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A Reassessment of the Late Miocene Rhinocerotidae of Anatolia Based on Recent Fossil Evidence

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Abstract This study aims to reassess the paleobiogeographic distribution and phylogenetic diversity of Rhinocerotidae species from the Late Miocene of Anatolia. Utilising data obtained from recent scientific publications and the New and Old World Neogene (NOW) fossil mammal database, the research identifies 105 rhinoceros-bearing fossil localities among 247 Late Miocene sites located across modern-day Anatolia and Thrace. Fossil evidence from these localities reveals the presence of ten rhinocerotid genera, including Chilotherium, Miodiceros, Acerorhinus, Dihoplus, Aceratherium, Stephanorhinus and Diceros. Based on spatial distribution, the fossil sites are categorised into three main geographic regions: Southern Anatolia, Western Anatolia, and Central Anatolia. Genera such as Chilotherium, Miodiceros, Acerorhinus, and Dihoplus were commonly recorded across all three regions. The findings demonstrate that Rhinocerotidae formed a significant component of Anatolia's Late Miocene mammalian fauna, showing notable taxonomic diversity during this period. The co-occurrence of rhinoceroses with other taxa adapted to open and woodland habitats—such as hyenas, felids, bovids, hipparionine equids, and proboscideans—suggests that the regional assemblages were strong representatives of the Pikermian chronofauna, which was widespread across Eurasia during the Late Miocene. While most Rhinocerotidae species vanished from Anatolia by the end of the Miocene, certain genera, including Chilotherium, persisted into the mid-Pliocene, indicating possible ecological refugia in the region.

Keywords Rhinocerotidae · Late Miocene · Anatolia · Paleontology · Paleobiogeography

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INTRODUCTION

Anatolia underwent significant geological transformations during the Miocene epoch (ca. 23–5.3 million years ago), driven by intense tectonic activity that ultimately shaped the region's current physiography. These tectonic processes not only defined the modern landscape but also established Anatolia as a strategic landmass connecting three major continents: Europe, Asia, and Africa (Rögl, 1999). Owing to its central location, Anatolia functioned as a critical biogeographic corridor that enabled the movement and interaction of terrestrial faunal assemblages across continents. As a result, its Miocene terrestrial deposits are particularly fossil-rich, preserving crucial evidence of past biodiversity and faunal dispersals.

Research on Miocene mammalian assemblages from Anatolia and surrounding regions reveals a pronounced ecological transition between the Early–Middle Miocene (23–11.2 Ma) and the Late Miocene (11.2–5.3 Ma) (Fortelius et al., 2002; Eronen et al., 2009; Mirzaie Ataabadi, 2010; Kaya et al., 2018). Whereas earlier intervals supported tropical to subtropical forested environments, the Late Miocene witnessed a climatic shift towards drier conditions, seasonality, and the expansion of open landscapes. This shift marked the onset of more modern, continental-type climates and led to the extinction of numerous taxa previously adapted to warm, humid ecosystems.

The earliest and most visible consequences of this environmental reorganisation emerged within the sub-Paratethys biogeographic province, where Anatolia occupied a central role (Rögl, 1999; Fortelius et al., 2002; Eronen et al., 2009). In this context, a novel mammalian fauna evolved—one that was increasingly adapted to seasonal, open environments. This community is known as the Pikermian chronofauna, named after the renowned fossil locality of Pikermi in Greece, dated to around 7 million years ago. Several fossil localities across Anatolia dating to the Late Miocene contain taxonomic elements that are emblematic of the Pikermian fauna. These assemblages predominantly feature species with hypsodont dentition, enabling them to consume coarse, abrasive vegetation such as grasses, as opposed to the softer leaves of forested ecosystems. Their ecological traits a strong adaptation to savanna-like environments and parallel the structure of modern Sub-Saharan African mammalian communities in both composition and trophic dynamics.

The spatial extent of the Pikermian chronofauna during the Late Miocene was considerable, with its influence traceable across vast stretches of Eurasia—from Eastern Europe to Northern China, and potentially into parts of East Africa. In this expansive biogeographic framework, Anatolia emerges not only as a centre of diversification for these faunas but also as a critical migratory thoroughfare that facilitated faunal exchanges between continents (Eronen et al., 2009; Kaya, 2017).

Accordingly, paleontological investigations in Anatolia provide essential data for reconstructing regional and continental-scale patterns of faunal turnover, paleoecological transformation, and climate-driven evolution during the Neogene. These studies underscore Anatolia's importance as a keystone region within the broader paleobiogeographic mosaic of Late Miocene Eurasia (Kaya et al., 2016).

