

Maragheh ungulate mesowear: interpreting paleodiet and paleoecology from a diverse fauna with restricted sample sizes

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This study explores the extent to which researchers might be able to interpret a fauna's paleoecology using mesowear analysis on ungulate maxillary molars when there are diverse taxa represented by few specimens. We compared our mesowear results on Maragheh ungulates with those of extant ungulates and with known mesowear score distributions of the two classical Greek Pikermian faunas of Samos and Pikermi, and with the late Miocene of China. The Maragheh equid and bovid species display a range of dietary abrasiveness, whereas the giraffids and chalicotheres have fairly abrasive mesowear signals. Despite small sample sizes for some taxa, our results are consistent with long-held taxon-based interpretations of Maragheh paleoecology: a Pikermian woodland habitat. In addition, our results are consistent with climatic changes of the Paratethyan realm at the end of the Miocene.

Introduction

The late Miocene Maragheh lagerstätte is located in the eastern Azerbaijan Province, NW Iran. It is a late Miocene, open country fauna of Pikermian age comparing closely with the other two “classical” Turolian age faunas of Pikermi and Samos, Greece (Bernor 1986, Bernor *et al.* 1996, Ataabadi *et al.* 2013). A Russian explorer, Khanikoff, has been credited with first finding the Maragheh site in 1840, which was explored in the second half of the 19th century by European

paleontologists, the French in the early 20th century and German, Dutch, Japanese and American teams in the 1960s and 1970s. Most recently, a joint Iranian–Finnish team collected fossils at Maragheh in the early part of the 21st century (see Ataabadi *et al.* 2013 for the most recent update). The Maragheh fossil beds are extensive, extend in range from 9.0–7.4 Ma (Bernor *et al.* 1996, Swisher 1996), and have both abundant and diverse fossil mammals that are represented in several European, Asian and American natural history museums.

In this contribution, we wish to develop a simple theme: to what extent can researchers interpret a fauna's paleoecology using the mesowear technique initially developed by Fortelius and Solounias (2000) as well as the newer method by Mihlbachler *et al.* (2011) when there are diverse taxa, most of which are represented by few specimens (see Table 1)? We will undertake this study using primarily the Howard University collection of Maragheh ungulate mammals collected by the UCLA–National Museum of Natural History, Iran (MMTT) expedition in 1974–1976 (Bernor 1986, Kostopoulos & Bernor 2011). We augment this collection with the hipparionine horse specimens that were collected by de Mequenem in 1905–1908 and that are housed at the Muséum National d'Histoire Naturelle, Paris (MNHN; de Mequenem 1925). We will compare our results with others specifically done on Pikermi, Samos (Solounias *et al.*

2010) and Pikermian faunas of China (*sensu* Eronen *et al.* 2009, Solounias *et al.* 2013) and use this Maragheh data set to pose hypotheses of ecological similarity between Maragheh, Samos, Pikermi and Chinese Baodean age faunas (*sensu* Qiu *et al.* 2013).

Material and methods

This study is predominantly based on equid material from the MNHN, Paris, and the University of Utrecht Paleontological collections (GIUP) as well as equid, chalicotherid, giraffid, and bovid specimens housed at Howard University, Washington DC. Other Maragheh material, which is common in a number of European museums and the American Museum of Natural History, New York, is available to significantly augment and expand our preliminary study

Table 1. Mesowear scores of all Maragheh ungulate specimens.

