrowing near the hypoconid. The posterolophid is well developed.

DP4 (Fig. 2L, M): The outline is subtriangular, with a protruding front end. The anteroloph is curved, with a weak contact with the protocone and isolated from the small paracone. The protoloph is short and connected to a big protocone. The protocone from CBR0C and BC1 is closer to the centre of the tooth than in the material from the other sites. The mesostyle is weak. The metacone is weakly developed. The metaconule is larger than the metacone, and it is almost isolated, only slightly connected to the metacone and the posteroloph, which is well developed, and connected to the hypocone and the metacone. In the material from CBR0C and BC1 the posteroloph is weaker than in the other sites and connected directly with the metaconule. The hypoconule is absent. The tooth from CBR0B is large in size.

M1 (Fig. 2N, O): The outline is quadrate, with four principal cusps. In MAB3, the anteroloph it is long and straight and in one specimen is connected to the paracone, and in the other it is not connected. The anteroconule is a small enlargement. The protoloph is straight, and downwards oriented in the middle of the tooth, and it connects the paracone with the protocone. The mesostyle is weak. The protocone and the hypocone are connected by a strong crest. In MAB3, the metaloph is strong, straight and either long (in one tooth) or short (in the other tooth). The metaconule is weak and connected to the posteroloph, except in the material from MAB5 where it is connected to the crest that runs from the protocone to the hypocone. In MAB3 the posteroloph may be, either long and strong (1 out of 2 specimens) or short (1 out of 2), and either connected to the metacone (1 out of 2) or not (1 out of 2).

M2 (Fig. 2P, Q): the outline is subquadrate, with four principal cusps. The anteroloph is long and straight, the anteroconule is a small enlargement that becomes narrower next to the protocone. The protoloph is straight and well developed, and it connects the paracone with the protocone. The mesostyle is either small, in one specimen, or absent, in another. The protocone and the hypocone are connected by a crest, which can be well developed (2 out of 4) or weak (2 out of 4). The metacone is well developed. The metaloph may be weak (1 out of 3) or strong (2 out of 3). The metaconule is either well developed (3 out of 4) or small (in the remaining tooth), and it is connected to the posteroloph. The last crest can be short (1 out of 4) or long (3 out of 4).

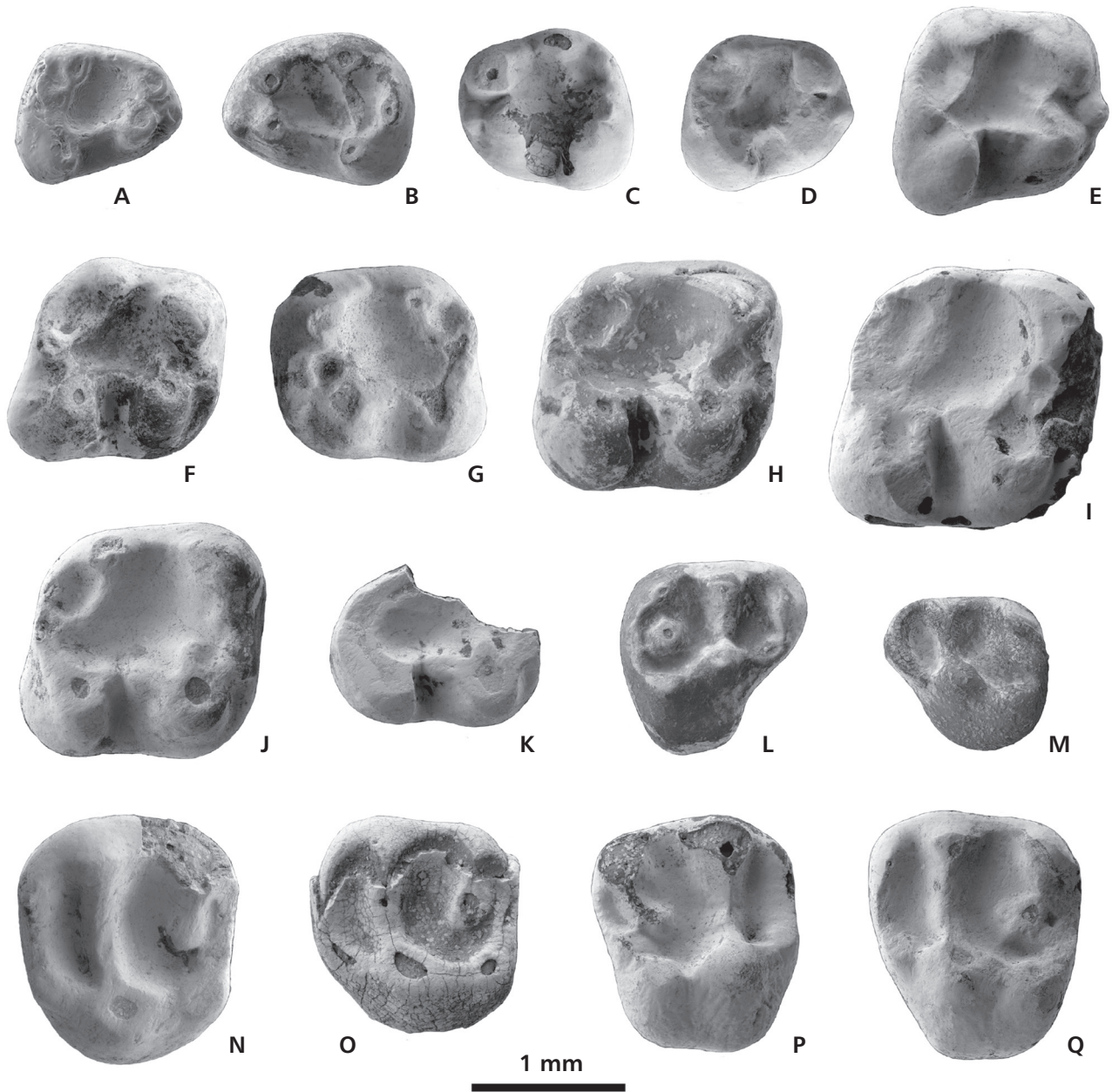
*Remarks.* – This ground squirrel is mentioned by Agustí *et al.* (1988) in the Ribesalbes-Alcora Basin, in the

