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1 **Tooth tales told by dental diet proxies: an alpine community of sympatric ruminants as**
2 **a model to decipher the ecology of fossil fauna**

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22

23 **Abstract**

24 Paleobiologists tend to use dietary information as an ecological indicator because
25 diet is a fundamental link between an organism and its environment. However, the ecological
26 information from fossilized hard tissues is often difficult to interpret, because links between
27 environment, diet, and hard tissue biology are insufficiently studied in modern communities.
28 To address this dilemma, we investigated dietary proxies commonly used by paleobiologists
29 in a 4-ruminant community from the French Alps. Dental microwear textural analyses are
30 applied to 82 specimens of roe deer, red deer, chamois, and mouflons. Intra-tooth serial
31 enamel stable carbon and oxygen isotope analyses of the structurally bound carbonate were
32 applied on eleven specimens, with isotope-based niche reconstructions, and inverse modeling
33 of original seasonally variable oxygen isotope inputs.

34 While microwear complexity largely overlaps, both inter-individual dispersion and
35 heterogeneity of complexity together with the anisotropy track dietary differences. The red
36 deer is likely more engaged in grazing than the two bovids, which both plot as mixed feeders.
37 When combined, dental microwear and carbon stable isotope analyses accurately reflect
38 known ecological separation between the chamois and the roe deer. Both stable isotopes
39 suggest niche separation by increasing enrichment from roe deer to red deer, to chamois;
40 mouflons appear to feed as generalists. In roe deer, which shows the highest enamel oxygen
41 isotope range (5.7 ‰), variation is nevertheless constrained compared to oxygen isotope
42 ranges observed in regional precipitation, where the mean annual range reaches 9.9 ‰.
43 However, through inverse modeling we estimate seasonal input ranges that average 9.7 ‰, a
44 result strikingly similar to regional values. Altogether, our data demonstrate that given
45 appropriate sampling strategies and modeling approaches, microwear and isotopic data can be
46 effective tools for demonstrating niche separation among multiple sympatric herbivorous taxa.
47 **Keywords:** Niche, Teeth, Stable Isotopes, Dental Microwear Textures, Ungulates, Europe

48 **1. Introduction**

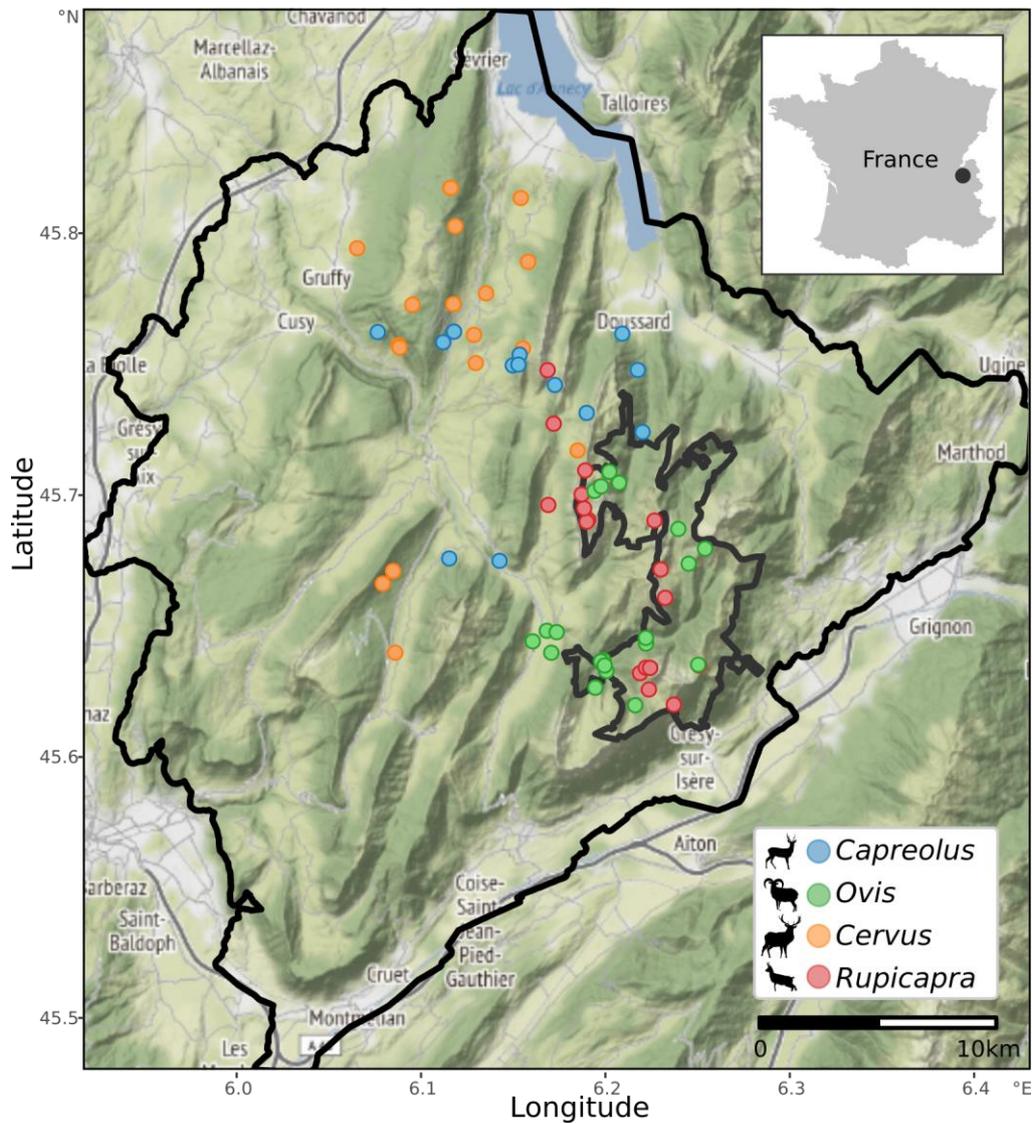
49 Exploring the diet of extinct species is essential to understand how they interacted
50 with their ecosystems, and how biotic and abiotic factors have both shaped their evolution.
51 Most soft tissues including stomach contents are rarely preserved in the fossil record, and
52 vertebrate paleontologists therefore base many paleodietary reconstructions on dental
53 morphology. Based on functional interpretations paleontologists identify plausible underlying
54 mechanisms driving evolution, and propose environmental reconstructions that constrain
55 climate models. For instance, the relative abundances of ruminants with low- and high-
56 crowned cheek teeth supposedly reflecting grazing versus browsing behavior have been used
57 to assess spatial and chronological variations in vegetation covers and climatic conditions
58 (e.g., Fortelius et al., 2002; Kaya et al., 2018).

59 Alternative approaches provide taxon-free tools to reconstruct the ecological traits.
60 Among them, the most widely used in mammal paleontology are traditional and non-
61 traditional stable isotopes (see Ben-David and Flaherty, 2012 and citations therein; Martin et
62 al., 2017) and dental microwear texture analyses (Ungar et al., 2008; Calandra and Merceron,
63 2016; DeSantis, 2016; Kaiser et al., 2016). However, prior to their application to fossils, these
64 proxies require validation using either in vivo experimentations (Merceron et al., 2016;
65 Ramdarshan et al., 2016, 2017; Schulz et al., 2013; Winkler et al., 2019) or well-constrained
66 modern communities of species with known ecological habits and life history traits (Merceron
67 et al., 2010; Berlioz et al., 2017; Bignon-Lau et al., 2017; Percher et al., 2018).

68 The present paper is a case study to explore how dental tissues reflect ecological
69 partitioning, through dietary habits and habitat use, among a modern community of four
70 sympatric ruminants. We here focus on two species of cervids (*Cervus elaphus*, and
71 *Capreolus capreolus*) and two of bovids (*Ovis gmelini musimon*, and *Rupicapra rupicapra*)
72 from the Bauges Natural Regional Park (BNRP) in the French Alps. These species have

73 different feeding behaviors and habitat use due to species-specific body-mass, digestive
74 morpho-physiological features and social-spatial behaviors (Redjadj et al., 2014 and citations
75 therein).

76



77
78 **Figure 1.** Location of specimens of roe deer (*Capreolus capreolus*, n = 18), red deer (*Cervus*
79 *elaphus*, n = 21), chamois (*Rupicapra rupicapra*, n = 21) and mouflon (*Ovis gmelini*
80 *musimon*, n = 22) from Bauges Natural Regional Park (BNRP). The inner limits correspond to
81 the National Game and Wildlife Reserve within the BNRP. White zones represent urbanized
82 areas, dark green forest and light green either lowland open fields or higher alpine meadows.
83

84 As Redjadj et al. (2014) have shown inter-specific differences in diet and habitat
85 within the Bauges ruminant community, we expect to observe corresponding differences in
86 dental microwear textures (Merceron et al., 2016; Ramdarshan et al., 2016; Schulz et al.,

87 2013; Scott, 2012) and stable carbon isotopes ($^{13}\text{C}/^{12}\text{C}$ ratio expressed as $\delta^{13}\text{C}$ value in permil
88 relative to VPDB; Vienna PeeDee Belemnite) in enamel (Bonafini et al., 2013; Drucker and
89 Bocherens, 2009). In addition, we expect the enamel oxygen isotopic composition ($^{18}\text{O}/^{16}\text{O}$
90 ratio expressed as $\delta^{18}\text{O}$ value in permil relative to VSMOW, Vienna Standard Mean Ocean
91 Water) to primarily reflect the $\delta^{18}\text{O}$ values of the ingested water, including drinking and/or
92 leaf water. Physiology (Kohn, 1996; Green et al., 2018a) and altitudinal ranges (Dansgaard,
93 1964; Rozanski et al., 1993; Gat, 1996; Bowen, 2010) will further impact body water and
94 enamel $\delta^{18}\text{O}$ compositions (See text-SI). The community of sympatric ruminants at the BNRP
95 representing 82 wild-shot individuals with known sex, age, place and date of death, sampled
96 over few months mostly during fall 2014 and 2015, provides a unique opportunity to
97 investigate ecological partitioning through different dietary proxies all issued from dental
98 tissues. This will allow us to draw conclusions how well a combined dental wear and stable
99 isotope approach on such a well-constrained faunal sample does reflect the environmental
100 conditions in mid-latitude mountainous C_3 plant ecosystem.

