



Bulletin of the Mineral Research and Exploration

<http://bulletin.mta.gov.tr>



Paleoecological investigation of the Miocene (23.03-5.33 mya) rodents (Mammalia: Rodentia) in Anatolia

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Research Article

Keywords:

Anatolia, Miocene,
Rodentia, Micromammal,
Paleoecology.

ABSTRACT

Anatolia's geographical location as a land bridge between Europe, Asia, and Africa, makes it an important passage for mammal migrations, with a rich fossil potential. However, detailed scientific studies on the Neogene paleogeography of Anatolia are scarce. Rodentia is among the major mammal groups generally adapting to different habitat types and rapidly evolving with the changing geography. Investigating this group provides data to increase the accuracy of ecological analyses. We selected Rodentia fossils from the Miocene excavation sites with published papers, and examined specimens of 14 families from 106 localities. Cricetidae, Muridae, Gliridae, and Sciuridae were found to be most dominant rodent families in Anatolia during the Early Miocene, indicating a high humidity, whereas ecological changes towards the end of this epoch led to a complex formation in the biogeography of micromammals. In the Middle Miocene, a 65% decrease in Muridae, the emergence of Eomyidae, and a significant increase in Spalacidae suggest a climate shift, towards tropical or semi-tropical conditions. In the Late Miocene, Muridae regaining its maximum level and becoming the most crowded family may indicate an unexpected rise in humidity, while the stable prevalence of Eomyidae and Castoridae point to the continuity of aquatic environments and humidity.

Received Date: 31.07.2021

Accepted Date: 30.06.2022

1. Introduction

Due to their rapid and wide geographic distribution and evolution, fossil groups of small mammals are extensively used in aging sediments belonging to the Neogene-Paleogene. These fossils contribute to the creation of an intra- and intercontinental biochronology of sediments, shedding light on the paleoecology and paleogeography of different regions. Anatolia's geographical position as a land bridge between Asia, Africa, and Europe during the Neogene-Paleogene, as it is today, has provided a passage for the intercontinental migration of mammals. Therefore, terrestrial sediments of the

Neogene-Paleogene period are widespread in Anatolia, containing fossils of several members of the mammalian fauna including rodents (Rodentia; mice, squirrels, moles, beavers, hedgehogs, etc.), lagomorphs (Lagomorpha), insectivorous mammals (Soricidae, Scandentia), and bats (Chiroptera). Rodentia constitutes the most crowded order among these small mammal groups. This order first occurred in the Late Paleocene according to paleontological data (Hartenberger, 1998), or in the Early Paleocene according to molecular studies (Wu et al., 2012). With approximately 30 families and an estimated number of more than 2.277 species, they constitute 42% of all extant mammal species (Carleton and Musser, 2005).

Citation Info: Vural, H., Özkurt, Ş. Ö. 2023. Paleocological investigation of the Miocene (23.03-5.33 mya) rodents (Mammalia: Rodentia) in Anatolia. Bulletin of the Mineral Research and Exploration 170, 15-30. <https://doi.org/10.19111/bulletinofmre.1139009>

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Including fossil records to this count may allow for a better understanding of the diversity of micromammals as a group (Chaline and Mein, 1979). In addition to species diversity, and the fact that they can be found on all continents except Antarctica, the extent of the evolutionary success of rodents is directly reflected in how they have adapted to almost all types of habitats including human settlement areas, besides their natural habitats such as trees, underground, deserts, steppes or forests, and even wetlands (Erdal, 2017).

Anatolia is a mainland formed by the merging of different continental parts. The closure of the Tethys Ocean, which was located between the two ancient supercontinents of Gondwana in the south and Laurasia in the north, and the collisions of both the Indian subcontinent and the Arabian Plate with Eurasia were the main critical events during Anatolia's terrestrial formation (Şengör and Yılmaz, 1981; Rögl, 1999). During the Oligocene epoch, Tethys was disconnected from the Mediterranean, and the Paratethys Sea was formed, covering a large portion of southeastern Europe, including the present-day Aral Sea, the Caspian Sea, and the Black Sea (Rögl, 1999). In the beginning of Miocene, land masses increased particularly in the Sub-Paratethyan bioprovince, which corresponds to the region where Anatolia is located. Around the Middle Miocene, connections were established between Paratethys and the Pacific, through the Indian Ocean, later to be closed off again. The connection between Paratethys and the Mediterranean established through the Eastern Anatolia was also closed with the collision of the Arabian Plate with Eurasia at the end of the Middle Miocene (Rögl, 1999). The connections of Paratethys with other oceans affected the intercontinental dispersal of mammals. During the Miocene, Paratethys gradually retreated, leading to an increase in the amount of land masses. Due to this increase, the fossil records of mammalian fauna in Anatolia are mostly known from the terrestrial sediments belonging to the Neogene.

Record of the African and Old World Miocene points to a decrease in humidity, accompanied by the diversification of seasonal open-air plants and animal communities (Bernor, 1984). The Miocene/Pliocene boundary indicates a shift in the environment and fauna, from warmer temperate seasonal climates to cooler temperate environments (Bernor, 1996). Although the

global cooling in this period is less significant than the ones in the Middle Miocene and the Pliocene/Pleistocene, the Late Miocene is characterized by very distinctive changes in terrestrial ecosystems. One of the most well-known changes is the strong dispersion of low-biomass plants: woodlands begin to replace forests, while savannas and grasslands spread and settle on a global scale (Van Dam, 1997). Ecological conditions of the Early Miocene indicate humid forest environments, dominated by low seasonality (Fortelius et al., 2014). In addition, paleobotanical findings from the Early Miocene sediments in Anatolia suggest the presence of humid and swamp-like areas in Western Anatolia, along with a sporadic presence of more open environments (Akgün et al., 2007; Akkiraz et al., 2011; Kayseri Özer et al., 2014). During the Middle Miocene, we see an increase of land masses in Anatolia (Rögl, 1999). Global temperatures reached maximum levels during these periods (Kaya, 2017). The ecological and environmental changes characterized by an increase in seasonality and a drought in the Late Miocene may be seen as the results of a parallel evolution in mammal species (Kaya, 2017).

This study aims to interpret the Miocene paleoecology of Anatolia, or to make ecological analyses regarding family groups with higher numbers of species by determining the Rodentia numbers in different localities and to identify the paleoenvironment in accordance with these analyses, based on database records published on Rodentia fossils obtained from several paleontological excavations carried out in Anatolia.

2. Material and Method

The data of our study consists of monographs and the surface investigation results of paleontological excavations carried out in Anatolian Miocene excavation sites, as well as scientific literature published on the paleoecology, paleoclimate, and paleobiology of the Miocene. We used the New and Old World Database of Fossil Mammals (NOW) as our main database (Fortelius et al., 2014). After obtaining the Rodentia order list from the NOW database, we excluded the specimens that were not published in any papers, and created a new data list. This final list contained Rodentia members from 106 localities, representing 14 families and around 130 species.