Specimen ID	Taxon	Tooth/cusp scored	Relief (H/L)	Cusp shape (S/R/B)	Mihlbachler score
MNHNMar3428_RLB8003	<i>Cremohipparium moldavicum</i>	lt. M2, p	H	S	1
MNHNMar_RLB7914	<i>Cremohipparium moldavicum</i>	rt. M1, p	H	S	1
MNHNMar62_RLB7915	<i>Cremohipparium moldavicum</i>	lt. M2, p	H	R	1.5
MNHNMar466_RLB8002	<i>Cremohipparium moldavicum</i>	lt. M2, m	H	R	1
MNHNMar1476	<i>Cremohipparium moldavicum</i>	lt. M2, p	H	R	1
MNHNMar469	<i>Cremohipparium moldavicum</i>	rt. M2, p	H	R	1.5
BMNHM3924	<i>Cremohipparium aff. moldavicum</i>	rt. M2, m	H	S	1
GIUP100-1958	<i>Cremohipparium matthewi</i>	rt. M2, p	L	R	3
MNHNMar1799	<i>Hipparion</i> sp.	lt. M2, p	L	R	3
KNHM-RLB8401	<i>Hipparion gettyi</i>	rt. M2, p	H	R	2.5
MNHNMar1474	<i>Hipparion prostylum</i>	lt. M2, p	H	R	1.5
MNHNMar1475	<i>Hipparion prostylum</i>	lt. M2, m	H	R	2.5
MNHMMar71	<i>Hipparion prostylum</i>	rt. M2, p	H	R	1.5
MMTT13/1342	<i>Hipparion campbelli</i>	rt. M2, p	H	R	2
MMTT13/1291	<i>Hipparion campbelli</i>	lt. M2, p	H	R	2
MMTT7/602	<i>Helladotherium duvernoyi</i>	rt. M2, p	H	R	3
MMTT7/2159	<i>Palaeoreas lindermayri</i>	lt. M2, p	L	R	3.5
MMTT7/2164	<i>Honanotherium</i> sp.	rt. M2, p	H	R	1.5
MMTT13/1346	<i>Tragoportex amalthea</i>	lt. M2, m	H	R	1.5
MMTT13/MCW80	<i>Gazella anycerus</i>	lt. M2, p	H	S	0
MMTT37/2300	<i>Ancylotherium pentelici</i>	lt. M1, p	H	R	2
MMTT7/2294	<i>Protragelaphus skouzesi</i>	lt. M2, p	H	R	1.5
MMTT13/1206	<i>Oioceros atropatenes</i>	rt. M3, p	H	R	1.5
MMTT13/1205	<i>Oioceros atropatenes</i>	lt. M2, p	H	S	0.5
MMTT13/1357	<i>Oioceros atropatenes</i>	rt. M2, m	H	S	1
MMTT13/1361	<i>Oioceros atropatenes</i>	lt. M3, p	H	S	0
MMTT1A/339	?Ovibovine indet	lt. M3, p	H	R	2

herein. We envision a future study of Maragheh ungulate paleoecology that includes more taxa and specimens and incorporates carbon and oxygen isotopic studies and use of soil phytolith analysis for a multi-proxy evaluation of Maragheh paleoecology. This paper is intended to pose an initial, testable hypothesis of Maragheh ungulate paleoecology as it compares to other Eurasian “Pikermian” faunas and extant African mammalian faunas following Eronen *et al.* (2009) and Solounias *et al.* (2010, 2013).

Mesowear scoring, on one tooth per individual, was undertaken using high-resolution photographs. In accordance with recent mesowear studies, we prefer to score the paracone over the metacone unless the former is damaged (e.g. Mihlbachler *et al.* 2011). Our results are based on two different approaches to mesowear analysis.

Fortelius and Solounias (2000) assessed paleodiet scoring based on the morphological profile of the paracone (or, if sharper, the metacone; cf. Kaiser & Fortelius 2003, Kaiser & Solounias 2003) of maxillary cheek teeth. Scored characters used in their mesowear approach are the buccal apical cusp shape (sharp, round and blunt) as well as the occlusal relief (high or low) in adult individuals showing normal occlusion. Kaiser and Solounias (2003) and later Wolf *et al.* (2012) and Melcher *et al.* (2013) extended this method on P4s to M3s in hypsodont horses, as has been adopted by us in subsequent studies. For most species in our Maragheh sample, however, the number of specimens is too low to provide reliable mesowear results according to the method of Fortelius and Solounias (2000). That technique relies on percentages of species in different shape categories and requires on the order of ten or more specimens per species (Table 1).

