

# Insectivore faunas from the Lower Miocene of Anatolia — Part 8: Stratigraphy, palaeoecology, palaeobiogeography

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Keywords: Insectivora, Anatolia, Early Miocene, biostratigraphy, palaeoecology, palaeobiogeography. This article deals with biostratigraphy, palaeoecology and biogeography of the Late Oligocene/Early Miocene insectivore faunas from Anatolia. With the exception of the much younger fauna from Kesköy, all faunas contain the same insectivore species. Kesköy contains the same genera, but mostly different species. It has been suggested that insectivores are of limited stratigraphical use due to the longevity of the taxa. This seems to hold true for the Early Miocene faunas from Anatolia.

Changes in the composition of the insectivore faunas are used to infer environmental changes. A rise in the abundance of insectivores near the MP 30/MN 1 transition is believed to be indicative of a climatic amelioration. The dominance of *Theratiskos* in Harami and Kesköy may reflect a somewhat dryer environment than indicated by the Kilçak assemblages.

Three periods of migration are deduced from the comparison of the stratigraphical distribution of the European and Anatolian insectivores. During the Late Oligocene various insectivores migrated into an area including Anatolia. Somewhere around the MN 2/MN 3 transition *Galerix* and *Desmanodon* migrated from Anatolia into Europe. During MN 4 we find a large number of migrations into Europe, e.g. that of *Dinosorex*. The palaeogeographical and ecological changes that allowed the various migrations are discussed.

## Contents

Introduction .....	101
Stratigraphy .....	102
Biostratigraphy .....	102
Stratigraphical distribution of the insectivores .....	103
Palaeoecology .....	104
Introduction .....	104
Ecology of insectivores .....	105
Palaeoenvironmental interpretations .....	108
Palaeobiogeography .....	112
Two bioprovinces .....	113
Who goes, who doesn't? .....	115
Mammal migrations and palaeogeography .....	116
Acknowledgements .....	118
References .....	118

## Introduction

This is the eighth and last paper in a series on Early Miocene insectivore faunas from Anatolia. The earlier papers (van den Hoek Ostende, 1992, 1995a, b, 1997, 2001a-c) focussed on the taxonomy of specific insectivore groups, describing the material

found in eight assemblages from Lower Miocene strata in Anatolia. The material originates from four lignite mines (see map of van den Hoek Ostende, 2001a, fig. 1), Kargi (three assemblages), Kilçak (four assemblages), Harami (three assemblages), and Keseköy (one assemblage). The material from a twelfth assemblage, Inkonak, was published outside the series in combination with the rodents from that locality (de Bruijn et al., 1992). In the current paper we will discuss the insectivore faunas, and look at the biostratigraphical, palaeoecological and biogeographical conclusions. A comprehensive paper in which the smaller mammal faunas will be discussed in combination with the palaeobotany and magnetostratigraphy of the Anatolian Lower Miocene is currently being prepared.

### Stratigraphy

Eleven of the insectivore assemblages studied were collected from four open cast lignite mines, that are situated in four different basins in Central Anatolia. Lithostratigraphic correlations between sections in different basins are impossible because the origin of the various basins is quite different. The relative stratigraphical position of the fossiliferous levels within individual mines is sometimes known from field data. This is the case for the three levels in the KYB mine of Kargi, for the three levels in the Harami mine and for two of the four levels in the Kilçak area. The Keseköy mine has yielded one assemblage only. A twelfth association that will be discussed below was collected from a road cut near Inkonak in the Sivas basin (de Bruijn et al., 1992).

The relative biostratigraphical position of the (sets of) assemblages from different mines is based on the evolutionary history of the dominant group of rodents: the Muroidea (Krijgsman et al., 1996).

### Biostratigraphy

The relative stratigraphical position of the fossiliferous levels in different basins is based on different stages of evolution in different genera of Muroidea as well as a gradual change in the composition of the muroid assemblages from *Muhsinia-Meteamys* dominated faunas assigned to the Late Oligocene towards *Eumyarion-Spanocricetodon/Democricetodon* dominated faunas of the Early Miocene. The assemblage of Keseköy is considered to be the youngest of our data set because it contains a number of groups that are not known from the other assemblages and are therefore considered to be immigrants into the area (*Megacricetodon*, *Debruijnia*, *Sayimys*). The tentative correlation of these assemblages to the European MP and MN zones was originally little more than a sophisticated guess, because the Anatolian muroid assemblages do not share one single species with those from Europe. Moreover, the family that provides the best markers for the Late Oligocene and Early Miocene in Europe, the Eomyidae, is absent in Anatolia until the Middle Miocene.

The palaeomagnetic studies of Krijgsman et al. (1996) on some of the sections that yielded the assemblages of small mammals support the stratigraphical succession suggested by de Bruijn. The correlation of the Inkonak and Harami sections to the geomagnetic polarity time scale as suggested by Krijgsman et al. (1996) and the fission track date provided by Dr P.A.M. Andriessen for a volcanic tuff that is strati-

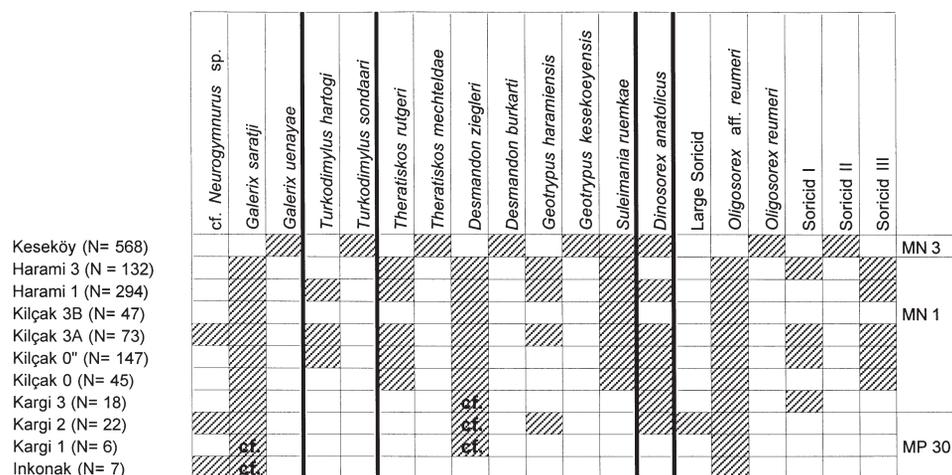


Fig. 1. Stratigraphical distribution of the Anatolian Lower Miocene Insectivores.

graphically some 15 m below the fossiliferous level of Keseköy (Krijgsman et al., 1996) allow a rough calibration to the MP-MN zonations (Kempf et al., 1997). This best fit suggests that the levels of Inkonak, Kargi 1 and Kargi 2 correlate with MP 30, that the Kargi 3 level and the Kilçak and Harami assemblages correlate with MN 1 and that the level of Keseköy correlates with MN 3. These correlations therefore constitute the time frame for the discussion of the changes observed in the insectivore assemblages. Calibration with the numerical time scale indicates that our insectivore assemblages roughly cover the interval between 24 and 18 MA.

