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Cainotheriids vs. lagomorphs: study of their ecological niche partitioning during the early miocene of the Ribesalbes-Alcora Basin (Castelló, Spain)

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ABSTRACT

Here we describe the fossil remains of *Cainotherium* aff. *huerzeleri* and *Lagopsis penai* from the Ribesalbes-Alcora Basin (Castelló, Spain). We also compare the relative abundance of cainotheriids vs. lagomorphs and discuss the possible direct interaction between both taxa, possibly indicating the competition between both families. The oldest locality in study has a predominance of *Cainotherium* followed by a dominance of *Lagopsis* in the next localities. Afterwards we see another interval where the relative abundance of *Cainotherium* is higher. However, after this period the relative abundance of *Lagopsis* increases again in one of the most recent sites, with a posterior modest increase in *Cainotherium* in the youngest locality that also sees a decrease in the abundance of *Lagopsis*. We can observe a pattern of one taxon attaining higher relative abundance when the other shows a decrease at the same time period, possibly indicating a direct competition between *Lagopsis* and *Cainotherium*.

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palaeocology; ecological
competition

Introduction

Cainotheriidae

The cainotheriids are small extinct artiodactyls endemic to Central and Western Europe, with the largest species reaching only the size of the extant *Tragulus javanicus* Osbeck 1765, the smallest of the Asian mouse-deer (~2 kg) (Blondel 2005). Usually, their remains are very abundant in the sites where they appear and their record spans from the late Eocene (MP18) to the middle Miocene (MN6) (Schmidt-Kittler 1987; Heizmann 1999). The distinctive features of their skeleton involve their distal humerus morphology, a well-developed fibula diaphysis, and the presence of large auditory bullae (Blondel 2005). The teeth of cainotheriids are brachydont, and the upper molars bear two anterior and three posterior cusps (Berthet 2003; Weppe et al. 2020b).

Although many ungulates endemic to Europe became extinct at the end of the Eocene (Sudre and Legendre 1992; Blondel 2001), the cainotheriids persisted beyond the Eocene/Oligocene boundary (Blondel 2005). Cainotheriidae contains two subfamilies: Oxacroninae, and Cainotheriinae. Both subfamilies appeared in the Eocene (Blondel 2005; Weppe et al. 2021). The Oxacroninae appear to be restricted to the Eo-Oligocene, while a species belonging to the genus *Cainotherium* is present in the Quercy localities of Escamps and Rosières 2 (Blondel 2005; Weppe et al. 2021) and the subfamily Cainotheriinae continuously appears in the fossil record during the Oligocene until its extinction in the Miocene. The first species recorded are *Oxacron courtoisii* (Gervais, 1852) from the MP18 of Sindou D (Quercy, France) and La Débruge (Vaucluse, France), and *Palembertina desplasi* (Weppe et al. 2020b) from the MP18-MP19 of Palembert (Quercy, France) (Weppe et al. 2020a). Also *Paroxacron valdense* (Stehlin 1906) from Escamps (Legendre 1980; Weppe et al. 2020b)

As mentioned above, the genus *Cainotherium* seems to appear at the end of the Eocene with a species present in the Quercy localities of Escamps and Rosières 2 (MP19). Another species of this genus seems to be present also in the MP23 in the Quercy localities of Pech Crabit and Roqueprune 2 (Weppe et al. 2021). During the late Oligocene (Chattian, MP28-MP30), it shows a northern and central European distribution; during the Aquitanian (MN1-MN2) the genus dispersed in Western Europe with a multiplication of the number of species, during the Burdigalian the number of species is maintained, but the number of species decreases in abundance (MN3-MN4; Berthet 2003). However, from the Langhian to the Serravallian (MN5-MN6), the number of species decreased considerably and was reduced to three before disappearing in the MN6 due to readjustment of communities, biotic factors and environmental changes (Heizmann 1999; Berthet 2003; Blondel 2005). This rapid decline manifests quantitatively, since in the basal Miocene this genus is very common within the European faunas, becoming scarcer during the first part of the middle Miocene and finally disappearing in some areas. However, in the Iberian Peninsula there was an expansion during the last part of middle Miocene (Hürzeler 1936; Heizmann 1999; Alarcón and Álvarez-Sierra 2009).

The genus *Cainotherium* is one of the smallest among the Artiodactyla, and it is endemic to Western and Central Europe (France, Germany, Portugal, Spain, and Switzerland) from the late Oligocene to the early-middle Miocene (Berthet 2003). The dental morphology of this genus is very stable (Möltzer 1975), and the taxon separation is only possible by differences of size and dental ratios, due to the morphology of the dentition follows the '*Cainotherium* plan' defined by Stehlin (1906) (Weppe et al. 2020a). The genus *Cainotherium* differs from the rest of the genera of the family due to the absence of diastemas between the premolars, premolars with

a strong cingulum or cingulid, the presence of squarer molars and generally a larger size (Alarcón and Álvarez-Sierra 2009). In particular, the ratio length of m3/length of P2 have proven to be very relevant to discriminate most of the species (Berthet 2003).

Basically, two large groups are recorded, one that encompasses small species, including *Cainotherium huerzeleri* (Heizmann 1983), *Cainotherium bavaricum* (Berger 1959), *Cainotherium gracile* Pomel 1946, *Cainotherium geoffroyi* Pomel 1853 and *Cainotherium miocaenicum* Crusafont Villalta and Truyols, 1955, and other including the larger species *Cainotherium commune* Bravard 1835, and *Cainotherium laticurvatum* Geoffroy-Saint-Hilare 1833. *Cainotherium lintillae* Baudelot and Crouzel 1974 falls within those two groups (Alarcón and Álvarez-Sierra 2009; Scherler et al. 2013; Mennecart 2015; Mennecart et al. 2016). Berthet and Huguene (2000) ruled out that this separation by size is the effect of sexual dimorphism that appears in other artiodactyls.

The systematic position of cainotheriids is uncertain and they have been linked to selenodont ungulates, like Tylopoda or Anoplotheria (Heizmann 1999; Geisler 2001; Geisler and Uhen 2003, 2005). According to the most recent studies *Cainotherium* phylogenetic position is, together with the Mixtotheriidae, the Anoplotheriidae and representatives of *Robiacina* a the sister clade to ruminants. Tylopoda split earlier in the tree, together with *Amphimeryx* and *Xiphodon* (Weppe et al. 2020a). For this work we follow the classification of McKenna and Bell (1997), modified by Theodor (2010) and reviewed by (Weppe et al. (2020a), (2020b)).

Specimens belonging to the genus *Cainotherium* are found in the several deposits of the Ribesalbes-Alcora basin (MN4). In this work we intend to describe the specimens found in these sites, and their possible direct biotic competition, including the possibility of the lagomorphs having an impact in the extinction of the last cainotheriids.

