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DIETARY TRAITS OF LATE MIOCENE HIPPARIONS FROM MARAGHEH REVEALED THROUGH DENTAL WEAR

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Abstract. Maragheh has yielded one of the richest mammal faunas of the late Miocene in the so-called Greco-Iranian Biogeographical Province in western Asia. This study investigates the paleoecology of fossil perissodactyls (equids) from the late Miocene of Maragheh, northwestern Iran. We used dental micro- and mesowear techniques to draw robust inferences about fossil equid dietary habits. Mesowear and microwear analyses were applied to the upper second molars of an hipparionine horse, aff. *Hippotherium brachypus*. For this purpose, we investigated samples from three fossiliferous localities: Ruhanioon, Azim Dareh, and Sizdaheaban. Six fossil specimens were analyzed for enamel meso- and microwear and results were compared to an extensive database of extant ungulates. Results indicated overlap of the Maragheh hipparions with the dietary signal of extant grazers and grass-dominated mixed feeders. This is consistent with the supposed vegetational habitat proposed by previous mesowear studies. The aff. *Hippotherium brachypus* hipparions from Maragheh were consuming a mixture of plants but with a preference for grasses. These results are consistent with paleoenvironmental reconstructions of the late Miocene dominated by open grassland areas among more wooded settings.

Introduction

The Late Miocene was dominated by the evolution of the Pikermian Chronofauna, also known as the Old-World large mammal Savanna Biome (Eronen et al. 2009; Kaya et al. 2018). This paleobiome had extremely diverse community structures of open-habitat adapted mammals including brachydonts (low-crowned teeth), mesodonts and hypsodonts (high-crowned teeth) taxa (Solounias et al. 2010). The great diversity of mammalian species of herbivorous groups like Equidae, Rhinocerotidae, Giraffidae, Bovidae and Proboscideans are typical for this paleobiome (Solounias et al. 1999). The evolution of this biome was provincial with most animals living in the mid-latitudes of Eurasia (Solounias et al. 1999; Eronen et al. 2009; Bernor et al. 2021).

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The late Miocene vertebrate fossil localities of Maragheh are situated in the eastern Azarbaijan province, in northwest Iran. They are renowned for preserving some of the richest fossil localities of the late Miocene in the so-called "Greco-Iranian" Subparatethyan Province (Bernor 1983, 1986), Biogeographical Province (Bonis et al. 1979) of the Pikermian fauna in western Asia (Bernor 1986; Eronen et al. 2009; Mirzaie Ataabadi et al. 2013; Kaya et al. 2018). They show high similarity with the classic Pikermian Chronofaunas of Samos and Pikermi in Greece (Bernor 1986; Bernor et al. 1996; Mirzaie Ataabadi et al. 2013). The fossiliferous sediments in Maragheh localities are volcaniclastic and fossils are preserved in fluvial and paleosol deposits (Sakai et al. 2016). The Maragheh Formation consists of several layers of andesitic volcanic sands and silts, tuff, and pumice. The maximum thickness of this Formation reaches 300 m, but the fossil-bearing sequence is confined to the lower 150 m (Mirzaie Ataabadi et al. 2013). Based on the single crystal argon ages of Swisher (1996) and chronologic correlations of the deposits by Bernor et al. (1996) and Atabaadi et al. (2016), the main Maragheh fossil fauna ranges from 9.0 to 7.4 Ma, corresponding to the mammal units MN11 and possibly early MN12 (Sawada et al. 2016; Mirzaie Ataabadi et al. 2016b).

Campbell et al. (1980) discussed the environment of the Maragheh Formation based on the faunal assemblage and suggested more closed habitat than previously thought, i.e., a savanna or woodland with wooded grassland nearby. Strömberg et al. (2007) indicated the presence of grasslands and C_4 grass based on phytoliths indicating a high temperature relative to other Pikermian localities. Fortelius et al. (2014) also concluded that the late Miocene Maragheh was dry, open habitat based on hypsodonty (tooth crown height) as an indicator of precipitations. The Maragheh assemblage corresponds to a time when the Eurasian hipparion were reaching their maximum diversity and species richness and adapted to open country woodlands with abundant grasses (Bernor et al. 2021).