### Stratigraphical distribution of the insectivores

The composition of the various insectivore faunas remains remarkably constant through time (Fig. 1). The same species are found in the assemblages from Kargi, Kilçak and Harami, but the large soricid from Kargi 2 has not been found in any of the younger assemblages. Soricid III, *Theratiskos*, *Suleimania*, and *Turkodimylus* are known from assemblages younger than Kargi 3 only. Van den Hoek Ostende (2001c) suggested that the absence of Soricid III, *Theratiskos* and *Suleimania* in Kargi could be explained by assuming that these are Asian immigrants that migrated into Anatolia after the deposits at Kargi were formed. For the dimyloid *Turkodimylus* this explanation is less likely, since Dimyliidae are known from Europe only. *Turkodimylus* represents a rare element in the Anatolian Early Miocene faunas. Its absence at Kargi may best be explained by the small sample sizes, although environmental control cannot be excluded.

Krijgsman et al. (1996) gave three possible ages for the Inkonak fauna, expressing a preference for an age of 25.3 MA (i.e. correlation with GPTS chron C8r). The change of *Muhsinia/Meteamys* dominated faunas to *Eumyarion* and *Spanocricetodon/ Democricetodon* dominated faunas seems to have taken place between Kargi 2 and Kargi 3.

Since this change coincides with a strong increase in the number of insectivores (Fig. 2), we assume that some change in the environment took place between Kargi 2 and Kargi 3. This change must have been relatively rapid, because there is no indication of a hiatus in the Kargi section and the stratigraphical distance between the two levels is c. 15 m. All localities between Kargi 2 and Harami 3 contain the same species of *Galerix*, *Geotrypus*, *Dinosorex* and probably also of *Desmanodon*. Assuming an age of 25.3 MA for Inkonak would imply that all of these species remained unaltered for over 2 MA. Though this is possible, an age of 23.6 MA (i.e. correlation with GPTS chron C6Cn.1r) for Inkonak seems more likely. Furthermore, following Kempf et al. (1997), an age of 25.3 MA would imply that Inkonak should be assigned to MP 28 in the Late Oligocene. This is contradicted by the muroids from Inkonak, which differ on the generic level from those found in the Middle Oligocene of Anatolia (Ünay & de Bruijn, 1987). An age of 23.6 MA would imply the correlation of Inkonak to the upper part of MP 30.

The largest change in the insectivore and rodent faunas studied is found between Harami 3 and Keseköy. This is not surprising given the age difference between the two localities. With the exception of the representatives of *Dinosorex* and *Suleimania*, the species found in Keseköy differ from those found in the older localities. The genera found in Keseköy are the same as those in the other assemblages, with the exception of cf. *Neurogymnurus*, an archaic element which is only found in Inkonak, Kargi 2 and Kilçak 3A, and Soricid III, which has its last occurrence in Harami 3.

The various rodent assemblages from the Early Miocene of Anatolia show more differences than the insectivore assemblages. Apparently the rate of evolution is higher in rodents than in insectivores. Thus the rodents seem to be more useful for stratigraphical purposes than the insectivores. Engesser & Ziegler (1996) considered insectivores less suitable as biostratigraphic markers due to their longevity. In the case of the Anatolian faunas this seems to hold true.

## Palaeoecology

### Introduction

The ecology of extinct mammals can be deduced from the habitats of extant relatives. For instance, we assume that fossil beavers lived in and near water as beavers do nowadays. The presence of beavers in a fossil locality is therefore considered indicative for a wet environment (Daams & van der Meulen, 1984). And since Petauristidae nowadays require trees, their fossils can be used as indicators for a wooded environment (de Bruijn & Ünay, 1989). The actualistic principle is applicable to a certain extent only. Particularly in those cases in which taxonomic groups had a larger distribution in the geological past, Galericinae for instance, we have to consider the possibility that they once occupied other ecological niches.

Functional morphology can also be used to determine the ecology of extinct species. Müller (1967), for instance, interpreted the peculiar bulbous teeth of Dimylidae as an adaptation for crushing the shells of molluscs. His interpretation was based on a comparison of the dentition of the Dimylidae with those of the African lizard

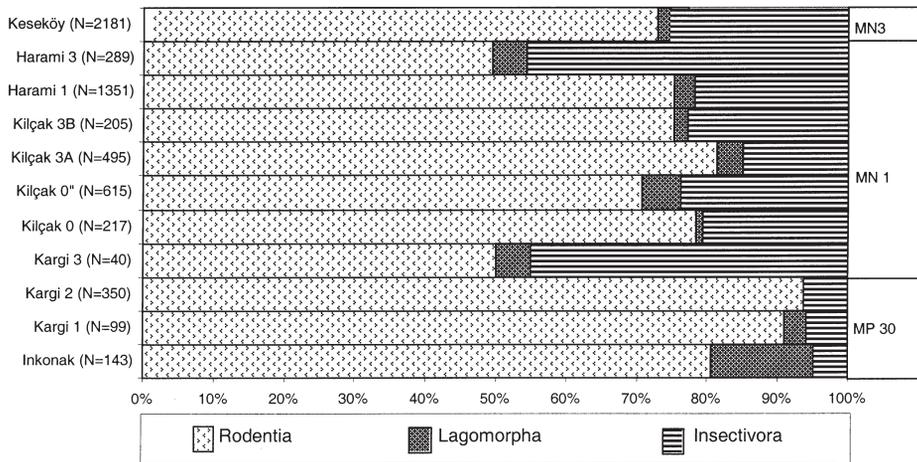


Fig. 2. The relative abundance of the various orders of small mammals.

*Varanus niloticus*. If Dimylidae fed on snails and other molluscs, they must have lived in a humid environment where snails could thrive. Therefore Dimylidae are associated with humid conditions. Some species may even have been semi-aquatic.

Another source for detecting the ecological preference of a taxon is the sedimentary environment in which it is usually found. The extinct rodent family Eomyidae is generally considered to have been forest dwellers on the basis of this principle (Mayr, 1979; van der Meulen & de Bruijn, 1982; Daams & van der Meulen, 1984; Daams et al., 1988).

Finally, van der Meulen & Daams (1992) reconstructed the ecology of a number of fossil genera by looking at their correlations with taxa of which the ecological preferences are known. These correlations proved to provide useful results.

