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Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)

Paleoenvironments inferred from phytoliths and Dental Microwear Texture Analyses of meso-herbivores☆

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ABSTRACT

The present study aims to assess the environmental conditions that prevailed during the late Miocene in the vicinity of Nikiti 2, Chalkidiki Peninsula (northern Greece). Here, a Dental Microwear Texture Analysis of three species of equids (20 specimens) and six species of bovids (76 specimens) is combined with analysis of the phytolith content of sediments from Nikiti 2. The latter analysis provided few remains of organic silica minerals; some were identified as short cells and are diagnostic of grasses. This is in accordance with previous studies of late Miocene sites in Anatolia which attested to the wide spread of grasslands in the Eastern Mediterranean at that time. Dental Microwear Texture Analysis completes the picture by exploring the diet of herbivores. This analysis concludes that *Hipparion sithonis* from Nikiti 2 had a diet composed of 80% of grass, making it the most committed to grazing component of the Nikiti 2 fauna. The two other equids from Nikiti 2, *H. philippus* and *H. macedonicum*, show affinities with variable grazers and mixed feeders. Among the Nikiti 2 bovids, *Nisidorcas planicornis* appears to have been a variable grazer and was the bovid most engaged in grazing. At the other end of the spectrum, ?*Miotragocerus* was least dependent on grasses. The two species of gazelles, *Gazella pilgrimi* and *G.* cf. *capricornis*, are best classified as mixed feeders. *Tragoportax amalthea* and *Palaeoreas lindermayeri* both plot between variable grazers and mixed feeders. The absence of browsers and the abundance of grass-eating species within the guild of meso-herbivores exclude the hypothesis of a forest during the late Miocene at Nikiti 2. Instead, it supports the existence of a savanna with grasses in a wealthy herbaceous layer together with accessible dicots (bushes, shrubs and forbs) exploited by medium-sized mammals. The absence of obligate grazers within the meso-herbivore guild suggests severe and repeated depletions of grassy vegetation (likely during seasonal droughts) forcing herbivores to widen their feeding habits to include browse. Such seasonality in food resources is consistent with paleoclimatic evidence especially with respect to seasonal changes in temperature.

1. Introduction

The late Miocene landscapes of the Eastern Mediterranean region have often been depicted as savannas. The contemporaneity of the exploration of Africa by Western scientists during the 19th century on the one hand, and excavations of fossil faunas in Europe on the other, clearly influenced interpretations of past environments from extinct faunas (Solounias et al., 1999). The existence of a late Miocene Eastern Mediterranean savanna has been challenged by Solounias et al. (1999) who instead interpreted fossil data as evidence of wooded landscapes in the Balkans and Anatolia at this time. However, the term savanna does not refer only to particular African mosaic landscapes and their peculiar associated fauna of large herbivores, but also to a wider range of habitats in South Asian and even Mediterranean biomes wherein trees occur in a continuous dense herbaceous layer (Smit et al., 2009; Ratnam et al., 2011; Lehmann et al., 2014).

In the last decades, alternative approaches based on faunal structure (Bernor, 1986; Bonis et al., 1992; Fortelius et al., 1996; Costeur and Legendre, 2008) or on sets of anatomical features considered as ecological proxies (Fortelius et al., 2003; Scott and Maga, 2005; Eronen et al., 2009) concluded that past landscapes in Eastern Mediterranean were mostly composed of open to mosaic

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habitats. None of these studies supported the presence of dense forested habitats (but see Solounias et al., 1999). Additionally, analysis of siliceous phytoliths found *in situ* in the sediments where fossil assemblages were unearthed strongly supports the existence of a C_3 grass-dominated savanna in Anatolia and surrounding areas during the late Miocene (Strömberg et al., 2007). Palynological assemblages indicate the presence of warm-climate and temperate-climate trees in conjunction with Mediterranean xeric species known today along the northern Mediterranean ridges (*Quercus ilex*, *Olea* sp., *Juniper*) as well as the presence of monocotyledonous plants and asteraceous dicots in the herbaceous layer (Jiménez-Moreno et al., 2007; Ivanov et al., 2011). Moreover, sites preserving macrofloristic assemblages strongly advocates for the presence of woody landscapes in Greece during the late Miocene (Velitzelos et al., 2014). These plants may have cohabited – supporting mixed habitats – or may have alternated through space – supporting contrasted open and forested habitats –, or even may have replaced each other through geological time, reflecting variations of climate conditions.

Alternative proxies to assess environmental conditions also include stable isotope and dental wear analyses. Carbon stable isotope analyses on tooth enamel of herbivores that evolved in the Balkans during the late Miocene depict a pure C_3 vegetal realm (Quade et al., 1994; Merceron et al., 2006, 2013, Rey et al., 2013). However, the C_3 vegetation was not only composed of dicots but also included grasses. Indeed, dental wear analyses on large herbivores have shown most of bovids and equids were mixed feeders with more or less affinities either with browsers or grazers (Merceron et al., 2005a, 2006, 2007, 2010; Koufos et al., 2006, 2009; Solounias et al., 2010).

