

Neogene gerbils from Europe

Agustí, J. & Casanovas-Vilar, I. 2003 - Neogene gerbils from Europe - in: Reumer, J.W.F. & Wessels, W. (eds.) - DISTRIBUTION AND MIGRATION OF TERTIARY MAMMALS IN EURASIA. A VOLUME IN HONOUR OF HANS DE BRUIJN - DEINSEA 10: 13-21 [ISSN 0923-9308] Published 1 December 2003

In this paper, a review of the gerbils that appear in the late Miocene and early Pliocene of Europe is presented. Among the Myocricetodontines, the presence of *Myocricetodon* is reported in Salobreña (Granada, Southern Spain), Almenara M (Castellón, Eastern Spain), Pino Mojón (Guadix-Baza Basin, Southern Spain) and Castelnou-3 and Font Estramar (Roussillon Basin, Southern France). Within the same subfamily, today's genus *Calomyscus* is present in Western Europe in Salobreña, Almenara M and possibly Font Estramar. In Eastern Europe, *Calomyscus* is present in the Ruscinian of Maritsa (Rhodes, Greece). Among the Taterillinae, they are restricted to Western Europe (Spain) and represented by two consecutive species, *Protatera almenarensis* and *Debruijnimys julii*. Both are closely related, although an ancestor-descendant relationship cannot be established between them. Finally, two supposed Gerbillinae, *Pseudomeriones* and *Epimeriones* are also considered. Both are considered as true gerbils, although their assignment to the subfamily Gerbillinae is questioned. Besides a number of features, *Epimeriones* differs from *Pseudomeriones* in its very different geographic range and also in its association with much more wooded environments.

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Keywords: Rodentia, Muroidea, Gerbillidae, Miocene, Pliocene

INTRODUCTION

In 1973, Hans de Bruijn published the first evidence of a fossil gerbil in Western Europe, in the form of a first lower molar of Gerbillidae indet. from the early Ruscinian of Gorafe 1 (Guadix-Baza Basin; de Bruijn 1974). This was one of the first strong evidences demonstrating the existence of faunal exchanges between Northern Africa and the Iberian Peninsula during the Messinian. Later on, new quotations of gerbils in several late Miocene and early Pliocene localities in Southern and Eastern Spain confirmed this faunal exchange: Salobreña, Alcoy, Almenara M, etcetera (Aguilar *et al.* 1984; Agustí 1989; Agustí 1991). The diversity of gerbil taxa also increased and thus a number of different genera and species were recognised in the

Spanish record: *Protatera*, *Myocricetodon*, *Calomyscus*, *Pseudomeriones*, *Epimeriones*, *Debruijnimys*.

At the same time, it has become increasingly clear that the presence of gerbils in Western Europe does not correspond to a single, isolated event, but that it was the consequence of a rather complicated process. In this paper we present an updated report on the taxa recorded so far in the European basins.

SUBFAMILY MYOCRICETODONTINAE

This subfamily, originally included among the cricetids, can be now regarded as a sort of 'stem group' for gerbils, assembling all those taxa which still retain a bunodont, brachyodont

dental pattern close to the Megacricetodontines. The inclusion of the Myocricetodontines within the Gerbillidae saved the monophyly of this family. However, and taking into account the two other subfamilies of gerbils, Gerbillinae and Taterillinae, the 'stem' character of the Myocricetodontinae clearly places them as a paraphyletic taxon, in which taxa are assembled on the basis of archaic shared characteristics (symplesiomorphic characteristics), instead of derived ones (synapomorphic characteristics). In this way, it appears that the various genera included within the subfamilies Gerbillinae and Taterillinae originated independently from different myocricetodontine genera, through quick processes of increasing hypsodonty and full development of lophodonty. The extant genera *Calomyscus* and *Mystromys*, once regarded as African cricetids, are now better placed among this group of archaic gerbils. The myocricetodontine record in Europe is restricted to the genera *Myocricetodon* and *Calomyscus*.