### Ecology of insectivores

Insectivores are among the most primitive living placentals. They have a primitive physiology and need a constant food supply. Insectivores are opportunistic feeders that live on a wide range of small invertebrates. Such invertebrates are particularly numerous in the topsoil of forests. The litter decomposers (e.g. worms, wood lice, centipedes and insects) and the accompanying invertebrate predators ensure a constant food supply for various insectivores. The importance of this fauna for insectivores can be inferred from the foraging habits of present-day shrews and moles. Many shrews forage for food in the leaf litter and soil (Churchfield, 1990). Shrew-moles burrow tunnels in the litter layer. Mole species that make deep subsurface burrows also dig shallow tunnels in the topsoil for feeding (Nowak, 1991). Since litter decomposers are an important food source for insectivores, we expect a larger diversity of insectivores in wooded areas than in grasslands.

Evaporation is an important threat to the live of for instance shrews. Most insectivores today are found in moist environments, although some shrews are known to

live in semi-arid areas. Therefore, a high percentage of insectivores in a fossil fauna can be used as an indication for a humid biotope. De Bruijn et al. (1996) considered the drop in the number of insectivores in Anatolia at the beginning of MN 4 (from 27 % in Keseköy to 9 % in Horlak 1) indicative of a drop in humidity. The insectivore faunas from the Daroca-Calamocha area, which are currently under study, confirm that the percentage of insectivores in the smaller mammal faunas provides a tool to estimate humidity. Most insectivores in that area come from localities from zones A-C (upper part MN 3-MN 4), which were recognized as representing relatively humid environments (van der Meulen & Daams, 1992). In zone D (MN 5), which is believed to represent a more open, arid environment, insectivore levels drop to around 1 %.

Our observations are in line with Reumer's conclusion (1995) that humid palaeoclimates seem to stimulate shrew proliferation. Soricidae are particularly abundant in periods with a relatively warm and humid climate. These climates are favorable for wooded environments, which provide a sufficient food supply for insectivores.

#### Galericinae

The Galericinae, the gymnures or moonrats, are a subfamily of the Erinaceidae. Moonrats are nowadays restricted to Southeast Asia. Three genera and six species are recognized (Hutterer, 1993). Most species live in mountainous areas at high altitudes in damp forests. Their diet consists of insects, other invertebrates and plant matter (Nowak, 1991). The largest living gymnure, *Echinosorex gymnura*, inhabits lowlands, where it can be found in primary and secondary forests, in cultivated areas and in mangroves. *E. gymnura* may live semi-aquatically, adding fishes and frogs to the usual gymnure diet. From an actualistic point of view, therefore, Galericinae would have to be considered indicative of wet environments. Ziegler (1983), however, pointed out that Galericinae once had a much larger geographical range which included most of Eurasia and North America. *Galerix exilis* is present in the German localities Steinberg and Goldberg. The fauna from these localities is considered indicative of an open environment. This means that at least some representatives of the genus *Galerix* were not restricted to forested areas. *G. symeonidisi*, on the other hand, appears in the Daroca-Calamocha area in zone A (upper part MN 3), and survives there up to zone Da (beginning MN 5), after which it is replaced by *G. exilis*. Zones A-C represent relatively humid and forested environments in the area (van der Meulen & Daams, 1992). Thus *G. symeonidisi* seems to have preferred more moist environments than *G. exilis*, which is confirmed by its presence in the lignite mine of Aliveri (Greece), the type locality of the species. The Galericinae are represented in our Anatolian faunas by cf. *Neurogymnurus* and two species of *Galerix*.

#### Heterosoricidae

Since the Heterosoricidae are extinct, the actualistic principle cannot be used to reconstruct the ecological preferences of the group. The only reference to the ecology of Heterosoricidae was made by Doukas (1986). He assumed that *Heterosorex ruemkae*, a species found in the lignite mine of Aliveri (Greece, MN 4) was a forest dweller. He based this assumption on the sedimentary facies of the locality and on the high percentage of forestdwellers, such as Petauristidae in the fauna. In the majority of our faunas, which, like Aliveri, have been recovered from beds between lignites, we find one species of the heterosoricid genus *Dinosorex*.

### Dimylidae

The Dimylidae, represented in the Lower Miocene of Anatolia by *Turkodimylus*, is an extinct insectivore family. Their peculiar dentition, with relatively wide and flat premolars and molars with bulbous cusps, is considered an adaptation to a diet primarily consisting of snails (Hürzeler, 1944; Müller, 1967). This implies that Dimylidae lived in moist environments in which snails could thrive.

### Talpidae

The humerus plays an important role in detecting the way of life of fossil moles. Moles with a very stout humerus are considered burrowers (*Geotrypus*, *Proscapanus*, *Talpa*), whereas those with a slender humerus are considered non-fossorial (*Desmaninae*, *Theratiskos*, *Desmanella*, *Myxomygale*). A number of extinct Talpidae (e.g. *Desmanodon*) has a humerus that is neither of the fossorial type, nor of the slender type found in shrew-moles. In our Anatolian faunas we find one type of mole with a strongly developed humerus (*Geotrypus*), one with a very slender humerus (*Theratiskos*) and one with an intermediate type of humerus (*Desmanodon*). The humerus of the fourth talpid genus found in the faunas, *Suleimania*, is not known.

Although the morphology of the humerus gives an indication of its function, its value for habitat reconstruction is limited. The extant American mole *Scapanus aquaticus* has a strongly developed humerus and is indeed a good burrower. The species is, however, also well adapted to life in the water. This semi-aquatic way of life would probably not be recognized, if the species was known from fossils only.

Burrowing moles are generally associated with fairly humid conditions, because they need moist soils in order to make their burrows. Very little is known about the habitat of *Scaptonyx* and *Scapanulus*, the only Recent moles with a moderately well-developed humerus. Presumably these moles hunt in the litter layer making shallow tunnels. Shrew-moles are nowadays found in the western United States (*Neurotrichus*) and in Japan (*Urotrichus*). *Neurotrichus* shows a preference for soft soils under trees and shrubs. *Urotrichus* is found in forests and grasslands (*U. talpoides*), and also inhabits coniferous mountain forests (*U. pilirostris*) (Nowak, 1991).

### Crocidosoricinae

Very little is known about the ecological preferences of the extinct Crocidosoricinae to which all shrews from our faunas belong (*Oligosorex*, Soricid I, II and III). The subfamily bloomed during the Early Miocene (MN 1- 4). In many aspects they probably had a way of life similar to that of present-day shrews. This is, however, of little help since shrews are nowadays by far the most diverse insectivore family and occupy a large number of different niches. Different Crocidosoricinae species probably will have held different niches also, but so far no specific ecology of a crocidosoricine has been determined.

Reumer (1994) noted that the diversity of the Crocidosoricinae in Europe decreased considerably after MN 4. This decrease in diversity was partly related to a pronounced decrease in humidity around the MN 4/ MN 5 transition, but mostly to the drop in temperature in MN 5 (Mid-Miocene cooling). The Crocidosoricinae that survived are mainly found in southern regions. This leads to the assumption that Crocidosoricinae were warmth-loving shrews adapted to the warm climates of the Early Miocene of Europe.