MATERIALS AND METHODS

This study is grounded in a comprehensive literature-based methodology. The research primarily draws upon published scientific studies concerning Miocene paleontology, paleoecology, paleoclimate, and paleobiology, as well as findings from field surveys and fossil excavations conducted in Anatolia. In addition to these sources, data were compiled from the "New and Old World Neogene Fossil Mammal Database (NOW)" (The NOW Community, 2025), with a specific focus on Late Miocene Rhinocerotidae occurrences in Turkey.

The collected data were synthesised and examined in relation to the taxonomic diversity and spatial distribution of Rhinocerotidae groups. Inferences were also drawn from related paleoecological studies to reconstruct the environmental conditions of the time. The study adheres to paleontological terminology and standards, particularly those concerning odontological and osteological characteristics. For systematic classification, the scheme proposed by Prothero and Schoch (1989) and Heissig (1999) was followed, as it provides the most recent and widely accepted taxonomic framework in the absence of a more updated phylogenetic model in the literature.

A comprehensive table of Rhinocerotidae fossil localities was compiled, organized according to MN (Mammal Neogene) zones. The average ages of these localities were estimated based on the midpoints of the MN unit age ranges to which each site is assigned, as per the chronology outlined by Steininger (1999) and adopted by the NOW database. To facilitate spatial analysis, the fossil localities were divided into three main geographic regions: Southern Anatolia, Western Anatolia, and Central Anatolia.

Origin and Evolution of Rhinocerotidae

The superfamily Rhinocerotoidea, which includes the family Rhinocerotidae, exhibits an extraordinary evolutionary history marked by morphological and ecological diversity (Nowak, 1991). Throughout their extensive Cenozoic radiation, rhinocerotoids adapted to various habitats and lifestyles. This group includes forms as varied as the cursorial *Hyracodon*, a sheep-sized runner; the semi-aquatic *Brachypotherium*, *Teleoceras*, and *Metamynodon*, whose body plans resembled modern hippos; the short-trunked, tapir-like *Cadurcodon* and *Aceratherium*; and the colossal *Paraceratherium* (formerly *Indricotherium* or *Baluchitherium*), which is considered one of the largest terrestrial mammals to have ever lived. In terms of fossil diversity, rhinocerotoids rival other perissodactyl groups such as horses (*Equidae*), tapirs (*Tapiridae*), and even extinct lineages like chalicotheres and titanotheres. During the Tertiary period, rhinocerotids were among the dominant large herbivores across Eurasia, Africa, and North America, often constituting a significant component of regional megafaunal assemblages. Contrary to their stereotypical modern image as horned giants, not all extinct rhinoceroses bore horns. In fact, many early rhinocerotids were hornless. The familiar horn configuration seen in extant species evolved independently in different lineages. The earliest horned forms exhibited two distinct, non-contiguous horn structures that were not initially fused into a single nasal horn. This mosaic evolution of cranial ornamentation a complex pattern of parallel evolution within the clade (Prothero et al., 1989).

The earliest known member of Rhinocerotoidea is *Hyrachyus*, which appeared in the Upper Wasatchian and Bridgerian North American faunal stages (Early to Middle Eocene). Although *Hyrachyus* displays several primitive traits resembling those of tapirs, leading Radinsky (1966, 1967) to initially classify it within Tapiridae, later studies by Prothero and colleagues (1986) recognized *Hyrachyus* as a basal rhinocerotoid. It had a broad geographic distribution, being reported not only from the western United States but also from Ellesmere Island in the Canadian Arctic (West et al., 1977), as well as from parts of Europe and possibly Asia (Radinsky, 1967), indicating a cosmopolitan range.

The dispersal of *Hyrachyus* into Europe during the Middle Eocene is attributed to the existence of a land bridge across the North Atlantic, linking North America and Europe. This corridor enabled faunal exchanges until the connection was severed (McKenna, 1975). Subsequently, transcontinental migrations continued periodically through Beringia, which connected Asia and North America. However, due to Europe's geographic isolation during the Late Eocene, the continent developed a distinctive endemic perissodactyl fauna, dominated by groups such as *Palaeotherium* and *Lophiodon*. These endemic taxa eventually disappeared in the Early Oligocene, giving way to more cosmopolitan ungulate assemblages (Prothero et al., 1989).

