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Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia)

Manon Hullot[1] · Pierre-Olivier Antoine[1] · Manuel Ballatore[2] · Gildas Merceron[3]

Abstract

Rhinoceroses were conspicuous elements in Cenozoic ecosystems, and studying the ecological behavior of extant species might unravel the ecology of their fossil kin. Microwear as a short-term recorder may detect subtle variations in the diet. Dental microwear texture analysis (DMTA) is extensively used to infer paleodiets. Yet, regarding ungulates, most microwear studies have been conducted on artiodactyls, and more particularly on ruminants (i.e., foregut fermenters), which may not be good models for hindgut fermenters, such as rhinoceroses. Moreover, rhinoceroses display a specific enamel ultrastructure with vertical Hunter–Schreger bands and a peculiar mastication cycle likely to impact tooth response to wear. Here, we studied the DMTA of the five extant rhinoceros species (17 specimens of *Ceratotherium simum*, four of *Dicerorhinus sumatrensis*, 21 of *Diceros bicornis*, 14 of *Rhinoceros sondaicus*, and 5 of *Rhinoceros unicornis*) and built up the present dataset. In parallel, we also compiled a taxon-based dataset of consumed plants for each rhinoceros species. Accordingly, we propose to reclassify the Indian rhinoceros (*Rhinoceros unicornis*) from mixed-feeder to variable grazer. Significant discrepancies were found between grinding and shearing facets on molars and between species on a given facet. Plotting the percentage of anisotropic specimens against that of complex specimens for each species discriminated well the different diets on both facets. This unprecedented dataset on rhinoceros texture microwear confronted to detailed diets appears critical for future diet reconstruction of fossil rhinocerotoids.

Keywords Enamel microstructure · Diet · Dental microwear texture analysis (DMTA) · Mastication · Megaherbivore · Rhinoceros

Introduction

Rhinoceroses are among the most emblematic and endangered mammals today. Indeed, all five extant species are on the red list of the International Union for Conservation of Nature (The IUCN Red List of Threatened Species. Version 2017-3. www.iucnredlist.org.), ranging from "near threatened" for the white rhinoceros to "critically endangered" for the black, Javan, and Sumatran rhinoceroses. The fragility of extant rhinoceroses was well illustrated recently by the loss of Sudan, the last captive male of the Northern white rhinoceros subspecies (i.e., *Ceratotherium simum cottoni*; Emslie 2012; Tunstall et al. 2018). The five extant species occupy a restricted geographic range in Central and South Eastern Africa for *Diceros bicornis* (black rhinoceros) and *Ceratotherium simum* (white rhinoceros), and in South Asia (mostly in India, Nepal, and Indonesia) for the three Asian species, *Dicerorhinus sumatrensis* (Sumatran rhinoceros), *Rhinoceros sondaicus* (Javan rhinoceros), and *Rhinoceros unicornis* (Indian rhinoceros; Antoine 2012; Rookmaaker and Antoine 2012). They live in various habitats like alluvial plain, jungle, or savannah and cover a wide range of vegetarian diets (Groves 1972; Groves and Kurt 1972; Guérin 1980; Laurie et al. 1983; Owen-Smith 1988; Hillman-Smith and Groves 1994; Groves and Leslie 2011). However, rhinoceroses were far more abundant in the past and the Rhinocerotoidea (including Hyrachyidae, Rhinocerotidae, Amynodontidae,

✉ Manon Hullot
manon.hullot@umontpellier.fr

[1] Institut des Sciences de l'Évolution, UMR5554, CNRS, IRD, Université Montpellier, EPHE, Place Eugène Bataillon, CC064, 34095 Montpellier, France

[2] 7 Via Antico Filatoio, Collegno, Italy

[3] Palevoprim UMR 7262, CNRS, Université de Poitiers, 86073 Poitiers, France

Hyracodontidae, and Paraceratheriidae for several authors) was the most abundant and ecologically diversified superfamily of Perissodactyla (Prothero et al. 1989; Tissier et al. 2018). Fossil Rhinocerotoidea were recorded in various areas of Eurasia, North America, Jamaica, Central America, and Arabo-Africa (Prothero et al. 1989; Domning et al. 1997), and up to nine species of rhinoceros were in some cases cohabiting in the same habitat (Antoine et al. 2010; Mihlbachler et al. 2018). Their great abundance and disparity (Cerdeño 1998) and their diversity in fossil assemblages suggest that the diet spectrum covered by extinct rhinocerotoids might have been even wider in past ecosystems. Since most rhinocerotoid families diversified and became extinct before the expansion of C4 grasslands (Miocene in age; Prothero et al. 1989; Cerdeño 1998; Gordon and Prins 2008), the use of stable carbon isotopes to distinguish their diets might not be adequate, except for Rhinocerotidae (Bentaleb et al. 2006; Martin et al. 2011; Uno et al. 2018). However, microwear and especially dental microwear texture analysis (DMTA) might help explore this past diversity.

Dental microwear results from attrition (tooth–tooth contact) and abrasion (food–tooth contact; Kaiser et al. 2013). Other parameters, such as crown morphology (Joomun et al. 2008), chewing direction (Charles et al. 2007), or enamel microstructure (Rensberger and Koenigswald 1980; Maas 1997) might affect the microwear pattern. Yet, diet composition and its physical properties greatly influence the microwear signature (Merceron et al. 2016; Hedberg and DeSantis 2016). Dental microwear is a short-term recorder, which only gives access to the diet of the last weeks or months before the death of the individual (Merceron et al. 2004b; Hoffman et al. 2015; Calandra et al. 2016). It is however a powerful tool to study diets, and it has been used extensively in the last decades to infer the paleodiets of various species (Merceron et al. 2004a; Boisserie et al. 2005; Ungar et al. 2016), but also interseasonal (Merceron et al. 2010; Percher et al. 2017; Berlioz et al. 2017) and interpopulational variations within a given species (Berlioz et al. 2017).