101

102 **2. Material and methods**

103 *2.1. Material*

104 The Bauges Natural Regional Park (BNRP; 45.69 °N, 6.14 °E) is a typical subalpine
105 massif located in the French Alps, with altitudes ranging from 250 m to 2217 m (see Figure 1
106 and Text-SI). Several studies have investigated multiple aspects of behavioral ecology of the
107 ruminants (chamois, red deer, roe deer and mouflon) inhabiting the BNRP. Among them,
108 Redjadj et al. (2014; see Text-SI and Table S1) made a comparative analysis of the feeding
109 ecology of these four large herbivores through a gender-balanced stomach content analysis
110 covering late summer until early winter period from 2003 to 2008. It is worth mentioning here
111 that the specimens considered in Redjadj et al. (2014) are not the same analyzed in the present

112 study. However, we used to interpret at best between species differences in dental dietary
113 proxies. It is also worth noting that stomach content or feces analyses reflect dietary
114 composition of the last few hours and days, respectively. However, the dietary proxies
115 extracted from dental tissues we investigate here reflect larger time windows: from at least
116 weeks, to months, to just over a year (Kierdorf and Kierdorf, 2000; Davis and Pineda Munoz,
117 2016).

118 *Cervus elaphus* is a mixed-feeding species (including both monocots and dicots)
119 with spatial variation in its diet (Gebert and Verheyden-Tixier, 2001). *Capreolus capreolus* is
120 a selective browser (Tixier et al., 1997). *Ovis gmelini musimon* is a mixed-feeding species.
121 Marchand et al. (2013) concluded that although grasses are the major food type, foliages from
122 shrubs and herbaceous dicots are the secondarily preferred food resources. *Rupicapra*
123 *rupicapra* is a mixed feeder grazing and browsing depending resource availabilities and
124 energetic requirements (Pérez-Barberia et al., 1997; see Text S1 and Table S1). The largest
125 ruminant (adult males: 151 kg; adult females: 98 kg; Text S1 and Table S1) at the BNRP, the
126 red deer *Cervus elaphus*, is a mixed-feeding species (including both monocots and dicots)
127 with spatial variation in its diet. Grasses account for about 30 % of the annual diet in many
128 regions through Europe but can surpass 80 % in Mediterranean habitats (Azorit et al., 2012;
129 Bugalho and Milne, 2003; Gebert and Verheyden-Tixier, 2001). At the BNRP, Redjadj et al.
130 (2014) found out that during late summer and early fall (the period during which most of the
131 specimens were shot), herbaceous monocots and forbs represent about 40 and 6 %,
132 respectively, of the stomach content as dry matter weight. Fruits, mainly apples and to a lesser
133 extent acorns (Redjadj et al., 2014) may account for up to 20 %. Foliages from various
134 evergreen and deciduous trees and shrubs (cumulative proportions reaching 23.6 %),
135 dominated by evergreen shrubs, notably brambles (*Rubus fruticosus*; Table S1), also form a
136 major fraction of the diet. It is worth noting that Suter et al. (2004) indicates that herbaceous

137 monocots represent between 50 and 60 % of summer diet of red deer in the Alps, which is
138 complemented with herbaceous dicots (forbs) that could represent up to 20 %. Although
139 comparisons between the two studies are difficult as the sampling methods differ, the seasonal
140 shift from graze to browse from summer to winter are reported for many Alpine populations
141 (Suter et al., 2004).

142 The second cervid, the roe deer *Capreolus capreolus* (adult males: 22.8 kg; adult
143 females: 21.4 kg; Text SI and Table S1), is a selective browser (Cibien, 1984; Cornelis et al.,
144 1999; Cransac et al., 2001; Storms et al., 2008; Tixier et al., 1997). Its diet mostly includes
145 dicot foliage, mosses, mushrooms, fruits including seeds. Herbaceous monocots barely reach
146 10 % of its diet; this occurs, however, only in spring. In late summer and early fall, roe deer
147 from the BNRP mainly focus on evergreen shrubs (bramble leaves) and forbs at about 44 and
148 25 % of the stomach content expressed as dry matter weight, respectively. Evergreen shrubs
149 reach almost 60 %, and forbs surpass 10 % in late fall and winter. What is surprising at the
150 BNRP is the very low amount of fruits in the roe deer diet for the two periods (3.4 and 5.8 %
151 of the diet, respectively) compared to the greater fruit intake among red deer at BNRP,
152 (Redjadj et al., 2014), and to roe deer populations in other locations (Tixier and Duncan,
153 1996). As expected, grasses represent less than 6 % of the roe deer diet for each of the two
154 seasons at the BNRP (Table S1).

155 The mouflons, *Ovis gmelini musimon* (adult males: 42.8 kg; adult females: 31.3 kg;
156 Text SI and Table S1) is a mixed-feeding species. Marchand et al. (2013) reviewed the
157 feeding ecology of this wild sheep. Although grasses are the major food type, foliages from
158 shrubs and herbaceous dicots are the secondarily preferred food resources. At the BNRP,
159 grasses represent 42 and 29 % (expressed as percentage of dry matter weight) of their diet for
160 each of the two investigated periods (Redjadj et al., 2014). Evergreen shrubs (16.2 %) and
161 forbs (15.7 %) are the secondarily preferred foods in late summer and early fall. In late fall

162 and winter, evergreen trees (mostly conifer foliages; 28.1 %) counterbalance the drop in
163 proportions of both forbs and grass component compared to the first period (Table S1;
164 Redjadj et al., 2014).

165 The chamois *Rupicapra rupicapra* (adult males: 34.5 kg; adult females: 29.7 kg;
166 Text SI and Table S1) is a mixed feeder grazing and browsing depending resources
167 availabilities and energetic requirements (Pérez-Barberia et al., 1997). For instance, recent
168 studies show that the chamois in Pyrenees may include less than 20 % grasses in its summer
169 and fall diets (Espunyes et al., 2019). Besides, grasses represent 44 % and more than 50 % in
170 summer and fall, respectively, of its diet at the BNRP (Table S1; Redjadj et al., 2014). Forbs
171 (22.4 %) and evergreen shrubs (19.6 %) complement the diet for the first period whereas the
172 drop in forbs is counterbalanced with evergreen trees (17.5 %) composing the secondary food
173 items (Table S1).

174 Mandibles were collected from early September to end of March during three
175 hunting seasons (2008/2009, 2014/2015 and 2015/2016), from adult animals (with worn
176 facets on M₂ and erupted or erupting M₃) shot during the legal hunting season both within and
177 outside the National Game and Wildlife Reserve (Figure 1). Most of the specimens were
178 sampled from late September to November 2015 (see Appendix 2). All samples come from
179 animals tagged with official annual hunting quotas delivered by the county prefects in
180 agreement with the environmental code (Art. R425-2 to 425-141 13). No animals were
181 harvested solely for the purpose of this study. A total of 11 and 82 adult specimens (with
182 erupted and worn second molars) were used for serial intra-tooth enamel stable isotope and
183 dental microwear texture analyses, respectively (see SI-Text and Appendices 1 and 2).

184

185 2.2. Methods

186 2.2.1. Enamel carbon and oxygen stable isotope analyses

187 About 100 μg of enamel powder per sample were serially extracted with a hand-held
188 microdrill, sampled along the crown from apex to cervix on both second and third lowers (see
189 Figures 2 and 3; Table 1; see Text SI and Appendix 1). The spatial location of sample
190 positions on each tooth was recorded to within 0.1 mm precision. No bleach treatment was
191 applied. Isotope analyses of structural carbonate in tooth enamel samples were performed on a
192 Thermo DeltaV mass spectrometer coupled to a Gasbench II gas preparation unit in which a
193 cold trap system at liquid nitrogen temperature is integrated. The system is setup as outlined
194 in Fiebig et al. (2005; see Text-SI).

