The southernmost record of fossil Castoridae (Mammalia, Rodentia) in Europe

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García-Alix A., Minwer-Barakat R., Martín-Suárez E. & Freudenthal M. 2007. — The southernmost record of fossil Castoridae (Mammalia, Rodentia) in Europe. *Geodiversitas* 29 (3): 435-440.

ABSTRACT
This paper tries to amplify the information about the poorly known fossil beaver *Dipoides problematicus* (Schlosser, 1902). This species has been found in several localities near the Mio-Pliocene boundary of the Granada Basin (southern Spain). During that time span, beavers are very scarce in southern Spain, but abundant in the Teruel region (northern Spain). Since they have specific ecological preferences, their presence in the Granada Basin and their absence in other southern Spanish basins have paleobiogeographical and paleoecological consequences.

KEY WORDS
Mammalia,
Rodentia,
Castoridae,
SE Spain,
Granada Basin,
Mio-Pliocene,
upper Turolian,
lower Ruscinian.

RÉSUMÉ
La mention la plus méridionale de Castoridae (Mammalia, Rodentia) fossiles en Europe.
Le but de ce travail est de révéler de nouvelles informations sur le castor fossile mal connu *Dipoides problematicus* (Schlosser, 1902). Des restes de cette espèce ont été trouvés dans plusieurs gisements proches de la limite Mio-Pliocène du Bassin de Grenade (sud de l'Espagne). Pendant cette période les castors sont très rares dans le sud de l'Espagne, mais abondants dans la région de Teruel, située plus au nord. Étant donné leurs exigences écologiques, leur présence dans le Bassin de Grenade et leur absence dans d'autres bassins du sud de l'Espagne revêtent une importance paléobiogéographique et paléoécologique.

MOTS CLÉS
Mammalia,
Rodentia,
Castoridae,
sud-est de l'Espagne,
Bassin de Grenade,
Mio-Pliocène,
Turolien supérieur,
Ruscinien inférieur.

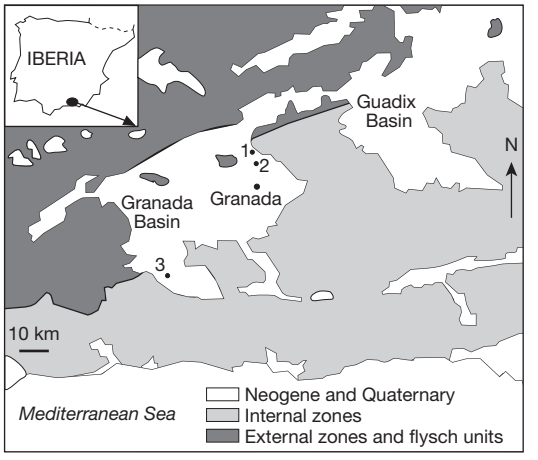

FIG. 1. — Geographical and geological context of the Granada Basin and situation of the studied section (after Braga *et al.* 1990): **1**, Calicasas section; **2**, Cantera de Pulianas section; **3**, La Dehesa and La Mina sections.

INTRODUCTION

Five fossiliferous localities in Mio-Pliocene fluvio-lacustrine sediments of the Granada Basin (southern Spain) have yielded fossil beaver material (Fig. 1). Their age is late Turolian and early Ruscinian (García-Alix 2006). References to Mio-Pliocene Castoridae in southern Spain are scarce; there are some summary references from the Granada Basin (Aguirre 1974; Boné *et al.* 1978; Padial 1986), but neither of these gives descriptions or measurements of the teeth. In the studied area only one species of Castoridae, *Dipoides problematicus* (Schlosser, 1902), is recognized. The sections where this species appears are (Fig. 1): Cantera de Pulianas section (code PUR), La Mina section (code MNA), La Dehesa section (code DHS) and Calicasas section (code CLC). The studied localities are: PUR-23, MNA-2, DHS-14, DHS-16 and CLC-3B. Except for CLC-3B, these sites correspond to the late Turolian and they are related with two independent deltaic complexes (García-Alix 2006): one in the east of the basin (PUR), and another one in the west of the basin (MNA and DHS). The locality CLC-3B from Calicasas section, early Ruscinian, is related with a lacustrine system in the east of the basin (García-Alix 2006).