Among these localities, Rodentia findings were found in the following sites: Balçıklidere, Akhisar, Altıntaş, Amasya, Ayseki, Bağıcı, Bayırköy, Bayraktepe, Belenyenice, Bostanyeri, Büyükanafartalar, Cumali, Çakıllı, Çandır, Dededağ, Dendil, Develiköy, Dumlupınar, Düzyayla, Eskisubası, Gördes, Göstere, Gözetlemederesi, Hancılı, Harta, Hayranlı, Hoşköy, İnkönak, Kalamış, Kaletepe, Kaleköy, Kaplangı, Karaçay, Karaözü, Kargı, Kavurca, Keseköy, Kılçak, Kinik, Kırca, Kumköy, Mahmutköy, Mahmutlar, Mürefte, Pişmanköy, Sabuncubeli, Sandıklı-Koçgazi, Sarıçay, Şemsettin, Sinaptepe, Sofça, Söke, Süleymanlı, Tuğlu, Yapıntı, Yeni Eskihisar, Yurtyenice, and Yukarıkızılca1. In addition to these, ongoing fossil excavations are currently being carried out in Kurutlu, Sofular, Yeni Yaylacık, Paşalar, and Çorakyerler.

We compiled the data for order Rodentia in Microsoft Excel 2007, and created graphics using the same software. We prepared the locality maps on the geological map of Anatolia. The percentages in graphics represent the ratio of the number of species in families relative to the number of species in other families.

3. Findings

3.1. Early Miocene Rodentia from Anatolia and Their Localities

As the tropical regions of the Late Oligocene and the Early Miocene expanded globally, the Early Miocene became dominated by green plants, as well as tropical and subtropical climates (Ataabadi, 2010). The Early Miocene was generally a humid period with high precipitation (Fortelius et al., 2002), and a complicated timeframe with weak seasonality and low temperatures (Utescher et al., 2000). While Muroidea was dominant in Anatolia in the Early Miocene, Gliridae and Eomyidae were dominant in Europe. This indicates a faunal barrier between the Afro-Arabic and the Eurasian plates. In this period, a few Asian mammalian taxa such as the genera *Cricetodon*, *Spanocricetodon*, and *Democricetodon* from the family Cricetidae, alongside *Vasseuroyms* and *Glirulus* from the family Gliridae emerged in Anatolia. These taxa have also migrated to the Balkans and Western Europe (Agusti et al., 2001; Koufos et al., 2005). *Glirulus*, *Democricetodon* and *Cricetodon* are inhabitants of

forest biotopes (Nargolwalla, 2009). This may indicate that the localities where these genera lived had an ecology where subtropical or tropical temperatures prevailed, along with humid conditions. Localities for the genera in question are Belenyenice, Dededağ, Dumlupınar, Gökler 4A, Hancılı 2, Harta, Kargı 1, Kargı 2, Kargı 3, Keseköy, Kılçak 3a, Kılçak 3b, Kılçak 0", Kınık, Kınık 2, Sabuncubeli, Söke, and Yapıntı for *Cricetodon*; Harami, Kargı 1, Kargı 2, Kılçak 3a, Kılçak 3b, Kılçak 0, and Söke for *Spanocricetodon*; Belenyenice, Harami, Harami 4, Kılçak 3a, Kılçak 0, Kılçak 0, and Kınık 1 for *Vasseuroyms*; and Keseköy and Söke for *Glirulus*. Genus *Debruijina* from the family Spalacidae was first seen in Anatolia in MN2. *Megacricetodon*, *Anomalomys* and *Karydomys* first appeared in Anatolia in MN3 (Alçiçek, 2010). The localities where these genera are found are Belenyenice, Dededağ, Dumlupınar, Hancılı 2, Harami, Hoşköy, Keseköy, Kınık 1, Söke, Yapıntı, and Yurtyenice for *Megacricetodon*; Belenyenice, Dededağ, Hancılı 2, and Söke for *Anomalomys*; and Dumlupınar, Söke, and Yapıntı for *Kardomys*. Forests constituted the predominant habitat type in the beginning of the Miocene, and the most common species of large mammals were the brachyodont (low-crowned teeth) forest forms, while species adapted to open environments were rare. Among the Rodentia fauna, Cricetidae was the dominant family. Not all species of this family are adapted to closed environments, although species of genera such as *Democricetodon* and *Eumyarion* definitely seem to prefer more closed environments (Van den Hoek Ostende, 2001). The Rodentia records of Anatolia from the Early Miocene are different from those of Europe and Central Asia. Some Rodentia species entered Anatolia in earlier periods. In this period, the scarcity of family Ctenodactylidae is replaced by Muroidea, which is marked by the emergence of *Eumyarion microps* as well as species belonging to *Deperetoyms*, *Democricetodon*, *Enginia*, and *Heterosminthus* (Ünay et al., 2003). The scarcity of Ctenodactylidae is reflected by the presence of only one genus (*Sayims*) found in Harta, Keseköy, and Yapıntı among all localities we investigated in Anatolia. From this period, the genus *Eumyarion* is found in localities Gökler 4A, Gördes, Hancılı 2, Harami, Kargı 2, Keseköy, Kılçak 3a, Kılçak 3b, Kılçak 0, Kınık 1, Kınık 2, Sabuncubeli, and Yapıntı; *Deperetoyms* is found in Gördes, Harami,

Kargı 2, Kargı 3, Kılçak 3a, Kılçak 3b, Kılçak 0, and Kınık; *Democricetodon* in Belenyenice, Gökler 4A, Gördes Hancılı 2, Harami, Harami 4, Harami 5, Harta, Hoşkøy, Kargı 3, Kesekøy, Kılçak 3a, Kılçak 3b, Kılçak 0, Kılçak 0, Sabuncubeli, Semsettin, Söke, Yapıntı, and Yurtyenice; and *Enginia* only in Yapıntı. The origin of Sciuridae is unknown. The first Anatolia records of it from this period are in Kargı 2 and Kılçak 0-3b (Ünay et al., 2003). Rodentia families identified from the Early Miocene paleontological excavation sites in Anatolia are Cricetidae (36%), Muridae (28%), Gliridae (15%), Sciuridae (10%),

Castoridae (3%), Dipodidae (3%), Anomalomyidae (1%), Ctenodactylidae (1%), Petauristidae (0.77%), and Spalacidae (0.77%) (Figure 1).

In paleontological studies carried out in Anatolia belonging to this epoch, the localities of Belenyenice, Dededağ, Dumlupınar, Gökler, Gördes, Hancılı, Harami, Harta, Hoşkøy, Inkonak, Kaplangı, Kargı, Kesekøy, Kılçak, Kınık, Sabuncubeli, Şemsettin, Söke, Yapıntı, and Yurtyenice are given on the map (Figure 2). Anatolian localities, where Rodentia families were seen, are also given as a list (Table 1).

