HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2022.2095910

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Late Miocene rhinocerotids from the Balkan-Iranian province: ecological insights from dental microwear textures and enamel hypoplasia

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ABSTRACT
The late Miocene is a period of increasing aridity and habitat openness in the south-eastern Mediterranean region. The impact of these changes has not been fully explored regarding rhinocerotids' ecology, although rhinoceroses were a major and diverse component of the Miocene mammalian faunas. Here, we investigate the palaeoecology of rhinocerotid specimens coming from 12 localities throughout the Balkan-Iranian zoogeographic province, and covering a large part of the late Miocene (MN9 to MN13). Microwear textures confirmed the hypothesised niche partitioning between the two main rhinocerotid species – *Ceratotherium* [*Ce.*] *neumayri* (mixed-feeder including grasses) and *Dihoplus pikermiensis* (browser) – but highlighted dietary overlap between *Ce. neumayri* and the co-occurring chilothere species at Maragheh, Samos and Pentalophos-1. Although microwear did not reveal clear spatiotemporal differences, we found obvious discrepancies regarding hypoplasia prevalence: Vallesian rhinocerotid teeth displayed more defects (Xirochori and Pentalophos-1: 16.26% of teeth affected) than Turolian specimens (all other localities: 9.72%). Similarly, rhinocerotid teeth from eastern localities (Samos and Maragheh; supposedly more arid), had a higher hypoplasia prevalence (13.52%) than their western counterparts (6.90%). Insights from rhinocerotids' ecology thus challenged space and time homogeneity within Balkan-Iranian province, and the associated savanna habitat, at least regarding the sample studied here.

ARTICLE HISTORY
Received 11 April 2022
Revised 24 June 2022
Accepted 27 June 2022

KEYWORDS
Vallesian; Turolian; Balkans; Rhinocerotidae; dietary preferences; Pikermian Biome

Introduction

The Pikermian Biome (*sensu* Solounias et al. 1999) is a classical Turolian (late Miocene) mammalian assemblage, supposedly homogeneous over the so-called Greco-Iranian biogeographical province (*sensu* de Bonis et al. 1979), later specified as Balkano-Iranian province (*sensu* Geraads et al. 2001; Spassov et al. 2018), or the Sub-Paratethyan zoogeographic province (*sensu* Bernor 1984). Although very popular, these notions are debated and questioned. Indeed, faunal homogeneity has been challenged (Kostopoulos 2009; Athanassiou et al. 2014), the classic savanna-like environment is controverted – with reconstructions ranging from sclerophyllous evergreen woodlands (Athanassiou et al. 2014; Denk 2016; Denk et al. 2018) to a savanna mosaic (Tobien 1967; Solounias et al. 1999; Spassov 2002; Merceron et al. 2006, 2016a) – and the temporal range of the Pikermian Biome could be more restricted than previously thought (see Pikermian chronofauna *sensu* Eronen et al. 2009 and the Pikermian Event *sensu* Kostopoulos 2009, with an age of 7.3–7.1 Mya after Kostopoulos 2009 and 7.42–7.27 Mya after Spassov et al. 2017). In fact, many rich localities of the Balkans, Aegean region, or eastern Anatolia have been linked to the Pikermian Biome sensu lato, such as Hadjidimovo, Gorna Sushitsa, Karaslari, Kiro Kuchuk, Samos, or Maragheh (Bernor et al. 1996; Spassov 2002; Kostopoulos 2009; Geraads et al. 2011; Danowitz et al. 2016; Spassov et al. 2018, 2019). However, the dating of large number of Southern Balkans Turolian sites is unsure, as few localities (e.g, Pikermi, Gorna Sushitsa and Asmaka; Böhme et al. 2017, 2018) have radiometric ages. Besides, many localities of this area fall within the 7.42–7.25 Mya interval (MN12), but very few in the preceding 8.7–7.5 Mya interval (MN11; Kostopoulos 2009; Geraads et al. 2011).

All these localities yielded typical species-rich large herbivore assemblages (e.g, ruminants and hipparionine equids) and several megaherbivores such as rhinocerotids, giraffids, and proboscideans (Solounias et al. 1999; Spassov 2002; Koufos et al. 2009a; Theodorou et al. 2010). The classic Turolian rhinocerotid assemblages are composed of one or two two-horned rhinocerotines (*Dihoplus* [*Dh.*] *pikermiensis* and/or *Ceratotherium* [*Ce.*] *neumayri*) and a similar number of aceratheriines either assigned to *Chilotherium*, *Acerorhinus*, or *Persiatherium* (Guérin 1980; Geraads 1988; Giaourtsakis 2003; Geraads and Spassov 2009; Athanassiou et al. 2014; Pandolfi 2016). In north-western Iran, Maragheh also yielded an elasmotheriine species (*Iranotherium morgani*) in addition to this classical rhinocerotine-aceratheriine fauna, making up to four distinct species and genera recognised at the same stratigraphic level (lower Maragheh biostratigraphic unit, ca. 9 Mya; Pandolfi 2016). Concerning rhinocerotids, in spite of widely homotaxic assemblages, obvious differences are visible in the distribution and relative abundance of the species across the Southeastern Mediterranean region, notably due to environmentally controlled provincial differences (Giaourtsakis et al. 2006; Athanassiou et al. 2014). Indeed, from West to East there is a shift in the dominance of *Dh. pikermiensis* associated with *Acerorhinus*

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/08912963.2022.2095910

species, to that of *Ce. neumayri* associated with *Chilotherium* species, in parallel to clear climate disparities and a gradient towards more aridity and less trees towards East (Fortelius et al. 2002; Giaourtsakis et al. 2006; Strömberg et al. 2007; Eronen et al. 2009; Athanassiou et al. 2014).

Recently, the ecology of various large herbivores in several emblematic localities has raised an increasing interest (e.g, Pikermi, Samos, Maragheh, Hadjidimovo; Merceron et al. 2006; Solounias et al. 2010; Konidaris and Koufos 2013; Danowitz et al. 2016; Orlandi-Oliveras et al. 2022). But, despite an abundant literature on the Pikermian Biome in general, their rhinocerotid component has always been under-investigated in this aspect (Giaourtsakis et al. 2006). Indeed, most works have widely focused on taxonomic issues (Giaourtsakis et al. 2006; Geraads and Spassov 2009; Giaourtsakis 2009; Athanassiou et al. 2014; Pandolfi 2016). As for ecological interpretation, dietary preferences of the two main rhinocerotid species (*Dh. pikermiensis* and *Ce. neumayri*) were classically hypothesised based on dental proportions (e.g, hypsodonty index) and similarity of occlusal pattern to modern rhinoceros species (Guérin 1980; Geraads and Koufos 1990; Geraads and Spassov 2009). In other words, independent proxies such as dental microwear, mesowear, or stable isotopy might provide original and useful palaeoecological inferences (Giaourtsakis et al. 2006). This is of particular concern, especially knowing that rhinocerotids were diverse and abundant large herbivores of the Pikermian fauna.

In this article, we propose a large-scale insight into the palaeoecology of the rhinocerotids from the Balkan-Iranian province based on the combination of dental microwear textures (dietary proxy) and enamel hypoplasias (environmental stress proxy). A dozen of localities were included in this study throughout the late Miocene (MN9-MN13), and ranging from southern Bulgaria, northern and southern continental Greece as well as Samos Island, to northwestern Iran. Those insights on rhinocerotids palaeoecology allowed us to discuss the supposed spatio-temporal homogeneity and the savanna biome of the region during late Miocene.

Materials and methods

We studied the rhinocerotid remains from 12 late Miocene localities included in the Balkan-Iranian province (Figure 1; Table 1) and spanning the entire late Miocene interval (MN9–MN13; Tortonian and Messinian standard ages; Vallesian and Turolian European Land Mammal Ages). Details about the localities can be found in Supplementary S1. The material studied here is curated in various European institutions: the Naturhistorisches Museum Wien (NHMW), the Aristotle University of Thessaloniki (AUTh), the Naturhistorisches Museum Basel (NHMB), the National Museum of Natural History at the Bulgarian Academy of Sciences (NMNHS) and the Palaeontological Museum 'D. Kovachev', Asenovgrad (PMA) – branch of the NMNHS. For all details on the specimens included in this study see Supplementary S2. Due to the COVID-crisis and to the relocation of the collections of the Muséum National d'Histoire Naturelle of Paris, we were unable to include Turkish localities in this dataset.

Dental Microwear Texture Analyses (DMTA)

Dental Microwear Texture Analysis (DMTA) is a short-term proxy of diet (few days to few months), widely used in palaeontology (Calandra et al. 2008; Merceron et al. 2010; Jones and DeSantis 2017; Bethune et al. 2019; Hullot et al. 2021). Here we used the protocol based on Scott et al. (2005), Scott et al. (2006) with sensitive-scale fractal analyses.

DMT was studied on silicone (Regular Body President, ref. 6015 – ISO 4823, medium consistency, polyvinylsiloxane addition type; Coltene Whaledent) negative replicas from wear facets of well-preserved molars. We sampled one tooth per individual (preferentially second molars regardless of position and side) and focused on two facets from the same enamel band, one grinding (occlusal) and one shearing (lateral; if present), as the inclusion of both grinding and shearing facets in microwear studies may improve dietary discrimination (Louail et al. 2021; Merceron et al. 2021). Localisation of these facets on upper and lower molars is detailed in Figure 2.

Silicone moulds were scanned with a Leica DCM8 confocal profilometer ('TRIDENT' profilometer housed at the PALEVOPRIM, CNRS, University of Poitiers) using white light confocal technology with a 100× objective (Leica Microsystems; Numerical aperture: 0.90; working distance: 0.9 mm). The produced scans (.plu files) were pre-treated with LeicaMap v.8.2. (Leica Microsystems). Pre-treatment included surface inversion (as scans were produced on negative replicas), replacement of the very few missing points (i.e, non-measured, less than 1%) by the mean of the neighbouring points, removal of aberrant peaks (automatic operators including a morphological filter see supplementary Information in (Merceron et al. 2016b), levelling of the surface, removal of form (polynomial of degree 8) and selection of a 200 × 200 µm area (1551 × 1551 pixels) saved as a digital elevation model (.sur) to be used for DMTA. The 200 × 200 µm surfaces were then analysed using the Scale-Sensitive Fractal Analysis with SFrax (Surfract, www.surfract.com) and LeicaMap.

Five texture variables are considered here:

- Anisotropy (exact proportion of length-scale anisotropy of relief; epLsar), which is an indication of the orientation concentration of surface roughness;
- Complexity (area-scale fractal complexity; Asfc), which measures the roughness at a given scale;
- Heterogeneity of the complexity (HAsfc) – here at two different scales 3 × 3 and 9 × 9 – reflecting the variation of complexity within the studied 200 × 200 µm zone;
- Fine textural fill volume (0.2 µm; FTfv) estimated by filling the surface with square cuboids of different volumes (see Scott et al. 2006 for details).

