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Title

On the record: the fossil mammals of Anatolia and Turkish Thrace in birds-eye view

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Abstract

The rich mammalian fossil record of Türkiye is of particular importance given the strategic position of the region between Eurasia and Africa. Nearly a century of research has provided valuable insights into the faunal developments, which are often separate from the western Eurasian mammal faunas. An analysis of the fossil record as it is recorded in the NOW database shows that there is a bias for the large mammal localities for the Late Miocene, where for the micromammals particularly the Early Miocene is well documented. Thus, the record still holds many possibilities for further research lines. But progress can not only be made by new discoveries, but certainly also by improving the record by revising existing collections.

Keywords

Mammal palaeontology, science history, Türkiye, fossil record, palaeontological databasing

Introduction

Saraç (2003) mentions in his report on the fossil mammal localities that Türkiye is the country with the highest density of fossil localities. Indeed, if it comes down to fossil mammals, the deposits of Anatolia are a true treasure cove. This richness in localities can be explained by the counterclockwise rotation and northward movement of the African Plate in respect to Eurasia, which, particularly in the later part of the Miocene, led to the formation of mountain ridges. The intramontane basins provided for many sedimentary environments with fossilization potential and an amazing fossil record, particularly where the Neogene is concerned.

The rich record is not the only reason why mammal palaeontologists have a particular interest in Türkiye. Almost any paper dealing with the fossil record of Anatolia mentions its strategic position between Europe, Africa and Eurasia. This makes it a central region in biogeographic studies. Over the last decades, there is also the growing realization that for much of its history, Türkiye was part of a different bioprovince than western Europe (e.g. Mein 2003; Eronen et al. 2009; Koufos and Konidaris 2011; Jafarzadeh and Konidaris 2020; Bilgin 2022; Marra 2025). From its relative isolation as part of the Balkan-Anatolian block in the Oligocene and Early Miocene, to a migration route south of the Paratethys up to a central area in the Greco-Iranian bioprovince in the Late Miocene, the Turkish faunas are part of a unique story. In 2016, the significance of Anatolia for palaeobiogeographical research was highlighted during an RCMNS (Regional Committee on Mediterranean Neogene Stratigraphy) interim workshop focussing on terrestrial ecosystems held in İzmir. The outcomes of this meeting were later published in a special issue of *Palaeobiodiversity and Palaeoenvironments*, entitled "*Taking the Orient Express? The role of Anatolia in Mediterranean Neogene palaeobiogeography*" (e.g., Alçiçek et al. 2019; Vasilyan et al. 2019; Bouchal 2019).

The current paper stems from a keynote lecture given at an RCMNS interim workshop held in Porrentruy (5-7 September 2025), organized by the same working group as the Izmir meeting. All of us authors have written or are writing their PhD thesis on Turkish fossil mammal assemblages. As such, we have made our contributions to the fossil record of the region, as have many others before us. At the same time, our group has also been involved in various studies on patterns in the fossil record using the New and Old Worlds (NOW) database (e.g., Van den Hoek Ostende et al. 2020, 2023). In this paper, we combine our love for the geological history of Türkiye and our interest in major patterns to have a critical look at where we stand when it comes down to the fossil record of Türkiye. In a time when scientists are required more and more to take the big picture into account based on available data, is the fossil record as it stands up to the task? What, if any, are the points of interest that may require extra attention? With our analyses we aim to see what challenges lie ahead, and which ones should perhaps be prioritized in a region of seemingly endless potential.

Early Years (1933-1975)

The first discoveries of fossil mammals in Türkiye date from the Ottoman period, but the systematic study of the fossil remains date from the early days of the Republican period (Sarıgül 2021a, b). A milestone in this respect is the publication by Malik and Nafiz (1933), in which they describe the mammal assemblage of Küçükçekmece as not only the first description of an entire fauna, but also the first paper solely written by Turkish nationals (Sen 2016).

Others followed in the footsteps of Malik and Nafiz (Kahya 2023). The study of mammal palaeontology in Türkiye came mainly under the umbrella of the anthropology departments (Sarıgül 2021b). The first proponent of this new school was Şevket Aziz (aka Kansu; 1903-1983), who, besides his studies in archaeology and (palaeo)anthropology also described mammals fossils. Also Muzaffer Süleyman (aka Şenyürek; 1915–1961) worked on mammals next to his specialism on primate and human dentitions. By contrast, Hüseyin Fikret Ozansoy (1913–2006) was a true mammal specialist, who made many contributions to the mammal palaeontology of Türkiye, including the first find of a hominoid, *Ankarapithecus meteai* (Ozansoy 1957). Apart from the official naming of this hominoid species, he presented in this paper the mapping, categorizing and biochronological dating of 31 fossiliferous localities across Anatolia and Thrace, providing an early and much needed framework for the, until then, poorly understood and highly fragmented Turkish fossil record. Later, he would expand on this framework, including a precise biostratigraphy of the Sinap section and additional descriptions of its faunas (Ozansoy 1965).

Altogether, these works of Ozansoy provided the scientific community with novel insights into the Turkish fossil record and solidified the role of Türkiye as an important migration corridor between Eurasia and Africa during the Miocene. Perhaps Ozansoy's greatest contribution to the field, however, was that he was instrumental in establishing both the Natural History Museum of the General Directorate of Mineral Research and Exploration (Maden Tetkik ve Arama Genel Müdürlüğü, commonly known as MTA) in Ankara and the Natural History Museum of Ege University in Izmir (Sarıgül 2021b). In doing so, he created repositories for both national and international palaeontologists to study the fossils of Türkiye, while at the same time creating a place where the Anatolian natural wealth in fossils could be shown to the general public (Kahya 2023).

International Cooperation (1975-)

Large Mammals

The last decades of the 20th century were the heydays for European mammal palaeontology, in which major progress was made in terms of taxonomy and

biochronology. Those were the days of illustrious names such as Leonard Ginsburg, Pierre Mein, Kurt Heissig, Volker Fahlbusch, Jorge Morales, Jordí Agusti, Hans de Bruijn, George Koufos, Ray Bernor and Şevket Şen. Notably, many of these names were also the founding fathers of the NOW database in the 1990s (Fortelius et al. 2023).

It is also the period in which there was a growing interest of foreign scholars in the Turkish fossil record. A major boost to mammal palaeontology in Türkiye came from a German-Turkish lignite exploration program in the late 1960s (Sickenberg 1975). During this program old localities were revisited and many significant fossil sites were discovered, including, for instance, the Middle Miocene hominoid locality of Paşalar (Schmidt-Kittler 1976; Alpagut et al. 1990; Begun et al. 2003a). The lignite program thus revealed the true richness of Anatolia in mammal localities, which led to Saraç's observation on the high density of sites.

At the same time, the close cooperation between the MTA and mammal palaeontologists stressed the importance of mammal fossils in dating terrestrial sediments. Sickenberg (1975) presented a biochronology based on 'Faunengruppen' (faunal groupings) named after a reference locality for each group. Notably, the biochronological system proposed by Sickenberg was hardly used. At approximately the same time, the Mammal Neogene (MN) system came into use (Mein 1975, 1979; Daams and Freudenthal 1981), which was based on reference localities in western Europe. This system quickly gained in popularity and was traditionally referred to as the MN zonation. Also the age of Turkish localities was commonly expressed in a designation to an MN unit. However, some authors warned about the usage of the MN system in Anatolia, as for part of its history it represents a different bioprovince than the region in which the MN system was defined (De Bruijn et al. 1992; Geraads et al. 2005). Nevertheless, MN units remain a very common way for mammal palaeontologists to communicate, and also Saraç (2003) assigned a large number of the Turkish localities to one or more MN units.

The taxonomic results of the German-Turkish expedition were published in a series of papers by specialists on the specific groups, including the suids (Hünermann 1975), rhinocerotids (Heissig 1975, 1976), proboscideans (Gaziry 1976), carnivorans (Schmidt-Kittler 1976), hipparionine horses (Staesche and Sondaar 1979), insectivorans (Engesser 1980), bovids (Köhler 1987), and cricetid rodents (Rummel 1998). As was common in those days, all of these papers were written in German.

A next major step in Turkish mammal palaeontology came from the expedition to the Sinap area (1989-1995) initiated by Berna Alpagut and Peter Andrews, both anthropologists and working together at Paşalar. The knowledge that Ozansoy had discovered *Ankarapithecus meteai* in the area back in 1953, may have been a big incentive for choosing this fieldwork area. At the same time, there had already been a rich history of excavation at the Sinap, including those of classical Anatolian

localities such as Çobanpınar, Kavakdere and İnönü (Sen 2003a). The PhD of Ozansoy (1958) was based on fossils of the Sinap, which he had brought to Paris. Later he would organize new excavations in the area, partly with French colleagues, and there were already a number of papers on the fauna of the area (e.g., Ozansoy 1965; Tekkaya 1970, 1973, 1974a, 1975). The new project, in which Fortelius and Kappelman replaced Andrews after the first season as co-organizers, aimed to capitulate on the earlier excavations and improve the biochronological resolution (Alpagut and Fortelius 1991). Unfortunately, the project was cut short in 1995 after the discovery of another specimen of *Ankarapithecus meteai* (Alpagut et al. 1996). This left the project in a peculiar situation, in which “Not a single member of the Sinap research group has been allowed to continue their studies of the fauna. Not one of her collaborators in this Sinap project group actually knows where the fossil material she [Alpagut] recovered is stored, or if they will ever be able to study it. (Sen 2003a, p. 14)”. Nevertheless, the results that were obtained were published in a monograph, dedicated to Fikret Ozansoy, several years later, notably without Alpagut (Fortelius et al. 2003). Most importantly, the monograph contained a chapter linking mammal localities to the Geomagnetic Polarity Time Scale (GPTS) (Kappelman et al. 2003a). In fact, a magnetostratigraphy of the Sinap had been published over a decade earlier (Sen 1991), but that was a true pioneering work at a time when the importance of correlating mammal faunas to the GPTS was just sinking in. The independent dating of the Sinap faunas provided the Turkish mammal record with important tie-points. For instance, it helped to show that the boundaries for MN 9 and MN 10, comprising the Vallesian, are remarkably similar in western Europe and in Anatolia (Braumuller et al. submitted).

In 2003, Gerçek Saraç completed a comprehensive report documenting more than 400 fossil mammal localities across Türkiye. This MTA report, written in Turkish, was never intended as an official publication, but turned out to be an influential work. According to Google Scholar, it has been cited 146 times in scientific papers and formed a major source on the Turkish mammal assemblages entered into the NOW database. As such it is clear that with his massive work, Saraç filled an important gap in our knowledge by making the fossil record to that point accessible in a comprehensive manner.