The first citation of *Myocricetodon* on the northern shores of the Mediterranean comes from the fissure infilling of Salobreña, in Southern Spain (province of Granada, Aguilar *et al.* 1984). Later, a second fissure infilling, Almenara M (= Casablanca M) provided an abundant population of *Myocricetodon* (Agustí 1991). A third mention of this genus in Spain comes from the locality of Pino Mojón, in the Guadix-Baza Basin (Sesé 1989). The record of this species in Pino Mojón is important since it is the first case in which the European myocricetodontines are not reported from fissure infillings but from a stratigraphical section that can be placed in the stratigraphical context of a basin.

However, the best representation of *Myocricetodon* comes from the locality of Almenara M. In this site, an abundant sample confirms the presence of a small sized *Myocricetodon* species in which the dominant morphotypes resemble *Myocricetodon parvus* in a number of features: double anterocone, persistence of longitudinal ridge and absence

of a lingual cuspule between the protocone and the hypocone. However, a number of teeth present a more derived morphology, in which the longitudinal ridge is lost and/or a lingual cuspule is present in the upper first molars, thus approximating the pattern observed in *M. seboui*. 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 (Jaeger 1977).

The population of Almenara M is also significant since it presents a much more northerly position than Salobreña and Pino Mojón (Guadix-Baza Basin). Salobreña is in the extreme south of the Granada province, on the southern Mediterranean coast of Spain. Its closeness to Africa would suggest an easy settlement of Southern Spain by these gerbils. However, this is not the case for Almenara M, on the eastern coast of Spain, about 500 km N. of Salobreña. From even further north are the few teeth of *Myocricetodon* sp. from the localities of Castelnou-3 and Font Estremar, in the Roussillon Basin (southern France, Aguilar *et al.* 1991). Therefore, the dispersal of this group of archaic gerbils was not restricted to Southern Spain, but they expanded far to the north, up to Southern France.

A second myocricetodontine genus, *Calomyscus*, is usually present in Northwestern Mediterranean localities joining *Myocricetodon*. *C. bailwardi*, the mouse-like hamsters, and another four species today represent *Calomyscus*. Nowadays they inhabit the steppes and arid rocky mountain slopes of Iran, Afghanistan, South Russia and Pakistan. Like *Myocricetodon*, it is present in a number of late Miocene-early Pliocene localities like Salobreña, Almenara M and with some doubt also in Font Estremar (Aguilar *et al.* 1984; Agustí 1989; Agustí 1991; Aguilar *et al.* 1991). However, and in contrast with *Myocricetodon*, *Calomyscus* is also present in the Eastern Mediterranean, represented by the