Reconstructing the dietary adaptations of fossil ungulates provides important information on species adaptations and habitat conditions of mammalian paleocommunities. Therefore, paleodiet studies provide valuable data on vegetational diversity and possible niche differentiation amongst the late Miocene Maragheh mammals. This paper will focus on the Equidae, a large family of perissodactyls, including horses and related extinct and extant taxa. Hipparionine horses are a group of extinct Equidae broadly defined as horses with hypsodont cheek teeth that have isolated protocones and tridactyl feet (Bernor et al. 2021). The hypsodont teeth with complex enamel plication and much cement suggests the consumption of abrasive food (MacFadden 2005). Nevertheless, equids show a remarkably wide dietary range from browsing to grazing and even mixed-feeding (Mihlbachler et al. 2011; Semprebon et al. 2019; Bernor et al. 2021; Saarinen et al. 2021; Cirilli et al. 2022).

Hipparionine horses are suitable for the application of paleodietary reconstructions as they are usually abundant in late Miocene mammal fossil faunas, their species diversity is high and their geographic and chronologic distribution is long and widespread. They are morphologically diverse and have been adapted to a broad range of habitats and feeding strategies (Bernor et al. 1989; Bernor et al. 2021).

In this paper, we used tooth microwear and mesowear techniques as powerful tools for gaining insight into local and global environmental trends (Merceron et al. 2004, 2007; Rivals et al. 2010; Semprebon et al. 2004). Over the past decade, integrated studies of microwear and mesowear have been undertaken for the inference of paleodiets (e.g., Rivals & Semprebon 2006; Rivals et al. 2007). The combination of the two techniques provides dietary information on two different timescales, mesowear averages the diet over a few months (Fortelius & Solounias 2000), while microwear reveals the diet in the last days of an animal's life (Grine 1986). The results obtained from the two methods are usually in agreement (Semprebon & Rivals 2007, 2010) but discrepancies often reflect seasonal changes in diet (Sánchez-Hernández et al. 2016).

There are a few paleodietary studies on the Maragheh fauna. Bernor et al. (2014), based on the comparison of the mesowear of Maragheh ungulates to other fossil localities, interpreted the Maragheh paleoenvironment and vegetation as a mosaic habitat, resembling a woodland. A later analysis of carbon and oxygen isotopes (Biasatti et al. 2015) on tooth enamel samples from three species of Maragheh hipparionines discovered that during the late Miocene there is a shift in carbon isotope values from C_4 to C_3 ecosystems. Yamada et al.

