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 dispersal 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.
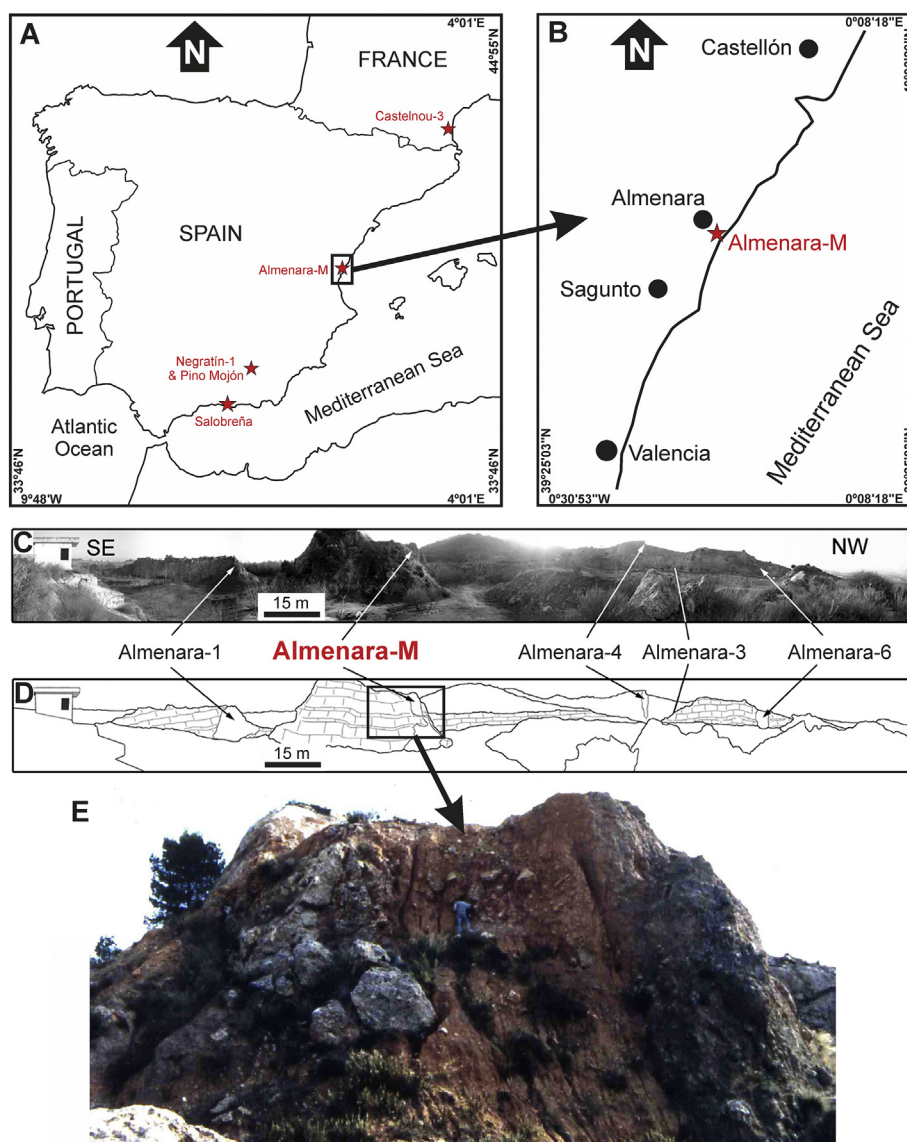
Fig. 1. A: geographical location of the European fossil sites yielding remains of *Myocricetodon*: Salobreña (Aguilar et al., 1984), Pino Mojón (Sesé, 1989), Negratín-1 (Minwer-Barakat et al., 2009a), Almenara-M (Agustí and Galobart, 1986) and Castelnou-3 (Aguilar et al., 1991). B: detail of the situation of the Almenara-M locality. C and D: photography and schematic reconstruction of the different fissure fillings within the Almenara karst complex. E: image of the Almenara-M fissure filling during the 1986 field campaign.

(2018). The most ancient mammal faunas from the basin were dated as late Turolian (MN13), with no evidence of older continental deposits (Minwer-Barakat et al., 2009b, 2012b).

The locality of Salobreña (Granada Province, southern Spain) corresponds to the infill of a karstic fissure in Jurassic limestones. In fact, the sample comes from some dropped blocks found at the base of a cliff, and the fossil-bearing level was never observed in situ (Aguilar et al., 1984). The rodent assemblage from Salobreña deserved a great interest since its discovery (Jaeger et al., 1977), because it represented the first finding of African rodents in Europe in relation with the MSC. This fauna was also assigned to the latest Miocene (Aguilar et al., 1984) on the basis of the presence of *Apodemus* cf. *gudrunae*, *Paraethomys meini* and "*Cricetus kormosi*" (which in fact correspond to *Apocricetus alberti* according to Freudenthal et al., 1998).

Finally, the locality of Castelnou-3 (Aguilar et al., 1991) is situated in the Roussillon (SE France), close to the town of Perpignan. This fossil site also corresponds to the infilling of a karst fissure, and represents the only European record of *Myocricetodon* out of Spain. The presence of *Apodemus* cf. *gudrunae*, *Paraethomys meini* and *Stephanomys dubari*

allowed the assignation of Castelnou-3 to the latest Miocene (Aguilar et al., 1991).

3. Material and methods

The described material from Almenara-M (Supplemental Information File) consists of 40 isolated teeth, including 18 M^1 (IPS82777-82779, 82781, 87684, 88263-88266 and 88268-88276), 3 M^2 (IPS88277-88279), 14 M_1 (IPS88280-88293) and 5 M_2 (IPS88294-88298), housed in the collections of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain).

The material from Negratín-1, originally described by Minwer-Barakat et al. (2009a), is curated at the Departamento de Estratigrafía y Paleontología, Universidad de Granada (Spain). The specimens from Pino Mojón (Sesé, 1989) are stored at the Museo Nacional de Ciencias Naturales (Madrid, Spain). The material from Salobreña (Aguilar et al., 1984) and Castelnou-3 (Aguilar et al., 1991) is housed at the Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier (France).

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Table 1
Measurements (mm) of the teeth of *Myocricetodon jaegeri* from Almenara-M.

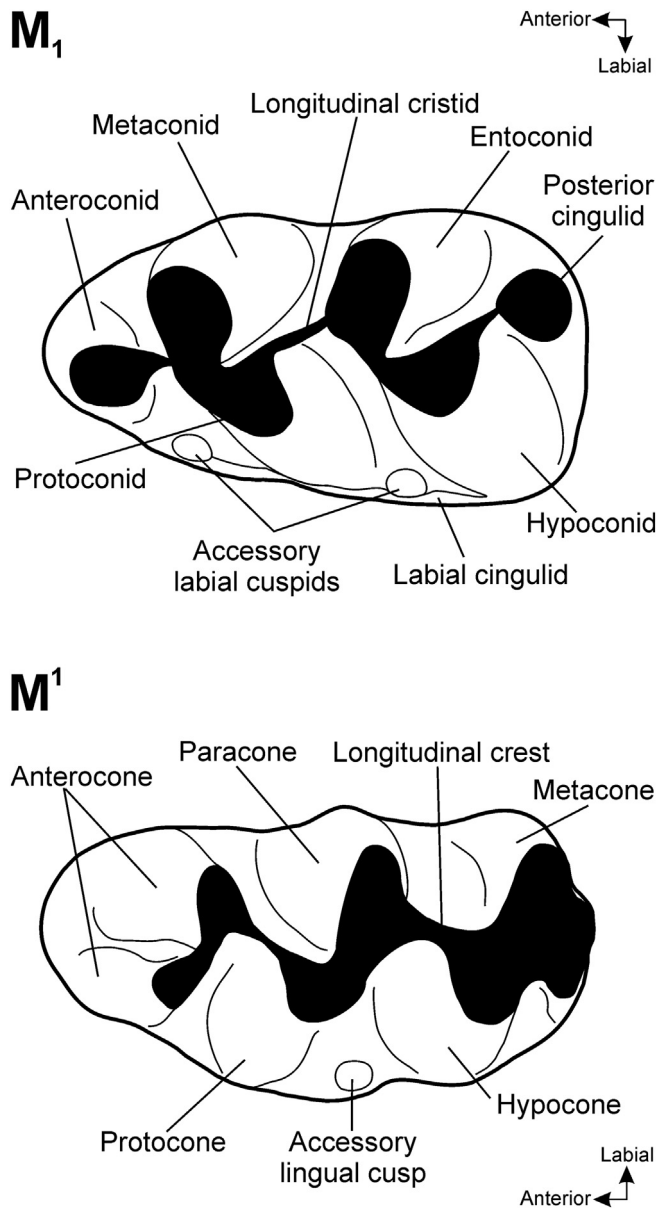|	Length				Width			
	N	Min	Mean	Max	N	Min	Mean	Max
M_1	14	1.19	1.29	1.38	14	0.68	0.75	0.81
M_2	5	0.80	0.89	0.96	5	0.69	0.74	0.78
M^1	16	1.39	1.52	1.61	15	0.73	0.79	0.84
M^2	3	0.89	0.95	0.99	3	0.72	0.76	0.79

Fig. 2. Nomenclature employed for the description of lower (top) and upper (bottom) teeth of *Myocricetodon*. Arrows indicate the anterior and labial sides of each tooth.