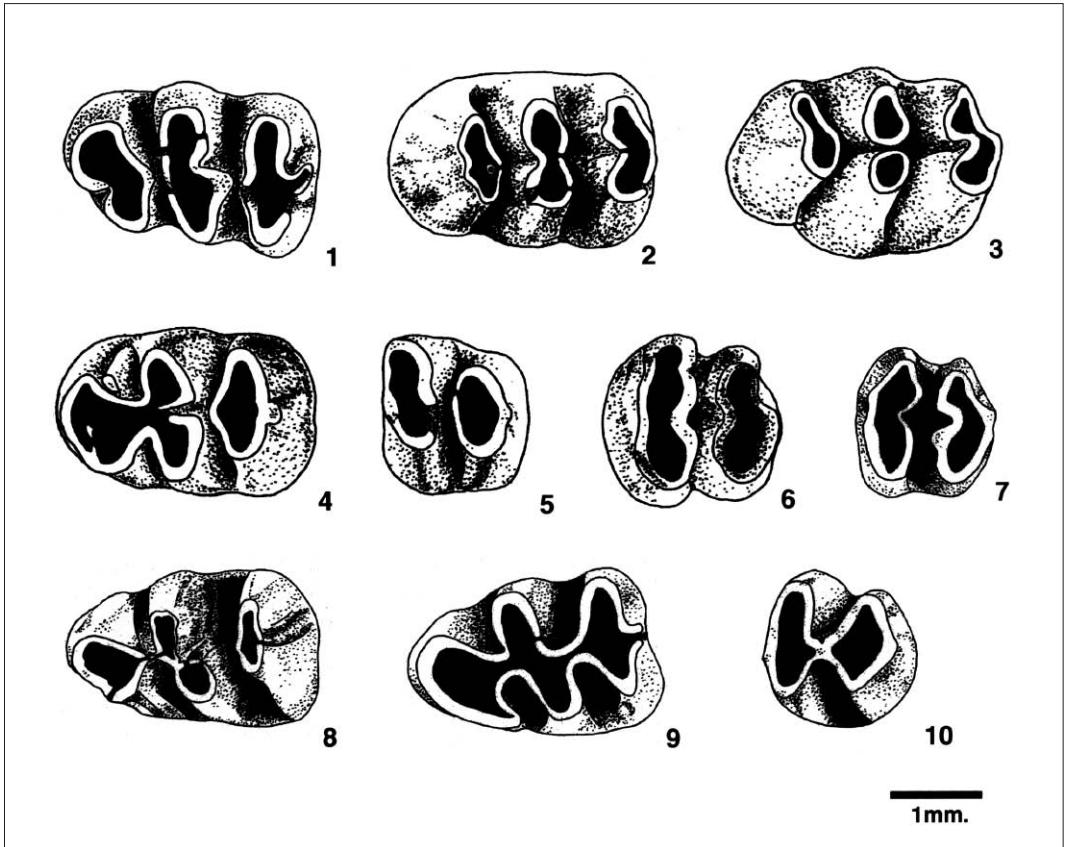


Figure 1. Some dental elements of Neogene gerbils. **1**: m1 of *Protatera almenarensis* from Almenara M; **2**: M1 of *Protatera almenarensis* from Almenara M; **3**: M1 of *Debruijnimys julii* from Asta Regia (reversed); **4**: m1 of *Debruijnimys julii* from Asta Regia (reversed); **5**: m2 of *Debruijnimys julii* from Asta Regia; **6**: M2 of *Debruijnimys julii* from Asta Regia; **7**: M2 of *Debruijnimys* sp. from Alcoy 4B (reversed); **8**: m1 of *Debruijnimys* sp. from Alcoy 4B; **9**: m1 of *Debruijnimys* sp. from Alcoy 4B; **10**: m2 of *Debruijnimys* sp. from Alcoy 4B.

species *C. minor* from the early Pliocene of Rhodes (de Bruijn *et al.* 1970). The oldest member of this lineage is *C. delicatus* from Salobreña. This is also the smallest species of the genus, which still retains a number of features that relate it to the Myocricetodontines, such as the possession of a cusped anteroconid in m1. The specimens recovered from Almenara M can probably be referred to this species, although they are placed in an intermediate position between the dimensions of *C. delicatus* and *C. minor*.

SUBFAMILY TATERILLINAE

This subfamily includes taxa with a molar pattern consisting of parallel ridges that are

not connected by a longitudinal spur. Nowadays, they are represented by larger gerbils of the genus *Tatera* and other smaller gerbils of the genera *Taterillus*, *Desmodillus* and *Gerbillurus*. The first description of a Miocene representative of this lineage was made by Jaeger (1977), who defined the new genus and species *Protatera algeriensis*, from the late Miocene (Turolian) of Amama 2 (Algeria). He proposed this species to be the ancestor of the living species of *Tatera*, the larger gerbils that today inhabit savannahs, desert and steppes of Southern and Eastern Africa and South Western Asia. After *P. algeriensis*, several *Protatera*-like taxa were subsequently described from different localities

Table 1 Distribution of characters in selected Neogene Taterillinae (*Abudhabia*, *Protatera*, *Debruijnimys*) from Western Eurasia and Northern Africa. ++ frequent; + present; (+) rare; - absent; characters: **1** m1 Anteroconid-Protoconid connection; **2** m1 Protoconid-Hypoconid connection; **3** Posterolophid present in m1; **4** Anterolophid present in m2; **5** Posterolophid present in m2; **6** m2 Protoconid-Hypoconid connection; **7** Anterolophid present in m3; **8** M1 Anterocone-Protocone connection; **9** M1 Protocone-Hypocone connection; **10** Anterolophe present in M2; **11** M2 Protocone-Hypocone connection; **12** M2 Paracone-Metacone connection; **13** Reduced Hypocone-Metacone complex in the M3.

