New findings of the genus Altomiramys (Mammalia, Gliridae) in the Lower Miocene (Agenian, Ramblian and Aragonian) of the Ebro and Ribesalbes-Alcora Basins (Spain)

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Abstract

Altomiramys (Gliridae, Myomiminae) is a very uncommon glirid in the rodent assemblages from the lower part of the Lower Miocene (Agenian to Ramblian) of the Iberian Peninsula. Only one species, Altomiramys daamsi, has been described from localities of Ramblian age (Loranca-1 and Ramblar-1). An unpublished second species, Altomiramys aff. daamsi, is mentioned in the locality of Cetina de Aragón, of Agenian age. New findings of this genus in the Ebro and Ribesalbes-Alcora Basin have allowed to expand the time range for this taxon to the later part of the Early Miocene (Aragonian). This increase of the material leads to a modification of the diagnosis of the genus.

Keywords: Early Miocene, Iberian Peninsula, biostratigraphy

1. Introduction

The diversity of dormice (glirids) in Europe during the Miocene (23-5.3 Ma) reaches 28 genera, with a maximum in the Lower Miocene (16.5 Ma). At the end of the Miocene, 23 of these genera were extinct (Daams 1999). A strong reduction of diversity came with the immigration of the modern cricetids (16.6 Ma) and the murids (9.8 Ma). The entry of these faunas coincided with a dramatic reduction in both number of species and relative abundance of the glirids in the rodent assemblages of Europe.

Altomiramys Díaz-Molina & López-Martínez, 1979 (Gliridae, Myomiminae) is a very uncommon endemic glirid in the rodent assemblages from the Lower Miocene (Agenian and Ramblian MN1-MN3, 23.0-16.6 Ma) of the Iberian Peninsula. So far, only one species, Altomiramys daamsi Díaz-Molina & López-Martínez, 1979, has been described from localities of this age (Loranca-1; Agenian, upper part of MN2, 20 Ma, Díaz-Molina & López-Martínez, 1979 and Ramblar-1; Lower Ramblian, lower part of MN3, 19.4-19.9 Ma, Daams, 1989) but an unpublished second species, Altomiramys aff. daamsi (Daams 1974, 1989, 1999), is mentioned from Cetina de Aragón, an older site from the early part of the Early Miocene (MN1). Therefore, the fossil record of this genus covers the span between MN1 and the lower part of MN3 (Fig. 1). The remains of Altomiramys are extremely scarce in the paleontological record, with only one specimen recorded in its type locality (Loranca-1) and 10 specimens in Ramblar-1. In this paper we describe new remains of this genus from the localities of Cuesta Agujeros-2 (CA-2) and Cuesta Agujeros-4 (CA-4) (Ebro Basin), and Mas de Antolino-5 (MAB-5, Ribesalbes-Alcora Basin).
2. Material and methods

2.1. Stratigraphical setting

The non-recurrent compositional and evolutionary changes of the European mammal fauna history have been extensively used as a relative-age tool for the continental sediments in which they are found (van der Meulen et al. 2011). Thaler (1966) was the first to propose a modern biozonation based on mammals for Paleogene and Neogene. A comprehensive framework for mammal history was provided by the MN zones. This system is based on Neogene mammal assemblages from Europe and North Africa (Mein 1975, 1979, 1990). According to this system, the Neogene is divided into seventeen units. It is ideally applicable, independent of regional factors or biogeography, and has been widely used during the past decades. Since its proposition, the MN-system has been used for correlations to different scales. The recognition of the MN units in several geographic areas has allowed the establishment of different ages from the MN boundaries (see bibliography in van der Meulen et al. 2011). Many of these proposals have been calibrated to the time scale with paleomagnetic and/or radiometric calibrations. For the time interval represented in the localities studied in this paper, we will use the calibrations contained in Larrasoaña et al. (2006), van der Meulen et al. (2012) and Ruiz-Sánchez et al. (in press).

The material from MAB-5, CA-2 and CA-4 was collected during paleontological excavations carried out in the past five years, using the standard methodology for collecting microvertebrate fossils (Hibbard 1950, Thaler 1966, Freudenthal et al. 1976, Daams & Freudenthal 1988). The terminology of dental morphology used to describe the glirid remains is taken from Freudenthal (2004) (Fig. 2). The lower case denotes lower teeth, upper case denotes upper teeth (m1, m2, M1, M2). The measurements are given in tenths of millimetres, and were taken on a Leica MZ75 binocular microscope by means of displacement of a mechanical stage connected to a Sony Magnescale measuring device.

The tooth of *Altomiramys* from MAB-5 is kept at the MGUV (Museu de Geologia de la Universitat de València) with the acronym MAB5-, and the five teeth from locality CA-2 and one from CA-4 are housed in the Departamento de Estratigrafía y Paleontología de la Universidad del País Vasco (UPV/EHU) with the acronyms CA2- and CA4-.