### Palaeoenvironmental interpretations

The localities used in this study lie in different basins that are geographically far apart. Nevertheless, it was noted that their taxonomical composition is remarkably constant (Fig. 1, Table 1), and we will use the available Anatolian insectivore record to reconstruct major changes in the environment. In the future a palaeoenvironmental study of the combined insectivore and rodent records will be carried out. All faunas are sampled from a similar facies (palaeosols), except the fauna from Harami 3, which was sampled from a laminated coal. The Keseköy locality is believed to have been formed at higher altitude (de Bruijn, pers. comm.) which may have influenced the composition of the fauna.

#### Climatic amelioration around the MP 30/MN 1 transition

Figure 2 shows the relative abundances of the various small mammal orders. Bats have been found in some of the localities, but these rare finds have been omitted. The older assemblages contain less than 10 % of insectivores. In Kargi 3, however, the number of insectivores increases dramatically. The high proportion of Insectivora in Kargi 3 may be partly due to chance in view of the small sample size. However, in all our samples from MN 1 and MN 3 the percentages of insectivores are higher than 20 %. In Kargi 3 and Harami 3 the insectivores even make up more than 40 % of the total fauna.

The increase in numbers of the insectivores is thought to be the result of an increase of the food supply (mainly invertebrates in the litter layer), in its turn related to a climatic amelioration during the MP 30/MN 1 transition. We do not know whether there was an increase in temperature, or humidity, or a combination of the two. The small assemblage of Kargi 2 shows that the climate before the amelioration was humid enough to sustain, at least locally, a food supply varied enough for seven different insectivore species. The presence of *Geotrypus*, a true burrower, argues against arid conditions. The climatic change around the MP 30/MN 1 transition may, therefore, have consisted (in part) of a rise in temperature.

The insectivore peaks of Kargi 3 and Harami 3 are not interpreted as maxima of climatic humidity. The Kargi 3 small mammal assemblage is too small for interpretations on the basis of its quantitative composition. The Harami 3 fauna has a special taphonomy (see above) and is supposed to reflect very humid local conditions only.

The increase in insectivores coincides with a change in the composition of the Muroidea. Inkonak, Kargi 1 and Kargi 2 are dominated by *Metamys* and *Muhsinia*. The younger assemblages are dominated by *Eumyarion* and *Spanocricetodon*/*Democricetodon*. This turnover of the rodent fauna confirms that an important environmental change took place in Anatolia around the MP 30/MN 1 transition.

#### Late MN 1 palaeoenvironmental change

Figure 3 shows the relative abundances of the insectivore families. Heterosoricidae and Dimylidae are rare. In agreement with the postulated generally humid climates during MN 1 and MN 3, the dimylid *Turkodimylus* is found in Kılçak 0'', Kılçak 3A, Harami 1, and Keseköy. It is common in Kılçak 3A (Fig. 5), the only locality in which beavers have been found.

Table 1. Percentages of insectivore species in the various assemblages.

<b>Inkonak</b>		<b>Kilçak 3A</b>	
<i>cf. Neurogymnurus</i>	14 %	<i>cf. Neurogymnurus</i>	1 %
<i>Galerix cf. saratji</i>	43 %	<i>Galerix saratji</i>	41 %
<i>Oligosorex aff. reumeri</i>	43 %	<i>Suleimania ruemkae</i>	10 %
<b>Kargi 1</b>		<i>Desmanodon zieglerei</i>	1 %
<i>Galerix cf. saratji</i>	50 %	<i>Theratisikos rutgeri</i>	3 %
<i>cf. Desmanodon zieglerei</i>	17 %	<i>Geotrypus haramiensis</i>	1 %
<i>Oligosorex aff. reumeri</i>	33 %	<i>Dinosorex anaticus</i>	1%
<b>Kargi 2</b>		<i>Turkodimylus hartogi</i>	14 %
<i>cf. Neurogymnurus</i>	5 %	<i>Oligosorex aff. reumeri</i>	25 %
<i>Galerix saratji</i>	32 %	Soricid I	1 %
<i>cf. Desmanodon zieglerei</i>	23 %	Soricid III	1 %
<i>Geotrypus haramiensis</i>	5 %	<b>Harami 1</b>	
<i>Dinosorex anaticus</i>	5 %	<i>Galerix saratji</i>	22 %
<i>Oligosorex aff. reumeri</i>	27 %	<i>Suleimania ruemkae</i>	12 %
Large soricid	5%	<i>Desmanodon zieglerei</i>	5 %
<b>Kargi 3</b>		<i>Theratisikos rutgeri</i>	45 %
<i>Galerix saratji</i>	56 %	<i>Geotrypus haramiensis</i>	1 %
<i>cf. Desmanodon zieglerei</i>	11 %	<i>Dinosorex anaticus</i>	9 %
<i>Oligosorex aff. reumeri</i>	11 %	<i>Turkodimylus hartogi</i>	2 %
Soricid I	22 %	<i>Oligosorex aff. reumeri</i>	4 %
<b>Kilçak 0</b>		Soricid I	1 %
<i>Galerix saratji</i>	38 %	<b>Harami 3</b>	
<i>Dinosorex anaticus</i>	2 %	<i>Galerix saratji</i>	20 %
<i>Suleimania ruemkae</i>	24 %	<i>Suleimania ruemkae</i>	27 %
<i>Desmanodon zieglerei</i>	2 %	<i>Desmanodon zieglerei</i>	6 %
<i>Theratisikos rutgeri</i>	2 %	<i>Theratisikos rutgeri</i>	31 %
<i>Oligosorex aff. reumeri</i>	31 %	<i>Geotrypus haramiensis</i>	2 %
<b>Kilçak 0''</b>		<i>Oligosorex aff. reumeri</i>	3 %
<i>Galerix saratji</i>	23 %	Soricid I	1 %
<i>Suleimania ruemkae</i>	20 %	Soricid III	10 %
<i>Desmanodon zieglerei</i>	3 %	<b>Keseköy</b>	
<i>Theratisikos rutgeri</i>	21 %	<i>Galerix uenayae</i>	17 %
<i>Dinosorex anaticus</i>	1 %	<i>Suleimania ruemkae</i>	1%
<i>Turkodimylus hartogi</i>	1 %	<i>Desmanodon burkartii</i>	7 %
<i>Oligosorex aff. reumeri</i>	27 %	<i>Theratisikos mechteldae</i>	46 %
Soricid I	1 %	<i>Geotrypus kesekoeyensis</i>	1 %
Soricid III	3 %	<i>Dinosorex anaticus</i>	4 %
		<i>Turkodimylus sondaari</i>	2 %
		<i>Oligosorex reumeri</i>	22 %
		Soricid II	1 %

The heterosoricid *Dinosorex* appears in Kargi 2, and is found in most assemblages. The absence of this genus in Harami 3 is believed to be environmentally controlled (van den Hoek Ostende, 1995a). The absence of Dimylidae in Harami 3 is not understood.