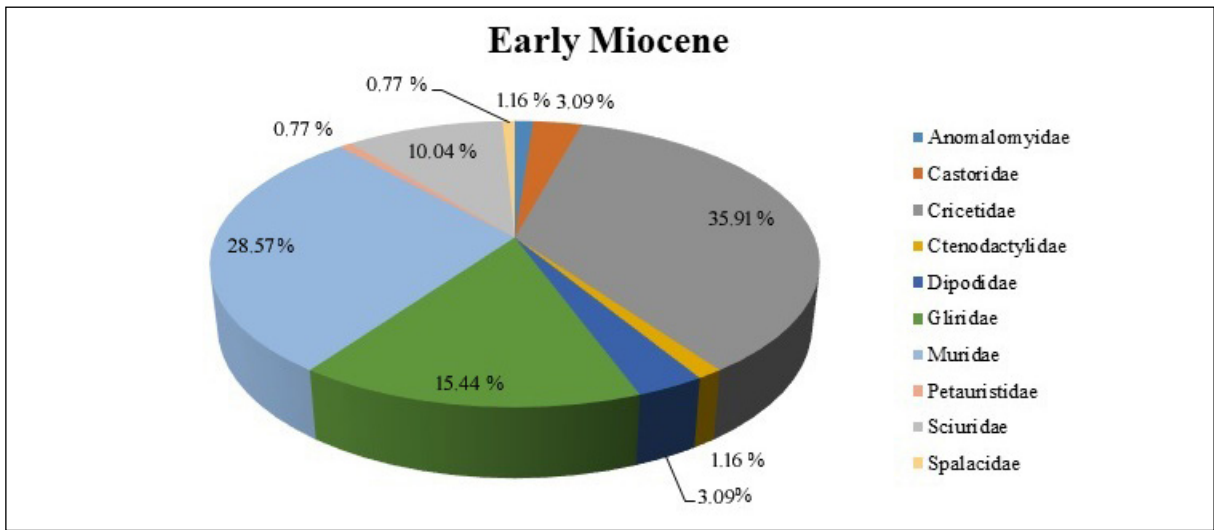


Figure 1- Early Miocene Rodentia findings from Anatolia.

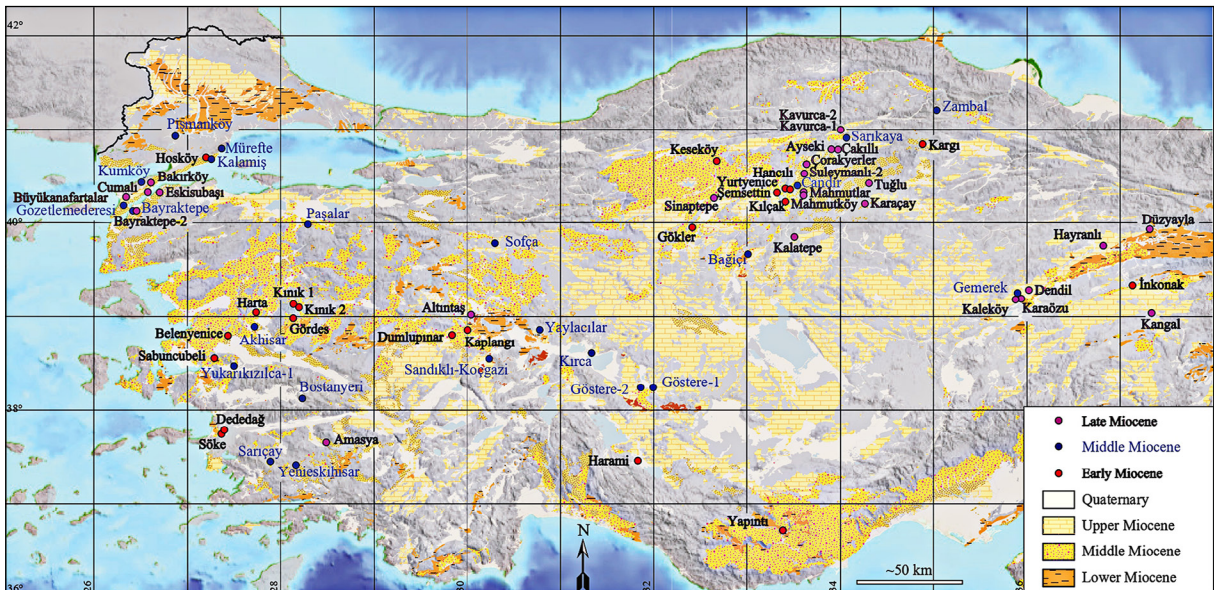


Figure 2- The localities in Anatolia, where Rodentia findings from the Miocene were found.

Table 1- Early Miocene Rodentia families from Anatolia, listed according to their localities.

LOCALITY	MN ZONE	Anomalomyidae	Castoridae	Cricetidae	Ctenodactylidae	Dipodidae	Gliridae	Muridae	Petauristidae	Sciuridae	Spalacidae
Hancılı 2	MN 4			X			X	X			X
Gökler4A	MN 2		X	X			X	X		X	
Keseköy	MN 3			X	X		X	X		X	
Kılçak3a	MN 1		X	X			X	X			
Kılçak 3b	MN 1			X		X		X			
Kılçak 0	MN 1		X	X		X	X	X		X	
Kılçak 0"	MN 1			X		X	X	X		X	
Şemsettin	MN 4			X			X		X	X	
Yurtyenice	MN 4			X			X				
Dededag	MN 4	X		X			X	X		X	
Söke	MN 3-4	X		X			X	X			
Kargı 1	MN 1			X				X			
Kargı 2	MN 1			X		X		X			
Kargı 3	MN 1			X		X		X		X	
Yapıntı	MN 3-4			X	X		X	X		X	
Harami	MN 2		X	X			X	X		X	
Harami 1	MN 2			X						X	
Harami 3	MN 2									X	
Harami 4	MN 2		X	X			X	X		X	
Harami 5	MN 2		X				X	X			
Dumlupınar	MN 4-5			X			X	X	X		
Belenyenice	MN 4	X		X			X	X			
Gördes	MN 3						X	X		X	
Harta	MN 3			X	X		X	X		X	
Kınık	MN 3							X			
Kınık 1	MN 3			X			X	X		X	
Kınık 2	MN 2		X	X			X	X			
Sabuncubeli	MN 3		X	X			X	X		X	
İnkonak	MP 30			X		X	X	X			
Hoşkoy	MN 4			X		X	X			X	
Kaplangı 1	MN 4									X	
Kaplangı 2	MN 4									X	

To make sense of the ecology of extinct mammals, it may be necessary to look at the ecology of their living relatives. It is a widely known fact that the family Castoridae (beavers) lives in or near water. We may say that the fossil relatives of this family also preferred similar environments. Therefore, the presence of Castoridae reflects the presence of wet environments (Daams and Ders Meulen, 1984). Gliridae, which is thought to have originated in Europe, appeared in Anatolia in the Late Oligocene

and the number of species belonging to this family also diversified in this period (Ünay, 1994). The family Castoridae is known from the localities of Gökler 4A, Harami, Harami 4, Harami 5, Kılçak 3a, Kılçak 0, Kınık 2, and Sabuncubeli. We can say that these localities match the ecology mentioned above. Cricetidae and Muridae, the families with the highest number of species, were recorded from the Central Anatolian, Western Anatolian, and the Mediterranean Regions, with respect to their current geographic

boundaries. Families Gliridae and Sciuridae, on the other hand, were only recorded from Central Anatolia with provided numbers, although they were seen in both Central and Western Anatolia.