![Fig. 1](image-url) Stratigraphic distribution of *Altomiramys daamsi* and *Altomiramys sp.* in different Spanish localities through the Lower Miocene (after Daams 1999 and this paper).
3. Results

3.1. Geological setting

The Ribesalbes-Alcora Basin is located in the East of Spain (Castellón Province) and is situated in the southern Maestrazgo, between the Sierra de Espadán and fallen blocks of the Desierto de las Palmas (Agustí et al. 1988). The deposits of this basin have been divided into five units (A, B, C, D and E) (Anadón 1983), and they consist of yellow and grey shales with banks of sandstone, dolomite and limestone beds. Agustí et al. (1988) in the section of Mas de Antolino, and after that Ruiz-Sánchez et al. (2010) and Furió et al. (2010) in the section of Mas de Antolino B, both in unit C of Anadón (1983), found several assemblages of mammalian remains. These localities contain faunal associations of Early Aragonian age (MN4). One of these localities, the rich association from the locality Mab-5, contains among other rodents, *Megacricetodon cf. primitivus* (Freudenthal, 1963) and *Ligerimys ellipticus* Daams, 1976, which allow to date this site as Early Aragonian (MN4) (Tab. 1).

On the other hand, the two other localities with *Altomiramys* remains analyzed in this paper are situated in the Ebro Basin. From the Late Eocene until the Late Miocene, this Basin was an endorheic depression. In the north-central area of this basin, the Tudela Formation has been defined, where the localities CA-2 and CA-4 are located. This Formation is composed of 650 meters of fluvial distal, palustrine and lacustrine sediments, accumulated during the Early and Middle Miocene (Larrasoaña et al. 2006) and it crops out extensively in the so-called Bardenas Reales of Navarra. The fossil sites presented in this work are located in the section of Cuesta de Agueros (CA-). The presence of *Armanomys daamsi* (Álvarez-Sierra et al. 1991) in CA-2 and *Armanomys* cf. *jasperi* Daams, 1991, in CA-4 allow an age attribution of these localities to the Late Agenian (local zone Y, MN2) and Late Ramblian (local zone A, MN3) (Ruiz-Sánchez et al. in press).

3.2. Systematics

According to the original diagnosis of the genus, *Altomiramys* is a glirid with upper molars with subrounded outline, a low crown and concave occlusal surface. The ridges are thin and well-separated, with precentroloph only, which joins the anteroloph in an arch-shaped ridge. The labial part of the posteroloph ends free (Díaz-Molina & López-Martínez 1979).

The material of this genus is very scarce, restricted to one tooth in the type locality, Loranca-1, four in Ramblar-1, and an indeterminate low number of unpublished material in Cetina de Aragón; to this now should be added five teeth in CA-2, one in CA-4 and another one in MAB-5.
**Tab. 1** Faunal list of the site MAB-5 (Ruiz-Sánchez et al. 2010, Furió et al. 2010).

**Faunal list of MAB-5**

<table>
<thead>
<tr>
<th>Order Rodentia</th>
<th>Family Gliridae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Glirudinus cf. modestus</em></td>
</tr>
<tr>
<td></td>
<td><em>Microdyromys sp.</em></td>
</tr>
<tr>
<td></td>
<td><em>Simplomys cf. julii</em></td>
</tr>
<tr>
<td></td>
<td><em>Altomiramys sp.</em></td>
</tr>
<tr>
<td>Family Cricetida</td>
<td><em>Megacricetodon cf. primitivus</em></td>
</tr>
<tr>
<td></td>
<td><em>Democricetodon/Fahlbuschia sp.</em></td>
</tr>
<tr>
<td>Family Eomyidae</td>
<td><em>Ligerimys ellipticus</em></td>
</tr>
<tr>
<td>Family Sciuridae</td>
<td>Sciuridae indet.</td>
</tr>
<tr>
<td>Order Insectivora</td>
<td>Insectivora indet.</td>
</tr>
<tr>
<td>Family Dimylidae</td>
<td><em>Plesiodimylus sp.</em></td>
</tr>
<tr>
<td>Infraclass Metatheria</td>
<td>Family Herpetotheriidae</td>
</tr>
<tr>
<td></td>
<td><em>Amphiperatherium frequens</em></td>
</tr>
</tbody>
</table>

**Fig. 3** *Altomiramys sp.* from Mas de Antolino-5 (MAB-5). M2 dext. (MAB-5-14). Scale: 600 µm.
Order: Rodentia Bodwich, 1821  
Family: Gliridae Muirhead, 1819  
Subfamily: Myomiminae Dams, 1981  
Genus Altomiramys: Díaz-Molina & López-Martínez, 1979

**Emended diagnosis**

A glirid with low-crowned molars and concave occlusal surface. The ridges are thin and well-separated. The upper molars have precentroloph and/or postcentroloph. The presence of extra ridges in the upper and lower molars is variable. The labial portion of the posteroloph ends free. There is no continuous endoloph.

