

Gerbillidae from the Miocene and Pliocene of Europe

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With 4 figures, 3 plates, 2 tables and 2 appendixes

Abstract

In this paper the distribution of Miocene and Pliocene Gerbillidae in Europe is described. It appears that only a few species of this family were present for only a short period of time (Upper Miocene-Lower Pliocene). The European Gerbillidae are related to forms from North Africa and Asia Minor and are thought to have immigrated in, at least, two waves during the Upper Miocene and Lower Pliocene into Europe.

Kurzfassung

In dieser Arbeit wird die Verbreitung von miozänen und pliozänen Gerbillidae in Europa besprochen. Nur wenige Arten dieser Familie traten für einen kurze Zeitraum auf. Die europäischen Gerbillidae sind mit nordafrikanischen und kleinasiatischen Arten verwandt. Es wird angenommen, daß sie in mindestens zwei Wellen während des Obermiozäns und Unterpliozäns nach Europa eingewandert sind.

Introduction

Only a few Gerbillidae species from the Miocene of Europe are recorded in the literature until now. The family seems to be of minor importance in the Miocene fauna's of Europe and moreover most of these genera and species were present for only a short time (appendix 1). However the species found in the European Miocene are part of a complex story of evolutionary history, with migrations, dispersions, extinctions and many uncertain origins.

First a general overview of the family is given, followed by a short introduction into the taxonomy, after which, in more detail, an overview of the three subfamilies is given with emphasis on fossil occurrences (only cheek teeth) especially those from Europe. Possible migration routes during and after the Messinian used by the European Gerbillidae are given at the end of this chapter.

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The Family Gerbillidae

The family Gerbillidae¹ (Table I) is represented by 16 extant genera and many species which occur mainly in (semi-)desert environments in Africa, the Arabian Peninsula and Asia. Extant Gerbillidae are not known from Europe. Some species are very well known because they are popular as pets (Internet: Gerbil Information Page) or used for laboratory research (*Meriones unguiculatus*) or are considered to be a plague, damaging and destroying crops and undermining irrigation works by their intensive burrowing and spreading diseases (*Tatera*, *Rhombomys*) (PRAKASH, 1975; NOWAK, 1991). Gerbillidae make simple or complex burrow systems for protecting their offspring or creating shelters against the dry and hot climate. Most of them are granivorous and some also insectivorous (PRAKASH, 1975; MUSSER & CARLETON, 1991; NOWAK, 1991). Gerbillidae are modified for terrestrial plains or desert life, they have a tendency for the hind limbs to be lengthened and the tail is normally fully haired. The cheek teeth are extremely hypsodont in progressive species, with continuously growing teeth in very specialised forms (*Rhombomys*). The cusps form transverse laminae which are separated by inner and outer folds (sinuses and sinusids). In primitive forms the teeth are not always separated into laminae (and are cuspidate), the sinuses are weaker and each lamina bears clear traces of two cusps (except the anterocone which has only one cusp). The M^3 is reduced (absent in *Desmodilliscus*), often cylindriform. The posterior lamina on M_3 is usually absent. The incisors may have a single groove, a faint double groove or be smooth. The outer enamel layers of the incisors are relatively thin compared to other muroids (ELLERMAN, 1941; MUSSER & CARLETON, 1991).

The family is divided into the subfamilies Myocricetodontinae, Taterillinae and Gerbillinae.

Taxonomy

Several papers concerning research on extant and fossil members of the Gerbillidae are listed in MUSSER & CARLETON (1991), many authors studied cytogenetic-, chromosomal-, biochemical-, anatomical-, physiological-, and fossil data.; a few examples are LAY (1972), TONG (1989) and BENAZZOU et al. (1984). These studies resulted in several taxonomical classifications of the Gerbillidae, between which large differences exist in the number of extant species (88-110), subspecies, subgenera or subfamilies (ELLERMAN, 1941; CHALINE et al., 1977; TONG, 1989; PAVLINOV et al., 1990; MUSSER & CARLETON, 1991; NOWAK, 1991). TONG (1989, page 110) concluded after combining the results of several research methods that a comprehensive taxonomical division of the Gerbillidae is impossible, but that the results illustrate the diverse patterns in the evolution of several characters.

In this paper we mainly deal with fossil material which largely consists of cheek teeth. The classification used in Table I² is therefore a classification in which morphology of the skull and cheek teeth are main elements. The classification of extant Gerbillinae from ELLERMAN (1941), who gives clear and consistent descriptions of extant genera and species, is extended with information on fossil Gerbillinae from a.o. CHALINE et al. (1977), TONG (1989) and WESSELS (1996).

¹ The ancestral group of this family lies probably in the Myocricetodontinae, therefore the family name should be Myocricetodontidae (WESSELS, 1996). But according to the International Code of Zoological Nomenclature the family name has to be Gerbillidae in agreement to the principle of priority.

² *Epimeriones* DAXNER-HÖCK (1972) (from the Miocene and/or Pliocene of Central Europe and Spain) is not included in the Gerbillidae (see DE WEERD et al., 1977; TONG, 1989).

Table I: The family Gerbillidae

Subfamily Myocricetodontinae LAVOCAT 1961

- Mystromys*³ WAGNER 1841
*Calomyscus*³ THOMAS 1905
*Myocricetodon*² LAVOCAT 1952
*Zramys*² JAEGER, MICHAUX & DAVID 1973
*Dakkamys*² JAEGER 1977a
*Mellalomys*² JAEGER 1977a
*Shamalina*² WHYBROW et al. 1982
*Punjabemys*² LINDSAY 1988
*Aïssamys*² COIFFAIT 1991
*Sindemys*² WESSELS 1996

Subfamily Taterillinae CHALINE, MEIN & PETTER 1977

- Tatera*³ Lataste 1882
*Taterillus*³ THOMAS 1910b
*Gerbillurus*³ SHORTRIDGE 1942
*Protatera*² JAEGER 1977b
*Abudhabia*² DE BRUIJN & WHYBROW 1994

Subfamily Gerbillinae ALSTON 1876

- Gerbillus*³ DESMAREST 1804
*Meriones*³ ILLIGER 1811
*Psammomys*³ CRETZCHMAR 1828
*Pseudomeriones*² SCHAUB 1934
*Rhomboomys*³ WAGNER 1841
*Pachyuromys*¹ LATASTE 1880
*Ammodillus*¹ THOMAS 1904
*Desmodillus*¹ THOMAS & SCHIWANN 1904
*Microdillus*¹ THOMAS 1910a
*Desmodilliscus*¹ WETTSTEIN 1917
*Brachiontes*¹ THOMAS 1925
*Sekeetamys*¹ ELLERMAN 1947
*Mascaromys*² TONG 1986
*Eulmus*² AMEUR 1991
*Debruijnimys*² CASTILLO & AGUSTI 1996

¹ only extant² only fossil³ extant and fossil

The most important characteristics for differentiating the genera in ELLERMAN (1941) are based on cranial- and cheek teeth characters as well as length and shape of the tail. For the skull and mandible these are: mandible with or without a coronoid process; size of mastoids and bullae; size and shape of the palatal foramina; size and shape of the zygomatic plate and shape of the skull (size of the frontals, size and shape of the rostrum). For the cheek teeth these are: ever growing or with roots; upper incisors: plain or grooved; hypsodont or bunodont; laminae with or without the original cusps; prismatic laminae; absence/presence of a third lower molar and absence/presence of a longitudinal crest.

A schematic overview of the characteristics of the extant and fossil Gerbillidae genera can be found in TONG (1989). Since then more fossil genera have been described. Table II gives

characteristics of the genera known from Miocene and/or Pliocene localities. Only cheek teeth characters are used, since these are usually the only fossil material available.

Characterisation of cheek teeth-elements on subfamily level

Myocricetodontinae

presence of a 'normal' or 'new' longitudinal crest in most alternating cusps
cingula usually present
 M_3 still has 2 'lobes'
accessory cusp(s) on lingual edge M^1

Taterillinae

strong reduction or absence of a longitudinal crest
cusps in rows (laminae)
reduction of the cingula
strong reduction of M^3 and M_3

Gerbillinae

development of a 'new' longitudinal crest
alternating cusps and/or cusps in rows (laminae)
reduction of the cingula
strong reduction of M^3 and M_3

Subfamily Myocricetodontinae

Myocricetodontinae are mainly known from the fossil record, its only extant members are *Calomyscus bailwardi* and *Mystromys albicaudatus*. The oldest Myocricetodontinae described until now is *Sindemys*³ from the upper Lower Miocene of Pakistan (WESSELS, 1996). A primitive species still with a „normal“ longitudinal crest and a mesoloph(id). A more primitive, but yet

Table II: Characteristics of Miocene and Pliocene Gerbillidae genera

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
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in almost (all) specimens

in some specimens

1 only M_1

in many specimens

none

2 only M_2

in 50%

unknown

3 often weakly developed

³ *Primus* (Murree FM, Early Miocene of Pakistan, DE BRUIJN et al., 1981) is possibly a member of the Myocricetodontinae, but more material and research is needed on this genus to determine its family rank.

undescribed, myocricetodontine is known from Keşköy (MN3, Turkey). In the Middle Miocene several Myocricetodontinae genera appeared (WESSELS, 1996). Some genera had a large geographical and stratigraphical distribution, for example *Myocricetodon* was present (Fig.1) for a long timespan in Pakistan (Sehwan and Potwar Plateau), North Africa (The Maghreb) and Namibia (Otavi Mountains) and for a short period of time in Turkey (Yeni Eskihisar), Kenya (Fort Ternan), Spain (Almenara-M) and France (La Tour). Not only *Myocricetodon* shows a wide geographical range of occurrences, *Mellalomys* and *Dakkamys* appear in Middle and Upper Miocene deposits of Pakistan, North Africa and probably Namibia (South Africa). Other Myocricetodontinae genera were successful (long time span) but did not migrate to other areas: *Zramys* is only known from the Middle and Late Miocene of North Africa (Appendix II). At the end of the Miocene almost all Myocricetodontinae vanished from the fossil record (except *Calomyscus*) and by then the first members of the Taterillinae had appeared in North Africa.

