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General palaeontology, systematics and evolution (Vertebrate palaeontology)

### The southernmost Miocene occurrence of the last European herpetotheriid *Amphiperatherium frequens* (Metatheria, Mammalia)

*Découverte la plus méridionale du dernier herpétothériidé européen Amphiperatherium frequens (Metatheria, Mammalia) au Miocène*

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#### ARTICLE INFO

##### Article history:

Received 14 December 2011

Accepted after revision 23 January 2012

Available online 7 June 2012

Presented by Philippe Taquet

##### Keywords:

Herpetotheriidae

Europe

Neogene

Aragonian

Ribesalbes-Alcora

Spain

##### Mots clés :

Herpetotheriidae

Europe

Neogène

Aragonien

Ribesalbes-Alcora

Espagne

#### ABSTRACT

The present work provides for the first time a detailed description of teeth attributable to metatherians in the Miocene fossil record of Spain, and justifies their generic and specific ascription. The fossil elements found correspond to *Amphiperatherium frequens*, the last herpetotheriid that inhabited Europe. This is so far the southernmost occurrence of this species, thus showing that its geographic range extended further southward than previously thought.

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#### R É S U M É

Ce travail donne la première description détaillée d'un métathérien trouvé dans des sédiments miocènes de l'Espagne et déterminé au niveau de l'espèce. Les fossiles trouvés appartiennent à l'espèce *Amphiperatherium frequens*, le dernier herpétothériidé ayant peuplé l'Europe. Il s'agit de la découverte la plus méridionale pour les métathériens, étendant ainsi considérablement leur aire géographique, une avancée nouvelle dans l'étude des faunes du Miocène européen.

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## 1. Introduction

Herpetotheriids have recently been found to be stem metatherians and the sister group of all living marsupials (Horovitz et al., 2009; Sánchez-Villagra et al., 2007). These metatherian mammals were rather common in central Europe during the Paleogene. They reached their maximum diversity during the Early Eocene, as demonstrated by the nine different species found in the sites of Avenay and Condé-en-Brie (Crochet, 1980). From then on, the group decreased in both relative abundance and number of species within mammal assemblages. The Oligocene represented a period of regular decline for the herpetotheriids on the European continent, beginning with six evolutionary lines and declining to only two (Crochet, 1980). The last known occurrences of *Amphiperatherium frequens* in the Middle Miocene from France, Germany and Switzerland (Fig. 1, Table 1) may represent the extinction of this group in central Europe before 13.8 ma, according to the dates of Kálin and Kempf (2009) and Abdul Aziz et al. (2010).

The Eurasian evolutionary history of the group outside central Europe is obscure. The fossil record of Cenozoic metatherians is particularly poor in Asia (Crochet et al., 2007; Ni et al., 2007), especially in Neogene sediments, which have provided merely three dental elements: two from Thailand (*Siamoperadectes minutus*, Ducrocq et al., 1992; Mein and Ginsburg, 1997) and one from China (*S. clandestinus*, Storch and Qiu, 2002). All of them have been found in localities equivalent in age to MN4 (Early Miocene).

The Cenozoic fossil record of metatherians in southwestern Europe is similarly scarce (Badiola and Cuesta, 2006; Crochet, 1980). Miocene Herpetotheriidae in Spain have been poorly documented, always restricted to indeterminate finds (Crochet, 1980; Ziegler, 1999) or personal communications (Robles et al., 1991). In the present work, we give for the first time a detailed description of teeth attributable to a Miocene herpetotheriid from Spain, and their generic and specific ascription are thoroughly justified.

## 2. Material and methods

Only upper dental elements have been recovered. The nomenclature for the description of the teeth and the reference lines to take the measurements follow Crochet (1980). Measurements were carried out at the Department of Geology of the University of Valencia, using a Leica MZ7<sub>5</sub> binocular microscope by means of displacement of a mechanical stage connected to Sony Magnescale measuring equipment. The fossil material is stored at the Museu de Geologia de la Universitat de València (MGUV) under catalogue numbers MGUV-25184 (MAB5-394), MGUV-25185 (MAB5-395), MGUV-25190 (MAB5-400), MGUV-25237 (MAB5-447), MGUV-25254 (MABOB-6), MGUV-25313 (MAB4-5), MGUV-25345 (BC1-30), MGUV-25579 (MTR1-4).

