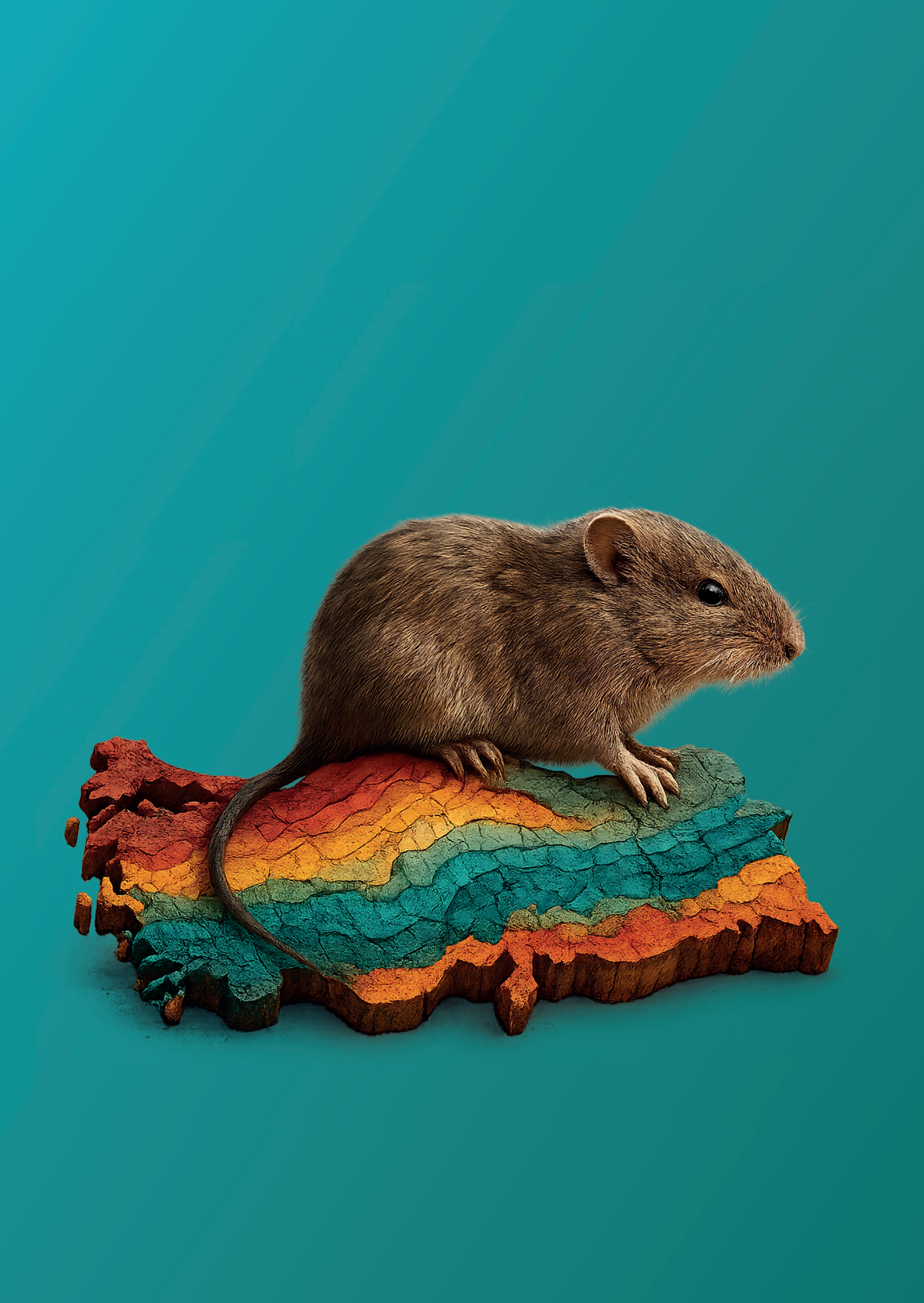
Taxonomic and paleobiological insights into small mammals from the Pliocene of Western Turkey: a comprehensive study of the locality of Afşar

Skandalos, P.



