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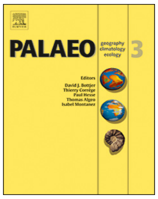

The European record of the gerbil *Myocricetodon* (Rodentia, Mammalia) and its bearing on the Messinian salinity crisis

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ABSTRACT

The gerbillid *Myocricetodon* is mainly known from the Miocene of Africa and Asia, but some small samples of this genus have been identified in southwestern Europe, interpreted as immigrants driven by the Messinian Salinity Crisis. However, the specific determination of these European populations and their relationships with African forms have proved controversial. The population from Negratín-1 (Guadix Basin, southern Spain) was attributed to the African species *Myocricetodon jaegeri*, but other European samples have still not been determined at the specific level. Here we describe the material of *Myocricetodon* from Almenara-M (eastern Spain), which represents the most abundant sample of the genus known from Europe, confirming its assignation to *M. jaegeri*. We also analyze material from Salobreña, Pino Mojón (southern Spain) and Castelnou-3 (southern France), concluding that these samples belong to the same species. The presence of these coeval and conspecific populations of *Myocricetodon* is explained by a single migratory event from northern Africa. The occurrence of *Myocricetodon*, interpreted as an indicator of warm and arid conditions, is restricted to southern and eastern Spain and the southeastermost extreme of France, being mainly limited to the Mediterranean coast. It is absent in other Iberian areas, such as the Granada, Cabriel and Teruel basins, despite their rich and well-studied record of late Miocene mammals. This distribution suggests the existence of different environmental (more humid) conditions in those areas during the latest Miocene, as already proposed for the Granada Basin. Our data also indicate that the presence of *Myocricetodon* in Europe was limited to a short interval close to the Miocene-Pliocene boundary, contrarily to other gerbils, namely *Debruijnimys,* which persisted during the Pliocene. This suggests that *Myocricetodon* could be extremely sensitive to environmental factors and its occurrence in Europe was linked to a specific moment of arid conditions.

1. Introduction

The Messinian Salinity Crisis (MSC) was a geological event of exceptional relevance in the history of the Mediterranean, and consisted in the nearly complete desiccation of this marine basin at the end of the Miocene (from 5.97 to 5.33 Ma), as a consequence of the closure of the connections between the Atlantic and the Mediterranean (Hsü et al., 1973, 1977). Tectonic convergence between the African and Iberian plates, together with eustatic and climatic factors, caused the progressive closing of the several marine gateways that connected the Atlantic Ocean and the Mediterranean Sea through southern Spain and northern Morocco (Krijgsman et al., 1999; Soria et al., 1999; Braga et al., 2006; Manzi et al., 2013; Flecker et al., 2015). This unusual situation led to drastic environmental changes in the Mediterranean, including extreme salinity fluctuations and the precipitation of large volumes of evaporites. The location and timing of the closure of the different gateways, as well as the existence of intermittent marine connections and freshwater sources, have been intensively discussed over the last decades and are still a topic of hot debate (Flecker et al., 2015; Van Baak et al., 2016; Capella et al., 2017; Tulbure et al., 2017). This event ended with the so-called "Zanclean flood", which occurred at the Messinian-Zanclean boundary (5.33 Ma), when the Strait of Gibraltar reopened and the Atlantic rapidly filled up the Mediterranean basin (Estrada et al., 2011).

Apart from major changes in the marine biotas, the MSC had significant consequences for the distribution of terrestrial vertebrate