MATERIAL AND METHODS

The nomenclature used in the descriptions of the teeth of Castoridae is that of Stirton (1935). Length and width have been taken perpendicularly with a precision calipers. Measurements are given in millimeters. Because of the large size of the specimens, they have been photographed with a digital camera Nikon Coolpix 4500, after whitening them with magnesium oxide. The specimens are kept in the Departamento de Estratigrafía y Paleontología of the University of Granada.

SYSTEMATICS

Order RODENTIA Bowdich, 1821
Family CASTORIDAE Hemprich, 1820

Genus *Dipoides* Jäger, 1835

Not *Dipoides* Schlosser, 1902, following Hugueney (1999).

Dipoides problematicus (Schlosser, 1902)
(Fig. 2)

NOMENCLATURAL REMARK. — Since the species *problematicus* is transferred from *Dipoides* Schlosser, 1902 to *Dipoides* Jaeger, 1835 (see Hugueney 1999), the correct form of the name is *Dipoides problematicus* (Schlosser, 1902).

MATERIAL EXAMINED. — Left jaw (p4-m2): PUR-23 174. Isolated teeth: lower incisor: PUR-23 175, CLC-3B 84; p4: DHS-16 214; m1-2: PUR-23 177, DHS-16 211; D4: PUR-23 181; P4: CLC-3B 83; M1-2: PUR-23 178, DHS-16 212; M3: DHS-16 213. The specimen DHS-16 216 is an undeterminable upper tooth. The worn specimen PUR-23 176 may be a p4 or m1-2. The specimens PUR-23 179, PUR-23 180, DHS-14 33 and MNA-2 51 are unspecified fragments with the typical "S"-structure of *Dipoides*.

MEASUREMENTS. — See Table 1.

DESCRIPTION OF THE MATERIAL FROM THE LOCALITY PUR-23

The lower incisor is convex-faced. The anterior surface is rounded and the section is oval-shaped with a lingual central channel (Fig. 2A).

TABLE 1. — Measurements (in mm) of the teeth of *Dipoides problematicus* (Schlosser, 1902) from the studied localities.

Element	Localities	Length				Width			
		N	Min.	Mean	Max.	N	Min.	Mean	Max.
p4	PUR-23	1		6.80		1		5.00	
	DHS-16	1		5.10		1		4.10	
m1, 2	PUR-23	3	5.10	5.27	5.50	3	5.00	5.03	5.10
	DHS-16	1		4.80		1		4.20	
D4	PUR-23	1		3.90		1		3.70	
P4	CLC-3B	1		7.70		1		6.60	
M1, 2	PUR-23	1		4.90		1		4.80	
	DHS-16	1		4.40		1		4.30	
M3	DHS-16	1		4.30		1		3.40	

The p4 has the "S"-structure. It is wider posteriorly than anteriorly. The hypoflexid is longer than the mesoflexid. The mesoflexid is curved. The hypostriid is deep, in contact with the base of the crown, like the mesostriid. The paraflexid and the parastriid cannot be observed due to the wear (Fig. 2B).

The m1-2 has the "S"-structure. The m1 and m2 are usually described together, since they are difficult to differentiate. The m1 and m2 of PUR-23 174 are morphologically identical; the main difference is that the m2 is slightly shorter than the m1. The greatest width is posterior. The hypoflexid is longer than the mesoflexid, and they have a labial and a lingual striid respectively, which seem to connect with the base of the crown. There are no paraflexid or parastriid (Fig. 2B).

A single small juvenile tooth seems to correspond to an upper deciduous premolar (D4) because its crown is markedly curved forward (Fig. 2C).

The M1-2 has neither a metastria nor a metaflexus. The hypoflexus and the mesoflexus are relatively deep. The parastria is very much reduced. The crown is convex forward.

DESCRIPTION OF THE MATERIAL FROM THE LOCALITY DHS-16

The p4, m1-2 and M1-2 are similar to those from PUR-23. The p4 have the paraflexid and the parastriid more developed than in the specimen from PUR-23 (Fig. 2E).

The M3 is lingually damaged. It is wider anteriorly than posteriorly. The hypoflexus is larger than the paraflexus, and the parastria is very short. The hypostria is very deep. The mesoflexus is curved and the mesostria reaches the base of the crown. Rounded metaflexus and reduced metastria. The crown is convex forward (Fig. 2F).

DESCRIPTION OF THE MATERIAL FROM THE LOCALITY CLC-3B

The lower incisor is like the one from PUR-23.

The P4 is wider anteriorly than posteriorly. The crown is convex forward. The hypostria is in contact with the base of the crown. Apparently, the hypoflexus and paraflexus are in contact and form a single flexus. The parastria is shorter than the hypostria and it is attenuated at medium height of the crown. The mesostria is longer than the parastria. The metastria and metaflexus are short (Fig. 2D).