Mihlbachler *et al.* (2011) recently proposed a new mesowear method that does not consider the shape-defining variables of the Fortelius and Solounias (2000) method. Instead, the Mihlbachler *et al.* (2011) method utilizes a template-based standard with seven qualitative stage series (0–6) that is a wear gradient from high relief and sharp (0) to low relief and blunt (6) shape in order to obtain a single score that incorporates both cusp shape and relief. These shape-scores are represented on the template or “ruler” by molds of representative hypsodont

equid paracone cusps arrayed according to their shape and relief gradient. One of the seven scores is assigned to each analyzed paracone if the shape of this paracone is equally as sharp as or sharper/higher than the reference cusp of that score on the template. Wolf *et al.* (2012) expanded the Mihlbachler *et al.* (2011) method by recognizing intermediate scores in 0.5 increments: 0.5, 1.5, 2.5, 3.5, 4.5, and 5.5. Mean mesowear scores were calculated for both the original and modified method and the results were compared to those reported by Mihlbachler *et al.* (2011). Two of the current authors (Bernor and Semprebon) scored these teeth and final scores were drawn by consensus view by Semprebon. A complete list of specimens studied and scored using both the Fortelius and Solounias (2000) and Mihlbachler *et al.* (2011) methods is given in Table 1. Table 2 provides the mean Mihlbachler *et al.* (2011) scores of the Maragheh species studied herein.

Results

A cluster analysis (Fig. 1), performed using Systat 6.0, compares the Mihlbachler *et al.* (2011) average mesowear scores obtained per taxon for species in the Maragheh assemblage (Table 2) with the mesowear scores of extant ungulates with known diets. Tables 1 and 2 include scoring for 7 hipparium taxa (*Cremohipparium moldavicum*, *Cremohipparium* aff. *moldavicum*, *Cremohipparium matthewi*, *Hipparium* sp., *Hipparium gettyi*, *Hipparium prostylum* and *Hipparium campbelli*), *Helladotherium duvernoyi*, *Palaeoreas lindermayri*, *Honanotherium* sp., *Tragoportax amathaea*, *Gazella anycerus*, *Ancylotherium pentelici*, *Protragelaphus skouzesi*, *Oioceros atropatenes* and ?Ovibovine *indet*. These Maragheh taxa have previously been described by Bernor (1986) and Bernor *et al.* (1996).

The cluster analysis (Fig. 1) revealed that the Maragheh ungulate taxa analyzed herein range from being at the extreme browser range (e.g., *Gazella anycerus*, *Oioceros atropatenes*, *Cremohipparium* aff. *moldavicum* and *Cremohipparium* *moldavicum*) which cluster between extant *Alces alces* and *Odocoileus virginianus* to intermediate feeders (e.g., *Tragoportax*

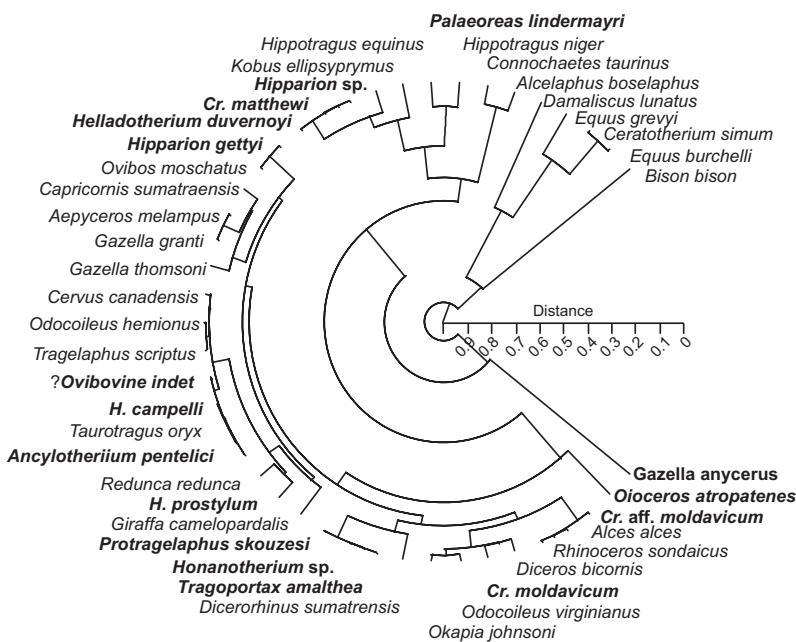


Fig. 1. Hierarchical cluster analysis of Maragheh ungulates compared with extant taxa.