Institutional abbreviations: **MGUV**: Museu de Geologia de la Universitat de València, Burjassot (Spain); **SCSIE**: Servei Central de Suport a la Investigació Experimental,

Valencia (Spain); **UV**: Universitat de València, Valencia (Spain).

Localities: **BC**: Barranc de Campisano; **MAB**: Mas d'Antolino; **MTR**: Mas de Torner.

## 3. Geographic and geologic setting

The fossil material described in the present work comes from different levels of the sections of Mas d'Antolino B (MABOB, MAB4 and MAB5), Mas de Torner (MTR1) and Barranc de Campisano (BC1). All of them are situated in the western area of the Ribesalbes-Alcora Basin, an intramontane basin in eastern Spain (Agustí et al., 1988; Anadón, 1983). These sections are made up of about 60 m of grey and yellow mudstones, sandstones and limestones, and they all belong to the Unit 3 Sequence defined by Anadón (1983). Twenty levels in these sections have provided micromammal fossil remains. The five beds recording the presence of herpetotheriids have provided a total of almost 200 fossil mammal teeth. The small mammal assemblages in these localities are detailed in Table 2.

The association of *Megacricetodon primitivus* and *Ligerimys* (either *florancei* or *ellipticus*) in the four localities where *A. frequens* is present is indicative of their Lower Miocene age (Lower Aragonian, zones B and/or C) (Daams and Freudenthal, 1988). The only site not recording *Megacricetodon* and *Ligerimys* is Mas de Torner 1. Nevertheless, its stratigraphic position with respect to the other four localities is unequivocally indicative of a similar age (Ruiz-Sánchez et al., 2010).

## 4. Systematic paleontology and description

Infraclass: METATHERIA Huxley, 1880

Family: HERPETOTHERIIDAE Trouessart, 1879

Genus: ***Amphiperatherium*** Filhol, 1879

*Amphiperatherium frequens* (von Meyer, 1846) (Fig. 2)

**dp3**: (MAB5-400; Fig. 2A, E: L=1.34; W=1.65; MAB5-447; Fig. 2B, F: L=1.41; W=1.78; MTR1-4; Fig. 2C, G: L=1.31; W=1.68; BC1-30; Fig. 2D, H: L=1.42; W=1.74). The metacone is the highest cusp. The paracone is only slightly lower than the metacone. A small and short anterior ridge originates from the top of the paracone. The protocone is much lower than the metacone. The paracone is discernible as a two-branch divergence of the preprotocrista in MAB5-400 and BC1-30, but it is not divided in MAB5-447 and MTR1-4. The centrocrista is less dilambdodont (more straight) than in definitive upper molars. The anterolabial corner is much protruding in occlusal view. In MAB5-400, the ectoflexus is rather straight and it displays stylar cusps A, B and C as small elevations placed at the labial edge. However, these stylar cusps are absent in MTR1-4, MAB5-447 and BC1-30 (only in the latter specimen there is a weak cusp A). In all the dp3s found, cusp D is always discernible and it is clearly the largest one of the stylar shelf. The metaconule is difficult to discern. In MAB5-400, the metaconule is represented by a faint swelling of the postprotocrista. The roots are not preserved in any specimen.

**Table 1**

Biostratigraphic chart with the localities with fossil remains of *Amphiperatherium*. In MN1 to MN4 from France and Germany, the order established by Ziegler (1999) prevails when no other indication of relative position exists.