195 Enamel formation (amelogenesis) of second and third molars differ in duration
196 from one species to another depending on the body mass and molar heights (see Text-SI). The
197 amelogenesis may last about 4 months for the roe deer second molar up to more than a year
198 for the third molar of the other ruminants because they are larger and have higher tooth
199 crown. Kierdorf and Kierdorf (2000) report that for the roe deer, enamel formation
200 (amelogenesis) of M2 begins *in utero* and terminates around 4 months of age. The roe deer
201 M3 is estimate to form between 4–9 months of age. For the red deer, the second molar begins
202 forming prior to 3 months of age and completes formation around 9 months of age; the third
203 molar begins forming at 9 months of age and completes prior to 26 months. We estimate the
204 fractionation factor ϵ between the carbon stable isotope composition of food resources
205 ($\delta^{13}\text{C}_{\text{diet}}$) and enamel carbonate using a body mass-dependent equation calibrated for foregut-
206 fermenting mammals (Tejada-Lara et al., 2018; Table 1; see Text-SI and Appendix 1). While
207 there is uncertainty in the optimal parameterization of ϵ (Clauss et al., 2020; Manthi et al.,
208 2019) in our calculations this offset differs by less than 1.1 ‰ between taxa. In parallel to
209 carbon isotope analysis of tooth enamel, for some individuals food remains stuck between
210 cusps and teeth in the jaw were sampled also for carbon isotope analysis, if present, to directly
211 assess the $\delta^{13}\text{C}$ values of ingested plants (see Text-SI and Table S2). Both food remains from

212 the teeth/jaw and $\delta^{13}\text{C}_{\text{enamel}}$ represent an unknown interval of time. We argue the plant
213 remains stuck in teeth is an epiphenomenon meaning the direct comparisons of these data
214 should be done with high caution. In any case, the $\delta^{13}\text{C}_{\text{enamel}}$ value of the very last sample to
215 mineralize on the M_3 is the most appropriate value to be compared with $\delta^{13}\text{C}$ measured from
216 food remains stuck between cusps and teeth. Based on the enamel oxygen isotope
217 composition, we propose an estimation of the oxygen isotope composition of the
218 environmental water ($\delta^{18}\text{O}_{\text{ew}}$) ingested by the ruminants from the BNRP following the
219 regression between enamel (i.e. structurally bound carbonate in the bioapatite) and ingested
220 water of Iacumin et al. (Iacumin et al., 1996; Table 1; Text-SI).

221 We also consider the niche breadth B_A (Levins, 1968) and the ecological
222 overlapping O_{Bauges} (Pianka, 1973) based on both $\delta^{18}\text{O}_{\text{ew}}$ and $\delta^{13}\text{C}_{\text{diet}}$ (see also Dantas et al.,
223 2017), and mixSIAR modeling based on enamel $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements (Jackson et al.,
224 2011). The niche breadth B_A estimating inter-individual dispersion and the ecological
225 overlapping O_{Bauges} are computed with the relative proportions of values plotting within pre-
226 defined isotopic bins (Table 2; Figure 4; see text-SI). Instead of using a mean value per
227 individual, which is a computation of n values representing an unknown time span, we here
228 simulate every n intra-tooth values in stable isotope composition along the M_3 as a single
229 snapshot of stable isotope composition (of the diet or environmental water ingested) of n
230 individuals randomly sampled. This means that the value sampled n_i is representative of an
231 individual i among a given population at any season around the year.

232 Lastly, we combine serial enamel $\delta^{18}\text{O}$ values with inverse modeling to estimate
233 $\delta^{18}\text{O}$ seasonality, a longtime goal of vertebrate isotope ecology (e.g. Passey et al., 2005;
234 Zazzo et al., 2010; Blumenthal et al., 2019). Specifically, we employ Bayesian inference with
235 a synchrotron-based empirical model of ruminant molar enamel formation (illustrated for *Ovis*
236 and *Rupicapra* in Figure 5), originally derived from a population of domesticated sheep, to

237 better infer potential seasonal variations in environmental $\delta^{18}\text{O}$ values that contribute to
238 measured spatial variations in tooth $\delta^{18}\text{O}$ (Green et al., 2018b; See Text-SI).

239 2.2.2. *Dental Microwear Texture Analysis*

240 Following standard procedures, replicas of the investigated dental facet on the
241 lower second molars were produced and then scanned using the surface profilometer confocal
242 DCM8 Leica Microsystems "TRIDENT" with a $100 \times$ lens (Leica Microsystems) at the
243 Palevoprim lab, CNRS and University of Poitiers, France (see details in Merceron et al.,
244 2016; See text-SI and Appendix 3). We target the disto-buccal facet of the protoconid or of
245 the hypoconid in case the former one was damaged. We do avoid grouping different dental
246 facets as they have different functions during mastication and thus significant differences in
247 dental microwear textures as shown by Ramdarshan et al. (2017).

248 After treating surfaces (see details in Merceron et al., 2016), the Dental Microwear
249 Texture Analysis (DMTA) was performed using the Scale-Sensitive Fractal Analysis using
250 Toothfrax and Sfrax software (Surfract, <http://www.surfract.com>) following Scott et al.
251 (2006). Four variables were extracted from the surface: complexity (Asfc), anisotropy
252 (epLsar), heterogeneity of complexity (HAsfc calculated with a 9-cell mesh) and Textural fill
253 volume (Tfv; Table 3, Appendix 3). Dispersion of the values are calculated following Plavcan
254 and Cope (2001) Levene equations (see Text-SI). After box-cox transformations, one-way
255 analyses of variance (ANOVAs) and pairwise comparisons were performed for each texture
256 parameter (Table 4, Figure 6; see Text-SI and Table S3). Furthermore, seasonal variations in
257 DMTA are explored on the mouflons as 10 of them were sampled in late summer/early fall
258 and 12 others in winter 2009 (see Text-SI and Table S4).

259

260 **3. Results**

261 *3.1. Enamel carbon isotope composition*

262 Individual mean molar enamel carbon isotope compositions ($\delta^{13}\text{C}_{\text{enamel}}$) for all four
263 ruminant species range from -18.4‰ to -14.3‰ VPDB (Table 1). The chamois (*Rupicapra*
264 *rupicapra*) has the highest mean $\delta^{13}\text{C}_{\text{enamel}}$ values both on lower M_2 and M_3 among the four
265 ruminant species while the roe deer (*Capreolus capreolus*) has the lowest values. The
266 mouflons (*Ovis gmelini musimon*) M_2 and M_3 , and red deer (*Cervus elaphus*) M_3 , show
267 intermediate values (Table 1; Figures 2 and 4). It is worth noting that a single high $\delta^{13}\text{C}_{\text{enamel}}$
268 value (-6.9‰ VPDB; not shown in Figure 2 but in Table 1 and Appendix 1) on a single
269 specimen (15MO8843) likely constitutes an undetected analytical error. The isolated high
270 $\delta^{13}\text{C}_{\text{enamel}}$ value, if not an analytical artefact, is perhaps either due the high intake of alpine
271 CAM plants or the few native C_4 plants at high altitudes and mid-to-high latitudinal biomes
272 (Osmond et al., 1975; Pyankov et al., 2010) which can have variable $\delta^{13}\text{C}$ values, depending
273 on local and seasonal conditions, or due to the consumption of cultivated maize in valleys.
274 Also, mouflons are known to perform seasonal altitudinal movements (Darmon et al. 2014)
275 and as there are a few areas of cultivated maize in the valleys and the possible existence of
276 some places where hunters spread maize for preventing damages caused by wild boar, we
277 cannot firmly exclude a high consumption of maize for short period. Apparently semi-
278 continuous isotopic compositions across sampled M_2 and M_3 reflect a relatively continuous
279 record of body fluid isotopic compositions during the earlier formation of the M_2 , and the
280 later formation of the M_3 .

281 The carbon isotope composition of the food resources exploited ($\delta^{13}\text{C}_{\text{diet}}$) are
282 calculated following the body mass-dependent diet-to-bioapatite fractionation equations for
283 foregut fermenting mammals following Tejada-Lara et al. (2018; Table 2). The calculated
284 mean $\delta^{13}\text{C}_{\text{diet}}$ values by tooth and specimen range from -30.5‰ and -26.6‰ VPDB. The
285 estimation of the seasonal variations in $\delta^{13}\text{C}_{\text{diet}}$ of food resources are given in Table 1
286 (Appendix 1).

287 **Table 1.** Enamel carbon and oxygen stable isotope composition $\delta^{13}\text{C}_{\text{enamel}}$ (‰ vs. VPDB) and
 288 $\delta^{18}\text{O}_{\text{enamel}}$ (‰ vs. VSMOW; mean *m*, standard deviation *sd*, minimal *min* and maximal *max*
 289 values, and amplitude Δ) of serial samples along second (M₂) and third (M₃) lower molars of
 290 the sympatric ruminants from the Bauges NRP, Alps, France. Carbon stable isotope
 291 composition of the food resources $\delta^{13}\text{C}_{\text{diet}}$ are calculated following Tejada-Lara et al. (2018 in
 292 supplementary material) with a shift depending on bodymass. An estimation of the oxygen
 293 stable isotope composition of the environmental water $\delta^{18}\text{O}_{\text{ew}}$ (‰ vs. VSMOW) is calculated
 294 after Iacumin et al. (1996).

