Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes

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Abstract

Major climatic and ecological changes are documented in terrestrial ecosystems during the Miocene epoch. The Rhinocerotidae are a very interesting clade to investigate the impact of these changes on ecology, as they are abundant and diverse in the fossil record throughout the Miocene. Here, we explored the spatio-temporal evolution of rhinocerotids' paleoecology during the early and middle Miocene in Europe and Pakistan. We studied the dental texture microwear (proxy for diet) and enamel hypoplasia (stress indicator) of 19 species belonging to four sub-tribes and an unnamed clade of Rhinocerotidae, and coming from nine Eurasian localities ranging from MN2 to MN7/8. Our results suggest a clear niche partitioning based on diet at Kumbi 4 (MN2, Pakistan), Sansan (MN6, France), and Villefranche d'Astarac (MN7/8, France), while ~~dietary~~ overlap and subtle variations are discussed for Béon 1 (MN4, France) and Gračanica (MN5/6, Bosnia-Herzegovina). All rhinocerotids studied were browsers or mixed-feeders, and none had ~~a~~ grazing ~~nor~~ frugivore diet. ~~Regarding hypoplasia, the~~ prevalence was ~~moderate (~~ 10%~~)~~ to ~~high (~~> 20 %~~)~~ at all localities but Kumbi 4 (~ 6 %), and documented quite well the local conditions. Sansan and Devínska Nová Ves (MN6, Slovakia), both dated to the MN6 (i.e., by the middle Miocene Climatic Transition, ca. 13.9 Mya), had moderate hypoplasia prevalence. Besides locality, species and tooth locus were also important factors of variation for the prevalence of hypoplasia. The very large hippo-like *Brachypotherium brachypus* was

one of the most affected species at all concerned localities (but Sansan), while early-diverging elasmotheriines were very little affected.

Keywords: paleoecology, Miocene Climatic Optimum (MCO), microwear (DMTA), enamel hypoplasia

Introduction

The Miocene is a key period in Earth and rhinocerotid evolutionary histories. Climatic conditions in Eurasia during the Miocene epoch are globally tropical and the typical habitat is forested (Cerling et al., 1997; Zachos et al., 2001; Bruch et al., 2007; Westerhold et al., 2020). It is the last warm episode of the Cenozoic era, although marked by great climatic changes prefiguring the setup of modern cold conditions (Westerhold et al., 2020). During early Miocene times, temperatures increased until reaching the Miocene Climatic Optimum (MCO) between ~17 to 14 Mya (corresponding to the late Burdigalian + Langhian standard ages; Westerhold et al., 2020). This optimum is followed by an abrupt cooling (the middle Miocene climatic transition [mMCT]; Westerhold et al., 2020) associated with faunal turnovers in Eurasia (Böhme, 2003; Maridet et al., 2007). The middle Miocene is marked by a relative aridity, associated with a global cooling (Bruch et al., 2007; Böhme et al., 2008).

Concerning rhinocerotids, Miocene times witness peaks in their alpha diversity about 22–18 Mya and 11–10 Mya (Antoine et al., 2010; Antoine and Becker, 2013; Antoine, in press). During the early and middle Miocene in Eurasia, four sub-tribes of Rhinocerotidae are encountered – Rhinocerotina, Teleoceratina and Aceratheriina (Rhinocerotinae), and Elasmotheriina (Elasmotheriinae) – and species of which are often found associated in fossil-yielding localities (Antoine et al., 1997, 2010; Heissig, 2012; Becker and Tissier, 2020; Antoine, 2002, in press). This abundance and the potential cohabitation of such large herbivores question habitat capacity and competition for food resources. However, the ecology of the rhinocerotids has rarely been explored or only been assumed based on morphological adaptations (Prothero et al., 1989; Prothero, 2005; Giaourtsakis et al., 2006). If the Rhinocerotina appear to be ecologically varied, the literature suggests a similar ecology for most elasmotheriines on one hand, as open environment dwellers adapted to though vegetation (Iñigo and Cerdeño, 1997; Antoine and Welcomme, 2000), and for the teleoceratines on another hand, as hipp

like rhinoceroses inhabiting lake side or swamps and probably browsing on low vegetation or even grazing (Prothero et al., 1989; Cerdeño, 1998).

In this article, we focused on the rhinocerotids from nine localities, covering wide temporal and geographical ranges (from MN2 to MN7/8 and from southwestern France to Pakistan). We assessed dietary preferences using dental microwear texture analysis, and stress sensibility via the study of enamel hypoplasia.

Material and methods

We studied the rhinocerotid dental remains from nine early and middle Miocene localities from France (Béon 1, Béon 2, Sansan, Simorre, and Villefranche d'Astarac), Germany (Steinheim am Albuch), Bosnia-Herzegovina (Gračanica), Slovakia (Devínska Nová Ves Spalte), and Pakistan (Kumbi 4, Balochistan), ranging from MN2 to MN7/8. The rhinocerotid assemblages are detailed in Table 1. The specimens are curated at the Naturhistorisches Museum Wien (NHMW), the Muséum de Toulouse (MHNT), and the Naturhistorisches Museum Basel (NHMB). For all details on the specimens included in this study see Supplementary S1. The localization of the studied localities is given in Figure 1. Further details on the localities are given in Supplementary S2.

Dental Microwear Texture Analyses (DMTA)

Dental Microwear Texture Analysis (DMTA) is ~~a powerful~~ approach to characterize dietary preferences at a short time scale (days to weeks prior the death of the individual; Hoffman et al., 2015; Winkler et al., 2020), widely used in paleontological and archeological studies (Grine, 1986; Rivals et al., 2012; Jones and DeSantis, 2017; Berlioz et al., 2018). We studied dental microwear texture on one well-preserved molar (germs and over-worn teeth excluded) per individual, preferentially the second molar (first or third otherwise), either upper or lower, left or right.

After cleaning the tooth with acetone or ethanol, two silicone (Regular Body President, ref. 6015 - ISO 4823, medium consistency, polyvinylsiloxane addition type; Coltene Whaledent) molds were made on a single enamel band, which shows two different facets acting as grinding and shearing (if present).

This shearing facet has a steep slope while the former is more horizontal and show several HSB band on the very enamel surface. To combine both type of facets with different functions indeed improves dietary reconstruction (Louail et al., 2021; Merceron et al., 2021). The enamel band on which we identified those two facets is localized labially near the protocone on upper molars and distally to the protoconid or hypoconid (if the protoconid is unavailable) on lower teeth (see supplementary S2).

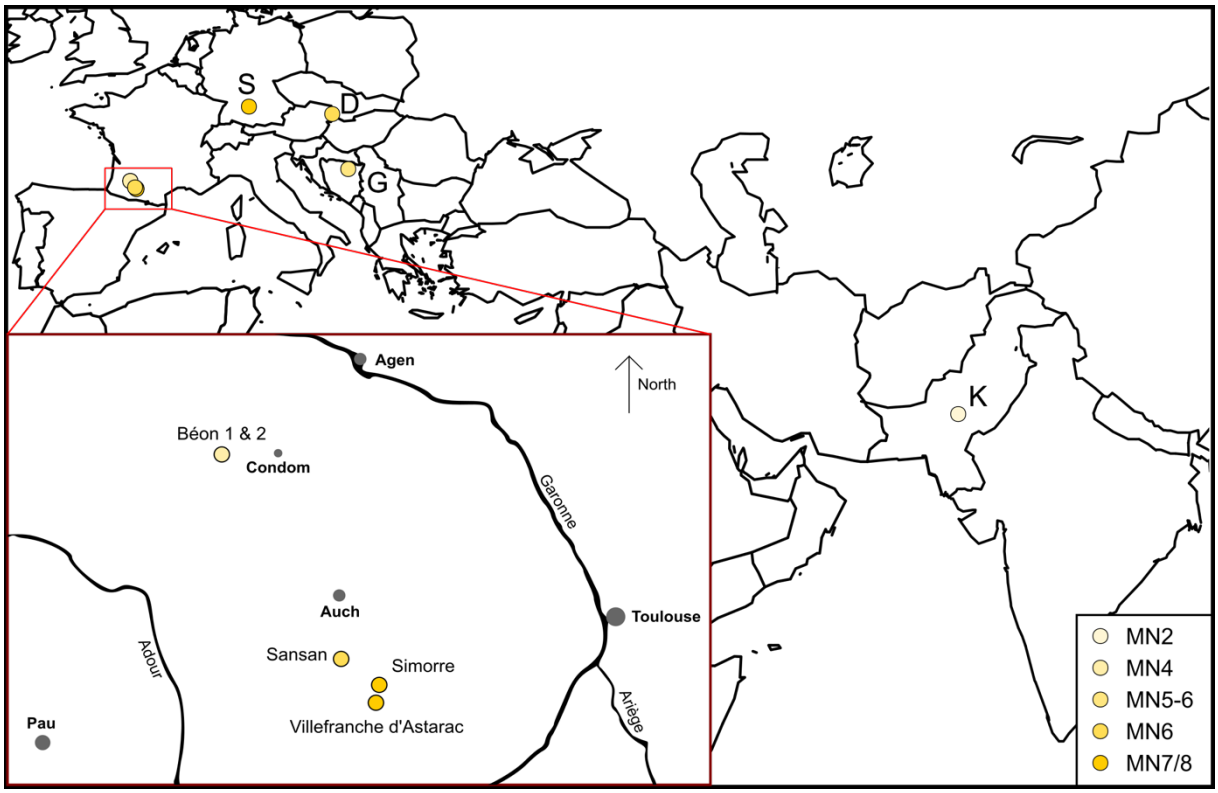

Figure 1: Geographical position of the studied Eurasian Miocene localities.

Localization of all localities in Eurasia. Red square is a zoom on the southwestern French localities, modified from Antoine and Duranthon (1997).

Color code by MN zones as detailed in A. Abbreviations from West to East: S- Steinheim am Albuch (MN7/8; Germany), D- Devínska Nová Ves Spalte (MN6; Slovakia), G- Gračanica (MN5-6; Bosnia-Herzegovina), K- Kumbi 4 (MN2; Pakistan).

