The high, the sharp and the rounded: paleodiet and paleoecology of Late Miocene herbivorous mammals from Greece and Iran

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Tiivistelmä/Referat – Abstract

The Late Miocene (11.6–5.3 million years ago) was a period of global climatic cooling and aridification. These events also had an effect on land mammals, which began to adapt to the increasingly open and grass-dominated biomes. The Eurasian Pikermian fauna is a well-known example of this evolutionary trend, including many species adapted to the new environment known as the Pikermian Biome in the Eurasian midlatitudes.

The aim of this study was to deduce the paleodiets of individual Pikermian herbivore taxa, to compare results across three localities as well as with with previous results, and to assess the biome they lived in. Fossil teeth of large terrestrial mammalian herbivores from three classical Late Miocene localities of the Pikermian Biome—Pikermi, Samos (Greece), and Maragheh (Iran)—were analyzed with the mesowear method. Mesowear is the wear of mammalian herbivore molar crowns, cusps, and facets that can be seen with the naked eye, and is determined by the animal's diet (browsing and/or grazing). The mesowear scores were used in a cluster analysis where the fossil taxa were clustered with modern taxa belongin to well-known dietary categories. The results indicated the dietary categories of the fossil taxa.

Among individual taxa, the Maraghean rhinoceros *Chilotherium persiae* gave a surprising browsing signal despite its hypsodonty. *Gazella* from Pikermi and Samos clustered with browsers to browse-dominated mixed feeders, while the sample from Maragheh indicated a more grass-dominated mixed diet. The antelope *Tragoportax* from Pikermi and Samos yielded results that indicate the Pikermian genus used more grass in its diet than the Samian one, even though Pikermi is regarded t have been more closed of the two localities. The abundant hipparionine horses, typical for the Pikermian Fauna and previously seen as an indicator of open savanna-like biomes, showed a wide range of diets, but none of the three hipparion populations included zebra-like grazers. The wide dietary range of the Maraghean mammals in the results suggests that Maragheh had a variable paleoenvironment that included both grassy openings and closed forest.

The results confirm those of previous studies, depicting a fauna consisting of browsers and mixed feeders with a notable lack of specialized grazers. This suggests that the Pikermian Biome wasn't as open as the modern East African savannas, which it has been classically compared to, but instead a varied woodland with grassy openings.

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Tiivistelmä/Referat – Abstract

Myöhäisessä mioseeniepookissa (11,6–5,3 mijoonaa vuotta sitten) maapallon ilmasto kehittyi viileämmäksi ja kuivemmaksi. Tämä vaikutti myös maanisäkkäisiin, jotka sopeutuivat elämään entistä avoimemmissa ja ruohovaltaisemmissa biomeissa. Euraasian keskileveyksillä niin kutsutussa Pikermi-biomissa elänyt fauna on tunnettu esimerkki tästä kehityksestä.

Tämän tutkimuksen tavoitteena oli vertailla Pikermi-faunan taksonien ravinnonkäyttöä kolmen tunnetun pikermiläisen lokaliteetin – Pikermin, Samoksen (Kreikka) ja Maraghehn (Iran) – välillä ja saatuja tuloksia aiempien tutkimusten tuloksiin, sekä arvioida eläinten elinympäristöä tulosten perusteella. Aineistona käytettiin myöhäismioseenissa eläneiden suurten kasvinsyöjänisäkkäiden hampaita. Hampaat analysoitiin mesowear-menetelmällä, jolla arvioidaan hammaskruunun, sen nystyjen ja nystyjen fasettien kulumista. Kulumisen on todettu määräytyvän sen perusteella, käyttääkö eläin ravintonaan pääasiallisesti lehtiä vai ruohoa. Mesowear-arvoja käytettiin klusterianalyysissä yhdessä tiettyihin ravintoluokkiin kuuluvien nykynisäkkäiden kanssa. Saatujen tulosten perusteella fossiilisten lajien ruokavalio voitiin määritellä.

Maraghehlaisen sarvikuono *Chilotherium persiaen* tulos yllätti, sillä laji on hampaistoltaan korkeakruunuinen ja siten näennäisesti ruohonsyöjä. Sen hampaat olivat kuitenkin kuluneet lehtiensyöjän tavoin. *Gazella*-suvun gasellit olivat pehmeää ravintoa suosivia Pikermissä ja Samoksella, mutta Maraghehn tulokset viittaavat ruohopitoisempaan sekaravintoon. Vaikka Pikermiä on pidetty lokaliteeteista metsäisimpänä, antilooppi *Tragoportax* Pikermistä söi tulosten mukaan enemmän ruohoa kuin samoslainen vastineensa. Pikermi-faunalle tyypilliset hipparionini-tribuksen hevoset osittautuivat ruokavalioltaan monipuolisiksi, mutta yhdessäkään kolmesta populaatioista ei ollut nykyisten seeprojen kaltaisia heinänsyöjiä. Maraghehn nisäkkäiden tuloksista ilmenevä laaja ravintoskaala osoittaa alueen paleobiomissa olleen monipuolisesti sekä avointa että suljettua maastoa.

Tulokset vahvistavat aikaisempien tulosten perusteella saatua näkemystä, jonka mukaan Pikermi-faunaa hallitsivat lehden- ja sekasyöjät, eikä erikoistuneita ruohonsyöjiä juuri ollut. Johtopäätös on, ettei Pikermi-biomi ollut nykyisten itäafrikkalaisten savannien kaltainen ympäristö, kuten klassisesti on väitetty, vaan se koostui puustomaasta, jossa oli siellä täällä ruohoa kasvavia aukeita.

Avainsanat – Nyckelord – Keywords
Myöhäismioseeni, suuret kasvinsyöjänisäkkäät, paleoruokavalio, paleoekologia, hampaiden kuluminen

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CONTENTS

1. INTRODUCTION

This is a study *based on*, but not *of* teeth. More than in any other division of paleontology, teeth have been the foremost subjects of paleomammalogical studies. Besides the evident reason of availability—teeth are the hardest part of the vertebrate body and are consequently abundant in the fossil record—the most important factor for the continued prominence of teeth in the field of paleomammalogy is their value as indicators of the evolutionary history and diets of their former owners. Unlike most other vertebrates, land mammals commonly preprocess their food through mastication before digestion. Mastication is made possible in mammals by the occlusion of teeth. Unlike other vertebrates, mammals do not have a continuously renewed tooth battery. Instead they rely on two sets of teeth (deciduous and permanent), which has enabled them to evolve teeth that occlude with high precision (the author's teeth notwithstanding). The ability to slice, crush, and grind food items with their teeth sets mammals apart from their evolutionary predecessor, and has been at the core of mammalian evolutionary specialization. This is especially true of herbivorous mammals, which chew their meals with a wide array of tooth types, all adapted to optimally reduce the plant matter of choice into a readily digestible pulp. The importance of teeth in the study of the evolution of mammals is crystallized in the words attributed to the great French pioneer of comparative anatomy, Georges Cuvier: ”Show me your teeth and I will tell who you are.” Here the wear of large herbivorous mammal teeth is used to evaluate the dietary categories and biomes of their owners.

The mammals of this study belong to the so-called *Pikermian fauna* from the late Miocene epoch of Eurasia. The late Miocene (~11.6–5.3 Mya) was a time of cooling and drying of the Earth's climate (Zachos et al. 2001, 2008, Eronen et al. 2012, Fortelius et al. 2014). This, along with the subsequent spread of grasslands, put an intense adaptational pressure on land mammal faunas. In the mid-latitudes of Eurasia the Pikermian fauna arose with adaptations to life in more open environments, such as hypsodont (high-crowned) teeth and increased cursoriality (for example, Bernor et al. 1996). So great are the apparent similarities between these faunas and the faunas of modern African savannas that they were classically interpreted to have lived in a savanna/steppe environment (Kurtén 1952, Solounias 1999 and references therein). Current studies, however, support the view that the biome of the Pikermian fauna (the *Pikermian Biome*) was a sclerophyllous evergreen woodland (Axelrod 1975, Bernor 1983, Solounias et al. 1999, Solounias et al. 2010).

The fossil localities of this study, Pikermi and Samos of Greece, and Maragheh of Iran, are part of the so-called Greco-Iranian Biogeographical Province of the Pikermian fauna (Bonis et al. 1979). These localities have been well known since the 19th century, and have been examined using a wide array of paleobiological methods (i.e. Solounias et al. 1999, 2010, Mirzaie Ataabadi et al. 2013, Bernor et al. 2014). Here a paleodiet study is performed by analyzing the macroscopic wear of the fossil cheek teeth of large herbivorous mammals from all three localities. The mesowear method, originally developed by Fortelius and Solounias (2000), quantifies and categorizes the wear of the crown of a molar tooth in selenodont and trilophodont herbivorous mammals, and can be used to classify animals as members of one of the following four dietary categories: grazer, graze-dominated mixed feeder, browse-dominated mixed feeder, and browser. Mesowear can thus also be used as a proxy for paleobotanical and paleoclimatological information.

The results are expected to show how the mesowear of the fossil taxa correlates with that of modern taxa whose diets are known from firsthand observation. Subsequently, the potential dietary differences between herbivores from Pikermi, Samos, and Maragheh will be compared. The implications of the results on the habitat and lifestyle of the animals, along with the vegetation and the climate of the study area, will be assessed. The results from individual taxa will be compared with previously gathered information. Also, unlike in the case of Pikermi and Samos, no extensive paleodiet studies have been made of the herbivorous mammals of Maragheh (Mirzaie Ataabadi, pers. comm. 2011). For its part, this study therefore supplements the ’big picture’ of the Greco-Iranian Province’s paleoenvironment. Suggestions for further research are also given.

2. BACKGROUND

In this chapter a look is taken at the bigger picture behind the climatic and evolutionary events that eventually lead to the emergence of the Pikermian Biome. First, the global climatic history is discussed. Second, the climatic events of the Eurasian midlatitudes—the Pikermian Biome's area of existence—are considered. Third, the evolution of grasslands is examined. Fourth, the evolution of the herbivorous mammals in Eurasia is reviewed. Fifth, and finally, the emergence of the Pikermian fauna and the history of its discovery is discussed.

2.1. A brief history of Earth's climate

The histories of Earth's climate, flora, and fauna are tightly interwoven. The evolution of the latter two can be used as a proxy for that of the former, and the planet's climate changes have always been the driving force behind the evolution of plants and animals. To understand the details of this study's fauna, its environment and evolution, a brief look at the history of Earth's climate during the Cenozoic era (the age of mammals, the past 65.5 Ma) is relevant. Information about Earth's past climates and temperatures has been deducted from oxygen and carbon isotope ratios from the calcium carbonate shells of minute sea organisms such as foraminifers (Zachos et al. 2001, 2008).

The world entered the Cenozoic era in so-called greenhouse conditions, with temperature and humidity levels much higher than present. The first epoch of the Cenozoic, the Paleocene (65.5-50 Mya), was not as warm as the preceding Cretaceous period, but global temperatures rose throughout the epoch (Zachos et al. 2001, 2008). This warming trend culminated in a series of rapid hyperthermal events in the latest Paleocene and the early Eocene (Ruddiman 2008, Zachos et al. 2008, Sluijs et al. 2009). Global temperatures rose by more than 5°C in less than 10,000 years during the first of these events (Zachos et al. 2001, 2008), known as the Paleocene-Eocene Thermal Maximum (or Eocene Thermal Maximum 1, ETM1). It and the Eocene Thermal Maximum 2 (ETM2) were the moment of highest global temperatures during the Cenozoic (Broccoli and Manabe 1997, Zachos et al. 2008). The following Early Eocene

Climatic Optimum (EECO) was not as transient, lasting for 2 Ma (Zachos et al. 2008). Fossil evidence of crocodilians living in the high arctic of the early Eocene indicate cold month mean temperatures of 5-7 °C in arctic latitudes during the EECO (Markwick 1994).

The EECO marked a turning point in the evolution of Earth's climate. Although one further climatic optimum, the Mid-Eocene Climatic Optimum, appeared ~42 Mya with tropical and mid-latitude sea surface temperatures being up to 30 °C and 25 °C respectively (Pearson et al. 2001), it didn't reverse the cooling trend that began after the EECO. Ice sheets started to form in Antarctica in late Eocene, and the Eocene-Oligocene boundary is marked by a remarkable drop in global temperatures as evidenced by oxygen isotope ratios from deep-sea benthic foraminifera (Zachos et al 2008).

At the advent of the Oligocene (34-23 Mya) the Earth had transitioned from the early Cenozoic greenhouse to dryer and cooler icehouse conditions. Permanent continental ice sheets were present in Antarctica (DeConto and Pollard 2003, Zachos et al. 2001, 2008). Continents had assumed positions closer to their modern situations. This altered the flow of sea currents, which had a global effect on the distribution of heat, moisture and salinity (Ruddiman 2008). The most notable tectonic changes were the closure of the Tethys Sea through the collisions of Africa and India with Eurasia, and the opening of the Tasman Gateway (37-33 Mya) and the Drake Passage (25-20 Mya) through the separation of Australia and South America from Antarctica (Ruddiman 2008). The closure of the Tethys blocked the warm circumequatorial current, and the opening of the subantarctic seaways isolated Antarctica from warm currents when the Antarctic Circumpolar Current began its flow through the newly opened passages. The current's positive effect on Antarctic glaciations was originally proposed by Kennett (1977). It has been both questioned (Mikolajewicz et al. 1993) and confirmed (Toggweiler and Bjornsson 2000) in later studies. In their model, Toggweiler and Bjornsson found that while the opening of Drake Passage cooled the southern high latitudes, it also warmed the northern high latitudes. DeConto and Pollard (2003) also found not the opening of the Southern Ocean gateways, but the declining atmospheric CO_2 concentration to be the foremost factor in the initiation of the Antarctic glaciation.

The late Oligocene saw temperatures rising to late Eocene levels (Zachos 2001, 2008). Episodic glaciation in the Northern hemisphere may still have been already possible at the Oligocene-Miocene boundary, ca. 20 Ma earlier than currently assumed (DeConto et al. 2008). The Miocene (23-5.3 Mya) was the point in Earth's climate history where the greenhouse conditions of the Paleogene finally transitioned to the Quaternary icehouse conditions (Bruch et al. 2007, Badger et al. 2013.). The Miocene began with temperatures comparable with the late Oligocene, and while the climate cooled slightly after the early Miocene, it warmed strongly again in the middle Miocene at 16.8-16.2 Mya (Shevenell and Kennett 2004, Zachos et al. 2001). This event is known as the Mid-Miocene Climatic Optimum (MMCO; Zachos et al. 2001, 2008). Böhme (2003) reports of mean annual temperatures in Central Europe of 17.4-22 °C based on the occurrence of fossil ectothermic vertebrates. Around this time, a permanent ice sheet formed in East Antarctica (Flower and Kennett 1994, Badger et al. 2013). From the MMCO on, Earth's climate gradually became cooler and cooler, culminating in the current Ice Age.