Lagomorpha

Lagomorphs are a diverse group, especially as far as it concerns of the fossil record. There are 12 genera and 75 extant species, and in the fossil record, more than 75 genera including over 230 species are described (López-Martínez 2008).

During the late early Miocene, two genera predominate in the Iberian Peninsula (Hordijk 2010): *Prolagus*, which evolved from the immigrant *Piezodus* (López-Martínez 1989), and *Lagopsis*, which descended from *Marcuinomys* (López-Martínez and Thaler 1975; Tobien 1978; López-Martínez 1989; Hordijk 2010).

All the fossil remains of lagomorphs recovered in the Ribesalbes-Alcora Basin belong to *Lagopsis*, which was widely distributed in Western Europe, although not as widespread as *Prolagus*, which colonised as far as North Africa (López-Martínez 2001). The stratigraphic range of *Lagopsis* encompasses the early and middle Miocene, although it is likely that some relict populations survived in Italy during the late Miocene (López-Martínez 1989; Dawson 2008). The genus *Lagopsis* became extinct as a consequence of the aridification and cooling of the middle Miocene (Erbajeva et al. 2015). In reference to the systematics of the group, we follow McKenna and Bell (1997), Angelone (2008, 2009), and Angelone and Sesé (2009), among others, who do not divide the Ochotonidae into distinct subfamilies. Unlike Averianov (2000) which includes the genus *Lagopsis* in the subfamily Lagopsinae, or Erbajeva et al. (2006), which includes it within the subfamily Ochotoninae.

Geological setting

The materials studied in this paper were recovered near the village of Araia d'Alcora (Ribesalbes-Alcora Basin, eastern Iberian Peninsula (Figure 1; Crespo et al. 2019a). Until now, up to 45 sites have been described from the seven sections comprise the synthetic stratigraphic column (see Figure 1 and Crespo et al. 2019a for details), consisting mainly of grey and yellow mudstones, limestones and sandstones, with almost 100 m of thickness. Mammalian remains are very abundant and partially published or under study (Furió et al. 2012; Crespo 2017; Crespo et al. 2018, 2019a, 2019b, 2019c, 2020a, 2020b, 2021a, 2021b) also noteworthy is the presence of a Konservat-Lagerstätte (Álvarez-Parra et al. 2021).

The studied stratigraphic column corresponds to the local biozone C from the Calatayud-Montalbán Basin (MN4, lower Aragonian, early Miocene), with an age range from 16.5 to 16 Ma according to van der Meulen et al. (2012) (Crespo et al. 2019a, p. 2021b). The presence of the genus *Ligerimys* (and the species present and its abundance) allow divided this stratigraphic column in two long local biozones (depending on the species present) and each biozones in two sub-biozones (depending on its abundance) (Crespo et al. 2021b).

Materials, methods, and abbreviations

The fossils under study are currently deposited at the Natural History Museum of the University of Valencia (MUVHN) with the field labels MCX-, MTR-, BC-, FS-, MAB-, and CBR-.

We follow the terminology for cainotheriids updated recently by Weppe et al. (2020b), while for the lagomorphs we follow López-Martínez (1974, 1989), with modifications by Hordijk (2010). We follow the length and width measurements proposed by Berthet (2003) for cainotheriids and by Hordijk (2010) for lagomorphs.

Abbreviations: BC, Barranc de Campisano; CBR, Corral de Brisca; FS, Foieta la Sarra; L, length; MAB, Mas d'Antolino B; MCX, Mas dels Coixos; MGUV, Museu de Geologia de la Universitat de València; MN, European Neogene Land Mammal units; MTR, Mas de Torner; W, width. Lower tooth positions are named as i, c, p, and m, and upper tooth positions as I, C, P, and M.

Systematic palaeontology

Order Cetartiodactyla Montgelard, Catzellis and Douzery 1997

Family Cainotheriidae (Camp and Van Der Hoof 1940)

Subfamily Cainotheriinae (Camp and Van Der Hoof 1940)

Genus Cainotherium Bravard 1828

Cainotherium aff. huerzeleri (Heizmann 1983)

Figure 2

Age
MN4

Localities

MCX1, MCX2, MCX3, MCX5, BC1, MAB0A, MAB3, MAB5, MAB7, MAB8, MAB11, CBR0A, CBR0B, and CBR1.