Few microwear studies have focused on rhinocerotoids and more particularly on Rhinocerotidae, i.e., the only family with living representatives (e.g., Schulz et al. 2013; Ballatore et al. 2017; Mihlbachler et al. 2018). The concerned results were often obtained using two-dimensional microwear techniques and were not fully satisfying in terms of reproducibility and comparison (Mihlbachler et al. 2012), number of specimens, or taxonomic sample. Moreover, very few of these studies acknowledge the peculiar masticatory cycle and structure of rhinoceros enamel. Indeed, rhinoceros display a specific enamel ultrastructure with vertical Hunter-Schreger bands (contrary to most mammals) and the first contact during mastication cycle does not occur between the classic couple paracone/protoconid (Fortelius 1985; Koenigswald et al. 2011). These differences are likely to impact tooth response

to wear. Thus, comprehensive dental microwear texture data are lacking for extant rhinoceros species despite being a necessary first step toward inferring paleodiets of their fossil kin, especially knowing that the very studied ruminants may not be adequate models for other large ungulates (Mihlbachler et al. 2016). Here, we provide a comprehensive database of enamel microwear textures among living rhinocerotids, coupled with dietary preferences, as well as consideration about the impact of mastication and enamel microstructure on enamel microwear textures.

Materials and methods

Specimen collection

The dataset is composed of a total of 62 wild-shot rhinoceroses (see detailed list in Supplementary S1) distributed as follows: 17 specimens of *Ceratotherium simum* (white rhinoceros; *C. s. simum* and *C. s. cottoni* merged), four of *Dicerorhinus sumatrensis* (Sumatran rhinoceros), 21 of *Diceros bicornis* (black rhinoceros), 14 of *Rhinoceros sondaicus* (Javan rhinoceros), and 5 of *Rhinoceros unicornis* (Indian rhinoceros). The specimens are hosted in different European institutions: University of Montpellier, France (UM), Musée des Confluences in Lyon, France (MCL), Muséum National d'Histoire Naturelle in Paris, France (MNHN), Musée Royal d'Afrique Centrale in Tervuren, Belgium (MRAC), University Museum of Zoology of Cambridge, United Kingdom (UMZC), and Naturhistoriches Museum of Vienna, Austria (NHMW). Estimated individual ages based on wear stages are given in Supplementary S1 according to Hitchins (1978) for the black rhinoceros and to Hillman-Smith et al. (1986) for other species. Individuals with unerupted or unworn (i.e., very young specimens), damaged, or lacking molars were excluded from the study. Some very old individuals with worn molars that had no enamel left were also excluded. Zoo individuals were also set apart from the dataset, due to the suspected existence of biased diets with respect to wild conditions (Deka et al. 2003) and discrepancies in tooth wear between wild and captive animals (Kaiser et al. 2009).

Compilation of plant consumption by living rhinoceroses

We collected detailed information on the diet of each extant species in the literature. When possible, we provided the prevalence of the species in the diet, the specific ingested parts (e.g., leaf, fruit, or branch), the feeding preferences, but also precisions concerning the seasonal availability, the toxicity, the mechanical properties, and the consumption by other animals (including humans) when available (see Supplementary S2). The literature was reviewed extensively and unpublished

studies such as PhD and master thesis were included as well. For every plant, we also checked if the taxonomic name was up to date on the Plant List website (2013; Version 1.1. http://www.theplantlist.org/).

Dental microwear textures analysis

We studied the shearing (without Hunter–Schreger Bands (HSB)) and grinding (with HSB) facets of the same enamel band on the lingual part of the protocone on upper molars and distally to the protoconid or hypoconid (if the protoconid facet was unavailable) on lower molars (Fig. 1; Ballatore et al. 2017). We have chosen to study the protocone/protoconid (or hypoconid) couple and not the paracone/protoconid couple for two reasons: (i) in rhinoceroses, the first contact during mastication does not occur between the protoconid and the paracone as traditionally thought (Fortelius 1985), and (ii) according to a recent study, there are significant differences in microwear between the paracone and the protoconid (Ramdarshan et al. 2017).

We followed a strict casting protocol developed in previous studies (Scott et al. 2005, 2006). The facet was cleaned twice with cotton swab soaked in acetone to remove dirt, glues, and dust. For each facet, two polyvinylsiloxane molds (Regular Body President, ref. 6015 - ISO 4823, medium consistency, polyvinylsiloxane addition type; Coltene Whaledent) were cast. The first mold removes the last dirts from the facet, and the second is used for further analyses. The facet was put flat under a Leica DCM8 confocal profilometer ("TRIDENT" profilometer housed at the Palevoprim lab, CNRS, and University of Poitiers) using white light confocal technology with a Leica 100× objective (Numerical aperture:
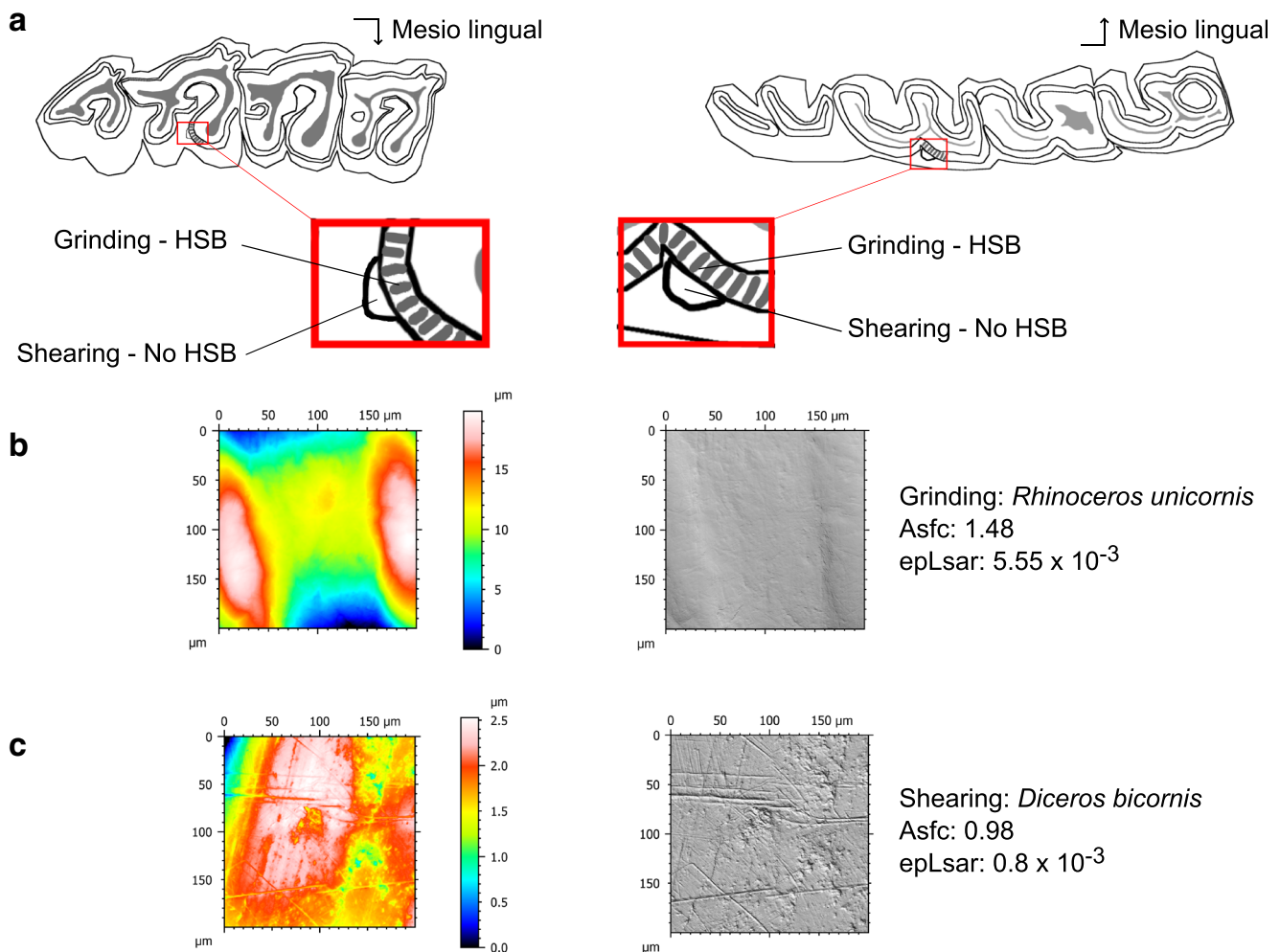