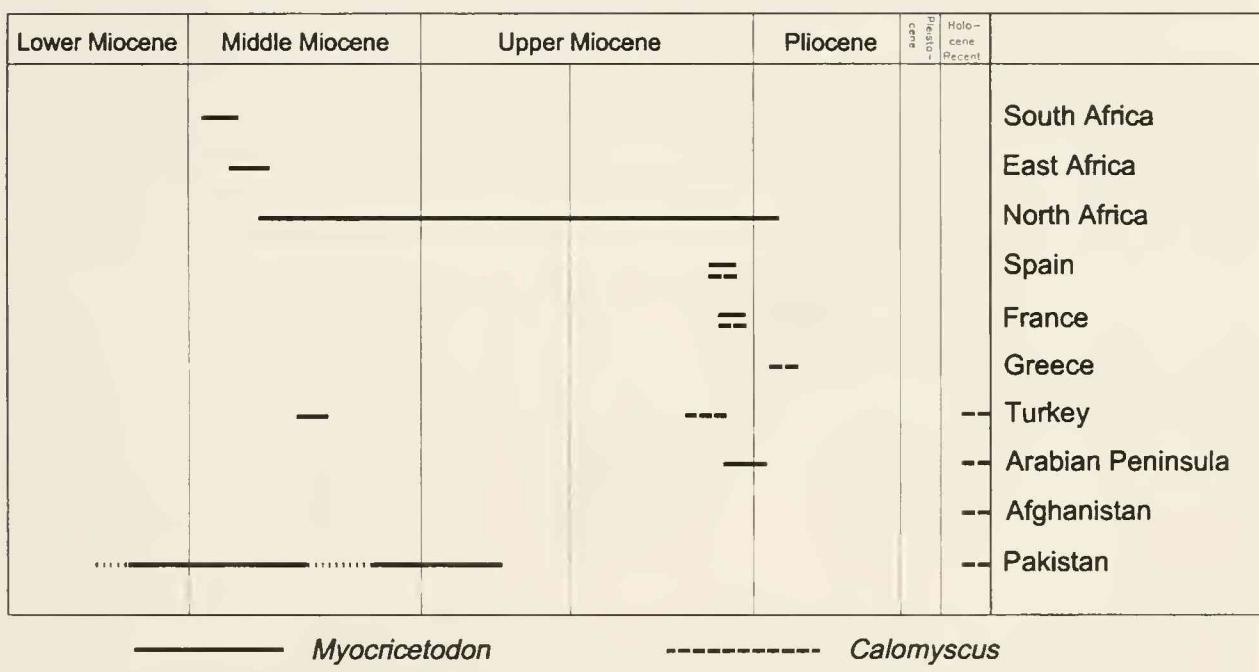


Figure 1: Distribution of Myocricetodontinae: *Myocricetodon* and *Calomyscus*

Longitudinal connections

1 - 'normal' longitudinal crest; 2 - 'normal' longitudinal crest but oblique; 3 - 'normal' longitudinal crest absent (upper molars); 4 - 'normal' longitudinal crest absent (lower molars); 5 - 'new' longitudinal crest, on labial or lingual edge (upper molars); 6 - 'new' longitudinal crest, in centre (upper molars); 7 - 'new' longitudinal crest, oblique (upper molars); 8 - 'new' longitudinal crest, on labial or lingual edge (lower molars); 9 - 'new' longitudinal crest, in centre (lower molars); 10 - 'new' longitudinal crest, oblique (lower molars)

11 - anterolophule (M^1) absent; 12 - anterolophulid (M_1) absent

Placement of the cusps

13 - alternating cusps (upper molars); 14 - alternating cusps (lower molars); 15 - transverse rows of cusps (upper molars); 16 - transverse rows of cusps (lower molars); 17 - strong laminae with cusps still clear; 18 - strong laminae, cusps incorporated

Divers characters

19 - mesoloph(id); 20 - simple anterocone; 21 - paraconus spur; 22 - (most) cingula reduced; 23 - accessory cusps; 24 - high crowned; 25 - M^3 one lobe; 26 - M_3 one lobe; 27 - upper incisors grooved

Myocricetodon is reported from four Upper Miocene South European localities: Salobreña (Plate 1, figs. 1, 2), Almenara-M and Pino Mojón in Spain and La Tour in Southern France. They resemble Moroccan *Myocricetodon* species from Afoud-5 and Lissasfa (GERAADS, 1998b) and probably migrated from Northern Africa into Spain during the Late Miocene.

Myocricetodon species can be divided into two groups (WESSELS, 1996). Group A includes all the species with a (almost) reduced 'normal' longitudinal crest, the tendency of arrangement of the cusps of the cheek teeth in transverse rows and the presence of the simple anterocone in M^1 . *Myocricetodon* species from group A occur in north, east and south Africa, their morphology could be seen as being ancestral to the Gerbillinae and/or Taterillinae (JAEGER 1977, TONG & JAEGER, 1993). Species of *Myocricetodon* group B show a large geographical distribution area: Pakistan, east, north and south Africa, Turkey, the Arabian Peninsula and Spain. The origin and migration pattern of *Myocricetodon* is not clear. Undescribed specimens from Keşköy (MN3, coll. Utrecht) of primitive Myocricetodontinae and from some localities from Namibia (coll. Mein) may give more information in the future.

Calomyscus (Plate 1) is considered to be a member of the Myocricetodontinae (AGUSTÍ, 1989). *Calomyscus* sp. is known from the Upper Miocene from Turkey (Süleimanlı; DE BRUIJN pers. comm.), *Calomyscus* cf. *minor* and *Calomyscus delicatus* from the Upper Miocene of Spain (Salobreña; AGUILAR et al., 1984), *Calomyscus* sp. from the Upper Miocene of France (La Tour; JAEGER & HARTENBERGER, 1989) and *Calomyscus minor* from the Lower Pliocene of Greece (Maritsa; DE BRUIJN et al., 1970). *Calomyscus bailwardi* is the only extant species. The main difference between all the *Calomyscus* species is size. *Calomyscus delicatus* is the smallest,

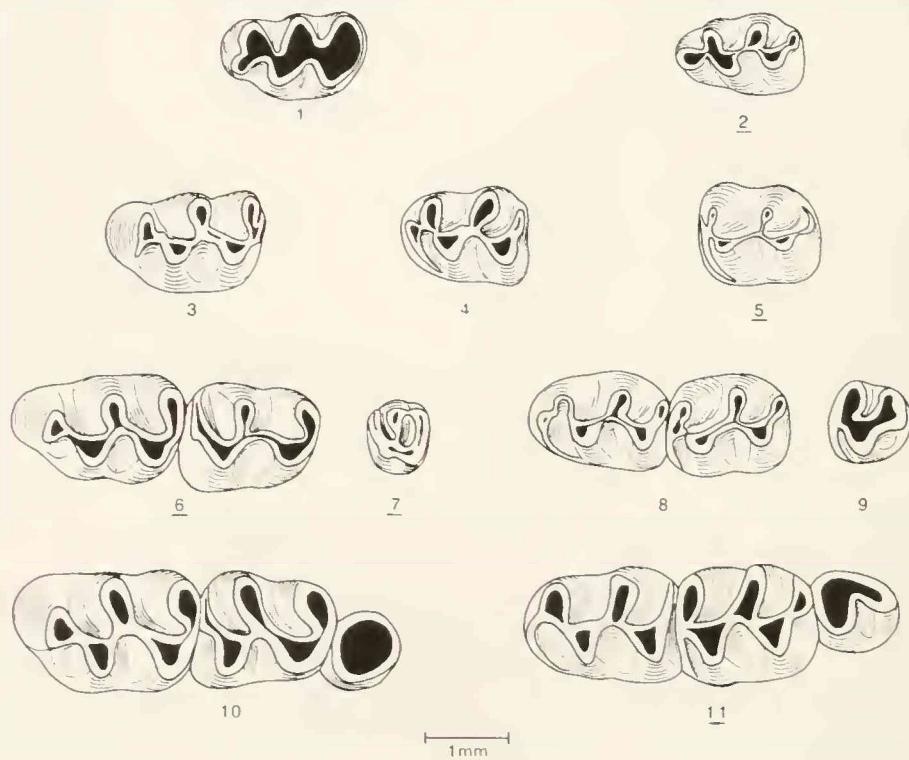


Plate 1: *Myocricetodon* sp. from Salobreña (Spain): fig. 1 M^1 sin (SAL114), fig. 2 M^1 dex (SAL115), AGUILAR et al., 1984.

Calomyscus delicatus from Salobreña (Spain): fig. 3 M^1 (SAL109, holotype), fig. 4 M^1 sin (SAL97), fig. 5 M^1 dex (SAL102), AGUILAR et al., 1984.

Calomyscus minor from Rhodos (Greece): fig. 6 M^{1-2} dex (no 786, holotype), fig. 7 M^3 dex (no 881), fig. 8 M_{1-2} sin (no 640), fig. 9 M_3 sin (no 728), DE BRUIJN et al., 1970.