Most members of the family Spalacidae (0.77%) are adapted to open meadowlands. The fact that they were less in number than the other Rodentia members in the Early Miocene may be the result of Anatolia's heavily forested ecology. However, although the members of Muridae (28%) and Cricetidae (35%) may not be reckoned as definite forest dwellers, they appear to be the two most dominant families during this period. Gliridae (15%) species constitute a group that was adapted to a humid and more closed ecology. The above-mentioned families form a complex pattern during this period. According to the analyses, it is possible to say that the ecology was dominated by deciduous trees, moist, and had partially open habitats.

3.2. Middle Miocene Rodentia from Anatolia and Their Localities

Ecological conditions of the Middle Miocene resemble those in the Early Miocene. In this period, the home ranges of numerous mammals that had immigrated from Africa expanded in Eurasia, while the Earth's tropical regions shifted towards the north and the middle latitudes of Eurasia due to an increase in Arctic glaciers and the cooling of polar regions. As a result, possibly a tropical and semi-tropical climate zone dominated the middle latitudes from Eastern Asia to Western Europe, including Anatolia (Kaya, 2017). Regional palynological evidence indicates a subtropical or tropical climate around the Mediterranean during the Middle Miocene (Akgün et al., 2007). In this period, Western Anatolia is generally represented by mixed mesophytic and evergreen forests. Some regions are characterized by broad-leaved deciduous forests (Kayseri-Özer, 2017). This period is characterized by Castoridae and Gliridae (MN6-8). Although *Cricetodon* and *Megacricetodon* of Asian origin were known from before, *Byzantinia*, *Myocricetodon* and *Pliospalax* are seen in this period for the first time (Alçiçek, H., 2010). Localities for these genera are Bağıçi, Bayraktepe, Derekebir, Pişmanköy, Yaylacılar, Yeni Eskişehir, Sandıklı-Koçgazi, Kırca, Gözetlemederesi, Sofça Akhisar, Kalamış for *Byzantinia*; Kalamış,

Sinap 64, Sinap 65, Yeni Eskişehir, and Bağıçi for *Myocricetodon*; Bayraktepe 1, Paşalar, Sarıçay, Sandıklı-Koçgazi, Kırca, Bağıçi, Pişmanköy, Göstere, Sofça, Yeni Eskişehir, and Sarıçay for *Pliospalax*. While *Eomyidae* of North American origin is seen in Central Asia and Europe, it appears in Anatolia during the Middle Miocene, and this may be related to the MN5 entry of *Keremidomys* and *Eomyops* species into Europe (Ünay et al., 2003). While *Eomyidae* was the dominant family in Europe during the Early Miocene, the first findings from Anatolia is MN5 unearthed in Çandır (Kaymakçı, 2000). The existence of families Castoridae and *Eomyidae* during this period indicates a paleoecology similar to that of the Early Miocene. While *Eomyidae* is seen in Europe in MN3, it is seen in Anatolia in MN5. This may indicate an ecology similar to that of Europe in localities where *Eomyidae* is seen in MN5.

Localities which provided the Middle Miocene Rodentia fossils from Anatolia were Akhisar, Bağıçi, Bayraktepe, Bostanyeri, Çandır, Derekebir, Dumlupınar, Gemerek, Göstere 1, Göstere 2, Gözlemederesi, Kalamış, Kırca, Kumköy, Mürefte, Paşalar, Pişmanköy, Sandıklı-Koçgazi, Sarıçay, Sarıkaya, Sinaptepe, Sofça, Yaylacılar, Yeni Eskişehir, and Zambal (Figure 2). The localities where Rodentia families of this period were seen (Saraç, 2003) are given as a list (Table 2).

The most crowded Rodentia group in the Middle Miocene is the family Cricetidae, with 32.35%; followed by Gliridae, which has the second higher numbers with 19.12%. Sciuridae has a ratio of 16.18%, while Spalacidae has 9.31%. Families with lower numbers are Muridae, with a ratio of 5.39%; Gerbillidae, with 4.41%; *Eomyidae*, with 3.92%; Dipodidae and *Petauristidae*, each with 2.94%; Castoridae, with 2.45%; and *Ctenodactylidae* and *Platacanthomyidae*, each with 0.49% (Figure 3).

3.3. Late Miocene Rodentia from Anatolia and Their Localities

In the Late Miocene, seasonality is assumed to have increased, while closed forest environments were replaced by more open habitats (Ataabadi, 2010). The Late Miocene is estimated to be a warmer period than today (Pound et al., 2012). Rising drought during the

Table 2- Middle Miocene Rodentia families from Anatolia, listed according to their localities.

LOCALITY	MN ZONE	Castoridae	Criceidae	Ctenodactylidae	Dipodidae	Eomyidae	Gerbilidae	Gliridae	Muridae	Petauristidae	Platacanthomyidae	Sciuridae	Spalacidae
Yaylacılar	MN 7-8		X										
Sandıklı-Koçgazi	MN 5-7		X		X	X		X				X	X
Kırca	MN 7-8		X					X				X	X
Bağici	MN 7-8		X										
Çandır	MN 6		X			X		X	X	X		X	
Sinap 64	MN 8						X						
Sinap 65	MN 8						X						X
Paşalar	MN 6	X	X	X	X			X	X			X	X
Bayraktepe 1	MN 7-8	X	X							X			X
Gözetlemederesi	MN 6-8	X	X									X	
Kumköy	MN 6-8		X					X					
Zambal 1	MN 6											X	
Sarıkaya	MN 5		X						X				
Bostanyeri	MN 6		X						X				
Yenicekent 1	MN 8-9		X										
Yenicekent 2	MN 8-9		X										
Yenicekent 3	MN 8-9		X										
Yenicekent 4	MN 8-9		X										
Pişmanköy	MN 7	X	X			X	X	X				X	X
Yukarıkızılca 1	MN 5-6		X					X	X			X	X
Göstere 1	MN 6-8								X				
Göstere 2	MN 6-8							X	X				X
Sofça	MN 7-8		X		X	X	X	X				X	X
Akhisar	MN 7-8		X					X					
Berdik 1	MN 7-8												X
Sarıçay	MN 7		X			X		X	X	X	X	X	X
Yeni Eskihisar	MN 7-8		X				X						
Gemerek	MN 6-8		X					X	X				
Mürefte	MN 5		X		X			X				X	
Kalamış	MN 7		X				X					X	