Meanwhile, during the Late Eocene, the three principal families of Rhinocerotoidea began diversifying across Asia and North America: Amynodontidae, Hyracodontidae, and Rhinocerotidae. These families are often definated by distinct features in their upper third molars (M3). In *Hyrachyus*, the M3 is subquadrate in shape, with prominent parastyles and metalophs. Amynodonts evolved molars that were elongated anteroposteriorly and exhibited a robust metastyle. In

contrast, members of Hyracodontidae and Rhinocerotidae show a reduced metastyle that is displaced lingually. In some derived hyracodonts and all true rhinocerotids, the metastyle is entirely lost, reflecting a transition toward triangular-shaped molars. Interestingly, in *Coelodonta antiquitatis*, the last rhinoceros genus of Europe, the M3 re-evolved a more classical quadrate shape, suggesting functional reversals or ecological pressures linked to its Pleistocene environment (Prothero et al., 1989).

This complex pattern of dental evolution, geographic dispersal, and ecological adaptation highlights the evolutionary plasticity of Rhinocerotoidea. Their fossil record not only documents significant phylogenetic transitions but also provides insights into the biogeographic history and environmental change during the Paleogene and Neogene.

Miocene Rhinocerotidae of Eurasia

During the Miocene epoch, Eurasia hosted a remarkably diverse and taxonomically rich assemblage of Rhinocerotidae, surpassing the relatively limited diversity observed in North America, which was largely confined to only three genera (Heissig, 1999). The Eurasian rhino fauna encompassed several major evolutionary lineages, reflecting adaptive radiation into various ecological niches and body forms. By the Middle Miocene (Vindobonian), the Menoceratine lineage had become extinct, and the dominant representatives included early Aceratheriini, primitive Rhinocerotinae, and *Brachypotherium*. The Aceratheriini clade comprised genera and subgenera such as *Aceratherium*, *Mesaceratherium*, *Alicornops*, *Chilotherium*, and *Dromoceratherium*. These forms exhibited various morphological adaptations. For example, *Aceratherium* was a medium-sized, hornless browser with brachyodont cheek teeth, a shortened proboscis, and limb proportions similar to modern tapirs (Eisenmann & Guérin, 1984; Hunermann, 1982). Its earliest representatives, including *A. platyodon*, *A. lumiarense*, *A. tetradactylum*, and *A. incisivum*, trace their lineage to the Late Oligocene species *A. paulhiacense* (Guérin, 1980; Antunes & Ginsburg, 1983).

Closely related genera such as *Dromoceratherium* and *Alicornops* expanded across Western and Central Europe, with species such as *D. mirallesi* and *A. simorrense* reaching as far as India (Heissig, 1972; Santafé-Llopis, 1978). A distinct lineage, *Chilotherium*, belonging to the Teleoceratinae and exhibiting hippopotamus-like proportions and hypsodont dentition, migrated from its Middle Miocene origin in the Siwaliks to China, the Middle East, and Europe, including localities such as Samos and the Iberian Peninsula (Guérin, 1980; Antunes & Ginsburg, 1983). Although many *Chilotherium* species have been described across Eurasia, only a few are widely accepted, such as *C. zernowi*, *C. samium*, and *C. kowalewskii* (Heissig, 1975).

Parallel to these developments, genera like *Brachypotherium*, which emerged from *Diaceratherium* in the Middle Miocene, became prominent grazers with semi-aquatic habits. Their fossil record spans from Europe to Africa and Asia, persisting into the Pliocene with species such as *B. perimense* and *B. lewisi*. These robust forms had reduced limbs and hypsodont teeth, a diet of abrasive vegetation and potential adaptation to wetland environments, much like the American *Teleoceras* (Prothero et al., 1989).

Another important taxon, *Prosantorhinus*, represented a smaller, short-legged Teleoceratine with brachyodont dentition. It was confined to Western Europe and became extinct by the end of the Vallesian (Guérin, 1980; Antunes & Ginsburg, 1983). Meanwhile, the *Dicerorhinus* group, including species such as *D. sansaniensis*, *D. steinheimensis*, and *D. orientalis*, appeared during the Orleanian and became widespread in both Western and Eastern Europe. *D. sansaniensis*, a medium-sized, horned browser, is considered the first unambiguous *Dicerorhinus* and has been proposed as a relative of the African *D. leakeyi.* Some *Dicerorhinus* species, like *D. schleiermacheri* and *D. orientalis*, were among the largest rhinoceroses of the Vallesian and Turolian. Although *Dicerorhinus* did not become highly diversified in Miocene Europe —possibly due to competitive exclusion by endemic taxa—it did include rare dwarf forms such as *D. steinheimensis*, the smallest known Neogene rhino (Prothero et al., 1989).

