Barbara Rzebik-Kowalska
Polish Academy of Sciences, Cracow

Distribution of shrews (Insectivora, Mammalia) in time and space

Rzebik-Kowalska, B., 2003 - Distribution of shrews (Mammalia, Insectivora) in time and space - 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: 499-508 [ISSN 0923-9308]
Published 1 December 2003

The oldest shrews, represented by the extinct family Heterosoricidae, were found in the Middle Eocene of North America. They lived also in Europe and Asia and finally disappeared in the Late Miocene. Their place of origin is still unknown. The 'true' shrews (family Soricidae) appeared for the first time in the Early Oligocene in Europe. They belonged to the extinct subfamily Crocidosoricinae. They were also found in Asia and North Africa and survived to the end of the Miocene or ?Early Pliocene (Gargano, Italy). They are considered to be of European origin. The remaining subfamilies i. e. Allosoricinae, Limnoecinae, Crocidurinae and Soricinae are not known before the Miocene. Allosoricinae were found in Europe and Asia Minor where they are known from the Early Miocene until the Late Pliocene. Probably their main evolution took place in Europe. The members of the extinct, and exclusively North American, Limnoecinae are known from the Early Miocene until the earliest Pliocene. The oldest remains of the Recent Old World subfamily Crocidurinae are known from the Middle Miocene of Asia Minor and Africa. In Europe, the first Crocidurinae are known from the Late Pliocene, in eastern Asia from the Pleistocene. Their great recent diversity in Africa and late appearance in Europe and eastern Asia suggest that their evolution took place mostly in Africa. Also the second Recent subfamily Soricinae is now extremely diversified. Their oldest remains were found in the Early Miocene of Europe and represented by the genus *Hemisorex*. More or less from the same time Soricinae are known from North America. They belong to the genus *Antesorex*. The first occurrences of the remaining species of the Soricinae are from the European Late Miocene, the end of the Middle Miocene of North America and the Late Miocene of Asia.

Correspondence: Barbara Rzebik-Kowalska, Institut of Systematics and Evolution of Animals, Polish Academy of Sciences, 31-016 Kraków, Slawkowska 17, Poland; e-mail: rzebik@isez.pan.krakow.pl

Keywords: Mammalia, Insectivora, Heterosoricidae, Soricidae, Tertiary, distribution.

INTRODUCTION

According to Reumer (1998), who presented a new approach to the classification of fossil and recent shrews, the shrews can be subdivided into two families, the Heterosoricidae and the Soricidae. This division is based on the different morphology of bones and muscles, which take part in the process of mastication (Reumer 1987). Some authors (Repenning 1967, Hutterer 1993, Storch *et al*. 1998) have not accepted this division and consider the heterosoricid shrews as a subfamily of the family Soricidae. Reumer's classification is adopted in the present article.

The family Soricidae consists of five subfamilies: Allosoricinae, Crocidosoricinae, Crocidurinae, Limnoecinae, and Soricinae. The exclusively North American subfamily Limnoecinae ranged from the Early Miocene to the earliest Pliocene. The subfamily

Soricinae includes seven tribes: Anourosoricini, Blarinellini, Blarinini, Soricini, Notiosoricini, Neomyini, and Beremendiini.

HISTORY OF DISTRIBUTION

Heterosoricidae VIRET & ZAPFE, 1952

The oldest shrews known so far belong to the extinct family Heterosoricidae. They were found in the Middle Eocene of North America in four localities of Wyoming (USA) and in one locality in Canada. They are represented by the genus *Domnina* COPE, 1873 with the unique species *D. gradata* COPE, 1873. In the Late Eocene the number of species doubled and their range was wider, but limited to the United States. The heterosoricid diversity increased again in the Early Oligocene. Besides three species of *Domnina*, a new genus *Pseudotrimylus* GUREEV, 1971 was described from Colorado and Wyoming (Harris 1998).