Additionally, we used an extant species dataset modified from that of Hullot et al. (2019), with two new specimens (one of *Rhinoceros unicornis* and one of *Rhinoceros sondaicus*), to facilitate the interpretation of dental microwear texture of the fossil material. It consists of 17 specimens of *Ceratotherium simum* (white rhinoceros) and 21 of *Diceros bicornis* (black rhinoceros) originated from Africa and the three Asian species with four specimens of *Dicerorhinus sumatrensis* (Sumatran rhinoceros), 15 of *R. sondaicus* (Javan rhinoceros), and five of *R. unicornis* (Indian rhinoceros).

Enamel hypoplasia

Enamel hypoplasia is a common marker of stress that is permanent, sensitive, but non-specific. Hypoplasia has been linked to many causes (more than a hundred in human; Small and Murray 1978), such as seasonality, birth, weaning or diseases (Goodman and Rose 1990; Bratlund 1999; Mead 1999; Rothschild et al. 2001; Franz-Odendaal et al. 2003; Niven et al. 2004; Upex and Dobney 2012). We studied enamel hypoplasia with the naked eye, as it provides a cheap, fast, and reliable insight (Hullot et al. 2021). We analysed all cheek teeth available, both deciduous and permanent, with the exception of damaged,

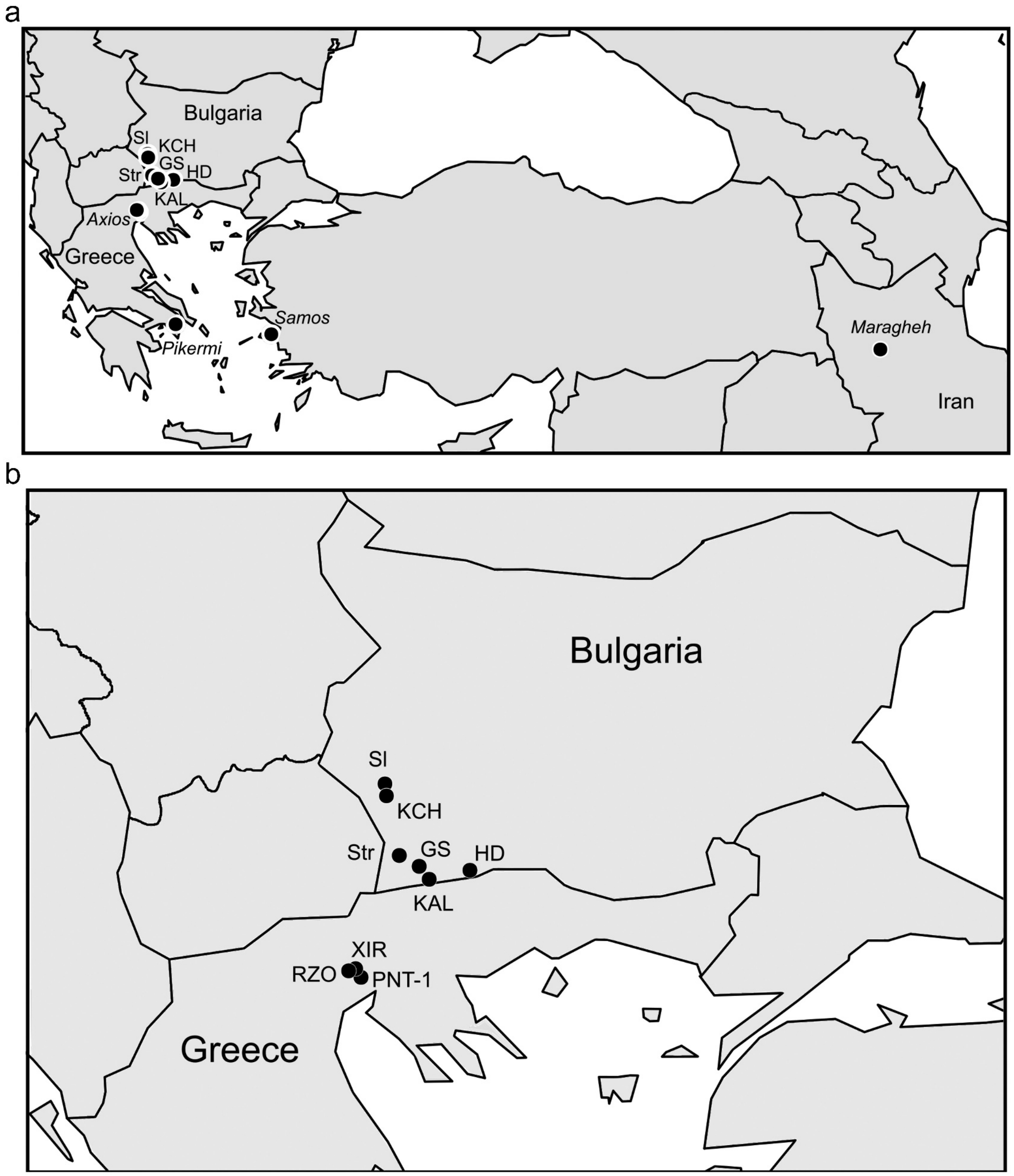

Figure 1. Localisation of the 12 late Miocene localities studied from the Balkan-Iranian province. a- Balkan-Iranian province and b- zoom on Bulgaria and Greece to precise the localisation of the continental localities. Eastern localities: Maragheh (9 to 7.4 Mya, MN10-MN12; Iran), Samos (7.8 to 6.7 Mya, MN11-MN13; Greece). Western localities: PNT-1 – Pentalophos-1 (late MN9-MN10; Greece), XIR – Xirochori (~ 9.6 Mya MN10; Greece), RZO – Ravin des Zouaves-5 (~ 8.2 Mya MN11; Greece), KCH – Kocherinovo (early MN11; Bulgaria), KAL – Kalimantsi (material studied here: 7.42–7.27 Mya, MN12; Bulgaria), HD – Hadjidimovo (> 7.44 Mya, MN11; Bulgaria), Str – Struymani-2 (MN11-MN12; Bulgaria), GS – Gorna Sushitsa (MN12; Bulgaria), Pikermi (7.33 and 7.29 Mya, MN12; Greece), Sl – Slatino (early Turolian; Bulgaria; see stratigraphic details in Spassov et al. 2006).

much worn, or not properly identified teeth. This exclusion concerned 75 teeth and left a total of 894 teeth (288 milk molars and 606 permanent premolars and molars) from the 12 localities included in the hypoplasia-aimed analysis. No standard protocol is available for hypoplasia analysis, but most studies refer to the *Fédération Dentaire Internationale* (1982) to identify hypoplasia defects (linear enamel hypoplasia [LEH], pitted hypoplasia, and aplasia). After identification, we recorded qualitative data (tooth affected, position of the defect on the crown, severity) and took calliper measurements (distance of the defect from enamel-dentine junction, width if applicable). The different types of defects and associated calliper measurements are illustrated in Figure 3.

Statistics and General Linear Mixed Models (GLMMs)

All statistics were conducted in R (https://www.R-project.org/), equipped with the following packages: reshape2 (Wickham 2007), dplyr (Wickham et al. 2019), lme4 (Bates et al. 2015), car (Fox et al. 2012), MASS (Venables and Ripley 2002). Figures were done using R package ggplot2 (Wickham 2011) as well as Inkscape v.0.91.

For GLMMs, we used the same bottom-up approach as in Hullot et al. (2021) based on a R code modified from Arman et al. (2019). An example of this code applied to DMTA variable epLsar (anisotropy) is given in Supplementary S3. For DMTA response variables were the five DMTA parameters (epLsar, Asfc, FTfv, HAsfc9, and HAsfc81), which were modelled using Gaussian family. The factors

Table 1. List of rhinocerotid species found in each locality of interest. Grey background indicates species not included in our sample and thus not studied here.

		Pentalophos-1 (late MN9-MN10)	Xirochori (MN10)	Maragheh (MN10-MN12)	Kocherinovo (MN11)	Ravin des Zouaves-5 (MN11)	Hadjidimovo (MN11)	Strumyani-2 (MN11-MN12)	Slatino (early Turolian)	Samos (MN11-MN13)	Kalimantsi (MN12)	Pikermi (MN12)	Gorna Sushita (MN12)
Rhinocerotinae													
Rhinocerotina													
	Ceratotherium neumayri	x		x		x		x		x	x	x	x
	Dihoplus pikermiensis						x	x		x	x	x	
	Dihoplus cf. *schleirmacheri*								x				
Aceratheriina													
	Chilotherium kilasi	x											
	Chilotherium samium									x			
	Chilotherium schlosseri									x			
	Chilotherium sp.		x										x
	Chilotherium persiae			x									
	Acerorhinus sp.				x				x		x		x
	Acerorhinus neleus											x	
	Persiatherium rodleri			x									
Teleoceraterina													
	Brachypotherium sp.										x		
Elasmotheriinae													
Elasmotheriina													
	Iranotherium morgani			x									
	Total	2	1	4	1	1	1	2	2	4	4	3	3

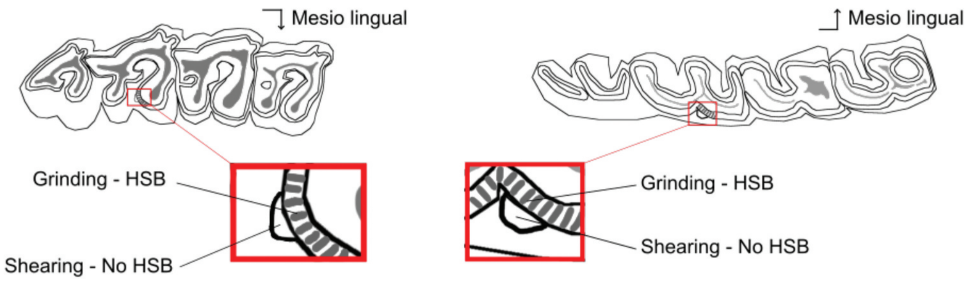

Figure 2. Localisation of the dental facets on rhinocerotid molars. Position of the two dental facets (grinding and shearing) on the second upper molar (left) and second lower molar (right). Both facets are sampled on the same enamel band with (grinding) or without (shearing) Hunter-Schreger bands (HSB). Illustration after Hullot et al. (2019).