Species	Specimen	Tooth	N	$\delta^{13}\text{C}_{\text{enamel}}$					$\delta^{13}\text{C}_{\text{diet}}$	$\delta^{18}\text{O}_{\text{enamel}}$					$\delta^{18}\text{O}_{\text{ew}}$
				<i>m</i>	<i>sd</i>	<i>max</i>	<i>min</i>	Δ		<i>m</i>	<i>sd</i>	<i>max</i>	<i>min</i>	Δ	
<i>C. capreolus</i>	CC2613	M ₂	6	-16.6	0.4	-17.0	-16.2	0.9	-28.7	22.8	0.3	23.1	22.3	0.8	-10.9
		M ₃	6	-18.4	0.5	-18.9	-17.6	1.3	-30.5	19.9	0.4	20.4	19.3	1.1	-13.7
	CC2653	M ₂	6	-18.4	0.2	-18.7	-18.1	0.6	-30.5	22.8	0.9	24.0	21.6	2.4	-10.9
		M ₃	6	-18.0	1.6	-18.8	-14.7	4.1	-30.2	19.3	1.6	22.5	18.3	4.2	-14.3
<i>C. elaphus</i>	CE4821	M ₃	9	-15.9	0.2	-16.2	-15.6	0.6	-29.1	22.3	0.5	23.0	21.7	1.3	-11.4
	CE0104	M ₃	8	-16.4	0.3	-16.9	-16.0	0.9	-29.6	21.7	1.4	23.7	19.6	4.1	-12.0
	CE4951	M ₃	10	-15.7	0.3	-16.2	-15.4	0.8	-28.9	22.6	0.6	23.4	21.4	2.0	-11.1
	CEF7104	M ₃	14	-16.0	0.3	-16.6	-15.5	1.1	-29.2	21.5	0.9	23.1	20.1	3.0	-12.1
	CEM2616	M ₃	10	-16.1	0.4	-16.7	-15.5	1.2	-29.3	22.3	1.2	23.9	20.5	3.4	-11.3
<i>O. gmelini</i>	MO8843	M ₂	16	-15.8	2.5	-17.2	-6.9	10.3	-28.2	21.3	1.5	24.0	19.5	4.5	-12.4
		M ₃	16	-15.7	0.8	-16.6	-14.7	1.9	-28.1	22.5	1.0	23.9	20.6	3.3	-11.1
	MO8847	M ₂	12	-16.3	1.0	-17.5	-15.2	2.3	-28.8	21.0	1.5	23.1	18.9	4.2	-12.7
		M ₃	15	-15.9	0.7	-17.1	-15.0	2.1	-28.4	21.6	1.5	23.8	19.2	4.6	-12.1
<i>R. rupicapra</i>	IS8932	M ₂	10	-14.9	0.4	-15.2	-14.1	1.1	-27.2	21.7	0.6	22.7	21.0	1.7	-12.0
		M ₃	11	-14.3	0.4	-14.7	-13.7	1.0	-26.6	22.9	0.7	23.9	21.7	2.2	-10.7
	IS8952	M ₂	9	-14.4	0.2	-14.8	-13.9	0.8	-26.7	23.8	0.7	25.0	22.7	2.3	-9.9
		M ₃	9	-14.4	0.3	-14.7	-13.8	0.9	-26.7	22.1	0.8	23.2	21.2	2.0	-11.5

295

296 The inter-individual and inter-species differences between the estimated enamel carbon
 297 isotopic compositions calculated from values from food remains stuck between teeth are quite
 298 similar with the $\delta^{13}\text{C}_{\text{enamel}}$ measured on the last enamel part to mineralize next the M₃ cervix
 299 (Table S2). Food item $\delta^{13}\text{C}$ composition differences reflect enamel patterns overall, with
 300 highest values observed in the chamois and mouflons, and lowest in the red and roe deer. All
 301 differences are < 2 ‰ VPDB.

302 The most narrow niche breath B_A based on $\delta^{13}\text{C}_{\text{diet}}$ is that of the chamois, with
 303 especially high values and nearly no or little ecological overlapping with the other sympatric

304 ruminants investigated. The mouflons and the red deer have the highest ecological
 305 overlapping when considering $\delta^{13}\text{C}_{\text{diet}}$ (Table 2).

306 **Table 2.** Niche breadth (B_A) per species are given in brackets next to the taxon name and
 307 ecological overlapping of the Bauges ruminants (O_{Bauges}) are given for $\delta^{18}\text{O}_{\text{ew}}$ and $\delta^{13}\text{C}_{\text{diet}}$
 308 respectively below and above the diagonal.

$\delta^{18}\text{O}_{\text{ew}} \backslash \delta^{13}\text{C}_{\text{diet}}$	<i>C. capreolus</i> (0.119)	<i>C. elaphus</i> (0.161)	<i>O. gmelini</i> (0.233)	<i>R. rupicapra</i> (0.060)
<i>C. capreolus</i> (0.405)		0.087	0.016	0.108
<i>C. elaphus</i> (0.472)	0.284		0.542	0
<i>O. gmelini</i> (0.552)	0.300	0.851		0.082
<i>R. rupicapra</i> (0.389)	0.085	0.918	0.929	

309

310 3.2. Enamel oxygen isotope composition

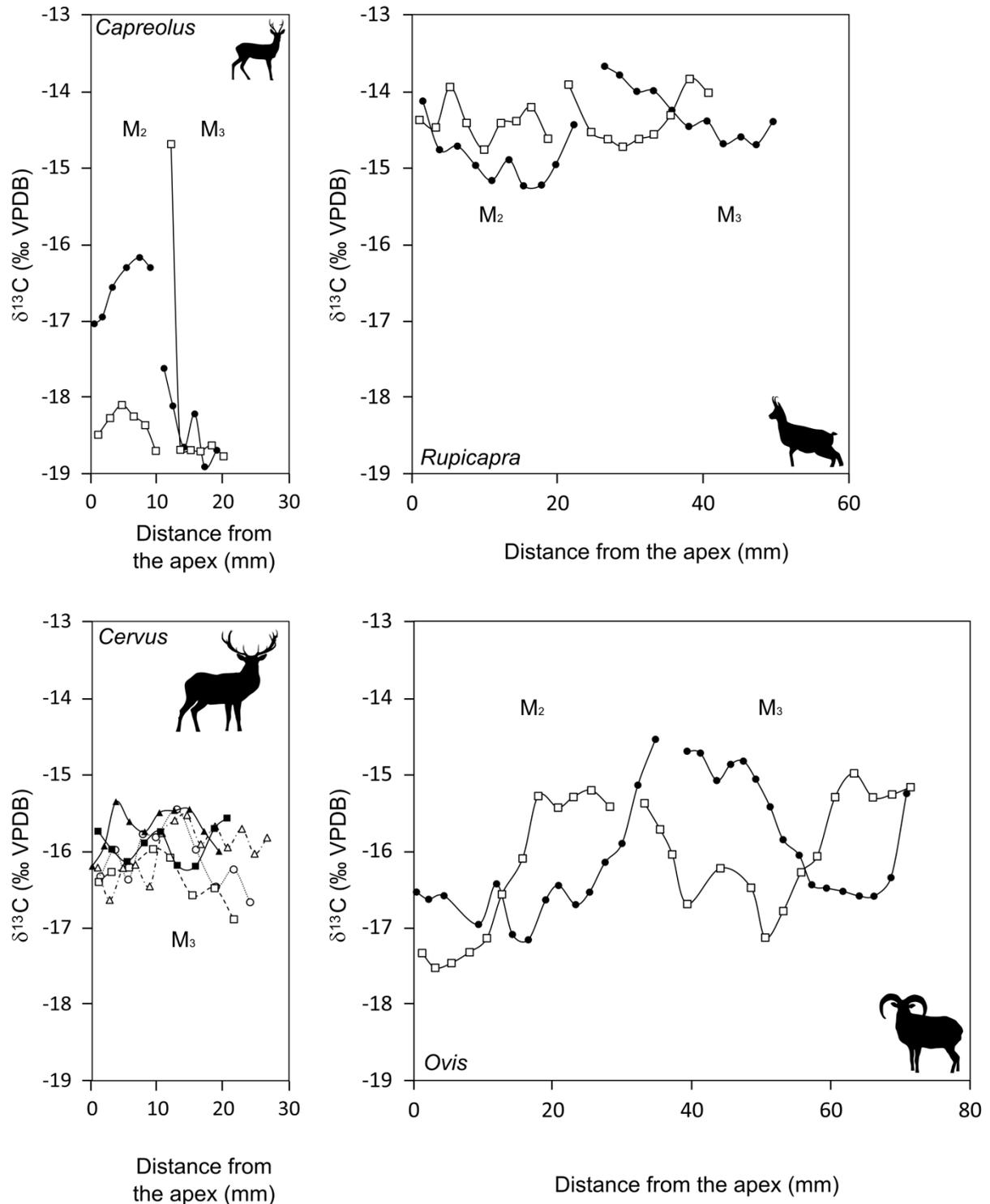
311 The chamois (*Rupicapra rupicapra*) has the highest mean $\delta^{18}\text{O}_{\text{enamel}}$ value (23.8 ‰
 312 VSMOW) and the roe deer (*Capreolus capreolus*) the lowest mean value (19.3 ‰ VSMOW).
 313 The mouflons (*Ovis gmelini musimon*) show the highest intra-tooth variability $\Delta^{18}\text{O}_{\text{enamel}}$
 314 (from 3.3 ‰ to 4.6 ‰ Table 2; Figure 3). The $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values (inferred from inverse modeling
 315 from enamel $\delta^{18}\text{O}_{\text{enamel}}$) of water ingested by the roe deer are the lowest of all analyzed
 316 ruminants (-14.3 ‰ to -10.9 ‰ VSMOW) but display the highest intra-tooth differences
 317 when $\delta^{18}\text{O}$ values of M_2 and M_3 are merged. High variations in oxygen isotope composition of
 318 water sources are also estimated for the mouflons. The highest $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values for the ingested
 319 water are recorded by the chamois.