CHAPTER 1

General Introduction

Afşar: A Window into Anatolia's Past

The study of fossils stands as a cornerstone in unravelling the mysteries of ancient ecosystems and the dynamic interplay between climate, tectonics, and biodiversity. Fossilised micromammals have become an essential tool for dating terrestrial sediments and reconstructing palaeoenvironments of the Cenozoic and particularly the Neogene and Pleistocene (e.g., Koufos, 2006; Minwer-Barakat et al., 2008; López Jiménez et al., 2018). When combined with different proxies, micromammals, particularly rodents, emerge as invaluable stratigraphic markers and paleoenvironmental indicators, offering insights into past environmental changes and the response of life to these changes. By tracking changes in micromammal faunas, researchers can discern the effects of climatic fluctuations and tectonic events on ancient landscapes on the biosphere.

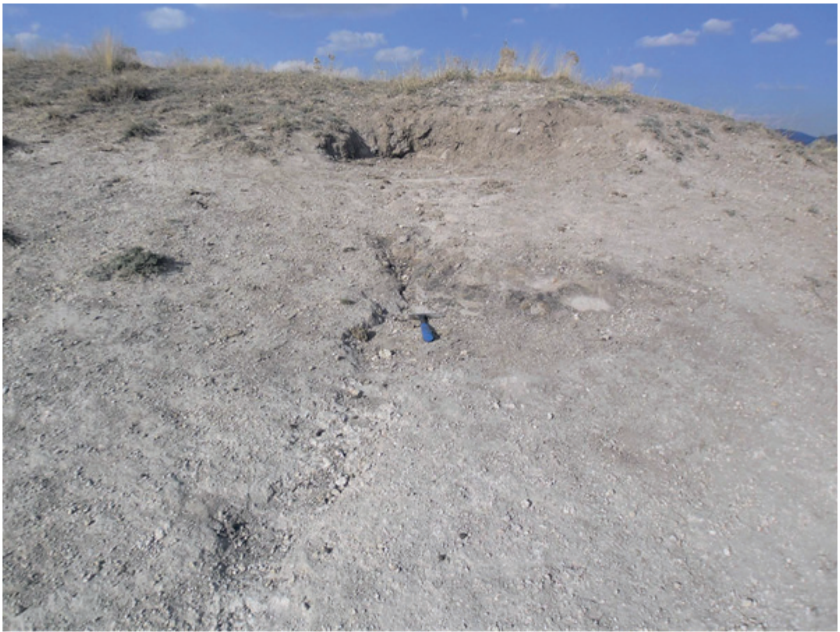
In the light of these discussions, we need to get a broad geographic overview on how environmental changes impacted different regions. Currently, the micromammal fossil record is heavily focused in Europe, with research predominantly conducted on the Miocene and Pleistocene epochs. The Pliocene, on the other hand, has received far less attention, even though in terms of climatic conditions, it provides a good proxy to the Holocene. Therefore, this thesis focuses on Turkey, a region with numerous Pliocene localities (Ünay and De Bruijn, 1998), but where the fossil record remains mainly unpublished (Van den Hoek Ostende et al., 2015).

During the last decade, an international consortium between Naturalis Biodiversity Center in Netherlands, Comenius University in Bratislava, MNCN/CSIC in Madrid and two Turkish Universities, Pamukkale University in Denizli and EGE University in Izmir came together aiming to reconstruct the faunal history of Anatolia. Initially, the group's research was primarily focused on the Early Miocene, but increasing interest from Turkish geologists has shifted the emphasis toward obtaining dating and environmental data from the late Neogene and Early Pleistocene. Their fieldwork has uncovered numerous promising sites in Anatolia in the vicinity of Burdur and Denizli. Anatolia plays an important role in the biogeography of mammals. Given its strategic position between Africa, Europe and Asia, it provided a corridor for many migrations of numerous species, including our own ancestors. Since its fossil record has been poorly studied (Van den Hoek Ostende et al., 2015) our current understanding of the Pliocene of the Eastern Mediterranean comes mostly from the other side of the Aegean, in Greece, where we have a more complete image of events. Localities such as the Ptolemais sections (Hordijk and De Bruijn, 2009) played a pivotal role by having both radiometric datings and a strong correlation to the geological time scale.