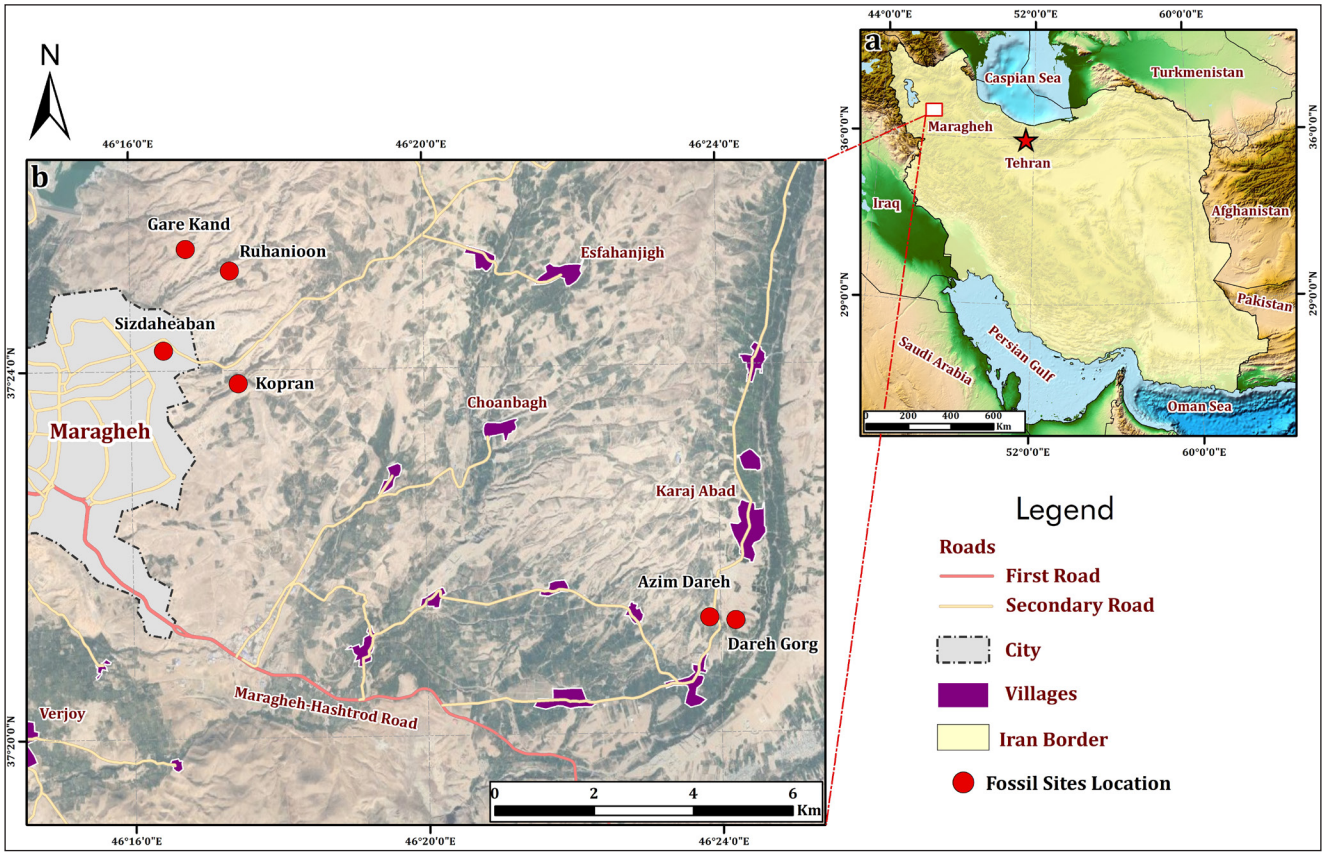

Fig. 1 - Geographic location of fossil localities in the Maragheh Basin, N.W. Iran.

(2016) provide mesowear data for sympatric bovid and equid species from a single quarry in a Middle Maragheh interval that supports the mosaic vegetation proposed by previous studies. In this study, we used tooth microwear and mesowear analyses on a small sample of hipparionine horses belonging to aff. *Hippotherium brachypus*.

The objectives are (1) to reconstruct the dietary traits and to evaluate the dietary flexibility in the hipparionine horse aff. *Hippotherium brachypus* and (2) to infer the habitat where these ungulates were living in the Maragheh area to improve the paleoenvironmental knowledge of this famous Formation.

Materials and methods

The materials were obtained from recent excavations led in 2013, 2015 and 2021 by Iran's Department of Environment (DOE) and the Iranian National Museum of Natural History (MMTT). The studied materials are stored in the collections of the Palaeontology and Paleodiversity Research Center of Iran (located in Maragheh). The fossil localities can be compared to the well-known MMTT-UCR (University of California, Riverside) sites (Bernor 1986; Mirzaie Ataabadi et al. 2013) as following (Fig. 1):

- Sizdaheaban locality belongs to the lower Maragheh interval and is correlated well with fossil sites in Kopran (MMTT 41, 43, 44, 48).

- Azim Dareh site belongs to middle Maragheh interval and is located in the main fossiliferous area of Maragheh Formation in Mordagh. It is close to the stratigraphic levels of MMTT 1B, C, 2, 4, 6.

- Ruhanioon locality also belongs to middle Maragheh interval and stratigraphically is comparable to MMTT 8, 23, 28, 36, 42 (Parizad et al. 2019, 2020).

In this study, six specimens of hipparions from Maragheh were sampled for mesowear and microwear analyses (Tab. 1; Fig. 2). All specimens of hipparions available in the collections of the Paleontology and Paleodiversity Research Center of Iran were sampled.

The skulls (PRCI-M 1010, 1011, 1012, 1013, 1015) belong to large individuals. They are well pre-