320 Regarding the niche breadth B_A based on $\delta^{18}\text{O}_{\text{ew}}$, the narrowest breadth is recorded
 321 for the chamois and the widest for the mouflons. Ecological overlapping is higher between the
 322 mixed feeding red deer, the mouflon and the chamois (Table 2). These patterns can be
 323 observed by comparing $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements across all single serial intra-tooth
 324 enamel samples. Among BNRP taxa, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enrichment or depletion tend to co-
 325 segregate (Figure 4). For example, species like the chamois with higher enamel $\delta^{13}\text{C}$

326 compositions have higher $\delta^{18}\text{O}$ values with little $\delta^{18}\text{O}$ variation, whereas species like roe deer
327 or mouflons have lower minimum $\delta^{18}\text{O}$ values, and greater ranges of $\delta^{18}\text{O}$ values.

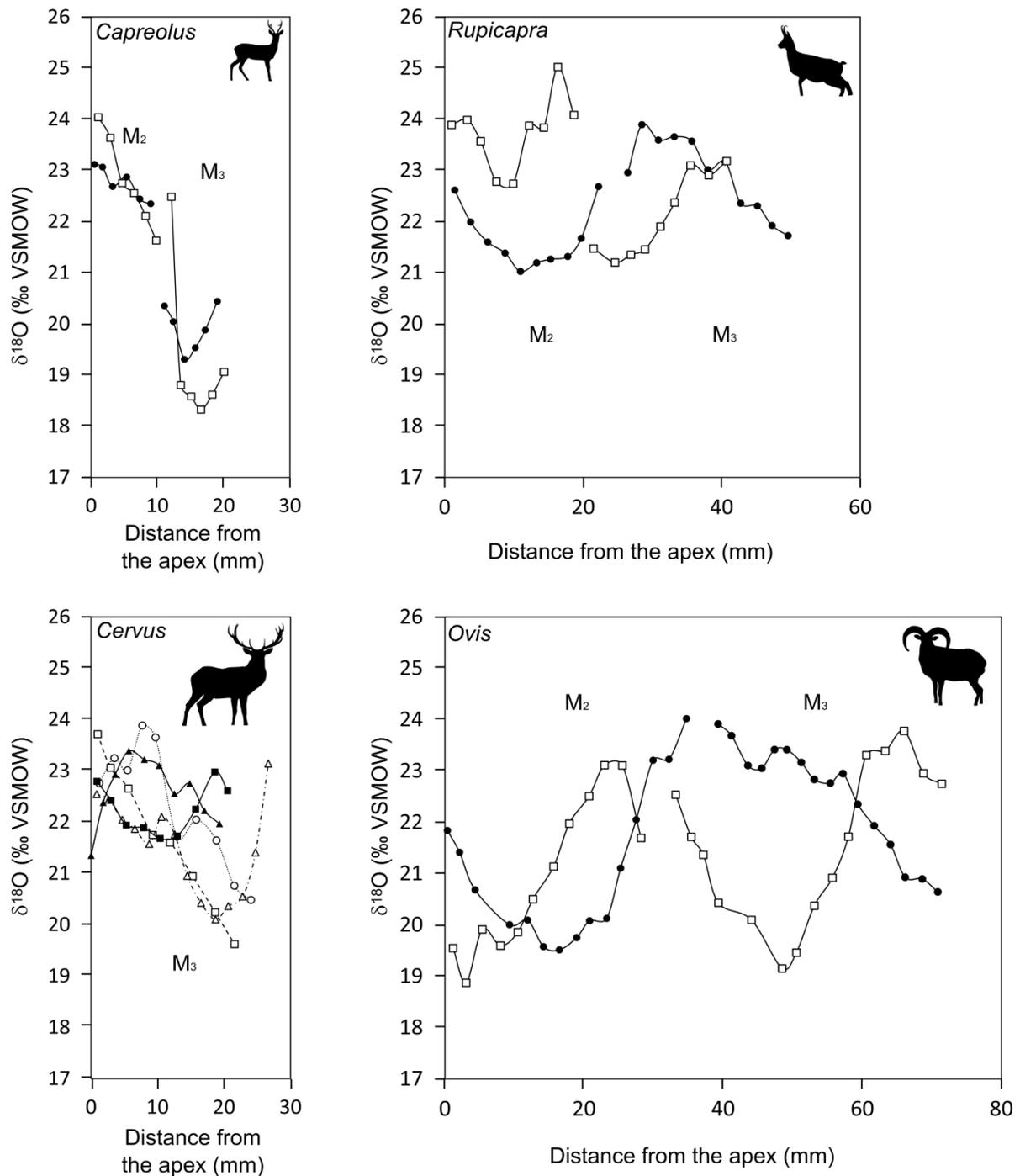
328 Reconstruction of estimated ingested seasonal $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ compositions recover what
329 appear to be annual cycles (Figure 5; Figure S1 and Figure S2), with average ranges of $\delta^{18}\text{O}$
330 variation in all teeth equal to $9.7 \pm 4.5 \text{ ‰}$ 1 S.D. The highest degree of variation is
331 reconstructed for the mouflons, where within-tooth reconstructed $\delta^{18}\text{O}$ ranges are 12.9 ± 2.9
332 ‰ 1 S.D. The lowest variation is observed among the chamois where reconstructed $\delta^{18}\text{O}$
333 ranges are from $7.4 \pm 1.9 \text{ ‰}$. Intermediate ranges are observed for the red deer ($9.3 \pm 3.2 \text{ ‰}$)
334 and roe deer ($9.46 \pm 7.8 \text{ ‰}$), with greater variability in roe deer resulting from a single very
335 high value at the cuspal margin of a M_3 .

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Figure 2. Variations in enamel carbon isotope composition ($\delta^{13}\text{C}_{\text{enamel}} \text{‰ VPDB}$) along the lower M_3 for red deer (*Cervus elaphus*), and of lower M_2 (left curves) and M_3 (right curves) for the three other species of ruminants (*Ovis gmelini musimon*, *Rupicapra rupicapra*, *Capreolus capreolus*) from the Bauges NRP expressed in mm from the apex of the M_2 . For all taxa except the red deer, the height dimension of the lower M_2 is added to the distance to the M_3 apex of the samples along the M_3 .



345
 346 **Figure 3.** Variations in enamel oxygen isotope composition ($\delta^{18}\text{O}$ ‰ VSMOW) along the
 347 lower M₃ of the red deer (*Cervus elaphus*) and along the lower M₂ (left curves) and M₃ (right
 348 curves) of the three other species of ruminants (*Ovis gmelini musimon*, *Rupicapra rupicapra*,
 349 *Capreolus capreolus*) from the Bauges NRP expressed in mm from the apex of M₂.
 350 For all taxa except the red deer, the height dimension of the lower M₂ is added to the distance
 351 to the M₃ apex of the samples along the M₃.

352
 353 3.3. DMTA

354 Among the four species, the red deer (*Cervus elaphus*) shows the lowest values of
 355 complexity (Asfc), and the roe deer (*Capreolus capreolus*) the highest. The two bovids

356 (*Rupicapra rupicapra* and *Ovis gmelini musimon*) significantly contrast with the two cervids
357 with lower values in anisotropy (epLsar; Tables 3 and 4; Table S3). The roe deer and the two
358 bovids have lower heterogeneity of complexity (HAsfc_{9-cells}; Table 3; Table S3) than the red
359 deer. There is no difference in textural fill volume (Tfv; Tables 3 and 4; Table S3). Regarding
360 dispersions, the roe deer has the highest values for Disp-Asfc and Disp-Tfv, and the red deer
361 the lowest ones (Tables 3 and 4; Table S3). Regarding the two other indices, the mouflons has
362 the highest Disp-epLsar, the roe deer and the chamois the lowest. The dispersion in
363 Heterogeneity of Complexity (Disp-HAsfc_{9-cells}) is maximal for the red deer and minimal for
364 the mouflons (Table 3). One way ANOVA on box-cox transformed data detects significant
365 differences in Anisotropy (epLsar), Heterogeneity of Complexity (HAsfc_{9-cells}), and
366 Dispersion in Complexity (Disp-Asfc, Tables 3 and 4, Figure 6; Table S3). Mouflons, the
367 only sample for which we could test seasonal variations, show significant differences in
368 textural fill volume (Tfv); the ones sampled in late fall and early winter having higher values
369 (Table S4).

370 **Table 3.** Descriptive statistics (mean m and standard deviation sd) as well as dispersion of
371 dental microwear texture parameters per species and per seasonal group for the mouflons.