REMARKS

The studied teeth have the typical "S"-pattern of *Dipoides*, and they are difficult to determinate due to the similarities between upper and lower teeth, which sometimes only differ in the curvature of the crown.

Stehlin & Schaub (1951) and Schaub (1958) distinguish three dental patterns in the teeth of Castoridae: pentalophodont basic pattern, "S"-pattern and laminar pattern. Our specimens have the "S"-pattern, which is shared by *Dipoides* and *Eucastor* Leidy, 1858.

Our material is medium-sized and has a simple "S"-pattern. The size and the structure agree with those of *Dipoides problematicus* from La Fontana, Valdecebro-3, Masada del Valle-5 and 7 (Van de Weerd 1976), Peralejos-E (Adrover *et al.* 1988),

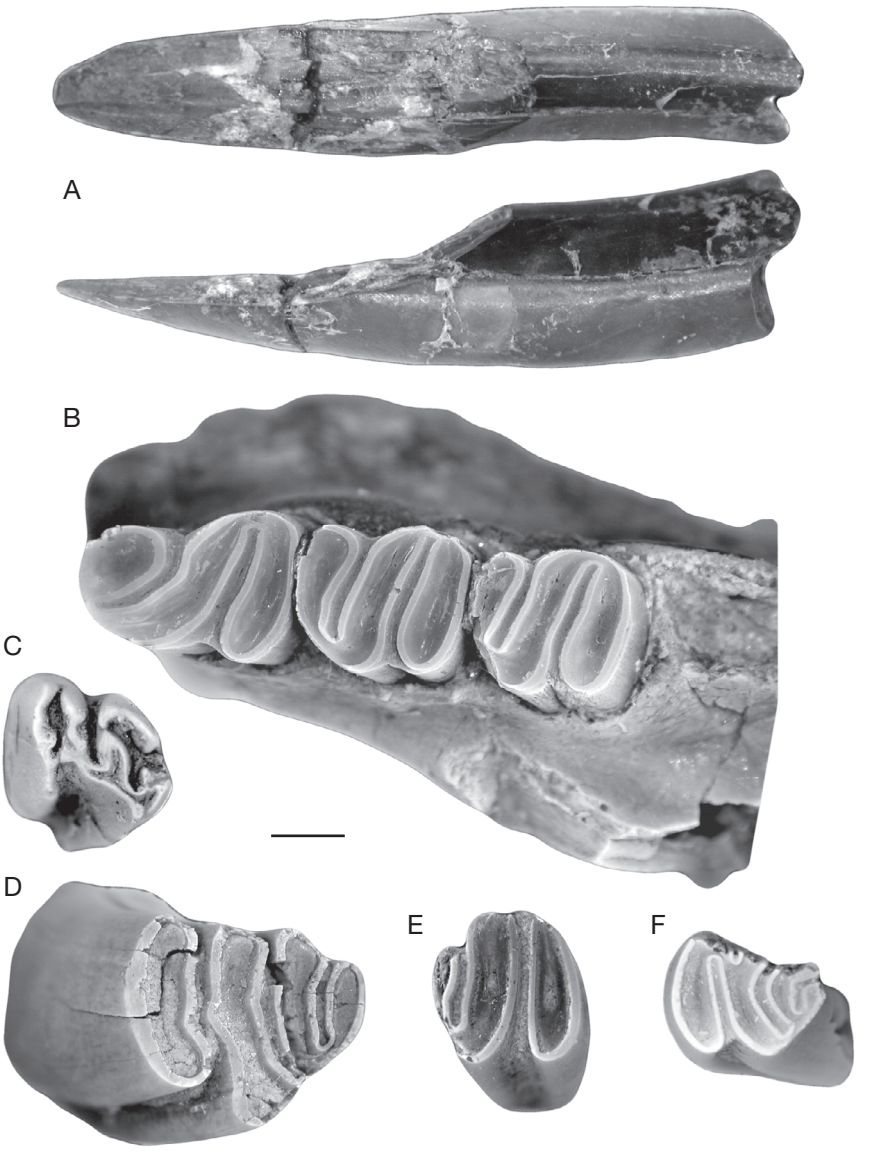

FIG. 2. — *Dipoides problematicus* (Schlosser, 1902) from the Mio-Pliocene boundary of Granada Basin: **A**, lower incisor (PUR-23 175); **B**, left p4-m2 (PUR-23 174); **C**, D4? (PUR-23 181); **D**, left P4 (CLC-3B 83); **E**, right M1-2 (DHS-16 212); **F**, Left M3 (DHS-16 213). Scale bar: 1 mm.