2.2. Late Miocene climate of Eurasian mid-latitudes

The Mid-Miocene Climatic Optimum came to its end 14-13.5 Mya (Böhme 2003, Zachos et al. 2001, 2008). The late Miocene (~11–5 Mya), with its great changes in climate and geography, restructured the distribution of biomes in Europe (Eronen et al. 2010a). These changes included a drop in mean annual temperatures and humidity, followed by increased seasonality of these parameters (Zachos et al. 2001, 2008; Bruch et al. 2007, 2011). In the late Miocene the geography of Europe was starting to resemble its modern configuration. There were, however, still significant differences, such as the Paratethys Sea in southeastern and Eastern Europe, which on their part must have had an effect on local precipitation and temperature (Harzhauser and Piller 2007, Eronen et al. 2010a). The major global contributors to the climatic changes were probably the uplift of the Tibetan Plateau through the collision of the Indian subcontinent with Asia and its strengthening effect in the late Miocene on the Asian monsoon circulation (Quade et al. 1989, An et al. 2001, Liu and Yin 2002, Eronen et al. 2010a), and the still open Panama seaway that weakened ocean heat transport to northern latitudes compared to modern conditions (Micheels et al. 2011). The exact elevation of the late Miocene Tibetan Plateau has been debated, but evidence points to an asynchronous uplift in different parts of the plateau, with estimates based on paleo-altitude studies suggesting an average height of the southern TP close to modern levels (Tang et al. 2013a and references therein). Recent studies (Tang et al. 2011, 2013b) point to a weaker than modern Asian summer monsoon in the late Miocene, while the East Asian winter monsoon was stronger, and the inter-annual variability on the Indian summer monsoon was as strong or even stronger than present. The formation of the Isthmus of Panama was a long and complex process (Bacon et al. 2015), and the depth of the Panama seaway probably varied before its complete closure ca. 4-3 Mya (Schmidt 2007). This may have lead to an increasingly variable climate in western Eurasia from the middle Miocene on (Eronen et al. 2012). The conditions were, however, still warmer and more humid than today, and the polar-equator temperature gradient was not as strong as it is now (Micheels et al. 2011). Still, the latitudinal temperature gradient had strengthened from mid-Miocene on due to increasingly cooler winter temperatures, causing steeper seasonality (Bruch et al. 2007). The late Miocene retreat of the Paratethys Sea in Central Europe gives a plausible explanation to this and the cooling of the winter temperatures (Bruch et al. 2007).

Evidence from ectothermic vertebrates suggests a mean annual temperature drop of more than 7°C following the MMCO (Böhme 2003). By the late Miocene the mid-latitudes of Eurasia (approximately 30° to 60° northern latitude) had become increasingly colder and dryer with stronger seasonality (e.g. Fortelius et al. 2002, 2003a, 2006, Bruch et al. 2007). Bruch et al. (2006) studied the late Miocene paleofloras in Central, Southern, and Southeastern Europe to deduct annual temperature and precipitation values. Extrapolated mean annual temperatures were 16-17 °C in Greece-Turkey-Caucasus. The increased seasonality was reflected by mean summer temperatures of 26-27 °C and mean winter temperatures of 5-9 °C. Annual precipitation ranged from 700 mm (southern Greece) to 1200 mm (Eastern Turkey, Caucasus). Quade et al. (1994) came to similar conclusions about the yearly late Miocene rainfall in the area of modern Greece and Turkey based on the abundance of paleosol carbonates, claiming annual precipitation of < 1000 mm from ~11 Mya onwards. Similar estimates were also given by Eronen et al. (2010b), whose results based on utilizing mean hypsodonty (see next paragraph for definition) gave late Miocene annual precipitation levels of 700-800 mm for northern Iran, and 800-1200 mm for Greece.

The fossil localities of Pikermi, Samos, and Maragheh, the sources of the material of this study, are all located roughly at 38° of northern latitude, making them prime examples of late Miocene mid-latitude environments. Paleoprecipitation maps created by using mean hypsodonty values of given areas in Eurasia indicate that by MN 11 (a European Land Mammal Zone, 8.7-7.75 Mya, see figure 1) hypsodonty had reached levels in northeastern Mediterranean that reflect modern precipitation values (Fortelius et al. 2002, 2006). Hypsodonty, the possession of high-crowned cheek teeth, is in general viewed as an adaptation to life in open, arid environments and feeding on tough, gritty plants, grass in particular (e.g. Stirton 1947, Van Valen 1960, Fortelius 1985, Janis 1988, Janis and Fortelius 1988, Jernvall and Fortelius 2002, Strömberg 2006, Damuth and Janis 2011, Kaiser et al. 2011). High mean hypsodonty in fossil mammal faunas is an indicator of low precipitation levels in the region where the fauna lived (Fortelius et al. 2002, 2003a, 2006, Eronen et al. 2010a, 2010b, 2012).

2.3. Evolution of grasslands

Today it may be difficult to imagine a world without vast grass-dominated biomes such as the savannas of Africa, the prairies of North America, and the pampas of South America. Abundant and diverse grasses are what characterize modern global vegetation, and mammalian herbivores that use grass as their main food resource are prevalent. Grasslands now cover more than 20% of the Earth's land surface (Edwards and Smith 2010). Against this background it might be surprising to realize that grasslands as dominant biomes, and grass as a common main food resource of herbivores, are both relatively recent phenomena on the geological timescale. Extensive grasslands only appeared in the late Oligocene-early Miocene (Strömberg 2005, Strömberg 2006, Janis 2008), and specialized grazers are even more recent, appearing only 10 Mya (Janis 2008). Prior to these events more or less closed forests had been the main biomes, and browsers dominated herbivore guilds (Janis et al. 2000, Janis 2008).

Evidence of grasses is known already from the late Cretaceous (Maastrichtian age, 70.6-65.5 Mya) in the form of fossil grass phytoliths (particles of intra-cellular opaline silica) from India (Prasad et al. 2005), but their rise to a characteristic feature of ecosystems took tens of millions of years. The emergence of grasslands also wasn't a synchronous process between continents (Strömberg 2011). The Cenozoic evolution of grasslands can be roughly summarized as follows: the appearance of open-habitat grasses using the C_3 and then the C_4 photosynthetic pathway in the Paleogene (65.5-23 Mya), the emergence of C_3 grass-dominated habitats in the mid-to-late Cenozoic, and, finally, the emergence of C_4 grass-dominated habitats in late Neogene of some regions (Osborne 2008, Strömberg 2011). Although the late Miocene rise of C_4 plants was a global phenomenon, it, like the rise of grasslands in general, as mentioned above, appears to have happened at different rates in each region (Latorre et al. 1997).

The evolution of the C_4 photosynthetic pathway of carbon fixation was a major adaptational breakthrough for grasses. Its significance is emphasized by the trait apparently having evolved independently several times in terrestrial plants (Edwards and Smith 2010, Osborne and Freckleton 2009, Sage 2004, Kellogg 2001). Even though only 3% of modern vascular plant species are C_4 grasses (Sage 2004), they account for ~20% of terrestrial carbon fixation (Osborne 2008), and are responsible for ~23% of terrestrial gross primary production (Still et al. 2003). 60% of C_4 plant species are grasses (Edwards and Smith 2010). The advantages of C_4 photosynthesis in comparison to the more common C_3 photosynthesis include a higher tolerance of drought and high temperatures, and a lower sensitivity to atmospheric CO_2 levels (Cerling et al. 1997). C_4 photosynthesis was therefore a prerequisite trait for the evolution of open grasslands in the dry tropical and subtropical environments of a world with low atmospheric CO_2 levels: C_4 grasses are now dominant in tropical and subtropical regions, while C_3 grasses dominate the cooler high latitudes (Cerling et al. 1997). Possible drivers of the C_4 expansion include increasing seasonal variability in temperature and rainfall (Latorre et al. 1997), lowering rates of atmospheric CO_2 during the Oligocene, and seasonal occurrence of fire (reviewed by Osborne 2008). Edwards and Smith (2010) found the evolution of the C_4 photosynthetic pathway in grasses to be mostly a response to increasing aridity, and to the move of grasses from the understory to open-canopy biomes, not to shifts between temperate and tropical biomes.

The evolution and spread of grasslands is linked to the general cooling and drying trend of Earth’s climate. Grasses started to become abundant when Earth’s climate started its shift from greenhouse to icehouse conditions in the Eocene (Jacobs et al. 1999, Osborne

2008, Strömberg 2011). The properties of grasslands have, for their part, contributed to the cooling and drying. Their albedo is high; they can act as a silica reservoir and a sink of atmospheric CO_2, CH_4, and water vapor; they have a capability to stimulate marine productivity and carbon burial by promoting the export of bicarbonate and nutrient cations to the oceans (Retallack 2001, Sage 2004, Kidder and Gierlowski-Kordesch 2005).

An aspect relevant for this study is that the appearance of hypsodont herbivorous mammals in the fossil record has classically been linked with the presence of grasslands (Solounias et al. 1999 and references therein). Hypsodonty as such is usually seen as an adaptation to increase tooth wear resistance, whether the wear is due to grittier food or abundant mineral particles in food because of increased aridity (e.g. Janis and Fortelius 1988, Fortelius and Solounias 2000). The synchrony of the emergence of these two phenomena in the geologic record, the adaptational hypsodonty hypothesis, and hypsodonty as an indicator of obligate grazing has been, however, put under question by recent research (Feranec 2003, Strömberg 2009, Mihlbachler et al. 2011, Strömberg et al. 2013). The evolution of the vegetation in the Pikermian Biome and the eastern Mediterranean will be reviewed in detail in Discussion.

2.4. Evolution of the Eurasian mammalian herbivore guild

The Cenozoic evolution of land mammals can be roughly divided in two phases: the time before and after the expansion of grasslands (Janis et al. 2000, Janis 2008). To this vegetational change is connected the great change in mammalian herbivore feeding: the use of grass as a principal source of nutrition instead of browse (Janis 2008). Several factors make grass a less desirable feed than browse (leaves and stems of dicotyledonous plants). Grass is less nutritious; more so than browse, it is filled with hard phytoliths; it often grows in open and more arid environments where extraneous grit and dust is more abundant than in closed environments. Also, the open environment itself, with few places to hide from predators, initially makes grassland a less advantageous habitat for herbivores. The sheer abundance of grass, however, makes it a resource too prominent left unused. Hence, herbivorous mammals from several lineages are now grazing the vast grasslands of modern Earth. In the beginning, however, the world belonged to forests and woodland and the browsing herbivores living in them.

In the lush greenhouse conditions of the Paleogene world, mammals diversified following the Cretaceous-Paleogene (KPg) extinction of the dinosaurs (Bininda-Emonds et al. 2007, Meredith et al. 2011, Wilson 2013). The first post-Mesozoic epoch, the Paleocene, was, in retrospect, a transitional phase in the evolution of mammalian herbivores, forms ranging from the unspecialized members of archaic clades such as ’Condylarthra’, Pantodonta, Dinocerata and Taeniodonta to the first representatives of the modern herbivore clades (Janis 2008).

The next epoch, the Eocene, witnessed the emergence of the two largest herbivore orders of the Cenozoic era: the odd-toed ungulates i.e. perissodactyls (horses, rhinos, tapirs etc.) and the even-toed ungulates i.e. artiodactyls (ruminants such as cattle, sheep, and deer; camels, pigs etc.) (Agustí and Antón 2002, Janis 2007, Janis 2008). While the Eocene forms of these orders were far from their modern representatives in evolutionary terms, the roots of many modern lineages were already present. In the late Eocene forests of Europe, the first ruminants of the family Gelocidae appeared, and several species of the horse-like browsers of the family Palaeotheriidae were among the dominant herbivores (Agustí & Antón 2002).

The Eocene ungulates showed specialized locomotory and feeding adaptations. Their limbs became longer and laterally less mobile (a sign of increased cursoriality, i.e. the ability to move fast and energy-efficiently over longer distances). Their brachydont (low-crowned) cheek teeth evolved enamel ridges (lophs) well suited for efficient browsing (Janis 2008). The Eocene also saw the appearance of some of the first herbivores with hypsodont molars in South America (Madden et al. 2010). This cannot, however, be interpreted as a definitive sign of specialized grazing, but perhaps of feeding in a more open environment with more dust and grit in food, possibly volcanic ash (Strömberg et al. 2013), which must have been plentiful, originating from the Andean orogeny (Gregory-Wodzicki 2000). Diverse grasses were already present in various environments worldwide at this point (Strömberg 2011), but specialized grazers had not yet evolved.

The Oligocene began in Europe with an extinction event called the Grande Coupure. Although possibly triggered by a cooling climate and its vegetational and other environmental consequences (Agustí and Antón 2002), the exact causes behind the Grande Coupure are still not well known (Eronen et al. 2015). The geography of Europe changed with the lowering of sea levels caused by Antarctic glaciations: what had been previously an archipelago was now a more continentalized mass of dry land, although the situation in the Mediterranean did fluctuate even later during the Miocene (Rögl 1999a, 1999b). Coinciding with this, several Asian mammal taxa dispersed to Europe via the connection formed by the closing of the Turgai strait that had run along the eastern margin of the Urals separating Europe from Asia (Rögl 1999a, 1999b, Agustí and Antón 2002). Among the herbivore immigrants were species of browsing rhinos and chalicotheres, and the true tapirid *Protapirus*, which took the place of the palaeotheres (Agustí and Antón 2002). Overall, the Oligocene faunas of Eurasia showed a progression towards a more ’modern’ assemblage of mammals, with browsing perissodacyls and artiodactyls with dental and locomotory features that indicate a more open vegetation at that time (Agustí and Antón 2002).

In the early Miocene, ~19 Mya, a land bridge emplaced between the continent of Africa and the Arabian Peninsula, and a wave of African taxa entered Eurasia. Among them were the deinotheres and the gomphotheres, both proboscidean megaherbivores, the latter giving the land bridge its name, the Gomphothere Land Bridge (Rögl 1999a, 1999b, Agustí and Antón 2002). This was the beginning of Western Asia acting as a hub for the dispersal of mammals across the Old World (Mirzaie Ataabadi 2010). Among the artiodactyls the horned ruminants made a big entrance, as the first cervids, giraffids and bovids appeared in Europe (Agustí and Antón 2002). On the perissodactylan front the arrival from North America of the browsing horse *Anchitherium* was a notable event (Forstén 1991, Eronen et al. 2010c and references therein). The rich browser fauna of the early Miocene of Central Europe lived in evergreen laurophyllous (broadleaved) and subhumid sclerophyllous forests (Kovar-Eder et al. 2008).

In the middle Miocene, after the warm period of the Mid-Miocene Climatic Optimum, the cooling post-MMCO climate meant the demise of Western Eurasia’s broadleaved evergreen forests (Utescher et al. 2007, Kovar-Eder et al. 2008, Rodríguez-Sánchez and

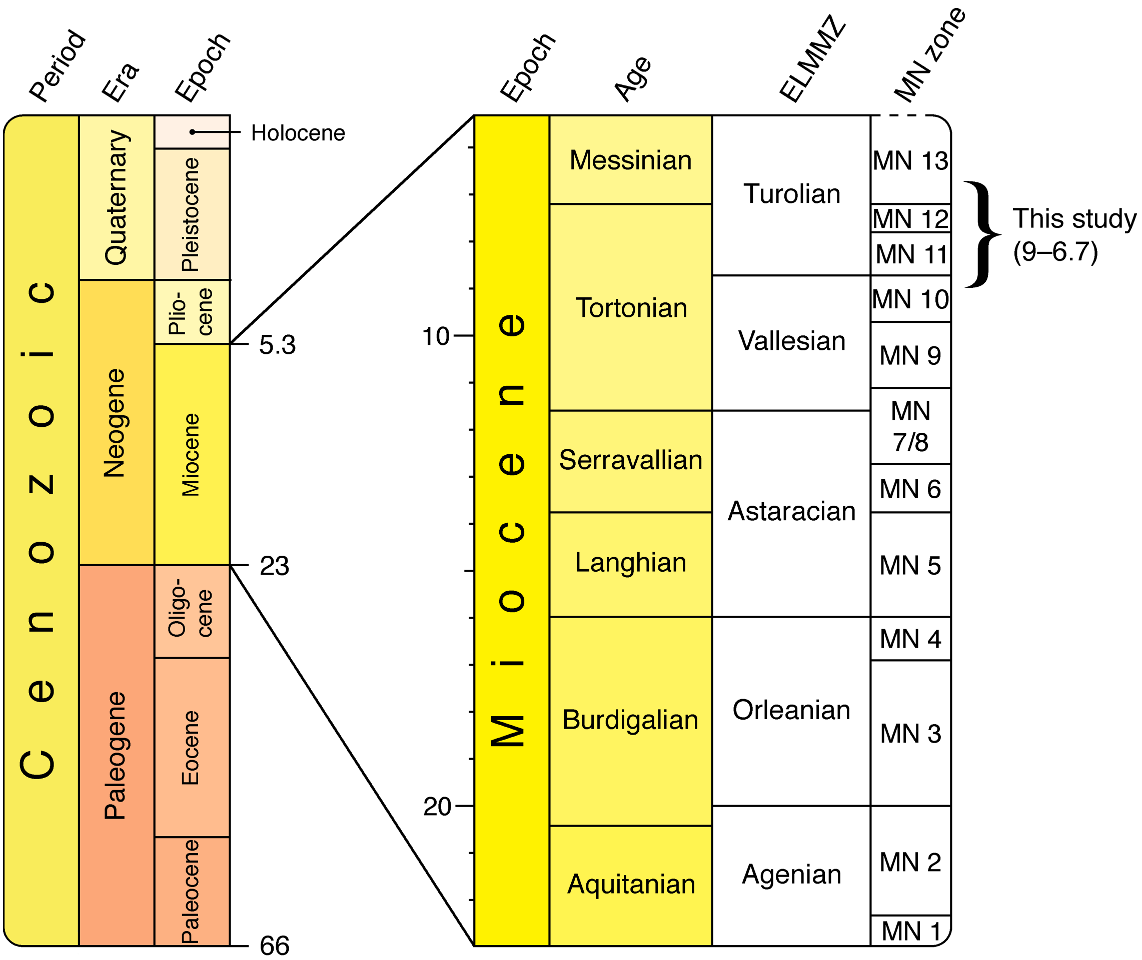


Figure 1. Timescale of the Cenozoic and the Miocene. Time is in millions of years. ELMMZ = European Land Mammal Mega Zone, MN zone = Neogene Mammal Zone. Based on Steininger et al. (1996), Agustí et al. (2001), and the ICS International Chronostratigraphic Chart 2015 (Cohen et al. 2013).