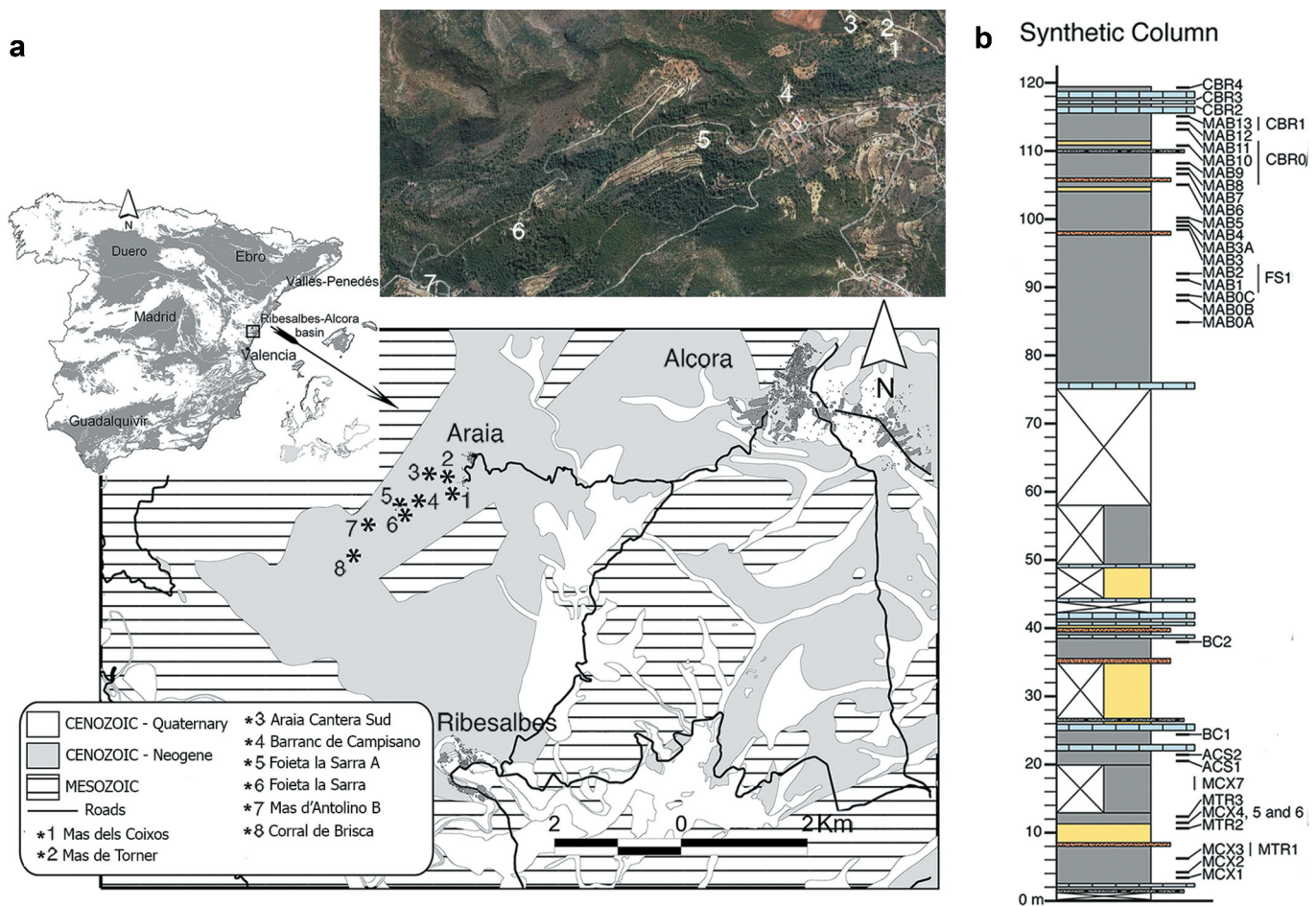


Figure 1. Geographic and geological setting of the Ribesalbes-Alcora Basin, showing the location of the outcrops of the campisano ravine. Modified from Crespo et al. (2018; 2019a)

Studied Material

MCX1: M fragment; MCX2: 1 P1; MCX3: 1 dp4, 1 p1, 2 p3, 1 p4, 1 m3, m fragment, 1 I/i, 3 M1, 1 M2, 1 M3, 3 M fragments; MCX5: 1 P3; BC1: premolar fragment; MAB0A: m fragment; MAB3: 2 p1, 2 p2, 4 p3, 3 premolar fragments, 6 m fragments, 2 I/i; MAB5: lower premolar fragment; MAB7: 1 p3, 1 premolar fragment; MAB8: 1 premolar fragment; MAB11: 1 p2, 1 p3, 1 p4, m fragment, 1 P1, 1P3, 1P4; CBR0A: 1 P1; CBR0B: 1 m1, 1 M2; CBR1: 1 p1, 1 premolar fragment, M fragment.

Measurements

see Supplemental online material 1.

Description

dp4: broken tooth, with the anterior lobe missing. The middle lobe is smaller than the posterior lobe.

p1: the tooth has an elliptical outline, with a cingulum surrounding the crown, more developed on the lingual side. The median ridge is slightly sinusoidal.

p2: the tooth is similar to the p1, but more elongated, the sinusoidal crest is more marked, with a small cusp in its anterior part.

p3: the tooth is similar to the p2, but more robust, with more developed cingulids and the central ridge curved towards the lingual part.

p4: the tooth has a subtriangular outline. The labial side is higher, the central ridge is situated on this side, having a sigmoidal shape and with a paraconid, protoconid and hypoconid. On the lingual

side there are two cusps, the metaconid and entoconid, which are joined to the labial cusps by ridges, forming a square. In the middle of this square there is a central conule. The labial cuspid is narrow and the lingual cingulum is absent.

m1: the tooth has a rectangular outline. The trigonid is slightly smaller than the talonid, the latter being more oblique than the former. The anterior cingulid is narrow. The metaconid and the protoconid show a similar height. The hypoconid is taller than the entoconid. The entoconid and posterior cingulid are broken.

m3: the tooth is broken. The anterior lobe is absent, while the middle lobe is mostly absent, leaving only part of the posterior lobe, which is missing the back part. Even so, the reduction of the talonid typical of this element can be observed.

Incisiform canine: the tooth is small with a subelliptical outline. It has a central ridge, slightly curved towards the labial part and the cingulum is poorly developed.

P1: the tooth has an elongated elliptical outline. The central ridge is slightly curved towards the labial side. The cingulum surrounds the tooth on the labial and lingual sides, being more developed on the lingual side.

P3: the tooth is similar to the P1, but larger, more robust and with more developed cingulums.

P4: the tooth has a subtrapezoidal outline. The tooth is very worn, although a decrease in the size of the cusps can be observed towards the lingual side. The paracone is the most developed and the protocone the smallest cone. The anterior and posterior cingulums are narrow and the styles of the labial side are developed.

