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On Neogene rodents of Eurasia: distribution and migrations

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The most recently published papers dealing with Eurasian rodents were compiled. The importance of dispersal migrations for our understanding of Eurasian faunal dynamics is stressed on the basis of selected rodent taxa. The rodent genera appeared in Asia generally earlier than their European relatives, evidences for the way of migrations. Many migrations may not have been preserved in the fossil record; however, most of them seem to originate in Asia, even if two or three examples show the contrary. Four main dispersal centres (China, Kazakhstan, Pakistan and Anatolia) were important during Neogene times.

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INTRODUCTION

Asian rodents are more diversified than European ones due to the smaller size of the latter area and the smaller latitudinal variation. Therefore, Asia acted as a faunal dispersal centre for Europe during the Neogene; the great majority of the exchanges were migrations from Asia into Europe (as in Paleogene times). Dispersal events from North America or Africa are rare and correlated with important tectonic or eustatic changes. Successful immigration may result in the appearance of new families on the new continent. On the Eurasian continent however, important barriers do not exist and small ecological variations initiate large changes in the distribution of the faunas. Therefore, migrations were numerous and led often to a change on genus level.

The beginning of the Neogene in Asia is difficult to identify. In Europe, the Paleogene-Neogene boundary is characterized in the rodents by the disappearance of the

Theridomyidae and Rhizospalacidae.

Unfortunately, these two families are unknown in Asia, and only geomagnetic data in calibrated sections can mark the beginning of the Neogene, except in Pakistan where the extinction of the Baluchimyinae seems contemporaneous with the Oligocene-Miocene boundary.

Western Europe can be seen as a trap for the East-West immigrants, because of its position at the Western end of the Eurasian continent and its triangular shape. Sometimes the temporal and spatial distribution of some invaders is very small. For example, the genus *Celadensia* is only known from a single latest Miocene locality in Italy, and from Teruel (Spain) during a short period at the Miocene-Pliocene transition. On the other hand, some immigrants settle and undergo evolutionary radiation. This is illustrated by the successful cricetid *Democricetodon* (with its probable origin in Anatolia), which is ancestral to several genera in Western

Europe. So, Western Europe periodically received faunal invasions, but it is difficult to localize the sources areas, which could be Eastern Europe, Central Asia, South-Western Asia, or the Far East. During the last decade, intensive field campaigns allowed to characterize some independent dispersal centres in Asia. Four such areas are now well known (corresponding to the main paleontological field activities): Mongolia, Kazakhstan, Anatolia, and Pakistan.

Rodents, which are the most numerous mammals, expanded widely since the Oligocene. Hartenberger (1998) gives a chart showing the major subdivisions and lineages. During the Neogene epoch, a few new groups diversified. Some of these new groups, especially the Muroidea, were very successful and produced many species and genera. McKenna & Bell (1997) have realized a remarkable review of all mammals at the supragenetic level, using a strict cladistic classification. In this case, the Neogene innovations are limited to some subfamilies. This classification is not convenient, because about fifty per cent of the rodents are part of the huge murid family. In this paper, the groupings of rodents used are those that are usually employed, but they are largely informal, because affiliations of many groups have not been solved satisfactorily. I will focus on those groups whose migrations have been demonstrated; for example, some old rodents like the apodontids living in China and in Central Europe during the early Miocene have no close relationship, and will, therefore not be discussed.

NON-MUROID RODENTS

The Neogene European Ctenodactylidae have been recently reviewed by De Bruijn (1999), who pointed to the fact that the Sardinian ctenodactylids show a tooth structure too complicated to be derived from a *Sayimys* pattern. But the genus *Prosayimys* from the Upper Chirtawarta formation of Zinda Pir Dome Pakistan (estimated age 20 Ma; Baskin 1996) has preserved the metalophid II, which is always present in the Early Miocene

Sardinian ctenodactylids. So *Prosayimys* could be the ancestor of the Sardinian ctenodactylids. During the Miocene, ctenodactylids disappeared from Asia. The youngest form *Sayimys chinjiensis* Baskin, 1996, is known from the Upper Vallesian of Pakistan. At the beginning of the Middle Miocene *Sayimys intermedius* (SEN & THOMAS, 1979) migrated to Rotem (Israel), to Al Sarrar (Saudi Arabia) and Djebel Zelten (Lybia, Africa). Ctenodactyloidea were also represented during Paleogene times in Asia by the Chappatimyids. An offshoot of this last group, the Baluchimyinae, survived until the earliest Miocene (Flynn *et al.* 1986, Flynn & Cheema 1994). The recent discovery of a representative of *Baluchimys* from an Eocene level from Thailand (Marivaux *et al.* 2000) has demonstrated an Eocene origin for the Baluchimyidae.