Arroyo 2011). They were replaced by increasingly mesophytic and sclerophyllous vegetation, of which the mesophytic plants are adapted neither to a particularly humid nor particularly dry environment, while the sclerophylls are adapted to seasonal droughts and lower winter temperatures (Utescher et al. 2007, Kovar-Eder et al. 2008). Still, western and central Europe remained more forested and relatively humid, while southeast Europe and the Mediterranean region became more open and dryer, with indicators of subhumid sclerophyllous forests and open woodlands (Utescher et al. 2007, Kovar-Eder et al. 2008). This was the beginning of the differentiated faunal provinces between these regions, the eastern Mediterranean region being called the *Greco-Iranian Province* (Bonis et al. 1979). This biogeographic region has also been variably called and defined as the Tethyan Province (Bernor 1979), the Sub-Paratethyan Province (Bernor 1984), the Greco-Irano-Afghan Province (Bonis et al. 1992), the Middle Asiatic Province (Geraads et al. 2002), the Balkano-Iranian Province (Spassov et al. 2004), the Greek-Iranian Province (Casanovas-Vilar et al. 2005) and the Balkan-Anatolia-Iran Province (Mirzaie Ataabadi 2010).

2.5. Evolution of the Pikermian fauna

The Pikermian fauna, so called after the fossil locality of Pikermi, Greece, was a highly diverse community of open-adapted mammals that lived in the mid-latitudes of Eurasia during the Turolian land mammal stage (8.7-5.3 Mya, Crusafont 1950, Solounias et al. 1999, Eronen et al. 2009). It reached its distributional peak at ~7 Mya, ultimately vanishing possibly because of increased seasonality and regional differentiation connected to changes of circulation patterns in the North Atlantic Ocean (Eronen et al. 2009, Kostopoulos 2009). The fauna's core area was in the Greco-Iranian Province, although at its peak it extended all the way from the Iberian Peninsula in the west to China in the east (Kurtén 1952, Deng 2006, Eronen et al. 2009, Casanovas-Vilar et al. 2010). Its rise has been associated with the climatic changes behind the Vallesian Crisis ~9.7 Mya at the end of the preceding Vallesian land mammal stage (11.6–9 Mya): the relative drying and increased seasonality of the climate and the subsequent spread of grasslands at the expense of the preceding Vallesian forests (Bernor 1983; Cerling et al. 1997; Utescher et al. 2000; Mosbrugger et al. 2005, Casanovas-Vilar et al. 2010). During the Vallesian, Western European faunas were dominated by forms more adapted to life in forest environments (Agustí and Moyà-Solà 1990, Casanovas-Vilar et al. 2005, Agustí et al. 2013). Among them were forest-adapted rodents, hominoids, tapirids, suid, cervid and moschid artiodactyls, and carnivores of the families Nimravidae and Amphicyonidae. In addition to the climatic causes, the pre-crisis fauna's 'supersaturated' level of diversity may have played part in its downfall. Agustí et al. (2013) argued the enriched diversity level of the fauna itself had reached a critical balance point: even a relatively minor oceanic-climatic factor might have been able to tip the scale and initiate a "House of Cards Effect". Meanwhile in Eastern Mediterranean, near Yulaflı in European Turkey, there is evidence of a mammal community living in a humid and forested environment in the late Vallesian/MN 10 (9.5–9 Mya) (Geraads et al. 2005). If this area acted as an ecological barrier between East and West as the authors suggest, it coincides well with the post-Vallesian expansion to the west of the Pikermian fauna.

The Pikermian fauna was characterized by an abundance of large herbivores, especially the presence of the three-toed, hypsodont hipparionine horses (from here on referred to as hipparions) (Kurtén 1952, Tobien 1967). The Beringian land bridge between Eurasia and North America emerged after a strong sea level drop at 11 Mya (Haq et al. 1988), which enabled the hipparions, along with a multitude of other North American taxa, to disperse into Eurasia in the Vallesian (Agustí & Antón 2002, Strömberg et al. 2007), where they ultimately replaced the brachydont anchitherine horses. The anchitherines, which had taken the same route from North America in the early Miocene (MN 3, 20 Mya, Forstén 1991) and were adapted to browsing in a forest or woodland environment are a good example of the great changes that took place in the climatic and vegetational realm of Eurasia in the late Miocene. There were incipient signs of anchitherine adaptation to the more open and arid conditions of the late Miocene (Eronen et al. 2010c), and indeed, the anchitherines and the hipparions coexisted briefly in Eurasia as shown by fossil evidence from the locality of Zheltokamenka, Ukraine (Gabunia 1981), dated to 10.5 Mya (Sen 1997). The hypsodont and more cursorial hipparions were, however, ultimately more successful in facing the challenges of a newly arid and open Eurasia. In fact, the hipparions may owe their successful dispersal to Eurasia through the harsh environment of the Beringian to their abilities to use highly fibrous low-quality food (grass) and feed virtually continuously, unlike the ruminants (Janis 1976). The hipparions were such a characteristic element of the Vallesian and Turolian faunas of Eurasia that these were classically known under the collective term *Hipparion fauna* (e.g. Kurtén 1952, Tobien 1967). The relative similarity and the presence of the hipparions was also the reason that Vallesian and Turolian faunas were previously considered to belong to a single Mammal Age called Pontian (Tobien 1967, Bernor et al. 1979, Koufos 2006). It has been proposed that counting together the Turolian faunas from southeastern Europe and Anatolia is oversimplification, and that there was no uniform fauna behaving synchronously in space and time in this area (Kostopoulos 2009). However, a faunal similarity study using Genus-level Faunal Resemblance Indices (GFRI) by Mirzaie Ataabadi et al. (2013) revealed Pikermi, Samos, and Maragheh as the most similar of Eurasian late Miocene faunas (GFRI over 60% in Pikermi and ~70% in Samos). Solounias et al. (2013) found the mesowear signal to suggest paleoecological uniformity from Spain to China in the late Miocene. As a geographically well-restricted assemblage of populations, which maintained its basic structure over a geologically significant time, the Pikermian mammal assemblage, even considering its local variations, can be reasonably classified as a chronofauna as defined by Olson (1952) (Eronen et al. 2009).

Upon its discovery and description in the early to middle 19th century the Pikermian fauna was thought to present steppe/savanna faunas in the style of the modern African savanna faunas (Solounias et al. 1999 and references therein). It is easy to understand why if one looks at a list of mammals typical to the Pikermian fauna. The African savannas are home to the most diverse local fauna of large land mammals found today, and the diversity of the Pikermian fauna even exceeded it (Solounias et al. 1999), all while it included several taxa similar to those now found in the east African savanna faunas. Beside the aforementioned hipparionine horses, which were specifically seen as the equivalents of modern zebras (see review in Solounias et al. 1999), the Pikermian fauna consisted of a highly varied assemblage of rhinoceroses, giraffoids, antelopes, proboscideans, aardvarks, hyaenids, and felids with a notable lack of cervids (e.g. Solounias et al. 1999, Agustí and Antón 2002, Eronen et al. 2009). Of the non-mammalian animals present in the fauna it is of note to mention the ostriches, now exclusively a feature of African grasslands (and the open and arid Middle East up to the 20th century). The presence of ungulates with hypsodont teeth, hypsodont equids in particular, is another significant factor that contributed to the popularity of the savanna scenario (again, see Solounias et al. 1999).

The savanna mosaic hypothesis has been a subject of intense scrutiny since the 1970s. Data from the fossil animals, plants, pollen, and paleosols of the subtethyan localities (now Greece and Turkey) have revealed a more detailed view of the Pikermian Biome’s paleoecology. A closer look at these results is taken in discussion. For its part, this study aims to add to the knowledge of the paleoenvironment of the Greco-Iranian Province with paleodiet data from the Iranian locality of Maragheh, from which very few species have been analyzed with paleodiet methods (Mirzaie Ataabadi 2011, pers. comm.).

2.6. The fossil localities – history, geology, taphonomy

The Pikermian fauna also has an illustrious history in addition to its prehistory. It has been studied since the 'Golden Age of paleontology' of the 19th century, when European and American institutions organized several extensive excavation expeditions to the classical fossil sites of Pikermi, Samos, and Maragheh. The fossils are more or less coeval, although there appears to be a mismatch between the geochronological and biochronological evidence (Mirzaie Ataabadi et al. 2013). The maximum age range of the fossils in this study is from ~9 Mya (MN 10/11, the oldest parts of the Maragheh Formation) to 6.7 Mya (in MN 13, the estimated youngest parts of Samos) (see below for details). The bulk of the fossils, however, originates from a much shorter timespan (Solounias et al. 2013, Mirzaie Ataabadi et al. 2013).

Pikermi, the namesake fossil locality of the fauna, is located 21 km east of Athens, Greece. George Finlay and Anton Lindermayer performed the first excavations at the locality in 1835 (Koufos 2006, Bernor et al. 1996). The entry of the Pikermian fossils into wider scientific attention is marked by a fortuitous anecdote: in 1837 a Bavarian soldier was arrested for grave robbery when he was trying to sell a fossil skull of the colobine monkey *Mesopithecus* filled with calcite crystals resembling diamonds to a layman's eyes (Bernor et al. 1996). Recently, excavations were carried out by the University of Athens at a new locality called Pikermi Valley-1, 500 m east-southeast from the classical locality, starting in 2008 (Theodorou et al. 2010). The Pikermi Formation is deposited against the southern side of the Pentéli Mountain, famous for being the source of the marble used in the construction of the Acropolis (Bernor et al. 1996). The fossils, heaped in fossil-bearing lenses within the silty matrix, are usually diagenetically flattened. The strata, consisting mostly of clayey silt derived from weathered limestone, are void of volcanics, which renders them undateable radiometrically (Bernor et al. 1996). According to Bernor et al. (1996) Pikermi is correlative with MN 11/12 (~8.3-8.2 Mya). Koufos (2006) points to faunal differences between Pikermi and the Mytilinii-1 locality of Samos (dated to 7.17–7.13 Mya, Kostopoulos et al. 2003) and therefore suggests a younger age for the former, possibly the upper part of middle Turolian. Solounias et al. (2010), however, claim an age near 8 Ma. Solounias et al. (2013) repeat the claim of an age of 8 Ma for Pikermi, citing the absence and presence of certain closely-related species in Pikermi and Samos, the age of the latter being known from direct dating. The authors also point out the smaller number of species in Pikermi compared to Samos and the core of Maragheh, which indicates a slightly older age for the former: a developing biome would have had a lower species count than a mature one.

The fossil localities of Samos in eastern Aegean archipelago are among the oldest known to humankind. Already the ancient Greeks (~1000 BC) recognized the fossiliferous beds as a place where the bones of ancient ”amazons” could be found (Bernor et al. 1996). These legends encouraged the Englishman C. I. Forsyth Major to search for fossils in Samos, which were earlier collected and given (or sold) to Italian tourists by locals. Several expeditions collected fossils from Samos starting from 1885-99 by Forsyth Major. One of the most notable was the gathering of the Frick Collection to the American Museum by Barnum Brown. The fossiliferous horizons are situated in the Mytilinii Formation, the second youngest of the five Miocene formations in Samos' eastern basin (Bernor et al. 1996, Kostopoulos et al. 2003). (”Mytilinii” Formation is the preferred form of Kostopoulos et al. [2003] to better reflect the Greek pronunciation of the word and to avoid confusion with the city of Mytilini on the island of Lesbos; the Samian formation has been usually known as the Mytilini Formation.) The Mytilinii Formation consists of five members (oldest to youngest): the Old Mill Beds, the Gravel Beds, the White Beds, the Main Bone Beds, and the Marker Tuffs (Kostopoulos et al. 2003). Although fossil mammal bones are known all the way through the Old Mill Beds up to the lowest part of the Marker Tuffs, most of the Samos fossils have been collected between these two from the Main Bone Beds, from which three fossil-bearing horizons have been recognized (Kostopoulos et al. 2003). The sediments of the Samos localities are volcanogenic: the Mytilinii Formation consists of floodplain deposits of volcanogenic marls and gravel with soil horizons and rhyolite pumice tuffs (Bernor et al. 1996, Kostopoulos et al. 2003). The volcanics make possible the direct radiometric dating of the horizons (Swisher 1996). In addition, the Mytilinii Formation has been dated magnetostratigraphically by Kostopoulos et al. (2003). The older of the fossil-bearing members of the Mytilinii Formation, the Old Mill Beds, is correlative with MN 11 (8.3 Ma by Bernor et al. 1996 or 7.6–8.3 Ma by Kostopoulos et al. 2003). The younger member—the Main Bone Beds—is correlative with MN 12/13

(≥ 7.1 Ma by Bernor et al. 1996), ~8–6.7 Ma by Kostopoulos et al. (2003), and an average radiometric age of 7.2 Ma for the upper part (Solounias et al. 2013). The time span for the main fossiliferous beds is estimated to be ~800 000 years (Solounias et al. 2013). The fossils occur in numerous pockets, which suggests concentration of the bones by flowing water on the flood plains.

The Maragheh fossil sites are located close to the town of Maragheh in northwestern Iran (Iranian Azerbaijan). The fossils were first collected by the French-Russian explorer Nicholas de Khanikoff (Nikolai Khanykov) in 1840 (Bernor et al. 1996). Subsequent expeditions from Naturhistorisches Museum, Vienna, British Museum of Natural History, and Muséum National d'Histoire Naturelle, Paris, gathered great collections of specimens (Mirzaie Ataabadi et al. 2013). The Maragheh localities have been the target of several excavations up to recent years (Mirzaie Ataabadi 2010). For more than 150 years they were the only source of information on Neogene faunas in Iran, until recently several new localities were discovered in (Mirzaie Ataabadi 2010, Mirzaie Ataabadi et al. 2013). Like in Samos, the sediments of the Maragheh localities are of volcanic origin, although alluviation rather than volcanic activity or lacustrine sedimentation built up the Maragheh Formation (Mirzaie Ataabadi et al. 2013). The Maragheh Formation consists of several nearly undeformed and coarsely stratified layers of andesitic volcanic sands and silts, tuff, and pumice (Bernor et al. 1996). The maximal total thickness of the formation reaches 300 m, of which the lower 150 m are fossiliferous (Mirzaie Ataabadi et al. 2013). Uniquely among the three classical Pikermian localities, Maragheh has a very clearly layered stratigraphy, which makes possible precise radiometric dating (Mirzaie Ataabadi et al. 2013). Based on the stratigraphic succession of hipparions the Maragheh fauna has been divided into three local biozones (Bernor et al. 1996). The fauna ranges temporally between nearly 9 Ma to less than 7.4 Ma, although most of the fossils are from the middle and upper parts of the fossiliferous section, dated 8.16–7.68 Ma (Mirzaie Ataabadi et al. 2013).