In most assemblages the Erinaceidae account for 40-60%, but in Kilçak 0'' and the three youngest faunas only for c. 20% of the insectivore fauna. The Soricidae also shows a decrease in the younger localities. The decrease in Erinaceidae and Soricidae is compensated by an increase in number of the Talpidae. The higher percentages of Talpidae in MN 1 are primarily caused by the genera *Suleimania* and *Theratiskos* that first appear in Kilçak.

The insectivore fauna of Kilçak 0'', with a relatively high proportion of *Theratiskos*, is remarkably equitable (Table 1, Fig. 5). Four species occur in percentages equal to or above 20%, in a range of 20-27%. We attribute this to special (though unknown) conditions of the local environment as in the case of Harami 3, the composition of which is only slightly less equitable than that found for Kilçak 0''. In Kilçak 3A and 3B the Talpidae account for less than 20%. Thus Figure 3 suggests a drop in the talpids after Kilçak 0'' followed by a marked increase after Kilçak 3B. However, the order of the Kilçak localities in the various figures is based on estimates in a poorly exposed section (de Bruijn, pers. comm.), and is by no means certain. We consider the increase of Talpidae at the cost of the Erinaceidae and Soricidae in the Harami and Keseköy faunas to indicate a palaeoenvironmental change of second order in comparison to the change around the MP 30/MN 1 transition.

In all faunas the Erinaceidae consists primarily of one *Galerix* species only. From their relatively high percentages in MN 1 and MN 3 (Fig. 5) we infer, that the ecologi-

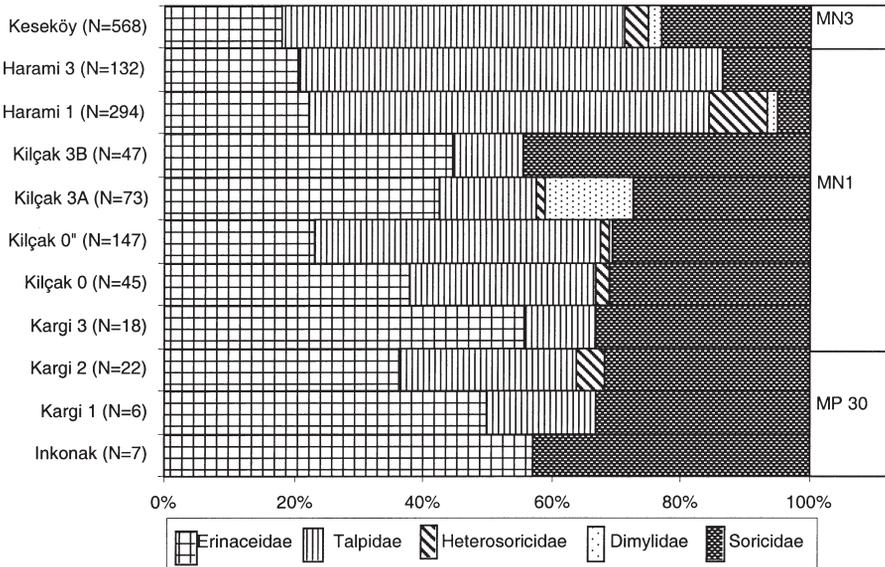


Fig. 3. The relative abundance of the various insectivore families.

cal preferences of *G. saratji* and *G. uenayae* were comparable to the forest-dwelling, extant representatives of the Galericinae and to *G. symeonidisi* (see above). On the other hand, *Galerix* is also dominant in the MP 30 insectivore faunules before the climatic change, so one might argue for it being an ubiquitous. We will return to this issue after the discussion of the talpids.

The relative abundance of the Talpidae genera is shown in Fig. 4. *Desmanodon* and *Geotrypus* are the only talpids in the small Kargi assemblages. The apparent drop of *Desmanodon* in Kilçak 0 coincides with the appearance of *Suleimania* and *Theratiskos*. *Geotrypus* is present in low numbers in Kargi 2, Kilçak 3A, the Harami assemblages, and Keseköy.

At its first appearance in Kilçak 0, *Suleimania* already makes up around 25% of the total insectivore fauna. Its numbers drop in Harami 1 but peak again in Harami 3. In Keseköy *Suleimania* is a rare element. *Theratiskos* in contrast, is more numerous in the younger assemblages. In Keseköy it is even the most common insectivore. The proportional decrease of *Theratiskos* in Harami 3 and increase in Keseköy are accompanied by an increase and decrease of *Suleimania*, respectively (Figs. 4, 5) indicating that the two represent opposite palaeoenvironmental signals. On the basis of the similarity of the dentition of *Suleimania* with those of Dimylidae, it was assumed that like Dimylidae it favoured humid environments (van den Hoek Ostende, 2001a). Furthermore, *Suleimania* is the more common mole in Kilçak 3A, which is in line with its preference for a wet environment. Assuming *Suleimania* favoured humid environments, *Theratiskos* probably represents a relatively dry element in the faunas. This is in line with what we would expect from a shrew-mole. Van Dam (1997) found that the uropsiline mole *Desmanella* is present in the Teruel Basin (Spain) throughout the Late Miocene, even when conditions were more arid. In view of their way of life similar to that of shrews, Uropsilinae are the moles that are least dependent on humid environments.

From Harami 1 onwards *Theratiskos* takes over the dominant position of *Galerix*.

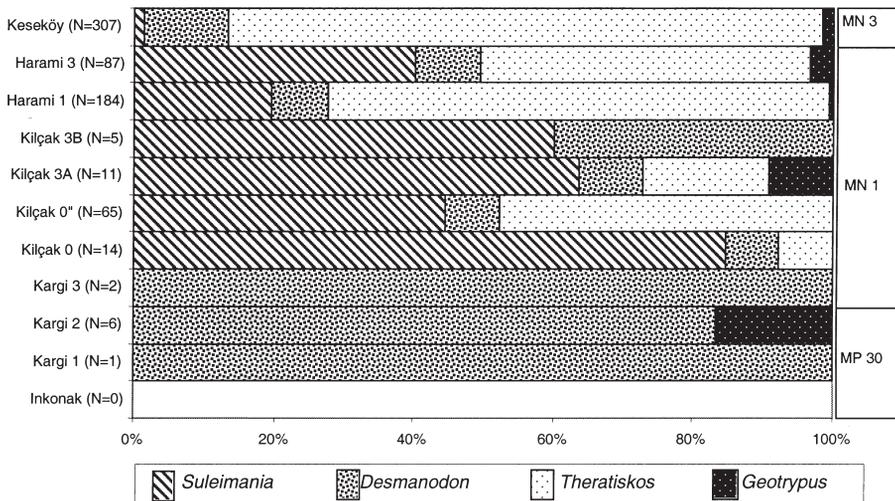


Fig. 4. Relative abundance of the talpid genera.