105 **Table 1: List of rhinocerotid species found at each locality studied**

		Kumbi 4	Béon 2	Béon 1	Gračanica	Sansan	Devínska Nová Ves Spalte	Steinheim am Albuch	Simorre	Villefranche d'Astarac
Rhinocerotinae										
	Mesaceratherium welcommi	x								
	Pleuroceros blanfordi	x								
	Protaceratherium sp.	x								
	Protaceratherium minutum		x							
	Plesiaceratherium naricum	x								
	Plesiaceratherium mirallesi		x	x						
	Plesiaceratherium balkanicum				x		x			
	Plesiaceratherium sp.			x						
Aceratheriina										
	Hoploaceratherium tetradactylum					x				
	Alicornops simorrense					x		x	x	x
Rhinocerotina										
	Gaindatherium cf. *browni*	x								
	Lartetotherium sansaniense				x	x		x		
	Dicerorhinus steinheimensis						x	x		
Teleoceratina										
	Brachypotherium brachypus			x	x	x		x	x	x
	Brachypotherium gajense	x								
	Diaceratherium fatehjangense	x								
	Prosantorhinus douvillei		aff.	x						
	Prosantorhinus shahbazi	x								
Elasmotheriinae										
Elasmotheriina										
	Bugtirhinus praecursor	x								
	Hispanotherium beonense			x						
	Hispanotherium cf. *matritense*				x					
	Total	9	3	5	4	4	2	4	2	2

106

107

108 In this article we followed a protocol adapted from Scott et al. (2005, 2006) with sensitive-scale fractal
109 analyses. Molds were scanned with a Leica DCM8 confocal profilometer ("TRIDENT" profilometer
110 housed at the PALEVOPRIM, CNRS, University of Poitiers) using white light confocal technology with
111 a 100× objective (Leica Microsystems; Numerical aperture: 0.90; working distance: 0.9 mm). The

obtained scans (.plu files) were pre-treated with LeicaMap v.8.2. (Leica Microsystems) as follows: the surface was inverted (as scans were made on negative replicas), missing points (i.e., non-measured, less than 1%) were replaced by the mean of the neighboring points and aberrant peaks were removed (see details in the supplementary Information in Merceron et al., 2016b). The surface was then levelled, and we applied a polynomial of degree 8 removal of form to temper for Hunter-Schreger bands reliefs in the DMTA parameters. Eventually, we selected a 200×200-µm area (1551 × 1551 pixels) within the surface, which we saved as a digital elevation model (.sur) and used to extract DMTA parameters through Scale-Sensitive Fractal Analysis with SFrax (Surfract, www.surfract.com) and LeicaMap.

Here we focused on five classical DMTA parameters: anisotropy (exact proportion of length-scale anisotropy of relief; epLsar), complexity (area-scale fractal complexity; Asfc), heterogeneity of complexity (heterogeneity of area-scale fractal complexity here at 3×3 and 9×9; HAsfc9 and HAsfc81), and fine textural fill volume (here at 0.2 µm; FTfv). The description of theses parameters is available in Scott et al. (2006).

To facilitate DMTA interpretation for fossil specimen, we used specimens of the five extant rhinocerotid species. This extant dataset was modified from that of Hullot et al. (2019), as precised below, and consists of 17 specimens of *Ceratotherium simum* (white rhinoceros), four of *Dicerorhinus sumatrensis* (Sumatran rhinoceros), 21 of Diceros bicornis (black rhinoceros), 15 of *Rhinoceros sondaicus* (Javan rhinoceros; one new specimen), and five of *Rhinoceros unicornis* (Indian rhinoceros; one new specimen).

Enamel hypoplasia

Hypoplasia is a common defect of the enamel resulting from a stress or a combination of stresses occurring during tooth development (Goodman and Rose, 1990). It is a permanent, sensitive, but non-specific indicator of stresses either environmental (e.g., drought or nutritional stress; Skinner and Pruetz, 2012; Upex and Dobney, 2012), physiological (e.g., disease or parasitism; Suckling et al., 1986; Rothschild et al., 2001; Niven et al., 2004), and/or psychological (e.g., depression in primates; Guatelli-Steinberg, 2001).

Enamel hypoplasia was studied with the naked eye and categorization of the defects followed the *Fédération Dentaire Internationale* (1982) as linear enamel hypoplasia (LEH), pitted hypoplasia, or aplasia. We studied all cheek teeth, both deciduous and permanent, but excluded 62 teeth to avoid false negative and uncalibrated defects, as enamel was obscured (e.g., tooth unerupted in bone, sediment occluding), broken or worn out, or as identification was impossible. This left 1401 teeth studied for the hypoplasia analysis – 294 milk molars and 1107 permanent premolars and molars – from the nine localities. In parallel, qualitative data (tooth locus affected, position of the defect on the crown, and severity) and caliper measurements (distance of the defect from enamel-dentine junction, width if applicable) were taken (details in Supplementary S3). Type of defects recorded, and caliper measurements are illustrated in Figure 2.

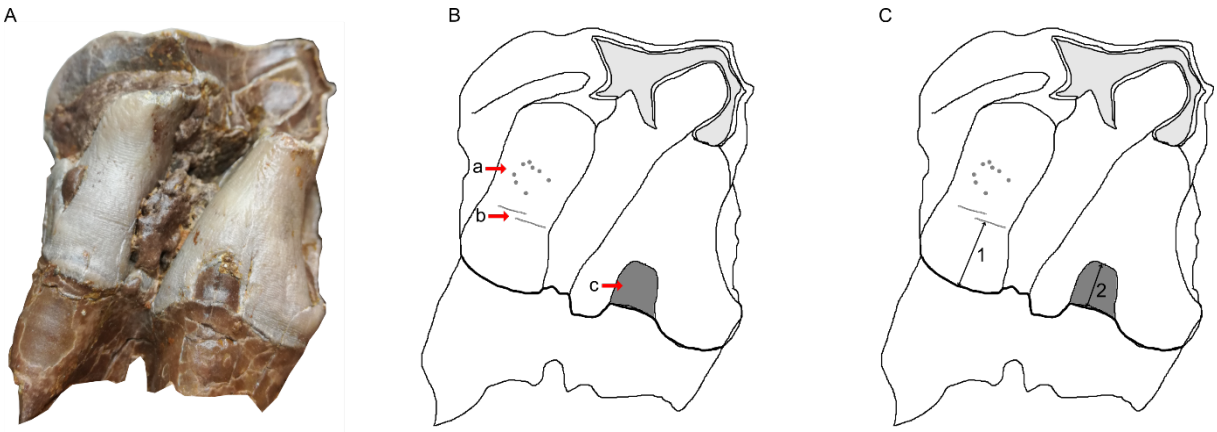

Figure 2: The three different types of hypoplasia considered in this study and the associated measurements

A- Lingual view of right M2 of the specimen MHNT.PAL.2004.0.58 (*Hispanotherium beonense*) displaying three types of hypoplasia

B- Interpretative drawing of the photo in A illustrating the hypoplastic defects: a- pitted hypoplasia, b- linear enamel hypoplasia, and c- aplasia

C- Interpretative drawing of the photo in A illustrating the measurements: 1- distance between the base of the defect and the enamel-dentin junction, 2- width of the defect (when applicable).

Figure from Hullot et al. (2021).

166 Statistics and GLMMs

167 Statistics were conducted in R (R Core Team, 2018: https://www.R-project.org/), equipped with the
168 following packages: reshape2 (Wickham, 2007), dplyr (Wickham et al., 2019), lme4 (Bates et al.,
169 2015), car (Fox et al., 2012), MASS (Venables and Ripley, 2002). According to the recent statement of
170 the American Statistical Association (ASA) on p-values (Wasserstein and Lazar, 2016; Wasserstein et
171 al., 2019), we avoided the use of the term “statistically significant” in this manuscript and the classical
172 thresholds as much as possible. Figures were done using R package ggplot2 (Wickham, 2011) as well
173 as Inkscape v.0.91.
174
175 General Linear Mixed Models (GLMM) on our data were constructed based on a R code modified from
176 Arman et al. (2019) and adapted to each tested response variable. An example of this code applied to
177 hypoplasia variable Hypo is given in Supplementary 4. DMTA response variables were the five DMTA
178 parameters (epLsar, Asfc, FTfv, HAsfc9, and HAsfc81) and we selected Gaussian family for the
179 GLMMs. Factors in the models were: specimen (number of the specimen; random factor), locality,
180 province, age (MN zones), genus, tooth (e.g., second molar, fourth milk molar), position (upper or
181 lower), side (left or right), cusp (protocone, protoconid, hypoconid), and facet (grinding or shearing).
182 For hypoplasia, response variables were Hypo (1 or 0 for presence or absence of hypoplasia,
183 respectively) for which we used Binomial family, Defect (e.g., LEH, Pits, Aplasia; converted to
184 numbers), Localization (position of the defect on the crown; mostly labial or lingual), Multiple (number
185 of defects), and Severity (0 to 4), modeled using Poisson family. The factors were: specimen (number
186 of the specimen; random factor), locality, province, age (MN zones), genus, tooth (e.g., first molar,
187 fourth premolar), position (upper or lower), side (left or right), and wear (low, average, high).
188 Additionally, for response variables Severity, Multiple, and Localization, defect was converted and
189 used as a factor.
190
191 The models were built with a bottom-up approach, starting with the only random factor of our dataset
192 alone (specimen) and adding factors incrementally for every set (e.g., 1|Specimen + Genus,
193 1|Specimen + Locality). New set was built has long as Akaike’s Information Criterion score (AIC) kept
194 decreasing. Few interactions (e.g., Genus x Facet for microwear, Genus x Tooth for hypoplasia) were
195 considered in the models, as most factors were considered independent and to avoid unnecessarily