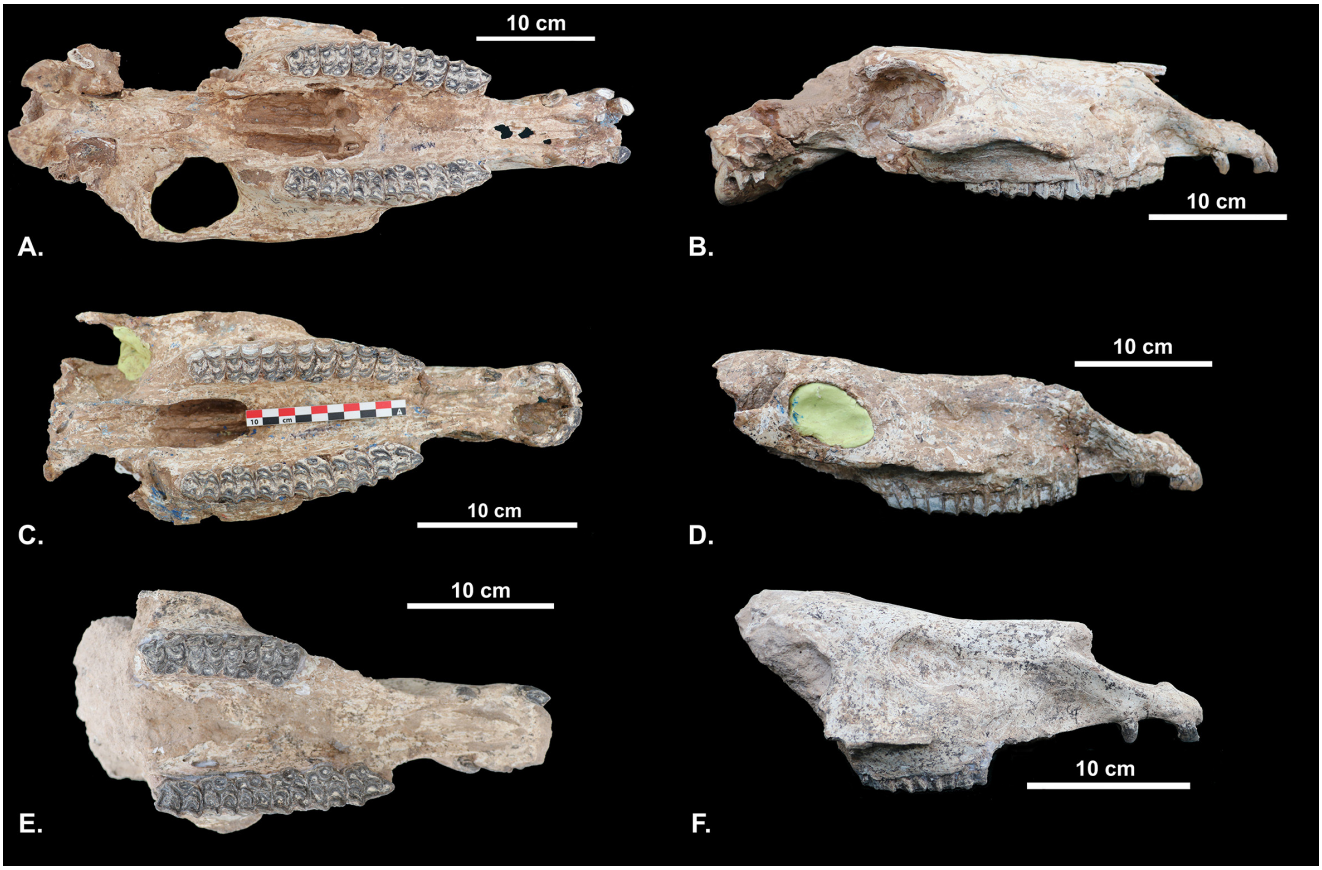

Fig. 2 - Hipparion skulls form Maragheh in ventral view (A, C, E) and lateral view (B, D, F): Ruhanioon locality, specimen PRCI-M 1012 (A and B); Ruhanioon locality, specimen PRCI-M 1013 (C and D); Sizdaheaban locality, specimen PRCI-M 1015 (E and F).

Specimen number	Locality
PRCI-M 1010	Azim Dareh
PRCI-M 1011	Azim Dareh
PRCI-M 1012	Ruhanioon
PRCI-M 1013	Ruhanioon
PRCI-M 1014	Sizdaheaban
PRCI-M 1015	Sizdaheaban

Tab. 1 - List of the hipparion specimens analyzed in this study.

served, lacking only the occipital part, except for PRCI-M 1010-1011 which are partially preserved. The muzzle is moderate and slightly robust. The nasal cavity is moderately deep. The nasal notch is retracted above the mesial border of P2. The orbit is well-preserved, round-ovoid shape, and its mesial margin is behind M3. The preorbital fossa (POF) is subtriangular to egg-shaped, relatively large, shallow deep and antero-posteriorly oriented. It is situated far (38-46 mm) from the orbit with no posterior pocketing and is well defined. The anterior rim of the POF appears above the medial part of P4. The posterior border of the POF is above the medial part of M2. The facial crest is strong and far from the alveoli and the ventral border of the POF. The anterior border of the facial crest is situated above the medial part of P4. The palate is elongated and relatively wide. The choanae are elliptical, deep and their mesial margin is situated at the mesial half of M2.