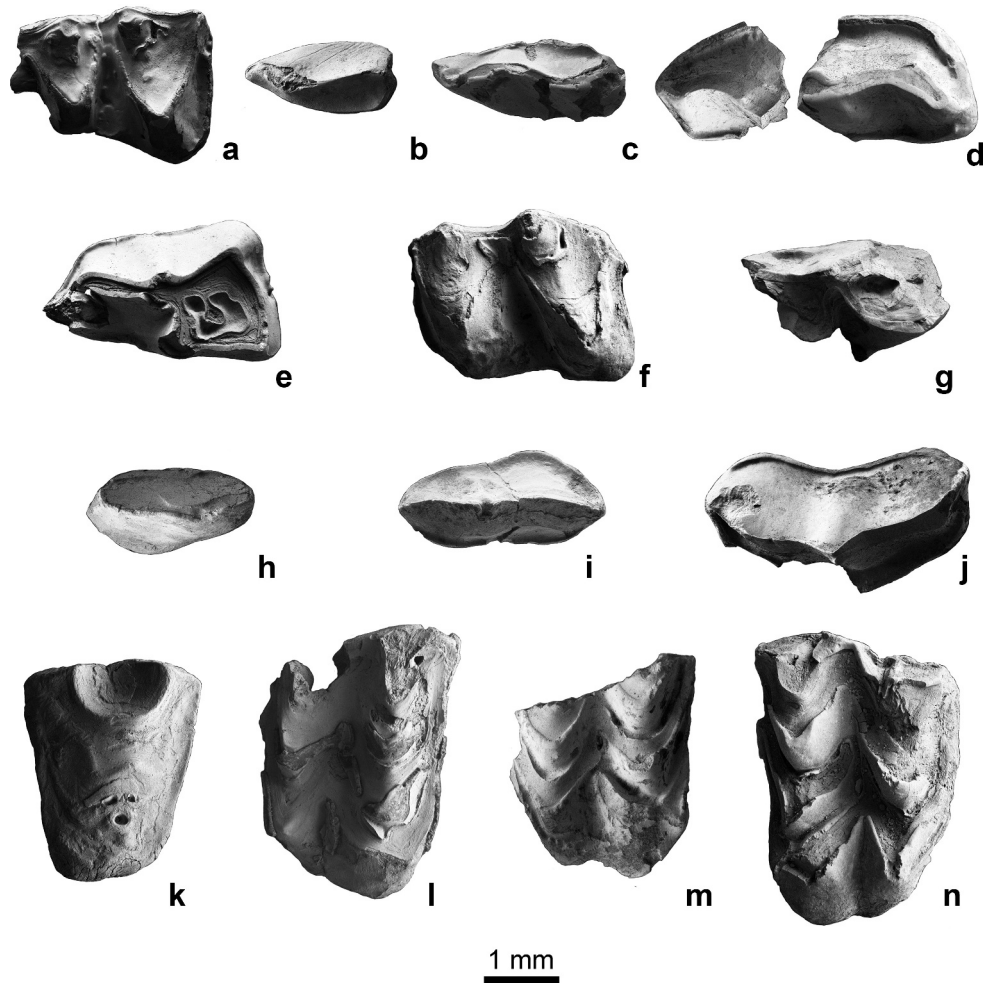


Figure 2. Teeth of *Cainotherium* aff. *huerzeleri* from the Ribesalbes-Alcora Basin. A- Left dp4 (MCX3-122); B- Left p1 (MCX3-24); C- Left p2 (MAB3-836); D- Left p3 (MAB7-3); E- Left p4 (MCX3-26); F- Left m1 (CBR0B-6); G- Left m3 (MCX3-28); H- Right incisiform canine. (MCX3-121); I- Left P1 (MCX2-5); J- Left P3 (MCX5-5); K- Left P4 (MAB11-14); L- Left M1 (MCX3-29); M- Right M1 (CBR0B-41); N- Right M2 (MCX3-118). Scale bar = 1 mm.

M1: the tooth has a subrectangular outline. The anterior lobe is narrower than the posterior. The centrocrest is broken. The anterior cingulum is developed. The protoconule is the minor cusp. The metastyle is developed. The metaconule is the major cusp, the metaconule being slightly smaller and the secondary cusp is lower.

M2: the tooth is similar to the M1, but the anterior part is wider.

M3: the tooth is broken, similar to M2, but larger.

Order Lagomorpha Brandt 1855

Family Ochotonidae Thomas 1897

Genus Lagopsis Schlosser 1884

Lagopsis penai Royo 1928

Figure 3

Localities

MCX2, MCX3, MCX5, MCX6, MTR2, BC1, MAB0A, MAB0B, MAB3, MAB5, MAB6, MAB11, MAB11B, MAB13, CBR0A, CBR0B and CBR1.

Material

MCX2: 1 p3; MCX3: 2 p3, 1 P3, 5 P4/M1/M2; MCX5: 1 DP4, 1 P3, 1 P4/M1/M2; MCX6: 1 P4/M1/M2; MTR2: 2 dp3, 2 dp4, 7 p3, 10 p4/m1/m2, 2 m3, 4 DP4, 3 P2, 6 P3, 9 P4/M1/M2; BC1: 1 dp4, 1 DP4, 2 P3, 3 P4/M1/M2; MAB0A: 1 P4/M1/M2; MAB0B: 1 dp3, 1 P3; MAB3: 1 dp3, 1 dp4, 3 p4/m1/m2, 1 P2, 4 P3, 5 P4/M1/M2; MAB5: 1 p3, 1 I, 3 P3, 4 P4/M1/M2; MAB6: 1 P3, 1 P4/M1/M2; MAB11: 1 P4/M1/M2; MAB11B: 1 p3; MAB13: 1 p4/m1/m2; CBR0A: 1 P3, 1 P4/M1/M2; CBR0B: 2 p4/m1/m2, 1 P4/M1/M2; CBR1: 1 p3.

Measurements

see Supplemental online material 1.

Description (based in the site MTR2)

dp3: The outline is sub-rectangular, consisting of three lobes. The anteroconid is well developed. The anteroflexid is deep and poorly cemented. The paraflexid is narrow, long and cemented. The protoflexid is wide, V-shaped and uncemented. The metaconid is small, but larger than the protoconid. than the protoconid. The mesoflexid and hypoflexid are wide, V-shaped and cementless. The entoconid and hypoconid are small, with the first two cusps being larger. Variability in other sites: The material from MAB0B and MAB3 are similar to that described previously.