**Tableau 1**

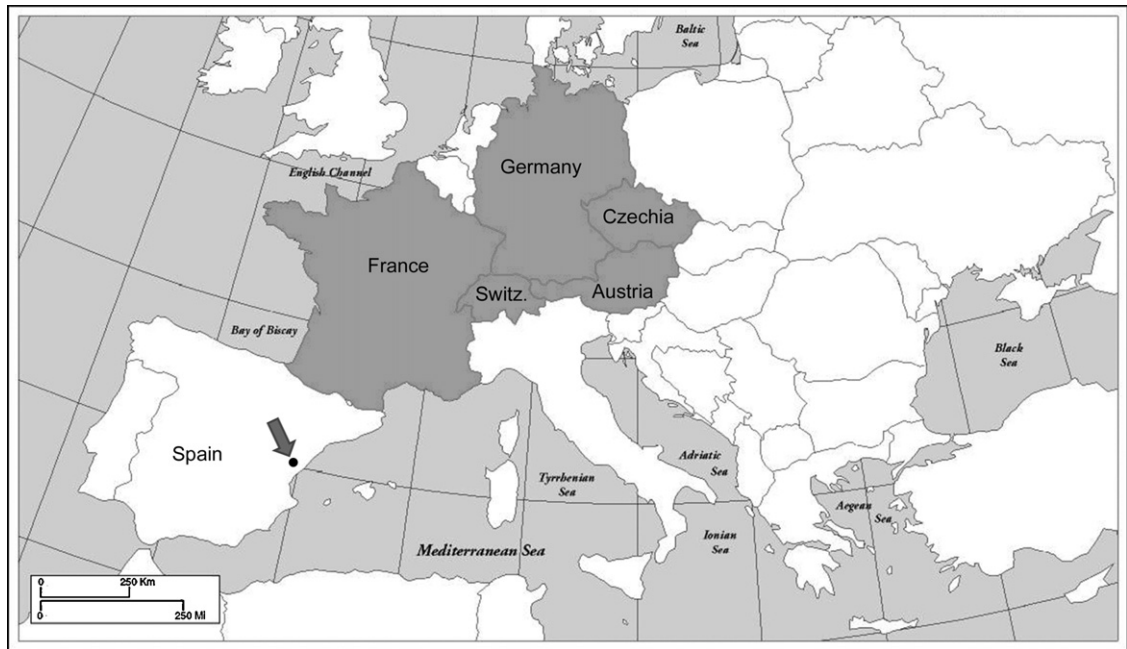
Cadre biostratigraphique, avec les localités qui ont fourni des restes fossiles d'*Amphiperatherium*. De MN1 à MN4 en France et en Allemagne, l'ordre établi par Ziegler (1999) est suivi quand aucune autre indication sur la position relative n'existe.

	France	Switzerland	Germany	Austria	Czechia	Spain
Datation	Aguilar et al. (1999, 2003)  Heissig (1989)	Kälin (1997)  Kälin and Kempf (2009) Kempf et al. (1997)	Heissig (1997)  Ziegler (2006) Abdul Aziz et al. (2010)	Daxner-Höck et al. (1998)  Harzhauser et al. (2002) Mein (1989)	Fejfar (1990)	Ruiz-Sánchez et al. (2010) This paper
MN7+8		Ergeten <sup>b</sup> Greuterschberg <sup>b</sup>				
MN6	Collet-Redon <sup>a</sup>	Schwamendingen Zeglingen Rümikon Sagentobel Uzwil- Nutzenbuech Chatzloch	Gallenbach 2b Gisseltshausen Untertzolling Laimering 3			
MN5		Vermes 1	Altenstadt <sup>c</sup> Hambach 6C Eitensheim Oggenhausen Oggenhof Affalterbach Massendorf Sandelzhausen Puttenhausen Niederaichbach Münchsmünster Langenmoosen	Teiritzberg Obergängendorf		
MN4	Vieux-Collonges Port-La-Nouvelle La Romieu	Eiboden Hubertingen Glovelier	Forsthart Rembach Rauscheröd 1b Erkertshofen 1  Erkertshofen 2 Petersbuch 2	Oberdorf 3+4	Dolnice	Mas d'Antolino 5 Mas d'Antolino 4 Mas d'Antolino 0B Barranc de Campisano 1 Mas de Torner 1
MN3	Beaulieu Estrepouy St.Vincent-de- Lamontjoie Serre de Verge	Goldinger Tobel 8 Bierkeller	Schnaitheim  Wintershof-West  Stubersheim 3	Maigen		
MN2	Balizac Bouzigues La Brète Laugnac Montaigu	Schaffhausen La Mèbre 698 La Chaux 7	Ulm-Uniklinik Haslach Eggingen Budenheim Frankfurt- Nordbassin Ulm-Westtangente			
MN1	Saulcet Plaissan St. Gérard-le-Puy Pyrimont-Challonges Les Cévennes La Paillade Paulhiac Relais des Cathares N.F.M.-Montpellier		Hochstadt Ravolzhausen Lautern 2 Weisenau Weissenburg 6			

<sup>a</sup> The age of this locality is still under discussion ranging from MN5 to MN7 (Aguilar and Clauzon, 1979; Heissig, 1989).

<sup>b</sup> These localities are considered MN8 *sensu* Kälin and Kempf (2009).