Calomyscus bailwardi (Recent): fig. 10 M^{1-3} sin (B.M.), fig. 11 M_{1-3} dex (B.M.), DE BRUIJN et al. 1970.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

C. bailwardi the largest. The origin of *Calomyscus*, a myocricetodontine with a simple anterocone (M^1) and a 'normal' longitudinal crest, is unknown. Some (undescribed) Myocricetodontinae from the Middle Miocene of Namibia (MEIN, pers. comm.) show these characters, but whether a relation exists with *Calomyscus* is unclear. The occurrences of *Calomyscus* in Europe and their absence in Africa during the Miocene and Pliocene indicate an (West)Asiatic origin with a dispersal at the end of the Miocene to Europe and Asia Minor. At the present day *Calomyscus bailwardi* is known from Syria, Turkmenistan, Azerbaijan, Iran, Afghanistan and Pakistan. It inhabits elevated areas of 400-3500 metres altitude, between evergreen oaks in monsoonal areas as well as barren scorched hills (NOWAK, 1991).

Subfamily Taterillinae

The origin of the Taterillinae lies probably in a species with a morphology of *Myocricetodon* group A (TONG, 1989; DE BRUIJN & WHYBROW, 1994; WESSELS 1996), these are characterised by the absence (in most specimens) of the longitudinal crest, the tendency to arrange cusps of the cheek teeth in transverse rows and by the presence of a simple anterocone (M^1).

Two genera appear in the upper Miocene (Fig. 2): *Protatera*, who is considered to be the ancestor of *Tatera* (JAEGER, 1977b) and *Abudhabia* (Plate 2), who is a possible ancestral form to *Taterillus* (DE BRUIJN & WHYBROW, 1994).

Protatera algeriensis (Plate 2, figs. 1-6), the oldest Taterillinae described until now is considered to be the ancestral form to *Protatera almenarensis* (Plate 2, figs. 7-12) from the Spanish Upper Miocene localities Almenara-M and Salobreña (AGUSTÍ, 1991). The oldest *Tatera* has been reported from the Lower Pliocene locality of Langebaanweg, South Africa (HENDEY, 1981). Later *Tatera* occurrences have been reported from several Pliocene and Pleistocene localities from East and South Africa (Appendix II). Extant *Tatera* species are common in many regions in Africa. Only one species, *Tatera indicus*, occurs outside of Africa, from Syria to India and Sri Lanka. *Tatera* inhabits grasslands, sandy plains and savannahs, but also woodlands and cultivated areas.

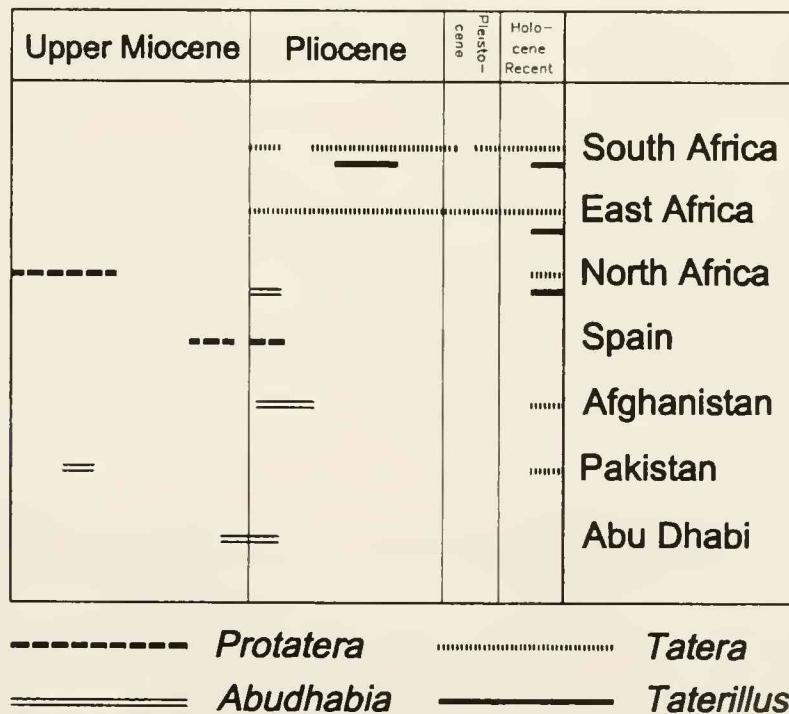


Figure 2: Distribution of Taterillinae: *Protatera*, *Tatera*, *Taterillus* and *Abudhabia*

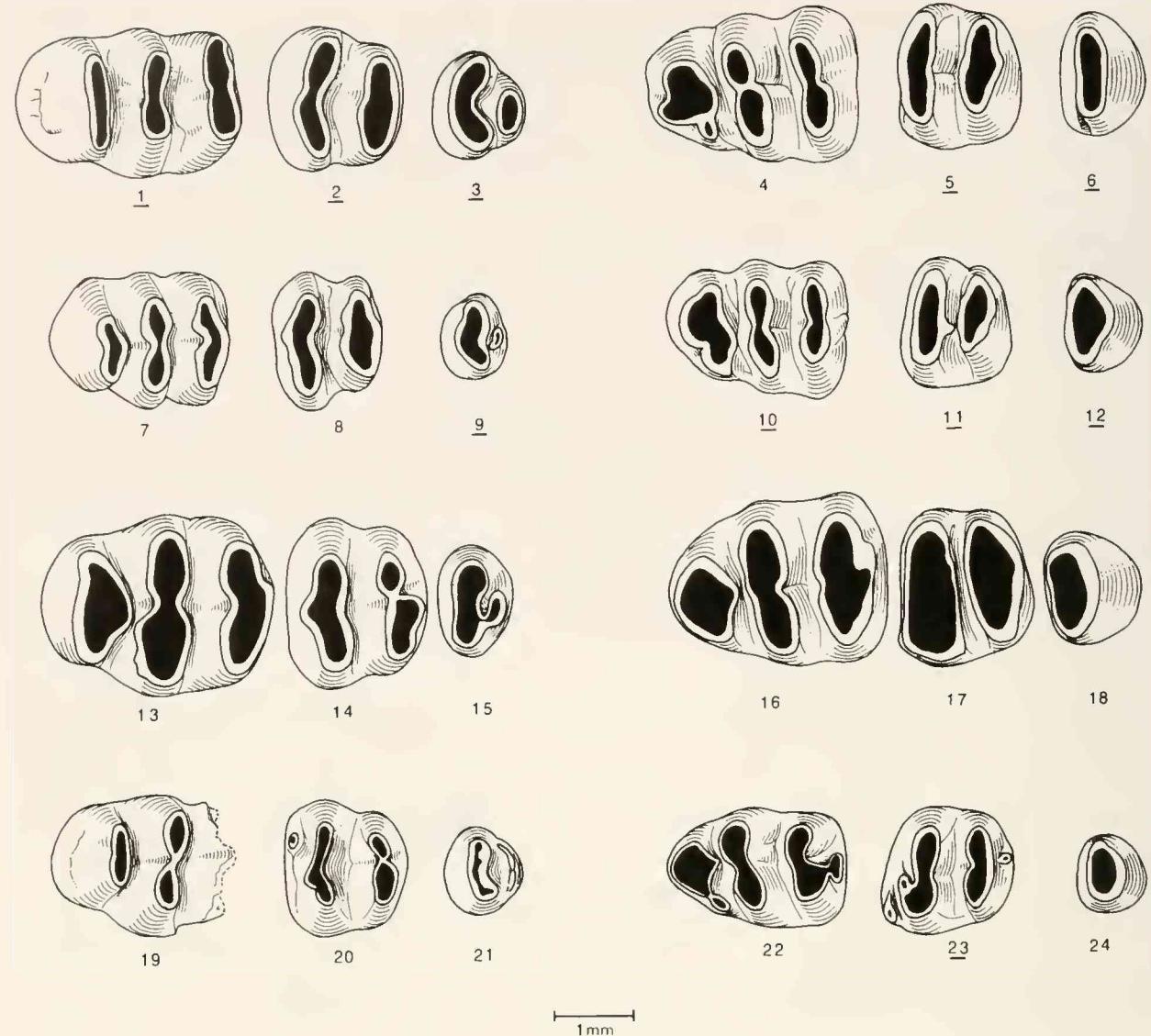


Plate 2: *Protatera algeriensis* from Amama 2 (Algeria): fig. 1 M¹ dex (A2-1, holotype), fig. 2 M² dex (A2-2), fig. 3 M³ dex (A2-3), fig. 4 M₁ sin (A2-5), fig. 5 M₁ dex (A2-4), fig. 6 M₃ dex (A2-7), JAEGER, 1977b.
Protatera almenarensis from Almenara (Spain): fig. 7 M¹ sin (ACS-M-11), fig. 8 M² sin (ACS-M-42), fig. 9 M³ dex (ACS-M-02), fig. 10 M₁ dex (ACS-M-33), fig. 11 M₂ dex (ACS-M-03), fig. 12 M₃ dex (ACS-M-37), AGUSTÍ, 1990.

Abudhabia kabulense from Pul-e Charki (Afghanistan): fig. 13 M¹ sin (AFG211, holotype), fig. 14 M² sin (AFG226), fig. 15 M³ sin (AFG241), fig. 16 M₁ sin (AFG217), fig. 17 M₂ sin (AFG239), fig. 18 M₃ sin (AFG246), SEN, 1983.

Abudhabia baynunensis from Abu Dhabi: fig. 19 M¹ sin (AAM572), fig. 20 M² sin (AAM574), fig. 21 M³ sin (AAM575), fig. 22 M₁ sin (AAM566, holotype), fig. 23 M₁ dex (AAM567), fig. 24 M₃ sin (AAM570), DE BRUIJN & WHYBROW, 1994.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

Protatera sp. from Pliocene deposits of Ibiza Island (Spain, MOYÀ-SOLÀ et al., 1984) is morphologically similar to *Protatera almenarensis* but larger, it must have settled on this island during the Messinian salinity crisis and got subsequently isolated (AGUSTÍ, 1990).