Measurements of the material from ALM-M (Table 1) have been taken using an optic calliper "Nikon measuroscope 10" connected to a monitor "Nikon SC112". The dimensions of the specimens from all the other localities can be found in the above mentioned publications. The nomenclature used in the descriptions of the teeth is explained in Fig. 2.

Micrographs of the material from ALM-M were taken using the Environmental Scanning Electron Microscope (ESEM) at the Universitat

de Barcelona. Micrographs of the material from NGR-1 were taken using the Zeiss 950 Scanning Electron Microscope of the "Centro de Instrumentación Científica", Universidad de Granada. Micrographs of the material from Pino Mojón were made in the Laboratorio de Técnicas no Destructivas, Museo Nacional de Ciencias Naturales (Madrid). Finally, micrographs of the teeth from Salobreña were taken at the "Service commun de microscopie électronique et analytique de l'Université de Montpellier".

4. Systematic paleontology

Family Gerbillidae Alston, 1876.
Subfamily Myocricetodontinae Lavocat, 1961.
Genus *Myocricetodon* Lavocat, 1952.
Myocricetodon jaegeri Benammi, 2001.

4.1. Emended diagnosis

Small species of *Myocricetodon*, with upper and lower first molars narrow and elongated. M_1 with prominent anteroconid. M_1 and M_2 with alternating labial and lingual cuspids and tubercular-shaped posterior cingulid. Longitudinal cristid connecting protoconid and entoconid in most M_1 and M_2. M^1 with anterocone divided in two asymmetrical lobes, paracone and metacone placed backwards with respect to the protocone and hypocone, and poorly developed longitudinal crest. Accessory lingual cusp in the M^1 absent or small, isolated or weakly connected to the protocone. M^2 with an anterior cusp instead of a crest-shaped labial anterolophid.

Myocricetodon jaegeri differs from *M. irhoudi, M. ouedi, M. ultimus, M. asphodelae* and *M. magnus* in the much smaller size, the proportionally narrower molars and the more accentuated asymmetry between labial and lingual cusps. It differs from *M. eskihisarensis, M. seboui, M. ouaichi* and *M. afoudensis* in the much less-developed accessory lingual cusp in the M^1. It further differs from *M. eskihisarensis* and *M. seboui* in the tubercular anterior cusp in the M^2, from *M. ouaichi* in the smaller size, and from *M. afoudensis* in the absence of transverse crests in the valleys between the cusps in the upper molars. It differs from *M. parvus* in the more prominent anteroconid in the M_1, the less-developed accessory lingual cusp and the better-divided anterocone in the M^1, and the tubercular anterior cusp instead of a crest-shaped labial anteroloph in the M^2. It differs from *M. cherifiensis* and *M. trerki* in the smaller size, the divided anterocone and the more frequent and better-developed accessory lingual cusp in the M^1.

4.2. Material attributed to the species

The material attributed to this species includes that from Afoud 5 (type locality, Morocco, Benammi, 2001), Argoub Kemellal (Algeria; Coiffait, 1991), Almenara-M (eastern Spain; Agustí, 1990), Negratín-1 (southern Spain; Minwer-Barakat et al., 2009a), Pino Mojón (southern Spain; Sesé, 1989), Salobreña (southern Spain; Aguilar et al., 1984) and Castelnou-3 (southeastern France; Aguilar et al., 1991).

4.3. Description of the material from Almenara-M

M_1 (Fig. 3A–I): Low-crowned molars, with the anteroconid large and prominent, higher than the other cuspids and undivided. Its connection with the protoconid-metaconid pair is weak. Metaconid, protoconid, entoconid and hypoconid are alternating. The labial cuspids are inclined anterolingually, whereas the lingual cuspids are inclined anteriorly. There is a longitudinal cristid connecting protoconid and entoconid in 12 out of 14 specimens. In the other two, the protoconid-metaconid pair and the hypoconid-entoconid pair are well separated by a transversal valley. The posterior cingulid is tubercular and oval, notably lower than the main cuspids and connected to the posterolingual part of the hypoconid. The labial cingulid is thin but well-marked
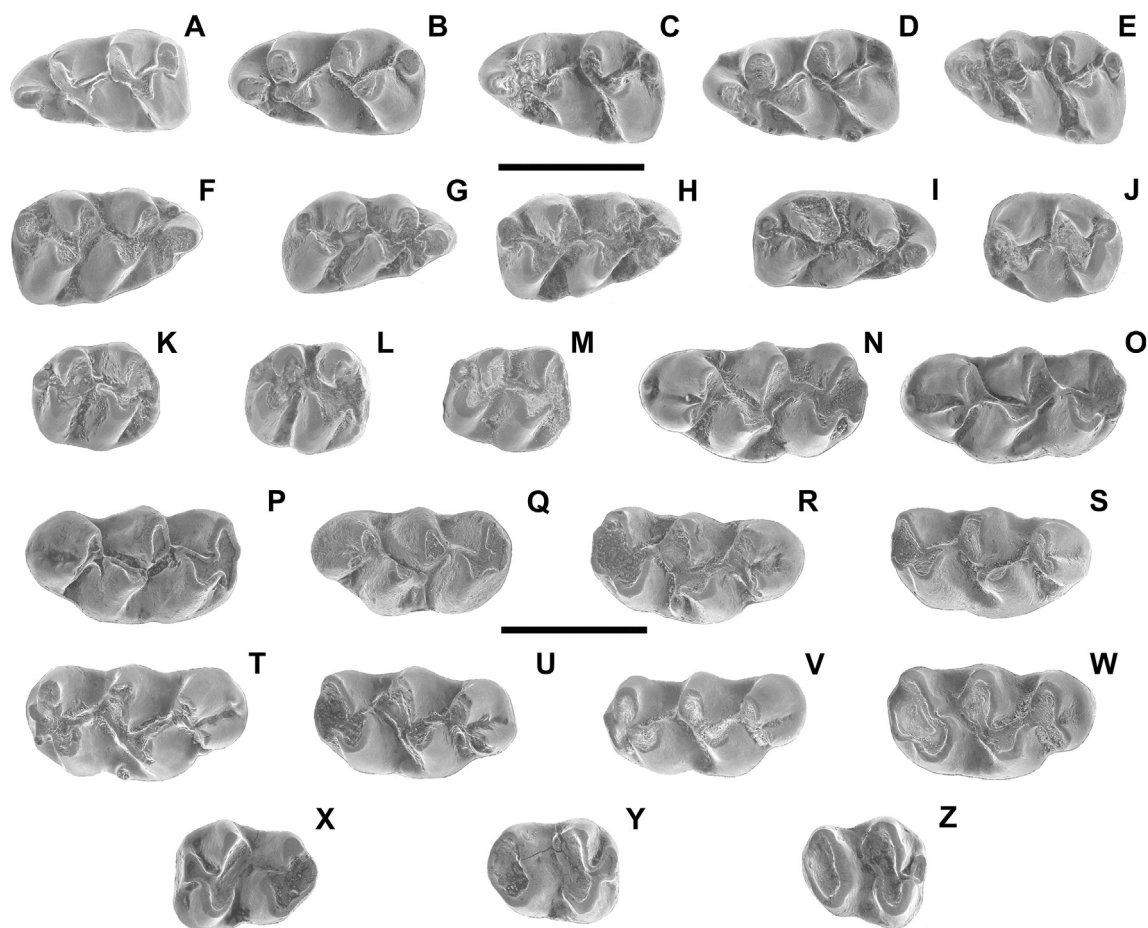
Fig. 3. Environmental Scanning Electron Microscope images of the teeth of *Myocricetodon jaegeri* from Almenara-M, housed in the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain). A: left M_1 (IPS88283). B: left M_1 (IPS88284). C: left M_1 (IPS88285). D: left M_1 (IPS88286). E: left M_1 (IPS88287). F: right M_1 (IPS88288). G: right M_1 (IPS88289). H: right M_1 (IPS88290). I: right M_1 (IPS88291). J: left M_2 (IPS88294). K: right M_2 (IPS88295). L: right M_2 (IPS88296). M: right M_2 (IPS88297). N: left M^1 (IPS88266). O: left M^1 (IPS88268). P: left M^1 (IPS88269). Q: left M^1 (IPS88270). R: right M^1 (IPS88271). S: right M^1 (IPS88272). T: right M^1 (IPS88273). U: right M^1 (IPS88274). V: right M^1 (IPS88275). W: right M^1 (IPS88276). X: left M^2 (IPS88277). Y: right M^2 (IPS88278). Z: right M^2 (IPS88279). Scale bar for all images represents 1 mm.
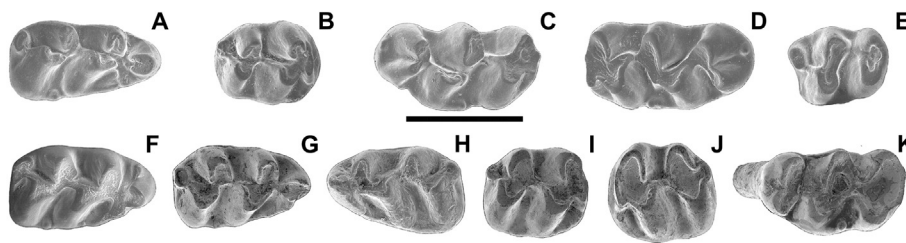
between the anteroconid and the protoconid, and weaker between the protoconid and the hypoconid. Nine specimens have a small accessory labial cuspid behind the anteroconid and another tooth has two minuscule cuspids in this position; seven specimens have another accessory labial cuspid between protoconid and hypoconid, and five teeth also have a small accessory cuspid on the lingual border, near the base of the anteroconid.