3. MATERIALS AND METHODS

3.1. Materials

The material for the study was acquired using the collections of Naturhistorisches Museum Wien (NHMW, Museum of Natural History, Vienna).

To acquire the mesowear data, fossil molars—preferably the second upper molar (M^2)—of large terrestrial herbivorous mammals were scored (measured and analyzed) according to the method developed by Fortelius and Solounias (2000). In most cases the scored teeth were attached to a piece of maxilla or a partial or complete cranium. In the case of a heap of miscellaneous teeth a single tooth from the set (for instance, a box of teeth) was measured. If the M^2 was absent or not in an acceptable condition, a first or third upper molar (M^1, M^3) was used—the mesowear signal is well observable from these as well. The taxonomy/nomenclature of the specimens had to be brought up to date afterwards. For example, a hipparionine specimen was not usually labeled as anything more than ”*Hipparion*”. Moreover, specimen labels and IDs were often incomplete or absent.

3.2. Methods

3.2.1. Mesowear analysis

Fortelius and Solounias introduced mesowear analysis in 2000 (Fortelius and Solounias 2000). The goal had been to develop an easy tooth wear analysis method that yields robust results quickly from a large sample of specimens. In contrast with another commonly used tooth wear analysis method, microwear analysis, mesowear is far less time-consuming, and gives results that paint a broader picture of a herbivore’s general feeding preferences during its life span. Microwear only tells about the animal’s last few meals (Teaford and Oyen 1989). Other authors have since developed the mesowear method further (e.g. Franz-Odendaal and Kaiser 2003, Kaiser and Solounias 2003, Mihlbachler and Solounias 2006, Mihlbachler et al. 2011, Solounias et al. 2014). Here, however, the ‘classical’ method of Fortelius and Solounias (2000) is used.

Mesowear is based on the relative dominance of attrition and abrasion in tooth wear. Attrition is wear dominated by teeth grinding against each other. It develops facets on the sides of the tooth cusp apices and keeps the intercusp valleys deep, resulting in a high crown relief and sharp cusps. In abrasion wear is caused by food chewed by the animal as it (and other extraneous matter that enters the mouth at the ingestion of food) grinds against the enamel. It masks the effect of attrition by wearing the facets and the cusps down, making them rounded and the intercusp valley shallower as the animal ages. The final result is a low crown relief with rounded or, in extreme cases, blunt cusps. Attrition is dominant in browsers, which consume soft leaves as their main food. In grazers abrasion is dominant due to rough and tough low-quality food that includes a

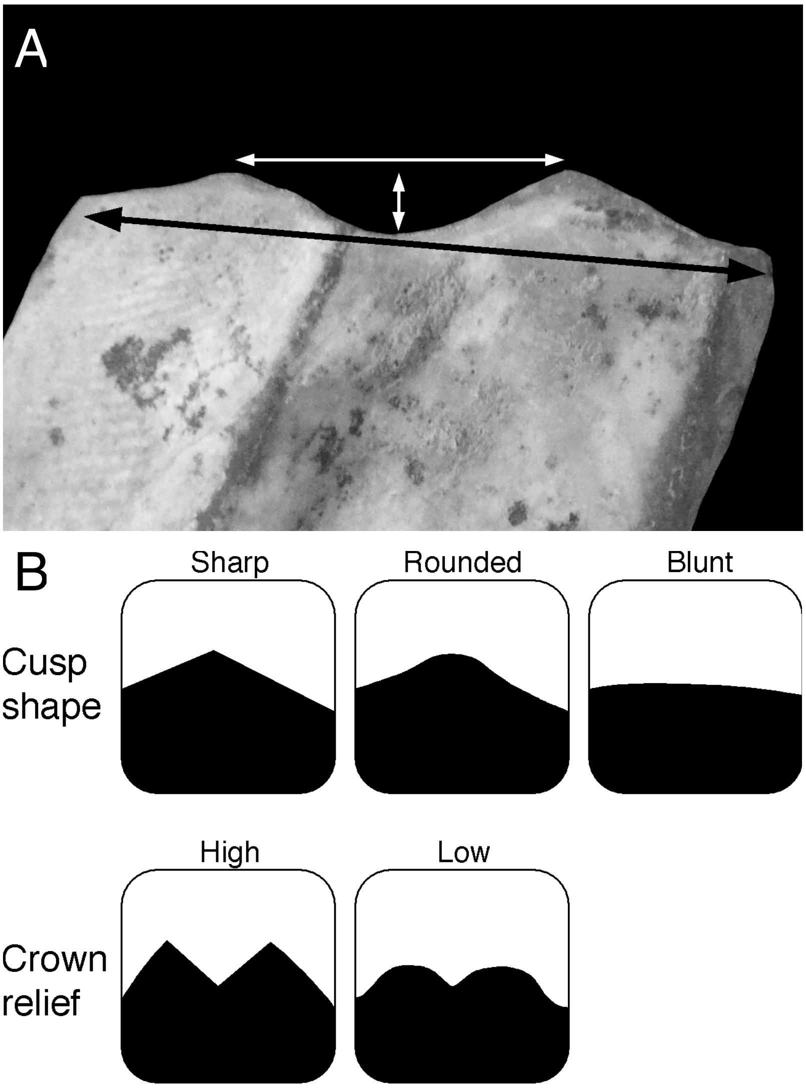


Figure 2. The mesowear scoring routine.
A) The crown of a hipparion molar from Maragheh showing the intercusp valley and the anteroposterior length of the crown which can be used to determine the crown relief value (*high* or *low*). Photo by author, © Naturhistorisches Museum Wien.
B) The idealized physical states of cusp shapes used in scoring and the crown relief. After Joomun et al. (2008).

greater amount of phytoliths and extraneous grit and dust.

Mesowear is observed from the buccal side of the tooth crown, preferably from the upper second molar (M^2). The examined specimens were selected in accordance to Fortelius and Solounias (2000): second upper molars (M^2) with intact buccal cusps, the paracone and the metacone, were favored, and the sharper of the two cusps was scored. Sometimes, e.g. in the case of a damaged or missing M^2, an M^1 or M^3 was chosen instead. Still, the mesowear signal has been demonstrated to be consistent among different upper teeth (Kaiser and Solounias 2003, Merceron et al. 2007). Teeth from individuals obviously too old or too young or otherwise ambiguous were excluded.

The mesowear values are scored from observing the wear stages of the tooth. The intercusp valleys are scored *high* or *low*, and the cusps are scored *sharp*, *rounded* or *blunt*. Mesowear can be observed with the naked eye or by using a slightly magnifying optical device. This can in some cases help scoring the cusp apices sharp or rounded. The scoring of the intercusp valleys as either *high* or *low* without exact measuring is easy after some training, but in borderline cases the value can be calculated as follows (figure 2): the depth of the intercusp valley is measured and divided by the anteroposterior length of the whole tooth. The measuring was done using a digital caliber. The limits between *high* and *low* values for selenodont forms (basically the artiodactyls) and plagiolophodont forms (equids) are 0.1 and 0.03 for rhinoceroses (Fortelius and Solounias 2000).

3.2.2. Cluster analysis

The values obtained from the scoring were put into a spreadsheet. For each taxon, the average percentages of the mesowear values *high profile*, *low profile*, *sharp cusps*, *rounded cusps*, and *blunt cusps* were calculated. These were then added to a matrix of corresponding data from modern herbivorous mammals the diet of which is well known. The data for the modern taxa are from Fortelius and Solounias (2000) with minor differences. All information concerning the data (taxon abbreviations, mesowear scores etc.) can be found in the appendices.

Next, a cluster analysis on the data including both the modern and the extinct taxa was performed using JMP versions 9 and 10 in Mac OS X environment. The clustering was hierarchical, using complete linkage and standardized data. Following the procedure of Fortelius and Solounias (2000), different combinations of the mesowear variables were analyzed. Here, for the sake of simplicity, the results of the combination that has been shown to give the most accurate signal (variables percentage of high profile, sharp cusps, and blunt cusps) (Fortelius and Solounias 2000, Croft and Weinstein 2008) are shown only. Percentage of round cusps is not used, because the cusp sharpness variables add up to 100 %, and therefore only two are needed in the analysis (Fortelius and Solounias 2000). In addition to the clustering with all of the modern taxa, a clustering of the fossil taxa and modern typical representatives of different feeding categories alone is also shown. The typical taxa are modern species whose diet is known with great certainty. A clustering that included the index of hypsodonty using typical modern species was also made.

Fortelius and Solounias (2000) showed that a three-variable analysis using the so-called ‘radical’ classification of ambiguous mixed feeders as either clear-cut browsers or grazers correctly classified modern species with a higher percentage than using the ‘conservative’ classification of species and/or less variables. When they included hypsodonty as a fourth variable, the percentage of correct classification rose even further. In the case of fossil taxa, however, including hypsodonty can give misleading results, because hypsodont taxa may have chosen to feed on browse despite their hypsodont adaptations. Adding hypsodonty can mask the ‘maverick’ feeding signal (see results for *Chilotherium* here).

4. RESULTS

4.1. Results of the mesowear analysis and the cluster analysis

The results of the clusterings can be seen in figures 3 and 4. A summary of the fossil taxa and their mesowear data can be seen in figure 6.

In the resulting dendrograms the fossil taxa are clustered along with modern taxa whose diet categories are well known. A dietary gradient from browsers in the upper end to grazers in the lower appears. Modern browsers are marked by capital letters (for example, AA for *Alces alces*, the moose), modern grazers with lowercase letters (i.e. bb for *Bison bison*, the American bison). Mixed feeders are marked with a combination of uppercase and lowercase letters (i.e. St for *Saiga tatarica*, the saiga). A capitalized last letter indicates fossil taxa. The first letter marks the locality of origin (Pikermi, Samos or Maragheh, i.e. mcP, *Chilotherium persiae* from Maragheh).

In the first dendrogram (figure 3) the fossil taxa sort into six different clusters on the browser-mixed-grazer scale. It must be noted that the gradient from extreme browsers at the top to extreme grazers at the end is not even: in principle, the clusters should show a straight browser-grazer continuum from top to bottom, but some sub-clusters (for example the one with extreme browsers like the giraffe GC) are situated lower or higher than they should, for unknown software-dependent reasons. This does not reflect the actual location of the taxa on the browser-grazer gradient.

Starting from above, *Gazella* from Pikermi and *Chilotherium persiae* cluster with the modern browsers the pronghorn AM, the giraffe GC, and the roe deer OL, plus the browse-dominated mixed feeders the springbuck Ma, and the ibex Ci.

The second cluster down the gradient is still very much browser-dominated. The *Gazella* from Samos, along with the *Tragoportax* of Samos, clusters with the browsers mule deer OH, southern tree hyrax DA, and lesser kudu TI, plus the browse-dominated mixed feeders wapiti Cc, bushbuck Ts, and eland To.

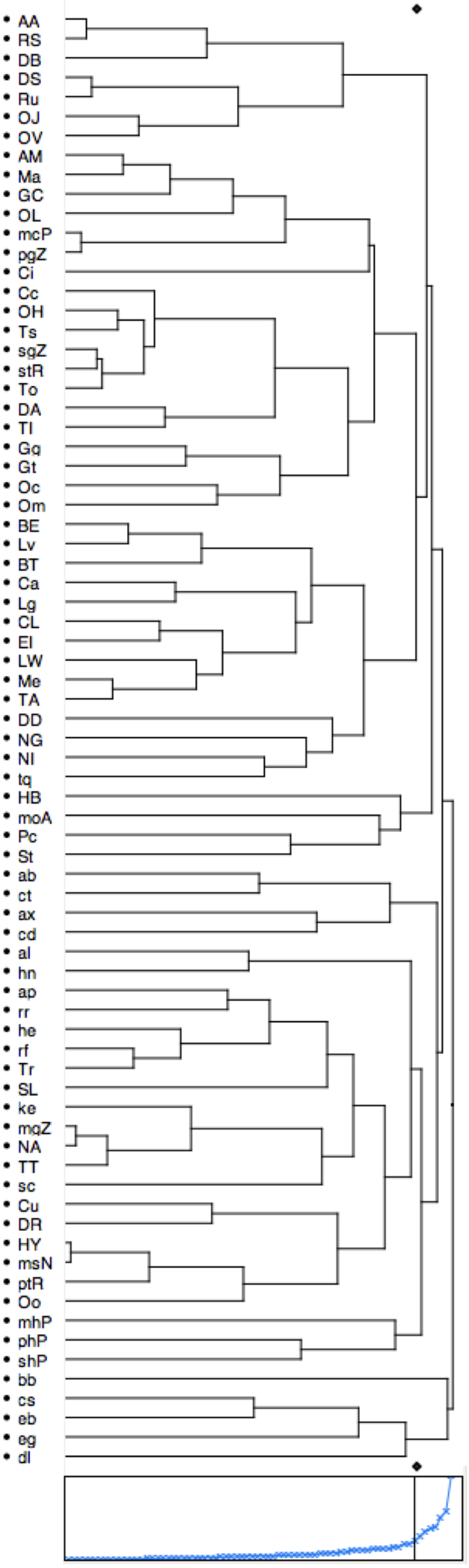


Figure 3. Dendrogram resulting from a clustering using values % high relief, % sharp cusps, % blunt cusps, including all modern species. Upper end = browsers, lower end = grazers.

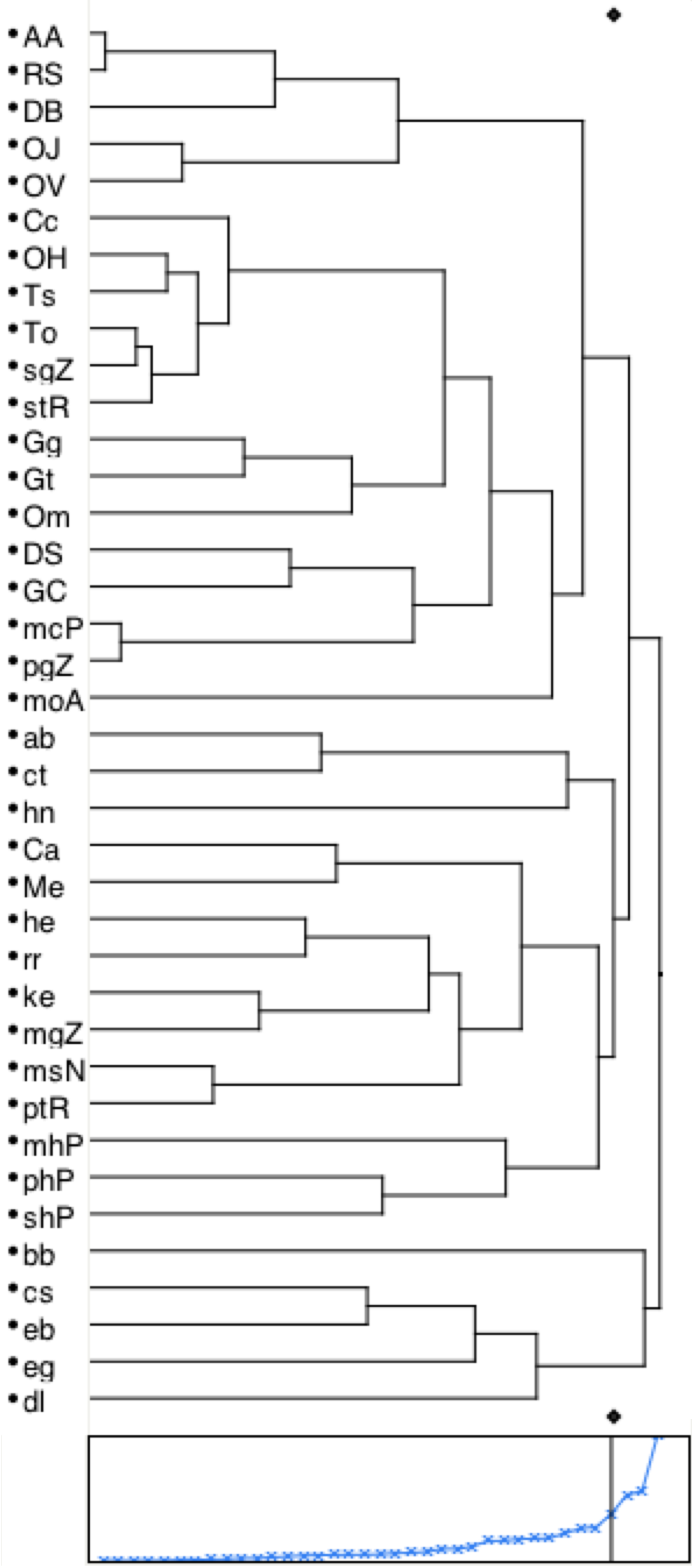


Figure 4. Dendrogram resulting from a clustering using values % high relief, % sharp cusps, and % blunt cusps, including modern species typical to their respective feeding categories and excluding the mabras. Upper end = browsers, lower end = grazers.