The PRCI-M 1014 skull belongs to a medium sized animal. It is smaller than other specimens and has relatively narrow short muzzle. The narial opening is positioned above the P2. The orbit is round and its anterior border is situated close to the posterior border of M3. The preorbital fossa (POF) is far (49 mm) from the orbit, sub-triangular in shape, relatively large and medially deep. It is antero-posteriorly oriented, well-defined posteriorly but not pocketed. The anterior rim of the POF is well ex-

pressed and appears above the medial part of P3. The posterior border of the POF is located above the posterior part of M3. The infraorbital foramen encroaching upon anteroventral border of the preorbital fossa. The facial crest is very strong and located far from the alveoli and the ventral border of the POF. The anterior border of the facial crest is situated above the medial part of P4. The palate is elongated and wide. The choanae are wide and their anterior border is situated at the contact between M2 and M3.

Although the facial morphology of the above-mentioned specimens resemble *H. prostylum* Gervais, 1849, here we follow Bernor et al. (2016) in assigning the Maragheh *H. prostylum sensu lato* samples to aff. *H. brachypus*. This is mainly due to the *Hippotherium* like metapodials accompanying these fossils which are not elongate-slender as they should be (Bernor et al. 2016; Watabe & Nakaya 1991). The studied specimens, similar to other material from Maragheh referred previously to *H. prostylum*, are characterized with a long preorbital bar, a lacrimal placed well posterior to the preorbital fossa. Preorbital fossa is reduced compared to other members of the *Hippotherium* clade. It is moderate to short in length, faintly egg- to C-shaped, antero-posteriorly oriented, shallow to very shallow dorsoventrally. Slight to no posterior pocketing is present. Medial depth is moderate to slight, the anterior rim is faint to absent and the peripheral rim being moderately to weakly expressed.

Tooth mesowear analysis

Mesowear analysis is a method of evaluating the diet based on the relative amounts of attritive and abrasive dental wear (Fortelius & Solounias 2000). It consists in categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices. Mesowear is scored macroscopically from the buccal side of the upper M2. A browsing diet, with low levels of abrasion, maintains sharpened apices. In contrast, a grazing diet with high levels of abrasion results in more rounded and blunted cusp apices. As cusp sharpness is sensitive to ontogenetic age (Rivals et al. 2007), only the adult individuals were analyzed. The method used here is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp to completely blunt with no relief (Mihlbachler et al. 2011). The average value of the mesowear data corresponds to the 'mesowear score' or MWS (Mihlbachler et al. 2011). To reduce inter-observer error, dental mesowear analysis was conducted by a single experienced researcher (FR).

Tooth microwear analysis

The microwear analysis was performed on the enamel surfaces of the occlusal surfaces which were examined using a stereomicroscope on high-resolution epoxy casts of teeth. We followed the protocol developed by Solounias and Semprebon (2002) and Semprebon et al (2004). First, the occlusal surface of each specimen was cleaned using acetone followed by 96% ethanol. Second, the full occlusal surface was molded using high-resolution silicone (Heraeus Provil novo Light Regular set), and casts were created using clear epoxy resin. Before the quantification of the microwear features, all casts were carefully screened under the stereomicroscope. Those with poorly preserved enamel or taphonomic defects were removed from the analysis, following the recommendation made by King et al (1999), El-Zaatari (2010) and Uzunidis et al (2021). The transparent casts were observed under oblique lighting with a Zeiss Stemi 2000C stereomicroscope at 35× magnification. Microwear features were quantified on the paracone of the upper M2 in a square area of 0.16 mm^2 using an ocular reticule. These features were classified as pits or scratches following the definition by Solounias and Semprebon (2002) and Semprebon et al. (2004). Pits are circular or sub-circular and have approximately similar widths and lengths, while scratches are elongated microwear features with straight and parallel sides. Gouges are depressions that are crater-shaped, with irregular and asymmetrical margins. Scratches and pits were quantified in four areas on the enamel surface, two areas on the paracone on the left molar and two on the right M2, all on the same facet and then averaged to obtain a single value per specimen. The analysis was conducted by a single experienced researcher (FR).

Comparison with data on extant ungulates

The meso- and microwear results were compared with a database constructed from extant ungulate taxa with known diets (Fortelius & Solounias 2000; Solounias & Semprebon 2002; Rivals et al. 2010, 2013, 2014) belonging to the following dietary categories: browsers, grazers and mixed feeders.