Fig. 1 Rhinocerotid dental microwear texture: location and examples of the studied grinding and shearing facets. **a** Analyses focused on shearing (without Hunter–Schreger bands) and grinding (with Hunter–Schreger bands) facets of the protocone and protoconid (or hypoconid) from upper and lower molars to conduct texture microwear analyses. Examples of shearing (B; *Diceros bicornis*: NHMW-4291) and grinding (C; *Rhinoceros unicornis*: NHMW-37591) surfaces are displayed in topography and black and white

0.90; working distance: 0.9 mm; Leica Microsystems). The scans were saved as a .Plμ file and pre-treated under Leica Map v. 7.4 (Leica Microsystems). The surface was inverted (as scans were produced on negative replicas), and missing (i.e., non-measured) points were replaced by the mean of the neighboring points. Aberrant peaks were removed with automatic operators including a morphological filter (see Merceron et al. 2016 for details). These surfaces were then leveled, and a 200 × 200-μm area was selected and saved as a digital elevation model (.sur) to be used for DMTA, and leveled. A final removal of form (polynomial of degree 8) and a last leveling were run in order to temper the potential effects of the HSB in the parameter calculations. These surfaces saved as .sur files were then analyzed using the Scale-Sensitive Fractal Analysis on Toothfrax and Sfrax softwares (Surfract, www.surfract.com) following Scott et al. (2006).

We used the four classical dental texture microwear 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 (HAsfc81)), and textural fill volume (here at 0.2 μm; FTfv). Anisotropy measures the orientation concentration of surface roughness. Complexity estimates the roughness at a given scale. Heterogeneity reflects the variation of complexity within the studied zone. Textural fill volume is estimated by filling the surface with square cuboids of different volumes (see Scott et al. 2006 for details).

Statistical analyses

We conducted all the statistical analyses on R (R Core Team 2017). First, we checked multivariate normality with the mardia test of the MVN package (Korkmaz S, Goksuluk D, Zararsiz G. MVN: An R Package for Assessing Multivariate Normality. The R Journal. 2014 6(2):151–162.). As our data were not multivariate normal, we used a Box–Cox transformation from the car package (Fox and Weisberg 2011). Then, we run a MANOVA from the MVN package. To make the MANOVA results precise, we conducted ANOVAs on each microwear parameter (anisotropy, complexity, FTfv, HAsfc81) by species and facet, by species only, and we performed Wilcoxon tests by facet only because there are only two groups (i.e., shearing and grinding). Eventually, we performed two kinds of post hoc tests, the Tukey's HSD and Fisher's LSD, that have different conservativities (HSD is more conservative) and that determine significant differences between group means in ANOVAs. The LSD test was from agricolae (de Mendiburu 2019). Eventually, all the graphs presented in this study were done using ggplot2 (Wickham 2016).

Results

Dietary overview for extant rhinoceroses

All living rhinoceroses are herbivores, but they differ in terms of plant species, type (e.g., herbaceous monocotyledon, herbaceous dicotyledon, or woody browse), and importance of each type in the diet (Fig. 2; S2). Diet categories are defined according to Scott (2012).

Diceros bicornis (Linnaeus, 1758): browser

Many studies were conducted on the diet of the black rhinoceros, mostly in South Africa and Kenya (Goddard 1970; Hall-Martin et al. 1982; Muya and Oguge 2000; Brown et al. 2003; van Lieverloo et al. 2009). Diceros bicornis is a browser found in various habitats ranging from desert to forest (Goddard 1968; Coetzee 1970; Guérin 1980; Hall-Martin et al. 1982; Young and Evans 1993; Kingdon and Hoffmann 2013). It may consume a wide variety of plant species (around 700; see S2), principally herbs and shrubs (Joubert and Eloff 1971; Hillman-Smith and Groves 1994; Kahlke and Kaiser 2011). However, most of the time 20 species or less represent 90% of the diet (Buk 2004; Kingdon and Hoffmann 2013). The diet is both season- and environment-driven (Goddard 1970; Mukinya 1977; Loutit et al. 1987) but not significantly age- or gender-dependent, at least in Tanzania (Goddard 1968). Ninety-eight percent of the feeding occurs under a 2-m height (Fig. 2) and preferentially between 0.5 and 1.5 m (Emslie 1999; Buk 2004).