Diatomyidae (Mein & Ginsburg 1997) constitute an independent Asiatic group of the ctenodactylids, they originated in Pakistan, and have two successive genera *Fallomus* (FLYNN *et al.*, 1986) and *Diatomys* LI, 1974. Flynn (2000) shows several morphological intermediate steps between these two diatomyid genera. Their molars are convergent with those of *Megapedetes*. During the Early and Middle Miocene, this group is known from Laddak, Thailand, China and Japan. The last occurrence is in the Pakistani site Y-797 (Nagri formation; 10.6 Ma).

Pedetidae are typically an African rodent family, but they are not documented during the Paleogene times. Three genera (*Parapedetes*, *Megapedetes* and a new undescribed genus) occurred simultaneously during the Early Miocene of East and South Africa. Among them, only *Megapedetes* can be occasionally found in the Middle Miocene of the South Eastern Mediterranean region; they are known from: Rotem (Israel, MN4; Wood & Goldsmith 1998), Chios (Greece, MN5; Tobien 1968) and Al Sarrar (Saudi Arabia, MN5; Thomas *et al.* 1982). *Megapedetes aegaus* is the last known Asiatic form of the Pedetids, known from

Bayrak Tepe 1 (MN7-8; Sen 1977).

Another African group, the Thryonomyidae, which are hystricognath rodents, occurs occasionally during the Miocene in Asia. Two different migrations reached the Indian subcontinent (Flynn & Winkler 1994). The first with the small *Kochalia* DE BRUIJN, 1986, is known from 11.3 to 12.5 Ma and the second with the large *Paraulacodus* HINTON, 1933, which is present only during a brief episode from 12.9 to 12.5 Ma.

There is nothing to add to the story of the Castoridae, described in detail by Huguency (1999), who shows that during the Neogene, the same genera of this group lived in Asia and Europe. However, Bendukidze (1997) mentions two genera (*Capacikala* and *Capatanka*) of American origin from the Early Miocene of Kazakhstan (but now, the latter is included in the genus *Palaeocastor*).

Gliridae belong to an old rodent radiation present in Eurasia since the Eocene. Many genera are exclusively European forms and the first idea supposed that Europe was the only dispersal centre for Glirids. However, the Oligocene-Early Miocene Glirids from Anatolia exhibit a great number of forms and are sometimes older than the European occurrences (Ünay, 1994). For example, *Glis* has been recorded from the Middle Oligocene of Anatolia (MP25) but is only known since MN4 in Europe. Similarly, *Glirulus* is known from Harami-1 (MN2) in Anatolia, and arrived in Europe in MN4. *Myomimus* existed in Keseköy (MN3) and Çandır (MN6), but arrived in MN9 in Europe (Daams 1999). During the Early Miocene, glirids are unknown in other districts of Asia, except in China where a tooth of *Glirulus* is recorded from the Late Oligocene of the North Junggar Basin (Wu *et al.* 2000). So Anatolia may have been a good centre for glirid dispersion to Europe or other parts of Asia.

At the beginning of the Middle Miocene, *Microdryomys*, *Miodryomys*, *Prodryomys* are known from Zaissan (North Asia; Kowalski & Shevyreva 1997). *Microdryomys* can be found in China in MN5. For this genus, its

European origin is clear, because it is known from Europe since MP25 and perhaps earlier. Probably by the way of Anatolia, *Dryomys* went to Africa during the Middle Miocene, where it can be found until the Lower Turolian. The recent genus *Graphiurus* could be a descendant of this African *Dryomys*. *Myomimus* was present in Pakistan from 13.8 Ma (HGSP 107, Banda Daud Shah) and occurs now in Iran and Turkmenistan.