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>A. baynunensis</i>	-	-	++	++	+	-	+	+(-)	-	+	-	-	+
<i>A. yadangensis</i>	+	-	++	+	+	-	+	+/-	-	+	-	-	+
<i>A. kabulensis</i>	-(+)	-	-(+)	+	+	-(+)	+	-(+)	-(+)	-(+)	-(+)	-(+)	+/-
<i>P. algeriensis</i>	-	-	-(+)	+	+	-	+	-	-	-	-	-	-
<i>D. almenarensis</i>	-(+)	-(+)	+	-	-	-	-	-(+)	-	+(-)	-	-	+
<i>D. julii</i>	++	+	+	-	-	-	-	-(+)	-	-(+)	-(+)	-(+)	+
<i>D. davidi</i>	++	+	-(+)	-	-	+/-	-	+/-	-(+)	-	-	+(-)	+

in Spain, Northern Africa, Arabia and Afghanistan, leading to a profusion of genera and species. In order to clarify the relationships between these taxa, a character analysis among the different genera and species has been developed. The distribution of characteristics is summarised in Table 1.

Abudhabia DE BRUIJN & WHYBROW, 1994

The species *Abudhabia baynunensis* DE BRUIJN & WHYBROW, 1994 is certainly the most archaic member of the subfamily, its dental morphology being very close to that of some advanced myocricetodontine species like *Myocricetodon magnus* JAEGER (1977). Archaic features in the lower molars include the retention of a well-developed posterolophid in m1 and m2 and the anterolophid in the m2 and m3. In the M1, the anterocone is often connected to the protocone, while the M2 retains a small anteroloph. De Bruijn & Whybrow (1994) also assigned the species *Protatera kabulense* SEN (1983) to this genus. However, this species presents a more derived dental morphology and lacks several of the archaic features present in *Abudhabia baynunensis*. In contrast, the character association of *Protatera kabulense* seems much closer to *Protatera algeriensis* than to *Abudhabia baynunensis* (see Table 1). Thus, common to *P. algeriensis* and *P. kabulense*

are the retention of the anterolophid, the very weak or absent posterolophid, the isolated protocone, the reduction of the anterolophid in the M2 and the relatively large M3. This association of characters is only seen in these two species, but not in *Abudhabia baynunensis* or in the species of *Debruijnimys* CASTILLO & AGUSTÍ, 1996. It turns out, therefore, that *Protatera algeriensis* and *Protatera kabulense* are more straightforwardly related with respect to other gerbil species.

Protatera JAEGER, 1977

The type species of this genus, to which most of the European and Asian large gerbils have been referred, is *Protatera algeriensis* from the Turolian beds of Amama 2 in Algeria. This is a large Taterillinae lacking most of the primitive features found in *Abudhabia*. For instance, the posterolophid is very reduced or absent in the lower molars, while in the M1 the anterocone is an isolated cusp. However, in contrast with these advanced features, the lower m2 and m3 still retain the anterolophid. Another peculiar feature of *Protatera algeriensis* is a relatively unreduced M3. This combination of derived upper molars and relatively primitive lower molars suggests an intermediate position between *Abudhabia* and the dental morphology seen in the extant *Tatera*, supporting the ideas of Jaeger (1977),

who placed this species in the ancestry of the latter genus.

Besides *Protatera algeriensis*, other species referred to *Protatera* have been *Protatera yadangiensis* MUNTHE, 1987, *Protatera kabulense* SEN, 1983, *Protatera almenarensis* AGUSTÍ, 1991, and *Protatera davidi* GERAADS, 1998. Based on the new material collected by a joint team of the University of Benghazi and the Institute of Paleontology M. Crusafont (Sabadell; unpublished material), the species *Protatera yadangiensis* from Sahabi (Libya; Munthe, 1987) is included in the genus *Abudhabia*, since its morphology closely fits that of *A. baynunensis* in the retention of most of the primitive characteristics mentioned for this species (see Table 1). However, the anteroconid is connected to the protoconid in several specimens of *P. yadangiensis*, a feature that is not found in *Abudhabia baynunensis* and weakly developed in *Protatera kabulense*.