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faunas, since the new paleogeographic configuration allowed the exchange of different taxa between northern Africa and the Iberian Peninsula. According to several authors, faunal exchanges between Africa and Spain started shortly before the onset of the MSC, and several migratory waves can be distinguished (Garcés et al., 1998, 2001; Agustí et al., 2006a; Gibert et al., 2013). One of these mammal migrations corresponds to the entry of the camel *Paracamelus* and the murid *Paraethomys* into the Iberian Peninsula, which has been magnetostratigraphically dated at ~6.2 Ma (Garcés et al., 1998; Gibert et al., 2013). These data are in agreement with the age of the oldest levels with European rodents identified in north Africa, situated in the Afoud section (Aït Kandoula Basin, Morocco) and also dated at ~6.2 Ma with paleomagnetic analyses (Benammi et al., 1996). Therefore, intercontinental mammal migrations started in both directions at least 200 kyr before the beginning of the MSC, indicating the existence of an ephemeral land connection between Africa and the Iberian Peninsula (Agustí et al., 2006a; Gibert et al., 2013; Flecker et al., 2015; García-Alix et al., 2016).

A second migratory wave correspond to the dispersal into the Iberian Peninsula of gerbils, subdesertic rodents that today inhabit the dry landscapes of northern Africa and southwestern Asia. Their record in Europe is scarce and starts clearly after the first occurrence of *Paraethomys*, so their entry has been related to the onset of the MSC and the spread of subdesertic conditions in the western Mediterranean (Agustí et al., 2006a; Minwer-Barakat et al., 2009a; Flecker et al., 2015). One of the few gerbillid genera identified in Europe is *Myocricetodon*. This genus, known from the late Aragonian (13.8–11.2 Ma) to the earliest Ruscinian (5.3–4.2 Ma), reached a great diversity in north Africa, where up to twelve species have been described: *Myocricetodon irhoudi*, *M. ouedi*, *M. ultimus*, *M. asphodelae, M. magnus, M. parvus*, *M. seboui, M. ouaichi, M. afoudensis, M. cherifiensis*, *M. trerki* and *M. jaegeri* (Lavocat, 1952, 1961; Jaeger, 1977a, 1977b; Coiffait, 1991; Benammi, 2001), which have been grouped in three different lineages (see later sections). The record in Asia is less abundant: the species *M. eskihisarensis* from Anatolia is the only Asian form related to the African lineages, being close to *M. parvus* and *M. seboui* (Wessels et al., 1987; Erten et al., 2016). Besides, there are some mentions of the genus from China (Qiu, 2001; Qiu et al., 2004) and Pakistan (*M. chinjiensis, M. sivalensis, M. tomidai*; Lindsay, 1988; Lindsay and Flynn, 2016), which do not seem to be closely related to the North African forms, and are not integrated in any of the above-mentioned African lineages (Benammi, 2001; López-Antoñanzas, 2009).

Unlike the cases of Africa and Asia, the record of *Myocricetodon* in Europe is extremely scarce and geographically restricted to the Iberian Peninsula and southernmost France. The first described evidence of this genus in the European continent is that from Salobreña, a karstic infill in southern Spain reported by Jaeger et al. (1977), who suggested that this occurrence was due to an Africa-Europe dispersion in the context of the MSC. However, Aguilar et al. (1984) observed notable differences between the undetermined specimens from Salobreña and all the African *Myocricetodon* species known at that time, thus refusing any African ancestor for *Myocricetodon* sp. from Salobreña and suggesting an Asian origin and a transmediterranean migration through Greece and Italy. Moyà-Solà et al. (1984) also claimed an Asian origin for *Myocricetodon* sp. from Salobreña and explained its presence in Spain by a migration through the desiccated Mediterranean.

Shortly after, the discovery of a more abundant sample of *Myocricetodon* in Almenara-M (ALM-M) in eastern Spain raised again the problem of the arrival of this genus into Europe (Agustí and Galobart, 1986). This work and further studies (Agustí, 1989, 1990; Agustí and Llenas, 1996) also proposed an eastern origin for the Spanish populations of *Myocricetodon*, based on the lack of similarities between the samples from Salobreña and ALM-M and the most recent (Turolian) north African *Myocricetodon* species known at that moment. In fact, these authors assigned the population from Almenara to *Myocricetodon* cf. *parvus* due to its resemblance with the middle Miocene species *M. parvus*. This taxonomic allocation, as well as the Asian origin of the Spanish forms of *Myocricetodon*, have been maintained even in relatively recent works (Agustí and Casanovas-Vilar, 2003; Agustí et al., 2006a), where these authors considered that "the apparent conservatism of the late Miocene *Myocricetodon* from Spain is a surprising fact, since the youngest *Myocricetodon parvus* is late Aragonian in age (Pataniak 6), while the youngest *M. seboui* is Turolian (Amama 2), but certainly pre-Messinian in age" (Agustí and Casanovas-Vilar, 2003; pag. 14). However, the rich sample from ALM-M has never been described in detail.