The Sinap volume appeared in the same year that Saraç (2003) presented his listing of the Turkish fossil record. Since then, obviously, work on the fossil mammal of Türkiye continued. That same year, a volume appeared on the hominoid locality of Çandır (Güleç et al. 2003). A similar monograph was published on the fauna of Akkaşdağı (Sen 2005) and later a volume was presented on Küçükçekmece (Sen 2016), the locality that played such an important role in the history of Anatolian mammal palaeontology. Without aiming to give a complete overview, papers appeared on faunas such as Yulaflı (Geraads et al. 2005), Şerefköy 2 (Kaya et al. 2012) and Kayaca (Konidaris et al. 2025), and detailed studies were published on bovids (Kostopoulos and Karakütük 2015; Kostopoulos et al. 2020, 2021),

carnivorans (Mayda et al. 2015; Morales et al. 2019; Van der Hoek et al. 2022), equids (Bernor et al. 2024; Kahya Parıldar et al. 2025), suids (Pickford 2016) proboscideans (Erten and Koralay 2020; Saarinen et al. 2025; Albayrak et al. 2025), to name but a few examples. Part of the studies on Anatolian mammal fossils are published in Turkish, and therefore quite hidden for the international audience (e.g., Mayda 2019; Taş and Erkman 2020). This certainly holds true for the PhD theses, which are still at most universities mandatory written in Turkish. Over the last decades, for instance, doctoral theses appeared on hyenids (Yavuz 2019), suids (Tarhan 2021), rhinoceroses (Güler 2023), and hipparionines (Şahin 2023),ha but follow-up papers for these theses in a more accessible language are rare.

Turkish Hominoids

We already noted that in Türkiye, mammal palaeontology traditionally resides at the universities under anthropology. It can therefore be no surprise that particular interest went out to those localities that were known to have a hominoid presence. To date, four Miocene hominid taxa have been discovered in Türkiye from different fossil horizons; *Ankarapithecus meteai*, *Kenyapithecus kizili*, *Griphopithecus alpani* and *Anadoluvius turkae*. In retrospect, the Turkish-German lignite explorations in the 1960s and 1970s have been instrumental in the discovery of all currently known Miocene, hominoid-bearing localities in Türkiye, with the exception of Sinap.

The first hominoid fossil in Türkiye, a partial mandible and associated dentition, was discovered in 1955 by Fikret Ozansoy in the Middle Sinap section (Ozansoy 1957). He described the material as *Ankarapithecus meteai*, naming the species after the Turkish capital Ankara and the MTA (Ozansoy 1965; Kappelman et al. 2003b). Moreover, a partial face (palate) was uncovered in 1967 by Ozansoy and his student Sevket Sen, and later described by Andrews and Tekkaya (1980). Ozansoy (1965) also mentioned an isolated upper P4, but unfortunately this specimen was neither figured, nor described and lost over time (Kappelman et al. 2003b). It wouldn't be until the excavations of 1995, led by Berna Alpagut, that we see additional specimens of *A. meteai* unearthed at Sinap. The 1995 specimens included two phalanges, a partial radius, an incisor, and a partial cranium and mandible that was described by Alpagut et al. (Alpagut et al. 1996; Kappelman et al. 2003b). With all this new available material, including a restoration of the palate found in 1967, David Begun and Erksin Güleç revised the genus in 1998, solidifying *Ankarapithecus'* position among other pongine-like Miocene apes (Begun and Güleç 1998).

In 1973, Ibrahim Tekkaya discovered a hominoid mandible at Çandır, which he described in 1974 as *Sivapithecus alpani*. He notes that the site had been studied since the 1940s, but the exact age of the locality had not yet been determined (Tekkaya 1974b). After two decades of detangling the phylogenetic relationships among Miocene hominoids from Eurasia and Africa, Andrews et al. (1996) reclassified the specimen as *Griphopithecus alpani*. The Çandır site was also

included in the German-Turkish lignite program, and its fauna was described as part of its results (e.g., Heissig 1976; Schmidt-Kittler 1976; Pickford and Ertürk, 1979; Engesser 1980; Köhler 1987). It wouldn't be until 1989 that extensive fieldwork at the site resumed (Güleç 2003). In 2003, multiple studies on the hominoid mandible were conducted, including its functional morphology (Güleç and Begun 2003) and on its implications on hominoid dispersal events (Begun et al. 2003a, b). That same year, an extensive survey of all macro- and micromammals at the site, complemented with a correlation to the GPTS, would finally confirm the Middle Miocene age of the locality, ending a debate lasting several decades (Krijgsman 2003).

Paşalar is probably the most famous Turkish mammal locality. It is with 55 taxa in any case the most diverse site (Fig. 1A). Note that for Çandır, the large mammals and micromammals are considered to come from two separate, closely adjacent localities, which combined would rival but not surpass the Paşalar diversity. In terms of numbers of hominoid specimens, Paşalar certainly holds the crown. This active digsite yielded nearly 2000 specimens belonging to two hominoid species (Mortzou and Andrews 2008).

The first formal excavations at Paşalar were initiated by the German Heinz Tobien in the late 1960s, already yielding 86 isolated hominoid teeth specimens. The hominoid teeth were first described by Andrews and Tobien (1977), who reported two distinct species: *Sivapithecus darwini* and *Ramapithecus wickeri*, for the larger and smaller morph respectively. In the following years, the taxonomic certainty of the Paşalar hominoids fluctuated, being subjected to both reclassification and abandonment of certain taxa (Greenfield 1979). Nevertheless, the hypothesis of two separate hominoids being present at the site persisted with the recovery of many additional specimens since the continuation of the excavations in 1983 (Alpagut et al. 1990; Waddle et al. 1995; Kelley and Alpagut 1999). In 1993, the identification of the larger morph would finally settle on *Griphopithecus alpani* (Martin and Andrews 1993), the species that had previously been recognized in Çandir (Tekkaya 1974b; Andrews et al. 1996). It would take another 15 years, however, to solve the mystery of the second hominoid species of Paşalar. In 2008, a reevaluation of two partial maxillae and a number of isolated teeth led to the recognition of the second species as *Kenyapithecus kizili*, based on a strong resemblance to *K. wickeri* from the contemporaneous Kenyan site of Fort Ternan (Kelley et al. 2008). This discovery once again established the position of Türkiye as an important biogeographic corridor for the dispersion of taxa between Eurasia and Africa (e.g., Kuhn 2010; Vural and Özkurt 2023; Guan et al. 2026; Skandalos 2025; Van de Weerd and Wessels 2026).

Also the Late Miocene locality of Çorakyerler was first mentioned in Sickenberg (1975). Erksin Güleç and her team described *Ouranopithecus turkae* from a maxilla and partial mandibles, discovered at the site in 1997 (Güleç et al. 2007). Ayla Sevim-Erol, part of the team describing *O. turkae*, would develop a long-lasting research

interest in Çorakyerler, uncovering a plethora of fossil vertebrate remains during the ongoing excavations since the beginning of 2000 (Sevim-Erol et al. 2016, Sevim-Erol 2023) and frequently publishing on the fauna and geology of the locality with (inter)national collaborators (e.g. Kostopoulos et al. 2020, 2021; Halaçlar et al. 2024; Alçiçek et al. 2026). The micromammals of the site were published by Ünay et al. (2006). The continuing efforts of Ayla Sevim-Erol and her team ensured that Çorakyerler is the second most diverse Anatolian mammal locality, featuring 46 taxa (Fig. 1A). In 2023, a newly found, partial ape cranium and the reanalysis of the specimen described earlier by Güleç et al. (2007) resulted in the identification of a number of differences between the Çorakyerler ape specimens and the Greek *Ouranopithecus*. Subsequently, the Çorakyerler hominoid was reclassified as belonging to a separate, new genus, *Anadoluvius turkae* (Sevim-Erol et al. 2023).

Besides the hominoid fossils, Türkiye has yielded fossil remains representing two distinct species of the genus *Homo*: *Homo neanderthalensis* and *Homo erectus*. The latter was discovered in 2002 by M. Cihat Alçiçek in a travertine quarry at Kocabaş after factory workers noticed fossilized skull fragments while cutting travertine blocks. Six years later, Kappelman et al. (2008) first reported on the fossil skull cap, identifying it as *Homo erectus*. Vialet et al. (2012) reconstructed the skull cap using 3D imagery. Their suggestion that the Kocabaş skull was close to the one from Zhoukoudian was later confirmed by a cladistic analysis (Vialet et al. 2018), firmly establishing the fossil as *H. erectus*.

Homo neanderthalensis was discovered in Karain Cave, where excavations were initiated in 1946 under the direction of İsmail Kılıç Kökten (Kökten 1947). Subsequent excavations yielded isolated teeth and additional non-dental human remains, which were identified as *Homo neanderthalensis* (Şenyürek 1949; Yalçınkaya 1988; Otte et al. 1998).

Micromammals

The study of micromammals (also referred to as small mammals) in Türkiye started much later than that of their larger counterparts. Systematic research on the fossils of rodents, insectivores, lagomorphs and bats started in the 1960’s in Europe, with pioneers such as Pierre Mein, Volkert Fahlbusch, Hans de Bruijn, and Thijs Freudenthal. It took a major boost when techniques were developed to screenwash large amounts of sediment in search of the little fossils (see Freudenthal et al. 1976; Daams and Freudenthal 1987). Micromammals quickly showed their worth in biostratigraphic and biochronological schemes, for the definition of land mammal stages (Daams et al. 1977, 1987; Daams and Freudenthal 1981), MN units (e.g., Mein 1990; De Bruijn et al. 1992; Van Dam et al. 2001), and local biostratigraphies (e.g., Kälin and Kempf 2009; Van der Meulen et al. 2012; García-Paredes et al. 2016) alike. In addition to the bio- and chronostratigraphic use, micromammals also proved to be important environmental indicators, also for large-scale ecological

changes (Van der Meulen and Daams 1992; Van Dam et al. 2006; Casanovas-Vilar et al. 2026).

The first detailed and comprehensive study on a micromammal fauna from Türkiye, was that of the Pliocene locality of Çalta (Sen 1977). Sen continued to publish a large number of papers on Anatolian palaeontology, but micromammals played a more modest role in these (e.g., Sen 1991, 2016; Sen and Sarıca 2011; Sen et al. 2019). In addition, small mammals had been collected during the German–Turkish lignite exploration programme reported by Sickenberg (1975), but these materials were published only in part and over a long period of time. The insectivores were described by Engesser (1980), while the cricetids were not published until much later by Rummel (1998).