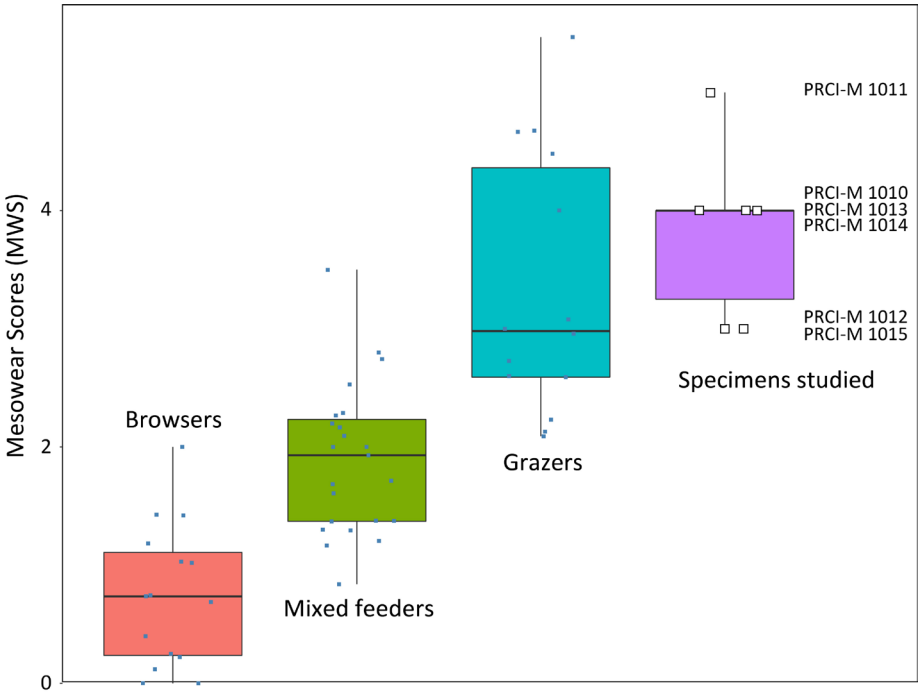

Fig. 3 - Mesowear scores for the sample of hipparions from Maragheh compared to extant ungulates with known diets i.e. leaf browsers, mixed feeders and grazers; data from Fortelius and Solounias (2000) and Rivals et al. (2010, 2013, 2014). The dots refer to the mean MWS and the error bars to the standard error of the mean.

Results

Tooth mesowear analysis

The mesowear analysis was performed on the six specimens, all having well preserved cusps. Cusp shapes are rounded and relief is either high or low. Mesowear scores (MWS) for the Maragheh hipparions range between 3 and 5 (Tab. 2; Fig. 3). These high mesowear scores indicate a diet with high abrasion. In comparison to modern ungulates with known diets, the mesowear values for the Maragheh hipparions overlaps with that of the extant grazers and the higher values of the extant grass-dominated mixed feeders (Fig. 3).

Tooth microwear analysis

Taphonomic alterations, like chemical and mechanical erosion, were frequent on the occlusal surfaces, but in all six specimens well-preserved areas were identified and quantitatively analyzed. The sample analyzed for tooth microwear is composed of six specimens with well-preserved enamel surfaces, the same specimens that were analyzed for tooth mesowear. The microwear pattern of the hipparionines from Maragheh is characterized by a relatively high numbers of scratches, from 20 to 24.5 scratches per counting area (Tab. 2; Fig. 4). On all samples, cross scratches were absent (i.e., all scratches had a bucco-lingual orientation as usually found in equids). The scratch width scores (SWS) were found to be equal to 1 in all specimens, indicating a mixture, in equal proportion, of fine and coarse scratches. The numbers of pits show intermediate values, from 16.5 to 19 pits per counting area and all specimens had large pits. Gouges were observed on five specimens out of six (gouges were absent for PRCI-M 1012). This microwear pattern suggests relatively high abrasion for all specimens.