The genus *Diceros*, ancestral to the extant African black rhinoceros, also extended into Europe and the Near East during the Late Miocene, with species such as *D. pachygnathus* and *D. neumayri*. Taxonomic debates persist regarding

the validity of some of these forms due to overlapping characteristics with *Dicerorhinus* (Wagner, 1848; Gaudry, 1862–1867; Heissig, 1975).

Additionally, the *Hispanotherium* group—part of the Iranotheriinae—originated in Early Miocene Asia and dispersed westward into Iberia, Anatolia, and beyond. Closely associated genera, such as *Caementodon* and *Beliajevina*, coexisted as smaller-bodied contemporaries (Antunes & Ginsburg, 1983).

In East and Southeast Asia, the Miocene rhinocerotid record reveals close affinities with the European taxa. Genera such as *Brachypotherium*, *Aceratherium*, *Plesiaceratherium*, *Chilotherium*, and *Dicerorhinus* are well-documented in China, India, Pakistan, and Iran (Heissig, 1972; Li et al., 1984). Species like *Chilotherium yunnanensis* persisted into the Early Pleistocene, while early members of the *Elasmotheriinae*, such as *Sinotherium*, appeared in the Turolian of northern China (Prothero et al., 1989).

In Africa, the earliest Miocene rhinocerotids include *Aceratherium campbelli* and *Brachypotherium snowi* from Libya and Egypt (Hamilton, 1973). The middle to late Miocene record includes several endemic and immigrant taxa, such as *Chilotheridium pattersoni*, *Paradiceros mukirii*, and *Kenyatherium bishopi* from Kenya and Uganda, alongside species of *Diceros* and *Dicerorhinus* (Prothero et al., 1989).

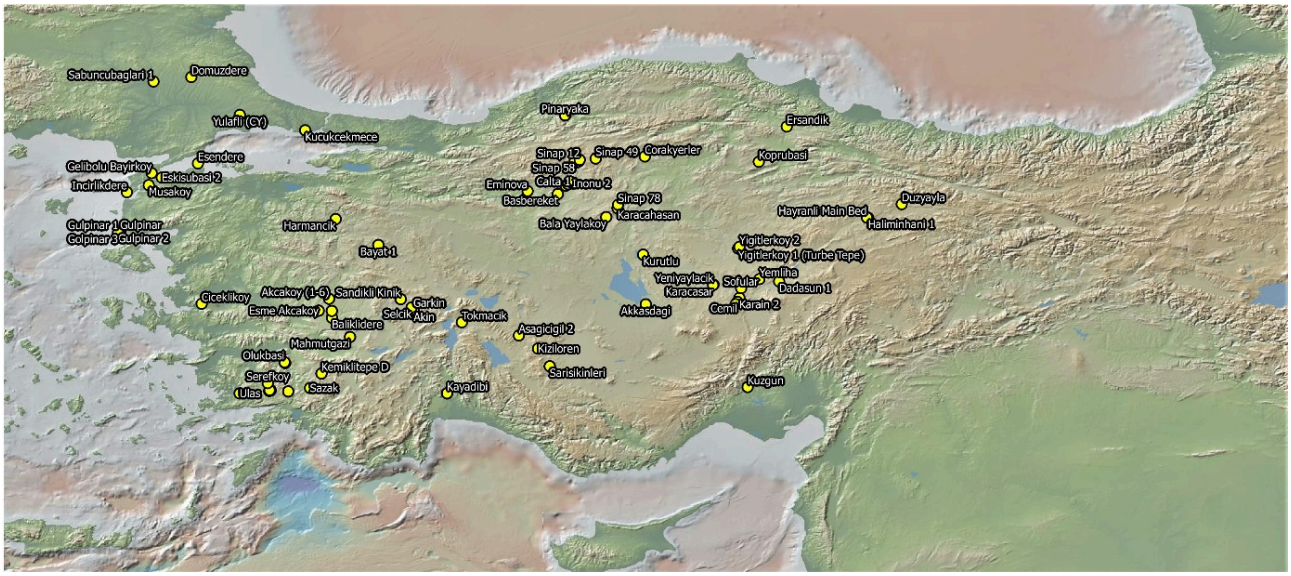
Overall, the Miocene Rhinocerotidae of Eurasia represents a period of significant diversification, dispersal, and ecological innovation. Many lineages independently evolved hypsodont dentition in response to the expansion of grassland habitats. This adaptation emerged convergently in multiple clades, including *Chilotherium*, *Chilotheridium*, *Teleoceras*, *Brachypotherium*, and Elasmotheriines. The coexistence of multiple rhino taxa in localities such as La Grive Saint-Alban (France) illustrates the niche partitioning that allowed for such diversity (Prothero et al., 1989).