classic locality of Araia, but the authors did not describe the material and they considered it as a doubtful form (cf.). The genus *Heteroxerus* is common in the Neogene from Europe (Cuenca-Bescós 1988, de Bruijn 1999), and it constitutes the best represented squirrel in the Ribesalbes-Alcora Basin sites. The species *Heteroxerus rubricati* is characterized by having upper molars with four principal cusps, the metaloph is incomplete, reduced and isolated or semi-isolated from the protocone and the metaconule is well developed (Cuenca-Bescós 1988). In the lower molars, the four cuspids are well developed, there is a well-developed entoconid, a reduced metalophid, a large anteroconulid and hypoconulid, and sometimes an anterior cingulid (Cuenca-Bescós 1988). Furthermore, for *H. rubricati*, this author proposes an emended diagnosis wherein she denotes the presence of an incomplete metaloph, either with a free ending or connected to the posteroloph, a complete or absent metalophid, and a scarcely present mesostylid. These characteristics can be observed in the material from Ribesalbes-Alcora Basin, and allow us to assign it to this species. *Heteroxerus rubricati* differs from *Heteroxerus vireti* Black, 1965 by a short and low entolophid, without connection with the hypoconulid, and the absence of the anterior cingulid. Additionally, in *Heteroxerus grivensis* (Forsyth Major, 1893) the anterior cingulid is absent (Aldana-Carrasco 1992).

Cuenca-Bescós (1988) divided the upper molars in four groups, according to the connections of the metaconule. The material here studied belongs to the morphologies 2 (without connection to the posteroloph) and 3 (with one connection to the posteroloph) for the M1 and M2; both morphologies are the most common in the Calatayud-Montalbán Basin. Regarding to the lower teeth, this author divided the morphologies in three groups (5 to 7) depending on the relative development of the anterior cingulid. In the Ribesalbes-Alcora Basin, the material belongs to morphologic group 5 (anterolophid absent in the p4 and very short in the molars). However, in BC1 there is a molar that belongs to group 7 (very long anterolophid). Overall, the morphological characters present in the material from the Ribesalbes-Alcora Basin are within the variability of the teeth from the Calatayud-Montalbán Basin. As for the morphometric variability, generally, the specimens are in the lower part of the variation range present in the Calatayud-Montalbán Basin, except for the material from BC1, and the upper molars from MAB3 that are rather medium-large in size.

*Occurrence.* – Mas dels Coixos 3 (MCX3), Mas de Torner 2 and 3 (MTR2 and MTR3), Barranc de Campisano 1 (BC1), Foieta la Sarra 1 (FS1), Mas d'Antolino B 3, 5, 8 and 11 (MAB3, MAB5, MAB8 and MAB11); Corral de Brisca 0B and 0C (CBR0B and CBR0C).





**Figure 2.** Teeth of *Heteroxerus rubricati* Crusafont et al., 1955 from the Ribesalbes-Alcora Basin. A – right dp4 (BC1-18); B – left dp4 (MAB3-674); C – left p4 (MAB3-672); D – right p4 (MAB3-675); E – right m1 (MTR3-2); F – right m1 (FS1-64); G – left m1 (MAB3-670); H – right m2 (BC1-150); I – right m2 (BC1-151); J – right m2 (MAB3-671); K – right m3 (MAB8-6); L – right DP4 (MAB11-13); M – left DP4 (CBR0C-1); N – right M1 (MAB3-666); O – right M1 (MAB5-137); P – left M2 (MAB3-668); Q – right M2 (MAB3-678). Scale bar is 1 mm.

**Genus *Atlantoxerus* Forsyth Major, 1893**

***Atlantoxerus blacki* de Bruijn, 1967**

Figure 3A–F

**Material.** – MCX1: 1 M1; MCX3: 1 M1/M2; MAB3: 1 d4, 1 p4, 1 D4; MAB5: 1 m1, 1 M1, 1 M3.

**Measurements.** – See Tab. 1.

**Description.** – dp4 (Fig. 3A): The outline is subtriangular. The anteroconulid is small and isolated. The metaconulid and the protoconulid are well developed, and connected by a short metalophid. The mesolophid and the mesoconulid are crest-shaped. The entolophid is well developed and connected to the entoconid. The posterolophid is long and complete.

p4 (Fig. 3B): The outline is subtriangular. The anteroconulid is absent. The metaconulid and the protoconulid are

well developed and connected by a short metalophid. The mesolophid is absent. The mesoconid is crest-shaped. The entoconid is poorly developed, and gives rise to a curved entolophid that is connected to the hypoconulid. The posterolophid is short and not connected to the entoconid.

m1 (Fig. 3C): The outline is subquadrate. The anteroconulid and the anterolophid are small, the latter is connected to the metaconid. The anterior cingulid is shorter than the anterolophid and it is connected to the protoconid. The metalophid is weak and almost divided in two. The mesostylid is absent and the mesoconid has a crest shape. The entoconid is the smallest of the four principal cusps. The entolophid is curved and connected to a well-developed hypoconid. The posterolophid is short and complete.