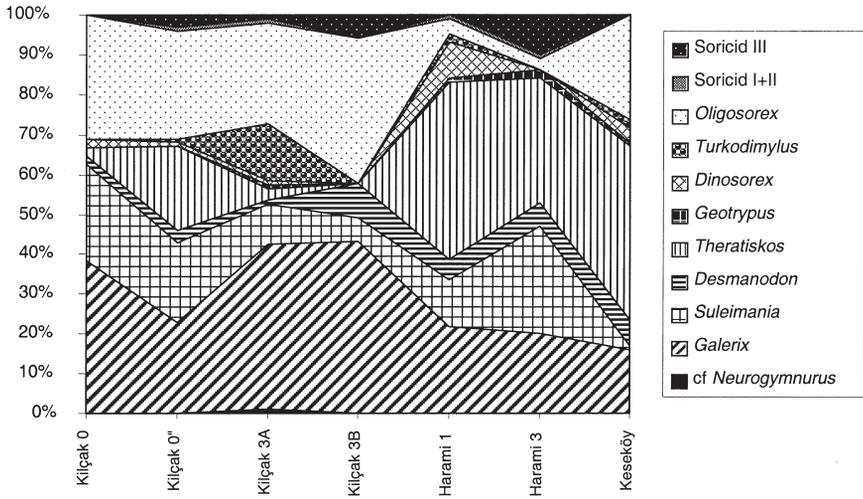


Fig. 5. Abundance of the various insectivore genera in the Kilçak, Harami and Keseköy assemblages.

Calculations of the correlation coefficients for the proportions of the MN 1 and MN 3 genera show that *Galerix* and *Theratiskos* are negatively correlated. We interpret this take-over as being due to an environmental change favouring *Theratiskos* by enlarging its habitat at the cost of that of *Galerix*. A (slight) decrease of humidity would be consistent with the interpretation of the ecology of *Theratiskos* and the first option given above for the preferences of *Galerix*. The increase of *Theratiskos* also coincides with the decrease of the soricids (mainly *Oligosorex*). Van den Hoek Ostende (2000a) argued that *Theratiskos* may have been in competition with the middle-sized *Oligosorex* aff. *reumeri* and Soricid I, and that the evolution of the first to *O. reumeri* and of the second to Soricid II in Keseköy towards smaller size was an adaptation to evade the competition. The increase in numbers of *Oligosorex* in Keseköy may be the result of this evolution. The common presence of Soricid III in Harami 3 appears to be related to local conditions. So we conclude that in late MN 1 a decrease in humidity took place, which favoured some species and was less favourable to others, but did not influence the overall diversity of the insectivores. After MN 3 the proportions of insectivores in the Anatolian small mammal faunas drop to about 10 %, suggesting a change to more arid environments (de Bruijn et al., 1996).

### Palaeobiogeography

This section is dedicated to the temporal and spatial relationships between the Anatolian insectivores and those from neighbouring areas, in particular Europe. We will discuss the immigration of representatives of insectivores into Anatolia and the subsequent dispersal/migration patterns in the course of the Late Oligocene and Early Miocene.

## Two bioprovinces

The Early Miocene smaller mammal faunas from Anatolia show considerable differences with those from Europe. Muroidea dominate the Anatolian faunas, whereas the co-eval rodent faunas in Europe are dominated by Eomyidae and Gliridae. In Europe two Oligocene murid lineages persist in MN 1 and 2, while MN 3 is characterized by the near-absence of Muroidea (only the aberrant cricetid genus *Melissiodon* has been encountered in this so-called Cricetid Vacuum). The differences between Anatolia and Europe are not only apparent in the rodents. Marsupials (the genus *Amphiperatherium*) are common in Europe throughout the Early Miocene and in part of the Middle Miocene. No marsupials have been found in Anatolia so far. The Early Miocene insectivore faunas of Europe and Anatolia show marked differences also. The erinaceid subfamily Galericinae is absent in Europe MN 1 and MN 2, but present in Anatolia, while the talpid genera *Desmanella*, *Asthenosaptor*, *Mygatalpa*, and *Paratalpa* are found in Europe, but not in Anatolia. The talpid genera *Theratiskos* and *Suleimania* and the dimylid *Turkodimylus* are known from Anatolia only.

Thus smaller mammals strongly suggest that Anatolia and Europe were different bioprovinces during the Early Miocene. Unfortunately, no larger mammals have been found in the Lower Miocene of Anatolia so far, so we cannot compare the megafauna of the two areas.

In the late Early Miocene, the mammalian faunas of Anatolia and Europe became more alike due to the immigration of various mammals. These migrations primarily took place in the course of MN 4. However, some groups already appeared in Europe in MN 3 (e.g. the equid *Anchitherium*, the anthracothere *Brachyodus*), while others appeared after MN 4. Among the European immigrants were various Muroidea which had their first occurrence in Anatolia (*Democricetodon*, *Megacricetodon*, *Eumyriodon*, *Cricetodon*), suggesting that Anatolia was potentially a centre of dispersal.

Below we will try to reconstruct the timing of migrations by comparing the stratigraphical ranges of taxa in Europe and Anatolia. First we will look at the insectivores only. Then we will compare the timing of the insectivore migrations with migration patterns of other animals from the literature.

### Insectivore migrations

Comparison of the stratigraphical ranges of insectivores in Europe and Anatolia provides a clue on the timing of migrations from Anatolia into Europe or vice versa. The ranges are summarized in Fig. 6.

Three genera, *Geotrypus*, *Oligosorex* and *Dinosorex* have their first occurrence in Europe. *Geotrypus* appears in MP 28 (Pêche-de-Fraysse, Crochet, 1974; Cournon-les-Soumeroux, Brunet et al., 1981). The first occurrence of *Oligosorex* and *Dinosorex* is also in Cournon-les-Soumeroux. *Dinosorex* is also known from Rickenbach (MP 29, Engesser, 1975). Apparently these insectivores migrated into Anatolia sometime during the Late Oligocene.