Oioceros atropatenes from Samos is joined only by three modern species, Bruce's yellowspotted hyrax HB, rock hyrax Pc, and saiga St.

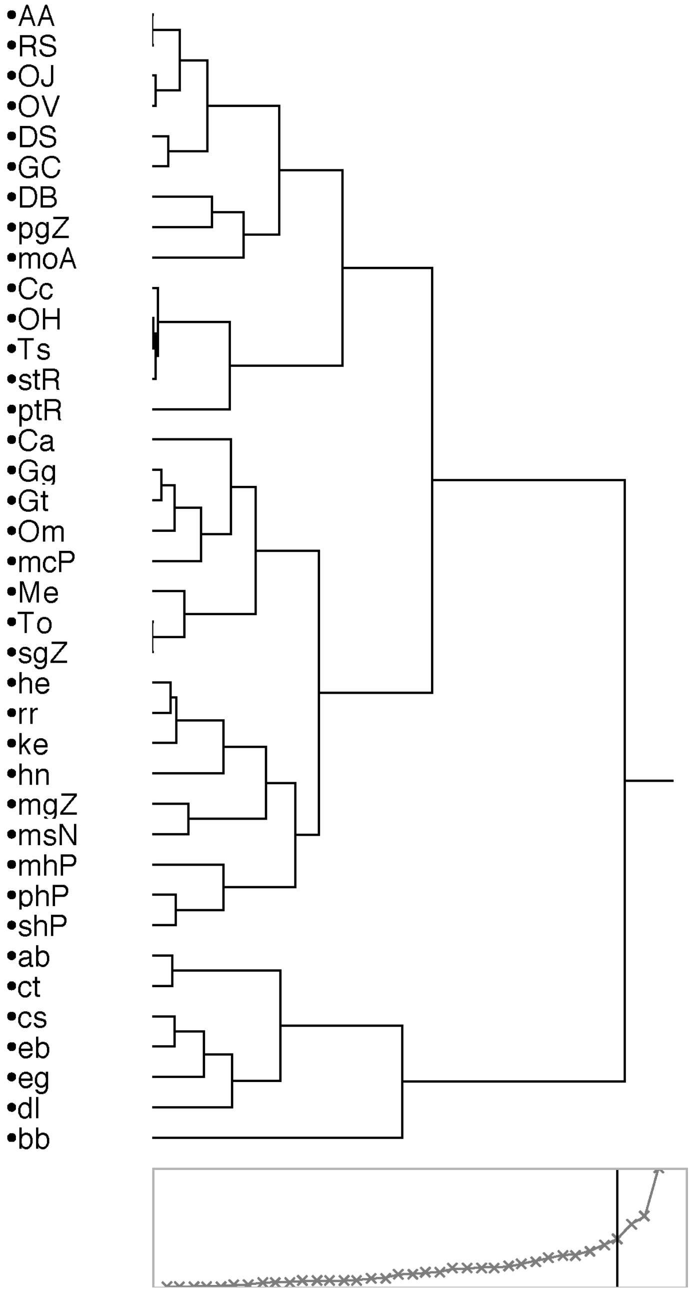


Figure 5. Dendrogram resulting from a clustering using values % high relief, % sharp cusps, % blunt cusps, and hypsodonty including modern species typical to their respective feeding categories and excluding the mabras. Upper end = browsers, lower end = grazers.

The fourth cluster is located in the grazer end of the continuum. Joining the *Gazella* of Maragheh are the grazers chital ap, bohor rr, roan antelope he, mountain reedbuck rf, common waterbuck ke, African buffalo sc, and the graze-dominated mixed feeder nilgai Tr. The apparent extreme browsers of this cluster, red forest duiker NA and greater kudu TT (TS), cluster here because of the so-called ”mabra syndrome” (Fortelius and Solounias 2000). The mabras (short for Minute Abraded Brachydont) are a group of small brachydont species usually classified as browsers such as water chevrotain HY, the duikers, the hyraxes, gerenuk LW and dibatag EI. In the mesowear study of Fortelius and Solounias (2000), however, they cluster with taxa with abraded teeth, e.g. grazers or graze-dominated mixed feeders. This apparent anomaly could be explained by their high intake of fruit (the water chevrotain and the duikers), opportunistic feeding that includes a high proportion of insects (the hyraxes) or highly selective feeding that results in so little attrition that even a small amount of abrasion masks it (Fortelius and Solounias 2000).

In the fifth cluster, the giraffid *Samotherium neumayri* msN from Maragheh and the *Tragoportax* of Pikermi cluster with sambar Cu, and oribi Oo. The erratic mabras are represented by bay duiker DR, and water chevrotain HY.

The sixth and final cluster of the first dendrogram includes all the hipparions of the study.

In the second dendrogram (figure 4) the number of included taxa is greatly reduced because of the inclusion of taxa typical to their feeding category only and the exclusion of the mabras. The fossil taxa are now found in four clusters only.

In the first cluster from above, *Gazella* and the *Tragoportax* from Samos are joined by wapiti Cc, mule deer OH, bushbuck Ts, and eland To. The extant species are all either browsers (mule deer) or browse-dominated mixed feeders. The cluster is virtually unchanged from the first clustering, the exclusion of the mabras being the only exception.

The second cluster has the Maraghean *Chilotherium* and the Pikermian *Gazella* together with the browsers giraffe GC and Sumatran rhinoceros DS as a newcomer in this company. Despite the location as the second cluster from above, this cluster actually has a stronger browsing signal than the first from above in this dendrogram (see page 25 for explanation). The Maraghean *Oioceros* is nested alone below the second cluster. Overall, the cluster is made up of browse-dominated mixed feeders.

The third cluster is nested in the graze-dominated end of the diet spectrum. The *Gazella* and the *Samotherium* from Maragheh and the *Tragoportax* from Pikermi are joined by the grazers roan antelope he, bohor reedbuck rr, and common waterbuck ke.

As they did in the first dendrogram featuring all of the recent species, the hipparions again cluster together here in the graze-dominated end of the diet spectrum. No fossil taxa cluster with the hard core grazers bison bb, white rhinoceros cs, Burchell's zebra eb, Grevy's zebra eg, and topi dl.

Because of the taxonomic resolution problem with hipparions, a histogram of the mesowear score distribution was made to regain some of the lost resolution (figure 7).

The hipparions of Maragheh (with the most specimens, 21) make two even peaks at the wear score categories *high and rounded* and *low and rounded* (8 specimens in each). Only two and three specimens fall into the categories *high and sharp* and *low and sharp* respectively.

In Pikermi, which has 7 specimens, the share of *high and rounded* is 5 against the 2 of *low and rounded*.

In Samos, with only 5 specimens, 3 are *high and rounded* while 2 are *low and rounded*.

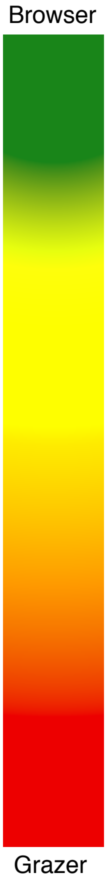
Figure 5 shows the dendrogram that was produced including the index of hypsodonty. The result does not differ greatly from the previous results, although the relocation of the rhino *Chilotherium* and the clustering together of the *Tragoportax* from Pikermi and Samos are noteworthy deviations (see discussion).

In figure 6, it is shown how the fossil taxa are distributed in the dietary categories *browser*, *browse-dominated mixed feeder*, *graze-dominated mixed feeder*, and *grazer.*

4.2. Limitations of the material and potential sources of bias

The material presented numerous qualitative and quantitative challenges. As is always the case with fossil material, the usability of a specimen depends on its condition. In general, teeth survive the diagenetic processes well, but in many cases the hard but brittle cusps of the fossil teeth were damaged, ergo rendered unusable in this study. Fortunately, the mesowear signal is usually reliably observed from M^1 and M^3 as well

Figure 6. Fossil taxa used, their relevant mesowear data, and approximate location on the browser-mixed-grazer dietary continuum. Crown height data from the NOW (New and Old Worlds) fossil mammal database (http://www.helsinki.fi/science/now).



Taxa	Locality	Sample	% sharp	% blunt	% high	Crown height
Chilotherium	Maragheh	12	66.67	0	100	hypsodont
Gazella	Pikermi	3	50	0	100	mesodont
Gazella	Samos	4	50	0	100	mesodont
Tragoportax	Samos	4	50	0	100	brachydont
Oioceros	Maragheh	3	66.67	0	66.7	mesodont
Samotherium	Maragheh	6	16.67	0	100	mesodont
Tragoportax	Pikermi	7	14.29	0	100	brachydont
Gazella	Maragheh	4	0	0	100	mesodont
Hipparionini	Pikermi	7	0	0	71.4	hypsodont
Hipparionini	Samos	5	0	0	60	hypsodont
Hipparionini	Maragheh	21	23.81	0	47.6	hypsodont

(Fortelius and Solounias 2000, Kaiser and Solounias 2003), which lowers the dependency on intact M^2s. The intended comparative aspect of this study was stymied by the lack of fossils of same species from the three localities, the low number of specimens, and the lack of taxonomic resolution.

The nomenclature of the specimens in NHMW's collections dates back to the latter half of the 19th century and the beginning of the 20th century. The effort to bring the species and genera of the study up-to-date was carried out as carefully as possible, but the risk of incorrect classification of the specimens remains. In many cases the species of the specimen could not be identified. Especially in the case of the hipparions, correct modern classification down to the species level would have resulted in a higher resolution in the results. While species-level identification would have been possible in theory, in practice such a task would have been beyond the scope of this study.

Part of the results must be treated with caution given the limited number of specimens. According to Fortelius and Solounias (2000), the mesowear signal stabilizes between 10 to 30 samples, and for fossils a sample of 5 specimens is acceptable. Below the 5-sample limit are *Oioceros* and *Gazella* from Maragheh (3 and 4 respectively), *Gazella* and *Tragoportax* from Samos (4 of both), and *Gazella* from Pikermi (3). Another possible cause of sampling bias is the purging of valid blunt specimens as individuals too old. Changing dietary preferences, caused by seasonal vegetation changes and/or migration, cannot be observed in the mesowear signal.

The low number of available specimens of the same taxa also hampered the cross-locality comparative aspect of the study. The hipparions were the most numerous fossils of the NHMW collection, but their potential was diminished by the lack of taxonomic resolution. The size of the teeth may have been a way to distinguish species from each other, but unfortunately the exact measurements were not written down. Therefore the hipparions did not yield species or genus level results. Aside from the hipparions, *Gazella* was the only genus in the study that spanned all three localities. Specimens of *Tragoportax* were available from both Pikermi and Samos.

5. DISCUSSION

5.1 On the results of individual taxa

The aceratherine rhino *Chilotherium* from Maragheh was represented by 12 specimens, which were all highly probably from *C. persiae*. The result was a clear browsing signal. This might seem peculiar at first, given the animal's apparent adaptations for grazing, such as hypsodont cheek teeth, a broad muzzle and short limbs that could have enhanced its ability to feed closer to the ground (Deng and Downs 2002, Heissig 1999). *Chilotherium* was a typical member of the Pikermian fauna, with species appearing from southeastern Europe to China, often with more than one species at the same locality. *C. persiae* is listed as a mixed feeder in the NOW database (http://www.helsinki.fi/science/now). Several factors might explain the result obtained here. First, *C. persiae* might have browsed on the lush herbaceous layer that was likely present in the Pikermian Biome (Koufos et al. 2011, Spassov et al. 2011). Second, *C. persiae* might have fed on aquatic plants. Moose, *Alces alces*, is an extant extreme browser that adds a great portion of water plants into its diet. The nasal region of moose and *Chilotherium*'s skulls show a similar retraction of the nasal bones. *Chilotherium* may well have had a similar fleshy, overhanging muzzle suited for foraging in shallow water. The characteristic flaring, enlarged, tusk-like lower incisors also largely explain the width of *Chilotherium's* muzzle, so its wide muzzle wasn't necessarily an adaptation to grazing as it is, for example, in the modern white rhino. Third, *C. persiae* might have specialized on the low-growing soft grasses like the recent Thomson's gazelle, *Gazella thomsoni*. (Incidentally, *Gazella* is also a genus with species whose molars range from brachydont to hypsodont.) Indeed, Biasatti (2009) argues, based on C and O isotope ratios and the deduced habitat, that *C. wimani*, a mesodont species from the late Miocene (9.5–6 Mya) of the Linxia and Tianshui Basins in north-central China, may have been a C3 grazer in a relatively closed environment. In the same study, Biasatti also mentions the possibility of a wallowing lifestyle in *Chilotherium*. Given some of its anatomical features—the similarity of the snout anatomy with the wallowing moose, a proportionally slender body, hippo-like short limbs and high-set orbits—*Chilotherium* may well have lived in shallow rivers browsing on water plants (Fortelius et al. 2003b).

Rhinocerotids, such as the Miocene–Pliocene North American rhino *Teleoceras*, are known to have assumed the role of hippopotami where the latter were absent. As such, browsing or a *high and sharp* mesowear score in a hypsodont species is not an exceptional phenomenon. The examples of the extant hypsodont herbivores with a high and sharp mesowear score—the dromedary (*Camelus dromedarius*), and especially the pronghorn (*Antilocapra americana*)—show how hypsodonty does not make an herbivore an obligate grazer (Fortelius 1985, Tubei 1985, Fortelius and Solounias 2000, Damuth and Janis 2011). In their mesowear study based on the method by Mihlbachler et al. (2011), Solounias et al. (2013) found the mesodont *C. habereri* from the late Miocene of China to have been a browse-dominated mixed feeder. As seen above, the teeth of *Chilotherium* species range from brachydont to hypsodont, with several species in each crown height category. This also indicates *Chilotherium* was a versatile genus able to adapt to a multitude of niches in the Pikermian Biome and to changes in its environment, such as warming and drying during the latest Miocene (Biasatti 2009). Including the index of hypsodonty to the clustering pulls *Chilotherium* towards the browse-dominated mixed feeders, while the mesowear variables alone produce a clear browsing signal for the rhino. This result highlights the difference between the mesowear signal and the hypsodonty signal, showing how hypsodonty and mesowear don’t necessarily produce similar results as hypsodonty is regarded as an adaptation for grazing. Since the modern species are, as mentioned above, typical to their feeding categories, and all of the modern typical grazers in the material are hypsodont, it is no wonder that using them in the clustering strengthens the ‘hypsodonty = grazing diet’ bond in the results. In their mesowear study, Solounias et al. (2013) mentioned hypsodonty to be a poor predictor of mesowear. Further paleodiet studies on *Chilotherium* from its entire range within the Pikermian Biome would bring more light upon its paleoenvironment, paleoecology, and dietary preferences.