During the Greek Plio-Pleistocene the environment changed from open woodlands to a more open, steppe-like landscape. This change initiated a number of migrations, presumably from the East (Koufos and Kostopoulos, 2016). From there, they have made their way further into Europe.

Other periods, particularly in the Miocene, indicate that Anatolia functioned as a source area corridor for many taxa. We hypothesise that the same holds true for the late Neogene, which implies that taxa adapted to more open environments in the drier regions of the Eastern Mediterranean, before entering the open plains that characterised the European landscape during the glacials. In order to test this hypothesis and to get a good picture of the palaeoenvironment changes in the late Neogene of the Eastern Mediterranean, research should focus on the micromammal remains on newly found and revisited localities from Turkey. Among the key areas that will contribute to the study of the Turkish Pliocene is the N-NW trending Dombayova graben in Western Turkey, that hosts the primary focus of this thesis, the Afşar section (Figure 1). Afşar was first identified as a fossil mammal site in the early 1990s and it was revisited and resampled during the framework of the Afyon and Burdur survey in 2017 (Demirel et al., 2019). Initially, our aim was to compare multiple localities from that region, but as fate would have, some samples were lost through mishaps. Before we could revisit the area, the COVID pandemic struck, and limited the possibilities for further fieldwork. Nevertheless, as it turned out and as this thesis will show, the material collected at the Afşar section (Figures 2-3) turned out to represent a pivotal, and yet unknown time slice in the faunal development of the Anatolian Pliocene, and yielded plenty of material to fill this thesis.

A



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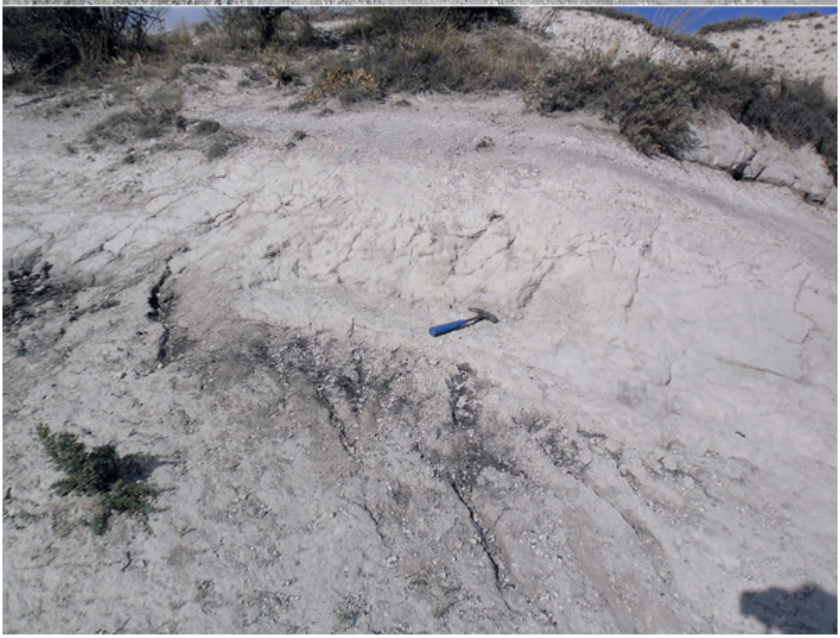

Figure 1. The Afşar section. (A) The top layer and (B) the lower layer where the fossil material has been recovered.