<sup>c</sup> *Amphiperatherium* was not found in new samplings from Altenstadt (Prieto et al., 2009). Data from Aguilar and Clauzon, 1979; Aguilar et al., 2003; Böttcher et al., 2009; Daxner-Höck et al., 1998; Engesser and Mödden, 1997; Engesser et al., 1993; Fejfar, 1990; Kälin, 1997; Kälin and Kempf, 2009; Mein, 1989; Prieto, 2011a, b; Ziegler, 1999, 2000.



**Fig. 1.** Map showing the countries with previously known Miocene occurrences of *Amphiperatherium* (grey-shaded). The new localities from Ribesalbes-Alcora Basin in Spain are indicated with an arrow.

**Fig. 1.** Carte montrant les pays où la présence d'*Amphiperatherium* au Miocène était déjà connue (en gris). Les nouvelles localités du bassin Ribesalbes-Alcora en Espagne sont indiquées par une flèche.

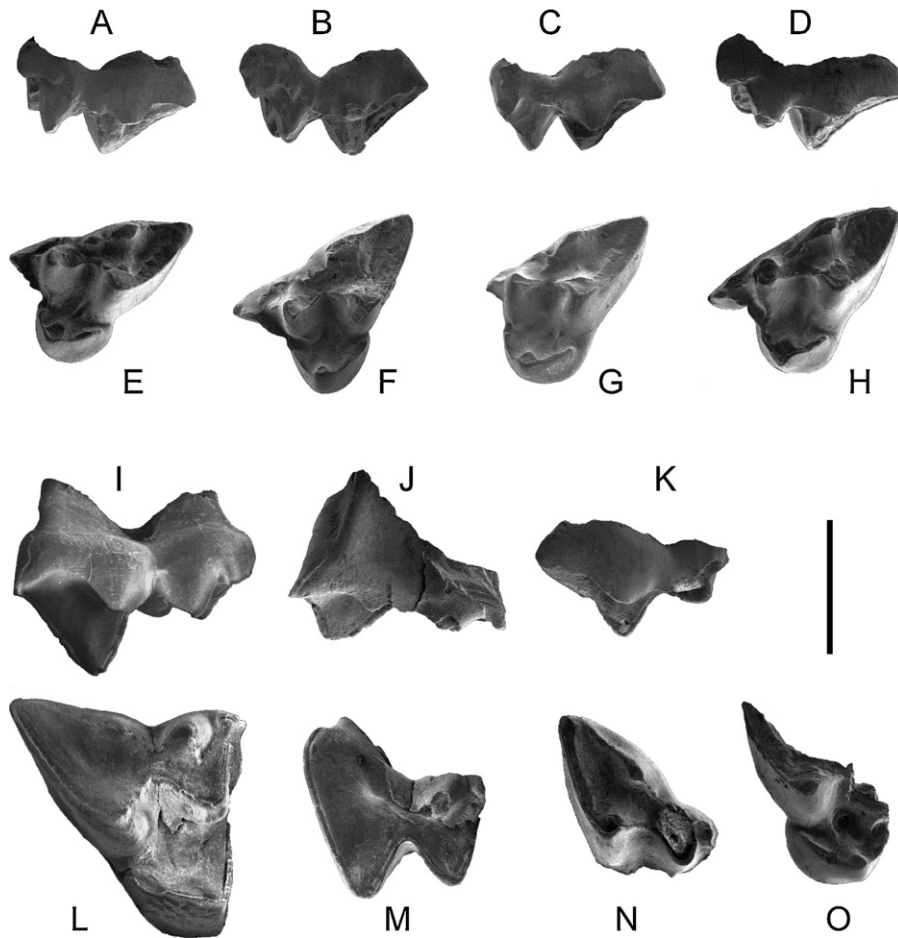
**Table 2**

Small mammal assemblage in the five localities from the Ribesalbes-Alcora Basin with fossil teeth of *Amphiperatherium*.

**Tableau 2**

Assemblage de micromammifères des cinq localités du bassin de Ribesalbes-Alcora, avec des dents fossiles d'*Amphiperatherium*.