The Gerbillidae indet. from Gorafe 1&4, Caravaca and Botardo C are close to *Protatera*, but more material is needed for an allocation. The taxonomical position of *Protatera davidi* (GERAADS, 1998b) from the Lower Pliocene of Morocco remains uncertain, GERAADS concludes that a new genus seems probable, but more information on Miocene and Pliocene Gerbillidae

is needed (an allocation to the Gerbillinae is a possibility because of the presence of clearly grooved upper incisors in this species).

Abudhabia is known from the Upper Miocene of Pakistan (*Abudhabia* sp.; FLYNN & JACOBS, in press) it represents the oldest occurrence of this genus, it is more primitive in morphology than *Abudhabia kabulensis* (Plate 2, fig 13-18) from the Pliocene of Afghanistan (SEN, in press). *Abudhabia baynunensis* (Plate 2, fig 19-24), from the Upper Miocene from Abu Dhabia (DE BRUIJN & WHYBROW, 1994; DE BRUIJN, in press), seems to be the most primitive form. The geographical distribution of *Abudhabia* (Fig. 2), with the inclusion of the Libyan „*Protatera yardangi*“ is large (DE BRUIJN & WHYBROW, 1994).

Abudhabia can be seen as an ancestor for *Taterillus* (DE BRUIJN & WHYBROW, 1994). Fossil *Taterillus* specimens are reported from the Middle Pliocene of Botswana and Namibia (PICKFORD et al., 1992). Extant *Taterillus* occur only in Africa, they inhabit treeless plains, thorny scrub savannahs, and woodlands.

Subfamily Gerbillinae

The origin(s) of the Gerbillinae probably lies in myocricetodontines with a morphology as found in *Myocricetodon* group A species: with the reduction of the 'normal' longitudinal crest, without accessory cusps and with a simple anterocone. But it is not possible to indicate one specific group or species within the Myocricetodontinae as being ancestral to all Gerbillinae. AGUSTÍ (1991) indicates that the Gerbillinae are possible polyphyletic, the diverse genera of the Gerbillinae were probably derived from different Myocricetodontinae species.

The first Gerbillinae to occur, *Pseudomeriones* (Fig. 3), is reported from the Upper Miocene of Turkey and Afghanistan: *Pseudomeriones latidens* SEN 1998 (Plate 3, figs. 17, 18) (Sherullah and Molayan in Afghanistan; Karaözü and Kaleköy in Turkey). A slightly more evolved species, *Pseudomeriones abbreviatus* (Plate 3, figs 1-6) occurs slightly later in Dendil (Upper Miocene, Turkey). This species is also reported from the upper Miocene and Pliocene of China

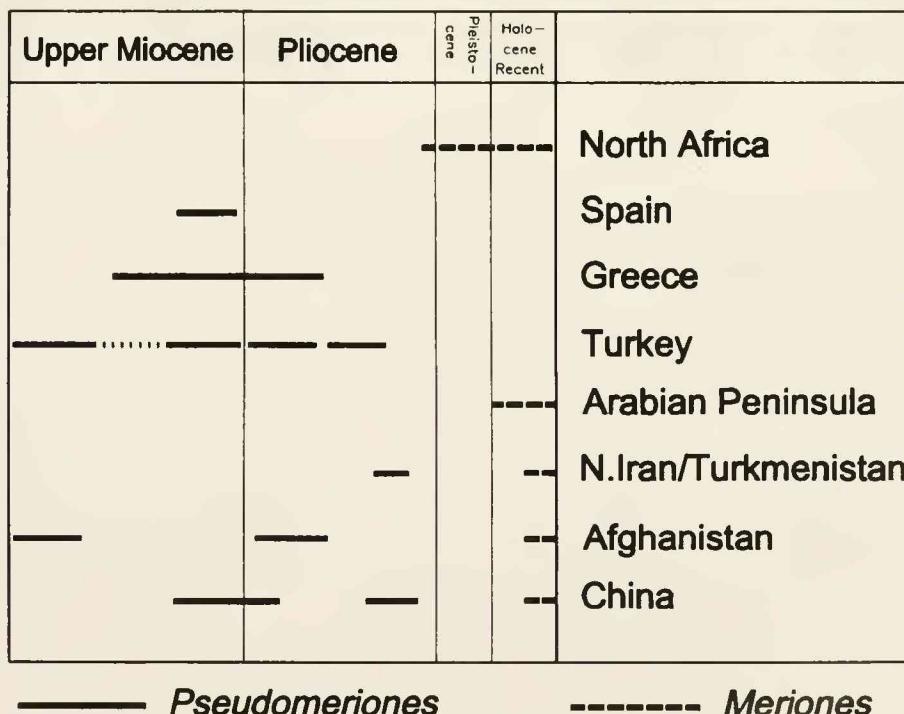


Figure 3: Distribution of Gerbillinae: *Pseudomeriones* and *Meriones*

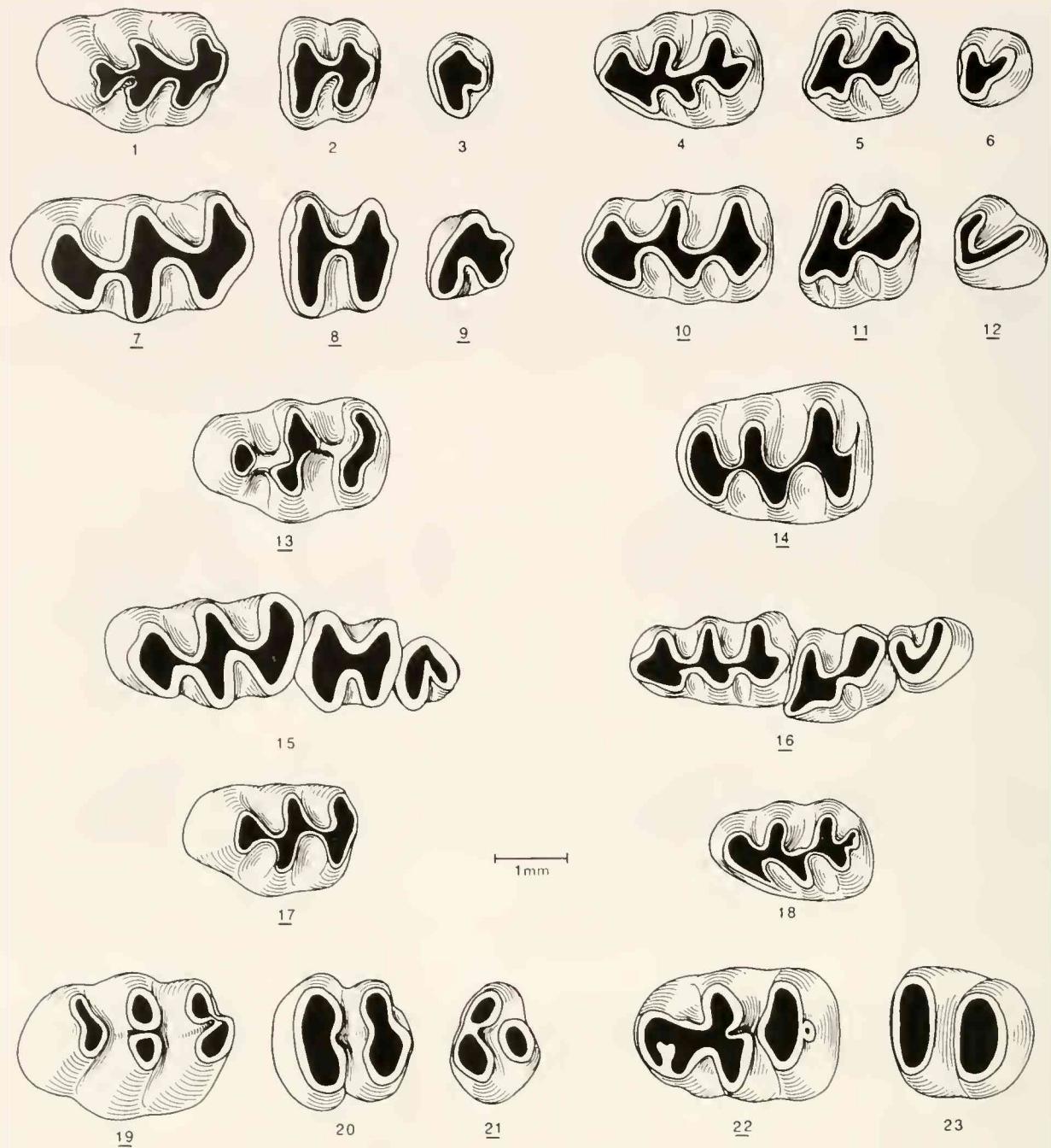


Plate 3: *Pseudomeriones abbreviatus* from Pul-e Charki (Afghanistan): fig. 1 M^1 sin (AFG253), fig. 2 M^2 sin (AFG286), fig. 3 M^3 sin (AFG343), fig. 4 M_1 sin (AFG370), fig. 5 M_2 sin (AFG370), fig. 6 M_3 sin (AFG383), SEN, 1983.

Pseudomeriones rhodius from Rhodos (Greece): fig. 7 M^1 dex (192), fig. 8 M^2 dex (171), fig. 9 M^3 dex (211), fig. 10 M_1 dex (164), fig. 11 M_2 dex (167), fig. 12 M_3 dex (187), DE BRUIJN et al., 1980.