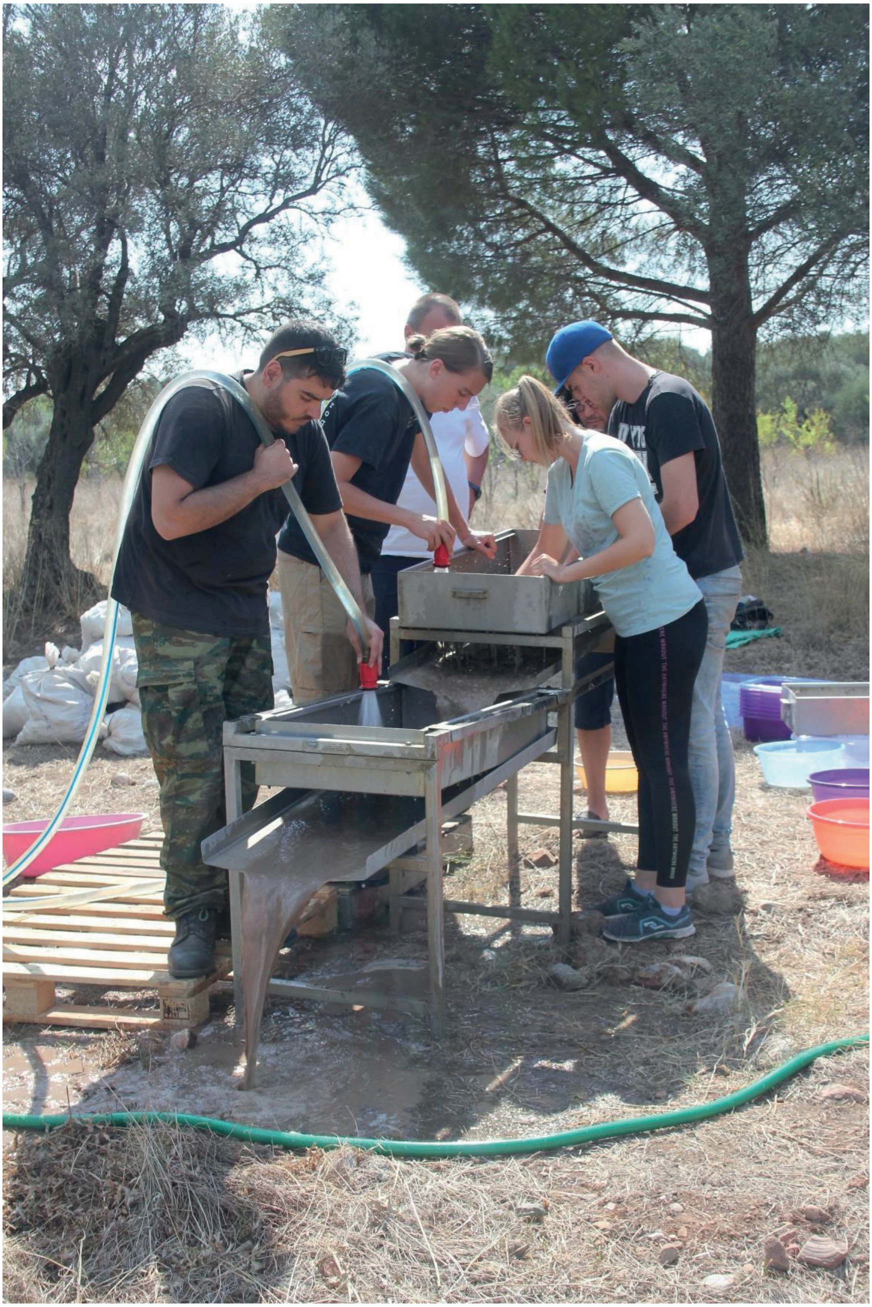

Figure 2. Sieving process for fossil material recovery from the locality of Afşar, separating microfossils from sediment.

In correlation to other Pliocene localities, the abundant fossil material recovered from Afşar will provide a comprehensive view of the evolution history of its species and it will position the section within the global chronostratigraphic framework. As we embark on this journey through Anatolia's micromammalian past, we are poised to uncover new insights into the evolutionary trajectories, climatic fluctuations, and faunal migrations that have shaped the region's ancient landscapes. Through collaborative research efforts and interdisciplinary approaches, we aim to unravel the intricate tapestry of Anatolia's paleontological heritage, offering invaluable lessons for understanding the challenges of the present and the uncertainties of the future.

Micromammals: biochronology, palaeoenvironments and taxonomy

Fossil teeth of rodents and other micromammal are recognized as an important tool for dating terrestrial sediments. This started a little over half a century ago, when methods were developed for the large-scale wet-screening of fossiliferous sediments. Originally developed in Leiden (Freudenthal et al., 1976), such sieve- systems were quickly deployed all over the world (e.g., Daams and Freudenthal, 1988), and were also used in the collecting of the Afşar assemblages.