By the end of the Miocene, the global faunal landscape was dramatically altered due to major climatic changes and events such as the Messinian Salinity Crisis. These environmental upheavals resulted in the extinction of several rhinocerotid lineages, including most Aceratheriini and Teleoceratinae, with only members of Rhinocerotinae and Dicerorhininae surviving into the Pliocene and beyond (Prothero et al., 1989).

RESULTS

Figure 1

Late Miocene Rhinocerotidae localities in Anatolia (based on the NOW Database; The NOW Community, 2025).



The Rhinocerotidae locality data from Turkey were extracted from the New and Old World Neogene Mammal Database (NOW) on 16 June 2025 (The NOW Community, 2025). This dataset was limited exclusively to Late Miocene records. A distribution map of these fossil localities was created using the QuantumGIS software, version 3.32.1.

Table 1

Late Miocene Rhinocerotidae Localities in Anatolia and Their Corresponding MN Zones.

LOCALITY	LOCATION	MN ZONE
Kurutlu	Kırşehir/Kaman	MN 9-13
Karacaşar	Nevşehir/Gülşehir	MN 9-10
Eşme- Akçaköy	Uşak	MN9
Sinap	Ankara/Kazan	MN9
Başbereket	Ankara	MN9-11
Ulaş	Muğla/Milas	MN9-10
Gebze	Kocaeli	MN9-10
Selçik	Afyon/Sandıklı	MN9-10
Bayraktepe	Çanakkale	MN10
Dadasun	Kayseri/Bünya	MN10
Sığındere	Çanakkale/Eceabat	MN 10
Yulaflı	Tekirdağ/Çorlu	MN10
Yeniyaylacık	Nevşehir/Gülşehir	MN 10
Hatunsaray/Sekisırtı	Konya	MN 10-11
Kayadibi	Konya	MN 10-11
Özkonak	Nevşehir/Avanos	MN 11-13
Yiğitler	Yozgat	MN11
Garkın	Afyon/Sandıklı	MN11
Paşabağı	Nevşehir/Göreme	MN 11
Bayat	Kütahya	MN11
Özlüce	Muğla	MN 11
Cemil	Nevşehir	MN 11
Eski Bayırköy	Muğla/Yatağan	MN11
Evciller Ağılları	Ankara	MN11
Karain	Nevşehir	MN 11
Harmancık	Kütahya	MN11
Taşkınpaşa	Nevşehir/Ürgüp	MN11
Gülpınar	Çanakkale/Ayvacık	MN11
Sofular	Nevşehir/Ürgüp	MN11
Çorakyerler	Çankırı	MN11
Balçıklıdere	Uşak/Eşme	MN11-12
Kınık	Afyon/Sandıklı	MN11-12
Haliminhanı-Hayranlı	Sivas	MN11-12
Düzyayla	Sivas/Hafik	MN 12
Sazak	Denizli	MN12
Akkaşdağ	Çankırı	MN12
Mahmutgazi	Denizli	MN12

LOCALITY	LOCATION	MN ZONE
Şerefköy	Muğla/Yatağan	MN12
Kemiklitepe	Uşak/Eşme	MN12
Esendere	İzmir/Karaburun	MN12-13
Amasya	Aydın/Bozdoğan	MN13
Yeni Eskihisar	Muğla/Yatağan	MN13

Fossil remains of the Rhinocerotidae family are common in the Late Neogene deposits of Asia, Europe, and Anatolia. Although they do not always provide sufficient chronostratigraphic resolution, they are valuable ecological indicators. During the Late Miocene, the Rhinocerotidae diversified and expanded rapidly in response to regional climatic changes. Two genera—*Chilotherium*, of Eurasian origin, and *Miodiceros*, of African origin—migrated into the Eastern Mediterranean during this period. While *Chilotherium* became widespread across much of Eurasia, *Miodiceros* was limited to the sub-Paratethys province, encompassing present-day Balkans, Ukraine, Anatolia, and Iran, as well as parts of Africa.

Within the Rhinocerotinae subfamily, the species *Miodiceros neumayri* (formerly *Ceratotherium neumayri*) and *Dihoplus pikermiensis* were present in the Eastern Mediterranean throughout the Late Miocene. *D. pikermiensis* is particularly well-known from fossil localities in Greece, including Pikermi, Samos, and Halmyropotamos.

