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Inferences on the paleodiet of *Dihoplus pikermiensis* (Perissodactyla, Rhinocerotidae) from the Late Miocene of North Macedonia through the application of dental mesowear analysis

Georgia Svorligkou[1] and Biljana Garevska[2]

1: Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, National and Kapodistrian University of Athens;
geosvorligk@geol.uoa.gr

2: National Institution Natural History Museum of North Macedonia – Skopje, Blvd. Ilinden 86;
b.garevska@musmacscinat.mk

Abstract

Three fossil rhinocerotids have been reported from the Late Miocene of North Macedonia: *Dihoplus pikermiensis,* Miodiceros neumayri and Chilotherium sp.. The material, which was collected by Professor Risto Garevski, comes from the North Macedonian sites of Kiro Kuchuk, Prsten and Umin Dol and belongs to the paleontology collection of the National Institution Natural History Museum of North Macedonia in Skopje. The present work marks the first report on the paleodiet of fossil rhinos from North Macedonia. We worked on the *D. pikermiensis* material from Kiro Kuchuk and Prsten using the mesowear ruler method. Our results indicate browsing habits for the species at both sites, in accordance with the literature.

Key words: dental mesowear, rhinoceros, paleodiet, feeding

Introduction

A notable number of fossiliferous localities have been reported from the Late Miocene of the Republic of North Macedonia. The first mention of fossils in the country comes from the Late Miocene of the Veles area, formerly known as Titov Veles (Schlosser 1921, Laskarev 1921). The most important fossiliferous localities of North Macedonia are Nerezi, Delchevo, Veles, Negotino, Kavadartsi, Valandovo and Dolni Disan, and the described faunas include mostly typical middle Turolian elements of the Pikermian biome, such as hipparionine horses, hyaenas, the primate *Mesopithecus pentelicus*, the tandem-horned rhinocerotids *Dihoplus pikermiensis* and *Miodiceros neumayri* and one species of the hornless rhinocerotid genus *Chilotherium* (Spassov et al. 2018). However, it is notable that the two tandem-horned rhinocerotids are not sympatric in Northern Macedonia, contrary to their very common and well-documented association in the Balkano-Iranian Zoogeographic Province (Giaourtsakis et al. 2006). Indeed, in North Macedonia, *M. neumayri* has only been reported from the site of Umin Dol, whereas the site of Marievo marks the westernmost limit of the genus *Chilotherium* in Europe (Geraads and Spassov 2009). The richest fossiliferous site of the country is Karaslari, featuring 22 mammal species of early Middle Turolian age (Spassov et al 2018).

In this work, we studied the dental mesowear of *Dihopolus pikermiensis* from North Macedonia, providing paleoecological data about the region for the first time. We proposed dietary inferences for this species at two localities, Kiro Kuchuk and Prsten, and discussed the implications at a regional scale. We also compared with other rhinocerotid specimens from various localities of the Balkans and the Eastern Mediterranean.

Fig. 1: Map of the fossiliferous sites of North Macedonia, with Kiro Kuchuk and Prsten in red font.

Abbreviations:

MMNH: Macedonian Museum of Natural History, Skopje; M: upper molar; P: upper premolar; d: dexter; s: sinister.

Material and Methods

In the present report, we examined the paleodiet of the rhinocerotid D*ihoplus pikermiensis* from the sites Kiro Kuchuk and Prsten. The material, which belongs to the Paleontology collection of the Natural History Museum of North Macedonia in Skopje, is relatively well preserved. The fossils were collected by professor Risto Garevski in the 1970s and consist of six skulls and one mandible, all attributed to *Dihoplus pikermiensis*.

With more than 15 mammal species reported, Kiro Kuchuk is the second richest fossiliferous site of North Macedonia, following Karaslari. The age of the site has been biostratigraphically determined to be early Middle Turolian. On the other hand, the site of Prsten is somewhat older; it has yielded a scarce number of fossil mammals, with its age determined as early Turolian (Spassov et al. 2018).