After the description of *Protatera kabulense* by Sen (1983), the genus *Abudhabia* was defined by de Bruijn & Whybrow (1994) to house this species and the archaic *Abudhabia baynunensis*. However, as argued in the last paragraph, *Protatera kabulense* presents a more derived dental morphology and lacks several of the archaic features present in *Abudhabia baynunensis* (see Table 1). In contrast, the character association of *Protatera almenarensis* does not support a close relationship between this species and *Protatera algeriensis*. *Protatera almenarensis* retains the posterolophid in the m1, but in the m2 and m3 the anterolophid is absent. In the upper molars, the M2 still retains a small anteroloph, while the M3 is more reduced than in *Protatera algeriensis* and *Protatera kabulense*. A trend towards developing a longitudinal spur between the anteroconid and the protoconid is observed in some teeth. This suggests an independent origin, directly from *Abudhabia baynunensis* or a closer species. As we will discuss in the next paragraph, there is even stronger evidence favouring the exclusion of the species *P. davidi*

from the genus *Protatera*.

***Debruijnimys* CASTILLO & AGUSTÍ, 1996**

This genus was included within the Gerbillinae by Wessels (1998) because of the presence of a longitudinal spur in the lower molars. However, as we will argue in the following paragraph, we do not think that this feature can be used as a diagnostic characteristic, since it probably evolved independently in a number of gerbil lineages. In the case of *Debruijnimys*, its upper and lower molar morphology is much closer to Taterillinae like *Abudhabia* or *Protatera* than to the true Gerbillinae like *Gerbillus* or *Meriones*. As stated, partial development of a connection between the anteroconid and the protoconid is seen in some archaic Taterillinae, and is fully expressed in *Debruijnimys*. In the most archaic members of *Debruijnimys* (from Alcoy), a low ridge appears connecting the base of the anteroconid to the metaconid or, in some cases, the protoconid to the hypoconid (these connections being fully apparent only in worn specimens). *Debruijnimys julii* CASTILLO & AGUSTÍ, 1996 from the middle Pliocene of the Jerez Basin is one of the youngest representatives of this genus. A number of findings in the early Pliocene of southern Spain usually reported as Gerbillidae indet. or *Protatera* sp. are likely to be included in this genus: Alcoy, Caravaca, Gorafe, Botardo and others. This includes the original Gerbillidae indet. of Gorafe-1 of de Bruijn (1974). The material from Alcoy is smaller and presents a number of archaic features that are already lost in the type species *Debruijnimys julii*. This material, therefore, belongs to a different, more archaic species within the genus.

A similar situation is found with *Protatera davidi*, from the Late Miocene/Early Pliocene of Lissasfa (Casablanca, Morocco). This species bears a longitudinal spur between the anteroconid and the protoconid and between the protoconid and the hypoconid. In contrast, the upper molars resemble *Protatera* and *Debruijnimys* in lacking any longitudinal

ridge. The lower molars have lost the anterolophids and the posterolophids. This character association relates this species more to *Debruijnimys* than to *Protatera*. With respect *Debruijnimys julii*, *Protatera davidi* is remarkably smaller, and therefore appears as a more archaic species. However, in contrast with the Spanish species, the posterolophid is weakly developed in m1 and it bears a better-developed posterior connection between the protoconid and the hypoconid-entoconid complex.

Regarding the origin of *Debruijnimys*, an ancestor-descendant relationship between *Debruijnimys* species and *Protatera almenarensis* seems difficult to accept, since the latter taxon is larger and has certain derived features which are absent in the oldest representatives of *Debruijnimys* (for instance, the very large anteroconid, in contrast with the reduced anteroconid seen in *Debruijnimys* sp. from Alcoy and in *D. davidi* from Lissasfa). However, according to a number of shared characteristics, *P. almenarensis* appears closer to *Debruijnimys* than to any other gerbil. The opposite hypothesis, that is, the possibility that an archaic *Debruijnimys* species would be in the ancestry of *P. almenarensis*, is more plausible, but in this case we face a 'reversed' chronology. Thus, typical *P. almenarensis* has been found in the Zorreras Formation of the Sorbas Basin (Martín-Suárez *et al.* 2000), which is correlated with the late Messinian. In contrast, all the *Debruijnimys* material so far found has proven to be Early Pliocene in age (or even Middle Pliocene, in the case of *Debruijnimys julii* from the Jerez Basin). Probably, the origin of *Debruijnimys* lies directly in a primitive species of *Abudhabia*, most probably *A. yardangiensis* from Sahabi.