Late Miocene is thought to have led to an increase in the amount of open environments in East Asia and East Africa, with hypsodont (high-crowned teeth) mammal species proliferating and becoming adapted to the savanna ecosystem (Eronen et al., 2009). According to studies, the species diversity is known to have increased to maximum levels around 10 mya, during the Vallesian age (Agustí and Anton, 2005). The Vallesian Crisis (9.7-9.6 Mya) was first described by Agustí and

Moya-Sola (1990). Increasing seasonality, and low winter temperatures in particular, brought an end to the evergreen subtropical forests of Western Europe (Fostelius et al., 2014). The Late Miocene vegetation was dominated by Asteraceae (the aster family), representing open environments with almost no trees (Yavuz Işık et al., 2011). In addition, the examination of pollen findings from the Mediterranean Basin suggested that the plant diversity gradually decreased

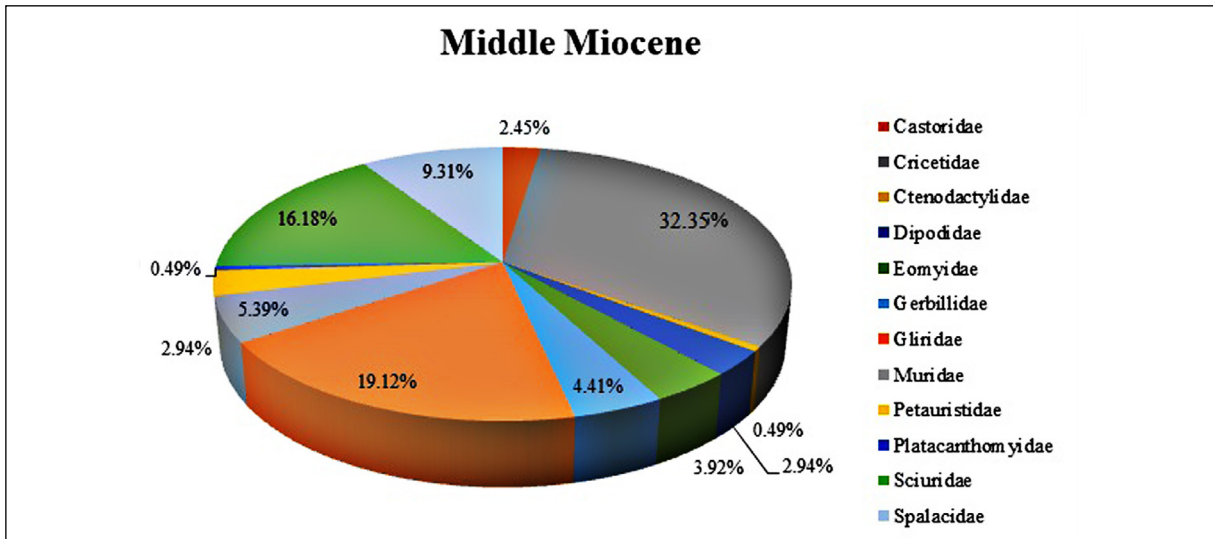


Figure 3- Middle Miocene Rodentia findings from Anatolia.

during the Middle-Late Miocene and Pliocene, and that the majority of these plant groups had very high water demand. It is estimated that the plants adapted to warmer climates proliferated (Jimenez Moreno et al., 2007). The decrease in Sciuridae and Cricetidae during the Late Miocene, as well as the diversification of Muridae species, can be interpreted as indicators of ecological change. The decline in Sciuridae is seen in its tree forms. This analysis shows us that arboraceous environments were replaced by open steppes.

The localities which provided Late Miocene Rodentia fossils from Anatolia were Altıntaş, Amasya,

Ayseki, Bayırköy, Bayraktepe, Büyükanafartalar, Cumali, Çakıllı, Çorakyerler, Dendil, Develiköy, Düzyayla, Eskisubaşı, Güney, Admired, Kalamış, Kaletpe, Kaleköy, Kangal, Karaçay, Karaözü, Kavrurca, Kütahya, Mahmutlar, Mahmutköy, Süleymanlı, and Tuğlu (Figure 2). For these localities, the frequency of the number of species of Rodentia families compared to other families are shown in a pie-chart (Figure 4), and their localities are given as a list (Table 3).

The most crowded group according to fossil findings is Muridae (24%), which displays a dispersal

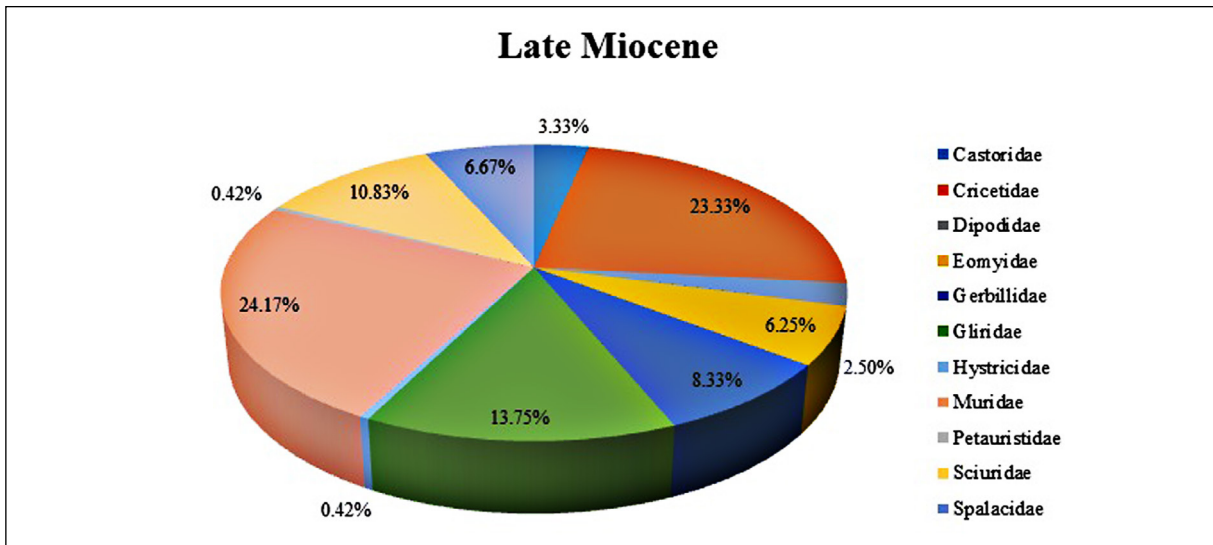


Figure 4- Late Miocene Rodentia findings from Anatolia.

Table 3- Late Miocene Rodentia families from Anatolia, listed according to their localities.