The material from Kiro Kuchuk and Prsten is generally in good preservation, with most cranial and mandibular features of the species easily noticeable. However, the dental mesowear analysis we opted to apply under the scope of this paper poses the restriction of utilizing only upper adult dentitions. For this reason, we did not include the numerous lower teeth available in the collection in the study, since they could not be used for mesowear analysis. Furthermore, we opted to focus this work exclusively on *D. pikermiensis*, as the only available *M. neumayri* skull, from the locality of Umin Dol, is too old and inadequately preserved in terms of dentition to allow for a mesowear study.

The material from the Macedonian Museum of Natural History has been thoroughly examined and extensively described by Spassov et al. 2018. The main cranial characteristics that allowed for the attribution of the studied material to *D. pikermiensis* were the following: the elongated nasals, the deep nasal notch, the horizontal ventral orbital surface, the position of the orbita above the anterior half of M2, the placement of the infra-orbital foramen above the posterior half of P3, the short cranial basis, the post-tympanic process overlapping the postglenoid process, infra-orbital foramen situated anteriorly (above the posterior root of P3); as far as the upper dentition is concerned, the main diagnostic characteristics of the species are the presence of a marked paracone fold, a slight constriction of both the pro-

tocone and the hypocone, a weak metacone fold on the P4, and the absence of a cingulum (Geraads 1988, Giaourtsakis et al. 2006, Geraads and Spassov 2009, Spassov et al. 2018).

We opted to study the paleodiet of *D. pikermiensis* through a dental mesowear analysis. Dental mesowear analysis is based on the classification of the tooth cusps into shape and relief categories, visible with the naked eye or with a hand lens. Dental wear is treated as two variables: occlusal relief and cusp shape. The upper teeth of browsing herbivores are characterized by high occlusal relief and sharp cusps, which is interpreted as attrition-dominated wear, whereas the dentitions of grazing herbivores tend to have low occlusal relief and blunt cusps, indicating an abrasion-dominated wear (Fortelius & Solounias 2000). This method can differentiate between grazing, mixed-feeding and browsing mammals, while also providing information about the dietary habits of the animal's last months, or even years (Ackermanns et al. 2020).

Under the scope of the present work, we opted for the application of the standardized method coined by Mihlbachler et al. (2011), known as mesowear 'ruler'. The cusp shape and occlusal relief are treated as a single parameter (cusp) and separated to seven categories, ranging from 0 (sharp cusp shape, high occlusal relief) to 6 (totally blunt cusp shape, absence of occlusal relief).

We opted for the mesowear ruler because, as a method originally crafted for the dentitions of another perissodactyl family (equids), it is better suited for rhinocerotids compared to methods originally designed based on artiodactyl ruminants (Hullot et al. 2021). Following the guidelines by Mihlbachler et al. 2018 and Hullot et al. 2021, we opted for the sampling of the second upper molar, right or left. Additionally, we followed Hullot et al. 2021, and only scored the paracone instead of choosing between the sharpest cusp (paracone or metacone) of the upper molar, as these two cusps may vary greatly in rhinos (Taylor et al. 2013). Finally, in order to reduce inter-observer error, the dental mesowear analysis was conducted by a single researcher (GS).

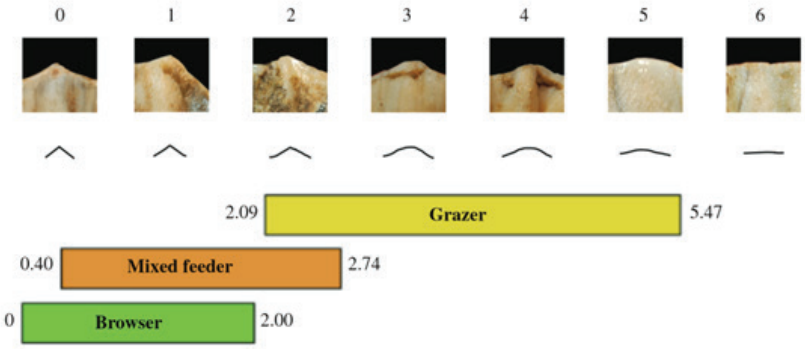

Fig. 2: Mesowear score using the mesowear ruler method by Jimenez-Manchon et al. 2022, illustrated with rhinoceros' (*Coelodonta antiquitatis*) dental cusps and interpretative drawings. By Hullot et al. 2024.