196 complex and rarely selected models (Arman et al., 2019). We selected the best candidate model as
197 the one with the lowest AIC and checked for over-dispersion (estimated through the ratio of deviance
198 and degrees of freedom). If needed, we corrected it through quasi-Poisson or quasi-Binomial laws
199 from the MASS package (Venables and Ripley, 2002) or by adjusting the coefficients table (multiply
200 type error by square root of the dispersion factor and recalculate Z and p values accordingly). In total,
201 340 models were compared across the 10 response variables (see electronic supplementary material,
202 S5, S6, and S7).
203
204 **Results**
205
206 Microwear
207 MANOVA (Species x Facet x Age x Locality) on all five main DMTA parameters (epLsar, Asfc, FTfv,
208 HAsfc9, HAsfc81) revealed low p-values for Species (df = 14; p-value = 8.6×10^{-4}), Facet (df = 1; p-
209 value = 6.5×10^{-4}), and Locality (df = 4; p-value = 0.014). The ANOVAs for each parameter,
210 highlighted at least a marked influence of Species (all parameters; p-values between 7.3×10^{-4} and
211 0.027), Facet (Asfc, p-value = 0.028; FTfv, p-value = 6.22×10^{-6}), Age (Asfc, p-value = 7.57×10^{-3}), or
212 Locality (epLsar, p-value = 0.01; Asfc, p-value = 1.7×10^{-4}). To precise the differences for Species and
213 Locality (factors with more than two states) we ran post hocs, results of which are detailed in Table 2
214 and Table 3. The more conservative post hoc (Tukey's honestly significant difference; HSD) revealed
215 very few noticeable differences in the microwear textures of the studied rhinocerotid specimens by
216 Species or Locality (low p-values relatively to other pairs; Table 2). The DMT of *Hoploaceratherium*
217 *tetradactylum* appears quite distinct from that of *Plesiaceratherium* spp. (epLsar, Asfc, HAsfc9 and
218 HAfsc81). Concerning Locality, Gračanica specimens stood out with very low values of complexity
219 compared to Sansan (p-value = 0.047), Simorre (p-value = 0.028), and Villefranche d'Astarac (p-value
220 = 0.032).
221
222 The least conservative post hoc (Fischer's least significant difference; LSD) highlighted more
223 differences in the DMTA patterns of the specimens regarding Species and Locality (Table 3).
224 *Alicornops simorrense* and *P. mirallesi* cluster together with higher anisotropy than *P. douvillei*, *B.*
225 *brachypus*, *B. gajense*, *M. welcommi*, *D. steinheimensis*, *H. tetradactylum*, and *L. sansaniense* (Table

3; p-value < 0.05). Concerning complexity, *B. gajense* and *H. tetradactylum* stood out for having higher complexities compared to all other species besides *M. welcommi* and *G.* cf. *browni*. Moreover, *G.* cf. *browni* was different from *B. brachypus*, both *Plesiaceratherium* species, and both *Hispanotherium* species regarding complexity and HAsfc81 (Table 3). For both DMTA parameters in which Locality had a noticeable effect (epLsar and Asfc), we found a cluster between Béon 1 and Gračanica opposed to one containing at least Simorre and Sansan (for Asfc: also Kumbi 4 and Villefranche d'Astarac; Table 3).

Table 2: Pairs (Species or Locality) with noticeable p-values after Tukey's honestly significant difference (HSD) by DMTA parameters.

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DMTA parameter	Pair (Species or Locality) with differences		p-value
Anisotropy			
	Plesiaceratherium mirallesi	*Brachypotherium brachypus*	0.066
		Lartetotherium sansaniense	0.054
		Hoploaceratherium tetradactylum	0.09
Complexity			
	Hoploaceratherium tetradactylum	*Hispanotherium beonense*	0.008
		Prosantorhinus douvillei	0.01
		Plesiaceratherium mirallesi	6.3×10^{-4}
		Plesiaceratherium balkanicum	0.051
	Gračanica	Sansan	0.047
		Simorre	0.028
		Villefranche d'Astarac	0.032
HAsfc9			
	Hoploaceratherium tetradactylum	*Plesiaceratherium balkanicum*	0.059
		Plesiaceratherium mirallesi	0.024
HAsfc81			
	Hoploaceratherium tetradactylum	*Plesiaceratherium balkanicum*	0.096
		Plesiaceratherium mirallesi	0.072

Table 3: Fischer's least significant difference (LSD) post hoc results by DMTA parameters

Groups (a, ab, abc, b, bc, and c) are indicated with a p-value threshold of 0.05, for the sake of clarity.

		a	ab	abc	b	bc	c
epLsar	**Species**	*A. simorrense* *P. mirallesi*	*G.* cf. *browni* *H. beonense* *H.* cf. *matritense* *P. balkanicum* *P. blanfordi*	-	*P. douvillei* *B. brachypus* *B. gajense* *M. welcommi* *D. steinheimensis* *L. sansaniense* *H. tetradactylum*	-	-
	Locality	Gračanica Béon 1	Villefranche d'Astarac Devínska Nová Ves Kumbi 4	-	Sansan Simorre	-	-
Asfc	**Species**	*B. gajense* *H. tetradactylum*	*G.* cf. *browni*	*M. welcommi*	-	*B. brachypus* *P. blanfordi* *A. simorrense* *D. steinheimensis* *L. sansaniense*	*P. douvillei* *P. balkanicum* *P. mirallesi* *H. beonense* *H.* cf. *matritense*
	Locality	Simorre Sansan Kumbi 4 Villefranche d'Astarac	Devínska Nová Ves	-	-	Béon 1	Gračanica
FTfv	**Species**	*H.* cf. *matritense* *B. gajense*	*P. blanfordi* *M. welcommi* *G.* cf. *browni* *D. steinheimensis* *H. tetradactylum* *P. douvillei* *H. beonense*	-	*B. brachypus* *A. simorrense* *P. balkanicum* *P. mirallesi* *L. sansaniense*	-	-
HAsfc9	**Species**	*G.* cf. *browni* *L. sansaniense* *H. tetradactylum*	*P. blanfordi* *B. gajense* *B. brachypus* *P. douvillei* *M. welcommi* *A. simorrense* *D. steinheimensis* *H. beonense*	-	*P. balkanicum* *P. mirallesi* *H.* cf. *matritense*	-	-
HAsfc81	**Species**	*G.* cf. *browni*	*B. gajense* *H. tetradactylum* *L. sansaniense*	*P. blanfordi* *P. douvillei* *M. welcommi* *A. simorrense* *D. steinheimensis*	-	*B. brachypus* *H. beonense*	*P. balkanicum* *P. mirallesi* *H.* cf. *matritense*

Besides at Béon 1, the microwear sampling was very restricted (n < 5), either due to low numbers of exploitable teeth available, or to the lack of well-preserved microwear texture on molars. In order to facilitate the understanding, the results are presented by locality (chronologically) and by species. At **Kumbi 4**, four species were considered for DMTA: *Pleuroceros blanfordi*, *Mesaceratherium welcommi*, *Gaindatherium* cf. *browni* (grinding only), and *Brachypotherium gajense* (grinding only). Figure 3 shows that Kumbi rhinocerotids display a great variety of microwear patterns. Only one specimen, belonging to *G.* cf. *browni*, is above the high anisotropy threshold of 5 x 10^{-3}, while all specimens of *B. gajense* and *G.* cf. *browni* but none of *P. blanfordi* display values above the high complexity cutpoint of 2. *Gaindatherium* cf. *browni* and *P. blanfordi* have large variations in anisotropy, from low values (~ 1 x 10^{-3}) to high (about 5 x 10^{-3}), but consistent values of complexity (around 3 and 1.4 respectively). Such a pattern associated with moderate (*P. blanfordi*) to high (*G.* cf. *browsi*) values of HAsfc (Figure 4) point towards mixed-feeding diets, probably with the inclusion of harder objects for *G.* cf. *browsi*. The signature for *B. gajense* is suggestive of browsing with low mean anisotropy (1.82 x 10^{-3}), but high means of complexity (4.58), FTfv (7.89 x10^{4}), and HAsfc (HAsfc9 = 0.36; HAsfc81 = 1). Eventually, *M. welcommi* presents low to moderate anisotropy values (< 4 x 10^{-3}), a moderate complexity (~ 1.5) and HAsfc, but high FTfv (> 4 x 10^{4}) on both facets (Figure 4), which denotes browsing or mixed-feeding habits.

At **Béon 1**, the DMT of the four rhinocerotids overlap contrary to that of Kumbi 4 rhinocerotids (Figure 3). The DMTA results are already detailed in Hullot et al. (2021). They suggest a mixed-feeding behavior for *H. beonense* with moderate anisotropy values (mostly < 4 x 10^{-3}), variable values of complexity (low-medium), moderate-high FTfv (around 4 x 10^{4}), and moderate HAsfc on both facets (Figure 4). *Plesiaceratherium mirallesi* is considered as a folivore due to low complexity (~ 1) and HAsfc values but relatively high anisotropy (above 5 x 10^{-3}), indicating an abrasive but not diversified diet. Concerning the teleoceratines, they display similar microwear textures (Figure 3; Figure 4), though *B. brachypus* has lower values of anisotropy (< 2 x 10^{-3}). This suggests that *B. brachypus* was probably a browser or a mixed-feeder, while *Pr. douvillei* was a browser favoring leaves.