LOCALITY	MN ZONE	Castoridae	Cricetidae	Dipodidae	Eomyidae	Gerbillidae	Giridae	Hystriidae	Muridae	Petauristidae	Sciuridae	Spalacidae
Sandık-Garkın	MN 11		X									
Kalamış	MN 8-9					X						
Sinap	MN 9								X			X
Sinap4	MN 9					X						X
Sinap12	MN 9					X			X			X
Sinap8A	MN 9					X			X			
Sinap41	MN 9											X
Sinap42	MN 9					X			X			
Sinap49	MN 10					X						
Sinap84	MN 9								X			X
Sinap108	MN 9								X			
Sinap120	MN 9											X
Amasya	MN 13											X
Amasya 2	MN 13					X			X			X
Direcik 1	MN 9											X
Cumali	MN 10-11	X	X				X		X			
Bakırköy	MN 12		X	X	X		X	X			X	
Büyükafartalar	MN 9-10		X									
Bayraktepe 2	MN 9	X	X						X		X	
Eskisubası	MN 9-10	X	X				X					
Çorakyerler	MN 10-11		X	X	X	X	X		X			X
Kalatepe 1	Late Miocene		X		X	X			X			
Kalatepe 2	Late Miocene				X				X			
Mahmutlar	Late Miocene					X			X			
Tuğlu	MN 9		X		X	X	X		X		X	
Çakıllı	MN 12-13								X			
Ayseki	MN 12-13		X				X		X			
Süleymanlı 2	MN 13		X			X	X		X		X	X
Kavurca 1	MN 10-13		X		X	X	X		X		X	X
Kavurca 2	Late Miocene		X				X		X			
Güney	MN 9		X									
Mahmutgazi	MN 11-12								X			
Dereikebir	MN 9		X				X		X			
Mahmutköy	MN 9-10		X			X	X		X			
Aşağıcıgil 1	MN 9		X				X		X			
Altıntaş 1	MN 9								X		X	
Kütahya A	MN 9										X	
Develiköy 2	MN 14					X			X		X	
Düzyayla	MN 12	X	X	X	X	X	X		X	X	X	
Hayranlı 1	MN 10-11						X				X	
Kangal 1	MN 13										X	
Kaleköy	MN 10-12		X			X	X		X		X	X
Dendil	MN 10		X			X	X		X		X	
Karaözü	MN 10-12		X	X	X	X	X				X	X

from the western part of Anatolia extending towards central regions. Another dense group, Cricetidae (23%), has a dispersal parallel to this. While the families Gliridae (13%) and Sciuridae (10%) are particularly dispersed in the western and inland parts; Gerbillidae (3%), Spalacidae (6%), and Eomyidae (6%) were dispersed in the central parts. The family Dipodidae (2%) maintained its density in South-Western Anatolia. The genus Dipodidae is seen in Anatolia, and differs from the Euro-Asian genera (Bruijn et al., 2013). Gerbillidae, Spalacidae, and Dipodidae sharing the same ecology is an indicator of the existence of an open meadowland, steppe and a semi-arid habitat in the Late Miocene. The decrease in Gliridae and Sciuridae during this period, compared to their densities in the Middle Miocene, can be ecologically characterized by a decline in forest environments. The dominance of Muridae species taking precedence over the dominance of Cricetidae, and the decrease in Gliridae both indicate a decline in moist and forested areas. However, the increase in Eomyidae was in contrast to the decline in humidity. This is because Eomyidae is a family of micromammals adapted to a moist and more closed ecosystem (Engesser and Kälın, 2017).

If we compare specific families (Figure 5) for a paleoecological evaluation of the Miocene findings from Anatolia; the family Castoridae preserving its density in the Early, Middle, and Late Miocene indicates the continuous existence of partial aquatic environments in Anatolia throughout the entire

Miocene (Table 4). While Castoridae was found in Anatolia until the 1950s, the family is currently unseen. Although the decline in Cricetidae seen in the Early Miocene until the Late Miocene does not provide information about the Anatolian ecology, the diversification of species in this family may indicate that its members had no difficulty in adapting to their habitat. The number of modern species belonging to this family seems to have reached the maximum. The family Gliridae, experiencing a decline in the late periods of the Middle Miocene until the Late Miocene, suggests that the species adapted to moist habitats of the ecology decreased in the Late Miocene, while a more continental climate became dominant. The current density of this family being almost equal to that in the Late Miocene suggests the Miocene ecology was similar to that of today. The fact that Gliridae reached its maximum level in the Middle Miocene, while Muridae dropped to its minimum level during the same period may propose an ecological dominance relationship between these two families. This parallel rise-drop forms the basis of environmental changes. The emergence of Eomyidae in the Middle Miocene and its continued existence through the Late Miocene, on the other hand, gives the impression that the habitat may have preserved its forest density in ecological terms. At the same time, Sciuridae maintaining its maximum level during the Middle Miocene indicates the continued existence of arboraceous environments.

As a general evaluation; families Gliridae and Sciuridae reach their maximum levels in the

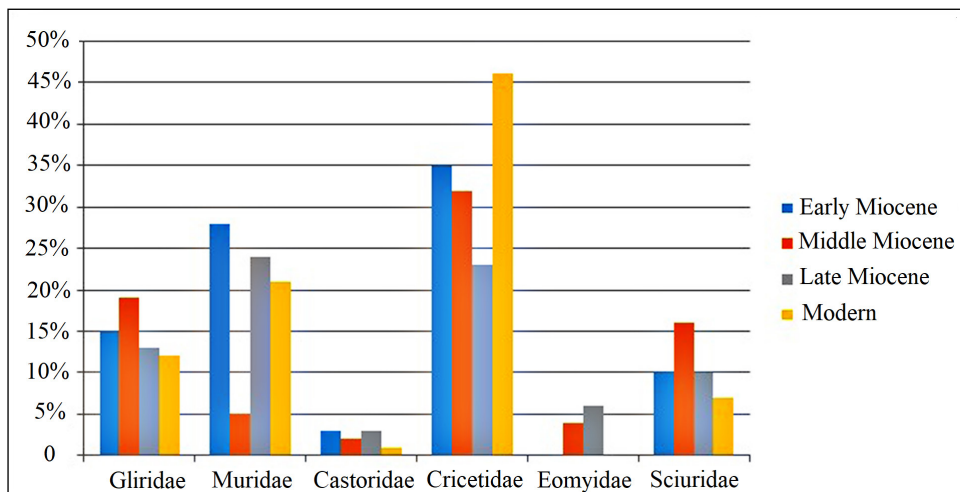


Figure 5- Comparison of the modern and Miocene Rodentia families of Anatolia.

Table 4- Modern and Miocene Rodentia families of Anatolia.