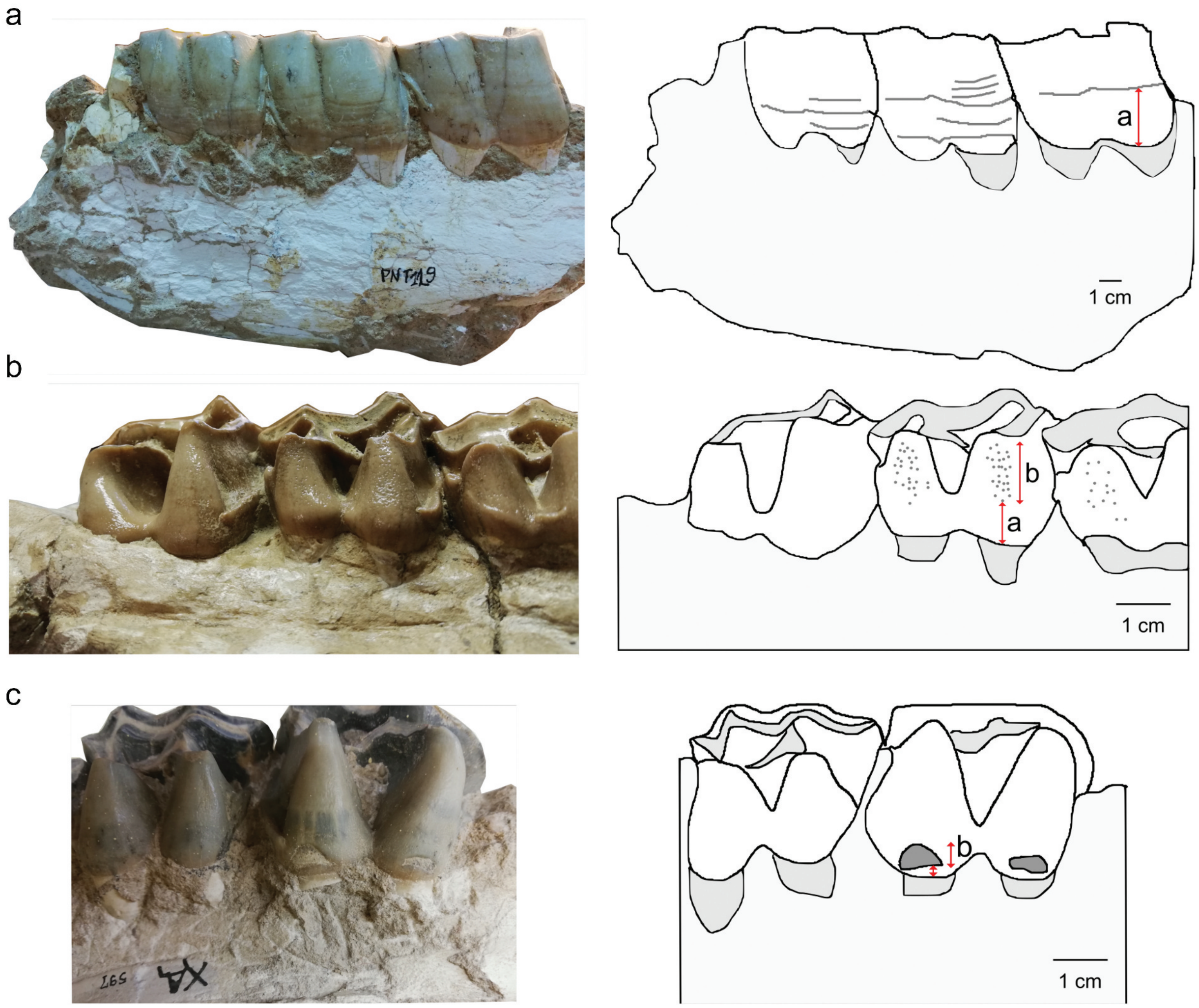

Figure 3. Different types of hypoplasia and associated measurements illustrated on rhinocerotid teeth. Left: photos of the specimens, Right: associated interpretative drawings of the photos with hypoplasia defects in dark grey. Approximate scale given for each specimen. a – Linear enamel hypoplasia (LEH) illustrated on the lower left teeth of the specimen PNT129 (*Ceratotherium neumayri* from Pentalophos-1; AUTh); b – Pits illustrated on the upper left teeth of the specimen 1911–0005-0041 (*Dihoplus pikermiensis* from Samos; NHMW); c – Aplasia on the upper right teeth of the specimen HD-597 (*Dh. pikermiensis* from Hadjidimovo; PMA). Measurements: a- Distance of the defect to the enamel-dentine junction, b- width of the defect (when applicable).

were: specimen (number of the specimen; random factor), locality, province, age (MN zones), genus, tooth (e.g, second molar and fourth milk molar), position (upper or lower), side (left or right), cusp (protocone, protoconid, or hypoconid), and facet (grinding or shearing). Hypoplasia response variables were Hypo (1 or 0 for presence or absence of hypoplasia) modelled with Binomial family, Defect (e.g., LEH, Pits, Aplasia; converted to numbers), Localisation (position of the defect on the crown; mostly labial or lingual), Multiple (number of defects), and Severity (from 0 to 4), for which we selected Poisson family. The factors tested were: specimen (number of the specimen; random factor), genus, province, locality, age (Vallesian or Turolian), tooth (e.g, first molar, fourth premolar), position (upper or lower), side (left or right), and wear (low, average, high). Additionally, Defect was converted and used as a factor for response variables Severity, Multiple, and Localisation.

The best model was selected using Akaike's Information Criterion score (AIC; lowest score), then tested for over-dispersion (estimated through the ratio of deviance and degrees of freedom) and corrected if necessary by using quasi-Poisson or quasi-Binomial laws from the MASS package (Venables and Ripley 2002) or by adjusting the coefficients table for Gaussian laws (multiply-type error by square root of the dispersion factor and recalculate z and p values accordingly). In total, 300 models were compared across the 10 response variables (see electronic supplementary material, S3, S4, and S5).

Results

Dental microwear

The p-values associated with MANOVAs (Species/Genus x Facet x Province/Locality) on all five main DMTA parameters (epLsar, Asfc, FTfv, HAsfc9, HAsfc81) were the lowest for Facet, ranging between 0.027 (Genus x Facet x Locality) and 0.047 (Species x Facet x Locality). For all other parameters (Species, Genus, Province, Locality), p-values were above 0.1 in every formula. The ANOVAs conducted for each DMTA parameter revealed low p-values for several factors suggesting an effect in the differences observed for all parameters but HAsfc81, as detailed in Table 2. Both types of statistical tests suggested that the differences in DMT patterns observed were mainly due to facet.

Median, mean and standard deviation of the mean (SD) were calculated by species, facet and locality. Besides at Maragheh, the sampling was very restricted (n < 5), either due to low numbers of cranio-dental specimens available, or to the lack of well-preserved dental microwear texture on molars. The results are detailed in Table 3. We also plotted anisotropy against complexity for all specimens (Figure 4).

The mean and median values of anisotropy for *Ceratotherium neumayri* were low ($< 2.5 \times 10^{-3}$) at Pikermi, Pentalophos-1, and Strumyani, moderate ($\sim 3 \times 10^{-3}$) at Maragheh and Kalimantsi, and high ($\geq 4.5 \times 10^{-3}$) at Ravin des Zouaves-5 and Samos on both facets (Table 3). For complexity, the values were moderate (> 1) for most sites on both facets, except for the shearing facet of Samos (0.68) and Ravin des Zouaves-5 (0.98), and much higher for the grinding facet at Strumyani-2 (1.98) and Samos (2.74). Only four specimens of *Ce. neumaryi* have anisotropy higher than the classic high anisotropy threshold of 5×10^{-3} on both facets: two from Maragheh, one from Samos, and one from Ravin des Zouaves-5 (Figure 4). Similarly, four specimens were above the high complexity cutpoint (Asfc = 2) but only on the grinding facets (none on the shearing ones): both specimens from Strumyani, one from Maragheh, and one from Pentalophos-1.

Mean and median of FTfv (in μm^3) for *Ce. neumayri* specimens were high ($> 4 \times 10^4$) on both facets for all localities but Pikermi (2.2×10^4), and shearing facet at Maragheh (3.4×10^4). Mean and median of HAsfc9 and HAsfc81 for *Ce. neumayri* varied greatly depending on the locality (Table 3). On the grinding facet, both Hasfc were low (≤ 0.2 for HAsfc9 and ≤ 0.5 for HAsfc81) at Pentalophos-1 and Ravin des Zouaves-5, but high (> 0.3 and > 0.6) at Pikermi and Samos. Values for the grinding facet at Kalimantsi and Maragheh were high for HAsfc9 (0.3–0.4) but moderate for HAsfc81 (> 0.5). On the shearing facet, HAsfc9 was moderate at Pentalophos-1 (0.25) and Samos (0.22), and high at Maragheh (> 0.3) and Ravin des Zouaves-5 (0.46), while HAsfc81 was moderate (0.5–0.6) in Maragheh, Samos, and Ravin des Zouaves-5, but low at Pentalophos-1 (0.49).

Dihoplus pikermiensis dental microwear textures were studied from Hadjidimovo and Pikermi only. This rhinocerotid had low mean and median values of anisotropy ($< 2 \times 10^{-3}$) at both sites and on both facets (Table 3). These statistics were high for complexity of the grinding facet (2.83) but low for the shearing facet (0.5) at Pikermi, and moderate (between 1 and 2) for both facets at Hadjidimovo. On Figure 4, we can see that all specimens of *Dh. pikermiensis* are below 2.5×10^{-3} for epLsar on both facets, and above 1 for Asfc on grinding facet. For both sites, FTfv was high on the grinding facet ($\sim 6.6 \times 10^4$) and low on the shearing one (Pikermi: 1.4×10^4 and Hadjidimovo: 2.6×10^4). Mean and median of both HAsfc were moderate to high on the grinding facet for both localities, and low-moderate on the shearing facets (Table 3).

Chilotherium [*Ch.*] species from the different sites (Maragheh, Pentalophos-1, Samos, and Xirochori) had various dental microwear texture profiles. *Chilotherium persiae* had the lowest mean value of anisotropy on both facets (grinding: 2.28×10^{-3}; shearing: 3.07×10^{-3}), while *Ch. kiliasi* from Pentalophos-1 and *Ch.* sp. from Xirochori had similarly high mean values on both facets (grinding: $\sim 4 \times 10^{-3}$; shearing: $\sim 6 \times 10^{-3}$). *Chilotherium schlosseri* from Samos had very low mean complexity on both facets (grinding: 0.64; shearing: 0.38). On the shearing facet, *Ch. persiae* and *Ch. kiliasi* displayed complexity mean around 1, while *Chilotherium* sp. from Xirochori had a complexity of 2.36. On the grinding facet the median Asfc was high (around 2) for all species but *Ch. schlosseri*. On the grinding facet, only three specimens (all from Maragheh; *Ch. persiae*) have epLsar values above the high anisotropy threshold (5×10^{-3}), while about half the specimens from Maragheh and both from Pentalophos-1 (*Ch. kiliasi*) are above the high complexity cutpoint (2; Figure 4). On the shearing facet, five specimens display high epLsar values (3 from Maragheh, one from Pentalophos-1, and on from Xirochori) and three have high Asfc values (same one from Xirochori, and two from Maragheh; Figure 4). FTfv had high values ($> 4 \times 10^4$) on the grinding facets of all *Chilotherium* species. On the shearing facet, FTfv was low for the specimen from Xirochori (1.5×10^4), moderate for *Ch. persiae* (Maragheh) and *Ch. kiliasi* (Pentalophos-1) with a mean around 3×10^4, and high for *Ch. schlosseri* (Samos; 5.7×10^4). HAsfc medians were high (> 0.3 for HAsfc9 and > 0.6 for HAsfc81) on the grinding facet all species but that at Xirochori (HAsfc9: 0.2; HAsfc81: 0.44). Hasfc medians on the shearing facet were low for *Ch. schlosseri* and moderate to high for all three other species.