In comparison to the dietary categories established in extant ungulates, the six specimens show some differences in microwear patterns (Fig. 4). Two specimens fall within the dietary space corresponding to the extant grazers while the others four fall in between the confidence ellipses of the extant browsers and grazers, i.e., they would be classified

Specimen #	MWS	Npit	Nscr	LP	G	SWS	XS
PRCI-M 1010	4	19	21	1	1	1	0
PRCI-M 1011	5	17.75	24	1	1	1	0
PRCI-M 1012	3	18.25	20	1	0	1	0
PRCI-M 1013	4	16.5	24.5	1	1	1	0
PRCI-M 1014	4	17	21.25	1	1	1	0
PRCI-M 1015	3	17	22	1	1	1	0

Tab. 2 - Results of the dental mesowear and microwear results for the hipparions from Maragheh.
Abbreviations: MWS = Mesowear score; Npit = Mean number of pits; Nscr = Mean number of scratches; LP = Presence (1) / absence (0) of large pits; G = Presence (1) / absence (0) of gouges; SWS = Scratch width score; XS = Presence (1) / absence (0) of cross scratches.

Fig. 4 - Bivariate plot of the numbers of pits and scratches for the hipparions from Maragheh. Plain ellipses correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (LB) and grazers (G) based on the reference database from Solounias and Semprebon (2002).

as mixed feeders (Fig. 4). The presence of large pits and gouges (Tab. 2) suggests that the hipparions also ingested a significant amount of dust or grit together with the vegetation (Semprebon & Rivals 2007; Semprebon et al. 2019). At the time of death, the hipparions from Maragheh were consuming a mixture of plants but with a preference for grasses.

Discussion

In this study, the paleodietary behavior of Maragheh hipparions was characterized by using mesowear and microwear analysis. Unlike mesowear, crown height, or gross craniodental morphology, microwear is thought to turn over rapidly making it a useful proxy for discerning seasonal, local and individual variations in diet. Microwear is also valuable for providing more specific dietary information about food items actually consumed than gross morphological assessments (Semprebon et al. 2017). Our mesowear and microwear results both show that the Maragheh hipparionine horses were significantly engaged in grass-dominated mixed feeding and grazing. In mesowear, comparison to modern ungulates with known diets shows that values overlap with extant grazers. Tooth microwear analysis compared to the dietary categories established in extant ungulates also demonstrates that the six specimens fall in or close to the dietary space corresponding to the extant grazers. These results differ somewhat in details but show similar patterns as in the previous study of Bernor et al. (2014), which showed a more diverse spectra among Maragheh hipparion diet, especially browsing and mixed feeding, but agree in the results from Yamada et al. (2016) that identified a grazing diet. On a longer chronologic range than in our study, Bernor et al. (2014) were the first to study the paleodiet of Maragheh herbivores through mesowear analysis. They showed that Maragheh hipparions span a spectrum of browse-dominated (*Cremohipparion moldavicum* Gromova, 1952), to more mixed feeding taxa (*Hipparion prostylum* and *Hipparion campbelli* Bernor, 1985), and to species exhibiting a preference to more grass (*Hipparion gettyi* Bernor, 1985, *Hipparion* sp. and *Cremohipparion matthewi* Kormos, 1911). They compared the mesowear of Maragheh ungulates to other fossil localities and concluded that a mosaic habitat with woodland and some open savanna environments existed in Maragheh. The Maragheh hipparions show a spectrum of dietary abrasiveness that fit well with the mosaic environment. The Maragheh bovid species also displayed a range of dietary abrasiveness, whereas the giraffids and chalicotheres had fairly attritional mesowear signals. They suggest that Maragheh ungulates adopted dietary browsing and mixed feeding habits. Yamada et

al (2016) also provided mesowear data for sympatric bovid and equid species from a single site in the Middle Maragheh succession. Their results represented dietary differentiations in Maragheh, consistent with the concept of a mosaic vegetational habitat as proposed by Bernor et al (2014). They show that the hipparionine horses were grazers, whereas, the bovids relied on a broader range of plant foods and were mixed feeders. The study of postcranial anatomy of hipparions, like aff. *H. brachypus*, show that cursorial, big, and robust metapodials were suited for living in more closed habitats. Other species often had long, thin metapodials suited for living in more open areas (Bernor et al. 2016).

Considering other diertary proxies, analyses of carbon and oxygen isotopes are scarce in Maragheh. Biasatti et al. (2015) based on samples from Maragheh hipparionines (*H. gettyi*, *H. campbelli*, and *C. matthewi*), concluded that there was a shift in carbon isotope values from C_4 to C_3 ecosystems before 8.2 Ma. According to Ballato et al (2010), the Iranian Plateau was rising throughout the late Miocene. Oxygen isotope analysis carried out in northern Iran support the presence of a humid climate suitable for woodland at this time, also supported by a decrease in aridity during 9.6-7.6 Ma.