The fossil rodent research in Türkiye received a major boost when Engin Ünay contacted Hans de Bruijn with the request to train her in micromammals. This was the start of a cooperation which would last decades, and started with studies on faunas from northwestern Türkiye (e.g., Ünay 1980, 1981; Ünay and De Bruijn 1984), surmounting in the PhD thesis of Ünay on the Oligocene rodents of Thrace (Ünay-Bayraktar 1989). The partnership became really prolific when Ünay and De Bruijn were joined by Gerçek Saraç, a geologist at the MTA. The team sampled terrestrial sediments all over Anatolia, providing dates for geological projects while sampling palaeontologically interesting localities in bulk. In that respect, their interest mainly went out to the Early Miocene, following the discovery that hamster genera indicative for MN 4 in western Europe occurred earlier in Anatolia. Localities like Harami (1 and 3), Keseköy, Kilçak (with four assemblages) and Kargi 1, 2, 3 yielded a wealth of material, which was published in a series of publications (e.g., De Bruijn and Saraç 1991; 1992; De Bruijn et al. 1993; 2003; 2006; Ünay 1994; Ünay and Göktaş 1999; 2000; Ünay et al. 2003; Wessels et al. 2001). Some selected hamster genera were published in the PhD thesis of Theocharopoulos (2000), while the publication on the insectivore assemblages formed the basis for the PhD thesis of Van den Hoek Ostende (1992, 1995a,b, 1997, 2001a,b,c,d).

As mentioned, the scientific focus of De Bruijn and Ünay lay very much with the Early Miocene, but the cooperation with the MTA resulted in (test) samples from different periods. Part of this material was published in a volume on the beginning of the Quaternary (Ünay and De Bruijn 1998). Although the paper contained a large number of localities, some of these contained one species only, indicating the limited material in the samples.

Decades of fieldwork all over Türkiye put Ünay, Saraç and De Bruijn in a unique position to create an overview on the micromammals of the region. In a volume celebrating the 70th anniversary of Hans de Bruijn, they published their “A preliminary zonation of the continental Neogene of Anatolia based on rodents” (Ünay et al. 2003). Although De Bruijn would continue to publish for many years, because of his age, he no longer made the long trips to Türkiye, and the cooperation with the

Turkish colleagues gradually came to an end. Undeniably, the team made a lasting impression on Turkish (micromammal) palaeontology. Recently, this was recognized by the International Commission on Geoheritage, as the collective proceeds of their fieldworks, stored at the museum of the MTA, was selected as a geo-collection.

Given their long-term cooperation with the MTA and their own interests, De Bruijn, Ünay and Saraç mostly approached fossil micromammals from a geological perspective. The usefulness of these fossils for dating terrestrial sediments in Türkiye did not go unnoticed, and inspired cooperation with geologists such as Orhan Kaya and Fikret Göktaş (e.g., Kaya et al. 1998, Göktaş 2014) and at a later stage also Cihat Alçiçek (Alçiçek et al. 2019). Micromammals also proved useful in the Vertical Anatolian Movements Project (VAMP) which was conducted as a cooperation between the European Science Foundation and Tübitak. As part of this project, Peter Joniak discovered the localities of Gökler, Tuğlu, and Tepe Alagöz (Joniak and De Bruijn 2015; Joniak et al. 2017; Čermák et al. 2019; Van den Hoek Ostende et al. 2019).

Joniak was also a member of the international National Geographic expedition entitled "*Palaeogeography of mammals following the collision of the African and Eurasian plates*". In 2015, this project aimed to enlarge the Early Miocene collections, combining the efforts of Turkish, Slovak and Spanish palaeontologists led by Lars van den Hoek Ostende. In their search for localities, they were heavily inspired by sites that were discovered by Orhan Kaya before his untimely death (Kaya et al. 2007). The project resulted in several publications prepared in collaboration with Serdar Mayda and Tanju Kaya from the Natural History Museum of Ege University (e.g., Bilgin et al. 2019, 2021, 2023; Joniak et al. 2019; Peláez Campomanes et al. 2019). It also supplied material for the PhD thesis of Melike Bilgin under direction of Peter Joniak (Bilgin 2022). De Bruijn and Ünay had already stressed the separate faunal development between Anatolia and central and western Europe (e.g., De Bruijn et al. 1992). Yet, when they published their biozonation (which is in fact a biochronology), they correlated most of their 'zones' one on one to MN units. Bilgin (2022), in refining the record, demonstrated that in fact the local units were strongly diachronous with the MN system.

So although a new generation of palaeontologists was getting into place, the focus of micromammal research remained very much on the Early Miocene. This is in itself not surprising. Serdar Mayda, who hosted the National Geographic team at EGE University, had done his PhD thesis under Orhan Kaya on the Early Miocene of Sabuncubeli (Mayda 2008) and Van den Hoek Ostende was a former student of Hans de Bruijn, and wrote his PhD on the insectivorans from the Early Miocene. Yet, Van den Hoek Ostende had come to Türkiye at the instigation of Cihat Alçiçek to work on Plio- and Pleistocene localities, such as Ericek and Bıçakçı (Van den Hoek Ostende et al. 2015b, 2015c). When it became clear that these localities were actually part of the Turkish PhD thesis of Hüseyin Erten (2013), the focus shifted

back to the Early Miocene. Erten continued to publish other parts of this thesis (Erten et al. 2014, 2015; Erten 2017, 2018), including Miocene and Quaternary micromammals. Other Late Neogene and Quaternary assemblages were published by Fadime Suata-Alpaslan (2009, 2011; Suata-Alpaslan et al. 2009), who had written a PhD under supervision of Engin Ünay on the Pliocene mammals from İğdeli (Suata-Alpaslan 2003). Also Ozan Erdal published on micromammals from the Quaternary (Erdal 2023; Erdal et al. 2018, 2019). More Pliocene and Quaternary localities were discovered during the project "Surveys for the identification of fossil localities of Neogene and Pleistocene periods in the province of Afyon and Burdur" led by Fatma Arzu Demirel. However, as the Covid19 pandemic struck, not all of the sites were elaborated. The exceptions are the assemblages from the Afşar section, which formed the basis for the PhD thesis of Panagiotis Skandalos (Skandalos and Van den Hoek Ostende 2023; Skandalos et al. 2024, submitted; Skandalos 2025). Thus, half a century after the first major micromammal presentation on a Pliocene locality (Çalta 2; Sen 1977, 1998), there are still few Late Neogene micromammal assemblages that have been fully described.

When we consider the Late Miocene, there is a peculiar parallel with the studies on the Pliocene. In this period too, there were early publications (e.g., Ünay 1980, 1981; Ünay and De Bruijn 1984), but little has been published since then. Micromammals were part of the Sinap expedition in the 1990s, but in the end only the hedgehog genus *Schizogalerix*, the Spalacidae , the Lagomorpha, and the murids and gerbils were published (Selänne 2003; Sarıca and Sen 2003; Sen 2003b, 2003c). Other than that, papers appeared on the glirids and the insectivorans from the localities of Hayranlı and Düzyayla in the Sivas basin (Kaya and Kaymakcı 2013; Furió et al. 2014). However, as in the Sinap, we don’t have a complete overview of the micromammal assemblage of those assemblages. A new Late Miocene locality, Sütlüce, was presented as being part of her PhD project by Altınbilek Köylü et al. (2025) at the Porrentruy meeting, and the insectivorans of that locality are published elsewhere in this volume (Van den Hoek Ostende et al. this volume). Some other Late Miocene finds featured in the taxonomic reviews Spalacidae (Sen and Sarıca 2011) and Sciuridae (Bosma et al. 2013, 2019). Such reviews are of particular interest, since they explicitly allow to compare material from different localities and ages. Such an overview will not be gained from looking at material from one locality alone, and as such reviews promote taxonomic stability.

Material and Methods

The data for this study were downloaded from the NOW database (The NOW Community 2026). As a first step, the dataset was filtered to contain only occurrences from Türkiye.

Data on the age of the localities were used to assign an MN unit (range), Epoch and European Land Mammal Age (ELMA). To evaluate the temporal resolution, an

additional metric was deployed, assigning each Neogene locality to one of three groups: ‘Well constrained / Single MN Unit’, ‘Independent dating’ (indicating an age derived from radiometric- or geomagnetostratigraphic dating), or ‘Wide Range / Multi-MN’ if the locality could not be restrained to a single MN unit or other relevant chronological unit. In every analysis of individual MN units, only localities constrained to a single MN unit were included.

To assess the faunal character of localities, assemblage categories were assigned. This resulted in either a micro, macro or mixed designation, based on the presence of micromammals (orders: Chiroptera, Rodentia, Eulipotyphla, Lagomorpha), macromammals (e.g. Proboscidea, Carnivora, Artiodactyla) or a mix of both orders. Taxonomic richness was calculated for each locality and defined as the number of unique genus and species combinations, treating indeterminate records (‘indet’ or ‘sp.’) as separate categories. To examine the regional distribution of Turkish and Greek hipparionine horses, occurrence data from Greece were integrated into the primary dataset. Each species occurrence was then evaluated on its geographic restriction, and characterized as being either exclusive to Türkiye, exclusive to Greece, or shared across both regions. Any issues we encountered in terms of missing data or updated classifications were corrected in the NOW database, after which analyses were resumed with a new download.

The remaining core dataset was converted to a table for further visual inspection and transparency purposes, exported as a spreadsheet using *openxlsx* (Schauberger and Walker 2025), and as a text document using *officer* (Gohel et al. 2026) with a modified tubular layout utilizing *flextable* (Gohel and Skintzos 2026).

All analyses were performed in R (R Core Team 2013), specifically RStudio version 2026.01.0, build392 (Posit team 2025). Core packages are derived from *tidyverse* (Wickham et al. 2019), including *dplyr* (Wickham et al. 2026) for data manipulation and *ggplot2* (Wickham 2016) for the data visualization. Composite figures (containing multiple plots) were created with *patchwork* (Pedersen 2025) and the tweaking of labels within figures was performed with *scales* (Wickham et al. 2025) and *ggrepel* (Slowikowski 2026). Base maps were derived from the Natural Earth Database, using *rnaturalearth* (Massicotte and South 2026), while the *sf* package (Pebesma and Bivand 2023) was used for plotting coordinates, fixing the map stretch and measuring distances to group localities into 100 km regional clusters.