The myrmecophagous Glirid *Plioselevinia* is known from MN15 of Weze (Poland) and Ivanovce (Czech Republic) and from MN16 of Hajnacka (Czech Republic) (Fejfar & Heinrich 1985). Its recent relatives live now in Kazakhstan. So, the migration of this group has been from West to East.

Sciuroidea were widely spread upon the whole Eurasiatic continent at the end of the Oligocene. During the Neogene, their diversification increased. Some ground squirrels invaded Africa in the Early Miocene just after the collision between African and Eurasiatic plates. We can observe two different routes for the migrations between Europe and Asia. The first is shown by *Atlantoxerus*, which is present at the beginning of Neogene of China, in the Suosuoquan Formation (MN1, Qiu *et al.* 1999). This genus appeared in Europe only in MN4 (de Bruijn 1999) and persisted until the Middle Pliocene (MN15). In Asia, the taxon disappeared after MN14 (Bilike, Qiu & Storch 2000). In the same group, *Sciurus* is supposed to arrive from North America during the Lower Pliocene. An opposite direction of migration is exemplified by *Ratufa*, which is found earlier in Europe than in Asia. In Europe, this genus is known from Ulm Westtangente (MN2) until Obendorf (MN4, de Bruijn 1998). In Asia, the first *Ratufa* is described from Li Mae Long (Thailand, MN4; Mein & Ginsburg 1997). Further, this genus is mentioned from several localities of the Potwar Plateau, Pakistan, between 9.7 and 8.5 Ma (Flynn *et al.* 1995). So, the case of *Ratufa* is an example of West to East migration.

Eomyidae have been exhaustively reviewed

by Engesser (1999). This author shows the precise date of migration of some Neogene Eomyids: *Pentabuneomys* appeared in Europe in MN3, and *Keramidomys* and *Eomyops* appeared in MN5. Unfortunately, their ancestors are unknown in Asia. This group shows a rare example of West-East migration with the genus *Megapeomys* that, original from Central Europe, shows a quick expansion reaching Japan (Fejfar *et al.* 1998).

Neogene Dipodidae of Eurasia belong to two different groups: Zapodidae and Allactaginae, which may represent two different families. McKenna & Bell (1997) recognize only one family, but divide the Sicistinae from the Zapodinae at subfamily rank. For European researchers, the Sicistinae and Zapodinae are more related to each other than either is to the Allactaginae. The dipodids have recently been revised by Daxner-Höck 1999.

In Europe, *Plesiosminthus*, a migrant descendant from the Oligocene Chinese *Parasminthus*, is known from the Late Oligocene (MP26) to the Early Miocene (MN2). A second immigration of an unknown zapodid occurs in MN3/4 (Petersbuch, Central Europe; Daxner-Höck 1999). The third immigration was that of *Eozapus* in the Late Miocene. This tiny animal is known from about twenty localities of Europe between MN10 and MN14. In Spain, its temporal distribution is divided into two: the first at the boundary MN10-MN11 within localities as Cucalon and Cascante-Cubla, the second one in the earliest Pliocene (Celadas 3-4-5-8). The latter was incorrectly assigned to *Sminthozapus* (Mein *et al.* 1983) as pointed out by Fahlbusch (1992). In France, *Eozapus* is recorded in the MN10 faunas of Amberieu 1 and 2, and Dionay. No occurrences are known from MN11 and MN12, but this genus reappeared in Lissieu MN13 (Mein 1999) and also in Celleneuve MN14. In Eastern Europe, *Eozapus* was found in Berislave (Nesin & Topachevsky 1999) and Podlesice (MN14). In China, *Eozapus* is not present before MN13 (Fahlbusch 1992) and a

related genus *Sinozapus* is known from Bilike (MN14, Qiu & Storch 2000). So *Eozapus* is earlier present in Europe than in Asia. *Sminthozapus* Sulimsky, 1962, is restricted to the Pliocene of East Europe. The genus *Sicista* first appeared during the Late Miocene of Kazakhstan and migrated westward to the Ukraine and eastward into China during the Pliocene. During the Pleistocene, *Sicista* made some short forays related to cold periods into Western Europe.