DP4: The tooth is broken and rounded with a truncated pyramid shape outline. The protocone is the best developed cusp. The protoloph is straight and connected to a low paracone. The metacone is small and connected to a well-developed hypoconule. The posteroloph is long.

M1 (Fig. 3D, E): The tooth from MAB5 is broken, it is large and with a rounded outline. The protocone is the highest cusp, with the hypocone lower than the protocone. The protoloph is straight. In the tooth from MCX1 the anteroloph is straight, long and open, the anteroconule is developed and the mesostyle is small. The paracone and the metacone are reduced and the protoloph is long and straight.

M3 (Fig. 3F): A large broken tooth with a rounded outline. The anteroloph is curved, with a small parastyle that ends near the paracone. The anteroconule is well developed. The protocone is the largest cusp. The paracone is small; it is connected by a straight protoloph to a small protoconule, and becomes narrower next to the protocone. The metaloph is long, poorly developed and divided in two. Both the metaconule and the hypoconule are well developed and connected to each other. The hypocone is poorly developed.

*Remarks.* – *Atlantoxerus* is a genus of ground squirrels that includes the extant Barbary ground squirrel [*Atlantoxerus getulus* (Linnaeus, 1758)]. It had not been described previously in the Ribesalbes-Alcora Basin. It can be easily distinguished from the genus *Heteroxerus*, in spite of their similar morphology, by its large size and its smaller anterolophid. (Cuenca-Bescós 1988, Peláez-Campomanes 2001). Furthermore, *Atlantoxerus* has more robust and rounded cusps, with well-developed anteroconules and hypoconules. The material studied here shows a complete anteroloph and a low metaloph connected to the posteroloph; this character is present in the material from some sites in the Calatayud-Montalbán Basin (Cuenca-Bescós 1988).

Peláez-Campomanes (2001) puts in synonymy *Atlantoxerus idubedensis* Cuenca-Bescós, 1988 with *A. blacki*. Following the emended diagnosis proposed by this author

for *A. blacki*, the material studied here presents a d4 with an anteroconulid and entolophid connected to the hypoconid; the p4 without anteroconulid; in the m1 the entolophid is connected to the hypoconid, and the metalophid is almost disconnected; the upper molars have a differentiated anteroconule and hypoconule; the metaconule is connected to the posteroloph and there is a small protoconule. These characters are described as diagnostic for this species and allow its distinction from the other early Miocene species of this genus. In addition, *A. blacki* differs from *Atlantoxerus martini* Aguilar, 2002 in its better developed anterior cingulid, and from both *A. martini* and *Atlantoxerus vireti* (Black, 1965) in its larger size (Aguilar 2002).

The biometric analysis shows that the d4 is in the lower limit size range of *A. blacki* within the Calatayud-Montalbán Basin, whereas the p4 is smaller and the m1 and M3 are located in the medium area, but narrower. This is in agreement with the great biometric variability described for this species by Peláez-Campomanes (2001).

*Occurrence.* – Mas dels Coixos 1 and 3 (MCX1 and MCX3), Mas d'Antolino B 3 and 5 (MAB3 and MAB5).

### Genus *Aragoxerus* Cuenca-Bescós, 1988

#### *Aragoxerus* sp.

Figure 3G, H

*Material.* – CBR0B – 1 p4; CBR1 – 1 m1/m2.