Pseudomeriones pythagorezi from Samos (Greece): fig. 13 M^1 dex (CM36284), fig. 14 M_1 dex (CM36305, holotype), BLACK et al., 1980.

Pseudomeriones tschaltensis from Çalta (Turkey): fig. 15 M^{1-3} sin (ACA917), fig. 16 M_{1-3} dex (ACA974), SEN, 1977.

Pseudomeriones latidens from Molayan (Afghanistan): fig. 17 M^1 dex, fig. 18 M_1 sin, SEN, 1983.

Debruijnomy julii from Asta Regia (Spain): fig. 19 M^1 dex, fig. 20 M^2 sin, fig. 21 M^3 dex, fig. 22 M_1 dex (AR36, holotype), fig. 23 M_2 sin, CASTILLO & AGUSTÍ, 1996.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

(Ertemte, Harr Obo), the Upper Miocene of Spain (Almenara-M) and the Lower Pliocene of Afghanistan (Pul-e Charki). Other *Pseudomeriones* species are *Pseudomeriones pythagorasi* (Plate 3, figs. 13-14) (Upper Miocene of Samos, Greece), *Pseudomeriones rhodius* (Plate 3, figs. 7-12) (Lower Pliocene of Maritsa, Rhodes, Ano Metochi and Monasteri, Greece), and *P. tchaltensis* (Plate 3, figs 15-16) (Upper Pliocene of Turkey). SEN (1983, 1998) and AGUSTÍ (1990) concluded that these species are very specialised and probably had a very limited geographical distribution.

All the *Pseudomeriones* species show a limited geographical and stratigraphical range of occurrence except *Pseudomeriones abbreviatus* which has the largest distribution. *P. latidens* seems to be the most primitive form of *Pseudomeriones* (SEN, in press). A possible evolutionary scenario for *Pseudomeriones* could be the transition of *P. latidens* into *P. abbreviatus* which migrated to China and Europe, where, in separated areas, it could develop into the more specialised forms.

Pseudomeriones is thought to be the ancestral form of *Mascromys* (Uppermost Pliocene and lowest Pleistocene of North Africa) and *Meriones* (TONG, 1989). The oldest *Meriones* comes from the upper Pliocene of North Africa (Aïn Brimba, Tunisia) and the Pleistocene of North Africa (Maghreb). Extant *Meriones* occur mainly in Asia, the Arabian Peninsula and Northern Africa. *Meriones* species live in clay and sandy deserts, low plains, cultivated fields, grasslands and mountain valleys. They can adapt to a wide range of temperature and humidity.

Another member of the Gerbillinae, *Debruijnimus* (Fig. 4 and Plate 3, figs 19-24), is recognised in Pliocene Spanish assemblages (Asta Regia, Bacochas 1, Alcoy, La Gloria 4). Before the gerbillines from Asta Regia (CASTILLO & AGUSTÍ, 1996) were found, the few gerbilline specimens from the Spanish Pliocene were seen as *Protatera* sp. or Gerbillidae indet. (AGUILAR et al., 1983; AGUSTÍ, 1991). The species from Asta Regia, *Debruijnimus julii*, has a longitudinal crest and are therefore not included in the Taterillinae. *Debruijnimus* sp. from Alcoy (Lower Pliocene) seems to be more primitive. CASTILLO & AGUSTÍ (1996) recognised this species also in the North African locality of Aïn Brimba (Upper Pliocene; Gerbillinae indet. TONG, 1989).

All other fossil Gerbillinae are found in Africa (Appendix II): *Gerbillus* in the Middle Pliocene of Botswana, the Upper Pliocene of North Africa (Marocco) and in the Pleistocene of North, East and South Africa. *Eulmus* occurs in the Middle Pliocene of North Africa and

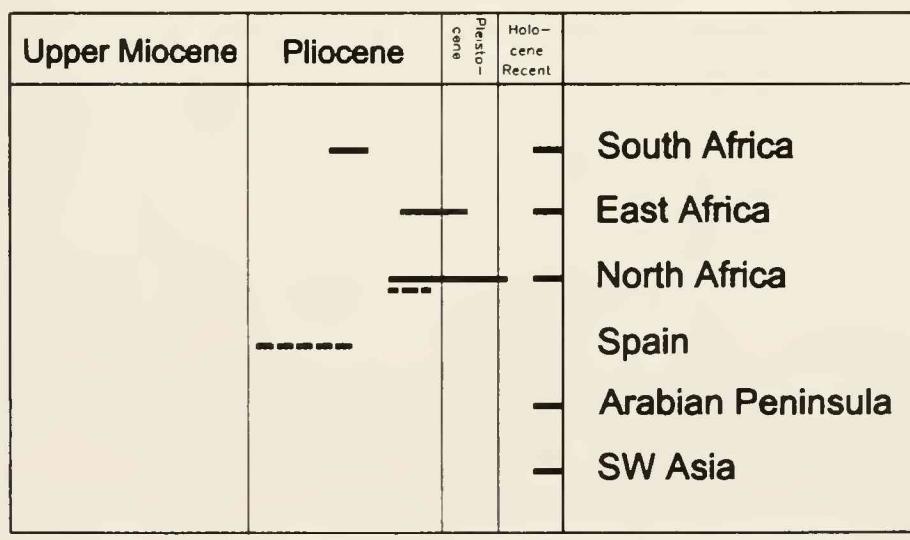


Figure 4: Distribution of Gerbillinae: *Gerbillus* and *Debruijnimus*

Psammomys occurs in the Late Pleistocene of Israel. In the Early Pleistocene of Asia *Rhombomys* is found. The status of '*Gerbillus*' from Celleneuve (France) remains unclear.

Gerbillus, the most prominent extant member of the Gerbillinae, has at least 38 species and occurs in dry biotopes of Africa, the Arabian Peninsula and SW Asia (Fig.4). The origin of *Gerbillus* is not yet understood, fossil *Gerbillus* species are known from Upper Pliocene and Pleistocene deposits from North Africa and Israel respectively. Extant *Psammomys* is found in the Northern Part of Africa and the Arabian Peninsula and inhabits dry country with sometimes only scant vegetation. *Rhombomys* inhabits sandy and clay deserts in the foothills of the mountains of Central Asia.

Migrations of the European Gerbillidae

In North Africa two phases of migration in the upper Miocene are recognised (COIFFAIT, 1991). Rodents with European affinities are found in the localities of Aïn Gueterra (Morocco, BRANDY et al., 1980), La voie Fereé (Tunisia, ROBINSON et al., 1982), Argoub and Kemellal (Algeria, COIFFAIT, 1991) and Afoud (Marocco, BENAMMI, 1997).

The first phase is documented by the arrival of several European species: *Apodemus guadrunae*, *Stephanomys*, *Ruscinomys* and *Prolagus michauxi*. The oldest locality (Afoud 1) is thought to be 6.1 Ma (BENAMMI et al., 1995), so European elements occur in North Africa well before the Messinian. The second phase is documented in the locality of Aïn Gueterra with the presence of *Cricetus barreri*, *Apodemus jeanteti* and *Eliomys truci*. This took place about the Mio-Pliocene transition.

A migration just before the Messinian from North Africa into Spain (Salobreña and Almenara-M; AGUSTÍ, 1991) is documented by *Myocricetodon cf. parvus*, *Protatera almenarensis*, *Protolophiomys* and *Dendromus*. The faunal exchange could have taken place through the Betic-Rif area, which formed a corridor between South-western Europe and Africa at the end of the Miocene (BENAMMI et al., 1995).

Pseudomeriones and *Calomyscus* are also considered to be immigrants into Spain, they occur in Spanish Miocene localities (Salobreña, Almenara-M) and *Calomyscus* also in France (La Tour). These taxa are known from the eastern part of the Mediterranean and probably migrated to western Europe by the northern Mediterranean exchange (GERAADS, 1998a) to France and Spain.

The origin of *Debruijnimus* (Lower Pliocene of Spain, Alcoy) and Gerbillinae indet. in several other Spanish localities is unclear but a migration by the northern Mediterranean exchange seems probable (AGUSTÍ & LLENAS, 1996; GERAADS, 1998a).

In Greece *Pseudomeriones* and *Calomyscus* are both considered to be immigrants from eastern regions (Turkey, Afghanistan).