The suitability of micromammal molars for the study of the past world of the Cenozoic is based on a number of properties. First of all, these dental elements fossilize well, given that they largely consist of enamel, the most durable material in the vertebrate skeleton. In addition, they can be found in large numbers, allowing us to study entire faunas. But most importantly, they have a species-specific morphology, which makes it possible to define and recognize extinct species.

The relatively rapid evolutionary changes in micromammals make them ideal for biostratigraphic and biochronologic purposes. This holds particularly true for the murids (e.g., hamsters, mice, and voles), which have the shortest average species duration among rodents (Van den Hoek Ostende et al., 2023). Little wonder, that the representatives of these families play a major role in biozonations, particularly in areas where multiple fossiliferous layers are available in superposition within sections (e.g., Van Dam et al., 2001; Van der Meulen et al., 2011; Casanovas-Vilar et al., 2016). In combination with the large mammals, such zonations are crucial in defining and subdividing European Land Mammal Stages and their biochronological counterparts, the European Land Mammal Ages (ELMAs). The definition of ELMAs requires basins with continuous sedimentation. Given the patchy nature of the terrestrial rock record, suitable regions for defining stages are rare, and mostly found in the unique record of the Iberian Peninsula. Some commonly used ELMAs, such as the Villanyian, which finds its basis is mammal assemblages from fissure fillings, and is as such per definition strictly biochronologic.

Next to the ELMAs, another system for the biochronology of mammal faunas was developed, the MN 'zonation' (De Bruijn et al., 1992; Mein, 1999; Steiniger, 1999; Van Dam et al., 2001). Today, it is the most commonly used system for dating Eurasian mammal assemblages. It finds its basis in a series of sixteen reference localities, each of which is deemed characteristic for its 'zone'. In addition, it is based on the first and last occurrences of its typical components. These first and last occurrences are largely based on respectively the emergence or disappearance of suitable habitats in a region. Therefore, they are not necessarily synchronous over large distances. In fact, Van der Meulen et al. (2011) demonstrated a substantial diachrony of MN boundaries of the Middle Miocene between well-dated sections in Spain, Switzerland, and southern Germany. It stands to reason that the further away we are from the regions where the MN 'zonation' was defined, the larger the chances for problems with diachrony become. Nevertheless, the MN system is still commonly used for dating Anatolian localities, and we will also refer to MN units in this thesis. Ünay et al. (2003) set up a preliminary rodent zonation for Anatolia, but as the regional zones are mostly directly correlated to the various MN zones, it does not provide much of an alternative and has been hardly used in literature. Bilgin (2022) demonstrated that, for the Early Miocene, the local zonation of Ünay et al. (2003) cannot be directly related to the MN system other than by accepting large diachronies.

Apart from their usefulness in stratigraphic and biochronological studies, micromammals are also valuable palaeoenvironmental indicators. As birds of prey are believed to be a primary accumulation agent (Andrews, 1990), micromammals are considered to represent a regional environmental signal, based on the action radius of their predators. However, semi-aquatic species or reed dwellers may represent a more local signal.

As we noted, evolutionary turnover in micromammals is high, particularly in murids. As a consequence, the ecological preferences of extant species can mostly only be used in Quaternary studies, as few recent species had their first occurrence before the Pleistocene. However, most modern genera saw their first appearance in the Miocene, so the wider preferences of the genus can be used as a proxy to the preferred habitats of the extinct relatives or ancestors. In addition, we can use morphological adaptations in the dentition, such as hypsodonty, or niche partitioning of the overall assemblages as valuable indicators of palaeoenvironments.

As in any palaeoenvironmental study, we need to be aware that reconstruction using micromammals are based on graveyard communities or thanatocoenoses, the composition of which is influenced by taphonomic factors. The quantitative composition of the assemblage is highly unlikely to represent the composition of the living community. For instance, the general dominance of murids in Neogene assemblages can be considered real, given the high diversity and their numbers in recent faunas. However, it is probably exaggerated in fossil assemblages because of the general short generation time and high reproduction of mice, voles and hamsters. Nevertheless, we can interpret changes in the quantitative composition of subsequent micromammal assemblages in similar depositional environments as changes in, for instance, climatic conditions. Ideally, such assemblages should be part of the same section, as is the case at Afşar, to minimize the influence of geographic difference influencing habitats.