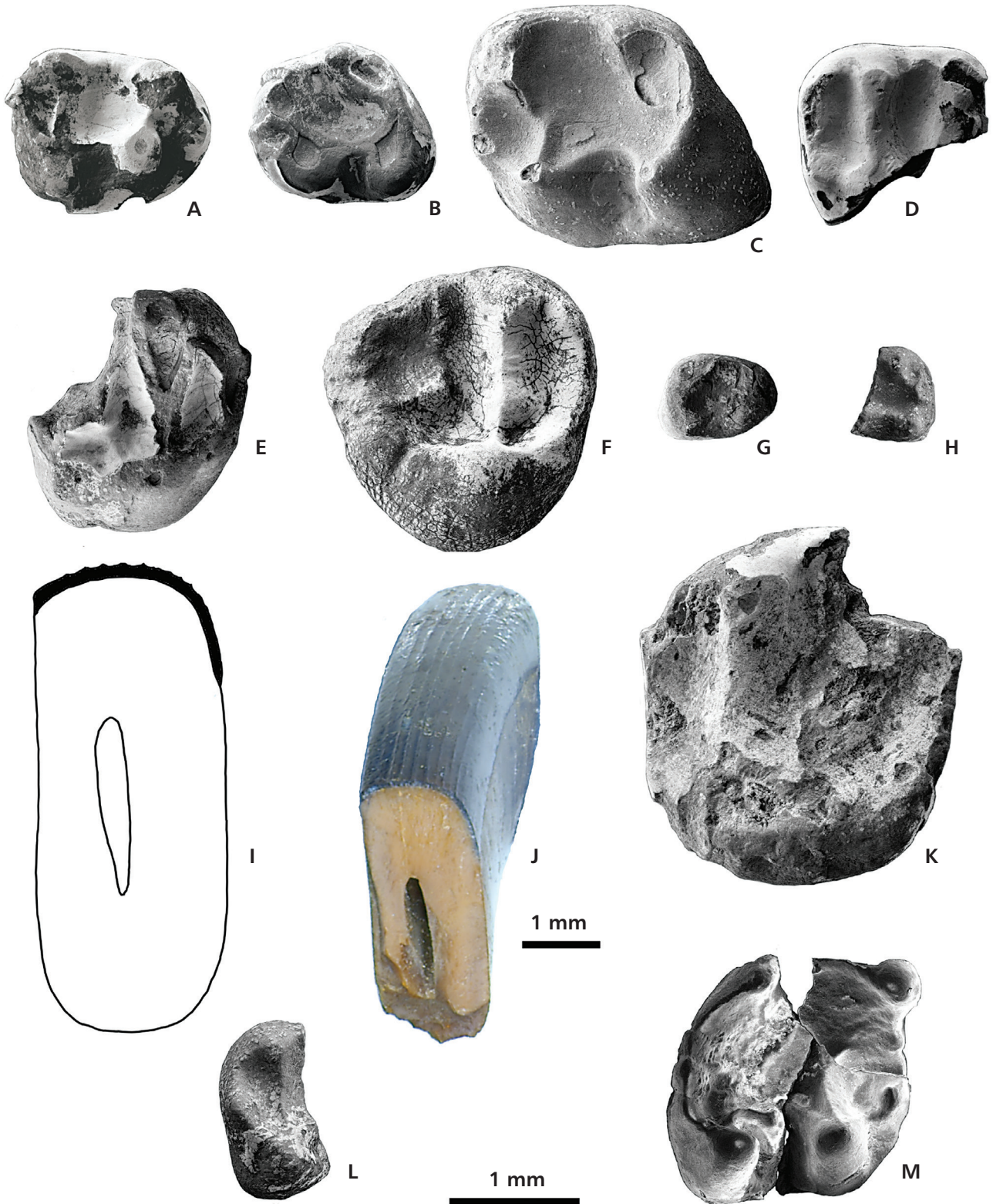
*Measurements.* – See Tab. 1.

*Description.* – p4 (Fig. 3G): The surface is rounded with a subelliptical outline. Only the four principal cusps are present, without conules. The senid is poorly developed.

m1/m2 (Fig. 3H): A broken tooth with a very small size. The anteroconulid is well developed and the metalophid is connected to it. The mesoconid has a crest-like shape. The senid is absent.

*Remarks.* – Among the fossil Sciuridae recovered in the Ribesalbes-Alcora Basin, the material ascribed to this ground squirrel shows the smallest size. Despite the fact that this material is fragmentary, some typical characteristics of this genus described by Cuenca-Bescós (1988) can be observed, such as the small size of the teeth, the absence of the senid and the labial cingulid and the small or absent anteroconulid. The material here described differs from *Aragoxerus ignis* (Cuenca-Bescós, 1986) in its better-developed cuspid (Cuenca-Bescós 1988) and from both *A. ignis* and *Aragoxerus* nov. sp. from Baixas and Saint Catherine (France) in its smaller size (Aguilar 2002). Although, *Aragoxerus* is considered a *nomen dubium* by de Bruijn (1999), or a synonym of *Heteroxerus* by Krystufek *et al.*





**Figure 3.** Teeth of the family Sciuridae (except *Heteroxerus rubricati*) from the Ribesalbes-Alcora Basin. • A–F – *Atlantoxerus blacki* de Bruijn, 1967; A – right dp4 (MAB3-673); B – left p4 (MAB3-669); C – left m1 (MAB5-717); D – right M1 (MCX1-5); E – left M1 (MAB5-44); F – left M3 (MAB5-716). • G, H – *Aragoxerus* sp.; G – right p4 (CBR0B-39); H – right m1/m2 (CBR1-44). • I, J – Marmotini indet.; I – (MAB3-696). • K – *Palaeosciurus* cf. *sutteri* Ziegler & Falhbusch, 1986, right M1/2 (MAB3-665). • L – *Spermophilinus* sp., left m1/m2 (MAB5-718). • M – *Aliveria* cf. *luteyni* de Bruijn et al., 1980; right m1/m2 (CBR0B-53). Scale bar is 1 mm.

(2016). The latter authors do not justify their synonymy and the remains described here are morphologically and biometrically distinct from the *Heteroxerus rubricati* of the sites from Ribesalbes-Alcora Basin. Therefore, and due to the scarcity of material, we prefer not to assign it to any particular species.

**Occurrence.** – Corral de Brisca 0B and 1 (CBR0B and CBR1).

Tribe Marmotini Pocock, 1923

**Marmotini indet.**

Figure 3I, J

**Material.** – MAB3 – 1 I.

**Measurements.** – See Tab. 1.

**Description.** – I (Fig. 3I, J): A fragment of a large upper incisor, with a subrectangular transversal section and an oval central channel. The enamel has ten central longitudinal crests.