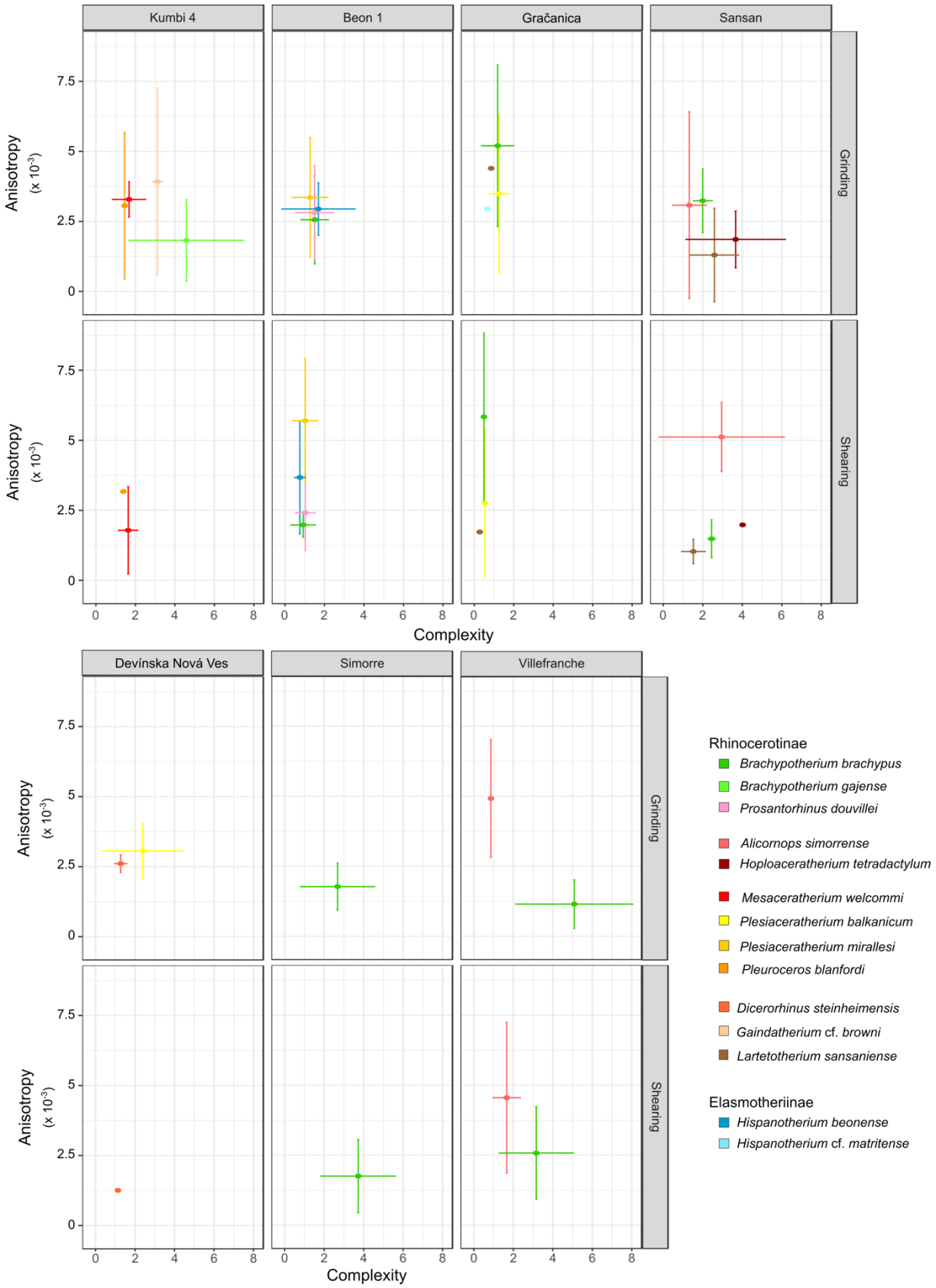
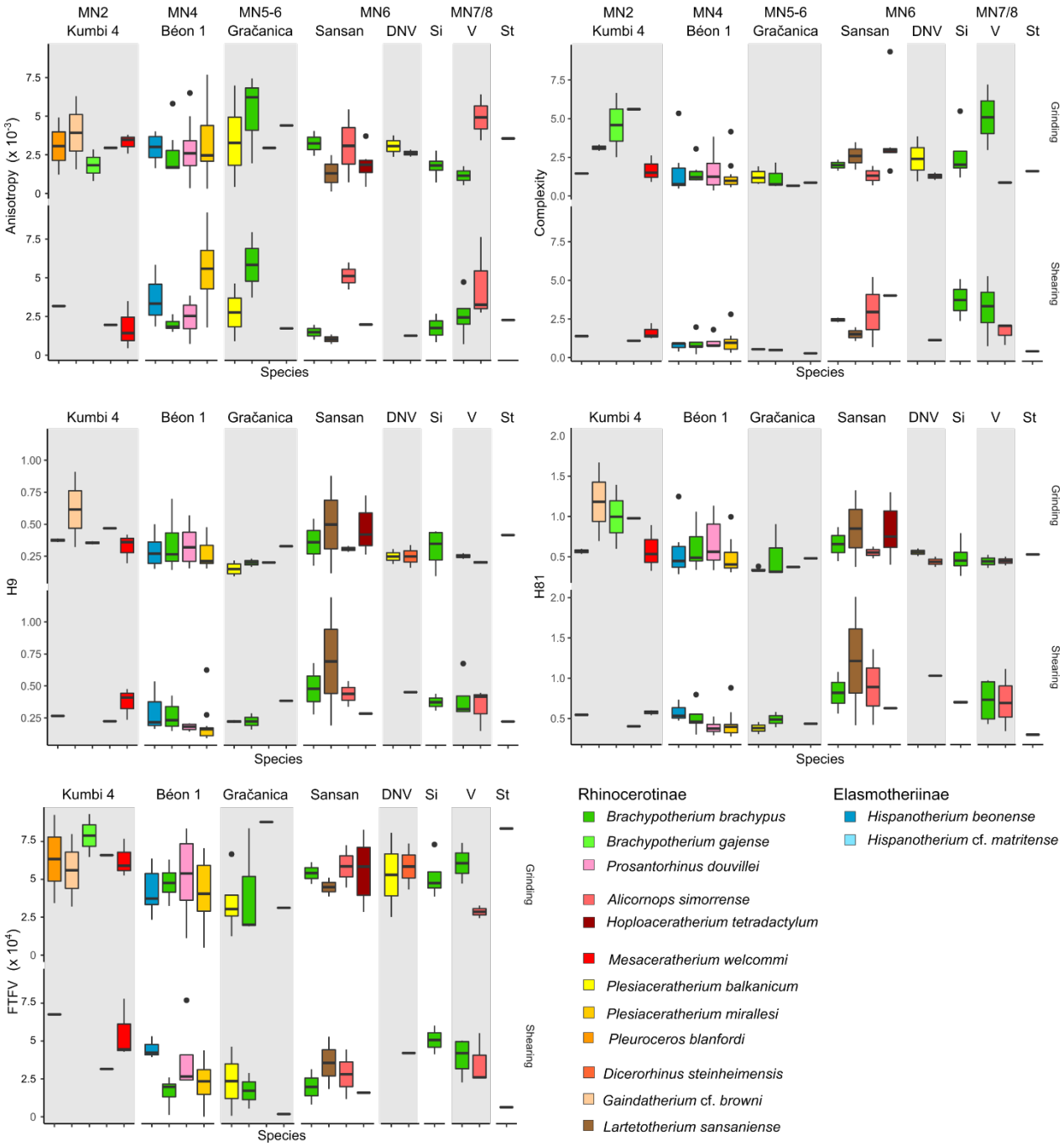


Figure 3: Dental microwear results of early and middle Miocene rhinocerotids plotted as mean and standard deviation of anisotropy against that of complexity by facet, locality and species

271 Localities organized chronologically. Steinheim am Albuch not shown as only one specimen was
272 studied. Color code by species as indicated in the figure.
273



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275 **Figure 4: Dental microwear results of early and middle Miocene rhinocerotids plotted as**
276 **boxplots of each DMTA parameter by facet and species.**
277 Time flows from left to right. DNV: Devínska Nová Ves, St: Steinheim am Albuch, Si: Simorre, V:
278 Villefranche d'Astarac. Color code by species as indicated in the figure and consistent with Figure 3.

279 At **Gračanica**, we also observe a great overlapping in the DMT. The complexity is very low for all
280 rhinocerotids studied (mostly below 1) suggesting soft food items. Anisotropy varies greatly but
281 HAsfc81 is consistently low (< 0.5) for all species (Figure 4). This points towards soft browsing or
282 folivory for all rhinocerotids at Gračanica.
283
284 At **Sansan**, the DMTA signatures of the rhinocerotids are more diversified and less overlapping,
285 similarly to Kumbi 4 (Figure 3). *Lartetotherium sansaniense* and *H. tetradactylum* have low values of
286 anisotropy (< 2.5 x 10^{-3}) and moderate (1-2; *L. sansaniense*) to high (> 2; *H. tetradactylum*) values of
287 complexity, recalling browsers. The high values of HAsfc (Figure 4) for both species are compatible
288 with a browsing diet. The other two species, *B. brachypus* and *A. simorrense*, are in the range of
289 mixed-feeders (Figure 3), and have compatible moderate to high values of HAsfc.
290
291 At **Devínska Nová Ves**, our restricted sample suggest browsing habits for both species *P. balkanicum*
292 and *D. steinheimensis*, with moderate values of both anisotropy (~ 2.5 x 10^{-3}) and complexity (mostly
293 between 1 and 1.5). FTfv is high on both facets (> 4 x 10^{4}) and HAsfc moderate (Figure 3; Figure 4).
294
295 At **Simorre**, *B. brachypus* specimens display low values of anisotropy (< 2.5 x 10^{-3} except two
296 specimens), and high values of complexity (> 2) and FTfv (> 4 x 10^{4}) on both facets. Values of HAsfc9
297 are high (> 0.3) on both facets, while that of HAsfc81 are moderate on the grinding facet (median =
298 0.45) and high on the shearing one (median = 0.7). These DMTA results suggest browsing
299 preferences with the inclusion of hard objects, probably fruits.
300
301 At **Villefranche d'Astarac**, *B. brachypus* and *A. simorrense* present well-distinguished DMT (Figure
302 3). *Brachypotherium brachypus* has low anisotropy values (< 2.5 x 10^{-3}) and high complexity ones (>
303 2.5) corresponding to a browsing signal, while the opposite is true for *A. simorrense*. The moderate
304 values of HAsfc for *A. simorrense* suggest that folivory is more likely than mixed-feeding for these
305 specimens and the corresponding individuals.
306
307 Eventually the specimen of *A. simorrense* from **Steinheim am Albuch** has a moderate anisotropy
308 (Grinding: 3.56 x 10^{-3}; Shearing: 2.27 x 10^{-3}), low (Shearing: 0.41) to moderate (Gringing: 1.6)

complexity, a high FTfv on the grinding facet (8.35 x 10^4) but low on the shearing one (0.63 x 10^4), and low HAsfc on the shearing facet but moderate-high on the grinding one (Figure 4). This pattern is consistent with browsing or mixed-feeding habits.