Results

The record in numbers

The Neogene mammal record from Türkiye represented in the NOW database comprises 506 localities. In total, 254 localities are classified as macromammal assemblages, corresponding to approximately half of the record. Micromammal

assemblages account for 174 localities, whereas mixed assemblages containing both macro- and micromammals are less frequent, with 78 localities (Fig. 2). This distribution immediately shows that the record is numerically dominated by macromammal localities, but it also indicates that the different components of the record are not equivalent in terms of sampling history or analytical value. The data indicate that fossiliferous localities are scarce in the eastern part of the country, as is visible in Fig. 3. This scarcity is likely due to limited accessibility and security related constraints that hinder fieldwork, rather than to a lack of favorable fossilization conditions in the region.

The distribution reflects a major structural feature of the record. When looking at the number of species per locality, the first thing that stands out is the large number of sites that have yielded one species only in large mammals (Fig. 4C). Such localities are often referred to as singletons and may represent chance finds on the surface, or during road or construction works. Their use is usually very limited and only in rare cases, such as the discovery of a near complete skeleton, can be identified with certainty. Their high number in Anatolia is somewhat unusual, for these finds rarely appear in the literature that usually forms the basis for entering data points into a database like the NOW. However, much of the Anatolian data was entered from the technical report of Gerçek Saraç (2003), that was based on the collections of the MTA. And since these collections are based on decades of fieldwork by the scientist of the directorate, one would expect that many a surface find from these explorations would have found its way into the collection. Such records are valuable as evidence for the presence of particular taxa, however their usefulness for palaeoecological reconstruction, faunal similarity analyses or regional diversity estimates is limited.

By contrast, micromammal localities are less numerous but tend to show higher taxonomic richness. This reflects differences in collecting practice. It is notable, however, that also in the micromammal assemblages, there is a high number of assemblages containing only one species (Fig. 4C). Micromammals are usually collected in bulk by wet-sieving sediment, and, with the possible exception of beavers and porcupines, are not typically found as a surface find. Presumably, the relatively high number of singletons derives from test samples stored at the MTA from the campaigns of Ünay, De Bruijn and Saraç, and listed in Saraç (2003). The nine singletons from the Late Pliocene/Early Pleistocene mentioned in Ünay and De Bruijn (1998) certainly would suggest so.

When studying a fauna, micromammal palaeontologists generally aim at retrieving around one hundred fossils. Depending on whether or not the insectivorans are included, the typical small mammal assemblage will have around ten species. Diversity also tends to differ depending on the age of the sample, with particularly the Early Miocene showing high levels of diversity. As we can see in Fig. 4C, assemblages containing over four species are most commonly micromammal assemblages, up to assemblages with more than twenty species, which are

generally the mixed assemblages. The most diverse micromammal assemblage is that of Keseköy, followed by Harami 1 (Fig. 1D), but these are ticking all the boxes in having both rodents and insectivorans studied, dating to the Early Miocene and an atypically large sample sizes of over one thousand Mm1Mm2 (Van den Hoek Ostende 2001d). Notably, out of the ten largest micromammal assemblages, nine are from the Early Miocene (Fig. 1D). The only exception is the Pleistocene assemblage from Yarımburgaz Cave (Santel and von Koenigswald 1998).

Mixed assemblages are even rarer and comprise only ~16 % of the Turkish record, but they are disproportionately represented among the richest localities (Figs 1A and 2).This is to be expected, as these localities combine both the large mammals and the micromammals, and therefore automatically have a broader range of taxa. The importance of mixed assemblages lies in this combination: macromammals provide biogeographic and palaeoecological information at larger spatial scales, whereas micromammals commonly offer finer biochronological and environmental resolution. Not only are they thus more informative, but they also provide a tie-point between assemblages that contain large or small mammals only. However, the category “mixed” in this paper should be interpreted with caution. We must bear in mind that we use a strict taxonomical division between micromammals and large mammals, the former comprising all records of rodents, eulipotyphlans, lagomorphs and bats. As a result, typical macro-mammal assemblages such as Şerefköy 2 (Kaya et al. 2012) or Kayaca (Konidaris et al. 2025) are considered mixed assemblages. The reversed may also be true, as also the predominantly micromammal assemblage of Sabuncubeli (De Bruijn et al. 2006) is considered a mixed assemblage for the presence of two small carnivorans (Morales et al. 2019; Kargopoulos et al. 2021). Therefore, the percentage of true mixed assemblages with a well-defined macro- and micromammal component is even lower.

A major factor in the rarity of mixed assemblages are the different taphonomic factors involved in the accumulation of large and small mammal fossils. Rivers can play an important role in accumulating carcasses and depositing them when energy levels drop. By contrast, the pellets of birds of prey are considered to be primary accumulation for micromammals, and in order for these pellets to be preserved, they need to be washed into a low energy environment such as pools and lakes. Because of these opposing energy requirements, a site requires specific taphonomic features in order to preserve both. However, in sections that preserve sediments of both higher and lower energy realms close together, we can find large and small mammals in close connection. The micromammals of Çandır 2 were collected from a bed in the vicinity of the main excavation, only two meters above the level of the main excavation (De Bruijn et al. 2003). For all practical purposes, they can be considered part of the same fauna, although in the NOW database (and our analysis) they are considered as a separate large and micromammal site.
There is a type of deposition that quite commonly produces mixed assemblages. Fissure fillings play an important role in mammal palaeontology in western Europe.

However, this type of deposit is rare in Türkiye. The fissures from Altıntaş have never been fully studied, and only the scuirids (Bosma et al. 2013) and murids (Wessels 2009) have been published. Only the Pleistocene fissure of Emirkaya yielded a complete, mixed assemblage, although largely identified at the genus level only (Saraç 2003).

Distribution in time

The temporal distribution of the fossil mammal record is far from uniform. This pattern is visible at several levels: in the absolute number of the localities through time, in the changing proportions of macro-, micro- and mixed assemblages, in the geographic spread of the record, and in the quality of temporal control. Therefore, the temporal distribution should not be interpreted simply as a curve of fossil abundance. Rather than that, it reflects the combined effect of geological exposure, sampling history, assemblage type, research focus, and database structure. This becomes clear when the full dataset is compared with the chronologically constrained subset used for analyses at the level of individual MN units. In the full dataset, macromammal localities dominate numerically, but in the temporally constrained assemblage dataset micromammal localities form the largest component. The difference is easily explained. Micromammals are generally considered to be more suitable stratigraphic markers. Their assemblages are gathered in larger numbers, making it easier to pinpoint entrances and extinctions.

We should also bear in mind that a biochronological scheme was published for the Neogene micromammals of Anatolia (Ünay et al. 2003), where, as yet, such an overview is missing for the large mammals. As a result, the apparent structure of the record changes according to the degree of temporal filtering. Localities that can be placed more precisely in time are not simply a smaller version of the full dataset; they more often than not reflect a different assemblage composition (Fig. 4D). Micromammal localities are therefore disproportionately important in the temporally resolved part of the record. This emphasizes the importance for establishing a biochronology for the large mammals. Without it, we lack the resolution to track biogeographical changes in time.

The Early Miocene record is strongly dominated by small mammal assemblages. This pattern already begins in the Agenian, which consists entirely of small mammal localities. It continues into the Orleanian, where micromammal localities remain by far the dominant component of the record. This reflects the historical importance of the Early Miocene small mammal studies in Anatolia (Fig. 4A, B). The Early Miocene signal should therefore be understood not only as feature if the fossil record itself, but also as the result of a long research tradition focused on small mammals biochronology, beginning with the work of De Bruijn, Ünay and Saraç and later continued by Bilgin, Joniak, Van den Hoek Ostende and collaborators. This “Early

Miocene micromammal boom" therefore, is one of the clearest examples of how focused sampling and detailed taxonomy can shape the structure of the fossil record. The Middle Miocene shows a more balanced composition (Fig. 4B). Macromammal localities form the largest component, but micromammal and mixed assemblages are also well represented. At the MN level, MN5 and MN6 show an increasing contribution of macromammal assemblages, whereas MN7/8 is almost evenly divided among macro-, micro- and mixed assemblages (Fig. 4D). The Astaracian therefore forms a transitional interval between the micromammal dominated Early Miocene and the more macromammal dominated Late Miocene record.

The Late Miocene shows the most prominent concentration of localities. In the Vallesian and Turolian, macromammal assemblages become the dominant component of the record. The Vallesian includes 53 localities, of which more than half are macromammal assemblages, while mixed assemblages also form a substantial proportion. In fact, there is a marked peak in both the number of macromammal and mixed assemblages in MN 9, accompanied by a more moderate high in the micromammal assemblages (Fig. 4D). At the same time, there is a peak in the localities with independent dating (Fig. 5B). This can all be attributed to the many Vallesian localities in the Sinap sections, many of which have been correlated to the GPTS. Note, however, that because of this correlation, also localities yielding one species only (e.g., Sinap 83 with its *Choerolophodon anatolicus*), appear in our analysis as well constrained. Moreover, we already noted that the micromammal component of the Sinap mixed assemblages was not fully elaborated due to circumstances. Obviously, the sections are still invaluable to the Turkish fossil record. In the biochronologic analysis of the Turkish Vallesian by Braumuller et al. (submitted), one third of the localities are from the Sinap, and are pivotal in assigning ages to the boundaries of the different units.

The Turolian shows an even stronger macromammal signal, with 30 of 50 localities classified as macromammal assemblages (Fig 4B). By contrast, the micromammal localities are at their lowest point, even with no localities confidently assigned to MN 11. This may in part explain the low resolution for Turolian localities. Around 40 % could not be assigned to an MN unit (Fig. 4B, D). With over 20 localities assigned to the unit, MN 11 seems to be a bit of an exception (Fig. 4D), but this can be related to the early Turolian localities in the Sinap sections, which also account for the high number of independently dated localities (Fig. 5B). Also from our own experiences, we recognize that distinguishing between the middle and late Turolian faunas is challenging (Koufos 2003, 2013, 2024), and the low number of MN 13 localities certainly looks somewhat suspicious in that respect.

The younger record shows a different pattern. The Ruscinian is strongly dominated by micromammal localities, which form 20 of the 24 localities in that stage. The Villafranchian also has a strong micromammal component, with 28 of 49 localities classified as micromammal assemblages.The Pliocene and Pleistocene record

contains a substantial number of small mammal localities, yet this part of the record has been less intensively developed than the Early Miocene micromammal record (Fig 4B, see also Skandalos 2025). In this respect, this micromammal record represents an important area for future work.