amalthea, Honanotherium sp., Protragelaphus skouzesi, Hipparion prostylum, Ancylotherium pentelici, Hipparion campbelli and ?Ovibovine indet.) which cluster between extant *Dicerorhinus sumatrensis* and *Tragelaphus scriptus*, to more grazing spectra taxa including *Hipparion gettyi*, *Helladotherium duvernoyi*, *Cremohipparion matthewi*, *Hipparion* sp. and *Palaeoreas lindermayri* that cluster between extant *Ovibos*

moschatus and *Hippotragus niger*. No Maragheh taxon scores in the more dedicated grazing range represented by the *Hippotragus niger* to *Bison bison* part of the range.

The seven fossil equid species yielded interesting results (Fig. 2). The Maragheh hipparions span a spectrum of dietary abrasiveness from those showing attritional (browse-dominated) wear features typical of browsers, such as that

Table 2. Mean mesowear percentages and mean Mihlbachler scores of Maragheh ungulate species.

Taxon	Sharp	Round	Blunt	High relief	Low relief	Mean Mihlbachler score
<i>Cremohipparion moldavicum</i>	33.33	66.67	0	100	0	1.2
<i>Cremohipparion</i> aff. <i>moldavicum</i>	100	0	0	100	0	1.0
<i>Cremohipparion matthewi</i>	0	100	0	0	100	3.0
<i>Hipparion</i> sp.	0	100	0	0	100	3.0
<i>Hipparion gettyi</i>	0	100	0	100	0	2.5
<i>Hipparion prostylum</i>	0	100	0	100	0	1.8
<i>Hipparion campbelli</i>	0	100	0	100	0	2.0
<i>Helladotherium duvernoyi</i>	0	100	0	100	0	3.0
<i>Palaeoreas lindermayri</i>	0	100	0	0	100	3.5
<i>Honanotherium</i> sp.	0	100	0	100	0	1.5
<i>Tragopontax amalthea</i>	0	100	0	100	0	1.5
<i>Gazella anycerus</i>	100	0	0	100	0	0
<i>Ancylatherium pentelici</i>	0	100	0	100	0	2
<i>Protragelaphus skouzesi</i>	0	100	0	100	0	1.5
<i>Oioceros atropatenes</i>	75	25	0	100	0	0.8
?Ovibovine indet.	0	100	0	100	0	2.0

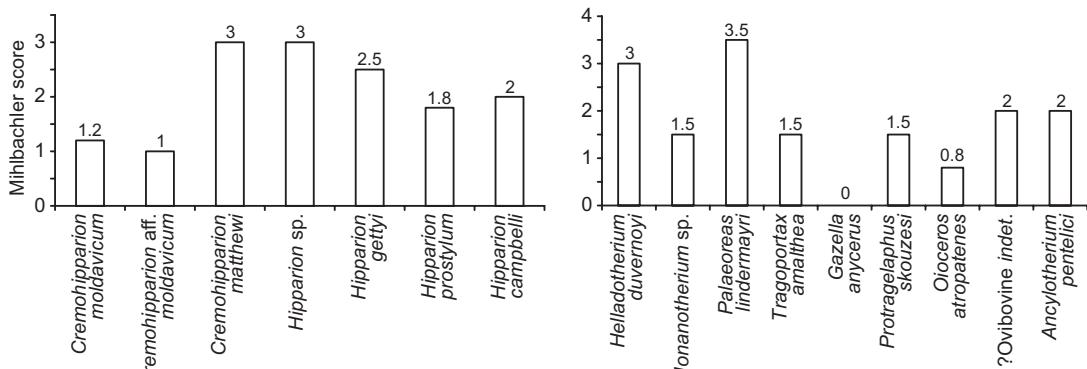


Fig. 2. The Mihlbachler *et al.* (2011) scores of Maragheh hipparions and other ungulates.

seen in *Cremohipparrison* aff. *moldavicum* and *Cremohipparrison* *moldavicum*, (scoring 1.0 and 1.2, respectively), to more intermediate abrasion taxa whose wear is typical of more balanced mixed feeding taxa such as seen in *Hipparrison prostylum* and *Hipparrison campbelli* (scoring 1.8 and 2.0, respectively) to species exhibiting a preference towards increased grass in the intermediate feeding part of the spectrum including *Hipparrison gettyi*, *Hipparrison* sp. and *Cremohipparrison matthewi* (2.5, 3.0 and 3.0, respectively). Larger samples sizes are needed to determine the actual dietary variability within taxon and between taxa and to better understand if there is actual dietary ecological separation that can be demonstrated for these taxa.