**Remarks.** – A large upper incisor has been found in MAB3. By its strong labiolingual compression, flattened anterior wall with finely striated enamel (Fig. 3J) restricted to anterior and, partially, labial walls but devoid the lingual wall belongs to a marmotine ground squirrel. Although, the cross-section of the incisor is similar to the genus *Spermophilinus*-like or *Tamias*-like appearance, shared by a number of primitive marmotins (Sinitza 2018), we discard *Spermophilinus* by its size, because it is larger than the remains of this genus found in this basin.

**Occurrence.** – Mas d'Antolino B 3 (MAB3).

**Genus *Palaeosciurus* Pomel, 1853**

***Palaeosciurus* cf. *sutteri* Ziegler & Falhbusch, 1986**

Figure 3K

**Material.** – MAB3 – 1 M1/2.

**Measurements.** – See Tab. 1.

**Description.** – M1/2 (Fig. 3K): A broken tooth with a rounded outline. The anteroloph is well developed. The only lingual cusp is the protocone, which is also well developed. The protoloph is lower than the metaloph and both form an acute V-shaped figure with the protocone. The metacone is well developed. The mesostyle is present and the metaconule is slightly developed. The posteroloph is well developed and straight.

**Remarks.** – The only marmotine tooth recovered differs from the others ground squirrels in the Ribesalbes-Alcora Basin in its larger size. It is characterized by a metaloph and a protoloph that converge to the protocone, an anteroloph and protoloph forming a U-shaped figure, and the presence of a mesostyle. This morphology is, after Cuenca-Bescós (1988), characteristic of the genus *Freudenthalia nomen dubium* [synonymized to *Palaeosciurus* by de Bruijn (1999)], *Palaeosciurus* according to Huguene & Bulot (2011) and *Tamias* after Bosma *et al.* (2013), but the latter lacks the mesostyle. Huguene & Bulot (2011) note that the morphological differences between *Palaeosciurus feignouxi* Pomel, 1853 and *Palaeosciurus fissurae* (Dehm, 1950) consist in the smaller size of *P. feignouxi*, which shows the metaloph and the protoloph arranged in V, while *P. fissurae* is larger and with both crests parallel. Just like *P. feignouxi*, the species *P. sutteri* shows the metaloph and the protoloph forming a V. This is also the case in MAB3, but in our specimen the metaconule is better developed than in *P. sutteri* (Ziegler & Falhbusch, 1986). In this way, the morphology allows us to assign the tooth from MAB3 either to *P. feignouxi* or to *P. sutteri*.

The morphometric measures show that the tooth from MAB3 is larger than in *P. feignouxi* and *P. aff. fissurae* from Estrepouy (France); additionally, it is slightly larger than in *P. sutteri* but similar in size to *P. cf. fissurae* from Serre de Vèrges (France) (Ziegler & Falhbusch 1986, Cuenca-Bescós 1988, Aguilar 2002, Huguene & Bulot 2011).

Based on morphological and metric similarities, this specimen has been determined as *Palaeosciurus* cf. *sutteri*.

**Occurrence.** – Mas d'Antolino B 3 (MAB3).

Subtribe Spermophilina Moore, 1959

**Genus *Spermophilinus* de Bruijn & Mein, 1968**

***Spermophilinus* sp.**

Figure 3L

**Material.** – MAB5 – 1 m1/2.

**Measurements.** – See Tab. 1.

**Description.** – m1/m2 (Fig. 3L): Anterior fragment of tooth. The anteroconulid is as high as the protoconid. The anterior cingulid is connected to the protoconid and the anterolophid is less developed, although it is connected to the metaconid, which is lower than the protoconid. The metalophid is weak, but complete, and it is connected to the crestid that connects the protoconid with the hypoconid. The central valley is low and it has a well-developed senid.



**Table 1.** Measurements of the teeth of squirrels from the Ribesalbes-Alcora Basin. L – length; W – width.

Element	Site	Measurement	n	Min.	Med.	Max.
<b><i>Heteroxerus rubricati</i></b>						
d4	BC1	L	1		1.25	
		W	1		1.32	
	MAB3	L	1		1.32	
		W	1		1.03	
p4	MAB3	L	2	1.15	1.16	1.16
		W	2	1.04	1.10	1.15
m1	MTR3	L	1		1.41	
		W	1		1.42	
	BC1	L	1		1.68	
		W	1		1.59	
	FS1	L	2	1.44	1.44	1.44
		W	1	1.29	1.35	1.41
	MAB3	L	1		1.54	
		W	1		1.34	
m2	BC1	L	2	1.68	1.75	1.81
		W	2	1.59	1.73	1.86
	MAB3	L	2	1.57	1.59	1.61
		W	2	1.49	1.58	1.67
m3	MAB8	L	1		1.51	
D4	BC1	L	1		1.25	
		W	1		1.21	
	FS1	W	1		1.33	
	MAB11	L	1		1.38	
		W	1		1.21	
	CBR0C	L	1		1.15	
		W	1		1.15	
M1	MCX3	L	1		1.47	
		FS1	L	1		1.31
		W	1		1.58	
	MAB3	L	2	1.44	1.47	1.51
		W	1		1.87	
	MAB5	L	1		1.41	
		W	1		1.55	
M2	MAB3	L	3	1.40	1.44	1.49
		W	2	1.66	1.67	1.68
<b><i>Atlantoxerus blacki</i></b>						
d4	MAB3	L	1		1.74	
		W	1		1.37	
p4	MAB3	L	1		1.43	
		W	1		1.32	
m1	MAB5	L	1		2.44	
		W	1		2.07	
M3	MAB5	W	1		2.44	
<b><i>Aragoxerus</i> sp.</b>						
p4	CBR0B	L	1		>1	
		W	1		>0.71	
	CBR1	W	1		0.84	
<b><i>Marmotini</i> indet.</b>						
I	MAB3	L	1		3.6	
		W	1		1.59	
<b><i>Palaeosciurus</i> cf. <i>sutteri</i></b>						
M1/2	MAB3	L	1		2.64	
		W	1		3.00	
<b><i>Spermophilinus</i> sp.</b>						
m1/m2		W	1		1.49	
<b><i>Aliveria</i> cf. <i>luteyni</i></b>						
m1/m2		L	1		>2.02	