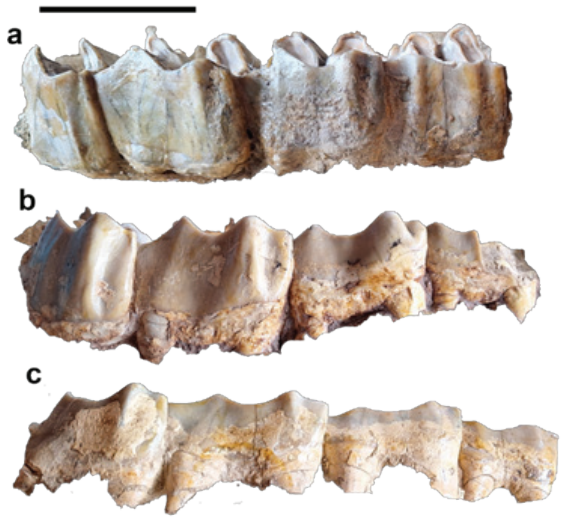

Fig. 3: Dentitions of *D. pikermiensis* from North Macedonia. a: MMNH-28439,upper left dentition (M3-P4) of D. pikermiensis from Kiro Kuchuk; b: MMNH-28444, upper left dentition (M3-P4) of D. pikermiensis from Prsten. c: MMNH-28442, upper right dentition (M3-P4) of D. pikermiensis from Kiro Kuchuk. Scale 10 cm.

Results

The second molars of the examined *D. pikermiensis* skulls are characterized by high occlusal relief and a relatively sharp cusp shape. The mesowear scores were compared to the mesowear score categories provided by Jimenez-Manchon et al. 2022, reporting low scores browsers for browsers (0-2), high scores for grazers (2.09–5.47) and intermediate ones for mixed-feeders (0.4-2.74). The median of the specimens in both localities is 2 (Table 1), indicating browsing or mixed feeding habits. The very small number of specimens (n<5) does not allow for statistical comparisons.

Specimen	Species	Site	M2s Score	M2d Score	Median
MMNH-28439	*Dihoplus pikermiensis*	Kiro Kuchuk	3	2	2
MMNH-28441	*Dihoplus pikermiensis*	Kiro Kuchuk	2	2	
MMNH-28442	*Dihoplus pikermiensis*	Kiro Kuchuk	2	-	
MMNH-28444	*Dihoplus pikermiensis*	Prsten	2	2	2

Table 1: the mesowear data extracted on the left (M2s) and right (M2d) second molars of the MMNH collection.

Discussion

It is interesting that, compared to the well-documented sympatry of at least two rhinos in the Balkan-Iranian Province (Giaourtsakis et al. 2006 and references therein), no sympatry of rhinocerotid species has been recorded in the Late Miocene of North Macedonia. The rhinos, actually, are relatively rare in the faunas of the country, with *D. pikermiensis* being the definite dominant rhinocerotid of the country.

Dihoplus pikermiensis is the dominant rhinocerotid of the Turolian faunal assemblages of North Macedonia. The species has been reported from many localities: it is the only rhino found in early Middle Turolian sites Kiro Kuchuk and Karaslari, as well as in the Middle Turolian site Belushka, early Vallesian site Prsten and, finally, Bashibos, the oldest site of the country, of Vallesian-lowermost Turolian age (Spassov et al. 2018). *Miodiceros neumayri* is the other tandem-horned rhino present in Northern Macedonia, reported only from the middle Turolian site of Umin Dol (Spassov et al. 2018). This species is a common perissodactyl in the Late Miocene of the Eastern Mediterranean, found in various sites of Greece, Turkey and Iran, with the site of Strumyani in Bulgaria marking its northernmost report (Giaourtsakis et al. 2006, Geraads and Spassov 2009, Spassov et al. 2019). The genus *Chilotherium* was also an important element of the Balkan-Iranian Province during the Turolian, with numerous species reported from Greece to China (Kampouridis et al. 2023 and references therein). In North Macedonia, the Late Miocene site of Marievo marks the westernmost report of the genus (Geraads and Spassov 2009, Spassov et al. 2018).