At this time (Early Oligocene) the first heterosoricid shrews appeared in Europe and Asia. In Europe they were represented by the genus, *Quercysorex* ENGESSER, 1975, with one species, *Q. herrlingensis* (PALMOWSKI & WACHENDORF, 1966) described from the German locality of Herrlingen 1 correlated to MP22. *Quercysorex* sp. cited from an older locality (MP21) in the Czech Republic is the oldest shrew known on the European continent (Fejfar & Kvacek 1993). The number of heterosoricid taxa in the Early Oligocene of Europe was most probably greater, since numerous remains are still unstudied. In Asia, the Early Oligocene heterosoricids were found in Mongolia (the Gobi Desert) and described by Sulimski (1970) as *Gobisorex kingae*. This finding constitutes the oldest record of shrews in Asia. Heterosoricids from the Late Oligocene of North America are not known. In Europe, several species (not all identified to species level) of two genera (*Quercysorex* and *Heterosorex* GAILLARD, 1915) were described. Among them *Q. herrlingensis*, *Q. ulmensis* ZIEGLER, 1998, *Q. huerzeleri* ENGESSER, 1975 and *Heterosorex neumayrianus* (SCHLOSSER, 1887) (Germany and Switzerland). *Quercysorex primaevus* (FILHOL, 1884), was cited from not precisely dated Oligocene layers in France (Rzebik-Kowalska 1998, Ziegler 1998).

At the Oligocene/Miocene boundary in North America, the number of the heterosoricids is again higher. They are represented by *Pseudotrimylus dakotensis* (REPENNING, 1967) and two species of *Domnina* (South Dakota, California and Idaho). The Early Miocene localities yielded still more diversified Heterosoricidae. There were two species of *Pseudotrimylus* and two to three species of a new genus *Wilsonosorex* MARTIN, 1978 (Colorado, South Dakota). In the Early/Middle Miocene a new genus (*Paradomnina* HUTCHISON, 1966) represented by *P. relicta* HUTCHISON, 1966 appeared in California (Harris 1998). The last ocurrence of the heterosoricids in North America was in the Middle Miocene. They were represented by new species of genera *Pseudotrimylus* and *Paradomnina* and by a new genus *Ingentisorex* HUTCHISON, 1966. The geographical range of all forms was limited to Oregon (Harris 1998).

In Europe, the Early Miocene Heterosoricidae were also numerous and represented by three species of the genus *Heterosorex* and two species of *Dinosorex*. Their geographical range was very wide, from Spain to Greece (Rzebik-Kowalska 1998). During the Middle Miocene in Europe, the number of Heterosoricidae was even greater than in North America: four species of *Dinosorex* and *Heterosorex* lived at that time from Spain to Poland and Slovakia (Rzebik-Kowalska 1998).

In the Middle Miocene, after a long absence since the Early Oligocene, the Heterosoricidae again appeared in Asia. They were found in China and described by Qiu (1996) as *Mongolosorex qiui*. Later, another heterosoricid shrew was discovered in Asia Minor and listed as *Dinosorex* sp. (Storch *et al*. 1998). During the Late Miocene heterosoricids became scarce and finally disappeared

from Europe and Asia. Their last occurrence in Europe was correlated to MN11 (*Dinosorex* sp. from Germany, Storch 1978), and in Asia to MN11/12 (*Heterosorex wangi* STORCH & QIU, 1991 from China, Storch *et al*. 1998). Up to then in Europe, three species of *Dinosorex* and one of *Heterosorex* survived in a large part of that continent. In Asia, besides *Heterosorex wangi*, *Mongolosorex qiui* was still present but became extinct at the beginning of the Late Miocene (MN9) (Storch *et al*. 1998).

The data presented above show that the oldest heterosoricid shrews (and the oldest shrews in general) were found in the Middle Eocene localities of North America. In the Late Eocene they were still present on this continent only. Until the Middle Miocene, when they disappeared from this part of the world, five genera with 12 named (and four unnamed) species inhabited the southwestern part of it (Harris 1998). It was as late as in the Early Oligocene that the Heterosoricidae appeared in Europe and Asia. In Europe, their representatives (three genera with eleven species) survived until the Late Miocene (MN11) (Rzebik-Kowalska 1998). In Asia, where the knowledge of fossil shrews is poor, we know only one species from the Early Oligocene of Mongolia, one species from the Middle, and one from the Late Miocene of China, and one unnamed species from the Middle Miocene of Asia Minor. The Chinese locality Lufteng is, so far, the youngest one (MN11/12) in which a representative of this family was found (Storch *et al*. 1998).