372

	N	Asfc			epLsar			HAsfc _{9-cells}			Tfv (µm ³)		
		m	sd	disp	m*	sd*	disp	m	sd	disp	m	sd	disp
<i>C. capreolus</i>	18	2.61	2.49	0.43	6.05	2.34	0.38	0.36	0.14	0.09	36152	19052	1.08
<i>C. elaphus</i>	21	1.36	0.57	0.18	5.99	2.63	0.42	0.55	0.48	0.13	36891	10049	0.24
<i>R. rupicapra</i>	21	1.79	0.97	0.23	4.26	1.78	0.38	0.39	0.22	0.10	36645	13018	0.36
<i>O. gmelini musimon</i> (all individuals)	22	2.02	0.88	0.25	3.76	2.56	0.54	0.33	0.10	0.06	34363	14738	0.44
Sample (late summer-early fall 2015)	12	2.01	0.74		3.33	0.21		0.35	0.11		27092	14338	
Sample (winter 2008-2009)	10	2.03	1.06		4.27	0.30		0.30	0.10		43089	10026	

373 *original values ($\times 10^{-3}$)

374

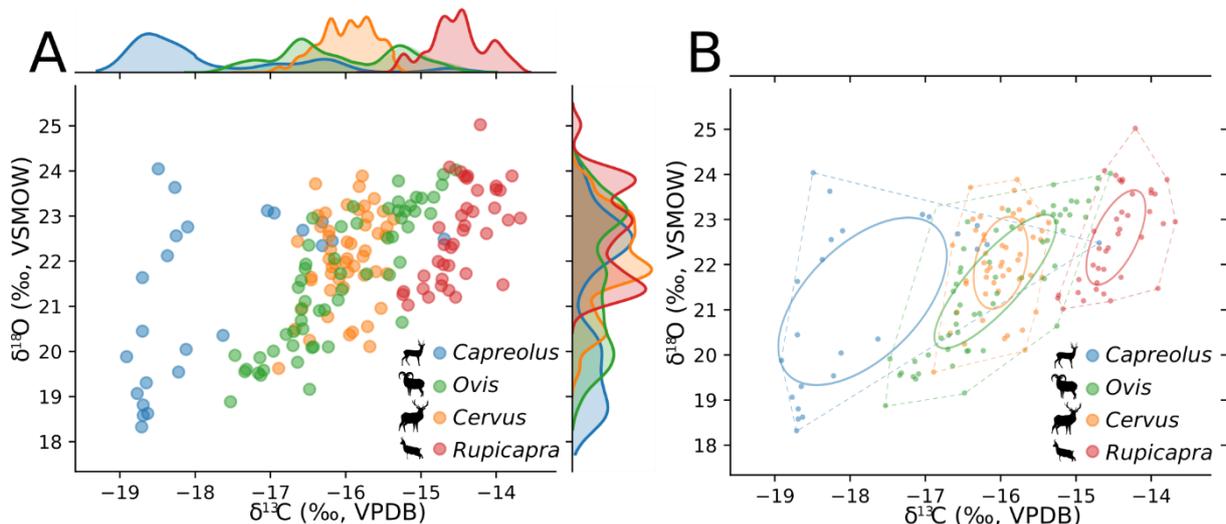
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377 Table 4. Summary of the analyses of variances on the box-cox transformed DMTA variables
 378 from ruminants of the Bauges NRP (complete results in Table S3).

	dof	F	p
Asfc			
Taxa	3	1.917	0.133
Residuals	78		
epLsar		F	p
Taxa	3	5.0279	<0.05
Residuals	78		
HAsfc _{9-cells}		F	p
Taxa	3	2.907	<0.05
Residuals	78		
Tfv		F	p
Taxa	3	0.1328	0.940
Residuals	78		
disp-Asfc		F	p
Taxa	3	2.7877	<0.05
Residuals	78		
disp epLsar		F	p
Taxa	3	0.7830	0.506
Residuals	78		
disp-HAsfc _{9-cells}		F	p
Taxa	3	0.6366	0.593
Residuals	78		
disp Tfv		F	p
Taxa	3	0.8252	0.483
Residuals	78		

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 382 **Figure 4.** A: Enamel carbonate carbon ($\delta^{13}\text{C}$) and oxygen isotope ($\delta^{18}\text{O}$) values from red deer
 383 *Cervus elaphus*, mouflons *Ovis gmelini musimon*, chamois *Rupicapra rupicapra*, and roe deer
 384 *Capreolus capreolus*. Overall, measurements segregate species by greater (chamois) or lesser
 385 (roe deer) carbon and oxygen isotopic enrichment. Kernel density estimates on each axis
 386 demonstrate that $\delta^{13}\text{C}$ distinguish chamois, red deer and roe deer relatively clearly, with
 387 mouflons feeding between these groups. B: mixSIAR modeling estimating isotope-based
 388 niche separation among taxa. The full range of observed variation is shown as a dashed line,
 389 while predictive ellipses in full lines show 40 % predictive ellipses for measurements from
 390 each population.
 391

392 4. Discussion

393 4.1. Inter-specific differences in diet

394 All $\delta^{13}\text{C}_{\text{enamel}}$ of permanent molars support that the four ruminants feed only on C_3
395 vegetation (Tables 1 and 5, Figure 2). Considering the relation specific to foregut-fermenting
396 mammals and body mass (Tejada-Lara et al., 2018) of the species at the BNRP (Redjadj et al.,
397 2014), the shift between diet and enamel carbon stable isotope composition varies from 12.1
398 ‰ for the roe deer to 13.2 ‰ for the red deer (Table 1; Appendix 1). Thus, the mean
399 calculated $\delta^{13}\text{C}_{\text{diet}}$ of the food resources for all four species ranges from about -30.5 ‰ to
400 -26.6 ‰, which supports the exclusive use of C_3 food resources, as C_3 plants have $\delta^{13}\text{C}$
401 values (Table 1; Appendix 1) ranging from -37 ‰ to -20 ‰ (with a mean value of -27 ‰;
402 see Kohn, 2010 for a review): far below the range seen for C_4 plants (from -18 ‰ to -8 ‰
403 with a mean value of -13 ‰; Smith and Epstein, 1971). The dominance of C_3 vegetation is
404 expected as BNRP dicots and monocots share similar C_3 metabolic pathways (Pyankov et al.,
405 2010).

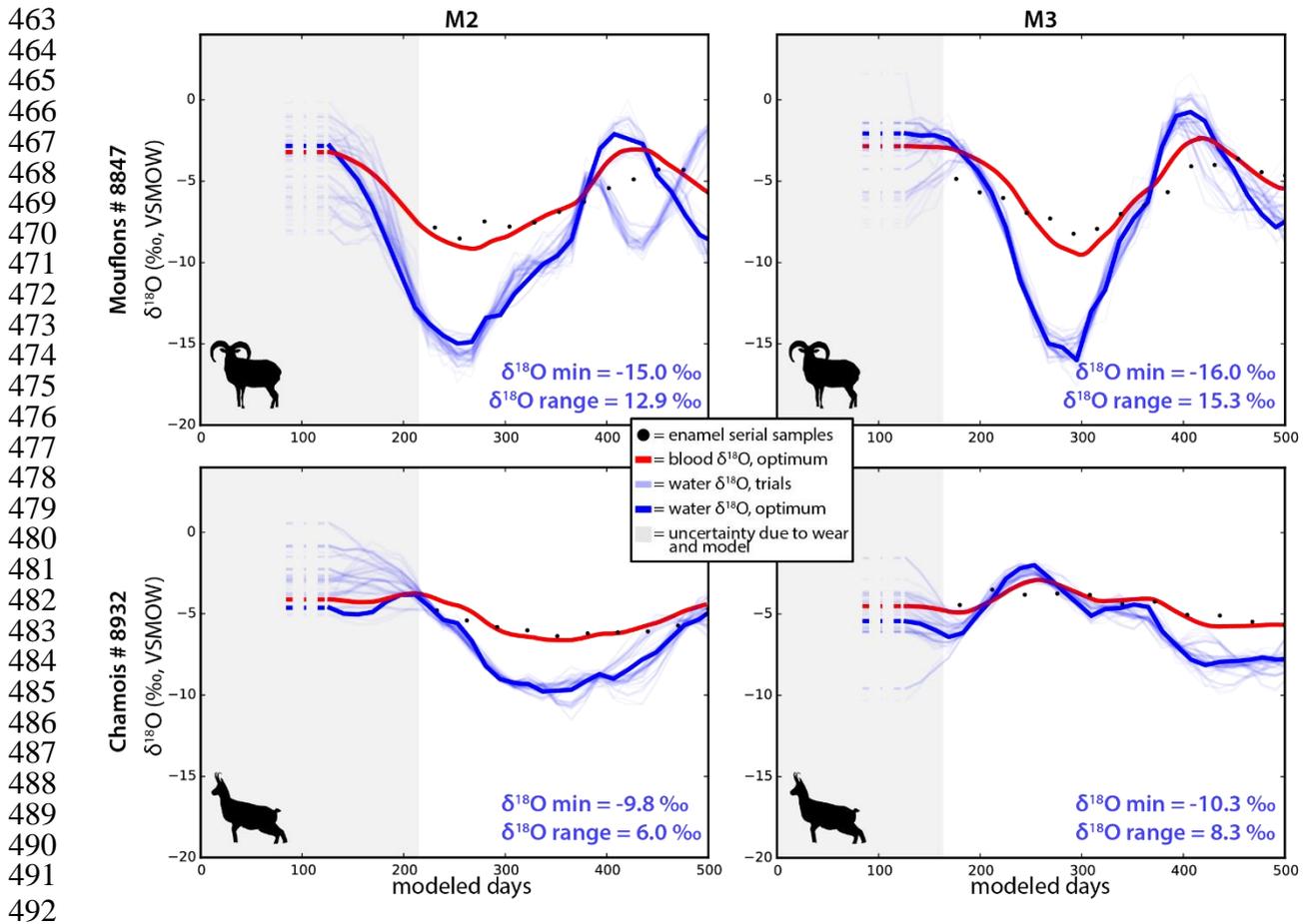
406 As Kierdorf and Kierdorf (2000) report that the amelogenesis of the second molar
407 of the roe deer begins *in utero* and continues about four months after birth, enamel $\delta^{13}\text{C}$ and
408 $\delta^{18}\text{O}$ values likely reflect a mixture of pre-weaning and post-weaning values. Thus the $\delta^{13}\text{C}_{\text{diet}}$
409 and $\delta^{18}\text{O}$ values derived from the roe deer M_2s are potentially biased by a milk suckling
410 enrichment effect, which may contribute to the especially large range of roe deer $\delta^{18}\text{O}$
411 compositions (Figs. 2–3; SI text Fig. S2): roe deer are thought to wean between 4–7 months
412 of age (Espmark, 1969). Because the other species are larger and have taller molar crowns, we
413 assume that a high proportion of their M_2 crown mineralizes after weaning and indeed reflects
414 food resources that compose the diet of these species.