M_2 (Fig. 3J–M): The crown is low, and the outline is rectangular, slightly longer than wide. Like in the M_1, metaconid and entoconid are located in an anterior position with respect to the protoconid and hypoconid respectively. The labial branch of the anterolophid is long and well-developed; it starts at the protoconid-metaconid intersection, descends bordering the anterolabial part of the molar and reaches the base of the metaconid. All the specimens have a low longitudinal cristid connecting the anterior part of the entoconid to the posterior part of the protoconid. The posterior cingulid is tubercular and low, smaller than in the M_1, and attached to the posterolingual part of the hypoconid. There are no accessory labial or lingual cuspids.

M^1 (Fig. 3N–W): Low-crowned, long and narrow teeth. The anterocone is divided into two well-differentiated lobes; the labial lobe is larger than the lingual one, and placed posteriorly with respect to it. In some specimens the lingual lobe of the anterocone is very reduced and the anterocone is markedly asymmetrical. Seven out of 17 complete specimens show a minuscule cusp, round or transversely elongated, on the anterior border of the tooth, at the level of the separation between

the two anterocone lobes. Paracone and metacone are transverse to the longitudinal axis of the tooth and placed in a posterior position with respect to the protocone and hypocone, respectively, which are oblique to the longitudinal axis. The labial lobe of the anterocone is connected to the protocone by a crest. The protocone and paracone are separated in the least worn specimens, and become connected with wear. In 16 specimens there is a crest connecting hypocone and paracone, variable from very low and weak to high and well-developed. Only in two teeth the protocone-paracone and hypocone-metacone pairs are completely separated. There is a short spur running lingually from the posterior face of the hypocone. The accessory cusp on the lingual border, between the protocone and hypocone, is present in ten specimens; it is variable in shape, from round to longitudinally elongated, isolated in eight teeth and connected to the protocone in the other two. In addition, five specimens have a very small, round accessory labial cusp on the posterolabial base of the anterocone.

M^2 (Fig. 3X–Z): The crown is low. There is a large anterior cusp, slightly shifted labially, lower than the main cusps and connected to the protocone. From this anterior cusp, two crests run labially and lingually, bordering the anterolabial and anterolingual parts of the tooth. The protocone is anterior with respect to the paracone. The hypocone is larger than the metacone; in the two most worn specimens these cusps are fused, forming a wide transverse ridge. There is a very weak spur on the anterior side of the metacone-hypocone complex, but it does not reach the paracone-protocone, so the anterior and posterior cusps are
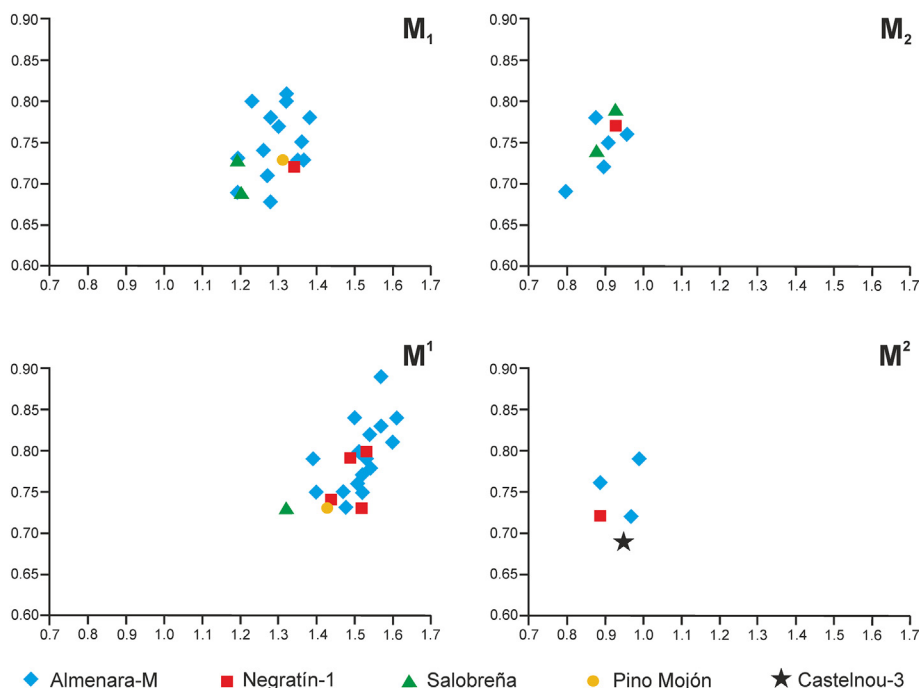
Fig. 4. Environmental Scanning Electron Microscope images of the teeth of *Myocricetodon jaegeri* from Negratín-1 (A–E), housed in the Departamento de Estratigrafía y Paleontología, Universidad de Granada (Spain), Pino Mojón (F), housed in the Museo Nacional de Ciencias Naturales (Madrid, Spain), and Salobreña (G–K), housed in the Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier (France). A: right M_1 (NGR-1 86). B: right M_2 (NGR-1 87). C: left M^1 (NGR-1 88). D: right M^1 (NGR-1 91). E: left M^2 (NGR-1 92). F: right M_1 from Pino Mojón. G: right M_1 (SAL-115). H: left M_1 (SAL-118). I: right M_2 (SAL-116). J: left M_2 (SAL-117). K: left M^1 (SAL-114). Scale bar for all images represents 1 mm.

separated by a wide valley. One out of three specimens has a minuscule accessory cusp between protocone and hypocone. There is no posteroloph.

4.4. Comparisons with the material from Negratín-1

The material of *Myocricetodon* from NGR-1 (Fig. 4A–E) consists of two M_1 (one of them fragmented), one M_2, four M^1 and one M^2, which were described in detail by Minwer-Barakat et al. (2009a). These teeth are very similar in size (Fig. 5) and overall morphology to those from ALM-M. Some characters show slightly different proportions in both populations and some other have been only identified in Almenara, as expected due to its larger sample size. For instance, some M^1 from Almenara have an extremely reduced lingual lobe of the anterocone, which is not observed in the specimens from NGR-1. Similarly, the tiny cusp that is present on the anterior border of all the M^1 from NGR-1 is absent in some molars from ALM-M. The only M^2 from NGR-1 has the anterior cusp in a slightly more labial position than the specimens from Almenara. Metacone and hypocone are completely fused in the single M^2 from NGR-1, whereas in the less worn specimens from ALM-M, these cusps are still slightly differentiated from each other. Some M_1 from ALM-M have a small accessory lingual cuspid near the base of the anteroconid, which is absent in the single complete tooth from NGR-1.

4.5. Comparisons with the material from Pino Mojón

The sample of *Myocricetodon* from Pino Mojón, originally described by Sesé (1989), only includes one M_1 (Fig. 4F) and one M^1, both very similar to the teeth from ALM-M. The M_1 displays the three accessory cuspids (two labial cuspids between anteroconid and protoconid and between protoconid and hypoconid, and a lingual one on the base of the anteroconid) that appear with different frequencies in the sample from ALM-M. The M^1 is similar in size to the smallest specimens from ALM-M, and morphologically identical, with the anterocone divided into two asymmetrical lobes and with the paracone and metacone placed in a posterior position with respect to the protocone and hypocone. This specimen lacks the accessory lingual cusp that is present in some molars from Almenara.

4.6. Comparisons with the material from Salobreña

We have carefully examined the material from Salobreña, first ascribed by Aguilar et al. (1984) to *Myocricetodon* sp., which consist of two M_1, two M_2 and one M^1 (Fig. 4G–K). The M_2 are similar in size to the specimens from ALM-M; the M_1 and M^1 are slightly smaller, although the difference is not significant (Fig. 5). The teeth from Salobreña are nearly identical in overall morphology to those from Almenara. The entoconid and the protoconid are connected in the two M_1 from Salobreña, like in most specimens from ALM-M. Only one of the two M_1 from Salobreña shows the small accessory cuspid close to the labial base of the anteroconid that is present in most specimens from ALM-M. The other accessory cuspids observed in some teeth from ALM-M (between the protoconid and the hypoconid and on the lingual base of the anteroconid) are absent in the specimens from Salobreña. The M_2

Fig. 5. Size graphs (length × width) of the M_1 (top left), M_2 (top right), M^1 (bottom left) and M^2 (bottom right) of all the European samples of *Myocricetodon jaegeri*. Measurements of *M. jaegeri* from Almenara-M are those presented in this work. Measurements from Negratín-1 after Minwer-Barakat et al. (2009a); data from Salobreña after Aguilar et al. (1984); data from Pino Mojón after Sesé (1989); data from Castelnou-3 after Aguilar et al. (1991).

from both samples are morphologically identical. The single M^1 from Salobreña is rather worn; so, the crests connecting cusps cannot be observed. It has a small and round accessory cusp on the lingual border, between protocone and hypocone, isolated from the main cusps. In addition, it shows a very weak cusp on the anterior border, between the two lobes of the anterocone, as a small swelling of the enamel.