SUBFAMILY GERBILLINAE

The only European genera tentatively assigned to this subfamily are *Pseudomeriones* and *Epimeriones*. As stated, we exclude the genus *Debruijnimys* from the Gerbillinae, which we consider more closely related to

Taterillinae such as *Abudhabia* and *Protatera*. *Epimeriones* also has been excluded from the gerbils by some authors (Tong 1989; Wessels 1998), by considering this genus as a case homoplasy within a group of unknown, hypsodont, gerbil-like late Miocene cricetids. However, we do not find any reason to exclude *Epimeriones* from the gerbils, while maintaining *Pseudomeriones* within them. The main difference lies on the peculiar geographic distribution of *Epimeriones*, which is basically a Western Eurasian dweller (Agustí 1989). Both genera, *Pseudomeriones* and *Epimeriones*, are basically Eurasian taxa, never having been recovered from an African site. Both also differ from other gerbils in their precocious first appearance in the early late Miocene of Europe.

Pseudomeriones SCHAUB, 1934

The species *Pseudomeriones abbreviatus* was originally described by Teilhard de Chardin (1926) from the King-Yan-Fou beds of Kansu (China). However, *Pseudomeriones* appears as one of the most widely distributed gerbil genus of the Neogene since, besides Inner Mongolia, its geographical range also covers Afghanistan, Turkey, Greece and Spain (where a tooth of *Pseudomeriones* sp. was recovered from Almenara M; Agustí 1989). In contrast to other gerbils, *Pseudomeriones* apparently never entered the African continent.

In comparison to other gerbils, *Pseudomeriones* appears as an unusually old gerbillinae. The oldest members of the genus have been reported from the late Vallesian-early Turolian beds of Dendil, Karaözü and Kaleköy in Turkey (Sümenen *et al.* 1990), and from the middle Turolian of Samos (*P. pythagoresi*, Black *et al.* 1980). In fact, *Pseudomeriones* appears as a typical dweller of the late Miocene Greek-Iranian bioprovince, its presence in Western Europe being restricted just to the Messinian levels of eastern Spain (Almenara M). Curiously, *Pseudomeriones* sp. from Almenara M fits the morpho-

hology of the original Chinese species *P. abbreviatus*, while this genus exhibits a considerable degree of specific variation in the Greek-Iranian bioprovince (*P. pythagoresi* in the late Miocene of Samos, *P. rhodius* de Bruijn, Dawson & Mein, 1970 in the early Pliocene of Maritsa, Rhodes, and *P. tchaltensis* SEN, 1977 in the early Pliocene of Çalta, Turkey).

Epimeriones DAXNER-HÖCK, 1972

The assignment of this genus to the family Gerbillidae has been questioned mainly by Tong (1989) and followed by Wessels (1998). However, Tong recognises "une forte ressemblance de ses molaires avec celles du genre *Meriones*" and also the presence of grooved incisors. Its exclusion from the Gerbillidae is based on some archaic dental features, such as the persistence of posterolophid in the m1 and the less reduced m3, but these are characteristics that are also present in other fossil gerbil genera (see Table 1). These features would also exclude *Pseudomeriones* from the Gerbillidae. Common to *Epimeriones* and *Pseudomeriones* and the typical gerbillines is the development of a longitudinal ridge in the lower molars. However, other data strongly suggests that *Epimeriones*, like *Pseudomeriones*, are not true Gerbillinae, and have to be included in a different subfamily. Thus, a characteristic feature of most Gerbillinae, the paracone-metacone connection in the M1 is absent in these Neogene genera.

But in fact, what really distinguishes *Epimeriones* from other Neogene gerbils are external features, dealing with its chronology, biogeography and paleoecology. Regarding its chronology, *Epimeriones* appears in the European fossil record much earlier than any other gerbil (*Epimeriones austriacus* from the early Turolian of Eichkogel; Daxner-Höck 1972). However, its range expands up to the Middle Pliocene of Poland (*Epimeriones progressus* KOWALSKI, 1974) from Kroczyce and the latest Pliocene of Roumania (*Epimeriones* sp. from Betfia-XIII; Terzea

1978).