GLMM: For all response variables (epLsar, Asfc, FTfv, HAsfc9, and HAsfc81), model support increased (i.e., lower AIC) when intraspecific factors (e.g., Facet, Genus, Locality) were included. The final models contained three to seven factors, including Specimen, the random factor, by default in all models. Facet was in the final models of epLsar and FTfv, Locality and Age were found in the final models of Asfc and both HAsfc. Details and comparison of all models can be seen in electronic supplementary material S5 and S6. Differences by Locality were also observed. Béon 1 had a lower complexity than Kumbi 4, Sansan, Simorre, and Villefranche (df = 119, α = 0.05, |t-values| > 1.7), while Tukey's contrasts highlighted lower values of Asfc for Gračanica than for Kumbi (p-value < 0.004), Simorre (p-value = 0.027), and Villefranche (p-value < 0.001). Moreover, Béon 1 had lower HAsfc9 and HAsfc81 values than Kumbi 4 and Sansan (df = 119, α = 0.05, |t-values| > 1.7). Tukey's contrasts also showed that Sansan had higher HAsfc9 and HAsfc81 than Gračanica (p-value ≤ 0.001). The sampling site (tooth locus, position, side) had sometimes a confounding effect. For instance, M2 had higher epLsar values than M3 (df = 119, α = 0.05, t-value = -1.95).

GLMM - Comparison to extant dataset: When compared to the extant dataset (see S8 for all details), we noticed that all fossil species had lower anisotropy values than the extant grazer *Ceratotherium simum* (white rhinoceros) and the folivore *Dicerorhinus sumatrensis* (Sumatran rhinoceros), although the classic t-value threshold was not reached for a few species (*P. blanfordi*, *G.* cf. *browsi*, *B. gajense* [only regarding *C. simum*], *P. mirallesi*, and *A. simorrense*; α = 0.95, |t-values| ≤ 1.7). On the contrary, *P. mirallesi* displayed higher values of anisotropy than the extant browsers *Diceros bicornis* (black rhinoceros; t-value = 1.93) and *Rhinoceros sondaicus* (Javan rhinoceros; t-value = 2.66). Regarding complexity, *C. simum* and *D. sumatrensis* had lower values than *B. gajense* and *H. tetradactylum*, while the extant browsers had higher values than *P. balkanicum*, *P. douvillei*, *P. mirallesi*, and *H. beonense* (α = 0.95, |t-values| > 1.7). All other DMTA parameters showed less differences between the extant and fossil datasets: *C. simum* and *R. sondaicus* had higher FTfv, HAsfc9, and HAsfc81 than *B. brachypus*, *P. balkanicum*, and *P. mirallesi* (α = 0.95, |t-values| > 1.7).

339 Hypoplasia

340 The overall prevalence of hypoplasia on rhinocerotid teeth from the early and middle Miocene
341 localities studied is high, with 302 teeth affected out of 1401, corresponding to over 20 % (21.56 %).
342 There are, however, marked discrepancies between species, localities, and tooth loci (Figure 5). The
343 most affected genera were *Plesiaceratherium* (104/357; 29.13 %), *Prosantorhinus* (97/370; 26.22 %),
344 and *Brachypotherium* (46/178; 25.84 %), but this resulted mostly from the dominance of Béon 1
345 specimens in our sample. *Brachypotherium brachypus* was often one of the most affected species at
346 all sites where the species was found, except Sansan (1/13; 7.69 %), contrary to *A. simorrense* often
347 found associated with the latter species and relatively spared by hypoplasia (maximum 4/35 = 11.43 %
348 of teeth affected at Simorre; Figure 6).
349
350 The prevalence was above 10 % for all localities except Kumbi 4, for which the overall prevalence is
351 low (6/99; 6.06 %; Table 4). Hypoplasia defects are quite rare at Kumbi 4 for all species studied, and
352 even null for the teleoceratine species (*D. fatehjangense* and *B. gajense*), *Bugtirhinus praecursor*, and
353 *Plesiaceratherium naricum* (Figure 6). Only *Pleuroceros blanfordi* appears a little more affected (4/42;
354 9.52 %), totaling four of the six hypoplasias observed at the locality. Hypoplasia was also relatively
355 limited at Sansan (14/132; 10.61 %) and Devínska Nová Ves (5/48; 10.42 %), with only *B. brachypus*
356 and *H. tetradactylum* affected at Sansan, and *D. steinheimensis* from the latter (Table 4 ; Figure 6). On
357 the contrary, the rhinocerotids from Béon 1, Béon 2, and Gračanica are very affected, with more than
358 25 % of the teeth presenting at least one hypoplasia at Béon 1 (216/832; 25.96 %) and Béon 2 (5/18;
359 27.78 %), and nearly 50 % at Gračanica (15/31; 48.39 %; Table 4). At these sites, the prevalence of
360 hypoplasia is high for all species but the elasmotheriines (Figure 6). Indeed, the elasmotheriines of all
361 sites were relatively spared (*H. beonense* at Béon 1: 13.04 %) or even not affected by hypoplasia (*B.*
362 *praecursor* at Kumbi 4 and *H.* cf. *matritense* at Gračanica).
363

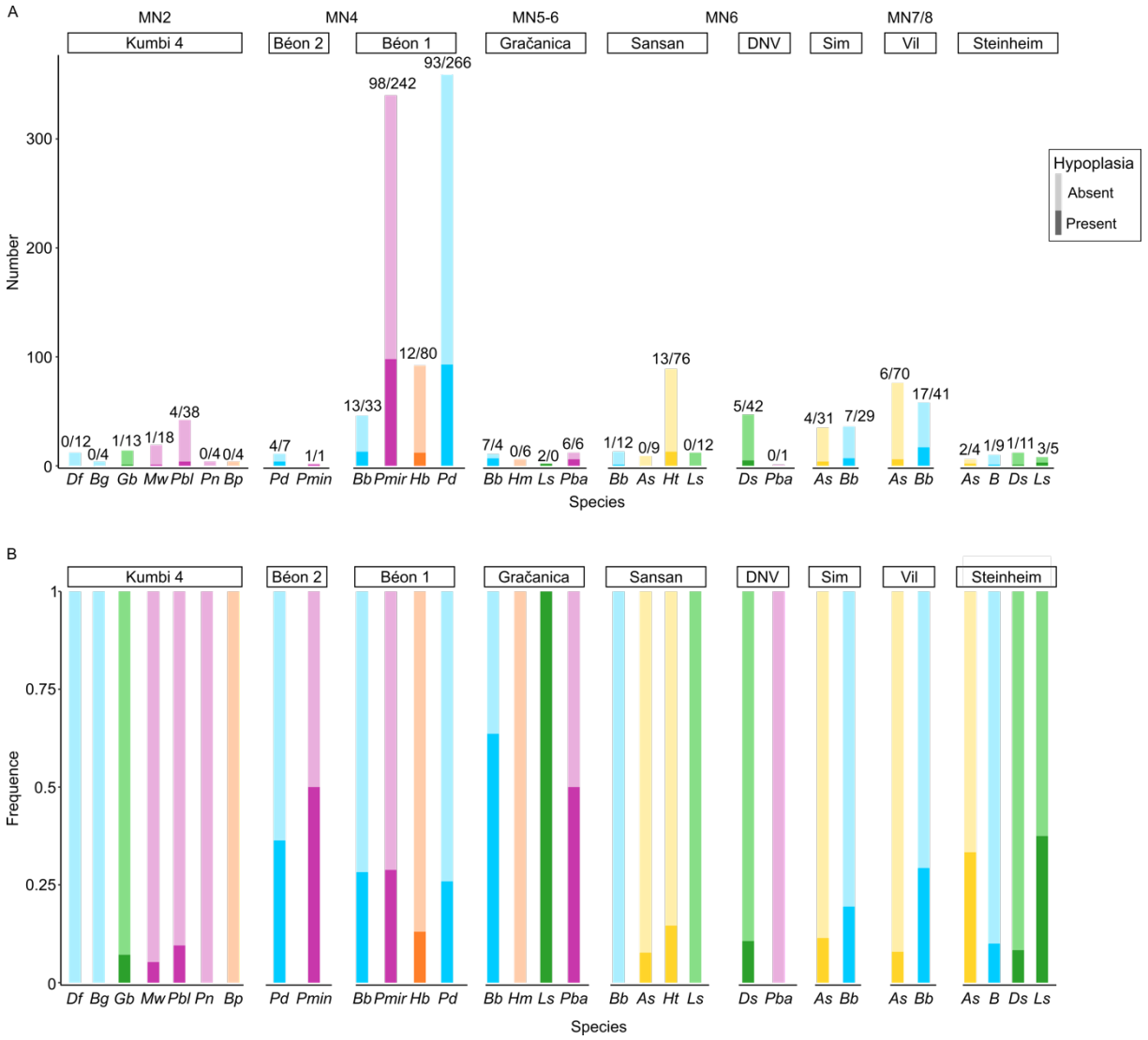

Figure 5: Number (A) and Frequence (B) of hypoplasia by Locality and Species

Numbers on barplot A indicate the number of hypoplastic teeth (dark colors) versus unaffected ones (light colors). Frequencies are calculated as the ratio of hypoplastic teeth on the total number of teeth (hypoplastic and normal). Sub-tribes colored in blue: Teleoceratina, in green: Rhinocerotina; in yellow: Aceratheriina, in pink: stem Rhinocerotinae, and in orange: Elasmotheriina

Abbreviations: DNV: Devínska Nová Ves, Sim: Simorre, Vil: Villefranche d'Astarac

Df: *Diaceratherium fatehjangense*, *Bg*: *Brachypotherium gajense*, *Bp*: *Bugtirhinus praecursor*, *Gb*: *Gaindatherium* cf. *browni*, *Mw*: *Mesaceratherium welcommi*, *Pbl*: *Pleuroceros blanfordi*, *Pn*: *Plesiaceratherium naricum*, *Pmin*: *Protaceratherium minutum*, *Pd*: *Prosantorhinus douvillei* (*P.* aff. *douvillei* at Béon 2), *Bb*: *Brachypotherium brachypus*, *Hb*: *Hispanotherium beonense*, *Pmir*: *Plesiaceratherium mirallesi*, *Hm*: *Hispanotherium* cf. *matritense*, *Ls*: *Lartetotherium sansaniense*, *Pba*:

Plesiaceratherium balkanicum, *As*: *Alicornops simorrense*, *Ht*: *Hoploaceratherium tetradactylum*, *Ds*: *Dicerorhinus steinheimensis*, *B*: *Brachypotherium* sp.