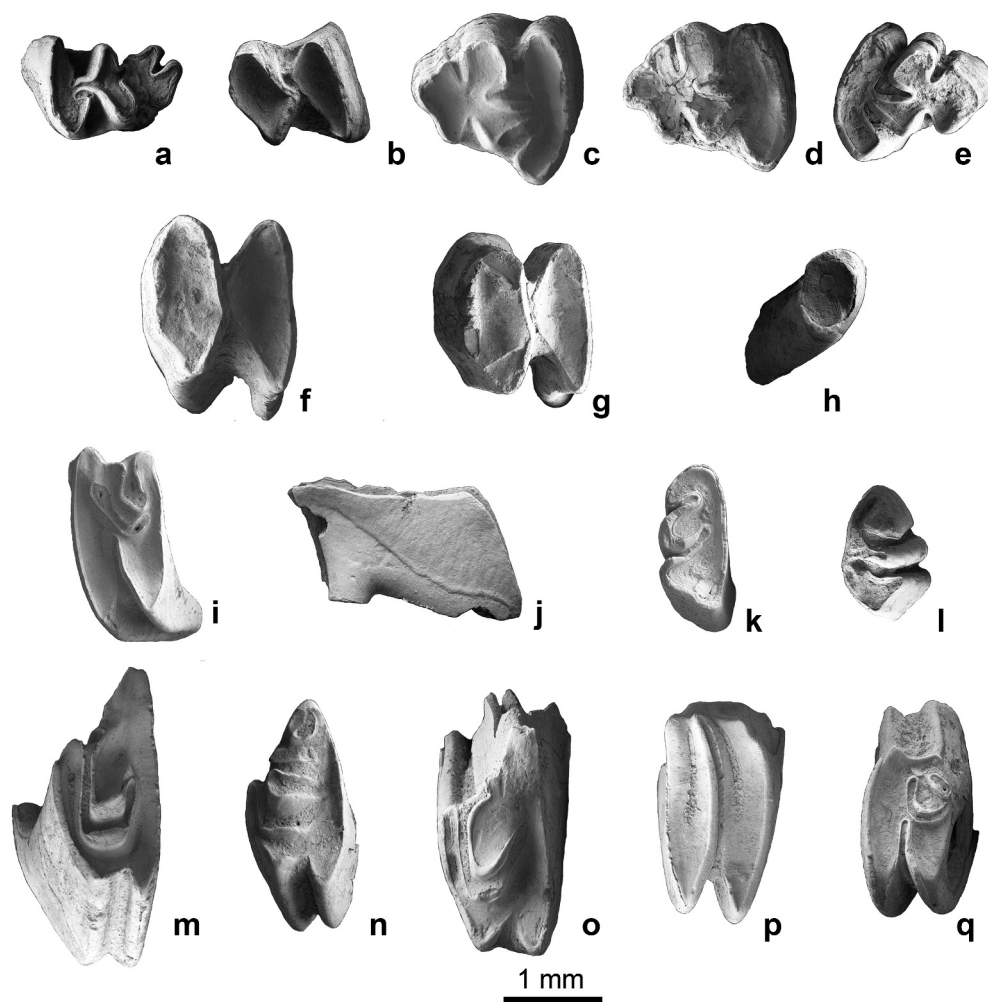


Figure 3. Teeth of *Lagopsis penai* from the Ribesalbes-Alcora Basin. A- Left dp3 (MTR2-173); B- Left dp4 (MTR2-179); C- Left p3 (MTR2-20); D- Left p3 (MTR2-22); E- Right p3 (MAB11B-5); F- Left p4/m1/m2 (MTR2-21); G- Left p4/m1/m2 (CBR0B-43); H- Right m3 (MTR2-33); I- Left DP4 (MTR2-160); J- Left DP4 (MTR2-163, lateral view); K- Left P2 (MTR2-174); L- Right P2 (MAB3-692); M- Left P3 (MTR2-155); N- Left P3 (MAB5-886); O- Left P3 (MAB6-3); P- Right P4/M1/M2 (MTR2-156); Q- Left P4/M1/M2 (MTR2-164). Scale bar = 1 mm.

dp4: tooth consisting of two lobes of similar width, with the trigonid longer, diamond-shaped and the narrower, oval-shaped talonid, joined in the middle. The base of the tooth is broad and connects both lobes. Variability in other sites: The material from BC1 and MAB3 are similar to that described previously.

p3: the outline is subtriangular. The anteroconid may be medium-size (2 out of 7) or well developed (5 out of 7), of similar size to the metaconid (2 out of 7) or larger (5 out of 7), in the form to metaconid (2 of 7) or larger (5 of 7), diamond to triangular in shape. The anteroflexid may be poorly developed (6 out of 7) or moderately developed (1 out of 7), and without cement (6 out of 7), or with it (1 out of 7). The paraflexid may be poorly developed (6 of 7) or almost absent (1 of 7), and without cement (3 of 7) or with it (4 of 7). The protoflexid may be poorly (2 out of 7) or moderately developed (5 out of 7), and without cement (5 out of 7) or with it (2 out of 7). The metaconid is lobular and well developed. The protoconid is triangular and poorly developed, the protoconulid is absent. The mesoflexid is triangular in shape and fully cemented. The hypoflexid may be narrow (2 out of 7) or wider (5 out of 7) and

cemented. The postlobe may be medium (3 out of 7) or long (4 out of 7). The hypoconid and entoconid may be poorly developed (4 out of 7) or well developed (3 out of 7), less developed than the metaconid (6 out of 7) or larger (1 out of 7), with the first cusp being slightly larger (1 out of 7) or similar (6 of 7). The posterior part is slightly rounded. It has no roots. Variability in other sites: The material from MCX2, MCX3, MAB5 and MAB11B are similar to that described previously.

p4/m1/m2: the tooth consisting of two lobes of similar width, with the longer, diamond-shaped trigonid and the narrower, more oval talonid, joined in the middle. The posterior part of the lobes has the thickest enamel. From p4 to m2 the teeth become progressively curved progressively. Variability in other sites: The material from MAB3, MAB13 and CBR0B are similar to that described previously.

m3: the tooth consisting of only one rounded lobe.

DP4: tooth with a sub-rectangular outline, consisting of two lobes, with slightly rounded anterior and posterior parts, and with the base wider than the crown. The mesoflexus and paraflexus are present and developed in the anterior lobe. The hypoflexus is deep, reaching to the middle of the tooth or

slightly closer to the labial side. The mesial hyperconus is wider than the distal one. It has two roots. Variability in other sites: The material from MCX5 and BC1 are similar to that described previously.

P2: the tooth has a sub-square outline. The postlobe is narrow and slopes anteriorly towards the lingual side, like the lagiconus, but this is more developed. The mesoflexus and paraflexus are long, narrow, curved towards the labial side and cemented, the second flexus being longer. The mesial hyperloph and distal hypercone form a triangle. The distal hyperlobe is straight. Variability in other sites: In the MAB3 specimen, the mesial hyperlobe and distal hyperconule form a triangle, being juvenile and unworn, the three lobes are observed to be independent.

P3: subtrapezoidal to sub-rectangular outline. The precone is narrow. The mesial hyperlobe is even narrower than the precone. The mesoflexus is very small. The paraflexus is long, cemented and hook-shaped. The mesial and distal hyperconus are small, the former being short and wide and the latter narrower and longer. The hypoflexus is small. The lagiconus is well developed. The postlobe is triangular. The distal hyperlobe is narrow, but wider than the mesial hyperlobe. Variability in other sites: the mesoflexus is well developed in two of three specimens from MAB5 (Figure 3.N), in two of four from MAB3 and in one of two from BC1. In individuals from MCX3, MCX5, MAB0B, MAB6 (figure 3.O) and CBR0A there are no notable differences.

P4/M1/M2: sub-rectangular tooth, consisting of two lobes, with slightly rounded anterior and posterior parts. The mesoflexus and paraflexus are absent, and they are only faintly visible in a specimen with little wear. The hypoflexus is deep, reaching to the middle of the tooth, or slightly closer to the labial side. The mesial hypercone is wider than the distal one. Variability in other sites: in material from MCX3, MCX6, BC1, MAB0A, MAB5, MAB6, MAB11 and CBR0A there are no notable differences. In two specimens from MAB3 the mesoflexus and paraflexus are still visible. In one individual from MCX5, both structures are also visible.