For a long time, the great morphological similarity of many taxa (including heterosoricids) from three northern continents aroused questions concerning their history. Where had they come from? Where was the centre of their dispersal? At what time and in which way had they spread? The Heterosoricidae were never found in Africa. Although in the sixties some species in Europe and North America were ranked in common genera (*Heterosorex*, *Trimylus*), Engesser (1979) proposed the opinion that there are no heterosoricid genera in common beteen Europe and America. As far as we know, North America and Asia had no genera in common either. The unique common genera inhabiting two continents (*Heterosorex* and *Dinosorex*) were found in Europe and Asia. Species of both of them appeared earlier in Europe (in the Late Oligocene) than in Asia (*Dinosorex* in the Middle and *Heterosorex* in the Late Miocene).

The morphological resemblance of organisms observed in North America, Europe and Asia has usually been explained by faunal exchange between those continents. As is generally known, in the Paleocene and in the Early Eocene northern Europe was connected with North America by the northern Atlantic bridge and was separated until the Early Oligocene from Asia by the Turgai Straits (although some brief contacts between them existed during that time). At the same time, Asia was united with North America by the Bering Bridge (Kramarenko 1974, Golonka 2000). It is also known that climatic conditions in the Early Eocene were more or less uniform in the Northern Hemisphere, from temperate and warm temperate in the north to subtropical in the south. Evergreen forests spread further northward in the Eocene, especially along seashores, as in the other Paleogene periods. This is confirmed by numerous localities of fossil flora, e.g. in the territory of north Asia, where palms were found until 64° northern latitude (Efimova 1961). Even the Bering area was much warmer in the Early Paleogene than in the Neogene. These conditions certainly facilitated the dispersion of many organisms. At that time we observe many common elements in mammal faunas of North America and Europe, the latter being only the eastern peninsula of North America. The same is true in the case of North America and Asia. At this time, few species were common to Asia and Europe.

Therefore, the Early Eocene was probably the period in which Heterosoricidae could spread between all three northern continents,

although it is difficult to say where they originated. Was it North America, where the oldest remains were found and where they only occurred during the Middle and Late Eocene? Or was it southeastern Asia, considered by many authors as the centre of evolution of most taxa of shrews? It is well known, that more Asiatic mammalian species spread from Asia to North America, especially in the Paleogene and the beginning of the Neogene, than in the opposite direction (Kramarenko 1974, Dawson 1999, Beard 1998). Moreover, if North American mammals crossed Beringia, they did not spread very far into Asia in most cases.

Unfortunately, the knowledge of fossil shrews from Asia is very limited. The Recent shrew fauna of this vast continent contains about 120 species, whereas during its entire long history only 60 species (among them four heterosoricids) have been discovered as fossils (Wolsan & Hutterer 1998, Storch *et al*. 1998). In the Middle Eocene the Bering and northern Atlantic bridges vanished, but the Turgai Straits was still present. These conditions resulted in the isolation of Europe, Asia, and North America. This isolation (with only some short contacts between Asia and North America and Asia and North Europe during this time), which continued in the Late Eocene, caused differentiation of faunal assemblages on three continents. Many endemic groups developed on each of them. In the Early Oligocene the Turgai Straits disappeared, enabling the mixing of many European and Asiatic mammals ('La Grande Coupure', Hartenberger 1983, Rögl 1998, Golonka 2000).