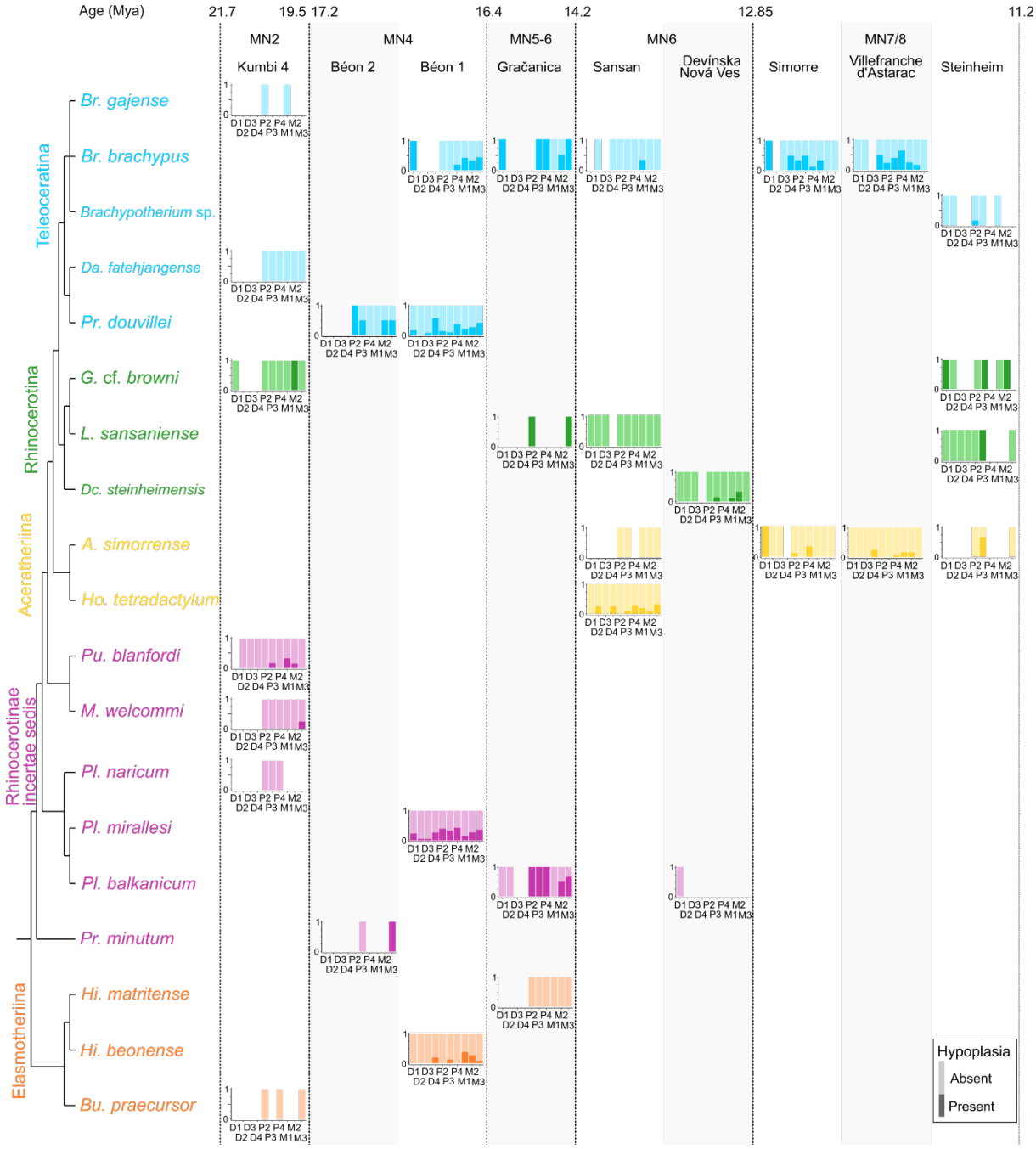

Figure 6: Prevalence of hypoplasia by locality, species and tooth locus plotted against phylogeny

Phylogenetic relationships follow formal parsimony analyses (Antoine, 2002; Antoine et al., 2010; Becker et al., 2013; Tissier et al., 2020).

384 Subtribes colored in blue: Teleoceratina, in green: Rhinocerotina; in yellow: Aceratheriina, in pink:
385 stem Rhinocerotinae, and in orange: Elasmotheriina
386 Dark colors: hypoplastic teeth; Light colors: unaffected teeth
387
388 **Table 4: Prevalence of hypoplasia by locality (number of specimens/percentages)**

	Hypoplastic	Normal	Percentage of hypoplasia
Kumbi 4	93	6	6.06
Béon 2	13	5	27.78
Béon 1	616	216	25.96
Gračanica	16	15	48.39
Devínska Nová Ves	43	5	10.42
Sansan	118	14	10.61
Simorre	60	11	15.49
Villefranche d'Astarac	111	23	17.16
Steinheim	29	7	19.44

389
390
391 Concerning the loci, milk teeth (47/294; 15.99 %) were overall less affected by hypoplasia than
392 permanent ones (255/1107; 23.04 %; Table 5). Indeed, besides at Béon 1, very few milk molars are
393 hypoplastic (one D1/d1 at Gračanica and Steinheim, two D1 at Simorre, two D2 and 1 d4 at Sansan, 4
394 D4/d4 at Villefranche d'Astarac). Upper and lower teeth were equally affected (Kruskal-Wallis, df = 1,
395 p-value = 0.11), with respectively 19.86 % (144/725) and 23.37 % (158/676) of teeth bearing
396 hypoplasia. The most affected locus was the fourth milk molar with 38.24 % (26/68), while the least
397 affected were second and third milk molars with around 4 % affected (3/68 and 3/72 respectively;
398 Table 5). Other loci particularly affected were fourth premolars (60/200; 30 %), third molars (50/188;
399 26.60 %), and second molars (49/202; 24.26 %; Table 5). Once again, these findings mostly result
400 from the dominance of Béon 1 specimens in the sample, and great differences in the hypoplasia
401 pattern are observed by locality (Figure 6). Indeed, if virtually all tooth loci are likely to be affected for
402 Béon 1 rhinocerotids, the pattern is less varied at other localities although it seemingly diversifies with
403 sample size (e.g., *H. tetradactylum* from Sansan and Villefranche d'Astarac). For instance, hypoplastic
404 teeth are nearly exclusively molars at Kumbi 4 (with only one defect on a p3), and permanent teeth at
405 Gračanica (only one defect on a D1; Figure 6).
406

Table 5: Prevalence of hypoplasia by tooth locus, regardless of provenance and taxon

Upper and lower teeth merged as they have a similar timing of development

	Hypoplastic	Normal	Percentage of hypoplasia
D1	71	15	17.44
D2	65	3	4.41
D3	69	3	4.17
D4	42	26	38.24
Total decidual teeth	47	247	15.99
P2	130	26	16.67
P3	138	33	19.30
P4	140	60	30.00
M1	153	37	19.47
M2	153	49	24.26
M3	138	50	26.60
Total permanent teeth	255	852	23.04

GLMM: For all response variables (Hypo, Defect, Multiple, Localization, and Severity), model support increased (i.e., lower AIC) when intraspecific factors (e.g., Tooth Loci, Genus, Locality) were included. When Genus was not forced into the models, the final models contained three to six 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, Localization, and Severity). Genus was in the final models of all variables but Localization. Position was in the final models of Hypo, Defect, and Localization, while Tooth, and Wear were in that of Hypo and Defect. Details and comparison of all models can be seen in electronic supplementary material S5 and S7.

Based on GLMMs results, we can assess the influence of Genus, Locality, and Tooth on the hypoplasia pattern. *Alicornops* was less affected than *Brachypotherium* (p-value = 0.015), while *Plesiaceratherium* was more prone to hypoplasia than *Hispanotherium* (p-value = 0.02). GLMMs revealed differences in the patterns of hypoplasia (i.e., type of defects and their frequencies) between *Brachypotherium* and the following taxa: *Dicerorhinus* (p-value = 0.0046), *Alicornops* (p-value < 0.001), and *Protaceratherium* (p-value = 0.034). Tukey's contrasts also revealed the lowest p-values between *Alicornops* and the following taxa: *Hispanotherium* (p-value = 0.064), *Plesiaceratherium* (p-value < 0.01), *Prosantorhinus* (p-value < 0.01), *Protaceratherium* (p-value = 0.05). Eventually

427 *Dicerorhinus* had a different hypoplasia pattern than *Plesiaceratherium* (p-value = 0.034) and
428 *Prosantorhinus* (p-value = 0.071).
429
430 Concerning tooth loci, all teeth but fourth premolars and third molars are less affected than fourth milk
431 molars (p-values < 0.05). The results further suggested that the most commonly affected loci were
432 third molars, fourth premolars and fourth milk molars, while the least affected were all milk molars but
433 the fourth. Concerning localities, Gračanica teeth were significantly more touched than Béon 1 and
434 Sansan specimens (p-values ≈ 0.01). Middle Miocene rhinocerotids present a hypoplasia pattern
435 distinct from that of early Miocene ones (p-value = 0.019). Similarly to GLMMs for DMTA, we observed
436 confounding effects. Slightly-worn teeth had less hypoplasia than average worn (p-value = 0.005) and
437 very worn teeth (p-value = 0.026).
438
439 **Discussion**
440
441 Dietary preferences and niche partitioning of the rhinocerotids studied
442 The comparison of the fossil specimens DMT to that of extant ones highlighted important differences.
443 This suggests that the dietary spectrum of extinct rhinocerotids might have been very distinct from that
444 observed in the living species (Hullot et al., 2019). However, the microwear textures of the fossils are
445 critically distinct from that of the only extant strict grazer *Ceratotherium simum*, banning such dietary
446 preferences for the studied fossil specimens. This finding is not surprising as grasses and associated
447 grazing ungulates expended only during latest Miocene in Eurasia (Janis, 2008). The reconstructed
448 dietary preferences based on DMTA are presented in Table 6 by locality and by species.
449
450 The DMTA results of fossil specimens on both facets (Figure 3; Figure 4) suggest a clear niche
451 partitioning based on feeding preferences for the rhinocerotid specimens studied at Kumbi 4, Sansan,
452 and Villefranche d'Astarac. Although DMT could only be explored in four out of the nine rhinocerotid
453 species present at Kumbi 4, the patterns observed indicate clear differences in the feeding behaviors,
454 even if leaf consumption seems to be a major component for all rhinocerotids studied but *B. gajense*.
455

Table 6: Dietary preferences inferred from textural microwear (DMTA) of the studied rhinocerotid specimens from different fossil localities of the lower and middle Miocene of Eurasia.