Based on a synthesis of previously published studies and data identified 105 localities with Rhinocerotidae remains out of 247 total Late Miocene fossil sites. These localities were classified into three geographical regions on a modern map according to the taxonomic status of the remains: Southern Anatolia, Western Anatolia, and Central Anatolia. The number of fossil-bearing localities identified in each region are as follows: 10 in Southern Anatolia, 35 in Western Anatolia, and 60 in Central Anatolia.

In the Late Miocene of Anatolia, members of the family *Rhinocerotidae* are represented by seven genera: *Chilotherium* (%39), *Miodiceros* (%37), *Acerorhinus* (%14), *Dihoplus* (%8), *Aceratherium* (%2) and *Stephanorhinus* (%1) (Table 2).

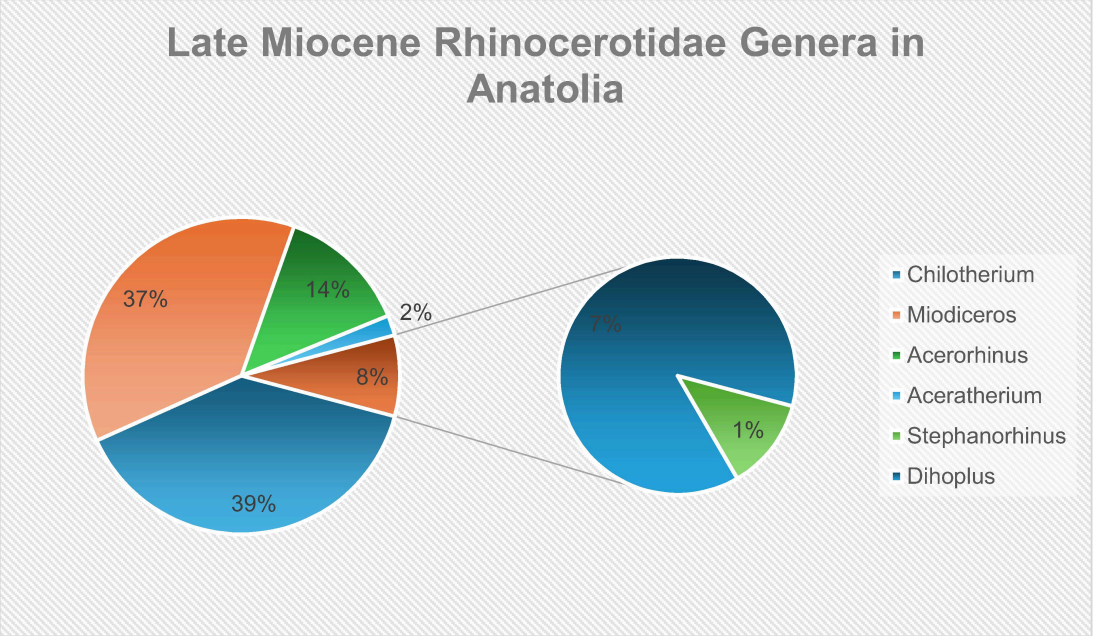
Among the Late Miocene localities, there are two genera with equal representation: *Chilotherium* (%38) and *Miodiceros* (%36). These rhinoceroses, possessing both brachydont and hypsodont teeth, included fruits, saplings, and tree bark in their diets. *Chilotherium* was both a grazer and a browser. Depending on the species, this genus had mesodont or brachydont teeth and mostly consumed non-abrasive food sources (Prothero et al., 1989; Nowak, 1991). In addition to being a typical genus of the Late Miocene, the ability of *Chilotherium* to feed as both a browser and a grazer may explain why it is one of the most commonly found taxa. The first known locality in Anatolia where it appeared is the Lower Vallesian-aged Eşme Akçaköy (MN9). *Chilotherium* lived for approximately 10 million years, from the Middle Miocene Astaracian stage (13.7 Ma) to the Early Pliocene (3.4 Ma). The last locality where it was seen in Anatolia is the Amasya locality in the Bozdoğan district of Aydın, dated to the end of the Turolian (MN13).

Miodiceros neumayri, on the other hand, due to its grazing diet and hypsodont teeth, likely consumed tough, abrasive grasses and tree bark. With the ecological transition during the Turolian, it must have inhabited open areas and ecotonal zones covered with grassland savannas. Although it had a wide distribution, it likely shared similar ecological niches with other browsing *Aceratheriini* species.