La Gloria-5, Valdecebro-6 and Villastar (Adrover *et al.* 1993; and direct comparison with material of *D. problematicus* from Villastar deposited in the University of Granada). The specimens from Granada Basin in general agree with, or are slightly larger than those from the type locality of *D. problematicus*, Salmendingen (Schlosser 1902), but our P4 and p4 are larger than these. The structure is in general similar to that of the specimens from Salmendingen, however, some teeth have a slightly more simplified dental pattern, especially the upper teeth. The parastria and paraflexus are very much

developed (sometimes the parastria is complete) in the upper teeth from Salmendingen, much more than in our upper teeth. Our M1-2 do not show metastria nor metaflexus. The parastriid and the paraflexid are very much developed in the lower teeth from Salmendingen.

The main difference between our teeth and those of *D. sigmodus* (Gervais, 1859), *D. majori* (Schlosser, 1903) and *D. anatolicus* (Özansoy, 1961) is that our specimens are smaller. Besides, *D. sigmodus*, *D. majori* and *D. anatolicus* have a more accentuated "S"-pattern. The "S"-pattern of *D. problematicus* is the most archaic. This genus is more diversified in North America than in Eurasia (Hugueney 1999), but we did not consider American species for the determination.

Dipoides problematicus and its descendant *D. sigmodus* form a western and central European lineage (Xu 1994; Hugueney 1999). *Dipoides anatolicus* and *D. majori* represent an eastern Mediterranean and Asiatic line (Xu 1994). Following Hugueney (1999), *Dipoides* may either be an immigrant from America that arrived in Europe in the early Turolian or it may be derived from the Spanish *Eucastor* subgenus *Schreuderia* Aldana-Carrasco, 1992.

Discussion

Beavers are large rodents that are present in North America since the Eocene and in Eurasia since the Oligocene (Hugueney 1999). They are very specialized mammals with concrete ecological preferences, so this group presents a great interest for paleoecological reconstructions (Hugueney & Escuillié 1995, 1996, 1997). Semiaquatic habitats and wet preferences are attributed to this group (Van de Weerd & Daams 1978; Van Dam & Weltje 1999). Fossorial castors, most diversified in North America, disappear at the end of the lower Miocene (Hugueney & Escuillié 1997). Shotwell (1963) noted that *Dipoides* is linked to puddle zones with slow water flow. The studied localities in the Granada Basin are related with very humid conditions and fluvio-lacustrine environment (García-Alix 2006); therefore, we agree with wet and semiaquatic preferences for *D. problematicus*.

Until now, Castoridae were not known from southern Spain, except for some superficial citations, as indicated above. *Dipoides* from the Granada Basin constitutes the only record of castorids from the Turolian and Ruscinian (late Miocene and early Pliocene) in the southern Spain. Earlier records are not found in the Granada Basin because the area was submerged until the late Tortonian. In view of the very complete fossil record from the southern Spanish basins of Guadix and Crevillente (Sesé 1989, 2006; Ruiz Bustos 1995; Martín-Suárez & Freudenthal 1998; among others), we interpret that the absence of Castoridae is real, and not due to a bias. Their presence in the Granada Basin and absence in the Guadix and Crevillente basins may be related to the different degree of humidity between these basins: the Granada Basin would have had wetter conditions in the latest Miocene-earliest Pliocene than the Guadix and Crevillente basins (Martín-Suárez *et al.* 2001; Minwer-Barakat 2005; García-Alix 2006). The oldest record of Castoridae in Guadix Basin, *Castor* sp., is from the lower Villanyian (Sesé 1989), when the wet conditions increased (Minwer-Barakat 2005).

Acknowledgements

This study was supported by the project "Dinámica de ecosistemas terrestres en el Neógeno de las cuencas del Levante español" (BOS 2001-1044) of the DGESIC, the program "Consolider Ingenio 2010" (CSD 2006-00041), and the research group RNM0190 of the "Junta de Andalucía". We want to thank M. Hugueney and P. Mein for their valuables comments. Comments and suggestions by two reviewers, S. Sen and E. Heizman, and by the editors, are much appreciated.

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Submitted on 28 February 2007;
accepted on 25 June 2007.