4.7. Comparisons with the material from Castelnou-3

The material from Castelnou-3 only consists of a M^2, which is broken at the level of the paracone; however, the outline is preserved, allowing the estimation of length and width (Aguilar et al., 1991). It is slightly narrower than the teeth from ALM-M (Fig. 5) and very similar in overall morphology, showing fused hypocone and metacone and no connection between these cusps and the protocone-paracone pair. It differs from the specimens from ALM-M in the smaller anterior cusp and in the lack of anterolabial and anterolingual crests.

4.8. Comparisons with the material from Afoud-5

The material from ALM-M has been compared with the sample from Afoud-5, type locality of the species *M. jaegeri*, which consists of very few teeth (Benammi, 2001). The morphology is very similar in both samples. The lower molars show alternating labial and lingual cuspids, a crest connecting protoconid and entoconid, and a tubercular posterior cingulid. The small accessory cuspid between protoconid and hypoconid observed in 7 out of 13 M_1 in ALM-M is also present in one of the two specimens from Afoud-5. The accessory lingual cusp of the M^1 is small and isolated in the six specimens from Afoud-5, like in most specimens from ALM-M. However, as expected due to the larger sample size, some M^1 from Almenara display a medium-sized accesory lingual cusp and some others lack this element. Besides, the division of the two lobes of the anterocone is better marked in the M^1 from ALM-M than in those from Afoud. The M^2 from Afoud 5 show a weak connection between paracone and hypocone that is absent in the specimens from ALM-M. The rest of morphological features are identical in both populations.

4.9. Wrong citations of Myocricetodon in Europe: Bacochas and Font Estramar

Some other European localities have yielded very few specimens that were assigned to the genus *Myocricetodon*. After an exhaustive revision of this material, we have concluded that these generic determinations were mistaken. Sesé (1989) reported a single M_1 from Bacochas (Guadix Basin), and assigned it to "*Myocricetodon* sp. 2" (in order to distinguish this specimen from "*Myocricetodon* sp. 1" from Pino Mojón, here ascribed to *M. jaegeri*). The M_1 from Bacochas is much larger (2.86×1.96 mm) and morphologically very different from all the other European samples of *Myocricetodon*. It displays a broad anteroconid weakly connected to the protoconid-metaconid pair, and a posterior ridge formed by the hypoconid and entoconid, which are fused. Contrary to *M. jaegeri*, in this molar the labial cuspids are not significantly displaced posteriorly with respect to the lingual cuspids. The specimen from Bacochas is virtually identical in size an morphology to the M_1 of *Debruijnimys almenarensis* from ALM-M (Agustí, 1990), so we consider that it can be confidently assigned to that species, also recognized in other late Turolian Spanish sites (Minwer-Barakat et al., 2009a; Martín-Suárez et al., 2000). The species *D. almenarensis* was still not described at the moment of the publication of the material from Bacochas, which explains the mistaken attribution of the mentioned specimen.

The single tooth assigned to *Myocricetodon* from Font Estramar in France (Aguilar et al., 1991, Pl. 2, Fig. 14) is an M_3, which cannot be compared with any other sample of *M. jaegeri* because this element is unknown for this species. However, the size of this tooth (1.30×1.07 mm) indicates that it cannot correspond to *M. jaegeri*, since it is notably wider than the M_1 and M_2 of this species. In any case, according to our observations, the generic ascription of the specimen from Castelnou is mistaken. Its morphology is quite simple: it consists of a protoconid-metaconid pair, with a small antelolabial cuspid, and a posterior complex formed by the fusion of hypoconid and entoconid. There is a longitudinal cristid joining these two pairs of cuspids. This specimen strongly resembles in size and morphology the M_3 of the murid *Stephanomys*, which is in fact an abundant element in the assemblage from Font Estramar. The only subtle difference is the presence of a small cingulid in the posterior side of the referred molar. Hence, this tooth probably belongs to *Stephanomys*.

4.10. Specific determination of all the European populations of Myocricetodon

The only European population of *Myocricetodon* that was formally determined at the specific level is that from NGR-1, assigned by Minwer-Barakat et al. (2009a) to the species *M. jaegeri*, which was previously described from Afoud 5 in Morocco and also recognized in Argoub Kemellal in Algeria (Benammi, 2001). The material from Salobreña, Pino Mojón and Castelnou-3 was not ascribed to any known species and was thus named as *Myocricetodon* sp. (Aguilar et al., 1984, 1991; Sesé, 1989). Regarding the sample from ALM-M, it was determined as *Myocricetodon* cf. *parvus* in previous works (Agustí and Galobart, 1986; Agustí, 1989, 1990; Agustí and Llenas, 1996; Agustí and Casanovas-Vilar, 2003; Agustí et al., 2006a). Minwer-Barakat et al. (2009a) pointed out the similarity between the sample from ALM-M and *M. jaegeri* from NGR-1, but a formal allocation to this species was not possible without a thorough description of the material from Almenara. Here we compare for the first time all the material of *Myocricetodon* recorded to date in Europe with the African species of this genus, aiming at reaching a specific determination for all the European samples.

First, it is worth noting that all the samples of *Myocricetodon* from Europe are noticeably similar to each other both in size and morphology. Fig. 5 shows that practically all the measurements of the teeth from NGR-1 and Pino Mojón fall within the size range of the most abundant population, ALM-M. One of the M_2 from Salobreña is slightly wider than those from ALM-M, whereas the M^1 is somewhat smaller. The only M^2 from Castelnou-3 is slightly narrower than the three specimens from ALM-M, although similar in length. Measurements of the European samples are also similar to those of the scarce teeth of *M. jaegeri* from Afoud 5 (Benammi, 2001) and Argoub Kemellal (Coiffait, 1991).

All the European populations of *Myocricetodon* are also similar to *M. jaegeri* from Afoud 5 in morphology, sharing all the features that characterize that species: upper and lower first molars narrow and elongated; M_1 with prominent anteroconid and alternating labial and lingual cuspids; M^1 with anterocone divided in two asymmetrical lobes, paracone and metacone placed backwards with respect to the protocone and hypocone, longitudinal crest weak but present in most specimens, accessory lingual cusp absent or small, isolated or weakly connected to the protocone.

We have analyzed the variability of some morphological traits in those samples that include at least two M_1 and M^1: Almenara-M, Negratín-1 and Afoud 5 (Fig. 6). In the M_1, the longitudinal cristid connecting protoconid and entoconid is present in all the specimens from NGR-1 and Afoud 5 (only 2 available teeth from each locality); similarly, this cristid is present in most specimens from ALM-M (11 out of 13). The frequency of the accessory labial cuspid between protoconid and hypoconid is also the same in the three studied samples: it is present in 1 out of 2 specimens in NGR-1 and Afoud 5, and in 7 out of 13 teeth in ALM-M. In the M^1, the longitudinal crest connecting hypocone and paracone also shows similar frequencies in the three samples: it occurs in 16 out of 18 specimens in ALM-M, 3 out of 4 teeth in NGR-1
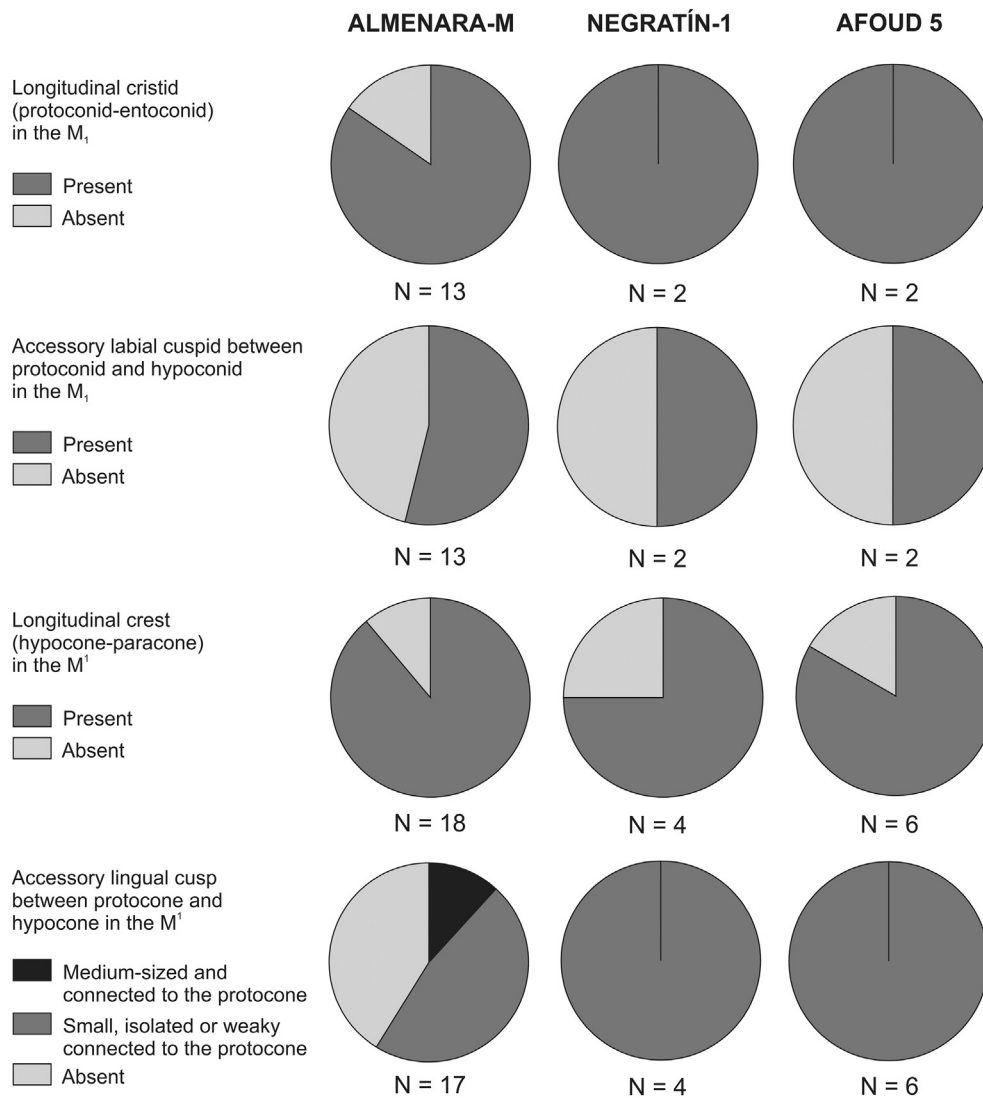
Fig. 6. Variability of some morphological traits in the M_1 and M^1 of *Myocricetodon jaegeri* from Almenara-M, Negratín-1 and Afoud 5. N: number of specimens in which each character can be observed.