The richness profiles add a further dimension to this pattern. Locality number and faunal information are not equivalent. Low richness localities are very common, especially among macromammal assemblages. By contrast, micromammal assemblages more often extend into intermediate richness classes, while the richest localities are generally mixed assemblages (Fig 4C). The richest localities include well-known mixed assemblages such as Paşalar and Çorakyerler, whereas the richest micromammal localities include Keseköy and Harami 1 (Fig 1A). This means that a temporal peak in locality number does not necessarily correspond to a peak in analytical value. An interval dominated by many low-richness macromammal localities may appear rich in terms of locality abundance, whereas an interval with fewer but well-sampled micromammal or mixed assemblages may be more informative for biochronology, faunal comparison and palaeoenvironmental interpretation.

The temporal structure of the Turkish fossil mammal record should therefore be understood as the product of several overlapping signals rather than as a simple reflection of changing mammalian diversity through time. The Early Miocene record is shaped above all by micromammal assemblages and by a research tradition in which small mammals were used to refine Anatolian biochronology (Bilgin 2022). By contrast, the Late Miocene record is numerically dominant, but this dominance is strongly linked to macromammal localities, intensively studied areas such as Sinap, and the greater visibility of large mammal remains in field surveys and historical collections. The greatest research interest goes, however, still to the hominoid localities, and decades of research efforts makes sites like Paşalar, Çandır, and Çorakyerler a league of their own (Fig. 1).

Taxonomic impediment

Having considered the quantitative aspects of the Turkish fossil record, the inevitable question arises about the quality of the record. Have localities been correctly dated and have species been correctly identified? As relevant as the question is, it is impossible to answer. First of all, the questions assume that we know what “correct” is, whereas some issues are the matter of ongoing debate. In addition, we are studying the record using the NOW database as a proxy for that record. Any perceived problems may actually lie with the database, for, for instance, still having out-dated information. An approximation of the quality of a record can be based on the validation of its finds. The validation refers to how well substantiated a source is. Full taxonomic descriptions will generally provide a firmer base for the data than faunal lists do. As we noted, a large number of assemblages have been entered

from faunal lists in the technical report of Saraç (2003), which have a low validation. At the same time, we have also seen that assemblages such as Akkaşdağı and Küçükçekmece have been fully described by a team of specialists (Sen 2005, 2016). In the case of micromammals, giving full descriptions of at least all the rodents in a fauna is far more common (e.g., De Bruijn et al. 2003, 2006; Bilgin et al. 2019, 2021, 2023; Skandalos et al. 2023, 2024, submitted). Therefore, the validation rate of micromammals will generally be higher than that of their larger counterparts. Nevertheless, with some of these descriptions and identifications being decades old, it is getting increasingly clear that part of the record is in need of revision.

Of course, the fossil record is imperfect by its very nature. Death assemblages will only preserve part of the living fauna and large scale excavations are costly, further limiting the proportion of a fauna that we can retrieve. The fossils that we find may not preserve the characteristics needed for a firm identification. So the question we should ask ourselves is not how good the record is, but if it is suitable for our biochronologic, palaeoenvironmental or biogeographical analyses. Such large scale analyses inevitably carry some noise in the data as a result from missing data or misidentifications. This holds true for any analysis based on species data and is known as the taxonomic impediment. Particularly in palaeontological studies based on faunal similarity (e.g. Eronen et al. 2009; Kaya et al. 2018; Madern et al. 2024), the taxonomic impediment is partly countered by carrying out analyses on the genus level (Alroy, 1996, 2003). In such a case, sometimes records identified to the genus level only are again filtered out, as they inherently carry a lower validation.

The taxonomic impediment can take all shapes and forms, and is often related to the material available. In an ongoing project of one of us (YB), we are making an attempt to place the combined Late Miocene large mammal assemblages from Greece and Türkiye in chronological order to create a biochronology for the Greco-Iranian bioprovince (Braumuller et al. submitted). Such a sequence should logically place members of presumed lineages in sequential order, which is actually one of the tools at our disposal to create the sequence. In the case of *Machairodus aphanistus* and its presumed descendant *Amphimachairodus giganteus*, however, this proved to be impossible. Although *Amphimachairodus*, as expected, makes its entrance at the beginning of the Turolian, *M. aphanistus* is still recorded in the Turolian localities of Kemiklitpe D, Karahasan, and Mahmutgazi. This is, however, part of a larger mosaic pattern throughout the distribution range of these large cats, with more plesiomorphic or apomorphic characteristics appearing in alternating assemblages. This mosaic is found particularly during the early Turolian, and makes a strict distinction between the two (chrono-)species impossible (Morlo and Semenov 2004).

One of the most notable examples in our studies on how the taxonomic impediment can influence the fossil record is the case of the hipparionine horses. As we mentioned, we combined in our ongoing biochronological analyses the records of Greece and Anatolia, under the assumption that these records are compatible.

Although regional differences are to be expected (e.g., Kostopoulos 2009), at the very least the fossil record of nearby Samos should be in sync with that of Anatolia. As it is, however, less than 50% of the hipparionine species are recognized in both countries (Fig. 6B). We do note that the relatively high percentage of solely Turkish species in MN 9, MN 15 and MN 16 (Fig. 6C) are an artifact because of sample size. There is only one Greek MN 9 locality (Pentalophos 1) and in the MN 15 and 16 only four species were recorded. Nevertheless, of the ten species that were recorded from Türkiye but not from Greece, half are actually known only from Türkiye. These are *Hipparion uzunagizli*, *Cormohipparion sinapensis*, *C. cappadocium*, *C. kecigibi*, and *C. sofularensis*. These seems to part of a wider tradition in hipparionine taxonomy, for also Hungary (*Hippotherium intrans*), Iran (*Hipparion gettyi*), Georgia (*Hipparion eldaricum*) and Greece (*Hipparion sithonis*, *H. phlegrae*) have species restricted to their borders. Such a regional distribution, particularly when linked to certain authors, could indicate an oversplitting in the taxonomy. In this respect, it is telling that the Turkish occurrences of *Plesiohipparion* cf. *longipes* [= *Cremohipparion* cf. *fissurae* in Becker et al. (2026)], *Hipparion prostylum*, *H. sebastopolitanum*, and *H. giganteum* were all recorded by European, and mostly Greek, authors (Koufos and Vlachou 2005; Geraads 2013; Koufos and Sen 2016). On the other hand, the renowned hipparionine specialist Ray Bernor was involved as (co-)author in all four named strictly Turkish species of *Cormohipparion* (Bernor et al. 2003, 2024; Kahya Parıldar et al. 2025). They are part of a pattern which led Bernor and Sen (2017) and Bernor et al. (2021) to suggest that the entrance of the hipparionine horses into Eurasia should be termed the “Cormohipparion” event, and that this genus of North American origin only evolved into other genera when crossing into Europe.

Another thing that stands out in Fig. 6A is the high number of *Hipparion* indet. in Türkiye. This is in itself not surprising. We already noted the large number of singleton localities and the strong representation of the Late Miocene in the record. Given that hipparionine horses are very common during that subepoch, many of the surface finds that comprise the singleton localities will belong to these horses. And such a find is impossible to determine beyond *Hipparion* indet., in which *Hipparion* is used sensu lato, possibly representing a number of genera. In addition, however, the figure also shows that named species have a higher number of occurrences in Greece, despite the overall record being more limited. This suggests that the Greek record has been studied in more detail, as we indeed know to be the case (Koufos et al. 2022).

An interpretation as solely a biogeographical signal for the differences observed between the Greek and Turkish record in Fig. 6 does not seem viable. The record seems to reflect differences in research history, taxonomic practice and the resolution of the available material. Indeed, in Turkish literature, we are already noticing the adaptation of ‘European’ names in the identification of hipparionine fossils (Yilmaz Usta et al. 2019; Şahin 2023). The case of the hipparionine horses serves as a sobering reminder that the patterns we discern in databases, albeit

biogeographical, palaeoenvironmental or phylogenetic, are as good as the data points allow. Similar, if less severe, cases of taxonomic impediment can be found throughout the NOW and other databases. The desire for unravelling the large patterns is understandable and should be applauded, but at the same time we must realize that we are still dependent on the precise identifications and reviews of taxonomic specialists. And in some cases, these reviews may be the most important way to make progress.

The taxonomic impediment is not restricted to fragmentary material or to records identified only above species level. It may also arise from the historical development of taxonomy itself. Some groups remain problematic because species limits have been unstable, as in the case of *Chilotherium*, which a large number of named species complicates comparisons between regions and studies. Methodological developments may have a similar effect. In their study on the arvicolids from Afsar, Skandalos et al. (2023) pointed out that an important character as the HH-index to indicate hypsodonty was often missing on older descriptions. In other cases older collections could not be assigned to taxa that had not yet been recognised in the relevant regional record. The recognition of *Qurliqnoria* in the Late Miocene of Anatolia provides an example; material studied before the description of the taxon could only be identified within the taxonomic framework available at that time. As Kostopoulos et al. (2020) indicated, other material from Turkish sites and in particular the Sinap is presumably attributable to the genus, but it requires a complete revision to get the full picture.

As the term itself already indicates, we tend to see the taxonomic impediment as a problem. However, from the examples given above, it is clear that it also opens opportunities. Because what data analysts perceive as a problem, provides a challenge for taxonomic specialists. It is in this interplay between interpreting data and improving on the quality of data points that true progress can be made. A vital role in this lies with the collection institutions. Because taxonomy, certainly in palaeontology, is in flux and problems can only be solved by revisiting the old collections. In fact, this touches upon one of the cornerstones of science, reproducibility. As such, palaeontologists should always bear in mind the long-term storage and accessibility of their fossils.

Epilogue

In line with the statement of Saraç (2003) that Türkiye is the country with the highest density of fossil localities, it is clear from our analyses that its fossil record is indeed very rich. However, the picture that we build up from the NOW database may not be entirely representative. Most of the database has been built up on the basis of literature, although, certainly in the early years of the database, alternative sources were also welcomed. In the early years of the database, many of its founders, including Mikael Fortelius, Ray Bernor, and Sevket Sen, also cooperated in the

Sinap project and had a keen interest in the Neogene faunas of Türkiye. As such, it is not surprising that the wealth of data from the technical report of Saraç (2003) found its way into the database, even though, as we discussed, much of the data has a low validation. Basically, a large number of singletons from chance finds or micromammal test samples were included in the NOW database for Türkiye, where such data were incorporated into the database to a lesser degree for other regions. This implies that the number of localities may be a bit of an overestimate, although the number of well-defined assemblages is still impressive. At the same time, it means that the quality of the record is higher than our analyses may imply, because with the singletons a certain amount of noise has been introduced in the data. Nevertheless, singletons also have their use, as they indicate the potential for fossil localities and provide data points for geographic distribution. However, for analyses of diversity, faunal similarity, palaeoecology or biochronology, we need to rely on sufficiently large assemblages. Overall, our dataset is a rather heterogeneous record in which high quality assemblages and low information occurrences coexist.