	MAB0B	MAB4	MAB5	MTR1	BC1
Lithology	Marls	Marls	Marls	Marls	Marls
<i>n</i> mammal teeth	8	6	150	10	22
<i>Amphiperatherium frequens</i>	x	x	x	x	x
<i>Plesiodimylus</i> sp.			x		x
Erinaceidae indet.		x			
Talpidae indet.					x
Insectivora indet.	x			x	x
Sciuridae indet.			x		x
<i>Democricetodon/Fahlbuschia</i> sp.			x	x	x
<i>Megacricetodon</i> cf. <i>primitivus</i>	x	x	x		x
<i>Glirudinus</i> cf. <i>modestus</i>			x		
<i>Microdyromys</i> sp.			x		
<i>Simplomys</i> cf. <i>julii</i>			x		x
<i>Pseudodryomys</i> cf. <i>ibericus</i>					x
Myomiminae indet.			x		
Gliridae indet.		x		x	x
<i>Ligerimys</i> aff. <i>florancei</i>	x				x
<i>Ligerimys ellipticus</i>		x	x		



**Fig. 2.** *Amphiperatherium frequens* from MAB0B, MAB4, MAB5, MTR1 and BC1, Ribesalbes-Alcora basin, Spain. **A.** MAB5-400, left dP3 (labial view). **B.** MAB5-447, left dP3 (labial view); **C.** MTR1-4, left dP3 (labial view). **D.** BC1-30, left dP3 (labial view). **E.** MAB5-400, left dP3 (occlusal view). **F.** MAB5-447, left dP3 (occlusal view). **G.** MTR1-4, left dP3 (occlusal view). **H.** BC1-30, left dP3 (occlusal view). **I.** MAB5-394, right M1 (labial view). **J.** MAB5-395, right M3 (labial view). **K.** MAB0B-6, left M4 (labial view). **L.** MAB5-394, right M1 (occlusal view). **M.** MAB5-395, right M3 (occlusal view). **N.** MAB0B-6, left M4 (occlusal view). **O.** MAB4-5, undetermined upper molar or premolar (occlusal view). Scale bar equals 1 mm.

**Fig. 2.** *Amphiperatherium frequens* de MAB0B, MAB4, MAB5, MTR1 et BC1, bassin de Ribesalbes-Alcora, Espagne. **A.** MAB5-400, dP3 gauche (vue labiale). **B.** MAB5-447, dP3 gauche (vue labiale). **C.** MTR1-4, dP3 gauche (vue labiale). **D.** BC1-30, dP3 gauche (vue labiale). **E.** MAB5-400, dP3 gauche (vue occlusale). **F.** MAB5-447, dP3 gauche (vue occlusale). **G.** MTR1-4, dP3 gauche (vue occlusale). **H.** BC1-30, dP3 gauche (vue occlusale). **I.** MAB5-394, M1 droite (vue labiale). **J.** MAB5-395, M3 droite (vue labiale). **K.** MAB0B-6, M4 gauche (vue labiale). **L.** MAB5-394, M1 droite (vue occlusale). **M.** MAB5-395, M3 droite (vue occlusale). **N.** MAB0B-6, M4 gauche (vue occlusale). **O.** MAB4-5, molaire ou prémolaire supérieure indéterminée (vue occlusale). Barre d'échelle : 1 mm.

**M1:** (MAB5-394; Fig. 2I, L: L = 1.93; W = 2.58). The metacone is the highest cusp. Protocone and paracone have a similar height. The metaconule is a faint elevation of the posterior end of the postprotocrista. The styler cusp B is the highest cusp of the ectoflexus. There is neither a styler cusp C, nor a ridge connecting the styler cusps A and B. The roots are not preserved in this specimen.

**M3:** (MAB5-395; Fig. 2J, M: L = 1.71). Only the labial half is preserved. The “v” shape of the labial margin suggests that this tooth is an M3. The wear affects the entire occlusal surface. The styler cusps A, B and D are only recognized as weak rather conical elevations.

**M4:** (MAB0B-6; Fig. 2K, N: L = 1.46). Only the labial side is preserved. The curvature of the crista of the right half in occlusal view (Fig. 2N) suggests that it might correspond to the metacrasta (posterior arm of the metacone) of an M4. Consequently, the paracone is the highest cusp, and the

paracrasta is the longest ridge of the preserved part. Cusp A is discernible as the anterolabial end of the paracrasta. The cusp B is immediately advanced to the labial notch and it is the most prominent of the ectoflexus. Cusp E is quite well developed. Cusps C and D are extremely reduced and they are difficult to discern.

**Undetermined Upper Molar or Premolar.** The specimen MAB4-5 (Fig. 2O) is an undetermined upper molar or deciduous premolar, lacking the anterolabial side.