In addition, Sesé (1989) documented the presence of two different forms of *Myocricetodon* in the localities of Pino Mojón and Bacochas (Guadix Basin), referred to *Myocricetodon* sp. 1 and sp. 2, which strongly differ from each other in size and morphology. Similarly, Aguilar et al. (1991) assigned to this genus one isolated molar from Castelnou-3 and another specimen from Font Estramar (southern France), constituting the only European mentions of the genus out of Spain. However, as will be explained in following sections, neither the tooth from Bacochas nor that from Font Estramar seem to belong to *Myocricetodon*. Finally, the assemblage from Negratín-1 (NGR-1) in the Guadix Basin is the only European population formally determined at the specific level. It was attributed to the species *Myocricetodon jaegeri*, originally described from Afoud 5 in Morocco (Benammi, 2001), which constitutes a solid argument for an African origin of this gerbil (Minwer-Barakat et al., 2009a).

However, the taxonomic determination of the rest of European populations of *Myocricetodon*, their relationships with African species and their way of entrance into the Iberian Peninsula, which have been the subject of discussion for many years (Aguilar et al., 1984; Agustí, 1990; Wessels, 1998; Agustí et al., 2006a; García-Alix et al., 2016), still need a thorough revision. In this work we analyze for the first time all the material of this genus recorded in Europe so far, aiming to clarify the paleoenvironmental factors that allowed its arrival into Europe and determined its geographical distribution.

2. Geographical and geological setting

The studied material of *Myocricetodon* comes from different fossil sites from the Iberian Peninsula and southernmost France, all of them situated relatively close to the Mediterranean coast (Fig. 1). The most abundant collection comes from Almenara-M, a level within the Almenara karst complex, which is located in an abandoned quarry next to the town of Almenara (Castellón, eastern Spain), in the eastern sector of the Iberian range. The paleokarst was developed in middle Triassic limestones and led to the formation of several fissure infillings, some of them yielding rich and diverse vertebrate remains, including small and large mammals (Gil and Sesé, 1984; Soto and Morales, 1985; Agustí and Galobart, 1986; Agustí, 1990; Furió et al., 2007; Furió and Mein, 2008; Agustí et al., 2011). Most of the fossil bearing levels correspond to the late Pliocene and early Pleistocene (Almenara-1, 3 and 4, see Agustí et al., 2011). Nevertheless, the infilling named as Almenara-M has yielded a small mammal assemblage characteristic from the latest Miocene, including the species *Apodemus gudrunae, Paraethomys meini* and *Apocricetus alberti* (Agustí et al., 2011).

The fossil sites Pino Mojón (Sesé, 1989) and NGR-1 (Minwer-Barakat et al., 2009a) are located in the Guadix Basin (southern Spain). This basin, situated in the central sector of the Betic Cordillera, was established as a separate intramontane basin in the late Miocene (Viseras et al., 2005). The sedimentary infill of this basin includes a phase of marine sedimentation during the Tortonian, another phase corresponding to the sea retreat at the end of the Tortonian, and a third phase of exclusively continental sedimentation in an endorheic basin context, from the late Turolian to the late Pleistocene (Soria et al., 1998; García-García et al., 2009). Recent biozonations of the continental stage of the basin based on small mammals were published by Minwer-Barakat et al. (2012a), Agustí et al. (2015) and Piñero et al.