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References

- AGUILAR, J.-P., L.D. BRANDY & L. THALER (1984): Les rongeurs de Salobreña (sud de l'Espagne) et le problème de la migration Messinienne - Paléobiol. contin., 14(2), 3-17.
- AGUSTÍ, J. (1986): Synthèse biostratigraphique du Plio-Pleistocène de Guadix-Baza (province de Granada, Sud-Est de L'Espagne) - Géobios, 19(4), 505-510.
- AGUSTÍ, J. (1989): On the peculiar distribution of some muroid taxa in the Western Mediterranean - Boll. Soc. Paleont. Ital., 28(2-3). 147-154.
- AGUSTÍ, J. (1990): The Miocene rodent succession in eastern Spain: a zoogeographical appraisal. In: E.H. LINDSAY et al. (Eds.). European Neogene Mammal Chronology. Plenum Press New York, 375-404.
- AGUSTÍ, J. (1991): Gerbillidés fossiles d'Europe occidentale. In: R. CHABAUD (Ed.). Le Rongeur et l'Espace., Le Berre & Guelte, 177-182.
- AGUSTÍ, J. & M. LLENAS (1996): The Late Turolian muroid rodent succession in eastern Spain - Acta zool. Cracov., 39(1): 47-56.
- ALSTON, E. R. (1876): On the classification of the Order Glires - Proc. Zool. Soc. London, 61-98.
- AMEUR, A. (1979): Biochronologie des formations continentales du Néogène et du Quaternaire de l'Oranie. Contribution micromammifères. Thèse de Doctorat de 3e cycle, Univ. Oran, 87 p..
- AMEUR-CHEHBEUR, A. (1991) Un nouveau genre de Gerbillidae (Rodentia, Mammalia) du Mio-Pliocene d'El Eulma, Algérie Orientale - Géobios, 24, 509-512.
- AVERY, D.M. (1995): A preliminary assessment of the micro mammalian remains from Gladysvale Cave, South Africa - Palaeont. Afr., 32, 1-10.
- BENAMMI, M. (in press, 1997): Deux nouvelles espèces de rongeurs dans le Miocène moyen continental du Jebel Rhassoul (Moyen Moulouya, Maroc) - Géobios.
- BENAMMI, M., B. ORTH, M. VIANEY-LIAUD, Y. CHAIMANEE, V. SUTEETHORN, G. FERAUD, J. HERNANDEZ & J.J. JAEGER (1995): Micromammifères et biochronologie des formations néogènes du flanc sud du Haut-Atlas Marocain: implications biogéographiques, stratigraphiques et tectoniques - Africa Geoscience Review, Vol. 2(2), 279-310.
- BENAZZOU, F. & F. ZYADI (1984): Présence d'une variabilité biométrique chez *Gerbillus campestris* au Maroc (Rongeurs, Gerbillidés) - Mammalia, 54: 271-279.
- BERNOR, R.L. (1982): A preliminary assessment of the mammalian biochronology and zoogeographic relationships of Sahabi, Libya - Gar. Sci. Bull., 133-139.
- BIRMAN, A.S., V.I. JEGALLO, L.M. RASTUETAIEV, L.I. KOSASKIY & N.S. CHEVIREVA (1971): Découverte de vertébrés pliocènes dans les dépôts molassiques du Kopet Dagh oriental (en russe) - Bjuulleten Moskovskogo obscchestva, Moscou, 46(2), 99-107.
- BLACK, C.C. & L. KRISHTALKA (1986): Rodents, Bats and Insectivores from the Plio-Pleistocene of sediments to the east of Lake Turkana, Kenya - Contr. Sci. Nat. Hist. Mus. Los Angeles, 372, 1-15.
- BLACK, C.C., L. KRISHTALKA & N. SOLOUNIAS (1980): Mammalian fossils of Samos and Pikermi. Part 1. The Turolian rodents and insectivores of Samos - Ann. Carnegie Mus., 49, 359-378.
- BRANDY, L.D. (1979): Etude de Rongeurs muroïdés du Néogène supérieur et du Quaternaire d'Europe, d'Afrique du Nord et d'Afghanistan. Évolution, biogéographie, corrélations. Thèse 3e. Cycle, Univ. Sc. Tech. Languedoc, 190 pp.
- BRANDY, L.D., M. SABATIER AND J.J. JAEGER (1980): Implications phylogénétiques et biogéographiques des dernières découvertes de Muridae en Afghanistan, au Pakistan et en Éthiopie - Géobios, 13(4), 639-643.
- BRUNET, M., J.P. CARBONNEL, E. HEINTZ & S. SEN (1980): Première découverte de vertébrés dans les formations continentales de Pul-e Charki, bassin de Kabul, Afghanistan. Implications stratigraphiques - Bull. Mus. Natn. Hist. Nat., Paris, 4e ser., 2, sect. C (3), 277-285.
- BRUIJN, DE H. (1974): The Ruscinian rodent succession in Southern Spain and its implications for the biostratigraphic correlation of Europe and North Africa - Senckenberg. Leth., 55(1/5), 435-443.
- BRUIJN, DE H. (1989): Smaller mammals from the Upper Miocene and Lower Pliocene of the Strimon basin, Greece. Part 1. Rodentia and Lagomorpha - Boll. Soc. Paleont. Ital., 28(2-3), 189-195.
- BRUIJN, DE H. (in press): Additional information on the Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. Int. Conf. Fossil Vertebrates of Arabia.
- BRUIJN, H. DE, M. DAWSON & P. MEIN (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). I, II and III - Proc. Kon. Ned. Akad. Wetensch., B 73(5), 535-584.

- BRUIJN, H. DE, S.T. HUSSAIN & J.J.M. LEINDERS (1981): Fossil rodents from the Murree Formation near Banda daud Shah, Kohat, Pakistan - Proc. Kon. Ned. Akad. Wetensch., B **84** (1), 71-99.
- BRUIJN, DE H. & P. WHYBROW (1994): A Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. Proc. Kon. Ned. Akad. Wetensch., B **97**(4), 407-422.
- CARLETON, M.D. & G.G. MUSSER (1984): Muroid rodents. In: ANDERSON, S. & J.K. JONES (Eds.): Orders and families of Recent Mammals of the World. John Wiley New York, 289-379.
- CASTILLO, C. & AGUSTÍ, J. (1996): Early Pliocene rodents (Mammalia) from Asta Regia (Jerez basin, South-western Spain) - Proc. Kon. Ned. Akad. Wetensch., B**99** (1-2), 25-43.
- CHALINE, J., P. MEIN & F. PETTER (1977): Les grandes lignes d'une classification évolutive des Muroidea - Mammalia **41**, 245-252.
- COIFFAIT-MARTIN, B. (1991): Contribution des Rongeurs du Neogene d'Algérie à la Biochronologie Mammaliene d'Afrique Nord-occidentale. Thèse Univ. Nancy-I, 389 p.
- CRETZCHMAR (1828) - Rüpell Atlas, p. 56.
- DAXNER-HÖCK, G. (1972): Die Wirbeltierfauna aus dem Alt-Pliozän (Pont) vom Eichkogel bei Mödling (Niederösterreich), IV: Gerbillinae (Rodentia, Mammalia) - Ann. Naturhist. Mus. Wien., **76**, pp. 143-160.
- DENYS, C. (1983): Les rongeurs du Pliocène de Laetoli (Tanzanie). Evolution, paléoécologie et paléobiogéographie. Approche qualitative et quantitative. Thèse 3e cycle, Univ. Paris VI, 492 p.
- DENYS, C. (1991): Un nouveau rongeur *Mystromys pocockei* sp. nov. (Cricetidae) du Pliocène inférieur de Langebaanweg (Région du Cap, Afrique du Sud) - C. R. Acad. Sci., ser 2, **313**, 1335-1341.
- DESMAREST (1804) - Nouv. Dict. Hist. Nat., **24**, Tab. Méth., p. 22.
- ELLERMAN, J.R. (1941): The families and genera of living rodents. Vol II. Trustees of the British Museum (N.H.) London, 690 p.
- ELLERMAN, J.R. (1947): A key to the Rodentia inhabiting India, Ceylon and Burma, based on collections in the British Museum - Journ. Mamm., **28**, 249-278; 357-387.
- FAHLBUSCH, V., QIU ZHUDING & G. STORCH (1983): Neogene mammalian faunas of Ertemte and Harr Obo in Nei Mongol, China - Scient. Sin., ser. B, **26**(2), 205-224.
- FLYNN, L.J & L.L. JACOBS (in press): Late Miocene small mammal faunal dynamics: the crossroads of the Arabian Peninsula. Int. Conf. Fossil Vertebrates of Arabia.
- GERAADS, D. (1993): Rongeurs et insectivores (Mammalia) du Pliocène final de Ahl al Oughlam (Casablanca, Maroc) - Géobios, **28**(1), 99-115.
- GERAADS, D. (1998a): Biogeographic relations of North African Pliocene rodents - Paleogeogr., Palaeoclimat., Palaeoecol., **137**, 273-288
- GERAADS, D. (1998b): Rongeurs du Mio-Pliocène de Lissasfa (Casablanca, Maroc) - Géobios, vol. **31**(2), 1998.
- HAAS, G. (1966): On the vertebrate fauna of the lower Pleistocene site Ubeidiya. Publication of the Israel Academy of Science and Humanities, Jerusalem, 68 p.
- HEISSIG, K. (1982): Kleinsäuger aus einer obermiozänen (Vallesium) Karstfüllung Ägyptens - Mitt. Bayer. Staatslg. Paläont. hist. Geol. **22**, 97-101.
- HENDEY Q.B. (1981): Paleoecology of the Late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context - Ann. S. Afr. Mus., Cape Town, **84** (1), 1-104.
- ILLIGER (1811): Prodr. Syst. Mamm.. Av., XVIII + 301pp., Berlin (Salfeld).
- JAEGER, J.-J. (1977a): Rongeurs (Mammalia, Rodentia) du Miocène de Beni Mellal - Palaeovertebrata, **7** (4), 91-125.
- JAEGER, J.-J. (1977b): Les Rongeurs du Miocène moyen et supérieur du Maghreb - Palaeovertebrata, **8** (1), 1-164.
- JAEGER, J.-J. & J.L. HARTENBERGER (1989): Diversification and extinction patterns among Neogene perimediterranean mammalia - Phil. Trans. R. Soc. Lond., B **325**, 401-420.
- JAEGER, J.-J., J. MICHAUX & B. DAVID (1973): Biochronologie du Miocène moyen et supérieur continental du Maghreb - C.R. Acad. Sc. Paris, sér D, **277**, 2477-2480.
- LATASTE, F. (1880) - Le Naturaliste Paris, I, p.313.
- LATASTE, F. (1882): Mammifères nouveaux d'Algérie (suite) - Le Naturaliste, Paris, 107-109.
- LAVOCAT, R. (1952): Sur une faune de mammifères Miocènes découverte à Beni-Mellal (Atlas Marocain) - C.R. Acad. Sc. Paris, **235**, 189-191.