Legumes were favored food items in many parks and may form more than 50% of the bulk diet in some habitats (Goddard 1968). In particular, species of thorn trees (Senegalia, Vachellia, and Acacia) were often preferred despite the presence of important herbivory deterrents, such as spines and ant mutualism (Emslie and Adcock 1994; Muya and Oguge 2000; Buk and Knight 2010). Similarly, although producing toxic latex and displaying spines, several Euphorbia species are really appreciated by the black rhinoceros (Emslie and Adcock 1994; Dudley 1997). Eventually, Grewia shrubs were recorded in most studies but with various contributions to the diet (Mukinya 1977; Hall-Martin et al. 1982; van Lieverloo et al. 2009).

Rhinoceros unicornis (Linnaeus, 1758): variable grazer

Rhinoceros unicornis is described in the literature as a mixed-feeder favoring grasses, such as Cynodon dactylon and Saccharum spontaneum (Laurie et al. 1983; Owen-Smith 1988; Dinerstein 1991; Fjellstad and Steinheim 1996). The proportion of grass in the diet varies according to the season between 70 and 89% (Laurie 1982). According to recent studies (Gagnon and Chew 2000; Scott 2012), the Indian rhinoceros classifies as a variable grazer, i.e., consumption of 60 to
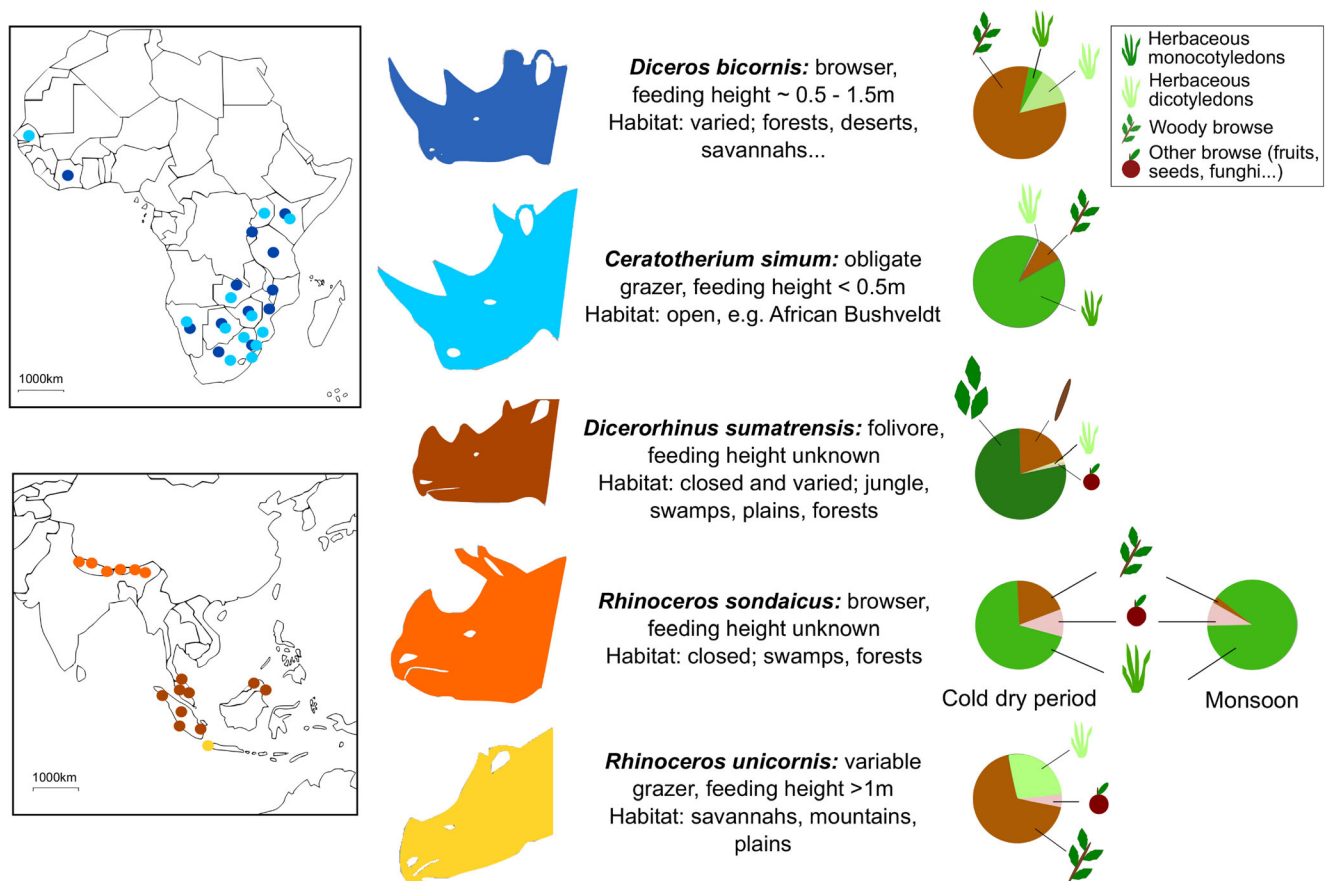
Fig. 2 Geographical distribution and diet of the five extant species of rhinoceroses. The Asian rhinoceroses are mostly found in protected areas forming discontinued patches in India and Nepal (*Rhinoceros unicornis*), in Sumatra and Malaysia (*Dicerorhinus sumatrensis*), and in Java (Ujung Kulon Reserve only; *Rhinoceros sondaicus*). *Diceros bicornis* is present in Western and Southeastern Africa (from Namibia to Kenya) overlapping with the range of *Ceratotherium simum* (e.g., Namibia, South Africa).

Points on the maps represent localities where rhinoceros presence was attested. Updated maps adapted from Antoine (2012) and Rookmaker & Antoine (2012). Graphical representation of the diets based on a review of the literature (see text 2.2, 3.1, and Supplementary S2). Other facts mostly from Coetzee (1970), Guérin (1980), Emslie (1999, 2012), Kahlke and Kaiser (2011), and Kingdon and Hoffmann (2013).

90% of grasses with a seasonal variation of the diet. This rhinoceros inhabits alluvial plain grasslands but might also be found in savannahs, mountains, jungles, and swamps (Laurie et al. 1983; Dinerstein and Price 1991). The browsing part in the diet is more important in the cool dry season (~November–mid February) and favored items include *Dalbergia sissoo*, *Litsea monopetala*, and *Mallotus nudiflorus* fruits (Laurie 1982; Laurie et al. 1983; Konwar et al. 2009; Bhatta 2011; Hazarika and Saikia 2012). Aquatic plants, such as *Hydrilla verticillata* or *Ceratophyllum demersum*, are also eaten (Laurie 1982; Owen-Smith 1988; Mary et al. 1998), as well as cultivated vegetables and crops when available (Laurie 1982; Laurie et al. 1983; Konwar et al. 2009; Bhatta 2011; Hazarika and Saikia 2012).