MODERN (Yiğit et al. 2006)	EARLY MIOCENE	MIDDLE MIOCENE	LATE MIOCENE
Castoridae 1.54%	Anomalomyidae 1.16%	Castoridae 2.45%	Castoridae 3.33%
Cricetidae 46.15%	Castoridae 3.09%	Cricetidae 32.35%	Cricetidae 23.33%
Dipodidae 4.62%	Cricetidae 35.91%	Ctenodactylidae 0.49%	Dipodidae 2.50%
Gliridae 12.31%	Ctenodactylidae 1.16%	Dipodidae 2.94%	Eomyidae 6.25%
Hystriidae 1.54%	Dipodidae 3.09%	Eomyidae 3.92%	Gerbillidae 8.33%
Muridae 21.54%	Gliridae 15.44%	Gerbillidae 4.41%	Gliridae 13.75%
Myocastoridae 1.54%	Muridae 28.57%	Gliridae 19.12%	Hystriidae 0.42%
Sciuridae 7.69%	Petauristidae 0.7%	Muridae 5.32%	Muridae 24.17%
Spalacidae 3.08%	Sciuridae 10.04%	Petauristidae 2.94%	Petauristidae 0.42%
	Spalacidae 0.77%	Platacanthomyidae 0.49%	Sciuridae 10.83%
		Sciuridae 16.18%	Spalacidae 6.67%
		Spalacidae 9.31%	

Middle Miocene. Seeing these two families at their maximum during this period, when compared to the rest of Miocene, indicates that Anatolia was a moist and forested habitat in the Middle Miocene ecosystem. The same period, the Middle Miocene, is also when Muridae drops to its minimum. The factor minimizing this family during the Middle Miocene is the ecological structure in moist and forested habitats. The presence of Castoridae during the entire Miocene suggests the ongoing presence of partial aquatic habitats throughout the epoch. The family Cricetidae experienced a linear decrease during Miocene, which may be due to Cricetidae passing on its dominance in different ecological niches to the members of other families. The occurrence of Eomyidae only in the Middle and the Late Miocene may have resulted from the paleoecological environment showing similar characteristics for Eomyidae during the Middle Miocene and the early periods of the Late Miocene.

4. Results

Terrestrial mammal ecosystems are mostly regionally or temporarily discontinuous, and are controlled by a combination of topographic, tectonic, climatic, and vegetational dynamics (Eronen et al., 2009). Anatolian paleogeography during the Miocene can be mainly summarized in three different stages. The first period, the Early Miocene in Anatolia, was dominated by low seasonality and mammal species adapted to moist and forested environments. The first Miocene faunas of Anatolia most likely represented very moist and possibly forested environments

(Fortelius, 2014). Although marshes were well established in some parts of Anatolia during the Early Miocene, we should be careful about overgeneralizing to assume that entire Anatolia was covered with lush forests at that period (Joniak et al., 2019). As this study focuses on Rodentia, the presence of Castoridae in Harami, Harami 4, Harami 5, Kılçak 3a, Kılçak 0, Kınık 2, and Sabuncubeli in the Early Miocene Anatolia indicates that these localities had woodlands and aquatic habitats with low flow rate. The occurrence of Dipodidae in Hoşk y, Kargı 2, and Kargı 3 localities does not show that these regions were much of closed environments as habitats. Rather, this family represents open steppes or semi-arid habitats. Even though the density of Sciuridae being lower than that of the Middle Miocene, and equal to that of the Late Miocene causes a hesitation concerning the forested environments, the diversity seen in Gliridae evens these ratios, suggesting that the woodlands were frequent. In addition, we may say that the Old World mammal faunas generally had homogeneous similarity patterns against the homogeneous environmental conditions in this period, especially towards the end of Early Miocene.

Although the Climatic Optimum period of the Middle Miocene was marked by a predominantly humid climate, regional precipitation data indicates that only some places were moist while others were relatively dry (Fortelius et al., 2002). The presence of Castoridae members in Pasalar, G ztlemederesi, Bayraktepe 1, and Piřmank y localities show that these localities had moist habitats. Based on their teeth

models, *Eumyarion* species in particular are thought to be more abundant in moist environments or sediments showing similar environmental conditions (Fortelius et al., 2002). The findings of Eomyidae members in Çandır, Sofça, Sarıçay, Karaçay, Kaletpe 1, Kaletpe 2, Düzyayla, Pişmanköy, Kavrurca, and Sandıklı-Koçgazi localities prove that these environments were also moist. As temperatures increased, Gliridae adapted to different habitats and geographically dispersed to a wider variety of locations in Europe and Asia. The dramatic downfall of Gliridae started at the beginning of the Middle Miocene, about 16 million years ago, and was triggered by environmental changes such as the seasonal expansion of open environments. According to Akkiraz et al. (2011), Anatolia was warm and moist in the Middle Miocene. On the other hand, the average hypsodonty measurements of herbivores and other extant large mammals from Greece through Afghanistan point to the existence of open and grassland ecosystems during the Middle Miocene (Fortelius et al., 2014). Anatolian Gliridae during the Middle Miocene consisted of *Microdyromys*, *Myomimus*, *Miodyromys*, *Peridyromys*, *Muscardinus*, *Vasseuromys*, *Glirulus*, and *Paraglis* species. The presence of these species in the family Gliridae represents the existence of deciduous trees and forests.

A tropical or semi-tropical climate prevailed dominated the Middle Miocene. Towards the end of this period, changes in environmental and climatic conditions caused the formation of a mixed pattern in the mammalian biogeography. A decrease in the density of Cricetidae by almost 25%, and in Muridae by about 65%, as well as significant increases in families such as Spalacidae and Eomyidae indicate a climate change in the Middle Miocene. The replacement of moist and forested areas that existed throughout the Miocene by an ecosystem with high seasonality and more open environments led to changes in the mammalian fauna.

In the Late Miocene, the grassland ecosystem became dominant and the number of large mammal species adapted to open habitats increased (Kaya and Kaymakçı, 2013). A significant faunal change was seen, from forest dwellers to ground-dwelling species. This change was characterized by *Myomimus* findings displaying a vegetational shift from forested environments of the Late Miocene to open forests and steppe-like habitats, as well as an increase in their

population size. Pollen analysis shows that the Central Anatolia Region was typically dry in the Late Miocene (Akgün et al., 2007). Biotic interactions of Gliridae with other small mammal groups such as Muridae should also be considered. Correspondingly, the biodiversity of Gliridae during the Late Miocene Anatolia is represented by six genera; *Glirulus*, *Microdyromys*, *Miodyromys*, *Myomimus*, *Muscardinus*, and *Ramys* (Kaya and Kaymakçı, 2013). This shows that the Muridae species entering Europe were pre-adapted to the conditions in more open ecosystems. At the very least, they would have to be present everywhere in order for the local fauna to have a chance of better coping with the environmental changes, and thus it seems reasonable to assume that Anatolia already had open environments and that the hamsters had already begun adapting to it (Joniak et al., 2019). While Muridae comprised approximately 24% of the entire Rodentia order in the Late Miocene, Gliridae comprised 13%. We may say that the decline seen in Gliridae during the Late Miocene, when compared to the Middle Miocene, was due to the ecological dominance of a dry environment.