Color code: brown/B – browser, blue/M – mixed-feeder, light green/F – folivore, no color/x – not studied

		Kumbi 4	Béon 2	Béon 1	Gračanica	Sansan	Devínska Nová Ves Spalte	Simorre	Villefranche d' Astarac	Steinheim am Albuch
Rhinocerotinae										
	Mesaceratherium welcommi	M								
	Pleuroceros blanfordi	M								
	Protaceratherium sp.	x								
	Protaceratherium minutum		x							
	Plesiaceratherium naricum	x								
	Plesiaceratherium mirallesi		x	F						
	Plesiaceratherium balkanicum				F		B			
	Plesiaceratherium sp.									
	Hoploaceratherium tetradactylum					B				
	Alicornops simorrense					M		x	F	M
	Gaindatherium cf. *browni*	M								
	Lartetotherium sansaniense				B	B				x
	Dicerorhinus steinheimensis						B			x
	Diaceratherium fatehjangense	x								
	Brachypotherium gajense	B								
	Brachypotherium brachypus			M	F	M		B	B	
	Brachypotherium sp.									x
	Prosantorhinus shahbazi	x								
	Prosantorhinus douvillei		aff.	B						
Elasmotheriinae										
	Bugtirhinus praecursor	x								
	Hispanotherium beonense			M						
	Hispanotherium cf. *matritense*				M					

This finding is in line with the inferred lush vegetation under warm and moist climatic conditions proposed for this locality, providing abundant and diverse feeding resources for the many large herbivores present (Antoine et al., 2010, 2013; Martin et al., 2011). The dietary preferences reconstructed for Sansan rhinocerotids suggest the co-occurrence of two browsers (*L. sansaniense* and *H. tetradactylum*, the latter including harder items in its diet) and two mixed-feeders (*A. simorrense* and *B. brachypus*), coherent with the (sub-)tropical forested environment reconstructed for that locality (Costeur et al., 2012), but at odds with the recent-like Miocene coolhouse as depicted by Westerhold et al. (2020; ~415 parts per million CO_2). This niche partitioning is probably accentuated by different habitat preferences: *H. tetradactylum* is mostly found in swamp or fluvial sediments

indicating wet habitat preferences contrary to *A. simorrense*, while *B. brachypus* seems intermediate and *L. sansaniense* generalist (Heissig, 2012). Eventually, we observed obvious differences in the dietary preferences for *A. simorrense* (folivore or mixed-feeder favoring leaves) and *B. brachypus* (browser including hard objects) at Villefranche d'Astarac, where a humid forested environment is hypothesized (Bentaleb et al., 2006).

On the contrary, an overlap of microwear textures, especially for the grinding facet, is observed for the localities of Béon 1 and Gračanica. Besides diet, different habitats and feeding heights might result in niche partitioning (Hutchinson, 1959; Arsenault and Owen-Smith, 2008). Concerning Béon 1, a partial niche partitioning due to habitat differences has been hypothesized for the rhinocerotids – swamps for both teleoceratines *B. brachypus* and *P. douvillei*, open woodland for *P. mirallesi*, and savannah-like open environments for *H. beonense* (Bentaleb et al., 2006) – and subtle dietary differences are discussed in Hullot et al. (2021) in the light of the combination of molar mesowear and dental microwear texture analysis. At Gračanica, 2D microwear and mesowear score already revealed an overlap in the dietary preferences of *Pl. balkanicum* and *B. brachypus* as two browsing species, although the latter is labelled as "dirty browsing", a dietary category (not defined by comparative datasets on intensively studied extant species with known diets) including species assumed to browse and incorporate soil particles. (Xafis et al., 2020). Although microwear sampling is restricted and includes premolars for the other two rhinocerotids (*L. sansaniense* and *H.* cf. *matritense*), it points towards different mixed-feeding behaviors, most likely with a dominance of grass in the diet of *H.* cf. *matritense* (Xafis et al., 2020). The very low values of complexity for all Gračanica rhinocerotids in our sample, combined to relatively high values of anisotropy (Figure 3; Figure 4), could suggest an important consumption of leaves for all species, as well as a very low amount of lignified tissues that would have required more grinding to get access to cell content. Interestingly, the reconstructed environment at this locality (based on mammal assemblage and flora) is a lowland swamp surrounded by a closed canopy-like environment (Butzmann et al., 2020; Xafis et al., 2020), meaning that leaves would have been an abundant resource. This recalls the feeding preferences and microwear textures of the extant *Dicerorhinus sumatrensis* (Sumatran rhino; Hullot et al., 2019). Eventually, the restricted DMTA samples from Devínska Nová Ves Spalte, Steinheim am Albuch, and Simorre suggest browsing

or mixed-feeding habits for all specimens studied, but did not allow to conclude on potential competition for food resources.

Interactions with co-occurring herbivores

Besides other rhinocerotid species, the individuals studied co-occurred with many other herbivore mammals. Although co-occurrence is not necessarily 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. Unfortunately, very little has been studied concerning the dietary preferences of the fauna at most of the studied localities with the notable exceptions of Gračanica and Sansan.

Indeed, recent studies on dental wear (micro- and meso- wear) or stable isotopy, suggested frugivory for some associated species such as tragulids (*Dorcatherium* spp. at all localities but Simorre and Villefranche; Aiglstorfer et al., 2014; Xafis et al., 2020), the middle Miocene Moschidae (*Micromeryx* spp. found at Sansan, Simorre and Steinheim am Albuch; Aiglstorfer and Semprebon, 2019) or the chalicothere *Metaschizotherium fraasi* (found at Steinheim am Albuch; Semprebon et al., 2011). Interestingly, no rhinocerotid specimens studied here seemingly favored fruits. Similarly, the lophodont suid *Listriodon splendens*, found at Gračanica, Devínska Nová Ves, and Simorre, might have favored grasses (Van der Made, 2003; Xafis et al., 2020), a resource not exploited by the rhinocerotids either. Otherwise, the vast majority of herbivore species were probably browsers or mixed-feeders, in good agreement with the statement by Eronen and Rössner (2007) that these forms were dominant between MN4 and MN9. This is for instance the case of the associated perissodactyl species *Anisodon grande* (Chalicotheriidae), which 2D microwear signal at Devínska Nová Ves suggests folivory (Semprebon et al., 2011), and *Anchitherium* spp. (Equidae) ranging from generalists to “dirty browsers” (Kaiser, 2009; Xafis et al., 2020).

Within browsers and mixed-feeders, resources partitioning is still possible (e.g., consumption of different plant parts or species) but might be difficult to detect in fossil communities. Moreover, other strategies can lead to niche partitioning, such as different habitat, different body mass, or different feeding height (Hutchinson, 1959; Schoener, 1974; Arsenault and Owen-Smith, 2008). Regarding body mass, most rhinocerotids studied are megaherbivores *sensu* Owen-Smith (1988; terrestrial

herbivores weighting more than 1000 kg), which implies specific feeding strategies and metabolic requirements. Megaherbivores are often treated as a separate herbivore guild, mostly disturbing that of mesoherbivores (4–450 kg ; Fritz et al., 2002; Calandra et al., 2008; Landman et al., 2013). Within megaherbivores, proboscideans frequently co-occurred with rhinocerotids at the studied localities and were mostly browsers or mixed-feeders, placing them as direct competitors for rhinocerotids. Indeed, the mesowear and 2D microwear suggest that *Prodeinotherium bavaricum* and *Gomphotherium angustidens* were browsers at Gračanica (Xafis et al. 2020), while the mesowear angle categorizes *P. bavaricum* from Sansan, *D. giganteum* from Villefranche d'Astarac and *G. angustidens* from Simorre as browsers, but *G. angustidens* from Sansan and Villefranche d'Astarac as mixed-feeders (Loponen, 2020). Such overlapping in the diet of proboscideans and rhinocerotids is observed nowadays between African elephants and black rhinoceroses (Landman et al., 2013). Interestingly, this competition is detrimental to the rhinoceros, whose individuals shift towards the inclusion of more grasses in presence of elephants (on a seasonal basis). Another possibility, as postulated by Xafis et al. (2020) for *Deinotherium* spp. and *Plesiaceratherium balkanicum* at Gračanica, would be different feeding heights between proboscideans and rhinocerotids, as the first ones were most likely feeding at the top of trees due to their larger size (some of the biggest Neogene mammals; Larramendi, 2015).

Hypoplasia prevalence and environmental conditions

We found that the hypoplasia prevalence and pattern (i.e., tooth loci affected) were very different depending on the locality and the species concerned. Except for Kumbi 4, the prevalence was relatively high (> 10 %) at all sites of our early-middle Miocene sample. Even though nine species of rhinocerotids are found at Kumbi 4, such a low prevalence is in agreement with previous results in the region over the Cenozoic (Roohi et al., 2015), and coherent with the very favorable, low-stress context hypothesized at this locality, that is a rich vegetation under a warm and humid climate (Antoine et al., 2013).