and 5 out of 6 molars in Afoud 5. Regarding the accesory labial cuspid that is present but small in all the M^1 from NGR-1 and Afoud 5, it shows some variability in the sample from ALM-M, being absent in 7 specimens, small and isolated or weakly connected to the protocone in 8 teeth, and medium-sized and connected to the protocone in 2 molars. This variability can be explained by the larger sample size in the population from ALM-M.

Concluding, the obvious similarity between the material of *Myocricetodon* from ALM-M, NGR-1, Salobreña, Pino Mojón, Castelnou-3 and the type-population of *M. jaegeri* from Afoud 5 allows us to consider that all of them belong to the same species.

4.11. Comparisons with other species of Myocricetodon

Comparison of the European samples with all other African and Turkish species of *Myocricetodon* reveals clear differences. Jaeger (1977a) identified three lineages within this genus (Fig. 7), which were completed in further works (Wessels et al., 1987; Coiffait, 1991; Benammi, 2001) in order to include newly described species. The first one is the large-sized lineage, including the species *Myocricetodon irhoudi, M. ouedi, M. ultimus, M. asphodelae* and *M. magnus*. The European samples can be distinguished from the species of that lineage mainly by their much smaller size (Fig. 8). Morphological differences are also

evident, since the first lower and upper molars of the species of the large-sized lineage are proportionally wider than those of *M. jaegeri*, have less-developed longitudinal crests (except for *M. asphodelae*) and a much less accentuated asymmetry between the labial and lingual cusps.

A second lineage, integrated by the species *Myocricetodon parvus, M. eskihisarensis, M. seboui, M. ouaichi* and *M. afoudensis*, is characterized by a large accessory lingual cusp in the M^1, which increases in size from older to younger species, becoming a well-developed tubercle. *Myocricetodon jaegeri* from ALM-M and other European localities is similar in size to *M. parvus, M. eskihisarensis* and *M. seboui*, slightly smaller than *M. afoudensis* and clearly smaller than *M. ouaichi* (Fig. 8). Morphologically, *M. jaegeri* differs from the species of that lineage principally in the much less-developed accessory lingual cusp in the M^1, which is reduced, isolated or weakly connected to the protocone, or even absent in some specimens. This difference is particularly evident with the three most recent species of the lineage, *M. seboui, M. ouaichi* and *M. afoudensis*, in which this lingual cusp is very large. These three species have also more developed longitudinal crests than *M. jaegeri*. Furthermore, *M. jaegeri* from ALM-M differs from *M. eskihisarensis* in the better differentiated lobes of the anterocone in the M^1 and in the tubercular posterior cingulid in the lower molars, instead of the crest-shaped posterior cingulid observed in the specimens from Yeni Eskihisar (Wessels et al., 1987). The M^2 of *M. eskihisarensis* and *M. seboui*
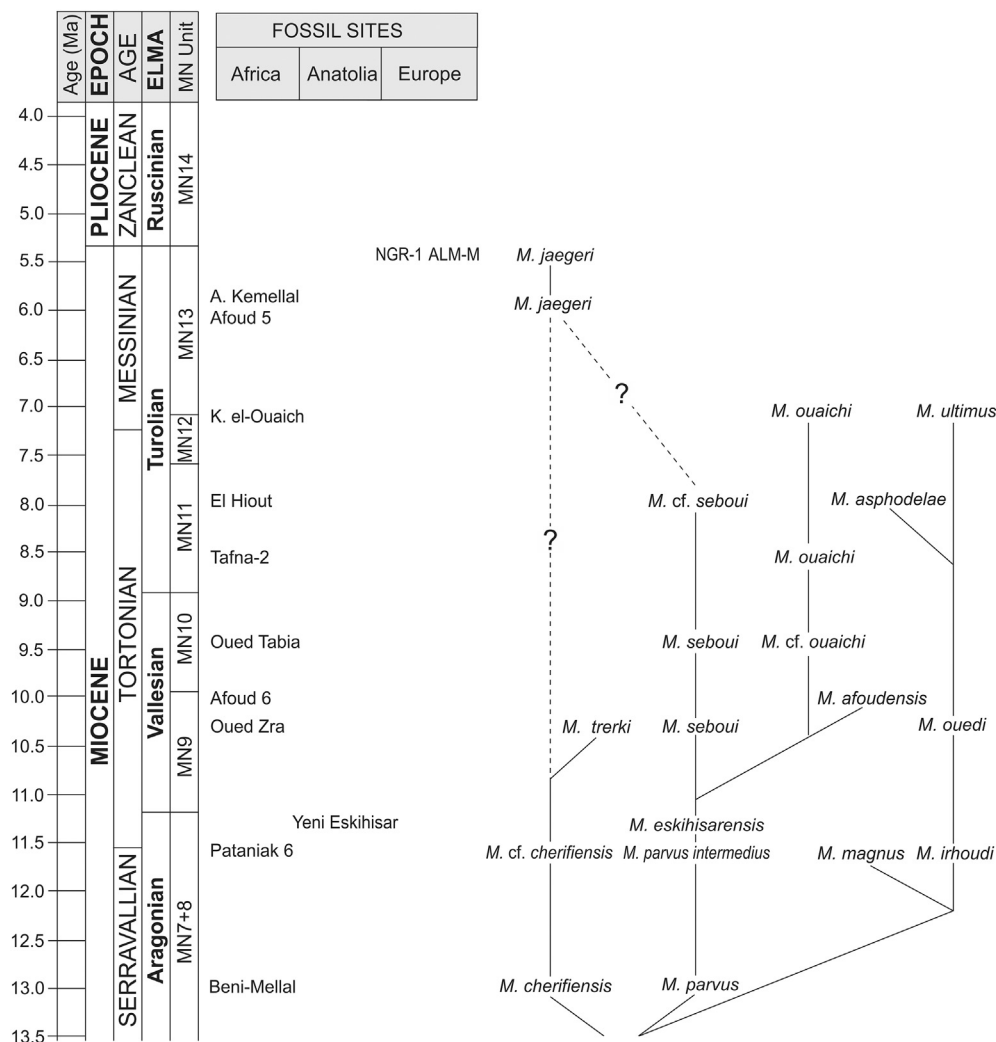
Fig. 7. Proposed phylogentic relationships of the different species of *Myocricetodon* described in north Africa, Anatolia and Europe. Dashed lines indicate uncertain relationships. Modified from Benammi (2001), Mein and Pickford (2010) and Mahboubi et al. (2015).

display a long labial anteroloph, instead of the tubercular anterior cusp connected to the protocone that is present in *M. jaegeri* from Almenara. In addition, the upper molars of *M. afoudensis* have several transverse crests in the valleys between the cusps, which are absent in those of *M. jaegeri*. With respect to *M. parvus*, despite its similarity in size with *M. jaegeri*, both species show clear morphological differences: the anterocone of the M^1 of *M. parvus* is simple or, less frequently, slightly divided into two lobes by a very shallow valley; the M^2 of *M. parvus* has a well-developed labial anteroloph and the M_1 is proportionally wider and has a less prominent anteroconid than in *M. jaegeri* from ALM-M.

Finally, the third lineage includes the species *Myocricetodon cherifiensis* and *M. trerki*, characterized by their medium size and the poorly developed accessory lingual cusp in the M^1. *Myocricetodon jaegeri* from ALM-M and other European sites is notably smaller than *M. cherifiensis* and much smaller than *M. trerki* (Fig. 8). Morphologically, in the M^1 of these two species the anterocone is undivided and the accessory lingual cusp is very infrequent, contrary to *M. jaegeri* from ALM-M.