- LAVOCAT, R. (1965): In: LEAKY L.S.B., Ed., Olduvai Gorge 1951-1961. Vol I: Fauna and Background, 17-18, Cambridge University Press, London.
- LAVOCAT, R. (1961): Le gisement de vertébrés Miocène de Beni-Mellal (Maroc.) - Notes et Mémoires du service géol. Maroc., 155, 52-67.
- LAVOCAT, R. (1978): Rodentia and Lagomorpha. In: MAGLIO, V.J. & H.B.S. COOKE (Eds). Evolution of African Mammals. Harvard Univ. Press, Cambridge, 69-89.
- LAY, D.M. (1972): The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents - J. Morphology, 138(1), 41-120.
- LI, C. W. WU & Z. QIU (1984): Chinese Neogene: subdivision and correlation - Vert. Palasiat., 22 (3), 163-178.
- LINDSAY, E.H. (1988): Cricetid rodents from Siwalik deposits near Chinji Village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae - Paleovertebrata, 18 (2), 95-154.
- MEIN, P., E MOISSENET & R. ADROVER (1990): Biostratigraphie du Néogène supérieur du basin de Teruel - Paleont. Evol., 23, 121-139.
- MOYÀ-SOLÀ, S., J. AGUSTÍ & J. PONS (1984): The Mio-Pliocene insular faunas from the West Mediterranean origin and distribution factors - Paleobiol. Continent., 14(2), 347-357.
- MUNTHE, J. (1987): Small-mammal fossils from the Pliocene Sahabi Formation of Libya. In: N.T. BOAZ, A. EL-ARNAUTI, A. WAHID GAZIRY, J. DE HEINZELIN & D. DECHANT BOAZ (Eds). Neogene paleontology and geology of Sahabi. Liss, New York, 135-144.
- MUSSER, G.G. & M.D. CARLETON (1993): Family Muridae. In: D.E. WILSON & D.M. REEDER (Eds). Mammal species of the World. A taxonomic and geographic reference. 2d edition. Smithsonian Institution Press, 501-756.
- NOWAK, R.M. (1991): Walker's Mammals of the world. Fifth edition. J. Hopkins Univ. Press, London, 1629 p.
- PAVLINOV, I.YA, YU. A. DUBROVSKY, O.L. ROSSOLIMO & E.G. POTAPOVA (1990): (Gerbils of the world). Nauka, Moscow, 368 p.(in Russian).
- PICKFORD, M. & P. MEIN (1988): The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana - C.R. Acad. Sci. Paris, 307, Sér. II, 1681-1686.
- PICKFORD, M., P. MEIN & B. SENUT (1992): Primate bearing Plio-Pleistocene cave deposits of Humpata, Southern Angola - Hum. Evol., 7(1), 17-33.
- POCOCK, T.N. (1987): Plio-Pleistocene fossil mammalian microfauna of southern Africa - a preliminary report including description of two new fossil Muroid genera (Mammalia: Rodentia) - Paleontologia Africana, 26, 69-91.
- PRAKASH, I. (1975): The population ecology of the rodents of the Rajasthan Desert, India. In: I. PRAKASH & P.K. GOSH (Eds.). Rodents in desert environments. Junk, the Hague, 75-116.
- QUI, Z. (1988): Neogene micromammals of China. In: P. WHYTE (Ed.). The Palaeoenvironment of East Asia from the Mid-Tertiary. Proc. 2nd Conf. Centre Asian Stud., Univ. Hong Kong, 834-848.
- ROBINSON, P., C.C. BLACK, L. KRISHTALKA & M. R. DAWSON (1982): Fossil small mammals from the Kechabta Formation, Northwestern Tunisia - Ann. Carnegie Mus., 51(12), 231-249.
- SABATIER, M. (1982): Les Rongeurs du site Pliocène à Homonidés de Hadar (Ethiopie) - Paleovertebrata, 12(1), 1-56.
- SCHAUB, S. (1934): Über einige fossile Simplicidentaten aus China und der Mongolei - Abh. Schweiz. Pal. Ges., 54, 1- 40.
- SEN, S. (1977): La faune de Rongeurs Pliocène de Çalta (Ankara, Turkey) - Bull. Mus. Natn. Hist. Nat., Paris (3), 465, Sci. Terre, 61, 89-172.
- SEN, S. (1983): Rongeurs et Lagomorphes du gisement Pliocène de Pul-e Charki, bassin de Kabul, Afghanistan - Bull. Mus. Natn. Hist. Nat., 4 ser., section C (1), 33-74.
- SEN, S. (in press): Rodents and Insectivores from the Late Miocene of Malayan in Afghanistan.
- SENUT, B., M. PICKFORD, P. MEIN, G. CONROY & J. VAN COUVERING (1992): Discovery of 12 new Late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia - C.R. Acad. Sci. Paris, 314, Sér. II, 727-733.
- SESÉ, C. (1989): Micromammíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada) - Trabajos Neogeno-Cuaternario, 11, 185-213.
- SHORTRIDGE, G.C. (1942): Field notes on the first and second expeditions to the Cape Museum's mammal survey of the Cape Province; with descriptions of some new subgenera and subspecies - Annals S. Afr. Mus., 36, 27-100.

- SÜMENGEN, M., E. ÜNAY, G. SARAC, H. DE BRUIJN, I. TERLEMEZ & M. GÜRBÜZ (1990): New Neogene rodent assemblages from Anatolia (Turkey). In: E.H. LINDSAY et al. (Eds.). European Neogene Mammal Chronology, Plenum Press, NY, 61-72.
- TCHERNOV, E. & R. CHETBOUN (1984): A new genus of gerbillid rodent from the early Pleistocene of the Middle East - J. Vertebrate Paleont., 4(4), 559-569.
- TEILHARD DU JARDIN, P. (1926): Mammifères du Tertiaire de Chine et de Mongolie - Ann. Pal., Paris, 15, 1-51.
- THOMAS, O. (1904) - Ann. Mag. Nat. Hist., 7(14), p.104.
- THOMAS, O. (1905) - Abstr. Proc. Zool. Soc. London, 24, p. 23.
- THOMAS, O. (1910a): New African Mammals - Ann. Mag. Nat. Hist., 8(5), p. 197.
- THOMAS, O. (1910b): Notes on African rodents - Ann. Mag. Nat. Hist., 9(2), 227-234.
- THOMAS, O. (1925): On the mammals (other than Ruminants) collected by Captain Angus Buchanas during his second Saharan Expedition - Ann. Mag. Nat. Hist., 9(16), p. 548.
- THOMAS, O. & H. SCHWANN (1904): On a collection of mammals from the British Namaqualand, presented to the National Museum by Mr. C.D. Rudd - Proc. Zool. Soc. London, 1904(1): 171-183.
- TOBIEN, H. (1975): Rodentia und Lagomorpha aus dem Känozoikum der Türkei. In: SICKENBERG et al.: Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogenstratigraphie - Geol. Jb, 15, 121-124.
- TONG, H. (1986): The Gerbillinae (Rodentia) from Tighennif (Pleistocene of Algeria) and their significance - Modern. Geol. London, 10, 197-214.
- TONG, H. (1989): Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord - Mém. Soc. Géol. France, 155, 1-120.
- TONG, H. & J.-J. JAEGER (1993): Muroid rodents from the Middle Miocene Fort Ternan Locality (Kenya) and their contribution to the phylogeny of Muroids - Palaeontographica, A 229, 51-73.
- WAGNER, J.A. (1841) - Gel. Anz. K. Bayer. Akad. Wiss. München, XII (52), p. 421.
- WEERD, VAN DER A., R. ADROVER, P. MEIN & D. SORIA (1977): A new genus and species of the Cricetidae (Mammalia, Rodentia) from the Pliocene of Southwestern Europe - Kon. Ned. Akad. Wetensch., B, 80 (5), 429-439.
- WESSELMAN, H.B. (1984): The Omo micromammals. Systematics and paleoecology of early man sites from Ethiopia. In: M.K. HECHT & F.S. SZALAY, Eds. Contributions to Vertebrate evolution, 219 p.
- WESSELS, W. (1996): Myocricetodontinae from the Miocene of Pakistan - Proc. Kon. Ned. Akad. Wetensch., 99(3-4), 253-312.
- WESSELS, W., E. ÜNAY & H. TOBIN (1987): Correlation of some Miocene faunas from Northern Africa, Turkey and Pakistan by means of Myocricetodontinae - Proc. Kon. Ned. Akad. Wetensch., B 90(1), 65-82.
- WETTSTEIN (1917) - Denkschr. Akad. Wiss. Wien., 94, p. 115.
- WHYBROW, P.J., M.E. COLLINSON, R. DAAMS, A.W. GENTRY & H.A. MCCLURE (1982): Geology, fauna (Bovidae, Rodentia) and flora from the early Miocene of eastern Saudi Arabia - Tertiary Research, 4(3), 105-120.
- YOUNG, C.C. (1927): Fossile Nagetiere aus Nord-China - Pal. Sin., C, 5(3), 1-82.