Discussion

Systematic position of the cainotheriidae from the Ribesalbes-Alcora Basin (MN4)

The differentiation at the species level was carried out according to morphometric criteria (Berthet 2003). However, the fragmentary nature of the specimens from the Ribesalbes-Alcora Basin makes impossible the full comparison meeting all the criteria described by Berthet (2003). Nevertheless, the material allows us to assign the new Iberian material to the group of smaller species of *Cainotherium*. In particular, the measurements obtained are mostly similar to those of *C. huerzeleri* from Steinberg, *C. cf. huerzeleri* from Alameda de Osuna (Spain) (Alarcón and Álvarez-Sierra 2009), and *C. cf. huerzeleri* from Vieux-Collognes and Francon (Berthet 2003) (Supplementary online material 2). However, a lot of the dimensions recovered from the specimens of the Ribesalbes-Alcora Basin such as the width of p2, P3 and P4, and the length of p1, p4, and M2 are smaller than any species of this genus previously described by Alarcón and Álvarez-Sierra (2009) or Berthet (2003), whereas the p3 is even longer than in *C. miocaenicum* from Sant-Mamet (MN4) which otherwise is generally much larger than all the specimens recovered in the Ribesalbes-Alcora Basin. Therefore, due to the scarcity and fragmentation of the studied material, with the absence of full jaws or maxillae, and having measurements smaller than the rest of species of the genus, we prefer to identify the new remains as *Cainotherium* aff. *huerzeleri*.

Cainotherium huerzeleri was described based on cranial and dental material from two localities of the Astaracian (MN6): Steinberg and Goldberg in the Nördlinger Ries (Southern Germany), with the first of these localities considered as the type site (Berthet 2003). Heizmann (1983) compared the skull of *C. huerzeleri* with the diagnosis of *Cainotherium* by Berger (1959, p. 39), and pointed out some differences such as the lower participation of the palatins in the palate or a greater width of the cervical skull behind the orbits. The lack of cranial material of *C. miocaenicum* and *C. bavaricum* did not allow Heizmann (1983) to take them into account. As Berthet (2003) later stated, the peculiar characters of *C. huerzeleri* dentition can easily be derived from *C. bavaricum*.

Berthet (2003) proposed that the evolution of *C. miocaenicum* (which appeared during the MN1 in France (e.g. Paulhiac) and remaining until the zone MN4 when it becomes no longer represented in Spain, which record starts in MN3, where it was initially considered as endemic.) originated – with continuous decrease in size and reduction of the length of the premolar row – *C. bavaricum* (MN5) which then evolved into *C. huerzeleri* (MN5-MN6), even dispersed to France, whereas *C. miocaenicum* remained confined to Spain and Portugal. This meant the ranges of the last cainotheriids were divided, a prelude to extinction.

Cainotherium huerzeleri is comparable in size to *C. gracile* and *C. bavaricum*, but the first one differs from the other two by a further reduction of the premolars (especially the anterior ones as we see in the specimens from the Ribesalbes-Alcora Basin), the size of P2 which is significantly smaller than the P3, and the m3/P2 ratio which is high, it is 1.46.

According to Berthet (2003) *C. huerzeleri* is distinguished from *C. bavaricum* by a slightly smaller size, remarkable shortening of the premolars, a p4 anterior half wider and with the median tubercle pushed back, the absence of enamel beads in the dimple of the third lobe of the m3, almost constant in *C. bavaricum*; a P4 frequently with a ridge directed backwards and bearing an inner tubercle, a lower tendency for the crests of the protoconule and protocone, a greater tendency to form secondary ridges and enamel beads on the upper molars, and a higher m3/P2 ratio.

Systematic position of the lagomorpha from the Ribesalbes-Alcora Basin (MN4)

The ochotonid *Lagopsis* is a very common genus in European faunal assemblages of the early Miocene (Hordijk 2010). It differs from its putative ancestor, *Marcuinomys*, by lacking roots on the definitive teeth and the lack of fossettes in the enamel of the upper molarized teeth. The morphology of the centroflexid of p3 differentiates it from the genera *Alloptox* and *Albertona*. It differs from *Paludotona* in having a very weak or no mesoflexus on P2, and in the presence of a p3 without paraflexus. It differs from *Prolagus* by the absence of an isolated anteroconid on p3, a bilobed m2 and the presence of the m3, and the upper molars are straighter and do not usually have pits in the enamel. *Ptychoprolagus* differs from *Lagopsis* by the same characters as *Prolagus*, besides having crenulations on its teeth. From the genera *Titanomys*, *Piezodus*, *Eurolagus* and *Gymnesicolagus*, it differs by not having roots on the teeth and the absence of fossettes on the upper molariforms (Hordijk 2010).

The material described here can be well ascribed to the species *Lagopsis penai*, characterised by: the absence of enamel fossettes (may be present in juvenile individuals); hypoflexus is deep, but it not reaches the labial side of the tooth; in the p3, the anteroconid is well developed and, in the majority of specimens, larger than metaconid; and the presence of anteroflexids; and has a more robust

tooth. On the other hand, the material in study, differs from *L. aff. penai* from the Ramblian has a smaller anteroconid on the p3, *Lagopsis verus* (Hensel 1856) has a different p3 anteroconid morphology, as well as an anteroflexid on this element with more frequent cement than the lack of this (López-Martínez 1984; Hordijk 2010).

The morphology of the material under study falls into category C as described for *L. penai* by López-Martínez (1984), characterised by more than 50% of specimens with the anteroconid somewhat compressed anteriorly and larger than the metaconid. Likewise, the rest of the characters agree with those described by López-Martínez (1984) and Hordijk (2010) for the populations of this species present in the sites of similar age in the Calatayud- Montalbán Basin. With regard to its shape, Hordijk (2010) points out the great variability that this species shows within the same population, as well as the morphometric stability over time, a fact that is confirmed in the material under study. Furthermore, the length of the p3 is within the range described by López-Martínez (1989) for the species *L. penai* and *L. cf. penai* from Europe, with a stratigraphic range from MN3 to MN5.

Palaeocology and biostratigraphy of *Lagopsis*

Pikas were one of the most numerous groups of small mammal communities in the Miocene, and one of the most common folivorous taxon present in these communities (Hordijk 2010). The lagomorph genera *Lagopsis* and *Prolagus* are usually very common during the early Miocene of Europe, although in Western Europe their abundance depends on the latitudinal gradient and the humid conditions (Mein 1984; López-Martínez 1989, 2001). Thus, the genus *Lagopsis* is more abundant in the Iberian Peninsula but *Prolagus* is more abundant in northern Europe, being associated also to a humidity gradient (López-Martínez 1989). *Prolagus* does not appear in the Ribesalbes-Alcora Basin, with only *Lagopsis* being present, probably associated with drier environments. This also occurs at the site Les Cases de la Valenciana (Vallès-Penedès Basin; Jovells-Vaqué et al. 2018).