Rhinoceros sondaicus (Desmarest, 1822): browser

Rhinoceros sondaicus is a browser including more than 100 species in its diet (Groves and Leslie 2011). It is found in dense jungles, swamps, and rain forests (Lydekker 1907; Ammann

1985; Groves and Leslie 2011). It favors leaves, shoots, and twigs (Ammann 1985; Owen-Smith 1988) but sometimes includes fruits and flowers of *Arenga pinnata*, *Carica papaya*, and *Leucaena leucocephala* in very small quantities (Hoogerwerf 1970). Ammann (Ammann 1985) reported that *Spondias pinnata*, *Amomum*, *Leea sambucina*, and *Dillenia excelsa* accounted for 44% of the diet. Other major species in the diet are *Glochidion zeylanicum* and *Dendrolobium umbellatum*, representing more than 20% (Hoogerwerf 1970). *Ficus* species are also well represented in the Javan rhino's diet. The World Wildlife Fund suggested a possible shift in the diet of this species toward less plant diversity (World Wildlife Fund 1982) compared to previous studies (Schenkel and Schenkel-Hulliger 1969) over the last decades, due to a critical demographic decline under severe human pressure.

Dicerorhinus sumatrensis (Fischer, 1814): folivore

In the literature, *Dicerorhinus sumatrensis* is depicted as a hyperbrowser mostly eating leaves, twigs, and small branches

of shrubs and trees (Groves and Kurt 1972; Guérin 1980; van Strien 1986). However, the frequent consumption of leaves (75% of mature leaves and 5% of young leaves; Flynn 1981) and especially that of monocotyledonous bamboos (*Bambusa*) and of silica-rich dicotyledons (e.g., Sapotaceae, *Styrax*) might challenge this classification and affect microwear in turn. The *Elastostema* species (dicotyledon) are reported to be most frequently eaten and *Garcinia* or *Styrax* species are favored (van Strien 1986). Some fruits, such as wild mangoes (*Mangifera lagenifera*), are sometimes included in the diet of this taxon (Evans 1904). More than 100 plant species were recorded by various authors but their contribution to the diet varies greatly (see S2). In the wild, this rhinoceros lives in various environments, ranging from altitudinal forests to swamps but never far from water and salt sources (Krumbiegel 1960; Groves and Kurt 1972; van Strien 1986).

Ceratotherium simum (Burchell, 1817): obligate grazer

Ceratotherium simum is an obligate grazer (i.e., more than 90% of monocots, diet constant). It lives in open environments like the African Bushveldt for the Southern subspecies (Player and Feely 1960) or non-dense *Combretum* forest for the Northern one (Heller 1913), which is probably extinct in the wild today (Emslie 2008; Milliken et al. 2009; Tunstall et al. 2018). It is area-selective and favors short grasses including species of *Panicum*, *Urochloa*, *Digitaria*, and *Cynodon* (Groves 1972; Guérin 1980; van Gyseghem 1984; Owen-Smith 1988). Around 30 species of grasses are recorded in the diet of this rhinoceros, both referred subspecies not differing significantly in their ecology (Groves et al. 2010). Extremely rare browsing has been reported for this species (i.e., 1% of forbs in annual diet; Owen-Smith 1988) and fecal analyses in Kruger National Park (South Africa) revealed a 90% proportion of C4 grasses in white rhinoceros dung (Codron et al. 2007). Such a diet implies a drastic and permanent abrasion of occlusal tooth surfaces. Indeed, tough and fibrous leaves of grasses contain high levels of silica phytoliths (Smith et al. 1971; Brizuela et al. 1986) and great amounts of exogenous grit might be ingested due to the low feeding height (Hummel et al. 2010).

Dental microwear textures of extant rhinoceroses

Mean, median, and standard deviation of the mean were calculated for anisotropy (epLsar), complexity (Asfc), fine textural fill volume (FTfv; textural fill volume at 0.2 μm), and heterogeneity of the complexity (HAsfc81) by species and by facet (shearing and grinding; Table 1). A permutational MANOVA on Box–Cox transformed data suggested significant differences in dental microwear texture depending on species (df = 16, p value = 0.009554) and facet (df = 4, p

value = 0.004148). No effect of the interaction of species and facet was observed (p value >0.1). The interspecific differences are explained both by anisotropy and complexity (ANOVA; Table 2). The differences between shearing and grinding facets are explained by complexity and FTfv (ANOVA; Table 2). No significant differences for heterogeneity of the complexity at any scale were observed neither by species (ANOVA, p value >0.1) nor by facet (Wilcoxon, p value >0.1).

Figure 3 plots reveal the significant differences highlighted by Fischer's least significant difference (LSD) and Tukey' honestly significant difference (HSD). Concerning facets, we found significant differences between grinding and shearing facets of *Diceros bicornis* for complexity and FTfv and of *Dicerorhinus sumatrensis* for complexity (HSD and LSD; Fig. 3). The post hoc tests also suggested significant differences of microwear between species. Indeed, mean anisotropy is higher on both facets in *C. simum* (grinding: $4.54*10^{-3}$, shearing: $5.59*10^{-3}$) and *Dicerorhinus sumatrensis* (grinding: $4.85*10^{-3}$, shearing: $6.51*10^{-3}$) than in *R. sondaicus* (grinding: $2.19*10^{-3}$, shearing: $3.07*10^{-3}$). Sometimes, interspecific differences were only significant on a single facet and/or using the less conservative LSD. For example, Fisher's LSD pointed different anisotropies on the shearing facet between *R. unicornis* and *C. simum* and between *R. unicornis* and *Dicerorhinus sumatrensis* (Fig. 3). The complexity of the shearing facet of *Dicerorhinus sumatrensis* is the lowest (mean Asfc = 0.5) and is significantly different from that of all the other species (HSD and LSD; Fig. 3).