Teeth of all representatives of *Acerorhinus* (from Gorna Sushitsa, Kocherinovo, and Kalimantsi) had low values of anisotropy, between 1 and 2×10^{-3} on both facets, except the shearing facet of the

Table 2. Factor showing an effect for each ANOVA formula on every DMTA parameters. epLsar: anisotropy, Asfc: complexity, FTfv: fine textural fill-volume, HAsfc: heterogeneity of the complexity. *: p-value < 0.05; **: p-value < 0.01; -: p-values > 0.05.

	epLsar	Asfc	FTfv	HAsfc9	HAsfc81
Species x Facet x Locality	Locality*	Facet**	Facet *	-	-
Species x Facet x Province	-	Facet**	Facet *	Province *	-
Genus x Facet x Locality	Genus:Locality*	Facet**	Facet *	-	-
Genus x Facet x Province	Genus:Province*	Facet**	Facet **	Province *	-

Table 3. Number of specimens (N), median, mean, and standard deviation of the mean (SD) of the DMTA parameters by locality, species, and facet. FTfv: fine texturall fill-volume, HAsfc: heterogeneity of the complexity; Gr. – grinding; Sh. – shearing.

			Anisotropy (x 10^-3)			Complexity			FTFV (x 10^4)			HAsfc9			HAsfc81		
		N	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD
Ceratotherium neumayri																	
Pentalophos-1 (MN9-10)	Gr.	2	2.16	2.16	0.36	1.98	1.98	1.22	5.60	5.60	0.63	0.20	0.20	0.02	0.45	0.45	0.07
	Sh.	2	1.49	1.49	1.83	1.31	1.31	0.26	4.85	4.85	0.50	0.25	0.25	0.01	0.49	0.49	0.07
Maragheh (MN10-12)	Gr.	7	3.12	3.11	1.73	1.83	1.69	0.72	5.75	5.82	2.61	0.32	0.42	0.20	0.51	0.62	0.22
	Sh.	5	2.44	3.62	3.05	1.06	1.14	0.55	3.42	4.63	3.24	0.35	0.32	0.06	0.55	0.54	0.10
Ravin des Zouaves (MN11)	Gr.	2	4.46	4.46	1.05	1.14	1.14	0.39	5.91	5.91	2.46	0.19	0.19	0.00	0.39	0.39	0.04
	Sh.	1	5.06	5.06	NA	0.98	0.98	NA	2.20	2.20	NA	0.46	0.46	NA	0.57	0.57	NA
Strumyani-2 (MN11-MN12)	Gr.	2	2.31	2.31	0.59	2.74	2.74	0.95	5.20	5.20	4.30	0.24	0.24	0.16	0.56	0.56	0.15
Samos (MN11-MN13)	Gr.	1	7.69	7.69	NA	1.28	1.28	NA	4.94	4.94	NA	0.83	0.83	NA	1.35	1.35	NA
	Sh.	1	8.75	8.75	NA	0.69	0.69	NA	4.01	4.01	NA	0.22	0.22	NA	0.52	0.52	NA
Kalimantsi (MN11-MN12)	Gr.	1	3.03	3.03	NA	1.37	1.37	NA	4.83	4.83	NA	0.32	0.32	NA	0.50	0.50	NA
Pikermi (MN11-MN13)	Gr.	1	0.19	0.19	NA	1.04	1.04	NA	2.27	2.27	NA	0.52	0.52	NA	0.68	0.68	NA
Dihoplus pikermiensis																	
Hadjidimovo (MN11-MN12)	Gr.	4	1.88	1.85	0.75	1.66	1.84	0.72	6.67	5.95	3.25	0.28	0.31	0.12	0.58	0.56	0.17
	Sh.	2	1.60	1.60	0.44	1.08	1.08	0.44	2.57	2.57	0.24	0.26	0.26	0.03	0.46	0.46	0.03
Pikermi (MN11-MN13)	Gr.	1	1.51	1.51	NA	2.83	2.83	NA	6.64	6.64	NA	0.35	0.35	NA	0.80	0.80	NA
	Sh.	1	1.69	1.69	NA	0.50	0.50	NA	1.43	1.43	NA	0.19	0.19	NA	0.43	0.43	NA
Chilotherium kiliasi																	
Pentalophos-1 (MN9-10)	Gr.	2	4.09	4.09	0.65	2.47	2.47	0.42	7.10	7.10	0.94	0.39	0.39	0.09	0.70	0.70	0.26
	Sh.	1	6.40	6.40	NA	0.82	0.82	NA	3.31	3.31	NA	0.38	0.38	NA	0.50	0.50	NA
Chilotherium sp.																	
Xirochori (MN10)	Gr.	1	4.55	4.55	NA	1.96	1.96	NA	8.28	8.28	NA	0.20	0.20	NA	0.44	0.44	NA
	Sh.	1	6.27	6.27	NA	2.36	2.36	NA	5.69	5.69	NA	0.19	0.19	NA	0.59	0.59	NA
Chilotherium persiae																	
Maragheh (MN10-12)	Gr.	13	2.28	2.75	2.08	1.56	1.82	1.04	4.57	4.84	1.91	0.38	0.40	0.13	0.71	0.70	0.20
	Sh.	9	3.07	3.54	1.91	0.96	1.46	1.35	3.06	4.16	2.66	0.31	0.48	0.40	0.60	0.79	0.55
Chilotherium schlosseri																	
Samos (MN11-MN13)	Gr.	1	3.88	3.88	NA	0.65	0.65	NA	7.08	7.08	NA	0.32	0.32	NA	0.65	0.65	NA
	Sh.	1	3.14	3.14	NA	0.38	0.38	NA	1.54	1.54	NA	0.12	0.12	NA	0.34	0.34	NA
Acerorhinus sp.																	
Kocherinovo (MN11)	Gr.	1	1.47	1.47	NA	4.31	4.31	NA	5.13	5.13	NA	0.45	0.45	NA	0.59	0.59	NA
	Sh.	1	1.65	1.65	NA	1.51	1.51	NA	2.99	2.99	NA	0.19	0.19	NA	0.49	0.49	NA
Kalimantsi (MN11-MN12)	Gr.	4	1.94	2.25	1.91	1.42	1.73	0.84	5.22	5.12	1.52	0.43	0.38	0.13	0.61	0.74	0.39
Gorna Sushitsa (MN11-12)	Gr.	1	1.28	1.28	NA	1.17	1.17	NA	2.67	2.67	NA	0.37	0.37	NA	0.51	0.51	NA
	Sh.	1	6.58	6.58	NA	1.23	1.23	NA	5.70	5.70	NA	0.29	0.29	NA	1.08	1.08	NA

specimen from Gorna Sushitsa (6.6 x 10^{-3}). Values of complexity were moderate, between 1 and 1.5, on both facets, except for the grinding facet of the specimen of Kocherinovo (4.3). FTfv was high (> 4 × 10^{4}) on the grinding facet at Kalimantsi and Kocherinovo, and the shearing facet at Gorna Sushitsa, moderate otherwise (> 2.5 x 10^{4}; Table 3). Eventually, HAsfc9 was high (0.3–0.5) on the grinding facet at all sites and low to moderate on the shearing ones (Kocherinovo: 0.19; Gorna Sushitsa: 0.29), while HAsfc81 was moderate (0.5–0.6) for all but the shearing facets of the specimen of Gorna Sushitsa (> 1).

GLMM

The results observed with basic statistics (mean, median) were retrieved with GLMMs, confirming the reliability of this approach. For all response variables (epLsar, Asfc, FTfv, HAsfc9, and HAsfc81), model support increased (i.e, lower AIC) when intraspecific factors were included (e.g, Facet, Genus, Province). When Genus was not forced into the models, the final models contained two to five factors, including Specimen, the random factor, by default in all models. Genus was in the final models of epLsar and HAsfc81, Facet in that of epLsar, Asfc and FTfv, and Province in that of HAsfc9 and HAsfc81. Details and comparison of all models can be seen in electronic supplementary material S3 and S4.

GLMMs results revealed the impact of Facet, Genus, and Province on the dental microwear pattern. We found more differences in dental microwear with GLMM than with the classic MANOVA/ANOVAs approach. Between Genus (corresponding to a single species except for *Chilotherium*) few differences were noticed: *Ceratotherium* has higher anisotropy than *Dihoplus* (df = 58; α = 0.05, t-value = −3.094), but lower complexity and HAsfc81 than *Chilotherium* and *Acerorhinus* (df > 60; α = 0.05, t-values > 1.7). The choice of the studied facet also appears crucial as the shearing facet has higher values of anisotropy (df = 58; α = 0.05, t-value = 2.14) but lower values of complexity and fine textural fill volume (df > 60; α = 0.05, absolute of t-value > 1.7) than the grinding facet. Eventually, Western localities specimens have lower HAsfc9 and HAsfc81 than Eastern ones (df > 60, α = 0.95, absolute of t-values > 1.7).

Besides the facet, the sampling site (tooth locus, position, side, cusp) had sometimes a confounding effect. Right teeth had lower complexity and HAsfc81 (df > 60, α = 0.95, absolute of t-values > 1.7) than their left counterparts. Similarly, upper teeth display higher anisotropy than lower teeth (df = 58; α = 0.05, t-value = 3.199), and the protocone has lower FTfv than the protoconid (df = 63, α = 0.95, t-value = −2.24). Eventually, second molars had higher epLsar values than third ones, but lower than first molars (df > 60, α = 0.95, absolute of t-values > 1.7). Tuckey's contrasts also highlighted that M3 had lower epLsar than M1 (p-value < 0.001).