Our mesowear and microwear results confirm the dietary plasticity of the Maragheh hipparionine horses that were able to shift from grass-dominated mixed feeding to grazing.

Our results show a difference in paleodiet reconstructions between mesowear and microwear. Nevertheless, this difference is not unusual in paleodietary studies. Semprebon and Rivals (2007, 2010) and Rivals and Semprebon (2011) using microwear and mesowear methods have demonstrated that the same taxon may have very different diets in different geographical locations. On the other hand, this difference might indicate a different paleoenvironment of fossil taxa. For example, it is evident that floodplain environments today in Pakistan are dominated by C_4 grasses, and C_3 vegetation is only present in non-floodplain (Waseem et al. 2021). So, animals living/feeding in different paleoenvironmental settings demonstrate different diets.

Another reason to explain discrepancies in paleodiet reconstructions of hipparions might come from their body size differences. In large-sized genera like *Hippotherium* diet ranges from browsing to mixed-feeding. Small species (body mass 50-110 kg) such as *Cremohipparion* were grazers while medium and large sized taxa (body mass ca. 150 and 200 kg) were mixed-feeders (Bernor et al. 2021). The same trend was identified for Pleistocene horses with large-sized species tending toward browse-dominated diets while small and medium-sized species having more abrasive diets (Saarinen et al. 2016, 2021).

The general consensus on hipparionine diet is that they were usually not extreme grazers like the *Equus* lineage, however, they were certainly adapted to using a wide mixed range of food, often with a preference for grass (Solounias et al. 2010). Other studies on the paleodiet of Pikermian biome hipparions show similar results compared to Maragheh. Solounias et al. (2013) sampled hipparions from Pikermi and Samos in their mesowear study. Four species of *Hippotherium* from Samos had diets that were slightly browse-dominated to grass dominated. But, *Cremohipparion proboscideum* Studer (1911) from Samos clustered clearly with browsing to browse-dominated mixed feeders (Fortelius & Solounias 2000). Later studies found the same species to be a grass-dominated mixed feeder (Solounias et al. 2013).

Kostopoulos and Bernor (2011) showed that the main Maragheh fossil horizons and Pikermi, are dominated by small-sized bovid taxa, while in Samos, the majority of bovids are medium-sized. The differences in the bovid body size spectra, in their view, indicate that environmental conditions were similar in Maragheh and Pikermi (more wooded) compared to Samos. Maragheh hipparions paleoecology shows that this 1.5 m.y. series of localities was more similar to Pikermi than to Samos (Mirzaie Ataabadi et al. 2013). Pikermi, however, based on the predominance of browsing and mixed feeding types of mesowear signatures, most likely had a mosaic habitat with woodland and some open savanna. No pure grassland or closed habitat existed (Solounias et al. 2010). Maragheh also had a mosaic habitat with woodland and some open savanna. The overall paleodiet studies (Yamada et al. 2016) show that this environment is suitable for many mixed feeding taxa and a few grazers, such as the hipparions of this study. Studies of the paleodiet from other Pikermian sites, such as Pikermi and Samos, show similar results (Solounias et al. 2010, 2013). Dental microwear study of the Turolian Molayan locality of Afghanistan, clearly indicates an open, arid environment, composed mainly of C_3 grasses and evergreen bushes (Merceron et al. 2004). Microwear analysis

of bovids in southwestern Bulgaria showed mixed feeding habits and leaf browsing diets. Thus, open wooded landscapes existed (Merceron et al. 2004). Diet reconstruction through mesowear analysis confirms the presence of a developed grassy cover in the Maragheh area, which constituted the main food source for hipparionines.

Conclusions

Previous studies, based on the predominance of browsing and mixed feeding taxa, depicted the paleoenvironmental context of the late Miocene of Maragheh as mosaic habitat including woodland and some open grasslands. Studies, including ours, show that hipparions from Maragheh were either grass-dominated mixed feeders or grazers. This indicates the presence of some open grass-dominated areas in the environment. In general, data suggests that the hipparion species of the late Miocene from Maragheh ate both browse and graze depending on the resources available in their habitat. The differences in the paleodiet of these mammals could be also related to their body size. It seems that smaller hipparion forms were predominately grass feeders and larger ones were mixed feeders. Paleoenvironmental differences may also explain the differences in the paleodiets, as certain food materials such as grass may be restricted to parts of the special environments and not be the most abundant in the environment.

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Declarations

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Conflicts of interest/Competing interests: None

Availability of data and material (data transparency): All materials are deposited in public institutions.

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