When considering the high quality assemblages, the well-studied assemblages of hominoid-bearing sites such as Paşalar, Çandir and Çorakyerler come to mind. In the Turkish academic system, mammal palaeontology resides under anthropology, and this will have been a key factor in the organization of decades of excavations on the sites by students of Berna Alpagut (Paşalar), Erksin Güleç (Çandir) and Ayla Sevim Erol (Çorakyerler). As a result, these sites stand out at important windows in time for the entire mammal fauna of Anatolia. That same interplay between anthropology and mammal palaeontology did not work out as well in the Sinap project. After the find of a primate skull, the work on other groups was all but cancelled (Sen 2003a). Nevertheless, the project proved of crucial importance to the fossil record of Türkiye. The correlation between the localities of Sinap Tepe and the GPTS provided crucial tie points for the biochronology of Anatolia (Braumuller et al. submitted).

Of course, there are large and well-studied mammal assemblages outside the hominoid localities. We mentioned the localities of Küçükçekmece and Akkaşdağı (Sen 2005, 2016), but these are certainly not the only sizable assemblages. However, a number of these, and certainly those from Sickenberg (1975) may have been overtaken by taxonomic progress and will be in need of revision. Our analyses suggest that much can be gained from such revisions, but at the same time we realize that there are many practical problems. Part of the material from the Sickenberg expedition is scattered over collection institutions in Europe and also collections in Türkiye itself are not always easily accessible. Not all Turkish colleagues are equally versed in English, and to make things more complicated, much of the relevant older literature is written in German, French or Spanish. Reversedly, there is also a lot of Turkish literature, particularly PhD theses, which have little impact for being overlooked. In the present day and age, we have

increasing access to translation tools to mitigate these problems, but it is clear that getting the much needed overview is an arduous task.

In the study of large mammals, there is a strong bias towards Late Miocene assemblages. Probably, this bias represents the presence of suitable environments for fossilization. Also in neighbouring countries, we see a high number of mammal localities from that period. Nevertheless, other periods are also represented in the record and perhaps two of the best studied assemblages, Paşalar and Çalta, represent the Middle Miocene and Pliocene, respectively.

The more equitable distribution of micromammal localities over time reflects that the suitable environments for fossilisation are of all ages. Micromammal localities typically constitute a fossiliferous layer of a couple to tens of centimeters in a section and can, compared to their macromammal counterparts, be relatively easily exploited. In this respect, the relative paucity of Late Miocene sites is surprising, certainly because at one time these were the first to be elaborated upon (Ünay 1980, 1981; Ünay and De Bruijn 1984). There is, however, a bias in the research effort on micromammals, and the largest and best recorded localities are from the Early Miocene, due to the work of De Bruijn and Ünay and at a later stage Bilgin and co-workers. This research was inspired by the clear faunal differences in the Early Miocene between Türkiye, as part of the Balkan-Anatolian block, and western and central Europe, and the consequences it held for the biochronology. However, now that we realise that Türkiye as part of the Greco-Iranian Bioprovince also had its own large mammal fauna during the Late Miocene, the study of the micromammals becomes equally important. For now, it is a major gap in our knowledge, but also in the Pliocene and Quaternary record there are still a lot of questions that await answering.

Apart from their importance in palaeobiogeographical and palaeoenvironmental studies, the micromammals hold another important quality. In the terrestrial sediments of the Turkish intramontane basins, they are the best tool for dating strata. This is the reason why geologists from the MTA as well as colleagues such as Orhan Kaya and Cihat Alçiçek showed such a keen interest in these fossils. However, in order to be optimally usable, the ‘biozonation’ of Ünay et al. (2003) needs to be revised and updated. More importantly, it must be considered as a regional biochronology that will only be correlated with the MN system a posteriori, in the way that Bilgin (2022) demonstrated for the Early Miocene part of the time scale.

Overall, almost a century after Malik and Nafix (1933) published their paper on Küçükçekmece, we can conclude that a strong record of fossil mammals has been built up. A record that does justice to the high density of fossil localities and confirms the important biogeographical role that Türkiye plays due to its strategic position between Eurasia and Africa. Most importantly, the fossil record shows that the region cannot be simply considered an eastward extension of the western Eurasian faunas,

but had its own faunal history. The faunal exchanges with other regions and local developments play an important role in understanding how mammalian faunas developed over time.

In some ways, the record is still a crude diamond awaiting polishing. Many new palaeontological discoveries lie ahead of us, and part of these discoveries will come from the ongoing excavations all over the country. This will particularly be the case for excavations that focus on the lesser known parts of the record. As we noticed, Early Miocene micromammals and Late Miocene large mammals are at present very well represented, while other periods have a less dense record. But many more discoveries can be made in the vast collections that have been gathered over the years, and in particular in comparing material from the different collections in comprehensive overviews. Major progress can be made in revisions, ensuring a consistent classification of Turkish fossils and those of the other countries in the region.

Mammal palaeontology is changing. We are looking at a period in which a generation of taxonomic specialists that built the record, particularly at the end of the last century, is retiring. Focus changes to studies on isotopes from mammal enamel, or studies based on the functional morphology of molars. More and more, computer-based studies are taking over, building models using vast amounts of data. These studies bring major advances, but we should never forget that the outcome of a model is as good as the quality of the data that it is based on. Taxonomic identifications are, and always will be, at the core of palaeontological work. Over the last decades, many European and American specialists have helped to shape the Turkish fossil record. However, as we noted, these taxonomic specialists are becoming rarer. As such, there lie opportunities for a new generation of Turkish scientists to advance and improve the record.

The way forward is therefore twofold. New fieldwork will continue to reveal important localities, especially in the regions and time frames that remain poorly represented in the current dataset. However, the analyses presented here suggest that equally important progress can be made by improving the resolution of the record that already exists. Its full potential will be reached only when the richness of the record is matched by equally strong taxonomic, chronological and database level resolution.

List of abbreviations
RCMNS – Regional Committee on Mediterranean Neogene Stratigraphy
NOW – New and Old Worlds database
MTA – Mineral Research and Exploration General Directorate
MN – Mammal Neogene unit
GPTS – Geomagnetic Polarity Time Scale
ELMA – European Land Mammal Age

Declarations

Availability of data and materials

The dataset supporting the conclusion of this article are available in the NOW Database repository, https://https://nowdatabase.org/ and within the additional files within the article.

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Authors' contributions

LHO - writing - original draft, conceptualization, formal analysis, writing - review & editing

MB - writing - original draft, formal analysis, writing - review & editing

PS - writing - original draft, writing - review & editing

SAK - writing - original draft, writing - review & editing

YB - writing - original draft, data curation, visualization, writing - review & editing

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Figures and figure captions

Figure 1. Comparative taxonomic richness across mammalian fossil assemblages in Türkiye. Species richness is calculated as the number of distinct species combinations represented in the NOW, including the ‘indet.’ species epithet as a separate species. A Global top 20 richest mammalian fossil sites in Türkiye, color coded by assemblage type. Assemblage types are characterized as macromammal (green), micromammal (blue) and mixed (purple) faunal assemblages. B Top 10 richest macromammal localities. C Top 10 richest micromammal localities. D Top 10 richest mixed-fauna assemblages.

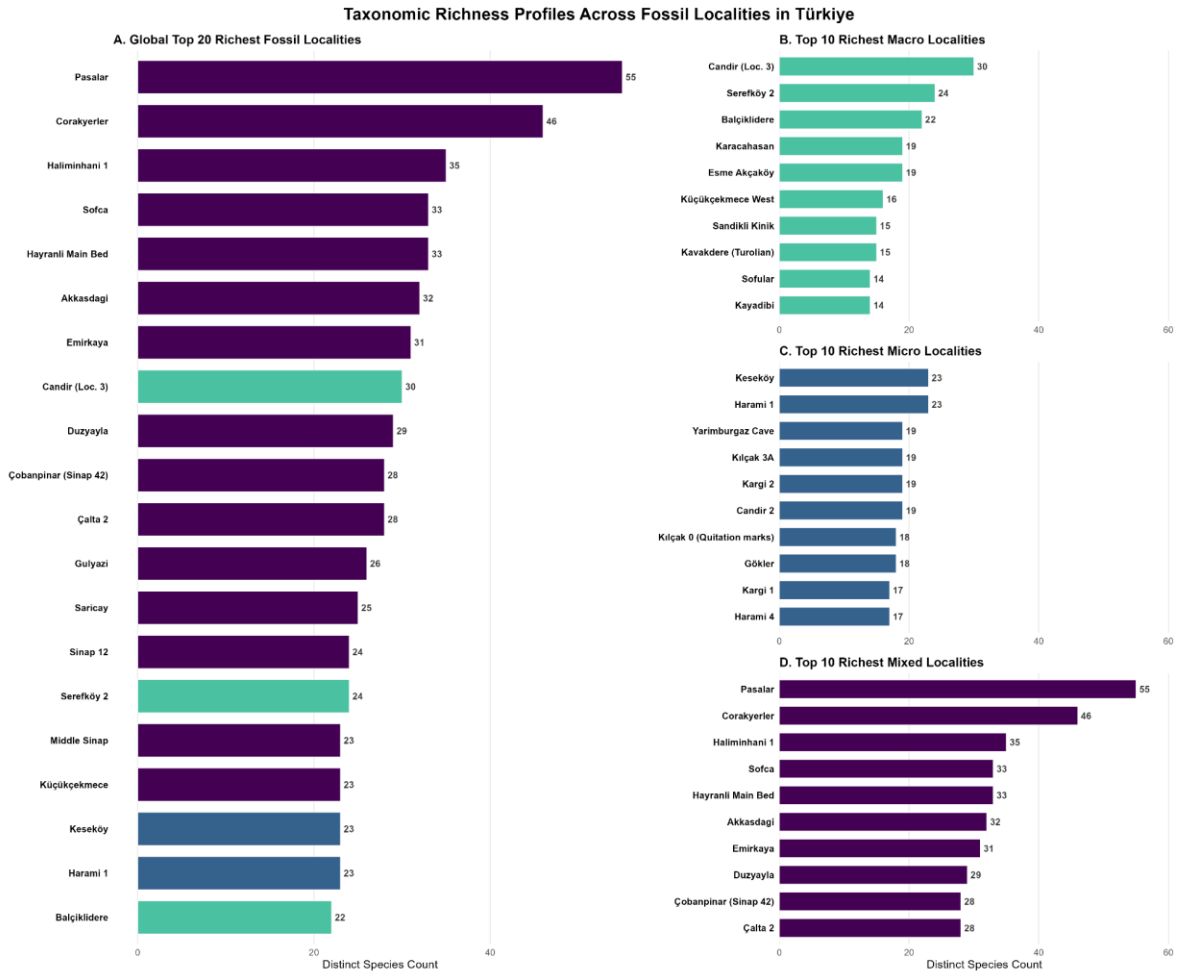


Figure 2. Donut chart showing a proportional representation of faunal assemblage category distribution across Cenozoic fossil localities in Türkiye recorded in the NOW database. Segments indicate the absolute number and total percentage of sites classified as macromammal (green), micromammal (blue) and mixed (purple) faunal assemblages.