GLMM – Comparison to extant dataset

When compared to the extant dataset, all fossil species had lower values of anisotropy than the grazing *Ce. simum* and the folivore *Dc. sumatrensis* (df = 165, α = 0.05, t-value threshold: ± 1.645). Moreover, *Dihoplus pikermiensis* had lower anisotropy than the browsing *Ds. bicornis* (t-value = – 1.71) and the variable grazer *R. unicornis* (t-value = – 2.18). Concerning

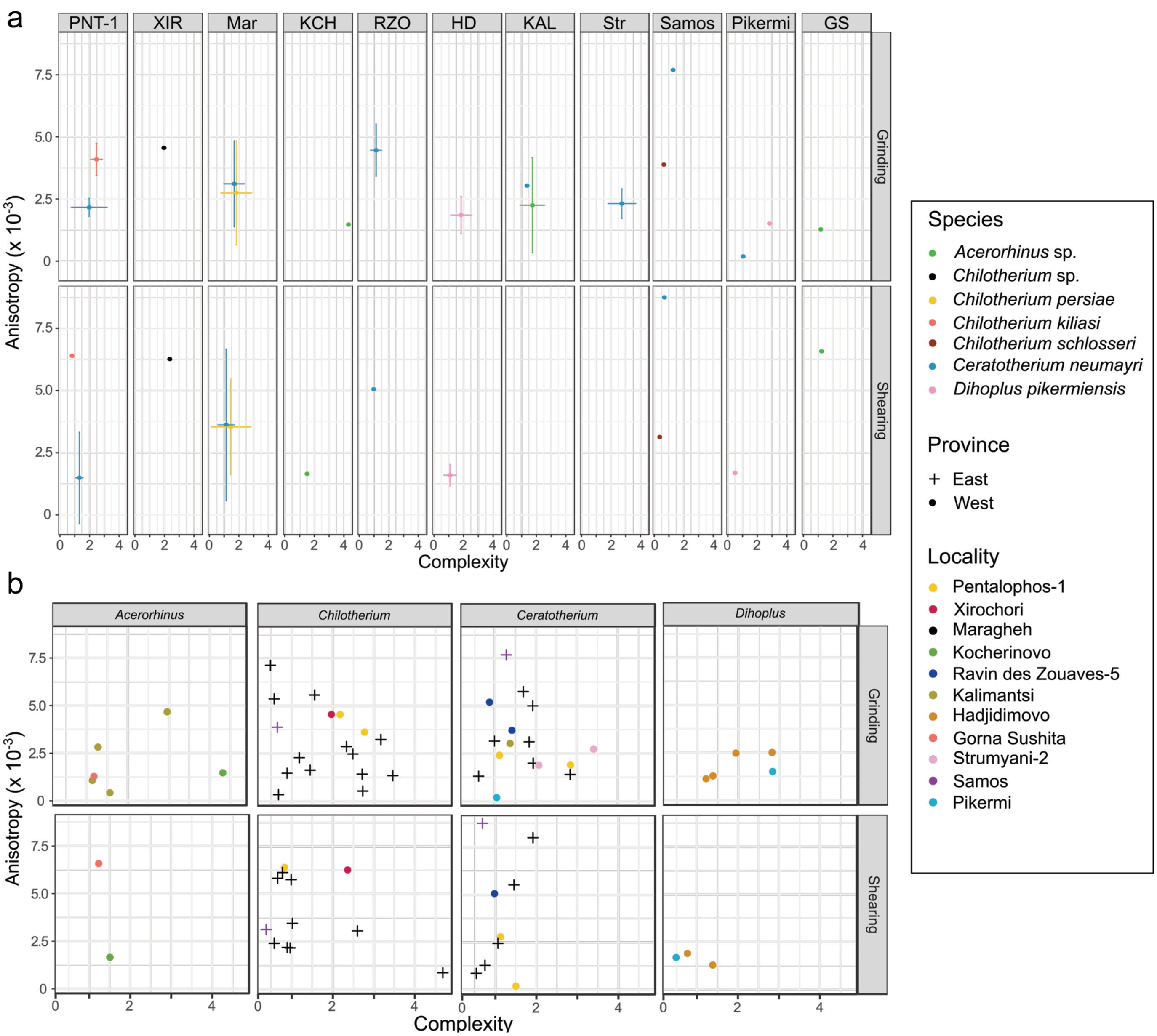

Figure 4. Dental microwear results of rhinocerotids from the Balkan-Iranian province plotted on anisotropy against complexity by facet, genus, species and province. a – Mean and standard deviation of the mean by locality, facet and coloured by species. b – All specimens studied separated by facet and genus, and coloured by localities. Colour code detailed on the right of the figure. Abbreviations: PNT-1: Pentalophos-1, XIR: Xirochori, RZO: Ravin des Zouaves-5, KCH: Kocherinovo, Mar: Maragheh, KAL: Kalimantsi, HD: Hadjidimovo, GS: Gorna Sushitsa, Str: Strumyani-2.

complexity, *Ce. neumayri*, *Chilotherium*, and *Dihoplus pikermiensis* had lower complexity values than both extant browsing species, *Ds. bicornis* and *R. sondaicus* (df = 165, α = 0.05, t-value threshold: ± 1.645). HAsfc81 values of *Ce. neumayri* were significantly lower than that of *Ce. simum* (t-value = – 2.33), *R. sondaicus* (t-value = – 2.77), and *Ds. bicornis* (t-value = – 1.87), while those of *Dh. pikermiensis* were significantly lower than the ones of only the extant grazing species *Ce. simum* (t-value = – 1.78), and the browser *R. sondaicus* (t-value = – 2.12). However, there were no critical differences in FTfv and HAsfc9 values between the extant and extinct rhinocerotids.

Hypoplasia

Out of the 894 rhinocerotid teeth studied throughout the Balkan-Iranian province, only 94 presented hypoplasia, corresponding to around 10.51%. This relatively moderate prevalence is however very distinct depending on the species, tooth locus, and locality considered (Table 4). Overall, milk molars (38/288; 13.19%) were more affected than permanent teeth (56/606; 9.24%; Table 4). Similarly, upper teeth (47/508; 9.25%) were less affected than their lower counterparts (47/386; 12.18%; Table 4). When all species and localities are merged (Table 4; Figure 5), the most affected tooth locus is D4/d4 with 35.06% (27/77 teeth being hypoplastic), while the least

Table 4. Prevalence of hypoplasia by species and tooth locus. Lower case stands for lower teeth and upper case for upper ones. D/d: deciduous teeth, P/p: premolars, and M/m: molars. -: no tooth available.

	Ceratotherium neumayri	*Dihoplus pikermiensis*	*Dihoplus* cf. *schleiermacheri*	*Chilotherium kiliasi*	*Chilotherium persiae*	*Chilotherium schlosseri*	*Chilotherium* sp.	*Acerorhinus* sp.	*Persiatherium rodleri*	*Iranotherium morgani*
d1	0/6	0/3	-	0/1	-	-	-	-	-	0/2
D1	0/10	3/15	-	0/2	0/18	-	-	0/2	0/1	0/3
d2	0/12	0/3	-	0/3	0/10	-	-	-	-	0/3
D2	0/10	3/15	-	0/3	2/9	-	-	0/1	-	-
d3	0/15	0/5	-	0/3	1/13	-	-	0/1	-	0/2
D3	0/11	2/15	-	0/3	0/8	-	0/2	0/1	-	-
d4	3/12	0/5	-	1/3	8/10	2/2	-	0/2	-	-
D4	2/8	3/15	-	1/3	7/12	-	0/2	0/1	0/2	-
Total Milk	5/84	11/76	-	2/21	18/80	2/2	0/4	0/8	0/3	0/10
p2	1/12	0/3	-	2/6	0/17	0/1	-	0/1	-	-
P2	2/12	0/6	0/1	0/2	0/27	-	0/2	0/5	0/3	-
p3	3/17	0/4	-	2/6	0/19	0/2	-	0/2	-	-
P3	2/12	0/6	0/1	1/2	0/25	-	-	2/8	0/2	0/1
p4	2/16	0/4	-	3/6	0/16	-	-	1/2	-	-
P4	0/11	0/5	0/1	0/2	0/26	-	-	0/5	-	-
m1	3/20	0/5	-	0/4	0/17	0/2	-	0/6	-	-
M1	0/17	0/5	0/1	0/2	3/30	-	1/2	0/4	0/2	0/1
m2	2/17	0/4	-	0/3	6/15	0/2	-	0/4	-	0/1
M2	0/10	0/6	0/1	1/3	3/29	-	0/2	0/5	2/2	0/1
m3	1/9	0/5	-	2/3	4/14	-	-	0/4	-	0/1
M3	0/11	0/5	-	1/3	5/22	-	-	1/6	-	0/1
Total Permanent	16/164	0/58	0/5	12/42	21/257	0/7	1/6	4/52	2/9	0/6
Total Lower	15/136	0/41	-	10/38	19/131	2/9	-	1/22	-	0/9
Total Upper	6/112	11/93	0/5	4/25	20/206	-	1/10	3/38	0/12	0/7
Total All	21/248	11/134	0/5	14/63	39/337	2/9	1/10	4/60	2/12	0/16

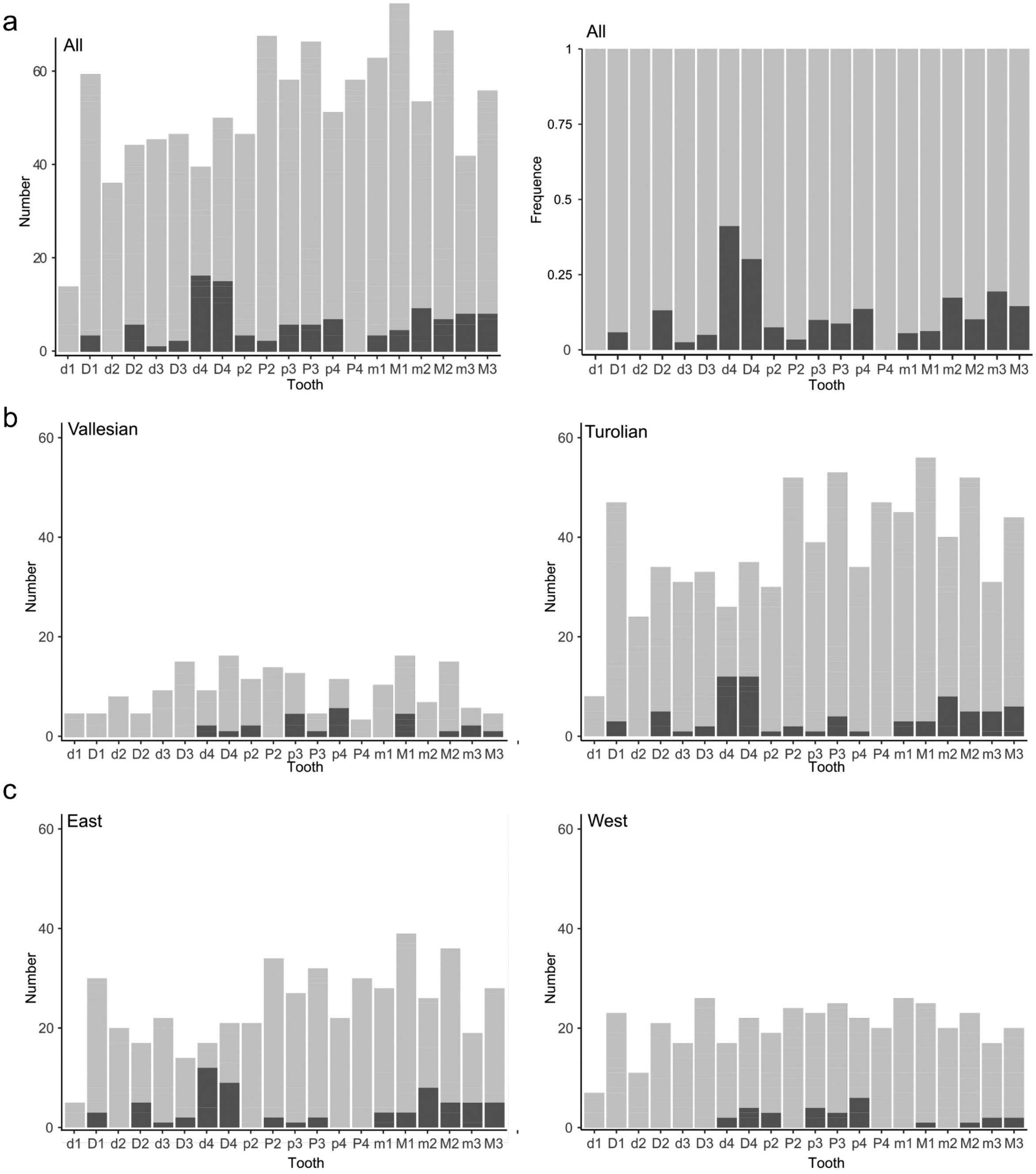

Figure 5. Prevalence of hypoplasia affecting the rhinocerotids of the Balkan-Iranian Province. a – Overall prevalence of hypoplasia (all specimens merged), in absolute numbers (left) and frequency (right). b – Comparison of the prevalence of hypoplasia at Vallesian localities (Pentalophos-1 and Xirochori; left) and Turolian ones (right). c – Comparison of the prevalence of hypoplasia at Eastern localities (Maragheh and Samos; left) and Western ones (right). Dark grey: hypoplastic teeth; Light grey: normal teeth.

affected are D1/d1 (3/63; 4.76%) and D3/d3 (3/79; 3.80%). We also found a relatively high prevalence for M2/m2 (14/105; 13.33%) and M3/m3 (14/84; 16.67%).