Drawing a comparison with the present-day pikas, the habitat preferences of this group are associated with different ecosystems ranging from grasslands to forests, but always with high densities of vegetation (López-Martínez 2001). Likewise, the increase in diversity of the family Ochotonidae is associated with the increase in C3 vegetation, together with an increase in temperature and humidity, while on the other hand, the family Leporidae is associated with the expansion of C4 plants, as well as low temperatures and dry environments (López-Martínez 2001; Ge et al. 2013; Flynn et al. 2014; Erbajeva et al. 2015). Ge et al. (2013) show how the increase in pikas was related to the increase of C3 plants and a rise in temperatures, until the middle Miocene, when C4 plants originate and temperatures dropped, with pikas declining their representation while rabbits expanded. Pikas nowadays have a preference for the consumption of C3 plants such as Astaraceae, Rosaceae and Fabaceae, with the maximum diversity and expansion of the Astaraceae family occurring at the height of the pikas (Ge et al. 2013). This fact could indicate an increase in MTR2 of this type of vegetation, as this is the site where pikas are most common.

Lagopsis reaches more than 50% of the remains in some sites in Zone B, with the species *L. penai* being the most abundant (MN4, Miocene) (Hordijk 2010; van der Meulen et al. 2012). In contrast, in the local zone Cb (MN4, early Miocene) this group has a particularly low abundance, and increasing in the deposits of the local zone Da (Hordijk 2010).

During the beginning of the middle Miocene there is a shift of dominance from the genus *Lagopsis* to the genus *Prolagus*, while during the rest of the middle Miocene (from local area Dd onwards) *L. penai* is replaced by *L. verus* (López-Martínez 1989, 2001; Hordijk 2010). The decrease in the abundance of lagomorphs along the local area Ca and Cb (Hordijk 2010), explains why they are more abundant in the oldest deposits of the Ribesalbes-Alcora Basin and progressively decreasing until they are scarcely represented in the most modern deposits, located in the local area Cb.

Cainotheriids vs lagomorphs at the Ribesalbes-Alcora basin

No studies have been made of the way of life of the Cainotheriidae family. According to Blondel (2001) or Berthet and Huguenet (2000), their brachyo-selenodont molars suggest a frugivorous/folivorous/grazer diet, although cainotheriids might have been more generalist feeders. Their morphology, especially of their hind limb, suggests an ecology rather close to that of the tragulids (see the reconstructed skeleton of *Cainotherium laticurvatum* in Hürzeler 1936). An unusual feature of this family of artiodactyls is the development of a large spongy tympanic bulla, a common occurrence among low-frequency hearing animals, as rodents that live in burrows or spend a considerable time below ground (Aitkin et al. 1982; Begall and Burda 2006; Pleštilová et al. 2016), although many artiodactyl groups have a spongy tympanic bulla (e. g. Hippos) and do not live in burrows. This is not possible to verify in current artiodactyls since none of them has this lifestyle (Theodor 2010).

Despite (Blondel 2005) suggesting Cainotheriidae were not affected by the immigration of different families of small artiodactyls and therefore, probably, they were not occupying the same exact ecological niche as them. The early Oligocene decline of cainotheriids from Quercy is not explained by abiotic factors and might be due by the competition with other group of artiodactyls, carnivores and glires (rodents and lagomorphs) (Weppe et al. 2021). According to (Heizmann 1999) during the early Miocene the decline of this family actually coincides with the increase in lagomorphs, suggesting possible similarities between their ecological niches.

In the Ribesalbes-Alcora Basin we can observe the presence of cainotheriids and lagomorphs in the same deposits with different relative abundances, which could possibly indicate the competition between both families (Figure 4, Supplementary online material 2), since no other artiodactyls have been recorded in the sites under study, although this does not mean that they were not present (see the complete faunal list at Crespo et al. (2019a)).

We see than in the oldest locality (MCX3) there is a predominance of *Cainotherium* followed by a dominance of *Lagopsis* in the localities MTR2 and BC1, peaking in MTR2 (Figure 4, Supplementary online material 2). Afterwards we see another interval where the relative abundance of *Cainotherium* is higher during MAB11, with the complete absence of *Lagopsis* in MAB7 and MAB8, although the sample in these sites is too low to be representative. However, after this period the relative abundance of *Lagopsis* increases again, attaining its highest level in CBR0B, one of the younger sites, with a modest increase in *Cainotherium* in the youngest locality with a decrease in the abundance of *Lagopsis*. We can observe a pattern of one taxon attaining higher relative abundance when the other shows a decrease at the same time period, possibly indicating a direct ecological competition between *Lagopsis* and *Cainotherium*.

As for the hypotheses on the disappearance of *Cainotherium* at the end of the MN6 it is very difficult to find a precise reason to explain the gradual disappearance of the genus and a whole series of