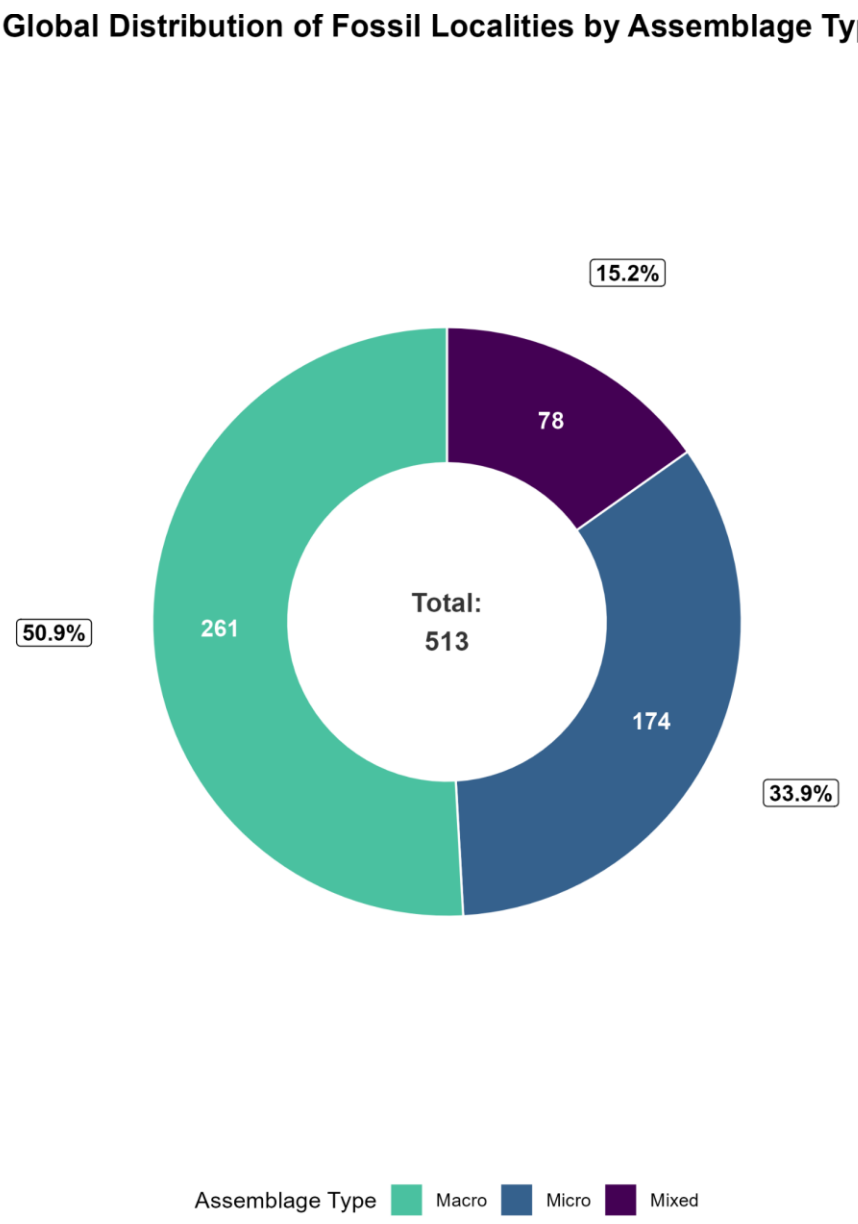


Figure 3. Spatial geographic distribution of Cenozoic fossil localities in Türkiye. Localities within a 100 km radius are clustered under a single geographic point. Individual sub-panels (A-L) show the spatial distribution of localities per chronostratigraphic level. The locality key table is provided in Appendix document S1. A Paleocene. B Eocene. C Oligocene. D Oligocene-Miocene Transition. E Early Miocene. F Middle Miocene. G Late Miocene. H Miocene-Pliocene Transition. I Pliocene. J Pleistocene/Holocene.

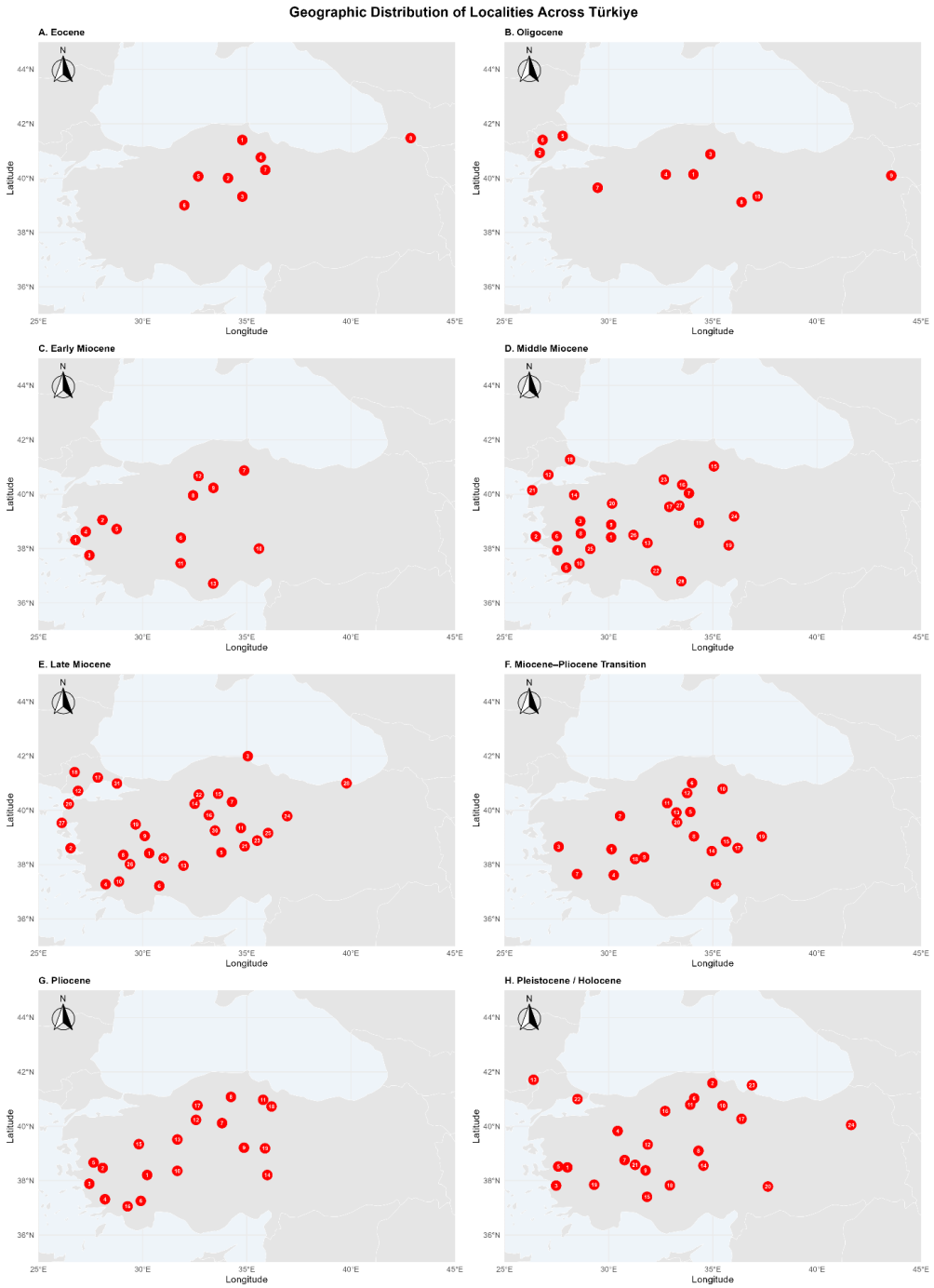


Figure 4. Spatiotemporal and stratigraphic representation of Turkish fossil localities by faunal assemblage category. Localities are characterized as macromammal (green), micromammal (blue) and mixed (purple) faunal assemblages. A Absolute frequency distribution of fossil localities stacked across geological (sub-)epochs. B Normalized proportional distribution of the three assemblage categories per European Land Mammal Age (ELMA). C Absolute distribution of taxonomic richness per assemblage category.