The present study aims to depict the ecological niche partitioning among herbivores and to assess the tree cover in the vicinity of Nikiti 2 during the late Miocene (early Turolian mammalian age, Mammal Neogene Zone MN11). Thus, the focus here is both on reconstructing habitats in terms of vegetation as well an exploration of niche dynamics among meso-herbivores. We combine Dental Microwear Texture Analysis (DMTA) to reconstruct feeding habits of meso-herbivores (equids and bovids) with an analysis of the phytolith assemblage recovered in sediment samples. Assuming that phytoliths become integrated in soils after plants die and decay, we expect that their remains found in the Nikiti 2 sediments reflect the local paleovegetation. DMTA was performed on equids and bovids not only because they are the most abundant taxa within the Nikiti 2 mammal assemblage, but also because, as primary consumers, they reflect primary production in the local habitats where they have evolved in. Thus, we infer that the presence of browsing ungulates and perhaps mixed feeders is associated with a wooded habitat. Similarly, an open habitat dominated by grassy vegetation is indicated by numerous grazing ungulates. A savanna combining a dense herbaceous layer (inclusive of dicots and monocots) with tree/bush/shrub layers should include mixed feeding species arranged along a browsing to grazing spectrum potentially in conjunction with some species fully committed to either grazing or browsing.

One of the main challenges when reconstructing the dietary habits of extinct species is not simply distinguishing browsers from grazers, but discriminating which mixed feeders depends more on grazing or on browsing. To overcome this challenge, we propose a new continuous variable reflecting the grazing–browsing continuum, the Wear Textural Index (WTI), derived from the two most useful variables in DMTA (anisotropy and complexity). Anisotropy is positively correlated with grazing habits whereas complexity is positively correlated with mastication of browse and hard items, such as seeds, twigs, and bark (Scott, 2012; Calandra and Merceron, 2016).

2. Material and methods

2.1. Material

2.1.1. Phytolith analysis

Four sediment samples were analyzed. The sample "NKT-Ourano" originates from the exact location of the Nikiti 1 site where the fossil remains of the hominoid *Ouranopithecus macedoniensis* were found (Koufos, 2016a, b). The sample "NIK-field" comes from the excavation site of the Nikiti 2 locality (Koufos, 2016a), whereas the sample "NIK-tusk" was collected in the uppermost level where an altered proboscidean tusk was recovered (Konidaris and Koufos, 2016). These three samples were gathered *in situ* by one of us (G.M., with G.D. Koufos in June 2014). A fourth sample, "NIK-lab" is composed of sediments associated with fossil mammals from Nikiti 2 stored at the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Greece.

2.1.2. DMTA

Seventy-six individuals of bovids representing six taxa and twenty specimens of equids belonging to three different species, all from Nikiti 2, compose the sample for DMTA ($n = 76$; Table 1; Appendix A). The DMTA sample is dominated by *N. planicornis* and *P. lindermayeri* (31.5% and 23.7%, respectively). The remainder of

Table 1
Descriptive statistics of dental microwear textural parameters of extinct species and modern bovids clustered in diet categories along the grazing–browsing continuum (see text for details).

		Asfc			epLsar ($\times 10^{-3}$)			WTI		
	n	**m**	SD	SEM	**m**	SD	SEM	**m**	SD	SEM
Extinct taxa										
N. planicornis	24	**2.10**	0.82	0.17	**5.23**	1.74	0.36	**0.141**	0.986	0.201
P. lindermayeri	18	**2.11**	0.78	0.18	**5.06**	1.42	0.33	**0.053**	0.959	0.226
T. amalthea	16	**1.95**	0.74	0.19	**4.81**	1.93	0.48	**0.060**	1.380	0.345
? Miotragocerus	5	**3.34**	1.71	0.76	**5.22**	2.29	1.02	**−0.846**	2.230	0.997
G. cf. *capricornis*	5	**2.04**	0.74	0.33	**4.08**	1.55	0.69	**−0.378**	1.176	0.526
G. pilgrimi	8	**2.07**	0.37	0.13	**4.65**	0.63	0.22	**−0.118**	0.382	0.135
H. macedonicum	9	**2.36**	0.74	0.25	**5.35**	2.20	0.73	**−0.003**	1.137	0.379
H. philippus	4	**2.05**	0.54	0.27	**5.36**	1.76	0.88	**0.248**	0.876	0.438
H. sithonis	7	**1.72**	0.56	0.21	**6.52**	0.83	0.31	**1.079**	0.658	0.249
Modern bovids										
Obligate grazers	46	**0.97**	0.26	0.04	**6.12**	0.89	0.13	**1.483**	0.449	0.066
Variable grazers	48	**1.58**	0.47	0.07	**5.13**	1.40	0.20	**0.510**	0.793	0.114
Browser–grazer Intermediates	41	**2.13**	0.91	0.14	**3.78**	1.53	0.24	**−0.597**	1.198	0.187
Generalists	47	**2.22**	0.69	0.10	**4.19**	1.08	0.16	**−0.462**	0.676	0.099
Browsers	47	**3.58**	0.98	0.14	**2.11**	0.59	0.09	**-2.578**	0.895	0.131

n: number of individuals per sample; m: mean; SD: standard deviation; SEM: standard error of the mean; WTI: Wear Textural Index; Asfc: complexity; epLsar: anisotropy.