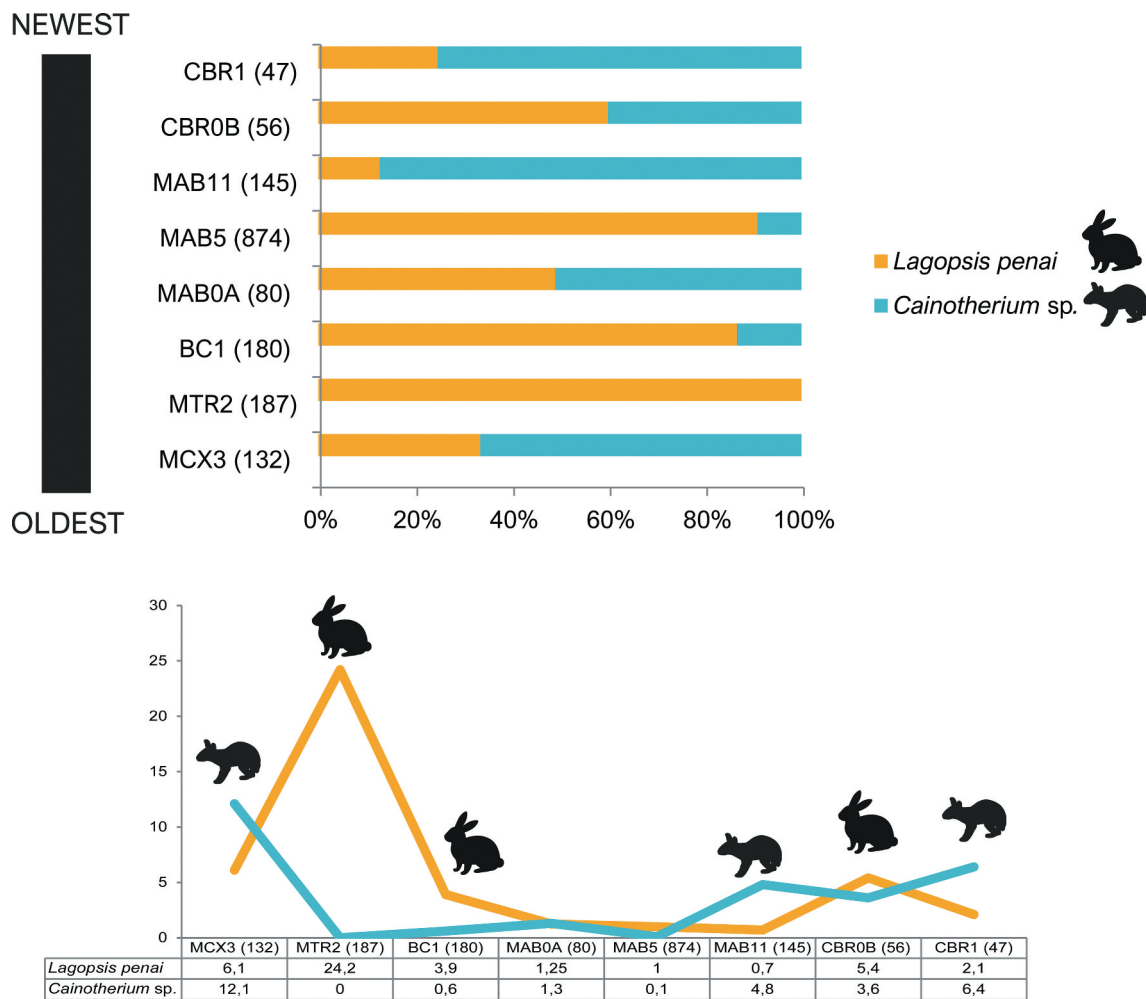


Figure 4. Relative abundances of *Cainotherium* aff. *huerzeleri* and *Lagopsis penai* from the Ribesalbes-Alcora Basin (early Miocene, MN4).

environmental, ecological or palaeogeographic changes as the readjustment of communities, biotic factors (e.g. direct competition for food with same sized competitors, dislodging of shelters, predation), and changes in vegetation, humidity and temperature (e.g. then a cooling phase and greater humidity at the end of MN5), and palaeogeographic events (e.g. Africa-Eurasia collision which allowed the establishment of exchanges between these continents for a long time and the arrival of new competitors, the filling of the rift of Limagne in MN2 led to the disappearance of one of the main areas of diversification of the genus *Cainotherium*) probably played a role (Berthet 2003).

Quoting Berthet (2003) 'Therefore not possible to appoint a single person responsible for the disappearance of *Cainotherium* which seems rather due to the convergence of many factors contributing to the weakening of an ancient wildlife complex even before immigration and the great faunal renewal of the middle Miocene'.

In the Ribesalbes-Alcora Basin, due to the faunal composition and the size of the other taxa (see Crespo et al. 2019a), the competition of the small artiodactyl *Cainotherium* with the lagomorph *Lagopsis penai* could represent a relevant biotic factor related to food competition. Both taxa are the most similar in size in the basin, and competition between shapes of equivalent size is the most direct (Berthet 2003). This is due also to both of them being very similar size herbivores with similar intake requirements influencing the availability, abundance and development of vegetation in the

area (Berthet 2003). Legendre et al. (1991) and Sudre and Legendre (1992) showed a coincidence between the regression of small artiodactyls and the diversification of rodents at the beginning of the Oligocene, but did not account for lagomorphs. There is also a competition event linked to the immigration, during the MN4, when a whole series of new cricetids arrive (Bruijn et al. 1992; Van der Meulen and Daams 1992), where cainotheriids are decreasingly scarce.

Lagomorphs are often mentioned as direct competitors of *Cainotherium* (Heizmann 1999; Berthet 2003). They appeared at the same time of the diversification of *Cainotherium*, in MP 28, with already strongly hypsodontic forms (Berthet 2003). However, at the beginning of their development in Europe, they probably did not play a big role in the competition with *Cainotherium*, since they did not prevent diversification and proliferation *Cainotherium* in Limagne; besides, they were tiny in size compared to *Cainotherium*, poorly diversified and not very abundant in the localities (Viret 1929; Berthet 2003).

However, from the MN3 onwards, when *Cainotherium* began to decrease in size and lagomorphs were getting larger, as we see in the Ribesalbes-Alcora Basin (MN4), direct competition probably came into play. This could also be the case with the locality of Steinberg (Heizmann and Falbusch 1983), where the abundance of the Lagomorphs may well have exerted mass pressure on a *Cainotherium* genus already in strong decline, as the population

there is represented only by a very high number of juvenile individuals, probably result of predation as is the case with numerous lagomorphs of this site (Heizmann and Fahlbusch 1983; Berthet 2003).

It is clear that once *Cainotherium* disappeared, the lagomorphs become extremely abundant in certain deposits, such as *Prolagus* in the levels of La Grive. As Berthet (2003) stated 'Is this the emergence Lagomorphs which caused the disappearance of the last Cainotherium or is it the place left empty by Cainotherium which favored their development?'

Another strong hypothesis points to an extinction related to predation and the changes in their social system. In this scenario similarly sized lagomorphs dislodged *Cainotherium* from shelters in which they protected themselves from predators at least until MN2. The adaptation to gregariousness of *Cainotherium* is suggested by the extremely abundant material hosted in older collections (both in the 'Quercy' and 'Saint-Gérard-le-Puy') (Berthet 2003). Herd lifestyle was increasing the viability of the individual because of the protection provided by the group, especially for young individuals. However, it appears that since the MN2b, *Cainotherium* no longer seemed to live in herds. It seems that after MN2, the abundance of *Cainotherium* diminished so much that one could only find small family groups, less able to protect themselves against predation. In MN5, the ranges of the two remaining *Cainotherium* species are disjointed, adding vulnerability against predators (Mc Kinney 1997; Berthet 2003). However, the disappearance of *Cainotherium* is certainly not due to a single carnivore, because we can note in the early Miocene great diversification in that order (Ginsburg 1999).

Other relevant extinction factors are related to palaeogeographic variations. Important tectonic events have played a big role in Miocene faunal changes as the Africa-Eurasia collision that allowed the establishment of exchanges between these continents (Rögl 1999) and the arrival of new competitors, as some kinds of rodents (Berthet 2003).

We agree with Berthet (2003) that there is not a single factor responsible for disappearance of *Cainotherium* but rather the convergence of many factors contributing to the weakening of the lineage and its posterior extinction during the middle Miocene.

In the Ribesalbes-Alcora Basin we see a succession of periods where we can appreciate a dominance of lagomorphs over cainotheriids, which in these localities show some of the smallest measurements found in the family showing a possibly weakened population probably affected not only by the competition with *Lagopsis* but with population fragmentation which increased the predatory pressures as the changing environment does not affect much.

Cainotherium could therefore be found in abundance in very varied biotopes; a radical change in the vegetation would have been necessary to explain his disappearance, which is not the case Huguency et al. (1982). Whereas temperature and humidity variations cooling and greater humidity at the end of MN5 could have accelerated the demise of *Cainotherium* (Van der Meulen and Daams 1992).

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