**Differential diagnosis**

The genus Altomiramys differs from other Miocene low-crowned Myomiminae in: wide valleys, thin and slanting ridges; it differs from Myomimus, Peridyromys, Pseudodryomys, Ramys and Vassequromys in: the complexity of dental pattern; it differs from Simplomys in: upper molars with more rounded outline and anterior valley that extends along the lingual border to the protocone; it differs from Peridyromys in: the metalophid reaching the metaconid; it differs from Plesiodyromys in: sharper edges, not reduced central structures and lack of the cingulum.

**Altomiramys sp.**

Locality: Mas de Antolino 5 (MAB-5)  
Material: 1 M2 (MAB-5-14, Fig. 3; size in Tab. 2)  
Description: The only specimen of Altomiramys sp. from MAB-5 is an M2 which has an anteroloph that ends below the protocone at the lingual border, disconnected from the paracone. The precentroloph is labially connected to the base of the paracone, extending almost halfway into the central valley. The postcentroloph is longer than the precentroloph, and parallel to this ridge, ending near the protocone. The metaloph and protoloph join at the lingual border. The posteroloph is connected to the protocone at the lingual border and labially not connected to the metacone.

Locality: Cuesta Agujeros 4 (CA-4)  
Material: 1 M2 (CA-4-1/3, Fig. 4F; size in Tab. 2)  
Description: This very scarce material is described in Ruiz-Sánchez et al. (in press). The tooth from CA-4 has narrow and well-separated ridges, with a long anteroloph, not connected to the protocone. The anteroloph and protoloph are connected to the paracone. A long precentroloph and a short-medium postcentroloph are present. Between precentroloph and protoloph a short prototrope is present.

**Altomiramys aff. daamsi** Díaz-Molina & López-Martínez, 1979

Locality: Cuesta Agujeros 2 (CA-2)  
Material: 2 m1 (CA-2-1/26 Fig. 4A, CA-2-1/27, Fig. 4B), 1 m2 (CA-2-1/25, Fig. 4C) and 2 M1 (CA-2-1/21, Fig. 4D, CA-2-1/22, Fig 4E); sizes in Table 2.  
Description: Five teeth are described in Ruiz-Sánchez et al. (in press) from this site. The lower molars have a low crown, narrow crests and broad valleys, with a long anterolophid,
Fig. 4  *Altomiramys* aff. *daamsi* from Cuesta Agujeros-2 (CA-2). A: m1 dext. (CA-2-1/26); B: m1 dext. (CA-2-1/27); C: m2 dext. (CA-2-1/25); D: M1 dext. (CA-2-1/21); E: M1 sin. (CA-2-1/22). *Altomiramys* sp. from Cuesta Agujeros-4 (CA-4). F: M2 dext. (CA-4-1/3). Scale: 1 mm. After Ruiz-Sánchez et al. (in press).

Tab. 2  Measurements of the teeth of *Altomiramys* from Loranca-1 (Díaz-Molina & López-Martínez 1979), Ramblar 1 (Daams 1989), CA-2 and CA4 (Ruiz-Sánchez et al. in press) and MAB-5 (this paper).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Element</th>
<th>Lenght</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Min.</td>
<td>Mean</td>
</tr>
<tr>
<td>MAB-5</td>
<td>M2</td>
<td>1</td>
<td>13.0</td>
</tr>
<tr>
<td>CA-4</td>
<td>M2</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>P4</td>
<td>2</td>
<td>9.3</td>
</tr>
<tr>
<td></td>
<td>M1</td>
<td>2</td>
<td>13.2</td>
</tr>
<tr>
<td>Ramblar-1</td>
<td>M2</td>
<td>3</td>
<td>13.8</td>
</tr>
<tr>
<td></td>
<td>m1</td>
<td>1</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>m2</td>
<td>1</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>m3</td>
<td>1</td>
<td>11.4</td>
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<tr>
<td>Loranca-1</td>
<td>M2</td>
<td>1</td>
<td>15.4</td>
</tr>
<tr>
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<td>M1</td>
<td>2</td>
<td>12.5</td>
</tr>
<tr>
<td></td>
<td>m1</td>
<td>2</td>
<td>12.1</td>
</tr>
<tr>
<td></td>
<td>m2</td>
<td>1</td>
<td>13.7</td>
</tr>
</tbody>
</table>
which may be connected to the protoconid. In 1 out of 2 m1 a posterotropid (Fig. 4A), and a short posterior spur in the middle of the mesolophid (Fig. 4B) are present. The upper molars have an anteroloph, which is isolated from the protocone and a precentroloph connected to the paracone. Protoloph and metaloph are connected, forming an oblique Y.