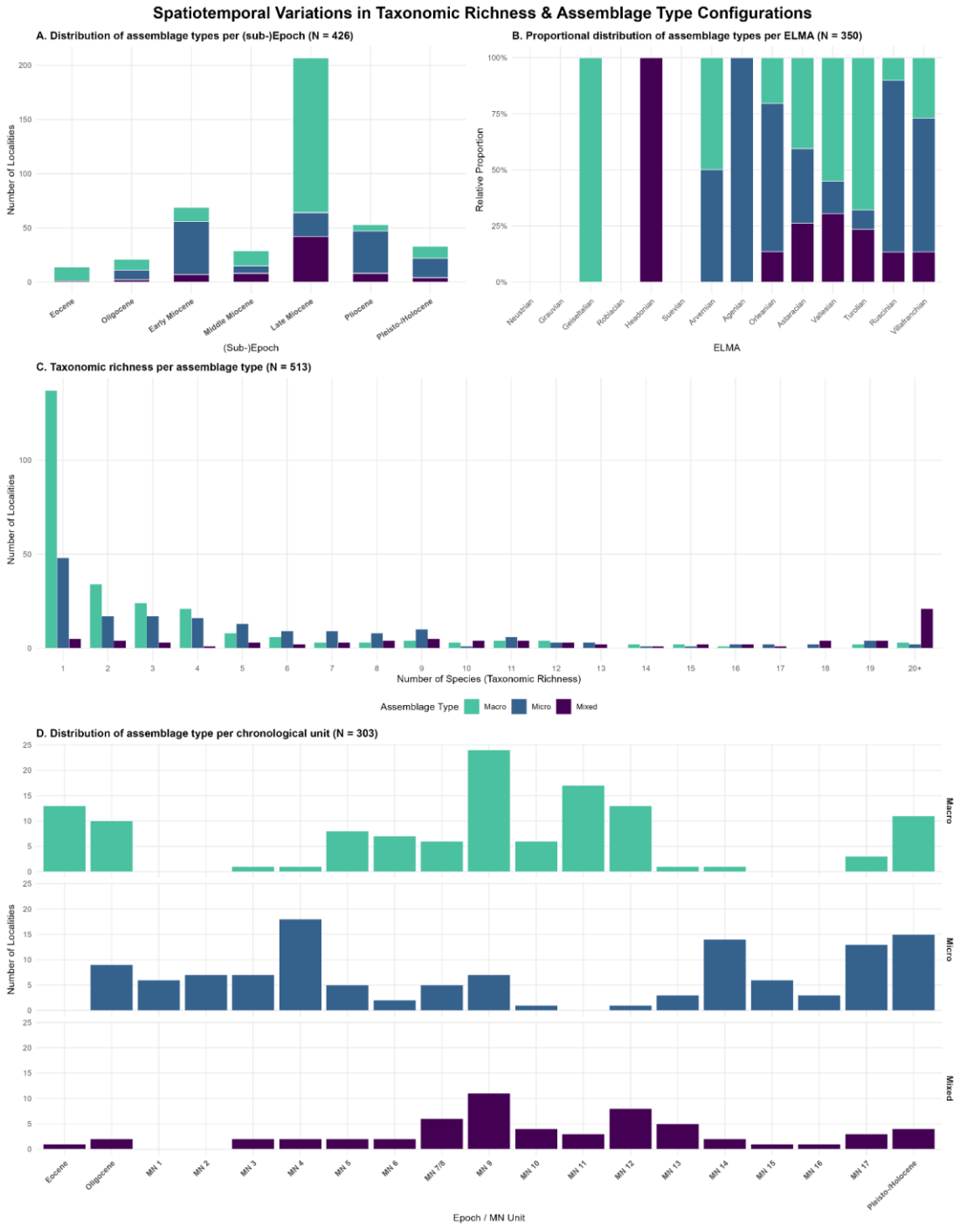


Figure 5. Dating resolution for mammalian fossil localities in Türkiye. Localities are categorized as independent (radiometric/magnetostratigraphic) dating (purple), well-constrained/single MN-unit (blue) and wide range/multi-MN unit (green) resolution types. A Donut chart showing the dating resolution of Neogene localities. Segments indicate the absolute number and total percentages of sites per dating resolution type. B Total absolute counts of well-constrained and independently dated sites across distinct biochronological boundaries, ranging from the Eocene through the Pleistocene/Holocene. C Normalized stacked bar chart showing the proportion of resolution types per European Land Mammal Age (ELMA).

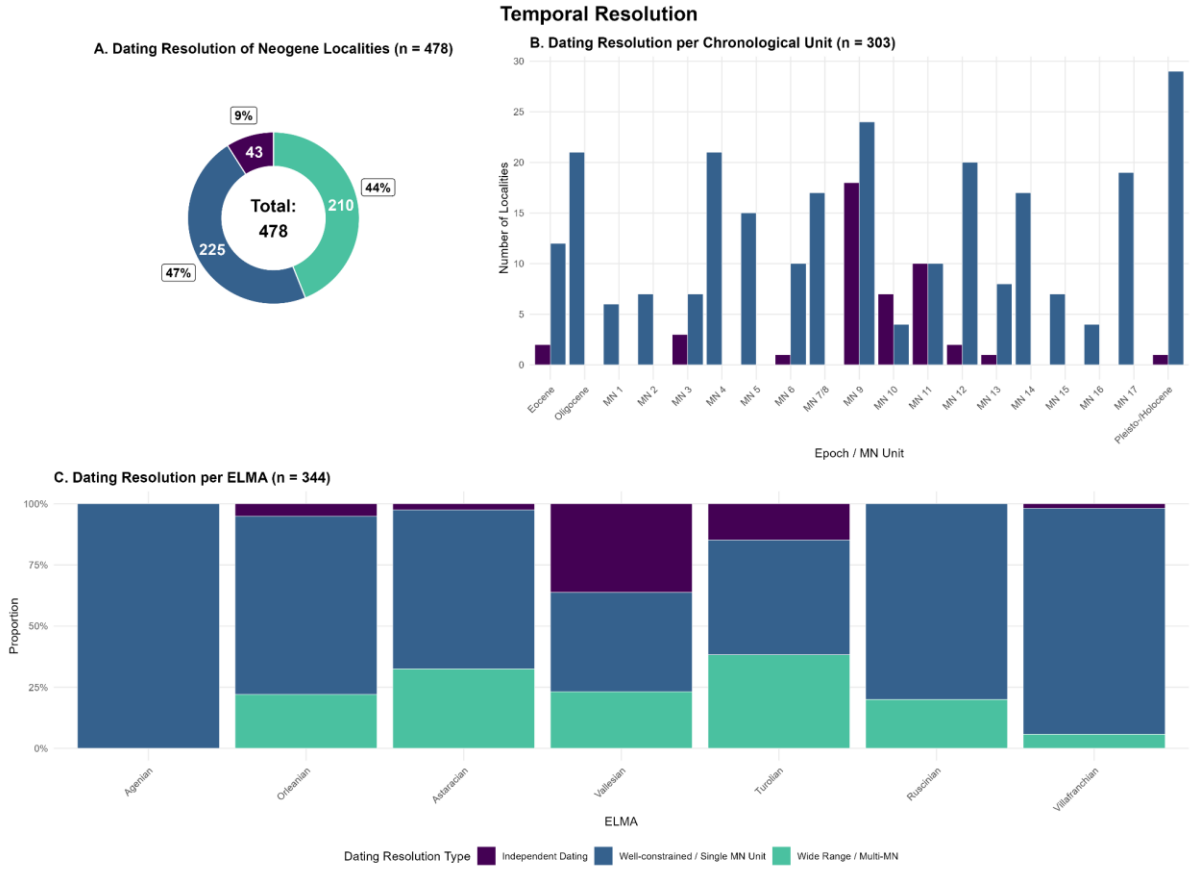
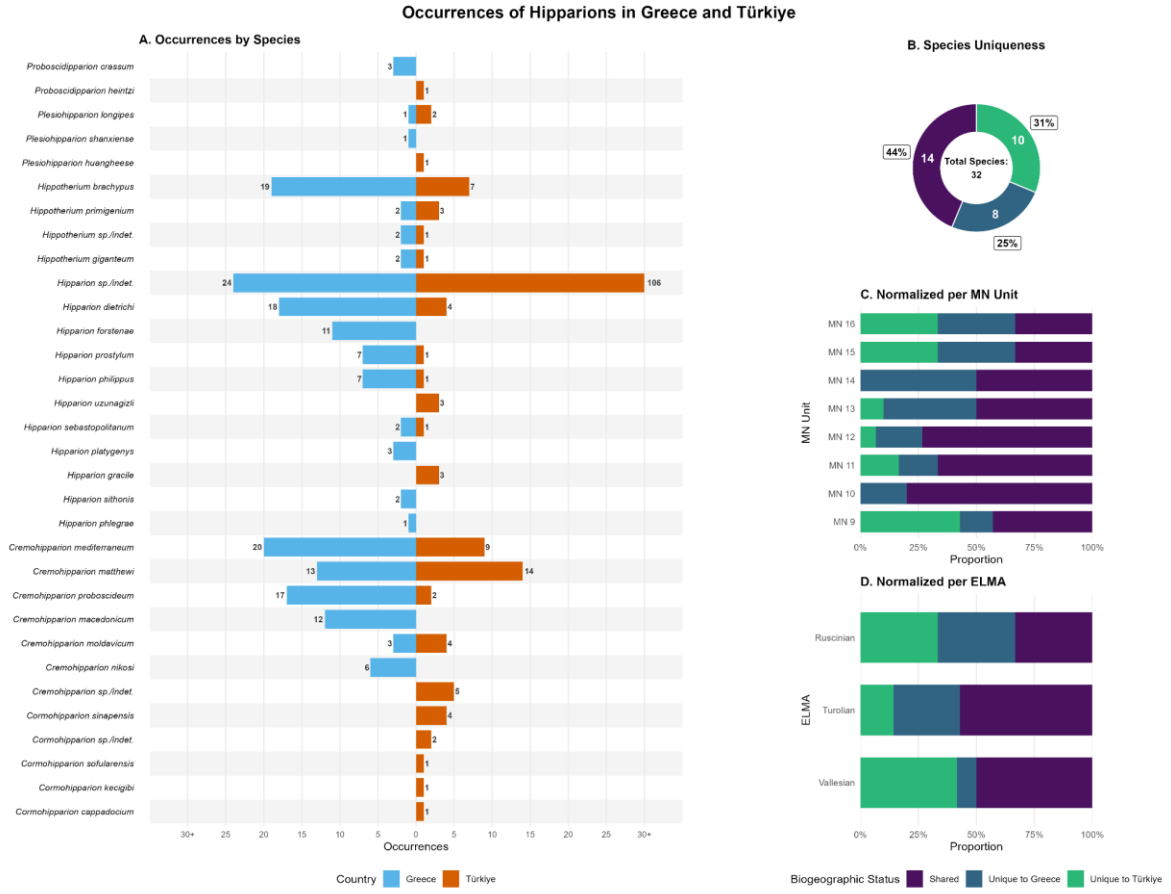


Figure 6. Comparison of the distribution of hipparionine horses across Türkiye and Greece. A Mirror pyramid chart tracking regional specific occurrence counts between Türkiye (orange, right) and Greece (blue, left). Data points exceeding 30 occurrences are cut off by the outer axis limit. B Donut chart indicating hipparionine species occurrence, i.e. the proportion and absolute number of taxa shared between regions (purple), restricted to Türkiye (green) and Greece (blue). C Normalized, stacked bar chart tracking species occurrences in Greece and Türkiye across Mammal Neogene (MN) Units, with identical color scheme. D Normalized, stacked bar chart tracking species occurrences across European Land Mammal Ages (ELMAs), with identical color scheme.



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