As far other localities of the Balkans are concerned, rhinocerotids have been reported in notable numbers from Bulgaria: *D. pikermiensis* is the only rhinocerotid from the early Turolian site Hadjidimovo; in the early-middle Turolian site Kalimantsi the species is sympatric with *Brachypotherium* sp., *Acerorhinus* sp. and *M. neumayri*; finally, at the early Turolian site Strumyani, *D. pikermiensis* is sympatric with *M. neumayri* (Geraads and Spassov 2009). As far as hornless genera are concerned, primitive chilothere *Eochilotherium samium* is reported from the early Turolian site Kromidovo; *Chilotherium* sp. and *Brachypotherium* sp. have been described from the middle Turolian site Ahmatovo; Turolian locality Gorna Sushitsa has yielded both *Acerorhinus* sp. and *Chilotherium* sp. along with *M. neumayri; Chilotherium* cf. *sarmaticum* has been reported from the early Upper Miocene of Oranovo; *Chilotherium* cf. *kowalevskii* is the sole rhinocerotid at the middle Turolian site Yambol; finally from the early Upper Miocene site Slatino, *Acerorhinus* sp and *D. pikermiensis* have been reported from the early upper Miocene site Slatino (Geraads and Spassov 2009, Hullot et al. 2022).

Greece has also yielded a notable number of fossil rhinoecrotids in the late Miocene

In the classical Turolian locality of Pikermi, *D. pikermiensis* is the main rhinocerotid of the fauna, along with M. neumayri and A. neleus (Giaourtsakis 2003, 2022, Athanassiou et al. 2014).

In Evia island, *D. pikermiensis* and *M. neumayri* coexist in the Turolian site of Kerassia with hornless *Acerorhinus neleus*, with *M. neumayri* being the main rhinocerotid (Giaourtsakis et al. 2006, Athanassiou et al. 2014), whereas in the synchronous locality of Halmyropotamos the only rhinocerotid present is *D. pikermiensis* (Giaourtsakis 2003, 2022 and references therein).

Rhinocerotids have also been reported from various localities of Axios valley, with a strong presence of *M. neumayri*, which has been described in the Turolian sites Dytiko, Ravin des Zouaves and Vathylakkos (Koufos 2006, Giaourtsakis 2022). The Vallesian sites Nikiti and Pentalophos also bear rhi-

nocerotids, with *M. neumayri* and *E. samium* reported from Pentalophos (Geraads and Koufos 1990, Geraads and Spassov 2009, Giaourtsakis 2022), whereas *D. pikermiensis* and *M. neumayri* coexisted in Nikiti-1 (Koufos 2006, Koufos et al. 2016, Giaourtsakis 2022).

The rich Turolian fauna of Mytilinii in Samos Island, Greece, has also yielded a number of rhinocerotid specimens, the majority of which belongs to *M. neumayri*, along with *D. pikermiensis* (Giaourtsakis et al. 2009), whereas the chilothere genera present on the island include both primitive *E. samium* and more derived *C. schlosseri* (Kampouridis et al. 2023).

The homogeneity of the Pikermian Biome as a savanna-like mammal community (Solounias et al. 1999) has been recently debated (Hullot et al. 2022 and references therein). In biogeographic terms, the Turolian faunas of North Macedonia should be clustered with the Western Local Faunal Assemblages (LFAs), including the Balkans and Northern Greece, which can be separated from the Eastern LFAs (Samos, Anatolia) from the during the Pikermian Large Mammal Event (sensu Kostopoulos 2009).