415 The dental microwear texture analysis complements the ecological picture provided
416 by $\delta^{13}\text{C}_{\text{enamel}}$ values. First, the two cervids have higher anisotropy than the two bovids (Tables

417 3 and 5). The two cervids, however, differ from each other in having contrasting complexities;
418 the red deer having lower values than the roe deer (Table 3, Figure 6). High anisotropy on
419 shearing molar facets have been empirically and experimentally associated with grass-eating
420 habits (Scott, 2012; Merceron et al., 2016). In the present case, the combination of high
421 anisotropy and low complexity for the red deer would advocate for a dominance of monocots
422 in the diet. By contrast, Redjadj et al. (2014) have found that monocots represent no more
423 than 40 % of diet in fall and winter. Our data would instead support a higher amount (Table
424 5), at least similar to the summer diet for Alpine red deer during which grasses may account
425 for up to 60 %; the remaining diet would be dominated by herbaceous dicots (Suter et al.,
426 2004). This is consistent with the fact that most of the red deer studied in the present study
427 were shot in October, so that dental microwear textures likely reflect summer food resources.
428 Several studies have challenged the hypothesis that anisotropy (epLsar) reflects only grass
429 consumption. For instance, Hedberg and DeSantis (2017) describing koalas or Merceron et al.
430 (2010) describing roe deer have shown that high anisotropy (epLsar) on shearing molar facets
431 is not specifically related to grass-eating habits but to tough leaf-eating habits requiring a
432 shearing motion during mastication. This appears to explain our observations at the BNRP.
433 Roe deer from the BNRP avoid fruits (3.4 and 5.8 % of the diet for the two periods; Table S1)
434 and mainly feed on forbs and evergreen shrubs, notably bramble foliage (*Rubus fruticosus*). In
435 addition to anisotropy, roe deer complexity (Asfc) and most specifically the dispersion of
436 complexity (disp-Asfc) are more than double those observed in the red deer (Table 3, Figure
437 6). This supports mechanically more diverse foods for the roe deer compared with the red
438 deer. Several specimens of roe deer browsing mostly on soft food have low values in
439 complexity (Asfc), whereas specimens with higher complexity consumed harder food items
440 (Ramdarshan et al., 2016). Indeed, while the high disp-Asfc seen in roe deer suggests
441 important inter-individual differences regarding mechanical food properties, the lower

442 heterogeneity of complexity (HAsfc_{9-cells}) supports a dietary spectrum, for any given
443 individual, that is constrained by its high feeding selectivity coupled with a low spatial
444 heterogeneity in resources (Table 5). This reflects smaller roe deer home range compared with
445 the red deer. In contrast, most of the red deer specimens share a mechanically diverse
446 spectrum of foods (low disp-Asfc and high HAsfc_{9-cells}), which reflects wider spatial
447 heterogeneity in resources and larger home range for all red deer individuals (Table 5).

448 The two bovids significantly contrast with the cervids with lower values in anisotropy
449 (epLsar). Their complexity values plot between the limits defined by the two deer (Table 3,
450 Figure 6). Chamois and mouflon fed on a mixed diet that was overall less tough, most likely
451 less abrasive but harder than that consumed by the red deer (Table 5). This reflects the low to
452 medium dietary portion (from 30 to 50 %) of herbaceous monocots for these bovids during
453 fall and winter (La Morgia and Bassano, 2009; Marchand et al., 2013; Redjadj et al., 2014;
454 Espunyes et al., 2019). Cransac et al. (1997) found out that for mouflons reintroduced in the
455 Caroux-Espinouse Mediterranean mountain habitats, in Southern France, herbaceous
456 monocots may account for less dietary intake in summer than in fall and winter. This is
457 exactly opposite the timing of herbaceous monocot consumption among red deer in the Alps
458 (Suter et al., 2004). Pérez-Barbería et al. (1997) found out that the shrub component increases
459 from spring to summer and grasses and forbs increase in early fall in the diet of Cantabrian
460 chamois. Besides, chamois and mouflons have lower heterogeneity of complexity (HAsfc₉₋
461 _{cells}) than the red deer, suggesting a dietary spectrum with a reduced diversity of mechanical
462 properties (Tables 3 and 5, Figure 6).



493 **Figure 5.** Measurements of enamel oxygen isotope compositions ($\delta^{18}\text{O}$ ‰, here shown as
 494 phosphate $\delta^{18}\text{O}$ -equivalent on the VSMOW scale, with an estimated PO_4 -water offset of 19.1
 495 ‰ subtracted from each measurement) are made serially down the tooth crown (black circles). These measurements are combined with a model of tooth formation to infer likely
 496 (light blue) and best guess (dark blue) histories of ingested seasonal $\delta^{18}\text{O}$ compositions in
 497 environmental and plant water. The $\delta^{18}\text{O}$ of blood water over time (red) is also estimated.
 498 Periods of uncertainty resulting from significant tooth wear or limitations in the synchrotron-
 499 based model of enamel formation are shown in light gray. Uncertainty also increases towards
 500 the end of the tooth, when enamel growth slows and incorporates ever greater periods of time
 501 into smaller spatial increments. Results suggest that compared to the chamois, mouflons
 502 ingest a greater range of environmental water $\delta^{18}\text{O}$ compositions, and in particular ingest
 503 lower $\delta^{18}\text{O}$ values, likely derived from snow in high altitude areas.
 504
 505

506 *4.2. Inter-specific differences in habitat use*

507 The carbon and oxygen isotopic compositions of the four ruminants appear to
 508 mirror their behavior and range at BNRP (Tables 1 and 5, Figure 4). Roe deer have by far the
 509 lowest $\delta^{13}\text{C}$ values of all the taxa, reflecting their browsing behavior in forested habitats
 510 (Table 5). Interestingly, roe deer also show the greatest range of $\delta^{18}\text{O}$ values: the M_2 $\delta^{13}\text{C}$ and

511 $\delta^{18}\text{O}$ measurements of both sampled individuals are higher than their M_3 measurements
512 (Table 1, Figures 2–4). This pattern would be consistent with $\delta^{13}\text{C}$ trophic enrichment and
513 elevated milk water $\delta^{18}\text{O}$ ingestion resulting from suckling during M_2 formation (Kierdorf and
514 Kierdorf, 2000), and relatively rapid M_3 formation in the following winter. By contrast
515 chamois enamel samples are the most ^{13}C - and ^{18}O -enriched and show less variation (Table 1,
516 Figures 2–4). This result is also observed in inverse modeling (Figure 5) and suggests the
517 consumption of both plant and water resources that are subject to low humidity and
518 evaporative enrichment. High $\delta^{18}\text{O}$ measurements among the chamois, who live at high
519 altitudes, may reflect a greater proportion of water obtained from vegetation and metabolic
520 water production. Mouflons and red deer have measured molar and reconstructed $\delta^{13}\text{C}$ and
521 $\delta^{18}\text{O}$ values that are intermediate between the high values observed in the chamois and the
522 low values of the roe deer (Figure 4–5).