Although Benammi (2001), in the original description of the species, allocated *M. jaegeri* in the third lineage, it displays certain similarities and differences with the species included in both the second (*M. parvus-M. seboui*) and third (*M. cherifiensis-M. trerki*) lineages. The size of *M. jaegeri* is similar to the species of the second lineage (*M. parvus-M. eskihisarensis-M. seboui*), whereas it is clearly smaller than *M. cherifiensis* and *M. trerki* (Fig. 8). In addition, the divided anterocone in the M^1 resembles more the species of the *M. parvus-M. seboui* group than those

of the *M. cherifiensis-M. trerki* lineage, in which the anterocone is simple. Finally, in *M. jaegeri* the development of the accessory lingual cusp of the M^1 is intermediate between these two lines: this cusp is absent or very weak in *M. cherifienis* and *M. trerki*, present in most specimens of *M. jaegeri* but generally small and isolated from the protocone, and very large and strongly connected to the protocone in the species *M. eskihisarensis* and *M. seboui*. For these reasons, we are cautious and prefer not to propose a conclusive ancestor-descendant relationship for *M. jaegeri*, considering that it could be either related to the *M. cherifiensis-M. trerki* or to the *M. parvus-M. seboui* lineages (Fig. 7).

Summarizing, the evident biometrical and morphological similarity between the European samples of *Myocricetodon* and *M. jaegeri* from Afoud-5, and the marked differences with the rest of African and Turkish species of the genus, allow a confident assignation of all the European populations to *M. jaegeri*. The similar age of all these localities and the fact that *M. jaegeri* is the only species of *Myocricetodon* described from the late Turolian reinforce this ascription. The previous determination of the population from ALM-M as *Myocricetodon* cf. *parvus* is, therefore, no longer valid, since the material from this Spanish locality shows clear differences with *M. parvus*, especially the deeply divided anterocone and the weaker accessory lingual cusp in the M^1.
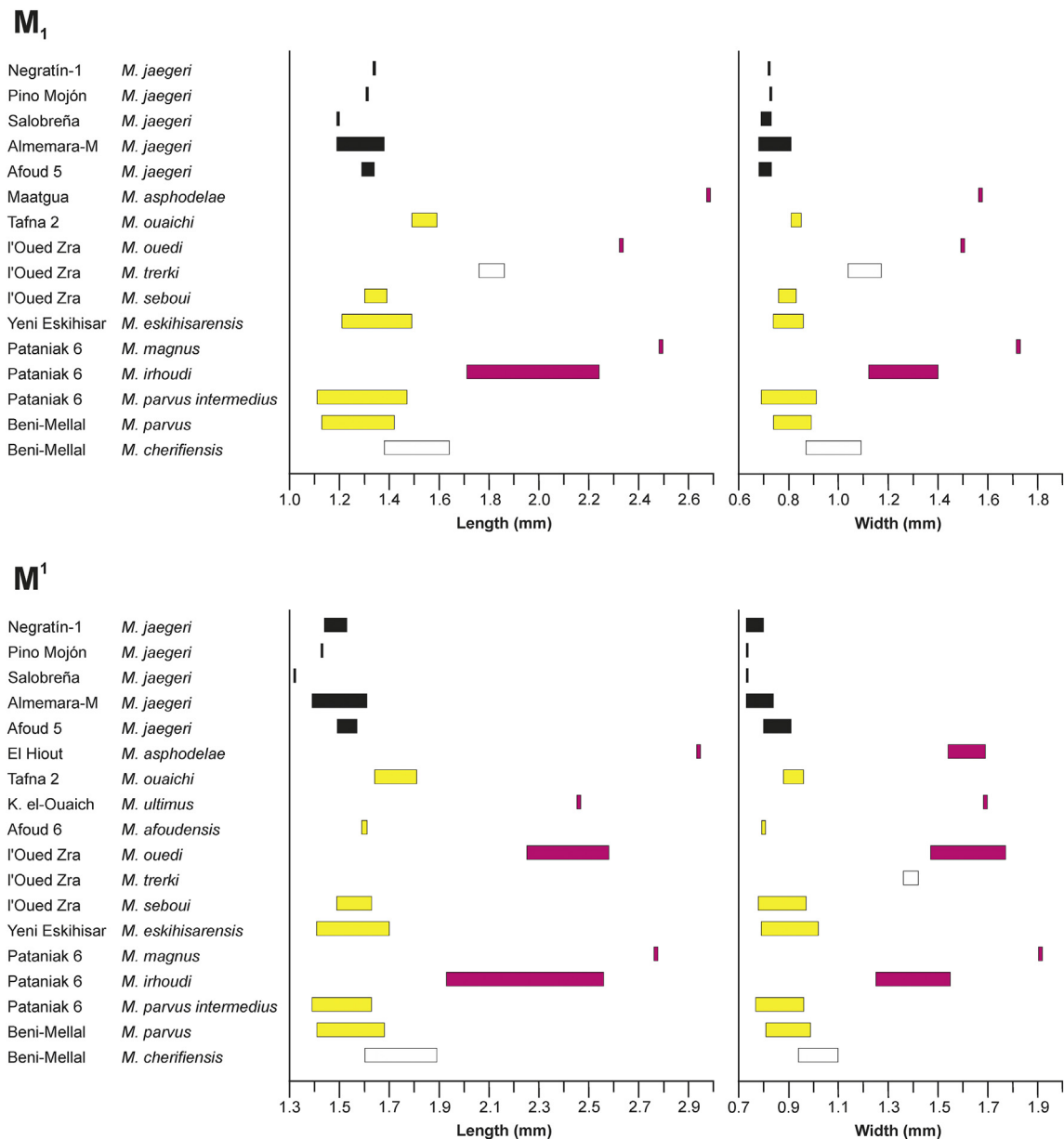
Fig. 8. Length and width ranges (in mm) of the M_1 and M^1 of all the African and Turkish species of *Myocricetodon* and the European samples of *M. jaegeri*. The measurements of each species correspond to its type locality, except for *M. ouaichi*, since the sample from Khendek-el-Ouaich is very scarce and thus the represented values correspond to the more abundant sample from Tafna-2 (Mahboubi et al., 2015). In the case of *M. asphodelae*, the measurements of the M^1 correspond to the type locality (El Hiout; Coiffait, 1991), but the values of the M_1 are those of the single specimen from Maatgua (Coiffait, 1991), because no first lower molar is available from the type locality. Data of *M. cherifiensis* and *M. parvus* from Beni-Mellal after Jaeger (1977b). Data of *M. parvus intermedius*, *M. irhoudi* and *M. magnus* from Pataniak 6, *M. seboui*, *M. trerki* and *M. ouedi* from l'Oued Zra and *M. ultimus* from Khendek-el-Ouaich after Jaeger (1977a). Data of *M. eskihisarensis* from Yeni Eskihisar after Wessels et al. (1987). Data of *M. afoudensis* from Afoud 6 and *M. jaegeri* from Afoud 5 after Benammi (2001). Measurements of *M. jaegeri* from Almenara-M are those presented in this work; data from Negratín-1 after Minwer-Barakat et al. (2009a); data from Salobreña after Aguilar et al. (1984); data from Pino Mojón after Sesé (1989). Ranges of the species included in the lineage *M. cherifiensis-M. trerki* are represented by white bars; ranges of the lineage *M. parvus-M. seboui* are represented in yellow; ranges of the lineage *M. irhoudi-M. ultimus* are represented by red bars; ranges of the species *M. jaegeri* are represented in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Discussion

5.1. Geographical distribution of M. jaegeri and paleoenvironmental constraints

The Iberian Peninsula holds an exceptional record of Neogene mammals; more specifically, latest Miocene-earliest Pliocene continental sequences with mammal remains are well represented in the eastern half of the Peninsula, cropping out in the Granada, Guadix-Baza, Sorbas, Almería-Níjar, Fortuna, Cabriel, Alcoy, Bajo Segura and Teruel basins (Mein et al., 1990; Garcés et al., 1998; Martín-Suárez et al., 2000; van Dam et al., 2001; García-Alix et al., 2008a, 2016; Minwer-Barakat et al., 2012a; Morales et al., 2013; Mansino et al., 2015, 2017; Gamonal et al., 2018; Piñero and Agustí, in press), with some sparse late Turolian fossil sites in the Pyrenees (Agustí et al., 2006b; Furió and Agustí, 2017). In addition, several latest Miocene karstic infillings have been identified in the Mediterranean coast (e.g., Salobreña and ALM-M). Therefore, the evolution of the small mammals assemblages of this age in Spain has been extensively studied and, indeed, several biochronological divisions for the continental late

Miocene have been established on the basis of the Spanish mammal record, including some Land Mammal Ages such as the Turolian and the Ventian (Fahlbusch, 1976; Morales et al., 2013). However, occurrences of the genus *Myocricetodon* are extremely scarce. In this section we discuss the factors that could have conditioned the presence or absence of this gerbil in different Iberian regions.