The bovid *Tragoportax*, a brachydont boselaphine antelope, clusters very differently in Pikermi and Samos. The Pikermian *Tragoportax* clusters with modern grazers or graze-dominated mixed feeders, while the *Tragoportax* from Samos clusters with browse-dominated mixed feeders and browsers. This is an interesting result, because the habitat of Pikermi has been interpreted as more closed than Samos (Solounias et al. 2010). *Tragoportax* in Pikermi might have been a pioneer genus, specializing in the recently increased grasses in its habitat. It must be pointed out that in this study *Tragoportax* is treated at genus level. Nevertheless, the result from Pikermi includes five *T. amalthea* and two *T.* sp. and can be considered reliable. The latter two are highly likely to be *T. amalthea*, it being the only species of *Tragoportax* known to be present in Pikermi (Bernor et al. 1996). The sample from Samos includes two of the more primitive *T. amalthea* and one *T. rugosifrons* (to which Solounias et al. 2010 deem *T. amalthea* ancestral, and found it to be a grazer in their light stereomicroscope microwear study), and also one *T. sp*. Taken individually, the two *T. amalthea* from Samos were scored *high and sharp* and *high and rounded* respectively. Since the relative percentage of the values is the same (50/50) when including the other taxa (*T. rugosifrons* and *T. sp*.), excluding them does not change the results. Previous studies have given varying results concerning the diet of *T. amalthea*. Solounias and Hayek (1993), Solounias and Moelleken (1993), Solounias et al. (1995), and Solounias et al. (2013) found *T. amalthea* to be a mixed feeder to possibly grazer, mixed feeder to grazer, a browser or a mixed feeder, and strongly browse-dominated mixed feeder, respectively. The first two studies were based on the analysis of the masticatory morphology, the last on SEM microwear. The present result puts *T. amalthea* firmly in the graze-dominated mixed feeder category. It is entirely possible, though, that *T. amalthea* had a different diet during different seasons and/or in different populations. The results of Solounias et al. (2010), for example, indicate that the diet of the hipparion *Hippotherium mediterraneum* (a.k.a. *Cremohipparion mediterraneum*, see the discussion of the results concerning the hipparions later in this chapter) differed between Pikermi and Samos, the Samos population being more inclined to graze than that of Pikermi.

Gazella, as stated above, was sampled from all three localities. Along the browser-grazer gradient, the strongest grazing signal comes from the *Gazella* of Maragheh, and the strongest browsing signal from Pikermi. *Gazella* from Samos falls in-between, although its companions in the cluster are either browsers or browse-dominated mixed feeders. The diet of extant gazelles is mixed as well. The extant Grant's gazelle is a browse-dominated mixed feeder (~22% grass), while Thomson's gazelle is a graze-dominated mixed feeder (~68% grass) (Cerling et al. 2003). According to Solounias et al. (2010) the modern gazelles prefer fresh short grasses and browse. This may explain the grouping of Thomson's gazelle in the browser/browse-dominated mixed feeder cluster by Fortelius and Solounias (2000). It is also known that in the modern grazing succession of the Serengeti plains in Tanzania, Thomson's gazelle 'finishes' the work of larger grazers by grazing on the softest and smallest grasses (Bell 1971). As such the results here are rather expected, with a known west-to-east humidity gradient as indicated by mean hypsodonty (Fortelius et al. 2002) which these results confirm. The results also indicate a strong dietary and ecological flexibility in *Gazella*. Because of a low number of specimens (3 from Pikermi, 4 from Samos, and 4 from Maragheh), however, care must be taken not to make too confident conclusions. Solounias et al. (2013), on their part, had 26 specimens of *G. gaudryi-deperdita* from Samos in their mesowear study, where the animal was deemed a browse-dominated mixed feeder. As was the case with *Tragoportax*, the clustering of *Gazella* was done at genus level. A clearer division of the material into species might have been even more daunting a task than in the case of the hipparions, as the taxonomy of fossil *Gazella* is notoriously convoluted. Species have often been split into several new species, and just as many times they have been clumped together again. This has long been a source of frustration for workers on the Pikermian fauna. Bibi and Güleç (2008) cite Teilhard de Chardin and Trassaert (1938), early workers on the Pikermian fauna: "Who among the palaeontologists would dare to proclaim his faith in the value and in the practical use of the various species of *Gazella* reported in the scientific literature for [the] Pontian only (Pikermi, Samos and Maragha)?" This has not kept people from trying. The latest reclassification comes from Kostopoulos and Bernor (2011), who recognize two species of *Gazella* from Maragheh, *G. capricornis* and *G.* cf *ancyrensis*, while establishing a new genus and species from *G. rodleri*, *Demecquenemia rodleri*. Solounias et al. (2010) list two species of *Gazella* present at Pikermi and Samos: *G. capricornis* and *G. pilgrimi*. Bernor et al. (1996) list *G. capricornis/deperdita* and "*G.*" *rodleri* as present in Maragheh, while Mirzaie Ataabadi (2010) updates this list to *G. capricornis* (*G. deperdita* in Bernor 1986), *"G." rodleri*, and *G.* cf. *ancyrensis*.

The mesodont Maraghean sivatherine giraffid *Samotherium neumayri* is represented by a sample of 6 individuals, of which 5 belong to the species *S. neumayri*. Because no other species of *Samotherium* are known from Maragheh, it is safe to assume the 6th individual, labeled *S.* sp. is also *S. neumayri*. *S. neumayri* clustered with graze-dominated mixed feeders in the first dendrogram (figure 3), and with clearly grazing modern species in the second clustering featuring only typical representatives of the diet categories (figure 4). These results correspond well to the results of previous studies that found *S. neumayri* to be a mixed feeder to grazer (e.g. Solounias and Moelleken 1993) and a clear grazer (Solounias et al. 2010, Table 2). Therefore, *S. neumayri* differs from the extant giraffe *Giraffa camelopardalis*, which is a highly specialized browser. Other species of *Samotherium* (*S. major* and *S. boissieri*) have also been interpreted as belonging to the same feeding categories (see Solounias et al. 1999 and Solounias et al. 2010 for summaries). In their mesowear study using the Mihlbachler scale (Mihlbachler et al. 2011), Solounias et al. (2013) found *Samotherium* (sensu lato) from Samos to be a mixed feeder with an emphasis on browse (score 2 on the Mihlbachler mesowear scale, for further details see Mihlbachler et al. 2011). It might be of interest to mention the Chinese late Miocene samotheres from the same study: the robust result from *S. boissieri* gives a clear mixed feeder signal (score 3 on the Mihlbachler scale).

Oioceros atropatenes, a spiral-horned antelope, is the most abundant species of the Maragheh bovid assemblage (Kostopoulos and Bernor 2011), but is represented here by only three specimens. Three species of *Oioceros* are known from the Greco-Iranian Province: *O. atropatenes* is a Maraghean species, the larger *O. rothii* is known from both Maragheh and Pikermi, *O. wegneri* from Samos (Bernor et al. 1996, Kostopoulos 2006, Kostopoulos and Bernor 2011, Mirzaie Ataabadi et al. 2013). The three specimens of the *Oioceros* sample are all confirmed to be *O. atropatenes*. The clustering of *O. atropatenes* with the modern hyraxes and the saiga in the first dendrogram (figure 3) is not informative in the sense that the hyraxes belong to the problematic mabra group (see materials and methods). That *Oioceros* clusters with them doesn't tell much about its dietary preferences. The saiga, on its part, is a hypsodont browse-dominated mixed feeder (Fortelius and Solounias (2000). In the 'typical' clustering (figure 4) *O. atropatenes* is alone in the larger browse-dominated mixed feeder cluster. In the NOW database (http://www.helsinki.fi/science/now) *O. atropatenes* is listed as a mesodont mixed browser/grazer, and, the small sample size aside, the results do match the animal's dietary category in NOW. Bernor et al. (2014), using the Mihlbachler mesowear scale (the average being 0.75), found the Maraghean *O. atropatenes* to be a browser from four specimens. The Mihlbachler mesowear score from the Pikermian *O. rothii* (five specimens, Solounias et al. 2013) was 1, which makes it a strongly browse-dominated mixed feeder. *O. rothii* and *O. wegneri* were deemed mixed feeder and browser, respectively, by light stereo-microscope microwear analysis by Solounias et al. (2010). As the same authors point out, however, members of the same genus or even the same species at different localities do not necessarily share a similar diet. All in all, dietary studies strongly point to *Oioceros* having been a browser to a browse-dominated mixed feeder.

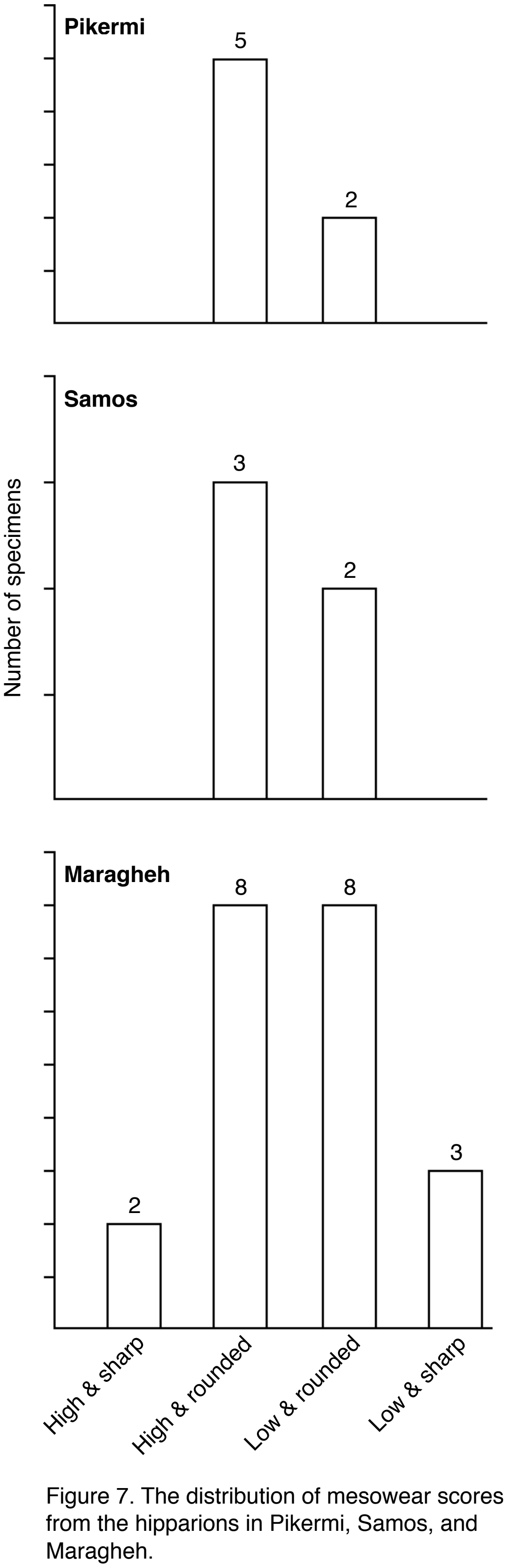


Figure 7. The distribution of mesowear scores from the hipparions in Pikermi, Samos, and Maragheh.

In the clustering, all hipparions from all three localities clump next to each other to the graze-dominated mixed feeder cluster. This was to be expected with such a coarse resolution as the hipparions were treated with, but closer inspection of the absolute numbers of mesowear values gave more detailed information (figure 7). The results of Maragheh stand out of the three with its even numbers of *high and rounded* and *low and rounded* profiles and cusps. Samos is close to these values with three and two of the same values respectively, but here the low number of specimens again undermines the robustness of the result. In Pikermi, the difference is clear between the two mesowear classes, with five against two. Although the diets of individual species still cannot be told, these results give an idea of the division of the hipparions' dietary regime at the localities. The proportionally greater number of low and rounded specimens in Maragheh indicates a greater intake of grass in Maraghean hipparions, which could point to more open, arid, and/or higher temperature environment. This correlates positively with the find of C_4 grasses emerging in Maragheh during the existence of the local Pikermian fauna (Strömberg et al. 2007). Also, the values of Pikermi—more *high and rounded* specimens indicating a mixed/browsing diet—fit with the view of Pikermi being more closed and humid than Samos (Solounias et al. 2010). Regional mean hypsodonty values (Fortelius 2012, pers. comm.), which can be used as a proxy for precipitation (e.g. Fortelius et al. 2002) indicate that Pikermi was relatively the most humid locality and Samos the most arid of the three. This is in part confirmed by Mirzaie Ataabadi et al. (2013), whose compilation of hypsodonty data shows that Pikermi had clearly the smallest number of hypsodont taxa (only ~7%), while in Maragheh over 30% of taxa were hypsodont. It is evidently the hypsodont and the brachydont taxa which make the difference, since the proportion of mesodont species is basically the same in all three localities (~30%). It could be speculated that the great number of specimen scored *low and rounded* in Maragheh is indicative of seasonal changes in dietary preferences: while extreme grazing results in *blunt* crowns, browsing during the wet season and grazing during the dry season could result in a *low* crown relief with *rounded* cusps.

Bernor et al. (2014) got results from Maraghean hipparions, and although their sample size was limited, it was clear that there were differences in the diets of individual hipparion species. In their study, *Cremohipparion moldavicum* gave a browsing-mixed signal, while *Hipparion prostylum* and *Hipparion campbelli* were clearly mixed feeders. Because the temporal range of the hipparion species in Maragheh is known (see next paragraph), a mesowear study using a larger sample could potentially reveal dietary trends in them. Solounias et al. (2013) sampled hipparions from Pikermi and Samos in their mesowear study, receiving results similar to this study. Four species of *Hippotherium* from Samos had diets that were slightly browse-dominated to graze-dominated. The Pikermian *Hippotherium primigenium* was a browse-dominated mixed feeder. Fortelius and Solounias (2000) had *Cremohipparion proboscideum* from Samos among the six fossil species included in their seminal mesowear study. In their results, *C. proboscideum* clustered clearly with browsing to browse-dominated mixed feeders (mule deer, roe deer, and springbuck). As the authors pointed out, this result might be indicative of *C. proboscideum* having had a proboscis, as old hypotheses suggest, which would indicate it was a specialized browser. Solounias et al. (2013), however, found the same species (a.k.a. *Hippotherium proboscideum*) to be a graze-dominated mixed feeder.

The systematics of the hipparions is, like that of the Pikermian gazelles, much-debated and convoluted. Solounias et al. (2013) cite Bernor (pers. comm. 2010), claiming only two species of hipparions present in Pikermi: the primitive *Hippotherium brachypus* and *Cremohipparion* (or *Hipparion*, Koufos 2013) *mediterraneum*. For Samos, the authors list six species: *C. proboscideum*, *C. matthewi*, *C. nikosi*, *Hippotherium* sp., *Hipparion dietrichi*, and *"Hipparion"* sp. The hipparions of Maragheh are as follows according to Mirzaie Ataabadi et al. (2013): *Hipparion gettyi* (oldest)*, Hippotherium brachypus* and *Cremohipparion moldavicum*, *Hipparion campbelli* (youngest), and *C.? matthewi* appearing jointly through most of the time with the previously mentioned species. The authors also mention the likelihood of many other small species of *Cremohipparion* appearing in Maragheh.