Allactaginae are first known from the latest Oligocene of Kazakhstan and Anatolia. Among the Miocene representatives, the genus *Protalactaga* had a wide Asian distribution during Early and Middle Miocene. It reached North Africa at the end of the Middle Miocene, but its African range is very restricted due to its extinction just before the arrival of *Hipparion*. *Protalactaga gabunii* (LUNGU, 1981) is an European allactagine, found in the Vallesian of Moldavia; it may be ancestral to *Lophocricetus*, an important genus during the Turolian of the Ukraine, Siberia and China. *Paralactaga* from the latest Miocene of China and Kazakhstan seems to be the ancestor of *Allactaga*, which had a wide distribution in Asia since the Pliocene and made some incursions in the Ukraine and Romania during the Late Pliocene and the Early Pleistocene.

MUROIDS

The Paleogene Paracricetodontinae has one surviving genus during the Early Miocene. This genus, *Mirabella* DE BRUIJN *et al.*, 1987, appears in Anatolia (*M. anatolica* DE BRUIJN & SARAÇ, 1992). A second species occurs in Keseköy at MN3. Later, the genus migrated into Greece in MN4 where it is known from Aliveri and Karydia. It is not recorded from younger faunas, so its temporal range is relatively short. De Bruijn & Saraç (1992) note the remarkable fact that there were probably two different migrations during the short range of the genus into Central Europe each one evidenced by only a single molar: a large one from the MN3 fauna of Reiden-Sertel

(Switzerland) and a smaller one from the MN4 fauna of Rembach (Germany). This example illustrates that many migrations may not have been preserved in the fossil record.

The Cricetodontinae are an important group of Muroids because of their wide geographic and long temporal distribution. Our knowledge about them has significantly increased, particularly through the fieldwork of Hans de Bruijn's team. The nominative genus *Cricetodon* LARTET, 1851, has first been recorded from the Middle Miocene of Western Europe. De Bruijn *et al.* (1993), have shown its existence in the Aegean region and Anatolia. The first representatives of the genus are characterized by three roots on first and second upper molars and a small size. The oldest known *Cricetodon* has been found at Inkonak (MP30, de Bruijn *et al.* 1991); from MN1 to MN3 in Anatolia *Cricetodon* was present, so this region should have been the dispersal centre for all Cricetodontids. Greece has been colonized during MN4 and Central and Western Europe during MN5. During the Middle Miocene, the genus *Cricetodon* is known from several Turkish localities like Pasalar, Çandır, Sarıçay; it is also known from the MN6 fauna of Belometschetskaya (North Caucasia, the type locality of *C. caucasicus* PICKFORD *et al.*, 2000). *Cricetodon* appeared early in China: *Cricetodon* sp. is mentioned from the MN1 locality of Suosuoquan (Qiu *et al.* 1999) and from Sihong during MN4 (Qiu 1996). *Gobicricetodon* QIU, 1996 appeared during the late Middle Miocene and Early Vallesian; this form has a size similar as the Western-European species, but still has three roots on its upper molars. Another Chinese genus *Plesiodipus* YOUNG, 1927 from the Middle Miocene is probably related to *Gobicricetodon*, and at the base of the Myospalacine radiation during the Late Miocene.

In Kazakhstan, the genus *Tsaganocricetus* TOPACHEWSKI & SKORIK, 1988, is represented by two different species. The older one, *T. turgaiensis* BENDUKIDZE, 1993 from

Kentjubeck (MN6), can be easily assigned to *Cricetodon*, but the type species *T. irtyschensis* Topachewski & Skorik, 1988 from the Vallesian locality of Semipalatynsk region, is a more derived form: brachyodont, but with a flat occlusal surface and cement filling the synclines; it is one of the numerous forms to be convergent with voles. (The Early Miocene age assignment of this genus in McKenna & Bell (1997) is erroneous).

Zramys JAEGER *et al.*, 1973, spread over North Africa during the final Middle Miocene and Late Miocene. Probably this migration came from Southwestern Asia, via Anatolia. At the end of the Miocene, another migration (with a Spanish origin) introduced *Ruscinomys* Depéret, 1890, into North Africa across the Gibraltar strait. In Western and Central Europe, other Middle Miocene cricetodontines have been found besides *Cricetodon*. The largest one is *Lartetomys* MEIN & FREUDENTHAL, 1971, which has three roots in its upper molars. *L. mirabilis* is a very rare species occurring in France during MN5. *Mixocricetodon dehmi* RUMMEL, 1997 (well represented in several German fissure fillings), is a junior synonym of *Lartetomys*.