Cricetidae members were the dominant species of Neogene rodent communities in Türkiye and its surroundings. Since they were widespread all over Eurasia, they provide biochronological correlations with the Neogene mammalian chronology of Europe (Erten et al., 2014). According to available Miocene fossil records from Anatolia, the family Cricetidae is represented by 12 genera; *Cricetodon*, *Democricetodon*, *Deperetomyx*, *Enginia*, *Karydomys*, *Lartetomys*, *Latocricetodon*, *Megacricetodon*, *Melissiodon*, *Meteamys*, *Mirabella*, and *Spanocricetodon*. Cricetidae constitutes 35% of the entire Rodentia order in the Early Miocene, 32% of the order in the Middle Miocene, and 23% in the Late Miocene. Cricetidae members are generally more associated with open environments, but this generalization does not seem valid for the first Miocene representatives of the family from Anatolia. The dominance of Cricetidae in Anatolia can be seen both paleoecologically and biogeographically. Smaller species of the genera *Democricetodon* and *Eumyarion* certainly seem to prefer more closed environments (Van den Hoek Ostende, 2001). The localities of Çandır, Düzyayla, Gördes, Harami 4, Harami 5, Sabuncubeli, Şemsettin, Kılçak0, Kılçak3a and Kılçak

3b, Yurtyenice, Söke, Kumköy, Yapıntı, Harami, Sofça, Harta, and Hoşkøy, where these species were seen, were possibly located in a deciduous woodland environment. On the other hand, *Megacricetodon* is a species that can cope better with open environments (Van den Hoek Ostende, 2001). The presence of *Palaeosciurus feignouxi*, a species of European origin, suggests a moist environment with dense vegetation. Localities of Gökler, Keseköy, Kılçak 0, Kılçak 3a, and Kılçak 3b, where *P. feignouxi* specimens were found, share the ecology of this squirrel species.

The number of Gliridae species coincides with the continental climatic events of the Cenozoic. The first Gliridae members appeared during Late Eocene through Early Oligocene, and the number of species remained limited. At the end of Late Oligocene and the beginning of Early Miocene, Gliridae experienced an increase in the number of species (Freudenthal, 1997). During this time, Gliridae numbers reached the highest paleobiodiversity peak of the family's history (5 to 60 species). During the Late Oligocene warming, *Microdyromys heissigi*, *Microdyromys praemurinus*, *Microdyromys monspeliensis*, and *Microdyromys legidensis* emerged. The earliest representative of *Peridyromys murine* (Mirambueno 1, MP 27) is known from the Late Oligocene in Spain (Freudenthal, 1997). In Miocene, seven genera of Gliridae lived in Türkiye; *Gliridinus*, *Glis*, *Vasseuromys*, *Microdyromys*, *Paraglrirulus*, *Miodyromys*, and *Bransatoglis* (Kaya and Kaymakçı, 2013). Environmental changes in Europe and the Eastern Mediterranean that occurred between the Middle and the Late Miocene caused a serious decrease in the number of Gliridae species that were adapted to a humid climate. While this family constituted 19% of the entire Rodentia order during the Middle Miocene, this ratio decreased to 12% in the Late Miocene. In the late periods of Miocene, forest and wetland ecosystems were replaced by steppes and clearings in forests. This change is characterized by an increase in *Myomimus* numbers during this period (Kaya and Kaymakçı, 2013). While this species was represented with only a few examples in the Early Miocene, the number of findings increases in Middle Miocene, almost reaching its maximum. The members of Gliridae generally have extremities well-adapted for climbing trees. Their diet includes fruits, nuts, insects, eggs, and small invertebrates. *Myomimus* is the only genus of this family that is not specialized

in arboreal life. *Dryomys*, a genus closely related to *Microdyromys*, is semi-arboreal. *Myomimus* lives in clusters of trees, on the ground, or in underground nests in Turkmenistan, Uzbekistan, Afghanistan, Iran, Palestine, Türkiye, and Bulgaria, all of which have open environments. On the other hand, *Dryomys* lives in dense mountain forests and bushes in Switzerland, some regions of Germany, Latvia, Türkiye, Iran, Mongolia, and in mountainous highlands of northern Pakistan (Kurtonur and Özkan, 1991; Nowak, 1999; Holden, 2005).

In the Late Miocene, as the paleoecology transformed into open environments and the drought increased in Anatolia, Rodentia families that were adapted to the moist and forested habitats were replaced by those adapted to steppe and savannah habitats. During the Late Miocene in Anatolia, the family Cricetidae started to decrease in density once again, the family Muridae increased the amount of its distribution areas compared to the Middle Miocene, while the families Sciuridae and Spalacidae experienced a relative decline. The family Gerbillidae was seen, and an increase was observed in the ecological dispersal of the family Eomyidae.

To generalize, the Anatolian paleoecology is thought to be dominated by a humid and temperate climate in the Early Miocene, a temperate and semi-tropical climate in the Middle Miocene, and a climate with more open and dry seasonal transitions towards the end of the Late Miocene. Also in the Late Miocene, meadowlands increased, while savannas and grasslands expanded (Kaya and Mayda, 2011; Demirsoy, 1999). Although a relatively warm period was detected in both Pliocene and Pleistocene, the climate was observed to change gradually and to enter a constant trend of cooling, along with increased cooling and expanding dry environments at higher latitudes (Janis, 1989).

If we compare the modern Rodentia fauna with that of the Miocene; the current density ratio of the family Castoridae to the entire order Rodentia is 1%, while it appears to be 3% in the Early Miocene, 2% in the Middle Miocene, and 3% in the Late Miocene. In the current ecology, this family reflects a sporadic presence of aquatic environments. The abundance in Miocene, on the other hand, indicates a higher amount

of aquatic environments than today. If we consider the family Dipodidae; its current density is about 5%, while this average ratio was 3% in Miocene, which may indicate that the Miocene ecology was more forested than today. The current density of the family Gliridae is 12%, which is close to its ratio in the Late Miocene. This close ratio may have resulted from Anatolia's location showing similar ecologies in both periods. The absence of the family Eomyidae today and its emergence in Middle Miocene may be due to the geographic change, and the family members entering Anatolia along with that change. The family's existence in Middle Miocene indicates that the humidity levels and the amount of forested areas in that period were different from the present. The members of Cricetidae preserved their dominance in the current ecology as they did in Miocene. The high diversity of the modern Rodentia fauna shows that Anatolia has a complex ecology. Likewise, we may say that the diversity of Rodentia fauna during Miocene indicates the presence of different habitats in its paleoecology. Regarding the period between the Early Miocene and the end of Middle Miocene, it may be more accurate to say the ecology was tropical and partially forested, rather than saying that it had an entirely closed and moist ecology. In the Late Miocene, the order Rodentia diversified and increased its biodiversity in Anatolia, which had its faunal peak as the rest of the world. Along with the ecological structure changing since the Late Miocene until the present day, we see an increase in the biodiversity of Rodentia species that became adapted to more arid steppes and open environments.

Acknowledgements

The authors would like to thank Prof. Dr. Nuretdin KAYMAKÇI from METU, for his valuable contributions on Anatolian geology and mapping, and Emin SEYFİ, a PhD student at Hitit University, Department of Molecular Biology and Genetics, for his recommendations on tables and figures.

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