Historically hipparions have been interpreted as grazers, whose appearance in the fossil record is an indicator of grasslands and more open biomes in general. This is mostly due to their hypsodonty and the savanna-like faunas they are associated with, where they have been assumed to have had the role of the modern zebras (see Solounias et al. 1999 and references therein). Although the zebra analogy isn't accurate, in that the hipparions were not extreme grazers like modern zebras, the appearance of the hipparions can still be seen as an indicator of more open environments in Eurasia. The subfamily Equinae of hypsodont horses (incl. hipparions and modern horses) appeared ~18 Mya in North America, and grasslands there had appeared at least 4 Mya prior to this (Strömberg 2006). There was, however, no delay toward the use of grass as food in North American horses, as evidenced by fossil anchitherine horse mesowear (Mihlbachler et al. 2011). This could be seen so that when the hipparions arrived, the region was already more or less open, and had possibly been so for a while.

Hipparions have been the subject of numerous paleodiet studies in the past (e.g. Hayek et al. 1992, Kaiser 2003, Solounias et al. 2010). The general consensus on hipparionine diet is that they were usually not extreme grazers like their extant relatives (Solounias et al. 2010). They were, however, certainly adapted to using a wide mixed range of feed, often with a preference for grass (Solounias et al. 2010). Their dietary flexibility may have been the key to their success in conquering the Old World. Kaiser (2003), using the ”extended” mesowear method (Kaiser and Solounias 2003), found two populations of *Hippotherium primigenium*, one of the first hipparions to enter Europe, in differing dietary categories at two contemporaneous localities in what is now modern Germany. The *H. primigenium* from the locality of Dinotheriensande, Eppelsheim, was a grazer, while the population of Höwenegg appeared to have mainly browse as its feed. As such, this is further proof of the trophic spectrum extension potential that hypsodonty gives to a species. It would be interesting to conduct similar studies on populations of other herbivorous mammals and, in the case of similar dietary flexibility, compare this with the temporal and spatial extent of their respective species or genera. Forms with greater dietary flexibility would be expected to show rapid and wide dispersal and persistence in deep time similar to the hipparions. An indicator of this could be that common species were chiefly responsible for the increase in hypsodonty when more open habitats expanded in late Miocene (Jernvall and Fortelius 2002). Raia et al. (2011) also found a positive correlation between hypsodonty and range size in some fossil ruminant species. Their results also indicated a higher speciation rate in hypsodont forms, which could be enabled at least in part by the dietary flexibility provided by hypsodonty.

It is worth noting that no sample was scored *blunt* in this study. This might be due to sampling bias (see chapter 4.2, page 32), but another plausible explanation is that the absence of *blunt* specimens indicates an environment that wasn’t open and/or grassy enough to wear teeth down to blunt levels (see next chapter). As late Miocene was also a time of increasing seasonality in the Eurasian mid-latitudes, the possibility of seasonal changes in diet must also be considered. Browsers and browse-dominated mixed feeders might have used more abrasive fallback food during drier and colder seasons. This would directly affect the mesowear signal.

It is important to take into account that the time spans from which the fossils of this study come from may affect the resolution of the results, even though most of the fossils are probably from a shorter age range than the maximum (see chapter 2.6). In Maragheh, the fossiliferous formation covers a time of ~1.4 Ma, in Samos ~1.6 Ma.

Significant climatic variation and consequences therefrom can take place in such time spans. A study comparing mesowear value ratios of same species from different time zones within one or several localities could yield information about the local variation of dietary preferences and consequently of local vegetation and climate through time.

5.2. The Pikermian Biome – a review and rumination

The view of the late Miocene eastern Mediterranean paleobiome has undergone significant changes from the days of its early researchers. The old view of a uniform, modern-day Serengeti-like region with a corresponding fauna has been proven too simple, as more detailed evidence has emerged. The precise type of the biome has been interpreted in several ways. The classical savanna interpretation, mostly based on faunal characteristics (e.g. Osborn 1910, Abel 1927, Kurtén 1952), has evolved to one that combines sclerophyllous evergreen woodland with interspersed grassy openings based on paleofloral reconstructions and paleodietary studies (Axelrod 1975, Bernor 1979, Solounias et al. 1999, Solounias et al. 2010, Bernor et al. 2014; but see Strömberg 2007).

The 'Savanna Myth' of the Pikermian Biome (so called by Solounias et al. 1999) painted an image of vast late Miocene grasslands grazed by a fauna similar to African savannas. C_4 grasses are the dominant form of grasses in modern subtropical and tropical grasslands. Recent studies have shown that the Pikermian fauna existed at the verge of the C_4 revolution, but was not quite yet part of it. In the Greco-Iranian Province, the eastern locality of Maragheh was probably the first to enter the C_4 world. Strömberg et al. (2007) report of the presence of potential C_4 chloridoid grasses in Maragheh, and also view this as an indicator of a somewhat warmer climate there compared to the western parts of the Greco-Iranian Province. The results of this study agree with this and the west-to-east humidity gradient of the late Miocene (Fortelius et al. 2002), with the hipparions of the eastern locality of Maragheh being more graze-dominated mixed feeders than the hipparions of the western locality of Pikermi. Other studies from localities further east from Maragheh, based on stable C and O isotopes and mean hypsodonty, support the view of an increasing eastward temperature and/or aridity gradient in late Miocene (Fortelius et al. 2002, Zazzo et al. 2002). Since high temperatures and seasonal aridity favors C_4 plants, it is to be expected that their rise in Eurasia began in the Asian mid-latitudes. The aforementioned authors also suggest this. East to Maragheh in the Siwaliks of northern Pakistan there is isotopic evidence of gradual C_4 expansion at 7.3 Mya, and from 6 Mya on the signal is almost purely indicative of C_4 grasslands (Quade and Cerling 1995). Further east still, in the late Miocene of the Chinese Loess Plateau, *Hipparion* and the gazelles of the *Gazella dorcadoides* type had a share of C_4 graze in their diet (Passey et al. 2007). C_4 plants also appear in the diet of mammalian herbivores at ~7.5 Mya in central Inner Mongolia, China (Zhang et al. 2009). In the eastern Mediterranean (excl. Iran), however, C_4 grasses appear to never have been an important element of the flora (Strömberg 2007, Cerling et al. 1997 – but see Urban et al. 2010). Cerling et al. (1997) also refer to ^{13}C isotopic evidence in their claim that there was a global C_4 event at 8-6 Mya, except in Western Europe and Eastern Mediterranean.

There is no doubt, however, that C_3 grasses were abundant in the Pikermian Biome. This is supported by phytolith (Strömberg et al. 2007), paleosol-isotopic (Quade et al. 1994) and paleodiet studies (Solounias et al. 1999, 2010, present study). Several lines of evidence point to the Pikermian Biome being a sclerophyllous woodland with a rich herbaceous undergrowth (Solounias et al. 2010, Koufos et al. 2011). Contrary to this, Strömberg et al. (2007) found the phytolith evidence pointing to a C_3 grass-dominated savanna-mosaic biome in Greece, Turkey, and Iran in late Miocene (~9 Mya). This result, however, must be seen as an outlier in the light of several other studies (see review in Solounias et al. 1999 and Solounias et al. 2010). A number of factors can cause a grass bias in the phytolith record: the significantly more prolific production of phytoliths in grasses and the effect of soil order type on phytolith preservation (Hyland et al. 2013), the possible effect on it of bedrock chemistry (Tsartsidou et al. 2007), and the negligible amount of phytoliths produced by some tree taxa (Bremond et al. 2004). Tsartsidou et al. (2007) report of an overrepresentation of grasses in samples from modern Mediterranean ecosystems, with phytolith production levels in grasses 20 times higher than in other groups. Also, there isn’t a long way from ’wooded grassland’ to ’grassy woodland’. Local variation in humidity and temperature, caused by topography and distance to sea, is also to be expected. Certainly an area as vast as the Eastern Mediterranean would have included a wide spectrum of habitats on both sides of the median woodland.

It is also entirely possible, perhaps even most likely, that the Pikermian Biome does not have any exact modern analogies. The results of Liu et al. (2012), using the lophedness and hypsodonty of herbivorous mammals as indicators of net primary productivity, showed that the Pikermian fauna plotted both in the dry part of temperate and mixed forests biome and in the humid part of temperate grasslands. This suggests that at least parts of the Pikermian Biome are not analogous with any single modern biome, but were instead a mix of several different paleobiomes. Bruch et al. (2006), in their paleoclimate study based on paleofloras, found no indication of a modern-type Mediterranean climate during the Tortonian (late Miocene, 11.6–7.2 Mya) in their study area, which stretched from Western Germany to Armenia. They also found the north-to-south humidity gradient to be weaker than today. Like the authors also did, however, the lack of data in their study from southern Balkans and Turkey must be noted. In a further paleoflora study, Bruch et al. (2011) found no support in their data for a Tortonian opening of vegetation in Eastern and Southern Europe. The vegetation reconstruction results of Kovar-Eder et al. (2006) from the late Tortonian of Crete (dated at 7.7–8.6 Ma) indicate that the island was covered by evergreen to mixed-mesophytic subtropical forests. Xeric grasslands in Europe are found between 12–8.5 Ma and 7–4 Ma only by the northern margin of the Black Sea according to Kovar-Eder et al. (2008). The novel method of reconstructing leaf cover index based on the plant cell derived shape of phytoliths (Dunn et al. 2015) could give new insights about the relative openness/ closedness of the Pikermian Biome's vegetation.

Solounias et al. (2010) do not see the extant African woodland as an appropriate model for understanding the Miocene of Pikermi and Samos, citing the notably higher hypsodonty levels of the modern African savanna and woodland ruminant species as the reason (as compared to the Pikermian species). As an explanation to this difference they give the differences in physiognomy between the present-day African woodland and the Miocene woodlands of the Mediterranean area. It must be asked, however, could the high hypsodonty levels in modern African woodland be a consequence of an invasion of by more hypsodont savanna species? As forests/woodland and savanna took turns expanding and contracting several times during the Pleistocene, the brachydont taxa must have suffered losses. Hypsodont taxa, on their part, do not necessarily need grasslands to survive (Feranec 2003). Instead they can opportunistically ‘revert’ to a diet that includes more browse or graze in a forest setting. This is also indicated by a mammal community study including the modern hypsodont ruminant species *Bos gaurus* (the gaur), *Bos javanicus* (the banteng), and *Syncerus caffer* (the African buffalo), the range of which includes tropical rainforests (Eronen et al. 2010b). Curiously, the abrasion level of modern African savanna is not much higher than that of Pikermi and Samos, despite the higher hypsodonty of the African fauna (Solounias et al. 2013). The latter phenomenon could be explained simply by the longer evolutionary history of the African taxa. Solounias et al. (2010) suggest the Kanha national park in India to be the closest modern analog to the Pikermian Biome. With abundant grass growing in clearings and along rivers in a woodland setting in Kanha, this parallel seems reasonable in the light of available paleontological evidence. Recent evidence of plant diversity being the main factor that defines species diversity in large mammal herbivore communities (Kartzinel et al. 2015) makes the high diversity of the Pikermian fauna understandable. Also, as modern herbivorous mammal species are able to partition their niches very precisely and efficiently in Kenyan semiarid savanna (Kartzinel et al. 2015), it is reasonable to assert the herbivores of the woodland Pikermian fauna had finely partitioned niches as well, again supporting the high species diversity.

6. CONCLUSIONS

The diet of herbivorous mammal taxa from the late Miocene fossil localities of Pikermi and Samos, Greece, and Maragheh, Iran, was studied using the original mesowear method introduced by Fortelius and Solounias (2000). The results mostly confirm previous paleodiet studies of the taxa from these localities, which show them having been browsers, browse-dominated mixed feeders or graze-dominated mixed feeders. Results obtained from *Gazella*, *Samotherium* and the hipparionine horses concur with the view that the habitat in the eastern locality of Maragheh was drier and/or more open than in the western Pikermi.

The most robust results come from the Maraghean rhinoceros *Chilotherium persiae*. They suggest the lifestyle of a wallowing browser of aquatic plants for *C. persiae*. The results from *C. persiae* are a good example of how mesowear can distinguish a species' dietary category that goes against that suggested by hypsodonty. With multiple species, *Chilotherium* was a widespread genus with a long evolutionary history. Because of these characteristics, *Chilotherium* would be an interesting genus to perform further paleodiet studies on. Mesowear studies using samples from same species from different localities and different species of differing tooth crown height would give more insight about the evolution of *Chilotherium*, its diet, and paleoenvironment.

The genus *Gazella* showed some dietary variability between the three localities. The mesowear signal from the Pikermian and Samian samples indicate the gazelles were feeding on browse or at least soft grass, while the Maraghean gazelles were grazers/ graze-dominated mixed feeders. Analysis of the boselaphine antelope *Tragoportax* gave surprising results, which indicate the Pikermian genus was more of a grazer than its Samian counterpart (although the sample from Samos was restricted in size). In the bigger picture this is an anomalous result, although not at all impossible.

Mesowear of the hipparions of Maragheh needs to be studied more precisely, as it could potentially yield information about the evolution of the dietary preferences of both single hipparion species and populations in deep time and the progression of the opening and aridification of the Maraghean habitat. The hipparions were only analyzed on tribe level, but the results indicate that the hipparions of Maragheh lived in a more open habitat and/or had more grass in their diet, while in Pikermi they probably had a more mixed diet in a more closed habitat. This indicates a more humid climate in Pikermi and more arid conditions in Maragheh. The results also make evident the hipparions' dietary flexibility most likely enabled by their hypsodonty. On the basis on the results obtained here and in previous studies it can be argued that although the level of abrasion in the Pikermian hipparions' diet was higher than in many other large herbivores in their habitat, they did not have a modern zebra-like role of extreme grazers in the Pikermian Biome.

Overall, the results of this study show that the taxa of the study were browsers (i.e. *Chilotherium*) to graze-dominated mixed feeders/grazers (i.e. the hipparions and *Samotherium*), but signals of extreme grazing were notably and clearly absent. The results confirm that the Pikermian Biome was one of many niches. Consequently, it is not at all unexpected that the taxonomic and dietary diversity was able to rise to such high levels in the Pikermian Biome, which most probably had a far more diverse flora than modern African savannas. For example, *Chilotherium* was able to choose a non-abrasive diet in spite of its hypsodont adaptations. The results support the view of the Pikermian Biome as a woodland biome with a rich herbaceous layer including abundant C_3 grass, able to support both a large number of browsing and a hitherto unusually wide range of grass-consuming large mammalian herbivores.

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APPENDIX 1

Fossil taxa studied and the mesowear scores of individual specimens.