Figure 4 shows the frequency of specimens per species with a high anisotropy (epLsar > 0.005) against that with a high complexity (Asfc > 2) for each facet. *Dicerorhinus sumatrensis* has a great proportion of anisotropic specimens (> 50%) and no complex specimens (0%) on both facets. On the grinding facet, *R. unicornis* presents many anisotropic specimens and an intermediate proportion of complex specimens, whereas on the shearing facet the percentage of anisotropic drops to ~ 33% and more specimens appear to be complex (Fig. 4). For *C. simum*, the number of anisotropic specimens is high (i.e., between 37.5 and 57%) and that of complex ones is low to intermediate (< 40%) on both facets (Fig. 4). Eventually, *Diceros bicornis* and *R. sondaicus* display similar tendencies on both facets with few anisotropic specimens (< 25%) and many complex specimens (grinding > 50%, shearing > 25%).

Discussion

DMTA and diet

The five extant species of rhinoceroses cover a wide array of herbivorous diets (Fig. 2; S2), ranging from obligate grazing

Table 1 Rhinocerotid dental microwear texture: median, mean and standard deviation (SD) of the mean of textural parameters by species and facet

	N	Asfc			epLsar ($\times 10^{-3}$)			FTfv ($\times 10^4$)			HAsfc81		
		Median	Mean	SD	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD
Grinding													
C. simum	16	1.64	1.97	1.16	4.57	4.54	1.66	4.81	5.26	2.36	0.68	0.76	0.57
D. sumatrensis	4	1.35	1.45	0.22	5.17	4.85	1.38	5.04	4.93	8.18	0.58	0.74	0.35
D. bicornis	18	2.57	3.35	2.70	2.99	3.05	1.56	5.69	5.42	1.71	0.66	0.78	0.41
R. sondaicus	12	2.38	3.14	2.52	2.00	2.19	1.25	5.99	5.82	1.94	0.67	0.98	0.73
R. unicornis	5	1.61	2.09	1.02	5.09	4.36	2.43	4.84	5.46	1.96	0.84	0.97	0.48
Shearing													
C. simum	14	1.43	1.54	0.66	6.21	5.59	2.91	4.84	4.82	2.10	0.74	0.86	0.37
D. sumatrensis	3	0.42	0.50	0.23	5.55	6.51	2.57	3.45	2.82	1.71	0.68	0.59	0.25
D. bicornis	16	1.33	1.59	0.84	3.63	3.48	1.93	3.40	3.52	2.21	0.65	0.74	0.2
R. sondaicus	12	1.89	2.13	1.43	2.15	3.07	2.49	5.28	4.96	2.27	0.68	0.75	0.23
R. unicornis	3	3.71	3.25	2.57	1.70	3.05	3.48	6.50	4.91	3.35	0.95	0.85	0.37

Asfc Area-scale fractal complexity, *epsLar* exact proportion of length-scale anisotropy of relief, *FTfv* Fine textural fill volume, *HAsfc81* heterogeneity of complexity with 81 cells

(*Ceratotherium simum*) to browsing (*Diceros bicornis* and *Rhinoceros sondaicus*). According to our review of the literature and the diet categories proposed by Scott (2012), we suggest to reclassify the Indian rhinoceros (*R. unicornis*) as variable grazer. Indeed, Scott (2012) defines variable grazing as the consumption of 60 to 90% of grasses with a seasonal variation of the diet. Figure 2 clearly shows a dominance of monocotyledonous grasses in the year round diet of *R. unicornis* and a clear seasonal variation of the diet.

The microwear signature for *C. simum* on both facets is high anisotropy and low complexity, which is in accordance with an obligate grazing diet (Scott 2012). Similarly, the two browsing rhinoceroses *Diceros bicornis* and *R. sondaicus* display a browsing signature (Scott 2012) with low to medium anisotropy and medium–high complexity on both facets (Fig. 3). *Rhinoceros unicornis* microwear pattern presents a discrepancy between grinding and shearing facets (Figs. 3 and 4). On the grinding facet, the complexity is low and the anisotropy high, whereas on the shearing facet *R. unicornis* displays a medium–high complexity and a low to medium

anisotropy. These differences might result from different causes. First, as very few skulls (five) of wild shot specimens were available for this species in the European collections visited, the tendencies observed might be primarily due to sampling bias (small sample effect). Conversely, a seasonal dietary shift is known to occur in *R. unicornis* (Laurie et al. 1983), from nearly exclusive grazing during monsoon times to variable grazing during the winter (Fig. 2). This shift shall certainly lead to different dental microwear textures according to the season, which may in turn bias the mean plotted in Fig. 3 depending on the season of death of the studied specimens (Merceron et al. 2010; Calandra and Merceron 2016; Percher et al. 2017; Berlioz et al. 2017). Unfortunately, this information is lacking in most cases (Scott et al. 2012), and more particularly in the present sample.

Eventually, *Dicerorhinus sumatrensis* has the highest values for anisotropy and the lowest for complexity (Table 1), suggesting soft but abrasive food items. This is in accordance with Loose's (1975) statement that this rhino is a "browser favoring soft food." Moreover, the Sumatran

Table 2 Rhinocerotid dental microwear texture: ANOVA results for facet and species on all textural parameters

	Asfc		epLsar		FTfv		HAsfc81	
	F value	Pr (>F)	F value	Pr (>F)	F value	Pr (>F)	F value	Pr (>F)
Species	2.606	*0.04071*	6.458	*0.000125*	1.023	0.39943	0.477	0.752
Facet	9.085	*0.00332*	1.083	0.300666	8.556	*0.00433*	0.217	0.643
Species × facet	1.118	0.35266	0.670	0.614524	0.778	0.54250	0.549	0.700