Despite the marked dietary variation they present, data on the paleoecology of rhinocerotids were relatively scarce compared to other herbivores (Hullot et al. 2022). In terms of paleodiet, *Dihoplus pikermiensis* has been described as a not highly specialized herbivore, a selective browser with low cheek teeth, favoring closed habitats characterized by dense vegetation (Giaourtsakis et al. 2006, Geraads and Spassov 2009, Hullot et al. 2022). In comparison, *M. neumayri* has been associated with occupying more arid and open landscapes and developing adaptations to feeding on increasingly lower and more hard bushy vegetation, such as the lack of incisors, the lengthening of the skull, the relatively convex mandible, the weakened protocone and strong mesostyle (Heissig 1999, Giaourtsakis et al. 2006, Geraads and Spassov 2009). Most recently, its dental signature was described as mixed feeding, including soft vegetation on the diet (Hullot et al. 2022). *Chilotherium* has been interpreted as a marsh or swamp dweller, with its short metapodials suggesting semi-aquatic habits (Beliaeva 1954), but this view has not had further support (Geraads and Spassov 2009). Based on data from the Balkan-Iranian Province, this genus has been interpreted as a mixed feeder, and a potential dietary competition or niche partitioning in cases of sympatry with *M. neumayri* (including the proximal to Kiro Kuchuk Bulgarian site of Gorna Shushitsa) has lead to the inclusion of harder browse items in the diet of the genus (Hullot et al. 2022). Moreover, the shape of the tusk can be interpreted as an adaptation to cutting this hard vegetation (Geraads and Spassov 2009). Finally, in the many cases of sympatry in the Balkan-Iranian Province, the two tandem horned species were probably not competing for the same ecological niches (Spassov et al. 2006, Geraads and Spassov 2009, Giaourtsakis 2022, Hullot et al. 2022).

With more than 15 fossil mammal species of Middle Turolian age, the fauna of Kiro Kuchuk is the second richest of North Macedonia, following only Karaslari, which has yielded 22 species. On the other hand, the material from Prsten is scarce, with an age determined to Early Turolian (Spassov et al. 2018).

Apart from *D. pikermiensis*, the other megaherbivores of Kiro Kuchuk are the large giraffine *Bohlinia attica* and the chalicothere *Ancylotherium pentelicum*. Both these animals have been decribed as browsers (Saraç et al 2002, Merceron et al. 2018). The presence of the primate *Mesopithecus pentelicus* would also indicate a forested environment. In conclusion, some degree of potential dietary competition may be expected between the megaherbivores, yet not enough data is available to support the hypothesis.

As far as Prsten is concerned, *D. pikermiensis* and the proboscidean *Choerolophodon* sp. (only one juvenile specimen) reported as the only megaherbivores of the site. *Choerolophodon* has been reported as a grazer feeding mostly on graminoids available on open habitats (Konidaris et al. 2016), therefore the two megaherbivores of the fauna would probably not be in dietary competition, as they would occupy different niches. This is a common trend in the Balkan-Iranian Province, where the co-existence of *Choerolophodon* and browsing/mixed feeding rhinocerotids is relatively common (Hullot et al. 2022).

The paleoecological reconstruction of North Macedonia during the Middle Turolian has been based on the faunal composition of the sites Karaslari and Kiro Kuchuk, and the paleoenvironment is described as dominated by open woodlands and bushlands (Spassov et al. 2018). This does not disagree with the result of our work on *D. pikermiensis* from Kiro Kuchuk, which we interpreted as a browser, coexisting either with other browsing megaherbivores (*B. attica, A. pentelicum*) or with grazing ones (*Choerolophodon* sp) in a variable environment.

Conclusion

The paleodietary data we collected from the upper dentitions of the *D. pikermiensis* fossils from North Macedonia support a browsing or mixed-feeding diet, which is supported by previous research. This rhinocerotid coexisted with other megaherbivores in Kiro Kuchuk and Prsten, yet a dietary competition is improbable. The late Miocene faunas of North Macedonia are similar to other synchronous Southern Balkans and continental Greece faunas. We support the need of a more synthetic study of the paleodiet of the various herbivores from North Macedonia in the future, using a combination of paleo-

ecological proxies such as microwear analysis and isotopic composition; we argue that a multi-proxy paleoecological study would help better reconstruct the paleonvironmental conditions of the area and, consequently, further understand an important part of the Balkan-Iranian Province during the Miocene.

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