**Remarks.** – This fragment of tooth belongs to a small ground squirrel, with characteristics not observed in the studied material of other taxa in the Ribesalbes-Alcora Basin. Examples are the very high anteroconulid or the long and sigmoidal metalophid, which is connected to the crest that links the protoconid to the hypoconid.

This morphology appears in *Spermophilinus* aff. *bredai* (von Meyer, 1848) from Forsthart, described by Ziegler & Fahlbusch (1986, fig. 4.5), although the contact between the anteroconulid and the protoconid is better developed in the material studied here. This character distinguishes our tooth from *Spermophilinus besanus* Cuenca-Bescós, 1988 of the Calatayud-Montalbán Basin (Cuenca-Bescós 1988). The occurrence of a complete metalophid distinguishes *S. besanus* from *Spermophilinus minutus* Zheng & Li, 1982, where the metalophid is residual. Nevertheless, this character is similar in *S. bredai*, where the metalophid could be complete (Zheng & Li 1982, Cuenca-Bescós 1988).

Morphometrically, the tooth studied here is situated in the lower part of the variability range of the m1 of *S. aff. bredai* from Forsthart and La Grive, or of *S. minutus* (Zheng & Li 1982, Ziegler & Fahlbusch 1986), and it is clearly smaller than in *S. besanus*, *S. bredai*, *Spermophilinus turoloensis* de Bruijn & Mein, 1968 and *Spermophilinus giganteus* de Bruijn, Dawson & Mein, 1970 (Cuenca-Bescós 1988, de Bruijn 1995, Vasileiadou & Koufos 2005).

Although the closest taxon seems to be *S. aff. bredai* from Central Europe, the observed differences and the scarcity and preservation state of the recovered material prevents us to assign it to a particular species.

**Occurrence.** – Mas d'Antolino B 5 (MAB5).

Subfamily Pteromyinae Brandt, 1855

### **Genus *Aliveria* de Bruijn, Van der Meulen & Katsikatsos, 1980**

#### ***Aliveria* cf. *luteyni* de Bruijn, Van der Meulen & Katsikatsos, 1980**

Figure 3M

**Material.** – CBR0B – 1 m1/2.

**Measurements.** – See Tab. 1.

**Description.** – m1/2 (Fig. 3M): A broken tooth with a subquadrangular outline. The surface of the enamel is wrinkled. The anteroconulid is small and connected to the protoconid by a short anterior cingulid. The anterolophid is bulbous. The metalophid is incomplete and not connected to the metaconid. The mesoconid is well developed and

sigmoidally connected with the hypoconid. The entoconid is an enlargement of the posterolophid, which is curved and has a bulbous-shape.

**Remarks.** – CBR0B is the only site that has yielded a fragmented tooth morphologically attributable to a flying squirrel. This tooth is characterized by the anterior cingulid, three well-developed cuspids and a posterolophid with conulids. These features are present in *Aliveria luteyni* from Rembach (Germany); this population was assigned to *Forsythia* aff. *gaudryi* Mein, 1970 by Ziegler & Fahlbusch (1986), but later, de Bruijn (1999) assigned the specimens to *Aliveria luteyni*. Furthermore, these features make this species clearly distinct from *Miopetaurista* cf. *dehmi* de Bruijn, Van der Meulen & Katsikasos, 1980 from Forsthart (Ziegler & Fahlbusch 1986). Overall, the studied tooth differs from *Miopetaurista neogrivensis* in its smaller size (Aldana-Carrasco 1992) and particularly, from *Miopetaurista diescalidus* Daams, 1977, which has a very wrinkled enamel and a small mesoconid (Daams 1977), while our tooth shows a slightly wrinkled enamel and a well-developed mesoconid. Besides, the well-developed anteroconulid makes this tooth clearly distinct from the genera *Albanensia* and *Forsythia*. Therefore, the genus most similar to the material from CBR0B is *Aliveria* (de Bruijn *et al.* 1980). At the species level, the absence of the entolophid is characteristic of the species *Aliveria luteyni*, as in the populations from Aliveri and the German sites of Rembach and Erkertshofen (de Bruijn *et al.* 1980, Ziegler & Fahlbusch 1986). In regard to the size, the tooth here described can be included, like the genus *Aliveria*, in the group of the middle-sized Pteromyiinae (Daxner-Höck 2004).