While *Acerorhinus* and *Dihoplus* were commonly found across all three regions, they showed different distribution patterns compared to the other two genera. The fact that species adapted to both grazing and browsing diets are found in the same localities supports the idea that they specialized in consuming different food resources. This suggests that, in the struggle for survival, they developed new strategies by exploiting different food sources, allowing them to share the same habitats.

Table 2

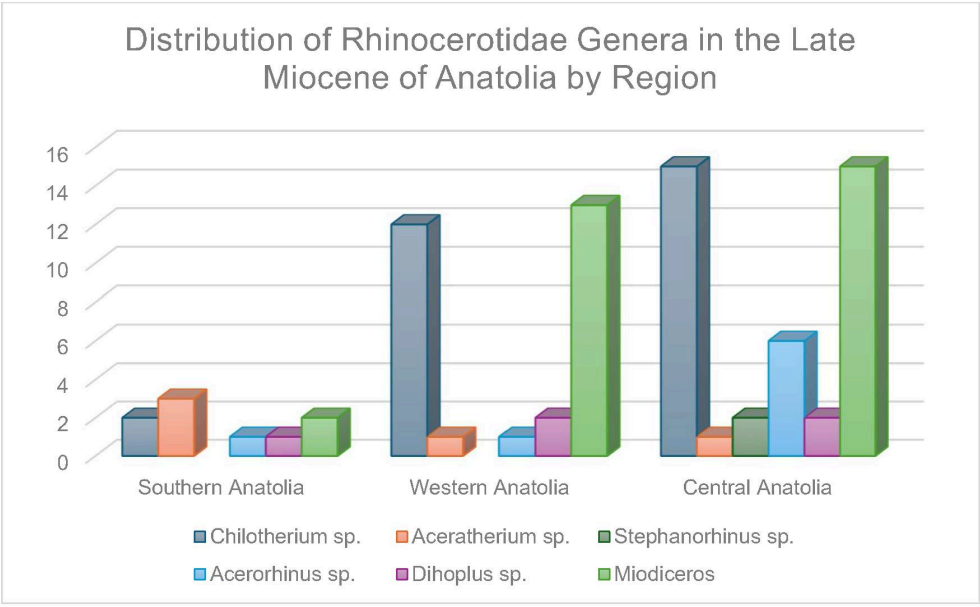
Rhinocerotidae Genera from the Late Miocene of Anatolia.



Among the 105 localities identified in Anatolia, when the distribution of Rhinocerotidae genera is examined by region, *Chilotherium* (39%), *Miodiceros* (37%), *Acerorhinus* (14%), and *Dihoplus* (8%) are commonly observed in all three regions (see Table 3). The differences are limited to their numbers/percentages. In Southern Anatolia, *Miodiceros* and *Diceros* are present; in Central Anatolia, *Chilotherium* dominates; whereas in Western Anatolia, *Stephanorhinus* and *Aceratherium* are absent (see Table 3). Overall, Rhinocerotidae species are distributed homogeneously across these three regions. Since the number of localities is higher in Central Anatolia, the fossil remains from this area are also more abundant compared to the other two. The absence of Rhinocerotidae remains in the Eastern and Southeastern regions of Anatolia is likely due to the lack of paleontological research in these areas or the absence of deposits from this period.

Table 3

Distribution of Rhinocerotidae Genera in the Late Miocene of Anatolia by Region.



According to the distribution pattern (see Table 3), the dominant community appears to consist primarily of hypsodont *Miodiceros* and *Aceratherine* species of large to medium body size, both of which are considered to have African origins. *Chilotherium* and *Miodiceros* exhibit distinct ecological adaptations. While the large-bodied *Miodiceros* species were better suited to open habitats, the medium-sized, short-limbed *Chilotherium* species adapted to more variable environments, including both semi-open and open landscapes.

DISCUSSION AND CONCLUSION

The development of fossil mammal communities during the Late Miocene was closely linked to the expansion and contraction of seasonal aridity across Eurasia. With the onset of mid-latitude drying, mammals with hypsodont feeding adaptations began to increase, and subsequent environmental, climatic, and paleogeographic processes accelerated this trend. Although equids and bovids are often cited as the best indicators of this ecological shift, rhinocerotids also reflect these climatic transition processes with notable clarity. Since the Oligocene, one or more rhinoceros species have been a significant component of the faunal communities in the most terrestrial habitats of the Northern Hemisphere. During the Late Miocene, Rhinocerotidae biodiversity increased, and their biogeographic distribution came to span large parts of the Old World. These taxa managed to cope with a variety of biotic and abiotic conditions, including environmental and climatic changes, interspecies competition, and migration.