Their suitability for both biochronological and palaeoenvironmental studies implies that micromammals can play a key role in understanding the response of the biosphere to natural climate change. Studies on the dense fossil record of Western Europe have confirmed this (e.g., Van der Meulen and Daams, 1992), but in order to understand how global changes affect different regions, there is a sore need to extend and improve the fossil record in other areas. As we noted, the Pliocene record of Anatolia is scanty at best, and the study of the Afşar assemblages is a major addition to the biochronology and palaeoenviroment of that epoch in southwestern Asia. But in addition to extending the record, micromammal palaeontologists are also faced with care for the quality of the record, i.e., ensuring the correctness of identifications.

Over the last century, major advances have been made in the taxonomy of fossil micromammals. New techniques were developed, such as the HH-index for Arvicolines as introduced by Rabeder (1981), which allows to assess hypsodonty independent of wear by measuring the height of enamel free areas. In this thesis, we introduce new methodology to assess Spalacinae molars independent of wear. Nevertheless, taxonomy is still an integrative part of micromammal studies. Taxonomic issues remain, partly because new techniques were not followed or simply because old identifications have not been checked as the taxonomy settled further. This thesis is no exception and four of the chapters are dedicated to the taxonomy of the various species from the Afşar section. Full descriptions are a prerequisite to ensure that future scholars can compare their material to that of the Afşar assemblages and as a basis for the identifications that allow us to elaborate the biochronology and palaeoenvironments of this remarkable section.

Thesis outline

The Afşar section emerges as a beacon for paleontologists seeking to decipher the enigmatic past of Anatolia's Pliocene epoch. The following chapters provide an overview of the micromammal research from this period, highlighting the intricate interplay between faunal diversity, paleoenvironmental conditions, and evolutionary processes.

The second chapter deals with the Arvicolinae Gray, 1821 and Cricetinae Fischer, 1817 from the Afşar section. The two subfamilies are considered closely related, as the Arvicolinae emerged as the surviving lineage of a number of cricetine lineages developed hypsodont dentitions at the end of the Miocene. The trend towards increased hypsodonty continues among arvicolines ever since their appearance at the beginning of the Pliocene. This, combined with their success as the most diverse murid family at the temperate latitudes of the Northern Hemisphere, makes them excellent stratigraphic markers for the

Pliocene and Pleistocene. However, consistently quantifying hypsodonty in assemblages with molars in different wear stages proved to be a challenge for paleontologists. The introduction of the so-called HH-index proved a valuable tool, allowing not only to distinguish between species of rooted arvicolines (as all Pliocene representatives are), but also assessing the evolutionary stages of assemblages within a species. However, particularly in older literature, this index is not always available, which provided a bit of an extra challenge in assessing the arvicoline assemblages from Afşar.

By contrast to the Arvicolinae, Cricetinae are less suited in determining the age of localities. The species from Afşar are all fossil representatives of extant genera. However, based on the preference of the recent species for open, steppe-like environments, the crictines from Afşar provide welcome paleoenvironmental indicators.

The third and fourth chapter deal with the Spalacinae Gray, 1821, a group from which Afşar yielded one of the largest fossil assemblages. The molars of Spalacinae are high-crowned and the morphology of the occlusal surface changes with wear, which makes the taxonomy of the group challenging. In the third chapter, a method is introduced to deal with those challenges. By artificially wearing the molars using CT- scanning, the timing of the various changes in different species can be documented. In the fourth chapter, the Afşar spalacine assemblages themself are described and identified.

The fifth chapter deals with the remainder of the rodent fauna and also describes the lagomorphs from the section. The murines are the second-most diverse group of the locality. In addition, the much rarer glirids, zapodids and dipodids from the localities are described, completing the taxonomic identification of all of the micromammal fauna with the exception of the insectivores.

The final chapter combines the data from the other chapters to synthesize an overview of the biochronology of the Afşar assemblages and to reconstruct the palaeoenvironmental changes that occurred between the two sections. Biochronologically, the section marks the transition between the Early and Late Pliocene. This makes the Afşar assemblages not just a welcome addition to the Pliocene record of Anatolia, but also makes the section a key point in understanding the transition that marked the onset of the Villafrachian Age.

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