The Miocene was the time of extensive faunal exchange between Eurasia and North America across the Bering Bridge. However, in large areas of the Northern Hemisphere, including Beringia, records on terrestrial mammals practically do not exist north of about 55o N (Dawson 1999). Several explanations are possible: older sediments had been destroyed by glaciers or covered by Quaternary layers; in the northern latitudes populations were limited; or taphonomic conditions were unfavourable for the preservation of remains. Even when the Bering Bridge sometimes formed again, the climate changed from warm temperate to cold temperate, which prohibited the cross-penetration of biota. At that time the Bering Bridge probably acted as a filter to mammalian dispersal. Engesser (1979) believes that it was probably impossible for small mammals, including Heterosoricidae, to cross such climatic and ecological barriers. The Heterosoricidae were evidently dwellers of warm regions as they were always found in assemblages containing taxa characteristic of tropical forests (e.g. gymnures - Hylomyinae). Moreover, the Heterosoricidae died out at the end of the Late Miocene when the deterioration of the climate, the cooling and desiccation, became evident.

With these facts in view, Engesser (1979) suggested other than dispersal explanations of heterosoricid similarity in North America and Europe after the Middle Eocene. According to him it could be a parallel evolution and/or conservation of primitive features.

Soricidae Fischer von Waldheim, 1917

Crocidosoricinae Reumer, 1987

The second group of Tertiary shrews is represented by small, primitive extinct species of the subfamily Crocidosoricinae. The subfamily was established by Reumer (1987) and is considered by many authors as ancestral to all other soricid shrews of the family Soricidae *sensu* Reumer (1987).

The Crocidosoricinae appeared for the first time in the Early Oligocene in Europe and most of their history is limited to this continent. The oldest remains are known from the German locality of Ehrenstein 8 (Early Oligocene, MP22). They were described as *Srinitium* cf. *marteli* and they represent the oldest known 'true' shrews (Ziegler & Heizmann 1991). Until the beginning of the Pliocene, when they disappeared, 14 named species of nine genera were found in Europe.

S. marteli HUGUENEY, 1976 was also found in the Early Oligocene (MP23) of France. In the Late Oligocene the number of taxa increased. Three to six species of three genera, *Srinitium* HUGENEY, 1976, *Ulmensia* ZIEGLER, 1989, and *Crocidosorex* LAVOCAT, 1952, were listed from France and Germany. The Early Miocene localities of Europe yielded a very rich fauna of Crocidosoricinae, at that time attaining the greatest differentiation (Reumer 1994). Thirteen species from eight genera (*Carposorex* CROCHET, 1975; *Clapasorex* CROCHET, 1975; *Crocidosorex*; *Florinia* ZIEGLER, 1989; *Lartetium* ZIEGLER, 1989; *Miosorex* KRETZOI, 1959; *Soricella* DOBEN-FLORIN, 1964; *Ulmensia*) were collected from ca. 50 localities. A drop in relative humidity and the following cooling around the Early/Middle Miocene boundary were probably responsible for their decreasing in geographical range and variety in the Middle Miocene. Only four genera, *Lartetium*, ?*Miosorex*, *Florinia* and *Soricella* survived in the Middle Miocene of Europe. Species of two genera (cf. *Crocidosorex* in Italy and *Miosorex* in Spain, France, and Hungary) were still found in Europe in the Late Miocene. The youngest Miocene localities (correlated to MN12) in which 'cf. *Crocidosorex*' was listed, are Casteani, Montemassi, and Ribolla in Italy (Rook *et al*. 1996). But probably, the remains do not represent a *Crocidosorex* but *Miosorex*.

Similar to the Heterosoricidae discussed, the Crocidosoricinae did not survive beyond the Miocene/Pliocene boundary. The unique exception is *Lartetium dehmi* (Viret & Zapfe, 1952) which was found in the ?Early Pliocene sediments of Pirro Nord Cave on the Gargano in Italy (De Giuli *et al*. 1987). So far the Crocidosoricinae have never been found in North America. One species similar to the European *Crocidosorex*, was listed by Storch *et al*. (1998) from the Early Miocene (MN4) of eastern China. Another, European, species of crocidosoricines, *Lartetium dehmi africanum* (LAVOCAT, 1961), was found in the Middle Miocene Moroccan locality of Beni Mellal in North Africa (Butler 1998).