4. Discussion

The very scarce material from the type locality, Loranca-1, impedes to know the variability of the diagnostic features of the genus. The study of the Altomiramys material from Ramblar-1 (Daams 1989) and the redescriptions of Pseudodryomys simplicidens (Simplomys simplicidens in García-Paredes et al. 2009) from Cetina de Aragón to Altomiramys aff. daamsi (Daams, 1989), allow to know its variability better.

The general shape of the teeth (upper molars with rounded outline; low crown, concave occlusal surface, ridges thin and well-separated) is very similar in all assemblages (Loranca-1, Rambler-1, CA-2, CA-4, Cetina de Aragón and MAB-5). However, the presence of a unique precentroloph, as mentioned in the original diagnosis, is variable. Thus, the postcentroloph is absent in the only tooth from the type locality, Loranca-1, in 1 out of 2 M2 from Rambler-1, in the only complete M1 from CA-2, and in all (37) specimens adscribed to A. aff. daamsi in Cetina de Aragón (Daams 1989).

The size of the material from CA-2 (MN2) is somewhat smaller than the material described by Daams (1989) from Rambler-1 (Tab. 2). The specimens from CA-2 show some morphological features, different from those of the type locality: development of a short posterior spur in the middle of the mesolophid (Fig. 4B) in 1 out of 2 m1, and the presence in 1 out of 2 m1 of a posterotropid (Fig. 4A).

In Cetina de Aragón have been cited P. ibericus and P. simplicidens (Altomiramys aff. daamsi sensu Daams, 1989). Among the m1 of gliroids from Cetina de Aragón, 15 out of 65 specimens lack extra ridges, another 15 have only a posterotropid and 35 have anterotropid and posterotropid. On the other hand, in Cetina de Aragón, 21 out of 91 m2 lack extra ridges, 44 have only a posterotropid, and 26 have anterotropid and posterotropid. According to García-Paredes et al. (2009), S. simplicidens lacks extra ridges. The absence of lower molars in the type locality of A. daamsi impedes to know the variability of this and other characters in the lower molars.

The general shape of the tooth from CA-4 (MN3) allows to adscribe this fragment to the genus Altomiramys. The precentroloph in the specimen from CA-4 is larger than in those from Loranca-1 and Rambler-1. The presence of a short prototrope (Fig. 4F) is similar to that described in 1 out of 3 M2 from Rambler 1.

The tooth of Altomiramys sp. from MAB-5 (MN4) is smaller than A. daamsi from the type locality, Loranca-1, and similar to the material from Rambler-1 (Tab. 2). The most striking feature of the M2 of Altomiramys from MAB-5 is the presence of two centrolophs, of which the postcentroloph is longer than the precentroloph. As has been remarked before, the postcentroloph is absent in the type locality Loranca-1 (one tooth) and in only 23% of M1.2 from Cetina de Aragón and 1 out of 2 M2 from Rambler-1.

5. Conclusions

A scarce material of Altomiramys has been found in the localities CA-2, CA-4 (Ebro Basin) and MAB-5 (Ribesalbes-Alcora Basin). The presence of Armantomys daamsi suggests a Late
Agenian age (upper part of MN2) for CA-2; *Armantomys* cf. *jasperi* gives a Late Ramblian age (upper part of MN3) for CA-4, and MAB-5 is attributed an Early Aragonian age (MN4) because of the presence of *Megacricetodon* cf. *primitivus* and *Ligerimys ellipticus*. These new findings allow to extend the record of the genus *Altomiramys* until the Early Aragonian (MN4).

The new findings of *Altomiramys* in the Ribesalbes-Alcora and Ebro Basins, allow a better knowledge of the metrical and morphological variability of this genus. Whereas the general shape, characterized by upper molars with subrounded outline, low crown, concave occlusal surface and thin and well-separated ridges, is constant in all assemblages from MN2 until MN4, the presence and development of the precentroloph and postcentroloph is more variable than stated in the diagnosis of the genus. While in the type locality, Loranca-1, (with only one tooth), the precentroloph is the only centroloph in the trigone, in the assemblages from Cetina de Aragón (MN2), Ramblar-1, CA-4 (MN3), and MAB-5 (MN4), the postcentroloph may also be present. In the same way, and despite the absence of lower molars in the type locality, Loranca-1, in the oldest assemblages of the genus *Altomiramys* (CA-2), the posterotropid may be present too.

Therefore, the diagnosis of the genus *Altomiramys* has been modified, including the possible presence of a postcentroloph in the upper molars and of a posterotropid in the lower molars.

6. References


New findings of the genus *Altomiramys* (*Mammalia, Gliridae*)


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