Recently, one isolated upper second molar has been recovered from the new French locality Four (MN6/7, Maridet *et al.* 2000). This tooth (LxW=3.31x2.68 mm) is more recent and more voluminous than the upper second molar of *L. mirabilis*. *L. mirabilis* and *T. irtyschensis* are the largest known cricetodontines. Is a lineage between these two species possible through the species of Four? A second species, described as *Lartetomys zapfei*, has been now correctly interpreted as a new genus *Karydomys* of the *Democricetodon-Copemys* group (Theocharopoulos, 2000).

Following the opinion expressed by de Bruijn *et al.* (1993), the genera *Deperetomys* and *Eumyarion* can be included in the Eucricetodontinae. Besides the morphological arguments, these two genera share also the same dispersal centre Anatolia and have the same first appearance date. *Deperetomys*

MEIN & FREUDENTHAL, 1971, has been firstly recorded from the latest Middle Miocene of Central and Western Europe. In Anatolia, new and older species have been described by de Bruijn *et al.* (1993) from Kargi II (MP30) and Kilçak 0 (MN1), and the younger MN4 locality of Gemerek. This latter find links the first species from Anatolia to the most recent species from Europe. *Metemys* de Bruijn *et al.*, 1992 is a large Cricetodontinae closely resembling *Deperetomys*, but its size in the latest Oligocene of Inkonak and Kargi is as large as the *Deperetomys* of the late Middle Miocene of Europe.

Eumyarion THALER, 1966 is a genus known in Europe from MN4 to MN9. In Anatolia, older species were described by de Bruijn & Saraç (1991) from MN1 of Harami to MN3 of Keseköy. Additionally, *Eumyarion* is already present in MP30 from Kargi (de Bruijn in Theocharopoulos 2000). As in the case of *Deperetomys*, Anatolia probably is the first dispersal centre of *Eumyarion*. The species found in this district are good ancestors for the European burrowing rodents, the Anomalomyiinae. *Eumyarion* appears also in Pakistan with *E. kowalskii* (Lindsay 1996), in the Chirtawata Formation of Zinda Pir Dome, calibrated to 20 Ma (early MN3). This last species seems a good ancestor for the rhizomyid radiation. Wessels & de Bruijn (2001) transfer this species to the genus *Prokarnisamys*. Later, the genus *Aralocricetodon* BENDUKIDZE, 1993 shows an ephemeral invasion of Rhizomyidae during the Middle Miocene of Kazakhstan. So two different kinds of burrowing rodents originated from *Eumyarion*.

A third group of specialized burrowing rodents are the Spalacidae. This family living in South West Asia and South East Europe has been recently well studied by Ünay (1999). The fossil record of this family seems to indicate Anatolia as the centre of origin and dispersion. The oldest known spalacid is *Debruijnina* from Keseköy (Anatolia, MN3), but until now, no potential ancestor has been found among the faunas from the older loca-

lities of Anatolia.

Another muroid from Anatolia is *Muhsinia*. This new genus was found at Inkonak (MP30) and Kilçak 0 (MN1, de Bruijn *et al.* 1992). It was tentatively positioned inside the group of the Pseudocricetodontidae by the authors, and finally stored into the Eucricetodontini by McKenna & Bell (1997). This genus bears some likeness to *Afrocrisetodon* LAVOCAT, 1977. This strange genus may be at the origin of an Afrocrisetodontine migration into Africa. It is a very low crowned muroid, with longitudinal ribs on the lower incisor and two metalophids on lower molars.

Democricetodontinae (or Copemyiinae) are one of the most frequent Neogene muroid rodents. The main genus *Democricetodon* FALBUSCH, 1964 is known as an Eastern immigrant in Europe, where its arrival indicates the beginning of MN4. As indicated by the etymology of its name, *Democricetodon* is a very common animal, often the dominant genus in small-mammal faunas. Recently, Theocharopoulos (2000) has reviewed the complete history of this group. Like so many muroid rodents, the origin of this group seems to have taken place in Anatolia descending from the Middle Oligocene genus *Lignitella* ÜNAY. *Democricetodon* itself appears in the earliest Neogene (Kilçak 0) and is present in all known Early Miocene localities and some Middle Miocene localities until MN6 from Anatolia. Çandır is the last known Turkish site where this genus present.