The first occurrence in Europe of the erinaceid *Galerix* is in the Spanish locality Ramblar 1 (unpublished data) at the beginning of MN 3. *Desmanodon* is believed to have its first occurrence in Europe in Navarette del Rio (uppermost MN 2), although it has to be noted that this material could not be identified with certainty (for

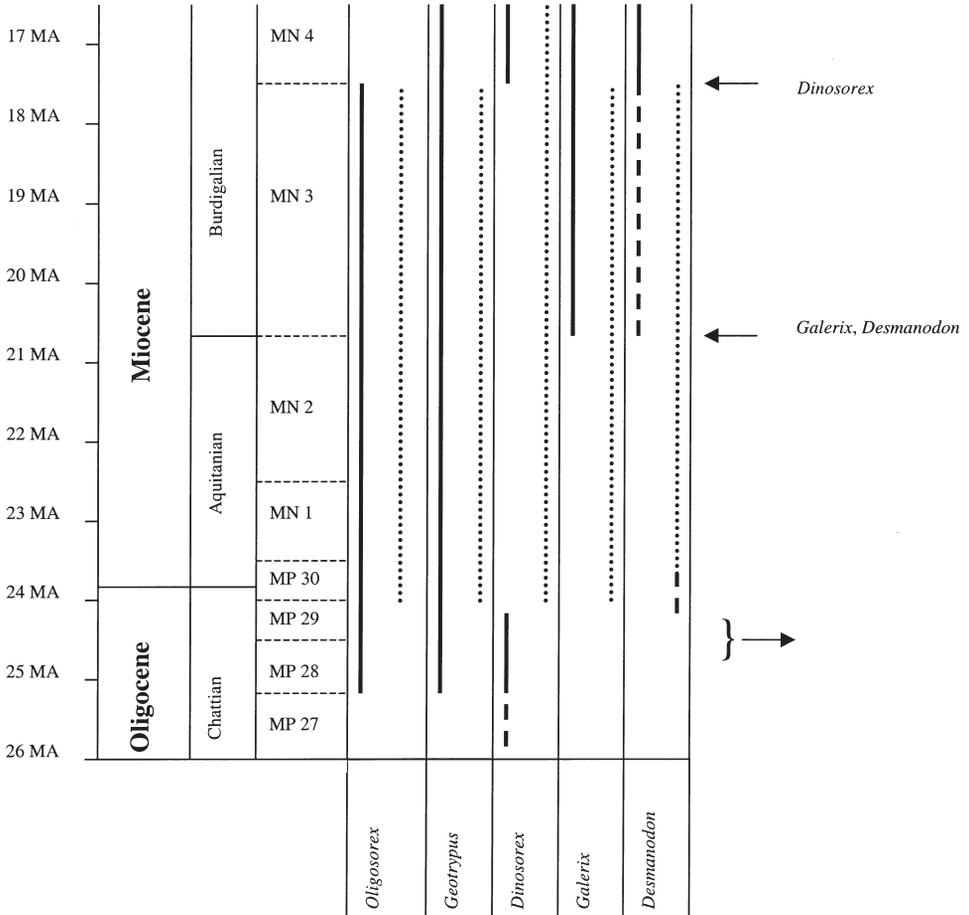


Fig. 6. Ranges of selected insectivore genera. Continuous lines indicate the ranges in Europe, dotted lines those in Anatolia/Greece. The arrows in the right-hand column indicate migration events. Arrows pointing to the right indicates a migration into Anatolia, to the left into Europe. Time-stratigraphic framework after Kempf et al., 1997.

discussion see van den Hoek Ostende, 1997). The oldest known representatives of *Galerix* and *Desmanodon* have been found in MP 30 localities in Anatolia (Inkonak for *Galerix*, Kargi 1 for *Desmanodon*). Thus migrations between Anatolia and Europe seem to have been possible around the beginning of MN 3.

The heterosoricid *Dinosorex* was absent in Europe throughout most of the Early Miocene, but lived in Anatolia (van den Hoek Ostende, 1995a). The genus re-appears in Europe near the MN 3/MN 4 transition, indicating that migrations were possible at that time as well. We therefore conclude that there were two episodes of insectivore immigration into Europe, the first near the MN 2/MN 3 transition, the second near the MN 3/MN 4 transition. This is in accordance with the conclusions of Ziegler (1989; 1990b), who noted that *Galerix*, the shrews *Hemisorex*, *Florinia* and *Miosorex*, and presumably also the talpid *Desmanodon* have their first occurrence in Europe in the

MN 3 faunas Stubersheim 3 and Wintershof West, whereas *Dinosorex* and the talpid *Proscapanus* appear in the MN 4 fauna Petersbuch 2. *Galerix*, *Desmanodon* and *Dinosorex* are presumed to be immigrants from Anatolia. The shrews *Hemisorex*, *Florinia* and *Miosorex* and the mole *Proscapanus*, however, have not been found in the Anatolian Early Miocene faunas and probably had another centre of dispersal.

#### Migration of other taxa

The insectivores suggest that there are three migration episodes. The first covers an ill-defined interval between MP 28 and MP 30, the second can be placed at the MN 2/MN 3 transition and the third at the transition MN 3/MN 4 (Fig. 6, right column). In this section we will explore whether these three migrational episodes correspond to migration patterns of other taxa.

A single molar of *Melissiodon*, a cricetid genus otherwise only known from Europe, was recovered at Kargi 2. The beaver *Steneofiber* teeth from Kilçak 3A are very similar to those of *S. eseri* from the Early Miocene faunas of the Allier (Stefen, pers. comm.). The herpetofauna of Kilçak and Harami contains numerous remains of the discoglossid frog *Latonia* (Claessens, 1995), which has its oldest known occurrence in the Upper Oligocene of Europe (Roček, 1994). Therefore it may also have been an immigrant into Anatolia.

During MN 3 a number of immigrants appear in the European faunas. The first occurrences of these genera is, however, not always near the MN 2/MN 3 transition, as is the case with the insectivores *Galerix* and *Desmanodon*. The horse *Anchitherium*, cervids and palaeomerycids appear in Spain in zone A, which is correlated with the upper part of MN 3 (Daams et al., 1998). The first occurrence of the anthracothere *Brachyodus* in Europe lies near the MN 2/MN 3 boundary (van der Made, 1996) and is therefore more or less coeval with the immigration of *Galerix* and *Desmanodon*.

The MN 3/MN 4 transition is traditionally drawn in southwestern Europe at the first occurrence of *Democricetodon* and the Proboscidea. Meanwhile, *Democricetodon* has also been found in the uppermost part of MN 3, albeit in small numbers (Daams et al., 1998). This cricetid is known from the Late Oligocene/Early Miocene faunas of Anatolia. The cricetids *Megacricetodon* and *Eumyarion*, which enter Europe later in MN 4, and *Cricetodon*, which migrates into Europe in MN 5, also have their first occurrence in Anatolia. Among the other MN 4 immigrants into Europe are the first Bovidae (*Eotragus*) and the creodont *Hyainailourus*.

Thus the migration events we deduced from the insectivores coincide with those of other taxa. Migrations in MN 3 are, however, not restricted to the lower part of that zone.

#### Who goes, who doesn't?

The MN 3 and MN 4 record in Anatolia and Europe still leaves many questions open. For instance, the largest change in the European mammal fauna is within MN 4. Relatively few migrants enter Europe in MN 3. Why did they not cross earlier, if a migration route was available? And why, if a corridor was open throughout MN 4, did taxa like *Eumyarion* and *Megacricetodon* enter Europe later than *Democricetodon*?