Significant *p* values are in italics

Asfc area-scale fractal complexity, *epLsar* exact proportion of length-scale anisotropy of relief, *FTfv* fine textural fill volume, *HAsfc81* heterogeneity of complexity with 81 cells
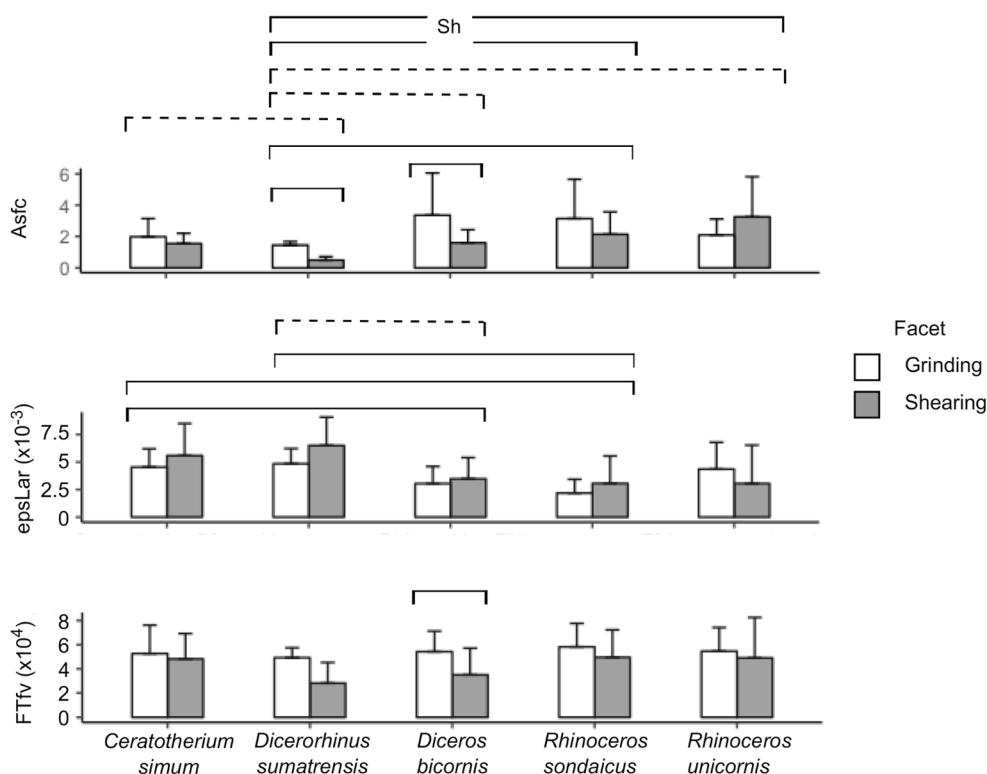
Fig. 3 Rhinocerotid dental microwear texture: bar plot of the mean values of three textural parameters (complexity, anisotropy, textural fill volume) depending on species and facet considered. The means and standard deviations of the textural parameters are plotted depending on the species and the facet. Shearing facets display higher complexity and lower anisotropy and textural fill volume, except for *Rhinoceros unicornis*. Each horizontal bar indicates significant interspecific differences according to Fischer's least significant difference (LSD) and Tukey' honestly significant difference (HSD) post hocs (plain lines; *p* value ≤ 0.05) or to LSD only (dashed lines; *p* value ≤ 0.05). Sh means significant interspecific differences only between shearing facets. Asfc: area-scale fractal complexity; epLsar: exact proportion of length-scale anisotropy of relief; FTfv: fine textural fill volume

rhinoceros mainly feeds on leaves (up to 80% according to Flynn 1981; Fig. 2) that are soft, which may explain the low complexity values observed (Scott et al. 2012; Calandra and Merceron 2016). Leaf-browsing is sometimes associated with intermediate values of anisotropy (Berlioz et al. 2017), but still

higher than the anisotropy associated with frugivores and generalists (Scott et al. 2012; Scott 2012; Percher et al. 2017). However, leaves and especially mature ones (75% of the diet of *Dicerorhinus sumatrensis*; Flynn 1981) are tough resulting in high anisotropy and low complexity through the
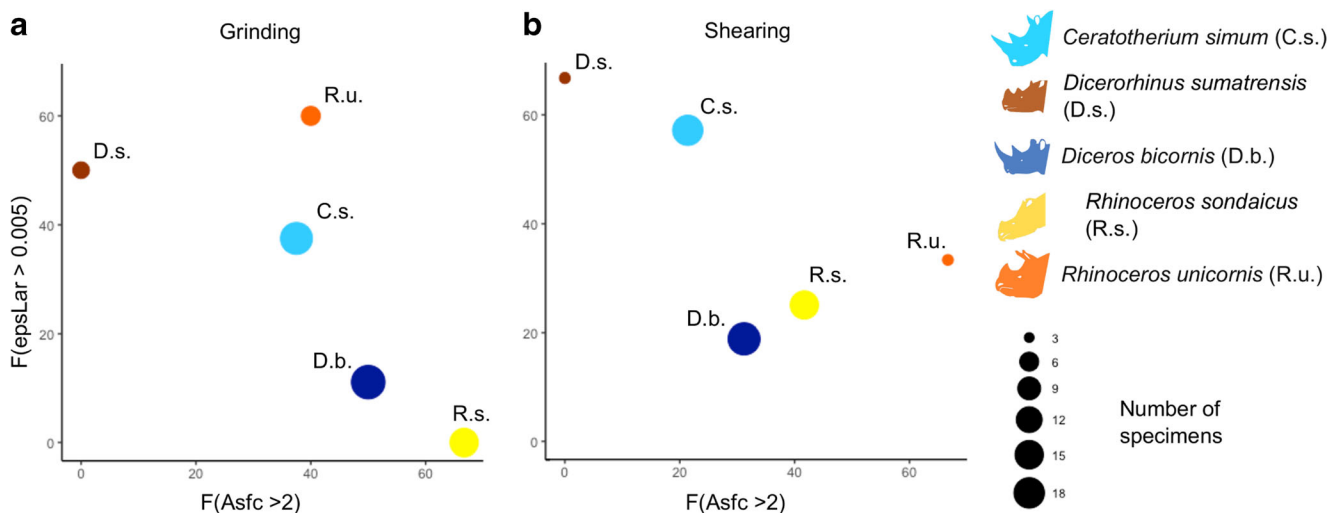

Fig. 4 Rhinocerotid dental microwear texture: frequency of specimens per species with high complexity (Asfc > 2.0) and high anisotropy (epLsar > 0.005). **a** Grinding facet. **b** Shearing facet. Circle diameter corresponds to the sample size for DMTA

phenomenon of polishing (Scott et al. 2012; Calandra and Merceron 2016; Percher et al. 2017). Several species favored by *Dicerorhinus sumatrensis* have indeed tough leaves, such as *Ficus elastica* or *Mangifera indica* (Choong et al. 1992), and the consumption of silica-rich plants like the monocotyledon *Bambusa* (for a discussion on the effect of bamboo consumption on microwear, see Rivals et al. 2014) or the dicotyledon *Styrax* is also reported (S2; Metcalfe 1961; van Strien 1986). Once again, the low number of specimens available (four) for this species pleads for nuanced interpretations.