The prevalence of hypoplasia is high at Béon 1 (>25 %) for all rhinocerotids except *H. beonense*, with molars being particularly affected with respect to other dental loci. Second and third molars are the last teeth to develop and erupt in rhinocerotids (Hitchins, 1978; Hillman-Smith et al., 1986; Böhmer et al., 2016), and stresses on these late-developed teeth have been correlated with environmental, seasonal

562 stresses in sheep (Upex and Dobney, 2012). Although subtropical wet conditions are reconstructed at
563 Béon 1 (just prior to the MCO), periodic droughts are also reported in the area at that time (Duranthon
564 et al., 1999; Hullot and Antoine, 2020). Interestingly, the least affected species is the elasmotheriine *H.*
565 *beonense*, an early representative of a clade adapted to relatively open and arid environments
566 (Cerdeño and Nieto, 1995; Iñigo and Cerdeño, 1997), and which displays a mixed-feeding diet (Figure
567 4). On the contrary, both teleoceratine species, often considered swamp dwellers, display a high
568 prevalence of hypoplasia (Figure 5).
569
570 We found a very high prevalence of hypoplasia at Gračanica, with nearly 50 % of the teeth bearing at
571 least one hypoplastic defect. The proposed age for the locality ranges between 14.8 and 13.8 Ma
572 (Göhlich and Mandic, 2020), which is an interval of great climatic changes. Indeed, though included in
573 the MCO, the interval from 14.7 to 14.5 Ma present an increased seasonality in precipitations, with
574 prolonged dry periods (Böhme, 2003). On the other hand, an abrupt cooling occurred between 14 and
575 13.5 Ma, correlating with the Mi-3 event (Zachos et al., 2001; Böhme, 2003; Holbourn et al., 2014;
576 mMCT of Westerhold et al., 2020). Besides this challenging environmental context for the
577 rhinocerotids, our DMTA results suggest a potential competition for food resources (Figure 3), that
578 could have generated stressful conditions.
579
580 At Sansan, the prevalence of hypoplasia is overall moderate (~ 10 %) and defects are only found in
581 two species out of four: *H. tetradactylum* and *B. brachypus* (only one M1). The pattern of hypoplasia
582 for *H. tetradactylum*, with various loci affected, suggests different stresses and timing, from *in utero*
583 (D2) to post-weaning (M3). It is quite remarkable, as the proximity of the MCO peak (Maridet and Sen,
584 2012) leading to seasonal warm and moist conditions (Costeur et al., 2012), would seemingly
585 constitute relatively low stress conditions for the concerned rhinocerotids.
586
587 The prevalence of hypoplasia at Devínska Nová Ves Spalte is also moderate (5/48; 10.42 %) and
588 restricted to *D. steinheimensis* (P3, M1, M2 only; Figure 6), although the locality dates from the
589 mMCT. However, despite this transitional climatic system, pollen data from the Vienna Basin, to which
590 the locality belongs, indicate that regional conditions remained tropical with few precipitation variations
591 (Sabol and Kováč, 2006), coherent with the absence of hypoplasia on third molars, that can be

592 correlated with seasonal stresses. The paleogeographic context seems to have played a major role,
593 as the taxonomic differences with Sansan are partly explained by different paleoenvironments:
594 Devínska Nová Ves Spalte was a forested area near the shoreline of the transgressive late Langhian
595 sea (Sabol and Kováč, 2006).
596
597 The rhinocerotids from the localities of the MN7/8 (Simorre, Villefranche d'Astarac, and Steinheim am
598 Albuch), a time of sea-level drop and comparatively dry climate (Legendre et al., 2005; Böhme et al.,
599 2011; Heissig, 2012; Westerhold et al., 2020), present higher prevalences but contrasted patterns
600 depending on the species and locality (Figure 5; Figure 6). However, contrary to what we could have
601 been expected regarding the environmental conditions, the most affected loci (P2, P3, D1) document
602 mostly early-life stresses (e.g., birth, juvenile disease), rather than environmental or seasonal stresses
603 (Niven et al., 2004; Upex and Dobney, 2012). At Steinheim, only *L. sansaniense* has hypoplasia on
604 other teeth than second and third premolars, suggesting mostly early life stresses. At Simorre, more
605 loci are affected (D1, P2-P3, P4, and M1) and the pattern is relatively similar for both co-occurring
606 species i.e., *B. brachypus* and *A. simorrense*. Hypoplasia on D1, that develops mostly *in utero*
607 synchronously with D4, could indicate birth-related stresses (Hillman-Smith et al., 1986; Mead, 1999;
608 Böhmer et al., 2016). Similarly, the M1 starts its development relatively early, attested by the presence
609 of a neonatal line in some rhinocerotid teeth (Tafforeau et al., 2007), revealing particularly stressful
610 conditions around birth. Eventually, the rhinocerotids from Villefranche d'Astarac document later-life
611 stresses, with hypoplasia recorded from D4 to M2 (not P2-P3 for *A. simorrense*). The fourth premolars
612 are particularly affected in *B. brachypus*, which could indicate harsh weaning or cow-calf separation
613 conditions.
614
615 Paleoecologic implications and changes
616 Several species or genera are retrieved in various localities overtime, but *B. brachypus* clearly has the
617 longest range (from Béon 1 [MN4] to Simorre + Villefranche d'Astarac [MN7/8], with Gračanica [MN5-
618 6] and Sansan [MN6] in the meantime). We observe a clear shift in the DMT of *B. brachypus* over time
619 from a mixed-feeding behavior at Béon 1, Gračanica, and Sansan to a clear browsing signal with the
620 ingestion of harder items (fruits, seeds, or even soil) at Simorre and Villefranche d'Astarac (Figure 3;
621 Figure 4). This result could be due to a change in the regional climatic conditions, from warm and

humid pre-MCO to cooler, more seasonal and arid post-MCO (Zachos et al., 2001; Böhme, 2003; Holbourn et al., 2014), perhaps leading to behavioral changes in this species (Cerdeño and Nieto, 1995), and/or to changes in local conditions.

Contrastingly, the DMT of *A. simorrense* remains quite similar from Sansan (MN6) to Steinheim (MN7/8; Figure 3; Figure 4). Interestingly, there are clear differences in the hypoplasia prevalence of these two species, *B. brachypus* being one of the most affected species in our sample. Such differences in the hypoplasia prevalence could reveal the existence of a competition for food and/or water resources. The pattern of hypoplasia at Simorre (D1, P2-P3) and Villefranche d'Astarac (D4-M1, P4-M2) suggests early life stresses for both rhinocerotids (Figure 6), mostly before weaning (Mead, 1999).

Concerning other species found at more than one locality (*L. sansaniense*, *D. steinheimhensis*, and *Plesiaceratherium* spp.), the hypoplasia patterns seem to be different at each locality, denoting a greater effect of local conditions than species-related sensitivities. Only the *Plesiaceratherium* species from Béon 1 and Gračanica exhibit comparable patterns (Figure 6), although it could be related to the high prevalence of stresses for individuals belonging to the concerned taxa at these localities. Overall, the elasmotheriines (*Bugtirhinus* and *Hispanotherium*) were seemingly spared by hypoplasia. Indeed, no tooth was hypoplastic at Kumbi 4 (*B. praecursor*; 0/4) and Gračanica (*H.* cf. *matritense*; 0/6). At Béon 1, for which a greater sample is available, *H. beonense* is the least affected species with 13.04 % (12/92) of hypoplastic teeth, nearly exclusively permanent (only one hypoplasia on a D4). If this result was not surprising at Kumbi 4, where low-stress conditions were inferred and very little hypoplasia recorded for all studied species, the difference to other associated species was particularly striking at Béon 1 and Gračanica. The microwear study of elasmotheriines is restricted in the literature, but it suggests the inclusion of a non-negligible part of browse resources in the diet, at least seasonally (Rivals et al., 2020; Xafis et al., 2020). This finding is in line with our DMTA results for *Hispanotherium* species (Béon 1 and Gračanica) suggesting mixed-feeding preferences (Figure 3; Figure 4). The increasing crown height observed in this clade over time could allow for accommodating to a greater variety of food items (Semprebon and Rivals, 2007; Damuth and Janis, 2011; Tütken et al., 2013), thus limiting nutritional stress, as observed in hipparionine equids, with

652 respect to anchitheriine equids (MacFadden, 1992; Janis, 2008; Mihlbachler et al., 2011). The classic
653 view of elasmotheriines as obligate open-environment rhinocerotids adapted to grazing – notably
654 based on representatives from the arid Iberic Peninsula (Iñigo and Cerdeño, 1997) – is thus somehow
655 challenged. This could mean that hypsodonty in this clade might counterbalance significant grit load
656 induced by feeding low in open environments, thus reflecting more the habitat rather than the diet, an
657 hypothesis that has already been proposed to explain hypsodonty evolution (Janis, 1988; Jardine et
658 al., 2012; Semprebon et al., 2019).
659
660 **Conclusions**
661
662 The study of the paleoecology of rhinocerotids from the early and middle Miocene of Eurasia revealed
663 clear differences over time and space between or within species. Though, DMTA results suggested
664 only browsers and mixed-feeders (no grazers nor frugivores) in the studied rhinocerotid sample, they
665 unraveled clear niche partitioning through food resources at several diachronous localities (Kumbi 4,
666 Sansan, and Villefranche d'Astarac). At other localities (Béon 1, Gračanica), a significant overlap of
667 microwear textures was observed, and more subtle differences in food preferences and other niche
668 partitioning strategies (habitat, feeding height) may have existed. Regarding enamel hypoplasia, which
669 is quite prevalent in the studied sample (except in the oldest and only South Asian locality, Kumbi 4), it
670 revealed clear disparities between localities, species, and dental loci. While the effects of climate
671 changes were not immediately obvious, we discussed more specific, local conditions that may explain
672 the observed stresses. Regarding a potential phylogenetic effect, we were able to highlight very
673 different sensitivities: while *B. brachypus* is highly affected by hypoplasia regardless of locality and
674 conditions, elasmotheriines (*Bugtirhinus praecursor* at Kumbi 4, *Hispanotherium beonense* at Béon 1
675 and *H.* cf. *matritense* at Gračanica) are pretty spared in contrast. Over time and depending on the
676 conditions, differences in DMT and/or prevalence of hypoplasia were observed for some species found
677 in several localities. This is notably the case for the feeding preferences of *B. brachypus*, oscillating
678 between browser and mixed feeder, or for the hypoplasia profiles of *L. sansaniense* and *D.*
679 *steinheimensis* denoting different stress periods and local conditions.
680
681

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