As in the case of the Heterosoricidae, the question arises concerning the origin of Crocidosoricinae. They have mostly been found in Europe. Although they are small in size, their absence or insignificant number in Asia and Africa does not seem to be artificial, because other very small fossil shrews (from the subfamily Allosoricinae) have been found in Asia Minor, West Siberia and China in several localities of the Middle and Late Miocene and the Late Pliocene. As Crocidosoricinae are older and more numerous in Europe than in Asia and Africa, some authors consider them to be of European origin. During the Early and Middle Miocene several events of faunal exchange took place between Eurasia and Africa. Most probably *Lartetium dehmi* reached West Africa from eastern Europe, along the southern coast of the Mediterranean Sea. In the Middle Miocene their passage from Spain was rather impossible. On the other hand, beginning with the Early Oligocene, dispersal between Europe and Asia was feasible. Were climatic and ecological conditions a filter for their dispersal to Asia?

Allosoricinae FEJFAR, 1966

This extinct subfamily consists of only two genera, *Allosorex* FEJFAR, 1966 and *Paenelimnoecus* BAUDELOT, 1972. Species of the last genus are very small, similar in size to one of the smallest Recent shrews, *Suncus etruscus* (SAVI, 1822). The inclusion of the genus *Paenelimnoecus* in the Allosoricinae is disputed by Storch *et al*. (1998), who referred to it as "Soricinae incertae sedis".

So far, the oldest representative of the subfamily, *Paenelimnoecus micromorphus* (DOBEN-FLORIN, 1964), was found in Europe. It was known from the Early Miocene (MN3, MN4) localities of the Czech Republic and Germany. In the Middle Miocene (MN6), another species of genus *Paenelimnoecus*, *P. crouzeli* BAUDELOT, 1972 was listed from France. Rare in the Early and Middle Miocene, *Paenelimnoecus* extended its range

into the Late Miocene. *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970) was discovered in several European localities dated from MN9 to MN13. It probably became extinct at the end of the Miocene; in the Early Pliocene it was replaced by another species, *P. pannonicus* (KORMOS, 1934), which survived until the Late Pliocene. The youngest (MN16) locality in which an unnamed *Paenelimnoecus* was found is Rbielice Królewskie 1A in Poland (Rzebik-Kowalska 1991, 1998).

Paenelimnoecus also occurred in Asia. The oldest, undetermined, forms were found in the Middle Miocene of Asia Minor. From the Late Miocene of Asia Storch *et al*. (1998) listed *P. obtusus* STORCH, 1995 in China (MN13) and two undetermined species of this genus in West Siberia (MN12, MN13). After a gap in the Early Pliocene, *P. chinensis* JIN AND KAWAMURA, 1997 was discovered in the Late Pliocene of China. The unnamed *Paenelimnoecus* in Daodi (MN16, China) is, so far, the youngest one with remains of the Allosoricinae (Storch *et al*. 1998). As seen above, the genus *Paenelimnoecus* has a long history in Europe, beginning with the Early Miocene. Outside Europe, its Middle Miocene remains were also found in neighbouring Asia Minor and West Siberia, whereas its oldest data from China come from the end of the Late Miocene (MN12 and MN13). These facts suggest its European origin and later dispersal in an eastern direction.

In the Early Pliocene a new member of Allosoricinae appeared in Europe. *Allosorex stenodus* FEJFAR, 1966 discovered in the Slovakian locality of Ivanovce (MN15). It was also found in Romania, in a locality of the same age (Radulescu *et al*. 1995). ?*Allosorex* sp. was mentioned from an older (MN14) locality in France (Guerin & Mein 1971). The genus *Allosorex* is known only from Europe.

Limnoecinae REPENNING, 1967

The extant exclusively North American subfamily Limnoecinae includes two genera (*Angustidens* REPENNING, 1967 and *Limnoecus* STIRTON, 1930) and three to four species. It stratigraphically ranged from the Early Miocene to the earliest Pliocene (Harris 1998).