Due to the aforementioned reasons and the scarcity of the material, we have left this tooth as *Aliveria* cf. *luteyni*, which constitutes the first cite of the genus *Aliveria* in Western Europe. Furthermore, this is probably one of the oldest representatives of the true flying squirrels in the fossil record (de Bruijn *et al.* 1980, Thorington *et al.* 2005, Casanovas-Vilar *et al.* 2018). We include *Aliveria* in the Pteromyiinae after McKenna & Bell (1997).

**Occurrence.** – Corral de Brisca 0B (CBR0B).

## Discussion

### Biostratigraphy

The use of squirrels as biostratigraphic markers is well established (Cuenca-Bescós 1988; and references therein). Although, their low abundance in the Ribesalbes-Alcora Basin prevented us to use them as such, they show a high diversity along the studied sections (Tab. 2).

**Table 2.** Percentages of frequency (%) of squirrels found in the Araia sections. Only sites with more than 45 teeth are represented, the number in parentheses next to the locality name represents the number of mammal teeth found at the site (modified from Crespo *et al.* 2019a).

Locality	Squirrels	Rest of rodents
CBR1 (47)	2.1	74.6
CBR0B (56)	9	64.3
MAB11 (145)	0.7	62.2
MAB5 (874)	0.5	69.8
MAB3 (807)	2.5	76.8
FS1 (63)	6.3	84.1
MAB0B (75)	0	38.7
MAB0A (80)	0	90.2
BC1 (180)	3.3	74.9
MTR2 (187)	0.5	64
MCX3 (132)	2.3	71.2

*Heteroxerus rubricati* is the most abundant squirrel (Tab. 2) in the studied basin, but also in the contemporaneous sites in the Iberian Peninsula. Its temporal range extends between the early and the upper Miocene (MN2–9) (Fortelius 2016). After Cuenca-Bescós (1988), García-Paredes *et al.* (2016) and Van der Meulen *et al.* (2012) in the Calatayud-Montalbán Basin its stratigraphic range starts in the Ramblian and ends at the top of the local zone G1 (MN6, Aragonian, middle Miocene). In the Vallès-Penedès Basin, it is very abundant in the MN4 and its last occurrence is in the upper Miocene, in the early Vallesian (MN9; Aldana-Carrasco 1992, Jovells-Vaquè *et al.* 2018). In the Magro Basin it appears in the sites Barranco de Candel and Buñol (Adrover *et al.* 1987, Robles *et al.* 1991) and almost all of the Morteral series (Ruiz-Sánchez *et al.* 2003). Finally, this species is present along the whole middle Miocene record of the Madrid Basin (Hernández-Ballarín & Peláez-Campomanes 2018).

The stratigraphic range of the species *Atlantoxerus blacki* is more restricted. In the Calatayud-Montalbán Basin it extends between the local biozones B (MN4, Aragonian, early Miocene) and Dc (MN5, Aragonian, early Miocene) (Van der Meulen *et al.* 2012), thus shortening the record given by Cuenca-Bescós (1988). In the Vallès-Penedès Basin this species is limited to the MN4 (Aragonian, early Miocene; Aldana-Carrasco 1992) and to the local biozone Dc in the Madrid Basin (MN5, middle Miocene; Hernández-Ballarín & Peláez-Campomanes 2018).

The genus *Aragoxerus* has been described in MN3 of the Calatayud-Montalbán Basin (Cuenca-Bescós 1988), and it appears later in MN4–6 in France (Aguilar 2002); its last record is in Crevillente 2 (MN11, Turolian, upper Miocene; Mazo & Montoya 2003; and references therein).

The species *Palaeosciurus sutteri* is typical for Central and Southwestern Europe and Turkey, with a temporal range that starts in MN4 and ends in MN6 (early – middle Miocene; de Bruijn 1999, Prieto et al. 2017, Bosma et al. 2018). The occurrence of this species in the Ribesalbes-Alcora Basin constitutes its first record in the Iberian Peninsula, and one of the last records of this genus in the same geographic zone. In the Calatayud-Montalbán Basin *Palaeosciurus* appeared at the end of the Agenian (Cuenca-Bescós 1988) and, according to García-Paredes et al. (2016), it became extinct in the Ramblian (local zone A, MN3, early Miocene). In the Vallès-Penedès Basin it has only been recorded, as *P. aff. fissurae*, in MN4 of the locality of San Mamet (Aldana-Carrasco 1992).

The genus *Spermophilinus* has a wide biostratigraphic record (de Bruijn 1999). In the Calatayud-Montalbán Basin, *S. besana* extends from the middle of the local zone B (MN4, early Miocene) until the middle of the local zone Dc (MN5, middle Miocene; Van der Meulen et al. 2012). In the early Miocene, in the Vallès-Penedès Basin, *Spermophilinus* only occurs in the site of Els Casots (MN4, early Miocene; Aldana-Carrasco 1992). Finally, in the Magro Basin, this genus is cited as *S. bredai* in Buñol (local zone C, MN4, early Miocene; Robles et al. 1991).

The flying squirrel *Aliveria luteyni* was described in the Greek locality of Aliveri, and was later reported in Karydia (also in Greece), both in the MN4 (early Miocene; de Bruijn et al. 1980, Doukas 2003). This taxon has also been found in other localities from Germany, Turkey and Serbia (here as *A. aff. luteyni*) with a similar age (de Bruijn 1999, Marković et al. 2016, Bosma et al. 2018). The record from the Ribesalbes-Alcora Basin is the first one for this genus in Western Europe. Probably, this genus originated in Turkey, where it shows a longer stratigraphic range, from the MN3 to the MN5 (early–middle Miocene; Kaya et al. 2007).