Once all localities and teeth are merged, *Ch. kiliasi* and *Ch. schlosseri* were the most affected species with both 22.22% of teeth bearing a defect (14/63 and 2/9 hypoplastic teeth respectively; Table 4), followed by *Ch. persiae* (39/337; 11.57%). The least affected species were *I. morgani* and the *Dihoplus* species from Slatino with no teeth hypoplastic (Table 4; Figure 6). Both two-horned rhinocerotine species, *Ce. neumayri* and *Dh. pikermiensis*, have similarly low overall hypoplasia prevalence, around 8% (21/248 and 11/134 hypoplastic teeth, respectively). All other species exhibit a similar prevalence, with around 7–9% of teeth being hypoplastic. Only one tooth out of ten (10%) is affected by hypoplasia for the *Chilotherium* sp. skull from Xirochori, and four teeth out of 60 (6.67%) for the *Acerorhinus* sp. specimens. No permanent tooth (0/58) is affected for *D. pikermiensis* but 14.47% (11/76) of milk teeth are hypoplastic.

Figure 5 highlights prevalence differences between Eastern localities (Samos and Maragheh) and Western ones (all others), and between Vallesian sites (Pentalophos-1 and Xirochori) and Turolian ones (all others). The Eastern localities presented twice as more frequent

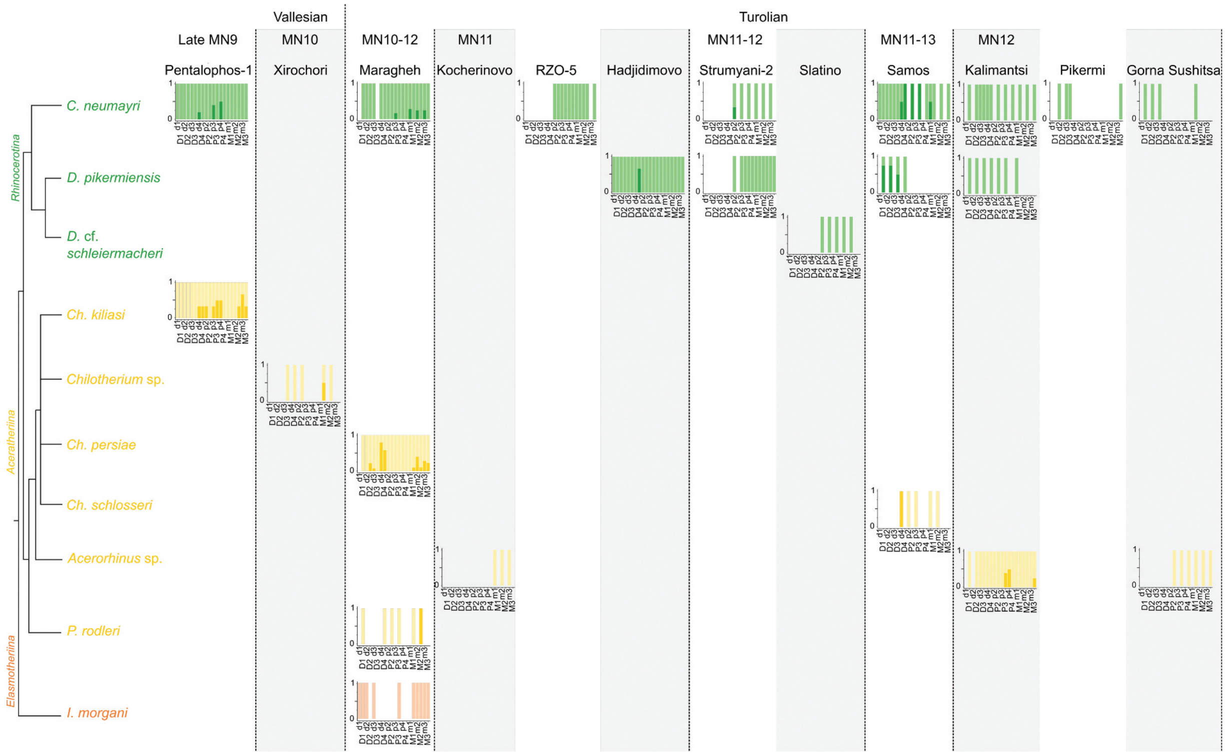

Figure 6. Compared prevalence of hypoplasia on rhinocerotid teeth from the Balkan-Iranian province by locality, species and tooth locus plotted against phylogeny. Barplots coloured by subtribes: green for Rhinocerotina, yellow for Aceratheriina, and Orange for Elasmotheriina; dark shades for hypoplastic teeth, light shades for teeth with no apparent hypoplasia. Phylogenetic relationships summarised from (Antoine 2002; Pandolfi 2016; Pandolfi et al. 2021; Antoine et al. 2022).

hypoplastic teeth in total (66/488; 13.52%) than the Western sites (28/406; 6.90%). Although it may not be obvious visually, rhinocerotids from Vallesian localities had a prevalence 1.5 times higher (20/123; 16.26%) than Turolian ones (74/761; 9.72%). The rhinocerotids from Samos were the most prone to hypoplasia with 27.94% (19/68) of their teeth bearing at least one defect. Hypoplasia was also frequent at Pentalophos-1 (19/123; 15.45%) and Maragheh (47/420; 11.19%). On the contrary, no hypoplasia was recorded in several localities having yielded only a few exploitable specimens, such as Gorna Sushista (two maxillaes, one skull), Kocherinovo (one mandible), Ravin des Zouaves (two skulls, one mandible), and Slatino (two maxillaes). The detail of hypoplasia counts and prevalence by species, locus, and locality is available in Supplementary S6.

The previous results are based on counts on each tooth as if it were isolated, but many specimens were mandibles and maxillaes (i.e, associated teeth). This means that some events of hypoplasia might have been counted more than once, as hypoplasia is likely to affect all co-developing teeth in a given individual, which may somewhat bias the interpretation of hypoplasia prevalence. For instance, 16.67% (2/12) of *Persiatherium rodleri* teeth present hypoplasia, but they all belong to the same skull, and both hypoplastic teeth (left and right M2) document the same hypoplasia event. Thus, Table 5 presents the results of hypoplasia prevalence when associated teeth are considered.

Overall, *Chilotherium* species seem to be particularly affected by hypoplasia. At Pentalophos-1, 66.67% of the specimens of *Ch. kiliasi* presented hypoplasia, while at Maragheh 47.06% of maxillaes and mandibles had at least one defect. Specimens of *Ce. neumayri* and *Dh. pikermiensis* at all localities seem less affected than the chilotheres. Nearly all dental material studied from Samos displayed hypoplasia, while at Kalimantsi only three remains, all of *Acerorhinus* sp, were affected (Table 5).

Clear phylogenetic differences are also evident on Figure 6. Although both restricted in specimens and species, the Elasmotheriina seem really spared by hypoplasia, a result also noted in other early to middle Miocene species (Hullot et al. 2022). On the contrary, Aceratheriina are very prone to having hypoplastic defects. Eventually, Rhinocerotina species are more or less affected depending on the locality. This could suggest that hypoplasia in this tribe reflects more the local conditions rather than a specific susceptibility to stress.

GLMM

For all response variables (Hypo, Defect, Multiple, Localisation, and Severity), model support increased (lower AIC) when intraspecific factors (e.g, Tooth Loci, Genus) were included. When Genus was not forced into the models, the final models contained two to seven factors, including Specimen, the random factor, by default in all models. Defect (converted to a factor) was in the final models of all concerned variables (Multiple, Localisation, and Severity). Age and Province were in the final models of Hypo and Defect, and Position was in that of Hypo and Localisation. Details and comparison of all models can be seen in electronic supplementary material S3 and S5.

Based on GLMMs results, we can investigate the influence of Province and Age on the hypoplasia pattern. Rhinocerotid teeth from Western localities are less affected by hypoplasia

Table 5. Number of rhinocerotid specimens affected by hypoplasia per type (mandible + maxilla or isolated tooth), species, and locality. Localities with a null prevalence of hypoplasia not shown in this table. – stands for no material available.

		Maxillaes and mandibles	Isolated teeth
Pentalophos-1			
	Ceratotherium neumayri	2/10	1/1
	Chilotherium kiliasi	6/9	-
Xirochori			
	Chilotherium sp.	1/1	-
Maragheh			
	Ceratotherium neumayri	1/6	4/19
	Chilotherium persiae	16/34	8/54
	Iranotherium morgani	0/5	0/5
	Persiatherium rodleri	1/1	0/1
Hadjidimovo			
	Dihoplus pikermiensis	1/9	0/9
Strumyani-2			
	Ceratotherium neumayri	1/2	-
	Dihoplus pikermiensis	0/2	-
Samos			
	Ceratotherium neumayri	2/5	-
	Dihoplus pikermiensis	2/2	-
	Chilotherium schlosseri	1/1	-
Kalimantsi			
	Acerorhinus sp.	3/7	0/3
	Ceratotherium neumayri	0/5	-
	Dihoplus pikermiensis	0/4	0/5
Pikermi			
	Ceratotherium neumayri	-	0/5
	Dihoplus pikermiensis	1/2	0/1

(p-value = 2.2 x 10^{-4}) than those from Eastern localities (Samos and Maragheh), but no significant differences in the nature of the defects were found. Vallesian rhinocerotids (from Pentalophos-1 and Xirochori) are more prone to hypoplastic defects on their teeth than Turolian ones (p-value = 1.03 x 10^{-3}), and the type of defects is also different (p-value = 9.21 x 10^{-3}). The only interspecific differences detected were between *Ce. neumayri* and *Dh. pikermiensis* (p-value = 0.036) or *Acerorhinus* (p-value = 0.052). Concerning tooth loci, all teeth but P4/p4 presented less hypoplastic defects than D4/d4 (p-values ≤ 0.001; except for M2/m2: p-value = 0.011 and M3/m3: p-value = 0.045).