## 5. Results

Taxonomically, the absence of a connection between the styler cusps A and B in the upper molars justifies their ascription to the genus *Amphiperatherium*. The species *A. frequens* is distinct from *A. exile* by having weaker styler cusps C and D, which sometimes disappear altogether

(Crochet, 1980). The complete absence of the styler cusp C in the M1 (Fig. 2L) and its almost complete reduction in M3 and M4 (Fig. 2M, N), support their specific ascription to *A. frequens*. The five characters for sub-specific identification proposed by von Koenigswald (1970) were reviewed by Crochet (1980), who concluded that actually none of them has a systematic significance. However, Ziegler (1999) considered the distinction of chronosubspecies in the Miocene (*A. f. frequens*, *A. f. erkertshofense* or *A. f. wintershofense*) justified, remarking that they are only determinable when sufficient material is available. Unfortunately, the scarce material found in Ribesalbes-Alcora Basin (with only upper teeth) and the variability observed in the dp3 found (the only repeated element) do not allow a sub-specific ascription.

It is noteworthy that the discovery of four left deciduous premolars indicates the presence of at least four different juvenile to subadult individuals. This is a highly unusual occurrence of young specimens, representing half of the total dental remains of the herpetotheriid sample from all layers. No lower dental elements have been found. This is probably because *Amphiperatherium* is, overall, a minimal component within the micromammalian assemblages in all these localities.

The limited presence of this taxon is probably a result of several climatic and environmental factors. It is worth to mention that most of the Miocene finds of *Amphiperatherium* in Europe correspond to Central European countries (Fig. 1), where the environmental conditions were rather humid (Utescher et al., 2011, and references therein). Ribesalbes-Alcora belongs to the Ibero-Levantine Province, which is characterized by wetter conditions than in other places of the Iberian Peninsula (Agustí, 1978, 1990; Agustí et al., 1984; Casanovas-Vilar and Agustí, 2007; Sesé, 1988). This is evidenced, for instance, by the presence of *Ligerimys* (Daams et al., 1988; Van der Meulen and Daams, 1992) or the flying squirrel *Miopetaurista* in the locality of Buñol (MN4, local zone C, Magro Basin; Daams, 1976, 1977). Nonetheless, a lesser degree of humidity in this region with respect to Central Europe could have resulted in less abundant populations of *Amphiperatherium* than in Germany, Switzerland or France.

Another point to consider is the age of the sites, which coincides with the Middle Miocene Climatic Optimum (17–15 Ma, Zachos et al., 2001). Not by chance, the extinction of *Amphiperatherium* in central Europe also coincides with the end of this climatic event. The warm temperatures could have played an important role permitting the southern expansion of environments and populations formerly limited to Central Europe. The Ramblian and the transition to the Early Aragonian are characterized by densely forested areas in some parts of Spain (DeMiguel et al., 2010). This picture suggests that the Ribesalbes-Alcora populations were close to the southern boundary of their suitable range, and more fragile to any climatic or environmental change. In last term, a northern retraction of this boundary combined with the fragmentation of the populations could have resulted in the regional extinction of *Amphiperatherium* in the Iberian Peninsula.

In any case, this is the first time that the presence of the herpetotheriid *A. frequens* is adequately documented in

the Miocene of Spain. Former references to the presence of herpetotheriids in the Neogene of the Iberian Peninsula were limited to identifications at the family level or personal communications to authors, giving no details nor figuring the material found. Consequently, this occurrence of *A. frequens* in the Early Aragonian (late Early Miocene) of the Ribesalbes-Alcora Basin represents the hitherto southernmost presence of this species in Europe, and the last record of a metatherian mammal in the Iberian Peninsula.

## Acknowledgements

We thank E. Navarro and A. Ibáñez (SCSIE, UV) for capable laboratory assistance. This research was supported by projects PIPH-2009 SGR 754 (AGAUR, Generalitat de Catalunya), CGL2011-28681 (Spanish Ministerio de Economía y Competitividad) and GVPRE/2008/320 (Generalitat Valenciana). The field work in Araia was supported from 2008 to 2010 by the Conselleria de Cultura of the Generalitat Valenciana. We acknowledge the useful comments on the manuscript provided by R. Ziegler, J. Prieto and two anonymous reviewers, which improved the quality of the paper.

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