The Granada Basin is one of the Iberian areas with a most complete micromammal record of the Miocene-Pliocene transition, with long and well-dated sections such as La Dehesa, Barranco del Purcal or Calicasas (García-Alix et al., 2008a). In spite of the common occurrence of several rodent species in the latest Miocene deposits of the Granada and Guadix Basins (e.g., *Occitanomys alcalai, Stephanomys dubari, Paraethomys meini, Apocricetus alberti*), which allow a good correlation between both areas, no record of *Myocricetodon* has been found in Granada. On the contrary, several taxa that indicate more humid conditions have been recognized in the Granada Basin, which are absent in Guadix at the end of the Miocene. This is the case of the occurence in the latest Miocene levels of La Dehesa of the beaver *Dipoides problematicus* (a species related to puddle zones with slow water flow) and the talpid *Desmanella*, which is explained by more humid conditions than in the neighboring Guadix Basin (García-Alix et al., 2007, 2011). Moreover, the water-mole *Archaeodesmana*, with a semi-aquatic lifestyle and linked to permanent streams, is identified in most latest Messinian levels in the Granada Basin (García-Alix et al., 2008a), whereas it is not recorded in Guadix until the Pliocene (Minwer-Barakat et al., 2008). As observed nowadays, the difference in the humidity conditions between both basins during the Turolian would be mainly due to the 'rain-shadow' effect of the Sierra Nevada and the Sierra de los Filabres mountains to the south of the Guadix Basin, which would have resulted in more abundant precipitations in the Granada Basin, favoring the development of permanent lakes and densely vegetated biotopes, in contrast to clearly drier climatic conditions in the Guadix Basin (García-Alix et al., 2008b). All these observations would be consistent with a geographical distribution of *Myocricetodon* limited to arid environments, since it does not appear together with mammals restricted to humid conditions.

In the Fortuna Basin, the evolution of the rodent faunas during the latest Miocene-earliest Pliocene was recently depicted by Piñero and Agustí (in press) in the Sifón de Librilla section, in which the Mio-Pliocene boundary is unambiguously marked by a valley incision produced during the MSC (Garcés et al., 2001). The latest Miocene levels (SIF-52, 61 and 79) have yielded a rodent assemblage very similar to those from NGR-1 and ALM-M including the species *Apodemus gudrunae, Occitanomys alcalai, Paraethomys meini* and *Apocricetus alberti*, but *Myocricetodon* is absent in the Fortuna Basin. However, the levels SIF-52, 61 and 79 show normal polarity and are correlated to chron C3An.1n, so in this case the absence of *Myocricetodon* may be due to an age slightly older than the arrival of gerbils to Europe (see next section) rather than to a paleoenvironmental factor. Similarly, in the Bajo Segura Basin, the sites of Crevillente-6 (Martín-Suárez and Freudenthal, 1998) and Sierra del Colmenar 1A (Gamonal et al., 2018), posterior to the arrival of *Paraethomys,* have rodent assemblages similar to those from NGR-1 and ALM-M, but *Myocricetodon* is absent. In these cases, it is difficult to elucidate whether this absence is due to temporal or paleoenvironmental reasons, since paleomagnetic data are not available, and Crevillente-6 and Sierra del Colmenar could correspond to a moment prior to the arrival of gerbils to Europe.

In the Zorreras section (Sorbas Basin, SE Spain) only two mammal-bearing localities have been assigned to the latest Miocene by means of paleomagnetic and paleontological data (Martín-Suárez et al., 2000), although both are extremely poor (only 4 and 12 rodent teeth were found in ZOR2B and ZOR3A, respectively). The presence of the gerbil *Debruijnimys almenarensis* in these levels enables a good correlation with NGR-1 and ALM-M. No remain of *Myocricetodon* has been found in Zorreras; however, in this case the absence of this taxon may well be due to an insufficient sample size. The same goes for the neighboring Almería-Níjar basin, where García-Alix et al. (2016) reported a single

tooth of *D. almenarensis* in the level named Gafares-2B, where only seven rodent teeth were recovered.

One of the most relevant late Turolian Spanish fossil sites is Venta del Moro (VM), in the Cabriel Basin (Morales et al., 2013). The murid and cricetid assemblage from VM is equivalent to those of NGR-1 and ALM-M, including *Apocricetus alberti, Occitanomys alcalai, Stephanomys dubari* and *Paraethomys meini*; however, *Myocricetodon* is not found in VM. In the same basin, *Myocricetodon* is also absent in La Bullana section (Mansino et al., 2015), assigned to the earliest Pliocene. The absence of this gerbil in VM can be explained by the age of this locality (~6.2 Ma), slightly older than the arrival of the gerbils to the Iberian Peninsula according to paleomagnetical data (Gibert et al., 2013; see next section), but a paleoenvironmental factor cannot be ruled out. As noted by Furió and Agustí (2017), the insectivore diversity is markedly different in ALM-M and VM, which are roughly equivalent in age and situated at the same latitude. Whereas ALM-M only has yielded two species (*Parasorex ibericus* and *Blarinella* cf. *europaea*), the assemblage from VM is more diverse, including at least one erinaceid, two talpids (among them the water-mole *Archaeodesmana*) and two soricids, which is indicative of more humid conditions.

The Teruel Basin is the Spanish area with a more complete continental record covering the late Miocene and the Pliocene. The latest Turolian is represented in several sites, such as Arquillo 4 and Celadas 2 (Van de Weerd, 1976; Mein et al., 1990; van Dam et al., 2001), where *Paraethomys* is present. However, despite the rich micromammal record of this area*, Myocricetodon* is also missing.

The northernmost record of late Turolian mammals from the Iberian Peninsula corresponds to the localities of Can Vilella (Cerdanya Basin) and Romanyà d'Empordà (Empordà Basin) in the Pyrenees, roughly equivalent in age to ALM-M and NGR-1. Again, the absence of *Myocricetodon* in these Pyrenean localities can be explained by different environmental conditions, since they have yielded remains of micromammals linked to humid environments, such as the beaver *Dipoides* or the talpids *Desmanella, Archaeodesmana* and *Talpa* (Furió and Agustí, 2017).

Summarizing, despite the abundant and diverse record of latest Miocene rodents in different Iberian basins, the gerbil *Myocricetodon* has been only recognized in the Guadix Basin (NGR-1 and Pino Mojón) and in different karstic infills placed along the Mediterranean coast (Salobreña, ALM-M and Castelnou-3, Fig. 9). In some cases, the absence of this genus can be explained by temporal reasons (Venta del Moro and the late Miocene levels from Sifón de Librilla are supposed to be older than the MSC and the arrival of gerbils to Europe), or to insufficient sample size (this is the case of Zorreras and Gafares in the Sorbas and Almería-Níjar basins). But, in general terms, we attribute the absence of this genus in some inner basins (Granada, Cabriel and Teruel) to environmental conditions that were different from those of eastern sites (Guadix Basin and coastal karstic localities). This interpretation is supported by other proxies, particularly the presence of taxa with specific environmental requirements and the abundance and diversity of insectivores, which is considered an indicator of humid conditions (Reumer, 1999; López-Antoñanzas and Cuenca-Bescós, 2002; Minwer-Barakat et al., 2010). Furió et al. (2011) described a latitudinal gradient in the composition of the western European insectivore assemblages, explained by the North-South gradient in precipitation that existed in the area during the Miocene; this gradient in rainfall can explain the absence of *Myocricetodon* in northern Spanish localities assigned to the latest Turolian, such as those from the Pyrenees and, to some extent, those from the Teruel area. But, in addition, another East-West gradient in humidity conditions must have existed, as already pointed out by Furió and Agustí (2017), to explain the differences in the insectivore associations between the latest Miocene localities from different Spanish areas. Fossil sites from the Teruel, Cabriel and Granada basins display high insectivore diversity and presence of indicators of humid conditions (*Desmanella, Archaeodesma*). In contrast, the same-aged sites of NGR-1 and ALM-M have only yielded remains of the galericini
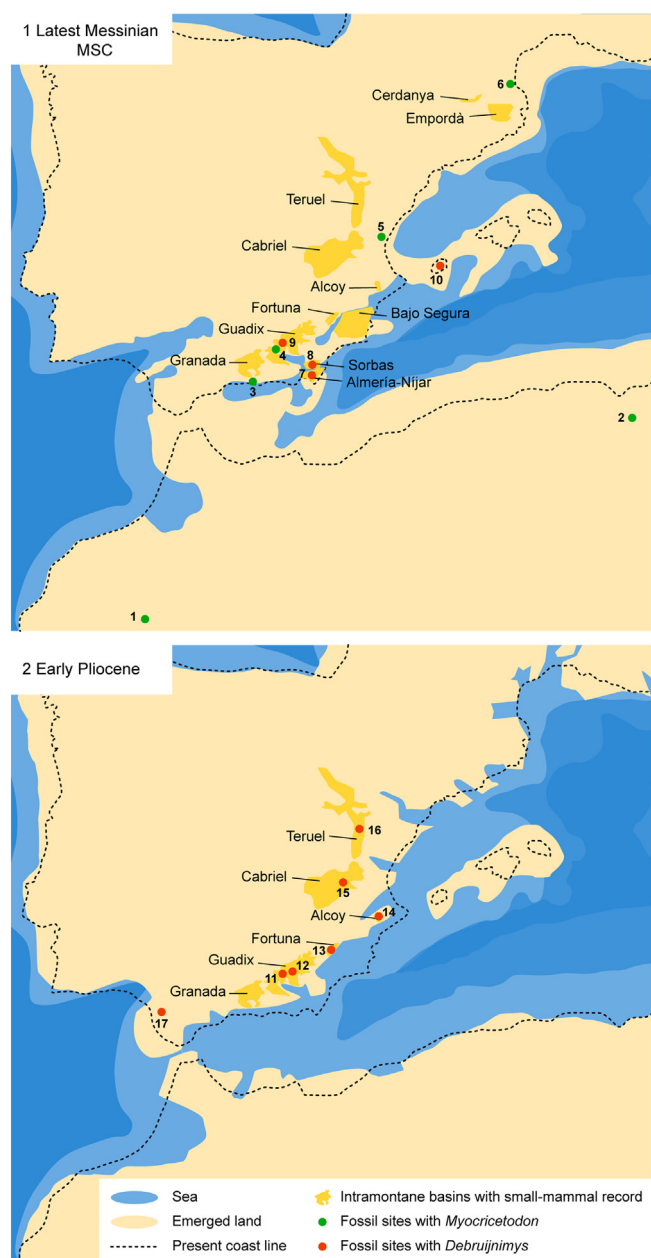
Fig. 9. Paleogeographic reconstructions of the Iberian Peninsula during the latest Messinian (Messinian Salinity Crisis) and the early Pliocene (modified from Popescu et al., 2009 and Vai, 2016), and distribution of fossil sites yielding remains of the gerbil rodents *Myocricetodon* and *Debruijnimys*. 1: Afoud 5. 2: Argoub Kemellal 1. 3: Salobreña. 4: Negratín-1 and Pino Mojón. 5: Almenara-M. 6: Castelnou-3. 7: Gafares-2B. 8: Zorreras 3A and 2B. 9: Bacochas. 10: Ses Fontanelles. 11: Gorafe-1. 12: Baza-1. 13: Sifón de Librilla-413. 14: Alcoy-N. 15: La Bullana-2B. 16: La Gloria-4. 17: Asta Regia-3.