Amongst the remaining ungulates (Fig. 2), the fossil giraffids (like the extant *Giraffa*) have mesowear signatures unlike the attritional wear of extant ungulate browsers and more typical of mixed feeders (i.e., *Honanotherium* sp.) and non-extreme grazers (i.e., *Helladotherium duvernoyi*). The chalicotheres, *Ancylotherium pentelici*, has a mesowear signature that shows intermediate levels of abrasion more typical of mixed feeders than pure browsers. Like the fossil equids, the Maragheh bovids display a variety of mesowear patterns from those showing attritional wear features typical of browsers (i.e., *Gazella anycerus* and *Oioceros atropatenes*) to ones suggesting more intermediate abrasion levels (i.e., *Tragopontax amalthea*, *Protragelaphus skouzesi*, and ?Ovibovine indet.), and finally more abrasive wear typical of non-extreme grazers (i.e., *Palaeoreas lindermayri*).

Thus Maragheh possesses a mixture of probable browsing species along with some individuals (15%) with mesowear scores in the 3 to < 4 range (i.e., typical of extant mixed feeders and non-extreme grazers).

Discussion

Solounias *et al.* (2010) published a comprehensive longitudinal study of Samos and Pikermi Greece ungulate paleoecology utilizing the mesowear and light microscope microwear methods. Solounias *et al.* (2013) made comparisons between the two classical Greek Pikermian faunas and the late Miocene Chinese Baodean age faunas. Bernor (1983, 1984) discussed the biogeographic provinciality and diachronic intercontinental biogeographic extension of the Sub-Paratethyan Pikermian Biome across Eurasia and Africa. Eronen *et al.* (2009) tested Bernor's earlier hypotheses using the NOW database (see <http://www.helsinki.fi/science/now/>) and outlined in detail the origin and progressive, diachronic dispersion of this biome between 12 and 7 Ma, its climax and ultimate community collapse (extinction) between 7 and 5.3 Ma.

Solounias *et al.* (2013) used tooth mesowear analysis to compare the paleodietary patterns of the classic late Miocene faunas of Pikermi and Samos, Greece to those of China and Recent African savanna and Recent African forest ungulates. We compared the relative Mihlbachler mesowear score distributions of Maragheh with those of fossil assemblages from Pikermi,