Other effects were also observed. For instance, upper teeth tended to have less defects than their lower counterparts (47/508 and 47/386 teeth affected, respectively; p-value = 0.045), and the defects are less frequently observed on the labial side (p-value = 0.016). Besides between upper and lower teeth, no difference in defect localisation (labial vs. lingual) was observed (p-values > 0.3). Concerning defect type, LEHs were more frequently multiple than pits, aplasia and other types of defects. LEH were also more often severe than pits or other defects (p-values < 0.02). Concerning pits, this result might be due to the way pits are recorded in the first place (i.e, several pits identified as a single hypoplasia event) and their aetiology (less ameloblasts disrupted than for LEH or aplasia).

Discussion

Dietary preferences of the studied specimens

Regarding DMTA, seven rhinocerotid species belonging to four genera (*Ceratotherium, Dihoplus, Chilotherium, Acerorhinus*) were studied. The reconstructed dietary preferences are detailed by locality and by species in Table 6.

The dental microwear texture profile (Figure 4) of *Ceratotherium neumayri*, with few specimens displaying high values of anisotropy (> 5 x 10^{-3}; grinding: 4/16; shearing: 4/9) and complexity (> 2; grinding: 4/16; shearing: 0/9), suggests quite soft food items and excludes pure grazing for the concerned individuals (except for the specimen of Samos). The moderate-to-high mean values of HAsfc9 and HAsfc81 at all sites (Table 3) point towards a certain intra-individual dietary versatility, incompatible with a monotypic diet such as pure grazing and strict folivory (Scott 2012; Ramdarshan et al. 2016; Merceron et al. 2018; Hullot et al. 2019), two dietary behaviours also excluded regarding the differences with the extant grazer *Ceratotherium simum* highlighted by GLMMs. Our results are instead compatible with a mixed-feeding behaviour. Such a diet is consistent with statements from the literature, as many authors stated that strict grazing similar to that of extant white rhinoceros (*Ceratotherium simum*) was very unlikely (Guérin 1980; Geraads and Koufos 1990; Giaourtsakis et al. 2006; Geraads and Spassov 2009) although this rhinoceros has adaptations to low-level vegetation (Geraads and Spassov 2009). The only other microwear (2D) study including this species (Solounias et al. 2010), suggested a grazing behaviour, contrary to our present specimen from Pikermi, but the study also included only one tooth from Pikermi (Figure 4).

Chilotherium species are also thought to be non-specialist grazers (Geraads and Koufos 1990; Geraads and Spassov 2009). Our results show a wide range of anisotropy values (Figure 4), and moderate-to-high Hasfc means (Table 3) for species assigned to this genus, recalling the microwear textures of *Ce. neumayri*. This suggests a similar mixed-feeding behaviour for *Chilotherium* spp. and *Ce. neumayri*. Therefore, competition for food resources may have occurred between these species around the localities where they co-occur (e.g, Samos, Maragheh, Pentalophos-1, and Gorna Sushitsa). However, several specimens of *Ch. persiae* (Maragheh; n = 6/13) and all of *Ch. kiliasi* (Pentalophos-1; n = 2/2) display high values of complexity (> 2) on the grinding facet, contrary to *Ce. neumayri*. This suggests the inclusion of harder browse items in the diet of these chilotheres, either due to competition (shift in the diet in harsh conditions) or to resource partitioning. In a previous study, the mesowear score of *Ch. persiae* (MS = 0.3; n = 12) even suggested browsing preferences for this quite high-crowned rhinocerotid (Jokela 2015).

Dihoplus pikermiensis has a browsing signature, with low values of anisotropy and moderate values of complexity (Figure 4), as expected based on the low-crowned cheek teeth of this rhinocerotine (Guérin 1980; Giaourtsakis et al. 2006; Geraads and Spassov 2009). The preliminary results (n = 3 from Pikermi) of 2D microwear from Solounias et al. (2010) pointed towards a grazing behaviour. This discrepancy can be explained by a sampling bias due to the restricted number of specimens in both studies. Thus, our results suggest that the main rhinocerotids of the Pikermian Biome, *Dihoplus pikermiensis* and *Ceratotherium neumayri*, had different dietary preferences and food niches, further reflected in their microwear textures, and as already proposed by previous studies (Giaourtsakis et al. 2006; Spassov et al. 2006; Geraads and Spassov 2009).

Table 6. Dietary preferences as inferred from textural microwear (DMT) of the studied rhinocerotid specimens from different fossil localities of the Balkan-Iranian province. Colour/Abbreviation code: brown/B – browser, blue/M – mixed-feeder, green/G – grazer, no colour/x – not studied here.

	Pentalophos-1	Xirochori	Maragha	Kocherinovo	Ravin des Zouaves 5	Hadjidimovo	Strumyani-2	Slatino	Samos	Kalimantsi	Pikermi	Gorna Sushitsa
Rhinocerotinae												
Ceratotherium neumayri	B		M		M		B		G	M	B	x
Dihoplus pikermiensis						B	B		B	B	B	
Dihoplus cf. *schleiermacheri*								x				
Chilotherium kiliasi	M											
Chilotherium persiae			M									
Chilotherium schlosseri									M			
Chilotherium samium									x			
Chilotherium sp.		M										x
Acerorhinus sp.				B				x		x		B
Acerorhinus neleus											x	
Persiatherium rodleri			x									
Brachypotherium sp.										x		
Elasmotheriinae												
Iranotherium morgani			x									

Our restricted pool of *Acerorhinus* sp. specimens points towards browsing or mixed-feeding behaviour. Browsing has already been proposed for some species of these genus based on dental morphology. Indeed, representatives of *Acerorhinus* have brachydont, non-prismatic crowns suggesting a diet based primarily on non-fibrous and non-abrasive food (i.e, browsing; Athanassiou et al. 2014). Moreover, the strong cingulum on the teeth might suggest the consumption of branches and thorns, as this structure has been proposed as gingiva protection during mastication of such hard objects (Heissig 2012). The consumption of hard objects should result in high values of complexity, as observed on the grinding facet of the specimen from Kocherinovo and one other from Kalimantsi. A browsing diet is also consistent with the reconstructed landscape at Kocherinovo, as dominated by open woodland and shrubland (Hristova et al. 2013).

Interestingly, all rhinocerotid species at Maragheh – *Ce. neumayri, Ch. persiae, I. morgani* (DMT not studied), and *P. rodleri* (DMT not studied) – are relatively hypsodont and adapted to open and dry environments (Pandolfi 2016). However, the link between hypsodonty and grazing is controverted. Indeed, hypsodonty might be either a way to compensate for the ingestion of more food due to poor nutritional quality, and/or a way to consume a greater diversity of resources, or even protect from excessive abrasion due to exogenous abrasive loads in open and dry environments (Semprebon and Rivals 2007; Damuth and Janis 2011; Jardine et al. 2012; Semprebon et al. 2019). A mixed-feeding diet has, for instance, been proposed for the subhypsodont elasmotheriines *Hispanotherium beonense* from Béon 1 (MN4; France) and *Hispanotherium* cf. *matritense* from Gračanica (MN5; Bosnia-Herzegovina), based on dental wear (micro- and meso- wear) data (Xafis et al. 2020; Hullot et al. 2021). Moreover, our DMTA results for *Ce. neumayri* and *Ch. persiae*, do not support a pure grazing diet for neither of them and suggest a potential niche partitioning or dietary shift due to competition.

Interactions with other mammalian herbivores

In addition to rhinocerotids, the fossil localities studied have yielded many other mammalian herbivores species such as other perissodactyls, artiodactyls and proboscideans (NOW Database 2020 and citations therein), as well as micro-herbivores (rodents, lagomorphs) but very few is known about their palaeoecology. Faunal lists by locality are detailed in Supplementary S1. Although co-occurrence is not a good proxy for ecological interactions (Blanchet et al. 2020), it is possible that some of these herbivores were competing for or partitioning food resources with the rhinocerotids. Niche partitioning can take place through different strategies, such as resources partitioning, living in different habitats, having different body masses or different feeding heights (Hutchinson 1959; Schoener 1974; Arsenault and Owen-Smith 2008).

Most species of perissodactyls (beside rhinocerotids) found in the studied localities are hipparions (*Cremohipparion, Hipparion*, and *Hippotherium*), as tapirs are relatively rare (Koufos 2006) and chalicotheres limited in number (S1). Exploitation of C3 grasses (mixed-feeding and grazing) is suggested by microwear analyses of several hipparion species from Samos and Pikermi (Koufos et al. 2009b; Solounias et al. 2010), as well as from Hadjidimovo, Kalimantsi, and Strumyani (Clavel et al. 2012), although most species do not fully rely on this resource (mixed-feeders; Orlandi-Oliveras et al. 2022). Regarding chalicotheres, *Ancylotherium* *pentelicum* studied at Pikermi and Samos, but also present at Hadjidimovo, Kalimantsi and Maragheh, has a dental microwear indicating the inclusion of harder objects such as branches or bark (Semprebon et al. 2011). Thus, it appears that hipparions, chalicotheres, and rhinocerotids exploited quite different niches, suggesting little or no competition for resources.

Artiodactyl species are also very common at the localities studied, and this clade is often considered to be a competitor of perissodactyls (Janis 1976). Indeed, the microwear signature of most bovids species points towards browsing or mixed-feeding preferences (Merceron et al. 2006; Solounias et al. 2010; Clavel et al. 2012), similarly to what is found for rhinocerotids. However, some artiodactyls (e.g, some bovids and giraffids) from Greek localities (Samos, Pikermi, Axios Valley) seem to have been grazers, a feeding preference not occupied by the rhinocerotids studied here (Quade et al. 1994; Merceron et al. 2007, 2018; Solounias et al. 2010). In contrast, no strictly grazing bovid species are found at Hadjidimovo, nor at Kalimantsi according to dental microwear and enamel carbon stable isotopes composition (Merceron et al. 2006).

Concerning proboscideans, *Choerolophodon* is the most abundant genus in our localities (*C. anatolicus* at Pentalophos-1, *C. pentelici* at Ravin des Zouaves-5, Xirochori, Pikermi and Samos; S1). Other proboscidean species are also found in the region (e.g, *Mammut* sp, *Deinotherium giganteum*), but they are not included in former studies dealing with the relevant deposits (e.g, Solounias et al. 2010). The dental microwear texture of both *Choerolophodon* species from the Axios Valley supports the consumption of herbaceous monocotyledons, consistent with the arid climatic conditions and the absence of this genus in Central, Western and Northern Europe (Konidaris et al. 2016). In his master's thesis, Loponen (2020) also finds a grass preference for *C. pentelici* from Maragheh using the mesowear angle. Thus, it is unlikely that *Choerolophodon* and rhinocerotids were competing for food resources on a yearly base. Such a niche partitioning is observed today between the Asian elephant (*Elephas maximus*) and the sympatric Indian rhinoceros (*Rhinoceros unicornis*), but not between the African bush elephant (*Loxodonta Africana*) and the black rhinoceros (*Diceros bicornis*) competing for browse resources at the expenses of the rhinoceros (Landman et al. 2013).