Parasorex ibericus and one soricid. This pattern is perfectly consistent with an absence of *Myocricetodon* in the more western Granada, Cabriel and Teruel basins due to more humid conditions.

5.2. The chronology of the arrival and persistence of gerbils in Europe

The origin and the way of entrance of the European populations of *Myocricetodon* have been discussed for long, with several authors defending an Asian origin and a transmediterranean migration ending in the Iberian Peninsula (Aguilar et al., 1984; Moyà-Solà et al., 1984; Agustí, 1989, 1990; Agustí and Casanovas-Vilar, 2003; Agustí et al.,

2006a). However, once all the European samples of *Myocricetodon* have been confidently assigned to the species *M. jaegeri*, originally described in a same-aged locality from Morocco, there is no doubt about the African origin of this gerbil and its arrival through the Betic-Rifian region in the context of the MSC, as already proposed by other authors (Coiffait, 1991; Geraads, 1998; Wessels, 1998). The African origin of *Myocricetodon* and the other gerbil that is commonly found in the Iberian Peninsula, *Debruijnimys*, is also supported by their absence in all the European continent except for Spain and the southeastern extreme of France. Moreover, these gerbils are not recorded in the Mediterranean islands, with the only exception of a mention of *Debruijnimys* in Ses Fontanelles (Eivissa island, Moyà-Solà et al., 1984; Agustí, 1989). This rodent could reach the island from Spain during the desiccation of the Mediterranean, without implying an eastern origin as proposed by the mentioned authors.

Recent works agree in considering that the gerbil arrival to Europe postdates that of *Paraethomys* and thus corresponds to a different migration wave. The first appearance of the murid *Paraethomys* in the Iberian Peninsula was dated around 6.2 Ma in the Fortuna Basin, coinciding with the chron C3An.1n (Garcés et al., 1998; Piñero and Agustí, in press). This age is consistent with that of VM in the Cabriel basin, also correlated with the chron C3An.1n and dated in 6.23 Ma (Gibert et al., 2013). Neither VM nor the latest Messinian levels from the Fortuna Basin (SIF-52, 61 and 79) have yielded any gerbillid remain, so it is reasonable to consider that these sub-desertic rodents arrived later. The joint presence of *Myocricetodon* and *Debruijnimys* in the latest Messinian sites of NGR-1, ALM-M and Salobreña suggests a common African origin and a coeval arrival for both of them, but the dating of this arrival deserves a further discussion. Agustí et al. (2006a) referred to the dispersal of these rodents as the "Gerbil Event" with a possible age ranging between 5.96 and 5.33 Ma, whereas Gibert et al. (2013) restricted the age of this event between 5.5 and 5.3 Ma. In fact, the only late Miocene gerbil-bearing sites in which paleomagnetic data are available are Zorreras (Martín-Suárez et al., 2000) and NGR-1 (Piñero et al., 2018), both showing clear reverse polarity and confidently correlated with chron C3r, ranging from 6.03 to 5.23 Ma. This way, the arrival of these genera to Europe can be constrained between 6.03 (base of the chron C3r) and 5.33 Ma (age of the reestablishment of the Atlantic-Mediterranean connections and, consequently, the interruption of the land bridges between Africa and Iberia). It is very probable, however, that this dispersal took place in the last part of this interval, since cyclostratigraphic studies in the Sorbas basin assign to the Zorreras member an age between 5.52 and 5.33 Ma (Krijgsman et al., 2001).

Besides their simultaneous arrival, the temporal extent and the geographical distribution of *Myocricetodon* and *Debruijnimys* in Europe were clearly different (Fig. 9). Whereas the record of *Myocricetodon* is extremely scarce, restricted to the latest Miocene and geographically limited to the Guadix Basin and the Mediterranean coast, *Debruijnimys* has been identified in various levels clearly assigned to the Pliocene. In the Fortuna Basin, *Debruijnimys* is found in the level SIF-413, situated above the erosional surface that marks the Mio-Pliocene boundary (Piñero and Agustí, in press). Similarly, remains of this gerbil have been found in other lower Ruscinian sites such as Alcoy-N in the Alcoy Basin (López-Martínez, 1989), La Bullana in the Cabriel Basin (Mansino et al., 2015), Gorafe-1 and Baza-1 in the Guadix Basin (de Bruijn, 1974; Piñero et al., 2017) and, northwards, in La Gloria-4 (Teruel Basin; Mein et al., 1990). The last record of the genus corresponds to the late Ruscinian (MN15) locality of Asta Regia-3 in the Jerez Basin (Castillo and Agustí, 1996), which is, in addition, its westernmost occurrence (Fig. 9).

The environmental conditions in the western Mediterranean region during the dispersal of *Myocricetodon* in Europe were mostly arid (Fauquette et al., 1999), changing into moderate-wetter conditions at the Messinian-Pliocene transition (Jiménez Moreno et al., 2010; Roveri et al., 2014; García-Alix, 2015). In addition, an increase in the mean

insolation (Laskar et al., 2004) coeval with a global warming stage (Zachos et al., 2001) gave rise to extremely high temperatures in the south of the Iberian Peninsula at the end of the Messinian (García-Alix, 2015). As a consequence, coral reefs briefly re-appeared in the western Mediterranean coastal shelves for the last time (Martín et al., 1999). In that context, *Myocricetodon* was only capable to occupy the south-westernmost part of Europe during this short span of particular environmental conditions at the end of the Messinian. On the contrary, *Debruijnimys* registered a longer presence and wider dispersion in Europe, reaching inner basins such as Teruel and Cabriel, and even the Jerez Basin, close to the Atlantic Ocean, where it has been identified together with arvicolid rodents, commonly associated with colder climates. Therefore, the geographical and temporal distribution of these genera seems to indicate that the environmental requirements of *Debruijnimys* were much more flexible than those of *Myocricetodon,* and this latter only inhabited a restricted area during particularly extreme climatic conditions. This hypothesis, however, should be tested with other data, such as microwear analyses, which would be conclusive to understand the ecological preferences of these gerbil rodents.

6. Conclusions

1. All the European samples of *Myocricetodon*, including those from Almenara-M, Negratín-1, Salobreña, Pino Mojón and Castelnou-3, are assigned to the species *M. jaegeri*, originally described from Afoud 5 (Late Turolian, Morocco). Other mentions of *Myocricetodon* from Europe (Bacochas and Font Estramar) correspond to wrong attributions.

2. *Myocricetodon* is considered an African immigrant that arrived to Europe in the context of the Messinian Salinity Crisis. Its arrival, coeval with that of *Debruijnimys*, is correlated to the chron C3r (6.03–5.23 Ma), although its dispersal probably took place between 5.52 and 5.33 Ma. There is no record of *Myocricetodon* in Europe during the Pliocene, contrary to *Debruijnimys*, which persisted in Spain until the late Ruscinian.

3. The distribution of *Myocricetodon* in Europe is limited to the Guadix Basin and sparse karstic sites in the Mediterranean coast of Spain and southeastern France. Its absence in some inner Iberian basins (Granada, Cabriel and Teruel basins) coincides with evidences of humid conditions during the latest Miocene (high diversity of insectivores; presence of the genera *Desmanella, Archaeodesmana* and *Dipoides*). We interpret that *Myocricetodon* was extremely sensitive to environmental conditions, and it was only able to live in Europe during a short timespan of dry and warm climate at the end of the MSC, occupying a narrow area where arid conditions were especially accentuated.

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