The increasing seasonality and aridification during the transition from the Vallesian to the Turolian led to the expansion of open habitats and savanna-like environments. These conditions provided a more favorable ecological setting for grazer taxa such as *Chilotherium* and *Miodiceros*, which were present in Anatolia. As a result, these genera maintained their dominance in the region until the beginning of the Pliocene.

Heissig (1975) and Kaya (1994), who studied *Chilotherium neumayri* specimens from the Upper Miocene of Anatolia and Greece, observed an increase in body size from the Upper Vallesian to the Upper Turolian. However, comparisons between the specimens from the mid-Turolian locality of Akkaşdağı (MN12) and those dated to the late Turolian challenge this size increase hypothesis (Şen, 2005; Pehlevan, 2006). Giaourtsakis (2003) also suggested that the limited number of specimens renders it difficult to determine the range of variation within the population.

The general trend, as observed in other large herbivorous mammals, indicates a shift toward larger and more hypsodont forms. This adaptation likely conferred advantages in increasingly seasonal and arid environments, enabling these animals to process tougher and more abrasive plant material during dry periods (Fortelius et al., 2003). They exhibited evolutionary responses to changing environmental and climatic conditions by adapting (through grazer-browser feeding strategies or body proportions), migrating in pursuit of food sources, or facing extinction. The fact that Rhinocerotidae species today survive only in savanna ecosystems has led many researchers to propose that the Late Miocene—particularly with the expansion of open habitats and grasslands—may have featured a savanna-like ecosystem. The taxonomic composition, including large felids, hyenas, some bovid species, and *Hipparion* forms, along with the increasing crown height of teeth (hypsodonty), strongly supports the hypothesis that a savanna ecosystem existed during the Late Miocene.

Among the 105 identified localities, detailed descriptions have been provided for 53 selected sites. When grouping these 53 localities according to their Upper Miocene biostratigraphic (biochronological) age assignments: 12 localities fall within the Vallesian stage (MN 9-10), 4 localities are dated to the transition between the end of the Vallesian and the beginning of the Turolian, and 37 localities belong to the Turolian stage (MN 11-13).

Localities belonging to the family Rhinocerotidae from the Turolian stage are more numerous compared to those from the Vallesian stage. The increasing seasonality and aridification observed during the transition from the Vallesian to the Turolian led to the expansion of open environments and savanna habitats, which offered more favorable ecological conditions for grazing taxa such as *Chilotherium* and *Miodiceros* in Anatolia. As a result, these genera maintained their dominance in the region until the beginning of the Pliocene.

The majority of identified fossil localities are dated to the Turolian stage, a time characterized by the highest levels of mammalian taxonomic richness and the documented presence of hominoid primates in the region (Fortelius et al., 2003).

Among the Upper Miocene localities in Anatolia that yielded Rhinocerotidae remains, two also contain hominid specimens in their associated faunal assemblages. The first is the Sinap locality. In levels 8A and 12 of Middle Sinap, dated to MN 9, the hominid *Ankarapithecus meteai* was discovered alongside Rhinocerotidae species such as *Acerorhinus zernowi*, *Acerorhinus* sp. nov., *Chilotherium kiliasi*, *Chilotherium cf. C. habereri*, *cf. Chilotherium* sp. (primitive), *Stephanorhinus pikermiensis*, and *Miodiceros neumayri* (Fortelius et al., 2003: 284). The second locality yielding hominid remains is Çorakyerler, dated to MN 10–11. The hominid discovered here has been identified as *Anadoluvius turkae* (Sevim Erol et al., 2023). The Rhinocerotidae taxa represented in the Çorakyerler fauna include *Miodiceros neumayri* and *Dihoplus* sp. (Sevim Erol, 2023).

Throughout the Late Miocene, the rich and diverse presence of rhinocerotid species in Anatolia can largely be attributed to the coexistence of arid-open grasslands and humid-semi-closed forested areas along the same temporal framework. A prime example of this is the ability of the genera *Chilotherium* and *Miodiceros* to share the same ecological niche despite their differing dietary adaptations. Moreover, the occurrence of these genera across numerous Anatolian localities for approximately 10 million years demonstrates their capacity to adapt to climatic changes. However, it is tragic that today these animals, now limited to parts of Africa and the savanna habitats of Asia, may not survive the current crisis brought about by human impact.

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