In Europe, *Democricetodon* became less frequent in the Late Miocene in relation with the presence of new (but related) genera. The last occurrences are in the early MN10 localities such as Masia del Barbo (Spain) and Suchomasty (Czech Republic). In Pakistan, *Democricetodon* is known from numerous species (Lindsay & Downs 1998) from Y-747 (18 Ma) to Nagri levels or perhaps later. In China (Qiu *et al.* 1999), the first occurrence is in the Sihong fauna, which is chronologically at the same level as in Europe, posterior to the fauna of Tunggur (MN7/8). The last occurrence is from Amuwusu (Nei Mongol,

early MN9).

In Anatolia, *Democricetodon* was preceded by the genus *Spanocricetodon* LI, 1977. *S. sinuosus* THEOCHAROPOULOS, 2000, is known from the latest Oligocene of Inkonak and from some MN1 localities. Later, this genus migrated to Pakistan where *S. khani* DE BRUIJN *et al.*, 1981, has been found in HGSP 116 from the Murree Formation (MN3), and in the coeval Zinda Pir Dome Y-113 (Lindsay 1998). Subsequently, *Spanocricetodon* expanded throughout Asia during MN4, as shown by the occurrence of *S. ningensis* (the type species) in Fangshan (China) and *S. janvieri* MEIN & GINSBURG, 1997, in Thailand. *Spanocricetodon* became extinct during MN4, it is considered to be an ancestral form to *Democricetodon*, *Primus* and perhaps also *Megacricetodon*. Theocharopoulos is the first paleontologist to write that *Protarsomys* LAVOCAT, 1977, was a member of the *Democricetodon* group that migrated into Africa. This genus is known from the Early Miocene of the East Africa and Namibia. A second migration wave (from Anatolia?), invaded East Africa in the late Middle Miocene.

Karydomys is a new genus erected by Theocharopoulos (2000) for a special democricetodontine lineage, characterized by a low anteroconid on m1, which is blade like and very close to the main anterior cusps. Only one species is known from Europe described by Mein & Freudenthal as a second *Lartetomys* species: *L. zapfei*, occurring in MN5 and MN6. Now, two different and smaller species have been described from the MN4 of Greece: *K. symeonidisi* and *K. boskosi*. An Asiatic origin is likely because some species were present in MN4 of Anatolia and also in MN5 of Kazakhstan.

Around the Middle to Late Miocene transition, some new democricetodontines appeared which are considered as the beginning of the Cricetinae. *Cricetulodon* HARTENBERGER, 1965, is the oldest representative. This species is a good marker for the beginning of MN9 in Western Europe. An earlier occur-

rence of the same genus is known from Bayrak-tepe 1 (MN7/8, Anatolia). Cricetines genera were very numerous during the Late Pliocene and Pleistocene. The main origin of these hamsters lies certainly in the vast open areas of Central Asia.

Two different kinds of specialized ‘cricetids’ occurred in the Late Miocene. The first are the so-called ‘gerbilloids cricetids’ with three genera showing migrations: *Blancomys* WEERD *et al.*, 1977 has been found in Spain and France between MN13 and MN16, but it was already present in Anatolia in the MN10 locality of Karaözü and Kaleköy (Sümengen *et al.* 1989). *Epimeriones* DAXNER-HÖCK, 1972, is known only from Europe, but its geographical range is expanding eastward during the Late Neogene. It is known from MN11 to MN13 in Central and Western Europe, and its more recent occurrences are in Eastern Europe till the lowermost Pleistocene (Terzea 1978).

Pseudomeriones SCHAUB, 1934 was considered as an aberrant gerbillid, but today, it is regarded as a gerbillid cricetid like *Epimeriones*. The oldest records are from several Vallesian localities in Anatolia (Sümengen *et al.* 1989). Later a Turolian migration brought this form to South East of Europe, where it is found until the Early Pliocene. During the Turolian, it is known also from Afghanistan and China, where it stayed until the Early Pliocene (Qiu & Storch 2000). The last record is found from Çalta (MN15) in Western Asia; but the most intriguing occurrence is from the Spanish locality of Casablanca-M, the only record in Western Europe of final MN13 age; it probably arrived there by way of North Africa (Agusti 1989).