The selectivity of the migration pattern suggests that ecological factors play a role

in deciding which taxa were able to extend their geographical range. Van der Meulen & Daams (1992) constructed a climate curve for the Early and Middle Miocene using rodent associations from the Daroca-Calamocha area. This curve shows no changes at the MN 2/MN 3 transition. Van der Meulen and Daams interpreted the Ramblian and Early Aragonian therefore as an interval that is characterized by stable environments. The rodent assemblages are dominated by K-selected species. For migrants it must have been difficult to find a niche in such a stable ecosystem. It is remarkable that the taxa that did enter, belong to (sub)families that were not present in the ecosystem before. Antracotheres were absent in Europe since MN 1 and Galericinae were absent since the Late Oligocene. Apparently the niches for these animals were again available, and were filled by *Brachyodus* and *Galerix* respectively. Equidae were newcomers in Eurasia, having evolved in America. The forest-dwelling horse *Anchitherium* proved very successful in finding a place in the Eurasian ecosystems.

The presumed entrance of *Desmanodon* in Europe at the MN 2/MN 3 transition cannot be explained in the same way, because the genus has a European counterpart in the closely related *Paratalpa*. The youngest finds of *Paratalpa* date from the lower part of MN 2, so it is possible, that the genus became extinct in the course of MN 2 and that *Desmanodon* took its place. Another possibility is that *Desmanodon* actively replaced *Paratalpa*. The latter, being an active hunter, may have been in competition with the various Uropsilinae (*Asthenoscaptor*, *Mygatalpa*). The humerus of *Desmanodon* indicates that this genus had a more fossorial life-style than *Paratalpa*, probably making shallow tunnels in litter. Thus, *Desmanodon* may have evaded the competition of the Uropsilinae, which may have given it the edge to replace *Paratalpa*.

The Anatolian insectivores that did not disperse into Europe all had an ecological counterpart. For *Dinosorex* this is *Heterosorex*, for *Turkodimylyus* and the dimyloid-like talpid *Suleimania* the various European Dimyliidae, for *Theratiskos* the European Uropsilinae and for the various shrews the European Crocidosoricinae. It is in this context surprising, that none of the Anatolian Muroidea migrated into Europe around the MN 2/MN 3 transition.

According to van der Meulen & Daams (1992), stable environments persisted in the lower part of MN 4 (Spanish zone B), although the landscape became more open. The migration of *Dinosorex* near the MN3/MN 4 transition is somewhat surprising. We assumed that the genus could not enter Europe at the beginning of MN 3 due to the competition with *Heterosorex*. Nevertheless the two genera are found together in the MN 4 locality Petersbuch 2. Possibly this is the result of the opening of the landscape. A mosaic of forests and more open spaces increases the number of niches. This could also account for the high equitability quotients found for zone B (van der Meulen & Daams, 1992).

### Mammal migrations and palaeogeography

In this section we will compare the migrations with palaeogeographical maps by Rögl & Steininger (1983), Dercourt et al. (1986), and Rögl (1998).

The reconstruction of the Mediterranean area during the Early Oligocene (Dercourt et al., 1986) shows Anatolia as part of a large island between Tethys and Paratethys. Large parts of present day Anatolia were still below sea level at that time.

During the Late Oligocene, larger parts of Anatolia had risen above sea level, judging from the palaeogeographic reconstruction by Rögl & Steininger (1983, pl. 3). This map shows Anatolia still as part of a large island, although Rögl and Steininger assumed a possible land bridge between Europe and Anatolia near present day Croatia. Provided this reconstruction is correct, such a land bridge could explain the migration of *Dinosorex*, *Geotrypus* and *Oligosorex* from Europe into Anatolia.

In the beginning of the Early Miocene, there are enormous differences between the smaller mammal faunas of Europe (glirid/eomyid dominated) and Anatolia (muroid dominated). This suggests that some kind of barrier for mammal migrations existed between the two regions. The palaeogeographic map for the Aquitanian by Rögl (1998) suggests that at that time Anatolia was an island again.

*Suleimania*, *Theratiskos* and Soricid III, which have their first occurrence in the Kılçak assemblages, were possibly Asian immigrants. Rögl & Steininger (1983, pl. 5) reconstructed a land bridge connecting Anatolia to Asia near present-day Afghanistan in their map for the Middle to Late Burdigalian. If this reconstruction is correct, this land bridge could have allowed the migration of Asian insectivores into Anatolia. However, it is not clear when this land corridor was formed. On the map of the Late Burdigalian by Dercourt et al. (1986) this land bridge is interrupted by a narrow marine corridor.

The next migration event in which Anatolian insectivores are involved is the migration of *Galerix* and possibly *Desmanodon* near the MN 2/MN 3 transition. The anthracothere *Brachyodus* enters Europe from Africa at about the same time. Neither Rögl & Steininger (1983) nor Dercourt et al. (1986) give a palaeogeographic reconstruction for this time slice. Van der Made (1996) explained the migration of *Brachyodus* by assuming that a land bridge was formed between Anatolia and Europe as a result of a eustatic sea-level drop. According to him this sea-level drop is the TB 2.1 regression of Haq et al. (1987). This regression would also have caused the formation of land bridges between North America and Asia and Eurasia and Africa that triggered large-scale faunal exchange between the continents. Van der Made correlated the TB 2.1 regression with both the MN 2/MN 3 transition and the Aquitanian/ Burdigalian boundary. He assumed that the land bridge disappeared as the sea level rose again. A land bridge as proposed by van der Made (1996) would provide a suitable migration route for *Galerix* and *Brachyodus*. However, the existence of such a land bridge is based on the assumption that the MN 2/MN 3 transition correlates with a sea level low.

The last insectivore migration we found is the entrance of *Dinosorex* in Europe at the beginning of MN 4. Among the other taxa that immigrate into Europe at the MN 3/MN 4 transition are the cricetid *Democricetodon*, the creodont *Hyainailourus*, and the Proboscidea. All of these taxa are of southern origin (*Dinosorex* and *Democricetodon* from Anatolia, Proboscidea and *Hyainailourus* from Africa). These migrations suggest that a migration route was available from Anatolia to Europe. Steininger et al. (1996) correlated the beginning of MN 4 with the base of the Paratethian stage Ottnangian. The palaeogeographical reconstruction of the western Paratethys during the Ottnangian (Rögl & Steininger, 1983: pl. 6) suggests no major barriers for mammals between Anatolia and Central Europe. The palaeogeographic map given by Dercourt et al. (1986) for the Late Burdigalian even shows Anatolia completely connected to Europe by a wide land corridor.

In summary, there are no major discrepancies between the insectivore migrations found and the reconstructions of the Late Oligocene/Early Miocene palaeogeography.

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