Appendix I: Occurrences of Gerbillidae in Europe

LOCALITIES IN SPAIN	MN zone / age	SPECIES
Asta Regia	MN 15	<i>Debruijnimus julii</i>
Bacochas 1	MN 13/14	<i>Debruijnimus julii</i>
La Gloria 4	MN 14	<i>Debruijnimus julii</i>
Alcoy	MN 14	<i>Debruijnimus</i> sp.
Ibiza (Ses Fontanelles)	MN 14	<i>Protatera</i> sp.
Gorafe 1&4	MN 14	<i>Gerbillidae</i> indet.
Botardo C	MN 13/14	<i>Gerbillidae</i> indet
Caravaca	MN 13/14	<i>Gerbillidae</i> indet.
Pino Mojón	MN 13	<i>Myocricetodon</i> aff <i>parvus</i>
Salobreña	MN 13	<i>Calomyscus</i> cf. <i>minor</i>
Almenara-M (Casablanca-M)	MN 13	<i>Protatera</i> sp. <i>Myocricetodon</i> aff. <i>parvus</i> <i>Calomyscus delicatus</i> <i>Protatera almenarensis</i> <i>Myocricetodon</i> sp. <i>Pseudomeriones abbreviatus</i>
LOCALITIES IN FRANCE	MN zone / age	SPECIES
Celleneuve	MN 14	" <i>Gerbillus</i> "
La Tour	MN 13	<i>Myocricetodon</i> sp. <i>Calomyscus</i> sp.
LOCALITIES IN TURKEY	MN zone/ age	SPECIES
Çalta	MN 15	<i>Pseudomeriones tchaltensis</i>
Iódeli	MN 14	<i>Pseudomeriones</i> sp.
Suleimanlı	MN 13	<i>Calomyscus</i> sp.
Dendil	MN 10	<i>Pseudomeriones</i> cf. <i>abbreviatus</i>
Karaözü	MN 10	<i>Pseudomeriones</i> cf. <i>latidens</i>
Kaleköy	MN 10	<i>Pseudomeriones</i> cf. <i>latidens</i>
Yeni Eskihisar	MN 7/8	<i>Myocricetodon eskihisarensis</i>

AUTHOR(S)	COLLECTION
CASTILLO & AGUSTÍ (1996)	UGS
SESÉ (1989); CASTILLO & AGUSTÍ (1996)	NMS
MEIN et al. (1990); CASTILLO & AGUSTÍ (1996)	NMS
CASTILLO & AGUSTÍ (1996)	CSS
MOYÀ-SOLÀ et al. (1984)	CSS
DE BRUIJN (1974); AGUSTÍ (1986)	UUN
AGUSTÍ (1989); AGUSTÍ (1991)	CSS
AGUSTÍ (1989); AGUSTÍ (1991)	CSS
SESÉ (1989)	NMS
AGUILAR et al. (1984); AGUSTÍ (1991)	UMF

AGUILAR et al. (1984); AGUSTÍ (1991) CSS

AUTHOR(S)

JAEGER & HARTENBERGER (1989)	UMF
JAEGER & HARTENBERGER (1989)	UMF

AUTHOR(S)

SEN (1977); SEN (1983)	MTA
SÜMENGEN et al. (1990)	MTA
DE BRUIJN pers. comm.	UUN
SÜMENGEN et al. (1990)	MTA
SÜMENGEN et al. (1990)	MTA
SÜMENGEN et al. (1990)	MTA
WESSELS et al. (1987)	MTA

LOCALITIES IN GREECE	Mn zone / age	SPECIES	AUTHOR(S)	
Maritsa (Rhodos) <i>Calomyscus minor</i>	MN 14	<i>Pseudomeriones rhodius</i>	DE BRUIJN et al.(1970); SEN (1983)	UUN
Kalithies	MN 14	<i>Pseudomeriones</i> sp.	DE BRUIJN (1989); BLACK et al. (1980)	UUN
Ptolomais (Lower FM, sect. 6)	MN 13/14	<i>Pseudomeriones</i> sp.	DE BRUIJN per. comm.	UUN
Monasteri	MN 13	<i>Pseudomeriones rhodius</i>	DE BRUIJN (1989)	UUN
Ano Metochi 3	MN 13	<i>Pseudomeriones</i> sp.	DE BRUIJN (1989)	UUN
Samos S3	MN 12	<i>Pseudomeriones pythagorasi</i>	BLACK et al. (1980)	CMU

UUN - Faculty of Earth Sciences, University of Utrecht, the Netherlands

MTA - Maden Tetkik va Arama Enstitüsü, Ankara, Turkey

CMU - Carnegie Museum of Natural History, USA

CSS - Institut de Paleontología AM. Crusafont, Sabadell, Spain

UGS - Department of Stratigraphy and Paleontology of the University of Granada, Spain

UMF - Université des Sciences et Techniques du Languedoc, Montpellier, France

NMS - Museo Nacional de Ciencias Naturales , Madrid, Spain

Appendix II: Fossil occurrences of Gerbillidae in Europe, Africa and Asia

Mystromys

Pliocene-Pleistocene

South Africa

Calomyscus

Upper Miocene-Lower Pliocene

SE Europe

Upper Miocene

SW Europe

Myocricetodon

Upper Miocene

Arabian Peninsula

Upper Miocene

SW Europe

Middle Miocene - Lower Pliocene

North Africa

Middle Miocene

South Africa

Middle Miocene

East Africa

Miocene

Pakistan

Zramys

Middle-Upper Miocene

North Africa

Dakkamys

Middle Miocene

North Africa

Middle-Upper Miocene

Pakistan

Mellalomys

Middle Miocene

North Africa

Lower-Middle Miocene

Pakistan

Shamalina

Lower Miocene

Arabian Peninsula

LAVOCAT (1978); POCOCK (1987); SENUT et al. (1992); DENYS (1991);
AVERY (1995)

DE BRUIJN et al. (1970); SEN (1983)
AGUILAR et al. (1984); JAEGER & HARTENBERGER (1989); AGUSTÍ (1991)

DE BRUIJN & WHYBROW (1994)
AGUILAR et al. (1984); AGUSTÍ (1991); SESÉ (1989);
JAEGER & HARTENBERGER (1989)
JAEGER (1977a,b); BERNOR (1982); HEISSIG (1982); TONG (1989);
COIFFAIT (1991); BENAMMI et al. (1995); GERAADS (1998b)
SENUT et al. (1992)
TONG & JAEGER (1993)
WESSELS et al. (1987); LINDSAY (1988); WESSELS (1996)

JAEGER et al. (1973); JAEGER (1977a,b)
AMEUR (1979); ROBINSON et al. (1982); COIFFAIT (1991); BENAMMI et al. (1995)

JAEGER (1977a); COIFFAIT (1991)
LINDSAY (1988); WESSELS (1996)

JAEGER (1977a); COIFFAIT (1991); BENAMMI et al. (1995); BENAMMI (1997)
LINDSAY (1988); WESSELS (1996)

WHYBROW et al. (1982)

<i>Punjabemys</i>		
Lower-Middle Miocene		Pakistan
<i>Aissaemys</i>		
Middle Miocene		North Africa
<i>Sindemys</i>		
Lower and Middle Miocene		Pakistan
<i>Tatera</i>		
Pliocene-Pleistocene		East Africa
Lower Pliocene-Pleistocene		South Africa
<i>Taterillus</i>		
Upper Pliocene		South Africa
<i>Gerbillurus</i>		
Upper Pliocene-Pleistocene		South Africa
<i>Protatera</i>		
Upper Miocene/ Lower Pliocene		SW Europe
Upper Miocene		North Africa
<i>Abudhabia</i>		
Lower Pliocene		Afghanistan
Lower Pliocene		North Africa
Upper Miocene		Arabian Peninsula
Upper Miocene		Pakistan

LINDSAY (1988); WESSELS (1996)

COIFFAIT (1991)

WESSELS (1996)

LAVOCAT (1965); SABATIER (1982); DENYS (1983); WESSELMAN (1984);
BLACK & KRISHTALKA (1986)
LAVOCAT (1978); HENDEY (1984); PICKFORD & MEIN (1988);
PICKFORD et al. (1992); SENUT et al. (1992); Avery (1995)

POCOCK (1987); PICKFORD & MEIN (1988)

LAVOCAT (1978); SENUT et al. (1992)

AGUILAR et al. (1984); MOYA-SOLÀ et al. (1984); AGUSTÍ (1990)
JAEGER (1977b); COIFFAIT (1991)

SEN (1977)

MUNTHE (1987)

DE BRUIJN & WHYBROW (1994); DE BRUIJN (in press)

FLYNN & JACOBS (in press)

Gerbillus

Upper Pliocene-Pleistocene	North Africa
Upper Pliocene-Pleistocene	East Africa
Middle Pliocene	South Africa

Meriones

Pleistocene	North Africa
Upper Pliocene	Israel

Pseudomeriones

Pliocene	Turkmenistan
Upper Miocene-Pliocene	SE Europe

Upper Miocene-Pliocene

China

Upper Miocene
Upper Miocene

Afghanistan
SW Europe

Desmodillus

Upper Pliocene-Pleistocene

South Africa

Mascromys

Upper Pliocene

North Africa

Eulmus

Upper Miocene-Pliocene

North Africa

Debruijnimus

Pliocene
Pliocene

Spain
North Africa

TONG (1989); GERAADS (1993)
LAVOCAT (1965); WESSELMAN (1984); TONG (1989)
LAVOCAT (1978); PICKFORD & MEIN (1988)

TONG (1989); MEIN & BESANCON (1993)
HAAS (1966); TCHERNOV & CHETBOUN (1984)

BIRMAN et al. (1971)
SEN (1977, 1983); BRUNET et al. (1980); BLACK et al., 1980; DE BRUIJN 1989;
SÜMENGEN et al. (1990)
TEILHARD DU JARDIN (1926); YOUNG (1927); SCHAUB (1934);
FAHLBUSCH et al. (1983); Qiu (1988); LI et al. (1984)
SEN (1983; in press)
AGUILAR et al. (1984); AGUSTÍ (1990, 1991)

AVERY (1995); SENUT et al. (1992)

TONG (1986, 1989)

AMEUR (1991)

SESÉ (1989); CASTILLO & AGUSTÍ (1996); MEIN et al. (1993)
CASTILLO & AGUSTÍ (1996)

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

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