## Palaeoecology

The genera *Atlantoxerus* and *Heteroxerus* are typical of warm and dry climates. *Atlantoxerus* has an extant representative (Barbary ground squirrel, *A. getulus*) that lives in African deserts (Van Dam & Weltje 1999, Minwer-Barakat 2005, García-Alix et al. 2008, Mansino et al. 2018). According to Minwer-Barakat (2005) and García-Alix et al. (2008) these genera are associated to open and denuded environments, and Menéndez et al. (2017) have reported the species *H. rubricati* in the semidesertic habitat of the site Somosaguas in the Madrid Basin. *Aragoxerus* might have shared these preferences, although there is no literature on this topic, but Cuenca-Bescós (1988) or Denys et al. (2003), among others, include this genus in the Xerini, that generally have a similar life style. The ground

squirrel *Heteroxerus* is the most abundant squirrel in the sites in study (Tab. 2).

The marmotine *Palaeosciurus* is a typical dweller of open to partially open habitats, similar to the ground squirrels in behaviour (Costeur et al. 2012). More specifically, the species *Palaeosciurus goti* has been described as a fossorial animal (Ginot et al. 2016), although this taxon would have no specific humidity or temperature requirements.

The other ground squirrel, *Spermophilinus*, lived in well illuminated woods interspersed with open herbaceous zones (Lungu 1981, Nicoara 2011), or in open habitats (Prieto et al. 2014). However, after an analysis of the dental microwear, Gusovsky & Sinita (2019) suggested that “the members of this genus were related to closed, forested biomes, where they consumed hard fruits, nuts, tree seeds and, rarely, insects, somewhat like many living arboreal squirrels do today”. *Spermophilinus* has been found throughout all Europe, which suggests that it had no specific temperature or humidity preferences.

The genus *Aliveria* probably represents one of the first gliding squirrels (de Bruijn et al. 1980). Different morphological characteristics (such as the convergent protoloph and metaloph, wrinkled enamel...) suggest they are convergent with the current flying squirrels. This is questioned by Thorington et al. (2005) and Thorington & Santana (2007), because these features appear in basal members of the group, next to the genus *Glaucomyia*, and the group of *Petaurista*. These authors show that these adaptations may result from a folivorous diet, and do not constitute an adaptation to flight. However, Casanovas-Vilar et al. (2018) consider the group of the Pteromyini (including *Glaucomyia*) as monophyletic and adapted to glide. In the other hand, newer data suggest that this group has a monophyletic origin in the late Eocene (with the genus *Hesperopetes*) or in the early Oligocene (with the genus *Oligopetes*) due to, these genera have a typical flying squirrel dental pattern (Heissig 1979, de Bruijn & Unay 1989, Korth 2017). Even so, this fact indicates a more or less closed wooded habitat, and this is widely accepted in the literature (Cuenca-Bescós 1988, de Bruijn 1999, Van Dam & Weltje 1999, García-Alix et al. 2008, Casanovas-Vilar et al. 2015). Furthermore, Van Dam & Weltje (1999) attribute wet preferences to the Pteromyini. Daxner-Höck (2004) classifies the flying squirrels in three groups according to their size, including *Aliveria* in the middle-size group. This author highlights some forms tolerant to dry conditions (as the genus *Hylopetes*) or others that dwell in evergreen boreal or mixed woods (as the genus *Pteromys*).

The genera *Aliveria*, *Spermophilinus*, *Palaeosciurus* and the Marmotini indet. have been found in only one site, and therefore they can be considered as transient stenotopic taxa, while *Heteroxerus* and *Atlantoxerus* that appear more frequently in the sites in study (Tab. 2) were resilient and eurytopic.



## Conclusions

The Ribesalbes- Alcora Basin, with continental sequences similar in age to those of the Calatayud-Montalbán area (local biozones Ca and Cb, MN4, early Miocene), has yielded a relatively diverse fauna of squirrels. The most abundant is the ground squirrel *Heteroxerus rubricati* and to a lesser degree *Atlantoxerus blacki* and *Aragoxerus* sp., the marmotine *Palaeosciurus* cf. *sutteri*, *Spermophilinus* sp., and Marmotini indet. and the flying squirrel *Aliveria* cf. *luteyni*. *Heteroxerus rubricati*, *Atlantoxerus blacki* and *Spermophilinus* are typical species from the Iberian early Miocene faunas. *Aragoxerus* is reported for the first time in the MN4 of the Iberian Peninsula, and together with the French record, it is the only cite from Europe. The species *Palaeosciurus* cf. *sutteri*, typical from Central and Southeastern Europe and from Turkey, constitutes the first record of this species, if it is confirmed, in the Iberian Peninsula, and one of the oldest in Europe. The occurrence of *Aliveria* cf. *luteyni* also constitutes the first record of *Aliveria* in Western Europe. The presence of a high diversity of squirrels, despite their low proportion when compared to other rodents, is indicative of the richness of habitats in the paleolake that filled the Ribesalbes-Alcora Basin in the early Miocene. The dominance of *Heteroxerus rubricati* and *Atlantoxerus blacki*, in lesser proportion, together with other species with humid preferences (Crespo 2017; Crespo *et al.* 2018, 2019a, b, c, 2020), indicates that these species were more eurytopic than previously thought.

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