Another group of democricetodontine rodents can be called “microtoid cricetids” evolving toward voles. They comprise numerous and independent lineages. Fejfar (1999) gives a good overview of these forms, distinguishing several morphological categories.

Microtocricetus FAHLBUSCH & MAYR, 1975, is the oldest European form whose molars

show a tendency toward prismatic structure. This genus lived only in MN9, from the Ukraine to France. *Rotundomys* MEIN, 1965, is less specialized and known essentially from MN10 in Western Europe only. *Microscoptes* SCHAUB, 1934, has hypsodont molars with a prismatic structure. It is present in MN12 at Cherevichnoe (Ukraine), from MN13 of Central Asia and MN14 of China. This genus is also known from North America during the Lower Hemphilian (which seems to be an older age).

Ischymomys ZAZHIGIN, 1992, which shows a similar dental structure, is known from the MN11 fauna from Frunzkovaz (Ukraine) and from MN12 of Petropavlosk (Kazakhstan).

One last group with mesodont molars and a trilophodont m1 consists of numerous genera, probably all derived from *Microtodon* in Eastern Asia from MN13 and MN14; some genera (like *Trilophomys* DEPÉRET, 1892 and *Baranomys* KORMOS, 1933) show a relative long temporal range during the Pliocene of Europe (from MN14 to MN16). Some others have had an extremely short temporal range, such as *Celadensia* MEIN *et al.*, 1983 that lived in Spain at the MN13-MN14 transition. *Bjornkurtenia* KOWALSKI, 1992 and *Baranarviamys* NESIN, 1996 have similar short ranges.

Aratomys ZAZHIGIN (in Gromov & Poljakov 1977) is known from the Eastern Asian localities Tchurno-kariakh (Mongolia, MN13) and Bilike (inner Mongolia, MN14). At first considered as a true vole by Fejfar (1997), this form has been placed in the cricetids by Qiu & Storch (2000).

Arvicolidae, or true voles, make up the most recent radiation among Muroid rodents; after their origin in North America, they rapidly spread over Asia and Europe during the Pliocene. *Promimomys* KRETZOI, 1955 is the only genus present in Eurasia during MN14, with two successive species (Fejfar *et al.* 1997). In MN15, *Mimomys* F. MAJOR, 1902 and *Dolomys* NEHRING, 1898 appeared in Western Europe at about 4 Ma. From MN16 onwards, the teeth have cement in

their synclines; the enamel free areas on the lateral walls of the teeth increased, and the thickness of the occlusal enamel became differentiated. The number of known forms increased and the story continued till the Pleistocene when forms with rootless molars appeared. This group, showing rapid morphological evolution of their teeth, is the most useful for detailed biochronology.

Megacricetodontinae seem to appear simultaneously (MN3) in two Asian regions: in Pakistan (Zinda Pir Dome; Lindsay & Downs 1998) and in Anatolia, (Keseköy, Theocharopoulos 2000). In the latter locality, two different species co-occur (de Bruijn, in Theocharopoulos). *Megacricetodon* FAHLBUSCH, 1964, arrived in China in the Sihong fauna (MN4) and reached Europe at the same time when this genus constitutes a major element among rodent faunas till MN9. In Europe, *Megacricetodon* disappeared without any descendants; however in Pakistan, it gave rise to a larger genus *Punjabemys* LINDSAY, 1988 and probably, some relative form was ancestral to the Myocricetodontinae (Gerbillidae) whose first representatives are difficult to distinguish from *Megacricetodon*. On this subject, see the divergent opinions of Wessels (1996) and LINDSAY & DOWNS (1998). A large review of gerbils can be found in Wessels (1998, 1999).

Myocricetodontinae arose probably in Pakistan; during the Early Miocene, they invaded Africa via Arabia. Known from North Africa, but also from Kenya and Namibia during the Middle Miocene, some forms reappeared in Spain during the salinity crisis (latest MN13). *Calomyscus* THOMAS, 1905 is a recent survivor of the Myocricetodontinae; some fossil specimens have been found in the uppermost Miocene of France and Spain, as well as in the lower Pliocene of Rhodes.