Locality	Taxon	Specimen ID	Relief	Sharp/ rounded	Notes
Pikermi	*Hipparion gracile*	A4668	h	r	
Pikermi	*Hipparion gracile*	1863.I.96 / WAT86818	l	r	
Pikermi	*Hipparion gracile*	1860.I.97	l	r	
Pikermi	*Hipparion gracile*	1860.XXXII.3 / WAT86822	h	r	
Pikermi	*Hipparion mediterraneum*		h	r	
Pikermi	*Hipparion gracile*	A4689	h	r	
Pikermi	*Hippotherium gracile*	1860.XXXIII. 2.A. / WAT86821	h	r	
Pikermi	*Tragoportax* sp.	1860 XXXII 37	h	r	
Pikermi	*Tragoportax* sp.	1860 XXXII 38	h	r	
Pikermi	*Tragoportax amalthea*	1863.I.66 & 67	h	s	
Pikermi	*Tragoportax amalthea*	1863.I.69	h	r	
Pikermi	*Tragoportax amalthea*	1863.I.68	h	r	
Pikermi	*Tragoportax amalthea (?)*	1854.III.45	h	r	
Pikermi	*Tragoportax amalthea*		h	r	Scored tooth M^1
Pikermi	*Gazella brevicornis*	1863.I.47	h	s	
Pikermi	*Gazella* sp.	1860 XXXII 21	h	s	
Pikermi	*Gazella* sp.	1854 III. 33	h	r	
Samos	*Hipparion schlosseri*	V114	h	r	
Samos	*Hipparion* sp.	V131	h	r	
Samos	*Hipparion* sp.	V357	h	r	
Samos	*Hipparion* sp.	V120	l	r	
Samos	*Cremohipparion matthewi*		l	r	
Samos	*Tragoportax amalthea*	V58	h	r	
Samos	*Tragoportax rugosifrons*	V70	h	r	
Samos	*Tragoportax amalthea*	V88	h	s	
Samos	*Tragoportax* sp.	1911 Samos V91	h	s	
Samos	*Gazella gaudryi*	V267	h	r	

Locality	Taxon	Specimen ID	Relief	Sharp/ rounded	Notes
Samos	*Gazella* sp.	V65	h	s	
Samos	*Gazella* sp.	1911 Samos V81	h	s	
Samos	*Gazella schlosseri*	A4777 / 1913.II.1	h	r	
Maragheh	*Hipparion gracile*	A4853	h	r	
Maragheh	*Hipparion*	KNHM-RLB 8402	l	r	
Maragheh	*Hipparion gracile*	KNHM-RLB-8404	h	r	
Maragheh	*Hipparion*	A4861	h	s	
Maragheh	*Hipparion gracile*	KNHM-RLB8404	h	r	
Maragheh	*Hipparion*	KNHM-RLB 8404 #4	l	s	Scored tooth M^1
Maragheh	*Hipparion*	A4847	l	r	
Maragheh	*Hipparion*		h	r	
Maragheh	*Hipparion gettyi*		l	s	
Maragheh	*Hipparion*		l	s	
Maragheh	*Hipparion gracile*	A4850	h	r	
Maragheh	*Hipparion* sp.	WAT8659	l	r	
Maragheh	*Hipparion* sp.		l	r	
Maragheh	*Hipparion*		l	r	
Maragheh	*Hipparion*		h	r	Scored tooth M^1
Maragheh	*Hipparion*	WAT86504, 505	l	r	
Maragheh	*Hipparion*		l	r	
Maragheh	*Hipparion*		h	r	
Maragheh	*Hipparion*		h	s	
Maragheh	*Hipparion gracile*		h	r	
Maragheh	*Hipparion*		l	r	
Maragheh	*Samotherium neumayri*	A4906	h	r	
Maragheh	*Samotherium neumayri*	A4903	h	s	
Maragheh	*Samotherium neumayri*	A4885	h	r	
Maragheh	*Samotherium neumayri*		h	r	
Maragheh	*Samotherium* sp.		h	r	
Maragheh	*Samotherium neumayri*		h	r	
Maragheh	*Gazella* sp.		h	r	
Maragheh	*Gazella deperdita*	Coll. Polak. 1886	h	r	

Locality	Taxon	Specimen ID	Relief	Sharp/ rounded	Notes
Maragheh	*Gazella deperdita*		h	r	
Maragheh	*Gazella*		h	r	
Maragheh	*Oioceros atropatenes*	Coll. Polak. 1886	h	s	
Maragheh	*Oioceros atropatenes*	Coll. Rodler	h	s	
Maragheh	*Oioceros atropatenes*		l	r	
Maragheh	*Chilotherium persiae?*		h	s	
Maragheh	*Chilotherium*	A4819	h	s	
Maragheh	*Chilotherium* sp.		h	r	
Maragheh	*Chilotherium persiae*		h	r	
Maragheh	*Chilotherium persiae*	A4822	h	r	
Maragheh	*Chilotherium persiae*		h	s	
Maragheh	*Chilotherium persiae*		h	s	
Maragheh	*Chilotherium persiae*	A4792	h	s	
Maragheh	*Chilotherium persiae*		h	s	
Maragheh	*Chilotherium persiae*	A4805	h	r	
Maragheh	*Chilotherium persiae*		h	s	
Maragheh	*Chilotherium persiae*		h	s	

APPENDIX 2

Complete list of taxa used (fossil and modern) and their statistical data used in the clustering.

Taxa	Common name	ID	Class	N	Diet	high	low	sharp	round	blunt	hyp	%round	%low	%sharp	%round	%blunt
Gazella (Pik)		pgZ	fo	3		3	0	2	2	0	m	100.0	0.0	66.7	66.7	0.0
Hipparionini (Pik)		phP	fo	7		5	2	0	7	0	h	71.4	28.6	0.0	100.0	0.0
Tragoportax (Pik)		ptR	fo	7		7	0	1	6	0	b	100.0	0.0	14.3	85.7	0.0
Gazella (Sam)		sgZ	fo	4		4	0	2	2	0	m	100.0	0.0	50.0	50.0	0.0
Hipparionini (Sam)		shP	fo	5		3	2	0	5	0	h	60.0	40.0	0.0	100.0	0.0
Tragoportax (Sam)		stR	fo	4		4	0	2	2	0	h	100.0	0.0	50.0	50.0	0.0
Chilotherium persiae (Mar)		mcP	fo	12		12	0	8	4	0	h	100.0	0.0	66.7	33.3	0.0
Gazella (Mar)		mgZ	fo	4		4	0	0	4	0	m	100.0	0.0	0.0	100.0	0.0
Hipparionini (Mar)		mhP	fo	21		10	11	5	16	0	h	47.6	52.4	23.8	76.2	0.0
Oioceros atropatenes (Mar)		moA	fo	3		2	1	2	1	0	m	66.7	33.3	66.7	33.3	0.0
Samotherium neumayri (Mar)		msN	fo	6		6	0	1	5	0	m	100.0	0.0	16.7	83.3	0.0
Alces alces	Moose	AA	ty	30	B	30	0	30	0	0	b	100.0	0.0	100.0	0.0	0.0
Antilocapra americana	Pronghorn	AM	no	45	B	42	2	32	12	0	h	95.5	4.5	72.7	27.3	0.0
Boocercus euryceros	Bongo	BE	no	32	B	31	0	11	16	0	b	100.0	0.0	40.7	59.3	0.0
Budorcas taxicolor	Takin	BT	no	43	B	39	2	15	23	0	h	95.1	4.9	39.5	60.5	0.0
Camelus dromedarius	Dromedary	CL	no	16	B	16	0	5	11	0	h	100.0	0.0	31.3	68.8	0.0
Dendrohyrax arboreus	Southern tree hyrax	DA	mb	20	B	20	0	11	9	0	b	100.0	0.0	55.0	45.0	0.0
Diceros bicornis	Black rhinoceros	DB	ty	35	B	34	0	32	2	0	m	100.0	0.0	94.1	5.9	0.0
Dendrohyrax dorsalis	Western tree hyrax	DD	mb	29	B	23	5	12	16	0	b	82.1	17.9	42.9	57.1	0.0
Cephalophus dorsalis	Bay duiker	DR	mb	28	B	26	2	4	22	2	b	92.9	7.1	14.3	78.6	7.1
Dicerorhinus sumatrensis	Sumatran rhinoceros	DS	ty	6	B	5	0	4	1	0	b	100.0	0.0	80.0	20.0	0.0
Ammodorcas clarkei	Dibatag	EI	no	7	B	7	0	2	5	0	b	100.0	0.0	28.6	71.4	0.0
Giraffa camelopardalis	Giraffe	GC	ty	69	B	63	4	46	15	0	b	94.0	6.0	75.4	24.6	0.0
Heterohyrax brucei	Yellow-spotted rock hyrax	HB	mb	11	B	4	7	9	2	0	b	36.4	63.6	81.8	18.2	0.0
Hyaemoschus aquaticus	Water chevrotain	HY	mb	19	B	18	0	3	15	0	b	100.0	0.0	16.7	83.3	0.0
Litocranius walleri	Gerenuk	LW	no	72	B	67	3	23	46	0	b	95.7	4.3	33.3	66.7	0.0
Cephalophus natalensis	Red forest duiker	NA	mb	6	B	6	0	0	6	0	b	100.0	0.0	0.0	100.0	0.0
Cephalophus nigrifrons	Black-fronted duiker	NG	mb	44	B	36	8	12	30	2	b	81.8	18.2	27.3	68.2	4.5
Cephalophus niger	Black duiker	NI	mb	32	B	29	3	11	19	1	b	90.6	9.4	35.5	61.3	3.2
Odocoileus hemionus	Mule deer	OH	ty	34	B	33	0	16	17	0	b	100.0	0.0	48.5	51.5	0.0
Okapia johnstoni	Okapi	OJ	ty	9	B	8	0	7	1	0	b	100.0	0.0	87.5	12.5	0.0
Capreolus capreolus	Roe deer	OL	no	68	B	65	3	49	17	2	b	95.6	4.4	72.1	25.0	2.9

Taxa	Common name	ID	Class	N	Diet	high	low	sharp	round	blunt	hyp	%round	%low	%sharp	%round	%blunt
Odocoileus virginianus	White-tailed deer	OV	ty	19	B	18	0	16	2	0	b	100.0	0.0	88.9	11.1	0.0
Rhinoceros sondaicus	Javan rhinoceros	RS	ty	6	B	5	0	5	0	0	b	100.0	0.0	100.0	0.0	0.0
Cephalophus silvicultor	Yellow-backed duiker	SL	mb	46	B	32	8	0	37	2	b	80.0	20.0	0.0	94.9	5.1
Tragelaphus angasi	Nyala	TA	no	24	B	20	0	7	13	0	b	100.0	0.0	35.0	65.0	0.0
Tragelaphus imberbis	Lesser kudu	TI	no	39	B	32	0	18	13	0	b	100.0	0.0	58.1	41.9	0.0
Tragelaphus strepsiceros	Greater kudu	TT	no	7	B	7	0	0	7	0	b	100.0	0.0	0.0	100.0	0.0
Capricornis sumatraensis	Serow	Ca	ty	28	M	27	0	7	14	1	h	100.0	0.0	31.8	63.6	4.5
Cervus canadensis	Wapiti	Cc	ty	20	M	19	0	9	10	0	b	100.0	0.0	47.4	52.6	0.0
Cervus duvauceli	Barashingha	Cd	no	57	M	34	17	6	32	12	m	66.7	33.3	12.0	64.0	24.0
Capra ibex	Ibex	Ci	no	30	M	28	1	14	8	2	h	96.6	3.4	58.3	33.3	8.3
Cervus unicolor	Sambar	Cu	no	21	M	19	2	3	17	1	b	90.5	9.5	14.3	81.0	4.8
Gazella granti	Grant's gazelle	Gg	ty	19	M	15	2	11	7	0	h	88.2	11.8	61.1	38.9	0.0
Gazella thomsoni	Thomson's gazelle	Gt	ty	147	M	129	17	85	59	2	h	88.4	11.6	58.2	40.4	1.4
Lama glama	Llama	Lg	no	32	M	32	0	10	21	1	h	100.0	0.0	31.3	65.6	3.1
Lama vicugna	Vicugna	Lv	no	12	M	12	0	5	7	0	h	100.0	0.0	41.7	58.3	0.0
Antidorcas marsupialis	Springbuck	Ma	no	26	M	25	1	19	7	0	m	96.2	3.8	73.1	26.9	0.0
Aepyceros melampus	Impala	Me	ty	17	M	17	0	6	11	0	m	100.0	0.0	35.3	64.7	0.0
Ovis canadensis	Bighorn sheep	Oc	no	39	M	26	4	17	14	0	h	86.7	13.3	54.8	45.2	0.0
Ovibos moschatus	Muskox	Om	ty	53	M	42	10	28	24	0	h	80.8	19.2	53.8	46.2	0.0
Ourebia ourebi	Oribi	Oo	no	128	M	123	5	28	99	1	h	96.1	3.9	21.9	77.3	0.8
Procavia capensis	Rock hyrax	Pc	mb	25	M	11	13	12	12	0	b	45.8	54.2	50.0	50.0	0.0
Rhinoceros unicornis	Indian rhinoceros	Ru	no	6	M	5	0	4	1	0	b	100.0	0.0	80.0	20.0	0.0
Saiga tatarica	Saiga	St	no	6	M	2	3	3	2	0	h	40.0	60.0	60.0	40.0	0.0
Taurotragus oryx	Eland	To	ty	15	M	14	0	7	7	0	m	100.0	0.0	50.0	50.0	0.0
Boselaphus tragocamelus	Nilgai	Tr	no	15	M	13	2	0	15	0	m	86.7	13.3	0.0	100.0	0.0
Tragelaphus scriptus	Bushbuck	Ts	ty	50	M	47	0	23	24	0	b	100.0	0.0	48.9	51.1	0.0
Alcelaphus buselaphus	hartebeest	ab	ty	77	G	43	33	13	44	19	h	56.6	43.4	17.1	57.9	25.0
Alcelaphus lichtensteinii	Lichtenstein's hartebeest	al	no	17	G	14	3	1	14	2	h	82.4	17.6	5.9	82.4	11.8
Axis porcinus	Hog deer	ap	no	24	G	21	3	2	22	0	b	87.5	12.5	8.3	91.7	0.0
Axis axis	Chital	ax	no	58	G	38	10	3	29	11	b	79.2	20.8	7.0	67.4	25.6
Bison bison	American bison	bb	ty	18	G	0	17	0	4	11	h	0.0	100.0	0.0	26.7	73.3
Ceratotherium simum	White rhinoceros	cs	ty	26	G	0	24	6	11	8	h	0.0	100.0	24.0	44.0	32.0

Taxa	Common name	ID	Class	N	Diet	High	Low	Sharp	Round	Blunt	Hyp	%round	%low	%sharp	%round	%blunt
Connochaetes taurinus	Wildebeest	ct	ty	61	G	33	27	11	26	15	h	55.0	45.0	21.2	50.0	28.8
Damaliscus lunatus	Topi	dl	ty	6	G	1	4	1	3	1	h	20.0	80.0	20.0	60.0	20.0
Equus burchelli	Burchell's zebra	eb	ty	124	G	0	121	41	40	41	h	0.0	100.0	33.6	32.8	33.6
Equus grevyi	Grevy's zebra	eg	ty	30	G	0	29	12	10	7	h	0.0	100.0	41.4	34.5	24.1
Hippotragus equinus	Roan antelope	he	ty	27	G	22	4	1	25	0	h	84.6	15.4	3.8	96.2	0.0
Hippotragus niger	Sable antelope	hn	ty	20	G	17	3	0	17	3	h	85.0	15.0	0.0	85.0	15.0
Kobus ellipsiprymnus	Common waterbuck	ke	ty	27	G	22	1	0	22	0	h	95.7	4.3	0.0	100.0	0.0
Redunca fulvorufula	Mountain reedbuck	rf	no	8	G	6	1	0	7	0	h	85.7	14.3	0.0	100.0	0.0
Redunca redunca	Bohor reedbuck	rr	ty	77	G	70	7	5	70	2	h	90.9	9.1	6.5	90.9	2.6
Syncerus caffer	African buffalo	sc	no	33	G	31	0	0	29	2	m	100.0	0.0	0.0	93.5	6.5
Tetracerus quadricornis	Chousingha	tq	no	21	G	19	2	6	15	0	m	90.5	9.5	28.6	71.4	0.0

Explanations

Class (not taxonomic): fo = fossil, ty = typical representative of its dietary class, no = no particular class, mb = mabra (see methods).

Diet: B = browser, M = mixed feeder, G = grazer.

Hyp (tooth crown height): b = brachydont, m = mesodont, h = hypsodont.

Notes

To heed doubtful cases Fortelius and Solounias (2000) used a 'conservative' and a 'radical' dietary classification to classify modern species.

The radical classification treated ambiguous species conservatively classified mixed feeders as browsers or grazers.

The present data uses the radical classification of species.

The IDs of greater kudu and serow were Ts and Cs, respectively, in Fortelius and Solounias (2000).