Crocidurinae MILNE-EDWARDS, 1872

Crocidurinae is one of the two subfamilies, which survived until Recent time. Data on their early history are extremely poor. Their oldest remains were described from two Middle Miocene localities from Asia Minor (MN7+8; Storch *et al*. 1998). From about the same age originate the remains of *Myosorex* sp. cited by Butler (1998) from Tunisia in Africa. Late Miocene (MN13) Crocidurinae were found in Asia Minor (Storch *et al*. 1998). In Europe, the oldest remains come from the Late Pliocene (MN16, MN17). They belong to two species of the Recent genus *Crocidura* WAGLER, 1832. From Austria *C.* cf. *obtusa* KRETZOI, 1938 was mentioned and *C. kornfeldi* KORMOS, 1934 from the Czech Republic, Hungary, and Slovakia (Rzebik-Kowalska 1998). All remaining data on fossil Crocidurinae of Asia, Africa and Europe are referred to the Pleistocene and Holocene.

Today, Crocidurinae contain mostly tropical forms of the Old World with 12 genera and 218 species. In Africa the subfamily shows the greatest diversity (nine genera and about 145 species, 106 of which belong to the genus *Crocidura*). In Asia the number of crocidurines is about half those above (5 genera and 69 species). Six species of two genera, *Crocidura* and *Suncus* EHRENBERG, 1832, which have successfully invaded the Palaearctic, are restricted to latitudes south of about 53° N and many of them are synanthropic (Wolsan & Hutterer 1998).

The apparently late appearance of the Crocidurinae in Asia (with the exception of Asia Minor) and Europe and their clearly African affinities suggest that they evolved mainly in Africa. During the Early and Middle Miocene intense faunal exchange between Eurasia and Africa occurred through SE Europe and Asia Minor (Dawson 1999).

This was probably also the time of exchange of Crocidurinae species between these continents.

Soricinae Fischer von Waldheim, 1817

The Soricinae are the second Recent subfamily of shrews. It consists of 11 genera and 117 species (Wolsan & Hutterer 1998). Today they occur in Eurasia and North America as well as in the northern part of South America. According to Repenning (1967), the boundary between two living subfamilies coincides with the position of the Miocene Tethys and this "explains an incredible degree of endemism with these shrews".

Today 7 genera with 52 species live in Asia, 5 genera and 60 species in America and 2 genera (*Sorex* Linnaeus, 1758 and *Neomys* Kaup, 1829) with 11 species in Europe. Most of the extant species on all continents belong to the genus *Sorex* Linnaeus, 1758, with exception of the northern part of South America, where species of the genus *Cryptotis* Pomel, 1848 are the only shrews present (Wolsan & Hutterer 1998).

The fossil record of the Soricinae is much better than those of the Crocidurinae, but it is still insufficient to fully understand their history and evolution. Fossil Soricinae were extremely diverse. So far 24 named fossil genera have been found in Europe, 20 in Asia and 16 in America; 13 genera were common in Asia and Europe and only one (*Sorex*) is common to Asia, Europe and America. Soricinae are absent in Africa, although one of their representatives, *Asoriculus maghrebiensis* (Rzebik-Kowalska, 1988), was found in the Pliocene / Pleistocene in Morocco. It probably came there along the southern shore of the Mediterranean Sea from Europe, where several species of this genus are known from the Late Miocene to the Middle Pleistocene (Rzebik-Kowalska 1988, 1998).

As mentioned above the subfamily consists of seven tribes. The representatives of these tribes are also known as fossils. The first five tribes (see Introduction) are known in America, while all tribes with the exception of Notiosoricini are present in Europe and Asia. The diversity of fossil soricine shrews in Europe and North America is large but in Asia and Africa the knowledge concerning them is clearly incomplete, therefore only data on the oldest taxa are presented below.

The oldest known soricine shrews belong to the genus *Hemisorex* Baudelot, 1967 (tribe Blarinellini). They are known exclusively from Europe. Their earliest remains described as ?*Hemisorex* sp., were found in Germany (Early Miocene, MN3; Ziegler 1989). *H. robustus* Baudelot, 1967 was collected in France in the Middle Miocene (MN6; Baudelot 1967), and *H. suchovi* Lungu, 1981 is known from the Late Miocene of Moldova (Lungu 1981). The youngest, remains of *Hemisorex* (Late Miocene, MN13), were found also in France (Guerin & Mein 1971). Soricinae were also found in North America. They belong to the genus *Antesorex* Repenning, 1967 (Soricini) and are dated to the middle and late Early Miocene (Harris 1998).