Taterillinae (Gerbillidae) arose with two close genera: the first, *Abudhabia* DE BRUIJN & WYBROW, 1994, originated in the Early Turolian of Dhok Pathan formation (Flynn & Jacobs 1999) and is later known from Saudi Arabia and Afghanistan. The second fossil

genus is *Protatera* JAEGER, 1977; it is a North African genus known from the Middle and Late Miocene. Some gerbils referred to the genus *Debruijnimys* CASTILLO & AGUSTÍ, 1996, are known from the lower Pliocene of Spain and had a North African origin. Murids also arose in Pakistan. We can imagine a succession of morphological transformations from *Megacricetodon* to Myocricetodontines, and finally to Murids. During these morphological changes of the molars, the longitudinal crest disappeared, the alternate major cusps took a twin position and new cusps appeared on the lingual border of the upper and labial side of the lower teeth.

Dendromurines are essentially an African group with some remnants of the longitudinal crest and only one supplementary lingual cusp (t4 = enterostyle). The only Asian rodent considered by Lindsay as a dendromurid is *Potwarmus* LINDSAY, 1988. This genus is known from Pakistan and Thailand. Its temporal range is from 18-14.3 Ma (Flynn *et al.* 1995). This genus migrated to Africa and was found in Gebel Zelten (Lybia) at the beginning of the Middle Miocene.

Antemus JACOBS, 1978, is the first murid showing the new cusp (t1 = anterostyle), which characterizes the Murinae. This form is known from 13.7-12.5 Ma (Flynn *et al.* 1995). *Progonomys* SCHAUB, 1938, is the first murid in Western Europe appearing at the beginning of MN10 (approximately 9.7 Ma). It appears earlier in Pakistan where finds of teeth are mentioned at 12.1 Ma (Flynn *et al.* 1995). *Progonomys hussaini* CHEEMA *et al.*, 2000 is also a primitive murid present between 10 and 11 Ma at the Potwar plateau. Some recently known archaic murids from Sinap Tepe I (MN9) are being studied by Sevket Sen. These finds implicate an earlier arrival of murids in Western Asia than in Europe. During the Late Miocene and particularly during the Pliocene, the number of murid genera increased considerably. Some fossil genera are known only from Asia, like *Ratchaburimys*, *Chardinomys*, *Wushanomys*, *Dianomys*, *Orientalomys*. Some others have

had a large distribution, being known from East Asia to Western Europe: it is the case for *Rhagapodemus*, *Parapodemus* and *Micromys*; the latter is still living today. Finally, some genera are known from Asia and from Africa like *Saidomys* and *Mus*. Murids spread quickly on Africa during the Late Miocene, especially for the group of *Acomys*.

CONCLUSIONS

During the Neogene the main migrations of rodents were from Asia to Europe, especially from Anatolia; this region has been a very important centre for speciation before MN4 (*Cricetodon*, *Democricetodon*, *Karyomys*, for example) and an important centre of dispersion to Europe by the South Aegean region. The same applies to Africa: dispersals from Anatolia (across Arabia) were more numerous and more various than from other regions. We mention for the Early Miocene: *Protarsomys*, *Muhsinia*, and some ground squirrels; for the early Middle Miocene: *Sayimys*; for the late Middle Miocene: *Dryomys*, *Democricetodon*, *Myocricetodon*; and for the Late Miocene the murids *Mus*, *Saidomys* and *Acomys*. A lower number spread from East Asia (eventually, from North America), or Central Asia. Migrations from Africa are only related to the Mediterranean crisis, at the end of the Miocene through the Gibraltar strait.

West-East migrations from Europe to Asia are seldom, but some have been assumed: we mentioned *Ratufa*, *Microdyromys*, *Plioselevinia*, *Megapeomys* and *Eozapus*. Beside these so important exchanges between Asian and European faunas, some groups like the Tachyoryctoidinae or Myospalacinae are exclusively Asiatic; they are limited to one continent and underwent no expansion phase.

With the biochronological development among mammals, the first appearance following a migration becomes more and more important. These first appearance data are really excellent in many cases but when the new districts are far from the original centre, some lateness may occur during the dispersal

event and a magnetostratigraphical control is desirable.

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