Stress susceptibility

The prevalence of hypoplasia on late Miocene rhinocerotid teeth from the localities studied here is overall low (10.51%). There are, however, great discrepancies depending on the locality, species, and tooth locus considered. Most localities had a null (Ravin des Zouaves-5, Gorna Sushitsa, Kocherinovo, Slatino) or very low (< 5%; Hadjidimovo, Kalimantsi, Pikermi, Strumyani-2) prevalence of hypoplasia, contrasting with the higher prevalences at Xirochori (10%), Maragheh (11.19%), Pentalophos-1 (15.45%), and Samos (27.94%). In the literature, hypoplasia in rhinocerotids has been reported in several sites, mostly of Pleistocene age (Bratlund 1999; Fourvel et al. 2015; Bacon et al. 2018). The prevalence and loci affected vary greatly, from nearly no teeth affected (e.g, Siwalik rhinocerotids, middle and late Miocene of Pakistan; Antoine in press) to more than 25% being hypoplastic at Coc Muoi (Pleistocene, Vietnam; 26.8% of rhinocerotid teeth affected and mostly permanent ones; Bacon et al. 2018), Béon 1 (late early Miocene, France; 25.96%; Hullot et al. 2021) or Gračanica (early middle Miocene, Bosnia-Herzegovina; 48.39%; Hullot et al. 2022).

The most affected loci were D4/d4 overall. These loci frequently bear hypoplasia at various localities (> 20% at Pentalophos-1, Maragheh, Samos, Pikermi) and for several species (15 to 59% of the D4/d4 of *Ce. neumayri, Dh. pikermiensis, Ch. persiae*). Hypoplasias on D4/d4 have already been noticed as frequent in rhinocerotids (Mead 1999; Hullot et al. 2021), and correlated to birth related stresses. Hypoplasia was also common on second and third molars overall. However, hypoplasia on these loci was restricted to rhinocerotids from Maragheh (*Ch. persiae, Ce. neumayri*, and *P. rodleri*), *Ch. kiliasi* from Pentalophos-1, and *Acerorhinus* sp. from Kalimantsi (Supplementary S5). Enamel hypoplasia on second and third molars have been correlated with environmental stresses (and not pre-weaning or pre-birth stress as those teeth mostly mineralise after the weaning), like seasonality, in extant sheep (Upex and Dobney 2012) and in an extinct giraffid (Franz-Odendaal et al. 2003). Seasonality is also likely to induce hypoplasia at these loci in rhinoceroses, as these teeth are the last to develop in rhinocerotids and may thus record post-weaning stresses (Hitchins 1978; Hillman-Smith et al. 1986; Böhmer et al. 2016). At all three sites certain aridity and seasonality are mentioned (Merceron et al. 2006, 2007; Geraads and Spassov 2009; Ataabadi et al. 2016) and could have been responsible for punctual stresses, such as food scarcity or drought.

Chilotherium species in general seem particularly susceptible to hypoplasia with 13.37% of the teeth being affected (56/419), and more than 20% for *Ch. schlosseri* at Samos (2/9; 22.22%) and for *Ch. kiliasi* at Pentalophos-1 (14/63; 22.22%). While at Samos, investigated rhinocerotid teeth seem to be particularly affected regardless of their taxonomic assignment, suggesting a particularly stressful environment in general, the situation is much more contrasted at Pentalophos-1 with *Ce. neumayri* relatively spared (5/60; 8.33%). These discrepancies between rhinocerotids from the same locality may therefore highlight specific susceptibilities to hypoplasia. The dental loci affected at Pentalophos-1 suggest early life stresses only for *Ce. neumayri* (d4, p3, p4), while *Ch. kiliasi* teeth present both early life stresses and seasonality-related ones (m2/M2 and m3/M3). Interestingly, DMT patterns suggested a potential competition between these species, which may have led to a dietary shift in *Ch. kiliasi* during period of shortage. Such a competition could be the cause of some of the observed hypoplasias. As opposed to chilothere species, *Dh. pikermiensis* presents very few hypoplastic teeth with the notable exception of Samos (where 8/16 teeth are hypoplastic), and no permanent tooth affected (0/58). Our results point towards less susceptibility to stresses in the studied elasmotheriine (*Iranotherium*, no hypoplasia recorded), Rhinocerotini (*Ceratotherium* + *Dihoplus*), contrary to the Aceratheriini (*Chilotherium* + *Acerorhinus*).

Impact of spatial (longitude), temporal, and environmental variations

We found that Western localities rhinocerotids were less affected by hypoplasia than their Eastern counterparts (Samos and Maragheh). This could be linked to the increased aridity towards the East (Fortelius et al. 2002; Giaourtsakis et al. 2006; Strömberg et al. 2007; Eronen et al. 2009; Athanassiou et al. 2014), creating harsher and more stressful conditions for the fauna, with punctual resource shortage. These drier conditions are supported by the presence of more hypsodont and mesodont forms at Maragheh and Samos than at Pikermi, but a clear aridity gradient from West to East has been disputed (Ataabadi et al. 2013). Similarly, Vallesian rhinocerotids (from Pentalophos-1 and Xirochori) are more prone to hypoplastic defects (20/123; 16.26%) than Turolian ones (74/761; 9.72%). During the Vallesian, climatic conditions changed drastically from a washhouse episode (10.2 to 9.8 Mya) to a cooler and drier phase

(9.7 to 9.5 Mya; Böhme et al. 2008). This event is known as the Vallesian crisis and resulted in a higher seasonality with cold winters and punctual unavailability of fruit resources, often associated with the extinction of hominoid species in Europe (Agustí et al. 2003), and resulted in more open environments (de Bonis et al. 1992a, 1992b). Interestingly, both Vallesian sites from the Axios-Valley are roughly coeval with this crisis (Pentalophos-1, late MN9 and Xirochori ~ 9.6 Mya; Koufos 2006).

Some authors, however, challenged the temporal homogeneity of this aridification event at the European scale, and suggested that Southeastern Mediterranean localities experienced it earlier, during the earliest late Miocene (11 Mya), and already had quite open and dry environments during the Vallesian interval (Koufos 2006), although aridity increased in the second half of the Turolian (Böhme et al. 2017). The high prevalence observed for enamel hypoplasia could thus only document relatively harsh conditions for rhinocerotids around these localities instead of the Vallesian crisis itself. The inclusion of more Vallesian localities from Southeastern Mediterranean region and the investigation of hypoplasia in other non-related taxa could help discriminate between these two hypotheses.

Concerning dietary preferences, no clear differences were observed neither between the species of both regions nor within species at different localities (Figure 4). This finding was surprising regarding previous studies and inferences. In Southern Bulgaria, a gradual aridification – notably between Hadjidimovo and Kalimantsi – is suggested by changes in dental microwear signals of bovids and by the presence of the open-habitat specialist *Ce. neumayri* in latter localities (Merceron et al. 2006; Geraads and Spassov 2009; Clavel et al. 2012). We did not observe such differences in the microwear textures of the studied rhinocerotids. Moreover, a series of adaptations are observed in the *Ce. neumayri* lineage (e.g, the gradual size growth, lengthening and lowering of the skull), linked with increasingly open and/or seasonal environments and their nutritionally inferior forage, indicating a probable progressive shift in the diet towards a coarser, mixed diet (Giaourtsakis 2009). Once again, we did not retrieve such a pattern in our DMTA results, but our sampling was restricted and DMTA unravel short-term insights of the diet.

Broader implications: palaeoenvironments, and the so-called 'Pikermian Biome'

Although our results did not suggest drastic differences in the feeding strategies of the rhinocerotids studied here, either over time or space, the hypoplasia prevalence highlighted probable discrepancies in the local conditions. Thus a space and time continuum of the ecosystems throughout the Balkan-Iranian province as hypothesised by the 'Pikermian Biome' *sensu* Solounias et al. (1999) is not supported.

The absence of true grazing rhinocerotids suggested by our DMT analyses is consistent with previous palaeoecological reconstructions based on tooth wear, carbon stable isotopes on enamel, phytoliths, and functional morphology that indicate very few C4-grasses in Turolian localities of the region (Strömberg et al. 2007). Similarly, a truly open savanna environment is very unlikely regarding our DMTA results, as most rhinocerotid species studied here must have greatly relied on browse resources. Due to Miocene climatic conditions (globally hot and wet) and low altitude, a C3 grassland is also doubtful (Solounias et al. 1999; Denk et al. 2018). These findings contradict the classical savanna biome proposed for the Pikermian fauna, as already tackled and discussed by several authors (Solounias et al. 1999; Athanassiou et al. 2014). The dietary preferences of the whole fauna are also way more diversified than in modern African savannas and they would more closely resemble modern Indian woodlands (Solounias et al. 1999, 2010). Despite the increased aridity and a tendency towards habitat openness, late Miocene terrestrial environments of the eastern Mediterranean were more likely dry woodlands or forests rather than grasslands (Strömberg et al. 2007; Clavel et al. 2012; Böhme et al. 2017, 2018; Spassov et al. 2018).

Conclusions

The study of the trophic palaeoecology of some late Miocene rhinocerotids from the Balkans (Greece and Bulgaria), Samos (Aegean region), and Maragheh (Iran) indicated clear spatio-temporal differences in the local conditions, as suggested by hypoplasia prevalence. The study of dietary preferences (dental microwear texture) confirmed the niche partitioning of the two most abundant species, i.e, *Ceratotherium neumayri* (mixed-feeder) and *Dihoplus pikermiensis* (browser). The combination of hypoplasia and DMT analyses highlighted potential competition between *Ce. neumayri* and associated chilothere species at the locality where they co-occur (Samos, Maragheh, Pentalophos-1). The dominance of rhinocerotid species depending on browse resources (leaves, branches, and fruits) seems to contradict the classical reconstitution of African savannah-type environments in the area in question. Thus, the palaeoecological insights provided by the rhinocerotid sample studied here allowed to somewhat challenge the concept of Pikermian Biome and Balkan-Iranian province, supposedly homogeneous over time and space.

Acknowledgments

We are indebted to the curators in charge of all the collections we visited: Dr. U. Göhlich (NHMW), Dr. N. Nedyalkov (PMA), Dr. L. Hristova (NMNHS), and Dr. L. Costeur (NHMB).

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the SYNTHESYS [AT-TAF-65]; Project PICS CNRS [IEA 08245];Doctoral Mobility Grant - Ecole Doctorale GAIA (n°584).

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