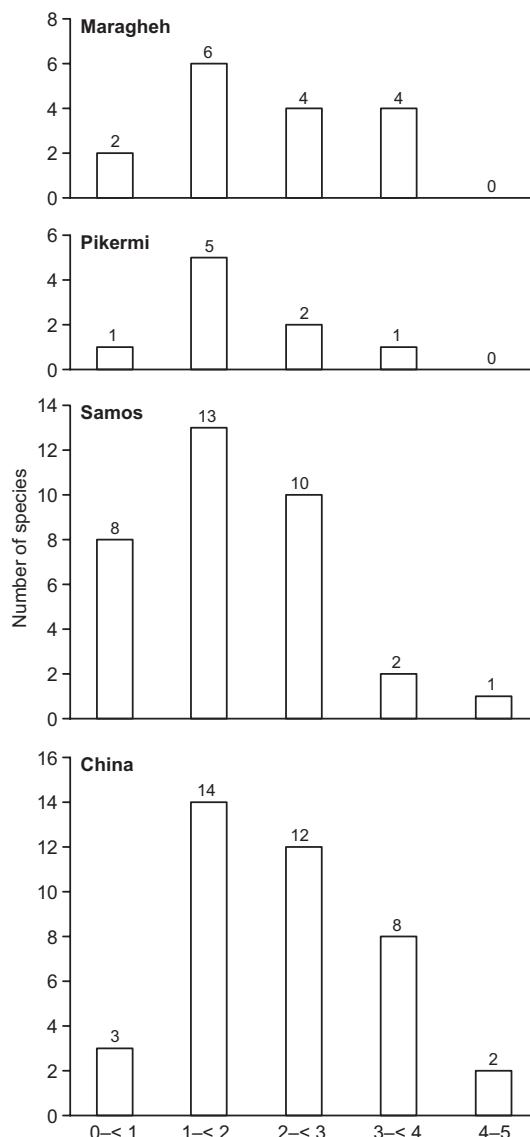


Fig. 3. The distribution of mean species mesowear scores (Mihlbachler *et al.* 2011) for Maragheh, Pikermi, Samos, and the late Miocene of China. Species are classed into five bins over the range 0–5 in mesowear score. No statistically significant differences in mesowear distribution were found among these four faunas (see text).

Samos, and China (adopted from Solounias *et al.* 2013; see Fig. 3). All four distributions appear similar, and a nonparametric test of the assemblage mean mesowear scores across the species means within each assemblage shows no significant statistical difference (approximative Kruskal-Wallis test: $\chi^2 = 0.7906$, $p = 0.837$; per-

formed using the *coin* package in R).

We recognize that our results must be viewed as preliminary based on the small sample sizes of the taxa available to us to study at this time. Nevertheless, this sample allows us to pose a hypothesis of Maragheh ungulate paleoecology. The results of this analysis are consistent with those found by Solounias *et. al.* (2010) for Pikermi and suggest a mosaic habitat with woodland and some open savanna based on the predominance of browsing and mixed feeding types of mesowear signatures present rather than a purely grassland or purely closed habitat. Our results are also consistent with climatic changes of the Central and Eastern Paratethys realm during the end of the Miocene from a warm and wet subtropical climate to a drier and cooler temperate climate (Dorofeyev 1966, Axelrod 1975, Fortelius *et al.* 2003, Strömberg *et al.* 2007, Eronen *et al.* 2009, Eronen *et al.* 2010a, 2010b). The Greek and Maragheh faunas fall during the cooling trend of this climatic change. Therefore a warm temperate woodland faunal reconstruction is consistent with what is currently known about the climate changes of this region in the late Miocene into the Pliocene and corroborates the observation that these faunas were all part of one large biome.

Conclusions

This study was intended to use our available sample of Maragheh ungulates to test the hypothesis that ungulate mesowear can offer insights into paleodiet and paleoecology when a diverse fauna with restricted sample sizes is used. We became interested in this hypothesis because of the common occurrence of fossil collections with these characteristics. It is important to establish specimen-based and species-resolved dietary variability over individual taxonomic ranges. We were able to obtain preliminary, but plausible, dietary information on individual Maragheh taxa from mesowear scores. Furthermore, we found that, indeed, the distribution of mesowear scores across the Maragheh species was similar to, and statistically indistinguishable from, the mesowear score distributions of more intensely sampled Greek and Chinese Pikermian faunas.

Previous work found an elevated percentage of hypsodont taxa in the Chinese faunas, relative to those from Greece, which may indicate a habitat difference (Solounias *et al.* 2010). Our analysis here suggests that if this is true, then assemblage-level mesowear distributions alone may lack the power to distinguish finer habitat differences that are better represented by additional kinds of data. However, the apparent faunal difference may also not indicate a contemporaneous habitat difference, but rather may reflect the longer chronologic range of the Chinese “Pikermian”-like faunas. The Chinese faunas are from the Bahean and Baodean and range from 11.1 to 5.3 Ma (Qiu *et al.* 2013) whereas the Maragheh, Pikermi and Samos faunas range from 9.0–6.7 Ma (Bernor *et al.* 1996).

This preliminary study suggests that Maragheh ungulates are typical of Greek Pikermian faunas (at least) in that they were principally adapted to browsing and mixed feeding trophic habits. As such, our study corroborates studies by Eronen *et al.* (2009) and Solounias *et al.* (2010, 2013).

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