Besides *Hemisorex*, the other old soricines of Europe were not found earlier than in the Late Miocene (MN9). At the beginning of the Late Miocene (MN9), the genus *Crusafontina* Gibert, 1974 (tribe Anourosoricini) appeared. This tribe consists of taxa extremely specialized in the structure of the teeth and masticatory system. Its only living representative (Asia), *Anourosorex squamipes* Milne-Edwards, 1872 is, according to Repenning (1967), the most specialized recent shrew. Species of this tribe survived in Europe to the Late Pliocene [MN16; *Kordosia topali* (Janossy, 1972), Hungary; Mészáros 1997].

The Asiatic Anourosoricini, *Anourosorex oblongus* Storch & Qiu, 1991, appeared later (MN11-12) in China. Another Late Miocene (MN12) shrew of this tribe in Asia belonged to the genus *Paranourosorex* Rzebik-Kowalska, 1975 found in the south of West Siberia. Until the Early Pliocene, probably more species appeared also in the south of West Siberia [*P. seletiensis* Storch &

ZAZHIGIN, 1996 (MN13), *P. gigas* RZEBIK-KOWALSKA, 1975 (MN14)] and in China (MN13) *P. inexpectatus* (SCHLOSSER, 1924). According to Storch & Zazhigin (1996), the West Siberian *Paranourosorex* belonged to a single evolutionary lineage with a range between the MN12 and MN14. The latest species, *P. gigas*, was also found in one European locality in Poland dated to MN14, and an unnamed species of this genus in the Late Pliocene (MN15) locality in the Ukraine (Topachevsky *et al*. 1988). *Paranourosorex*, a genus of Asiatic origin, probably spread to Europe in the beginning of the Pliocene (Storch & Zazhigin 1996). In North America, the tribe was represented by two species of the genus *Anouroneomys* HUTCHISON & BOWN, 1980 ranging from the latest Middle Miocene to earliest Pliocene in Nebraska and Oregon. They present the oldest remains of Anourosoricini in the Northern Hemisphere (Harris 1998).

Besides the above-mentioned shrews some other taxa also appeared in the Late Miocene sediments of Europe. They were: *Petenyia* KORMOS, 1934 (MN9, Blarinellini), *Amblycoptus* KORMOS, 1926 (MN12, Anourosoricini), *Asoriculus* KRETZOI, 1959 (MN13, Neomyini), *Deinsdorfia* HELLER, 1963 and *Sorex* (MN13, Soricini). Two of these genera, *Petenyia* and *Sorex*, also appeared in Asia but a little later, in MN12 and MN11-12 respectively. Moreover, *Blarinella* THOMAS, 1911 (MN11-12), *Alloblarinella* STORCH, 1995, *Cokia* STORCH, 1995, *Paenepetenyia* STORCH, 1995 (all Blarinellini, MN13) and *Zelceina* SULIMSKI, 1962 (Soricini, MN13) were found for the first time in Asia. In the Early Pliocene *Alloblarinella* and *Cokia* were also found in Europe (Rzebik-Kowalska 1998, Storch *et al*. 1998). Species of the Blarinini first appeared in North America at the end of the Middle or Late Miocene, while in Asia and Europe they are known only known from the Early Pliocene.

The exclusively fossil Beremendiini are known from Eurasia. They were represented by three genera: *Beremendia* KORMOS, 1934, *Peisorex* KOWALSKI & LI, 1963 and *Lunasorex* JIN & KAWAMURA, 1996. Their oldest remains belonging to *Beremendia* were found in Early Pliocene (MN14) localities of Europe. It survived until the earliest Middle Pleistocene. In Asia, representatives of this tribe are known from Late Pliocene until the Middle Pleistocene (Rzebik-Kowalska 1998, Storch *et al*. 1998).

Unfortunately the origin and the place of evolution of most Soricinae taxa remain, so far, unknown.

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