Influence of other parameters than diet on DMTA

Despite some significant differences between rhinoceros species (Fig. 3), there are no visual clusters in their dental texture microwear (classic plot of anisotropy against complexity, principal component analysis, factor discriminant analysis; see Supplementary S3). This is congruent with previous studies that showed lower diet discrimination in perissodactyls than in ruminants for instance (Mihlbachler et al. 2016). Several factors other than food properties might affect the microwear signature and explain this absence of clear diet clusters in rhinoceroses, such as the extremely modified structure of their enamel (Rensberger and Koenigswald 1980; Boyde and Fortelius 1986; Koenigswald et al. 2011) or the

differences in mastication cycles (Fortelius 1985; Abrams 2016) compared to ruminants.

Regarding enamel microstructure, rhinocerotoids are quite different from other ungulates. Indeed, in some parts of their enamel, they display vertical Hunter–Schreger bands (HSB) that are associated with a better resistance to abrasion and crack propagation in lophodont teeth (Rensberger and Koenigswald 1980; Koenigswald et al. 2011). Thus, one may expect a different response to wear from that of the transverse HSB enamel of most placentals, including ruminants (Koenigswald et al. 2011). In fact, the facets with HSB (i.e., grinding facet) often displayed a higher complexity and textural fill volume than the ones without HSB (Table 1).

Concerning mastication processes, rhinocerotids are also distinct from other ungulates, which could be reflected in their microwear signature (Charles et al. 2007). Most studies on ungulates were conducted on the paracone/protoconid couple, as they usually are the first cusps to contact during mastication (Fortelius 1985; Abrams 2016). Still, in rhinoceroses the previous statement is wrong and the first cusps to contact during the chewing stroke are the hypoconid on M2 and the protocone on M1 (Fortelius 1985). Moreover, every facet has one or several different functions (e.g., phase I or II, or number of interactions) in the masticatory process and the structure of enamel (i.e., presence or absence of HSB) varies within the tooth, thus modifying facet reaction to wear as well
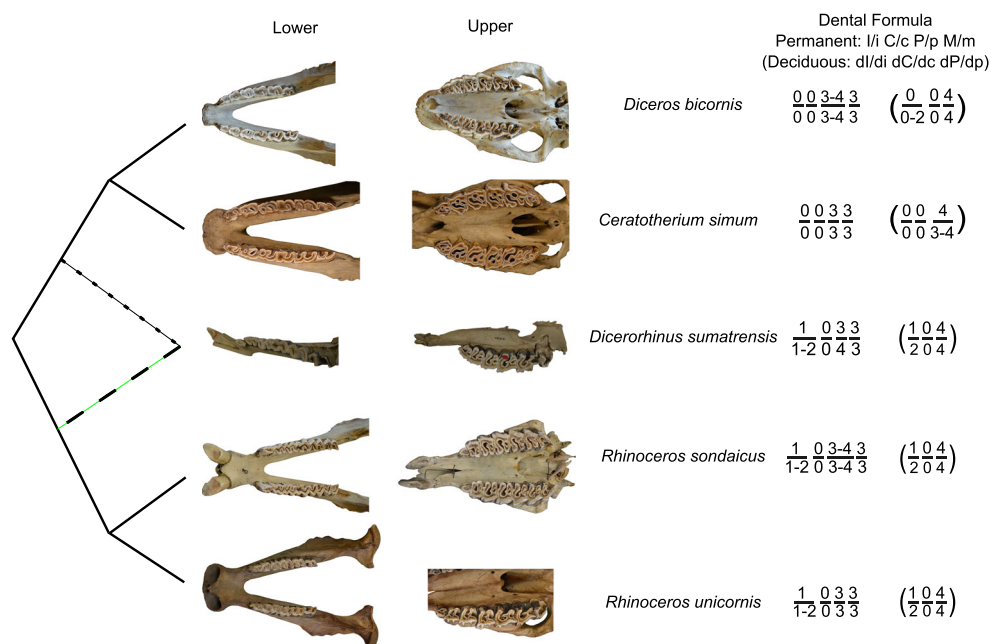

Fig. 5 Phylogeny and dental morphology of extant rhinoceroses. Upper and lower tooth rows, as well as dental formulae are plotted against rhinocerotid phylogeny for each species: *Diceros bicornis* (MRAC-7987), *Ceratotherium simum* (MRAC-5925), *Dicerorhinus sumatrensis* (UMZC-H6385), *Rhinoceros sondaicus* (MCL-5000-2041), and *Rhinoceros unicornis* (MNHN-2009.400). We chose to display adult specimens (M3 fully erupted and in wear) having a complete dentition with limited wear on associated mandible and maxilla, which was not possible for *Dicerorhinus sumatrensis* and *R. unicornis* as very few specimens were available for this study. The position of *Dicerorhinus sumatrensis* is still disputed: "horn hypothesis" in blue short dashes (Antoine 2002) or "geographic hypothesis" in green long dashes (Welker et al. 2017). Capital letters stand for upper teeth and lower case for lower ones; d is for deciduous. I: incisor, C: canine, P: premolar, M: molar

(Ramdarshan et al. 2017). Lastly, one could assume that a potential phylogenetic inertia might affect the microwear pattern. Indeed, the two species of *Rhinoceros* display similar dental morphologies, and it is the same to a lesser extent for the closely related African rhinoceroses *C. simum* and *Diceros bicornis* (Fig. 5). However, ecologies and diets within these phylogenetic clusters are truly different (Fig. 2), discrediting the hypothesis of a phylogenetic niche conservatism (see the review of Losos 2008). Yet, studying the phylogenetic signal (Blomberg and Garland 2002) in rhinoceros texture microwear would be very interesting. But to do so one would need a resolved and reliable phylogeny, which is not the case of that of extant rhinoceroses. Indeed, rhinoceros phylogeny—and especially the position of *Dicerorhinus*—remains debated (Fig. 5; Antoine 2002; Willerslev et al. 2009; Welker et al. 2017).

Nonetheless, we plotted the percentage of anisotropic specimens (epLsar > 0.005) against that of complex specimens (Asfc > 2) for each species and revealed crucial differences in microwear between the diets (Fig. 4). We used the cutpoints proposed by Scott et al. (2012) because despite having been defined for primates, they fall between the median values of browsers and grazers from diverse groups. Although still perfectible in terms of sampling, the current dataset on rhinoceros DMTA could be of critical help to reconstruct the diet of fossil Rhinocerotoidea.

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