Another peculiar feature of *Epimeriones* is its geographical range, almost entirely restricted to Eastern and Central Europe (Austria, Poland, and Romania). In Western Europe, two teeth have been reported in the late Turolian of Lissieu. Quite surprisingly, it appears abundantly represented in the late Turolian of Can Vilella, in La Cerdanya, an intramountainous basin in the Catalan Pyrenees. In contrast with other Miocene gerbils, apparently *Epimeriones* seems absent from the Greek-Iranian province, Asia and, of course, Africa.

The peculiar zoogeographic distribution of *Epimeriones* probably lies in the different ecological requirements of this genus with respect to other gerbil genera. If we just consider the closely related *Pseudomeriones*, it appears associated at Almenara M to *Stephanomys* aff. *ramblensis*, *Occitanomys adroveri*, *Apodemus* aff. *gudrunae*, *Paraethomys miocaenicus*, *Apocricetus* aff. *alberdiae*, *Ruscinomys lasallei*, *Blancomys* sp., "*Protatera*" *almenarensis*, *Myocricetodon* cf. *parvus*, *Calomyscus* sp. and *Eliomys truci*. The abundance of *Stephanomys* aff. *ramblensis*, *Protatera almenarensis*, *Myocricetodon* cf. *parvus* and the presence of *Ruscinomys lasallei* and *Blancomys* sp. in Almenara M strongly suggest very arid, (sub)desertic conditions. However, in the almost coeval levels of Can Vilella, in the Pyrenees, *Epimeriones* appears associated with *Apodemus* aff. *gudrunae*, *Kowalskia* aff. *lavocati*, *Eozapus* aff. *intermedius*, *Muscardinus vireti* and *Paragilirulus lissiensis*.

The presence of forest indicators like *Muscardinus vireti* and *Paragilirulus lissiensis*, the very different murid and cricetid composition of the fauna, lacking typical xeric Iberian elements like *Stephanomys*, *Occitanomys* and *Ruscinomys*, strongly suggest a very different, wooded habitat from that occupied by *Pseudomeriones*.

CONCLUDING REMARKS

According to the character association from Table 1, we propose the following generic re-assignment of the Western European gerbil species:

Genus *Abudhabia*

- A. baynunensis*
- A. yardangiensis*

Genus *Protatera*

- P. algeriensis*
- P. kabulense* (provisionally, may belong to a separate genus of its own).

Genus *Debruijnimys*:

- Debruijnimys* sp. (Alcoy),
- D. davidi*
- D. julii*
- D. almenarensis* (tentatively).

The chronology of the gerbil dispersals around the Messinian is not yet fully understood, although work in progress in the Librilla section (Fortuna, Murcia) will clarify this aspect in the next few years. However, what clearly appears is the existence of at least two distinct waves of colonisation of the Northwestern Mediterranean basins. The first wave is best represented by the fissure infillings of Salobreña and Almenara M, and involved the entry of a number of taxa of Asian origin, such as *Pseudomeriones* sp., *Calomyscus* minor, *Protatera almenarensis*, *Blancomys* sp. Despite the Asian character of these faunas, in Salobreña there are also some taxa of undoubtedly African affinities, such as *Protolophiomys*. A Middle Eastern origin for these faunas, as suggested by Moyà-Solà *et al.* (1984), would explain the coexistence of both Asian and African species in these faunas.

In contrast to the main Asian character of the faunas from Salobreña and Almenara M, the second wave of gerbil immigrants was probably of African origin, as deduced from the close relationship between *Debruijnimys*

julii and some Northern African taxa like *Abudhabia yardangiensis* from Sahabi and *Debruijnimys davidi* from Lissasfa. The age of this second wave is probably late Messinian, since *Debruijnimys* is usually found in early Pliocene, Ruscian levels, persisting in Southern Spain up to the middle Pliocene.

ACKNOWLEDGEMENTS

We acknowledge Dr Hans de Bruijn (Utrecht) for providing a set of casts of *Abudhabia baynunensis*. We also acknowledge helpful comments by O. Fejfar and W. Wessels. This paper has been supported by the project BOS2001-1044 of the Spanish Ministry of Science and Technology.

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Received 22 June 2001

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM
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