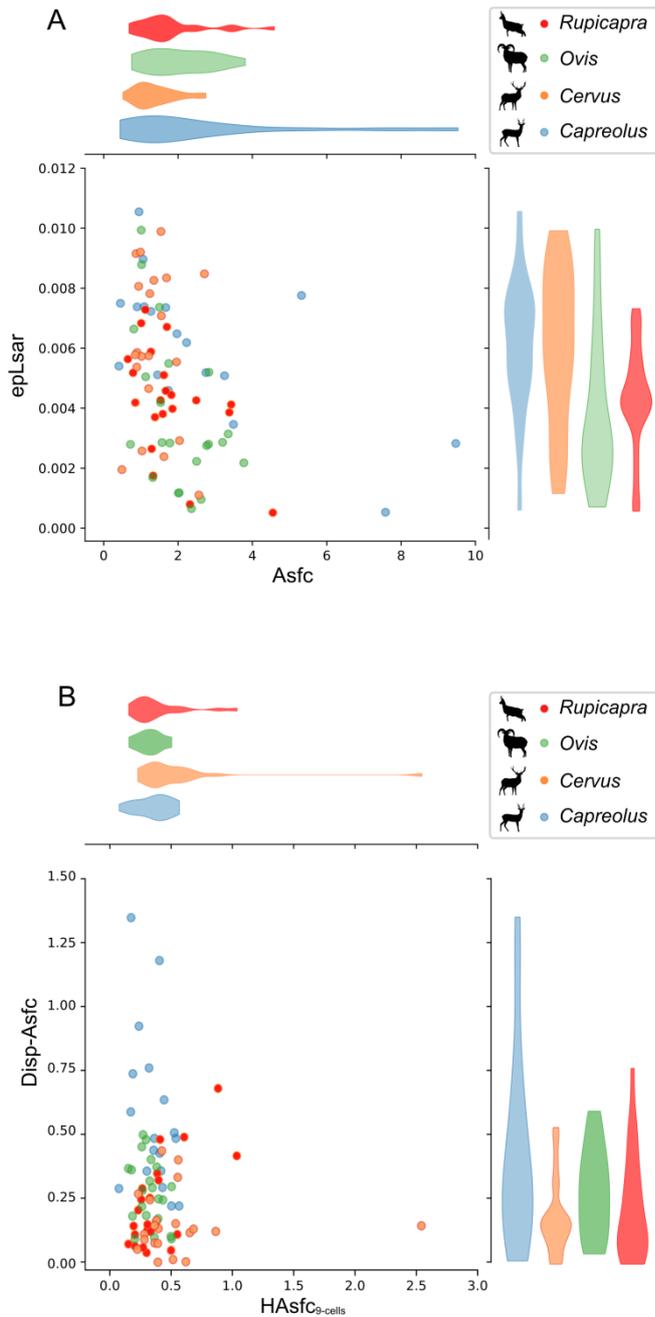
523 The isotopic ecology of vegetation in the BNRP helps to explain these general
524 patterns. Understory plants are exposed to lower light intensity and higher CO_2 concentration
525 (^{13}C -depleted CO_2 from biomass degradation) favoring the fractionation of light ^{12}C into plant
526 tissue during photosynthesis (Van der Merwe and Medina, 1991). Therefore, $\delta^{13}\text{C}$ values of
527 subcanopy C_3 plants under dense tree cover can be up to 5 ‰ lower than for the same species
528 of plants in more open habitats (Bonafini et al., 2013). Such differences in carbon isotope
529 fractionation in open versus under canopy conditions is then recorded in the dental tissues of
530 the mammalian herbivore species which browse or graze on these plants. When $\delta^{13}\text{C}_{\text{enamel}}$ on
531 third molars are considered (the M_3 mineralizes after weaning for all four species), the roe
532 deer (–18.4 ‰ and –18.0 ‰ VPDB) appears as the most forest-dwelling ruminant at the
533 BNRP with an estimated $\delta^{13}\text{C}_{\text{diet}}$ ranging from –30.5 ‰ to –30.2 ‰ (Tables 1 and 5, Figure 2,
534 Appendix 1). It is worth noting that the specimen CC 2613 likely shifts its home range to a
535 more open area while growing as its M_3 (–16.6 ‰ VPDB) has recorded less negative

536 $\delta^{13}\text{C}_{\text{enamel}}$ values compared to the M_2 (-18.4 ‰ VPDB). With roe deer having a significantly
537 smaller home range (from 20 to 60 ha depending on gender and density; Kjellander et al.,
538 2004) than red deer, the variations in $\delta^{13}\text{C}_{\text{enamel}}$ between individuals likely reflect the
539 differences in tree cover from one habitat to another. Specimen CC 2613 was shot at the “Roc
540 des Boeufs” station, an area between 1000 m and 1600 m high with a lower tree cover than
541 the Golet Station from 1200 m to 1600 m high where the second specimen comes from.
542 Although the five red deer were shot at different stations in the BNRP and their higher tooth
543 crowns indeed have the potential to record more dietary variations during a longer time span,
544 their low inter- and intra-tooth variation in $\delta^{13}\text{C}_{\text{enamel}}$ compared with the roe deer, strongly
545 suggest that the red deer has i) a wider home range, covering several micro-habitats buffering
546 by then any micro-habitat scale effects and ii) a slightly more open habitats than the roe deer
547 (Table 5).

548 The chamois displays the highest $\delta^{13}\text{C}_{\text{enamel}}$ values, indicating use of the largest
549 fraction of food resources from open habitats of the four ruminant species (Tables 1 and 5,
550 Figure 2). With intermediate $\delta^{13}\text{C}_{\text{enamel}}$ values (Table 1, Figure 2, Appendix 1), mouflons
551 show intra-tooth variations in $\delta^{13}\text{C}_{\text{enamel}}$ of about 3.0 ‰ across all samples, whereas variation
552 in the chamois is lower, at 1.6 ‰. This reflects seasonal altitudinal displacement (Table 5), as
553 mouflons move up to higher altitude settings in late spring and return to lower altitudes in
554 winter (Darmon et al., 2014). This variability in the mouflons is supported by reconstructions
555 of blood and environmental water $\delta^{18}\text{O}$ values (Table 5, Fig. 5; SI text and Figure S1). It is
556 worth noting that the high $\delta^{13}\text{C}_{\text{enamel}}$ value in one of the two mouflons, if not an artefact, is
557 also associated with an increase in $\delta^{18}\text{O}_{\text{enamel}}$ (not shown in Figures 2 and 3, see Table 1 and
558 Appendix 1), supporting not only a shift to a diet with higher $\delta^{13}\text{C}$ values but likely a change
559 of habitat (i.e. ingested water) as well.

560 Although all ruminants at the BNRP have grown up in a pure C₃ ecosystem, the
561 species differ in their niche breadth B_A, with the chamois having the most constrained niche
562 breadth characterized by the consumption of pure C₃ food resources in open habitats all
563 around the year (Tables 2 and 5; Figure 4). The mouflon has the widest niche breadth and has
564 a minor ecological overlapping with the chamois. The ecological overlapping is actually the
565 highest between the mouflon and the red deer, though mouflons δ¹³C values indicate that it
566 may be feeding in between niches occupied by the three other taxa (Figure 4). There is also a
567 low ecological overlapping between the two cervids, the roe deer occupying more closed
568 habitats than the red deer (Tables 2 and 5).

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573 **Figure 6.** Dental microwear texture complexity and anisotropy values (Asfc, epLsar, A) and
574 disparity and heterogeneity of complexity (Disp-Asfc, HAsfc, B) from red deer *Cervus*
575 *elaphus*, mouflons *Ovis gmelini musimon*, chamois *Rupicapra rupicapra*, and roe deer
576 *Capreolus capreolus*. Overall, anisotropy significantly segregates the two bovids from the
577 cervids. While complexity shows no significant variation, disparity of complexity
578 significantly discriminates the roe deer from the red deer, and heterogeneity of complexity the
579 red deer from the two bovids.

580

581 4.3. Seasonal variations in diet, habitat, and altitudes

582

The large intra-tooth variation in $\delta^{13}\text{C}_{\text{enamel}}$ support that the most mobile species is
583 the mouflon (Tables 1 and 5, Figure 2). Regarding DMTA, mouflons are the only species for

584 which the sampling in two seasons makes an assessment of the inter-season variation
585 possible. The sheep from late fall and early winter have significantly higher textural fill
586 volume (Tfv) than specimens sampled in late summer and early fall (Table S4). Knowing that
587 mouflons tend to decrease their consumption of grasses from 42 % to 29 % from late summer
588 to winter counterbalanced by more conifer foliage up to 28.1 %, we might interpret this
589 increase of textural fill volume as a trend towards more browsing (Tables S1 and S4).
590 However, the absence of significant difference in the other variables on one hand, and the fact
591 that the samples not only differ in season but also in year of sampling (2009 vs. 2015) make it
592 difficult to interpret differences in textural fill volume. Moreover, earlier works yielded
593 contrasted results regarding this variable, with grazers having higher values than browsers in
594 one study (Merceron et al., 2016) and lower values in the other (Scott, 2012).

595 Because mouflons, red deer and chamois molars form over longer periods (about
596 10 to 15 months for the M₃ versus less than 6 months for the roe deer M₃), they are especially
597 useful for the reconstruction of local seasonal patterns (Figure 5, Figure S1–S2). A sample of
598 472 measurements from nearby Thonon-les-Bains (about 80 km from the BNRP) monthly
599 recorded precipitation $\delta^{18}\text{O}$ values ranging from -17.8 to -0.4 ‰ between 1963 and 2012
600 (IAEA/WMO, 2020). Mean precipitation $\delta^{18}\text{O}$ range from the site at any given year is $9.9 \pm$
601 2.9 ‰ 1 S.D. Only 37 % of total site variation is recorded directly by enamel carbonate $\delta^{18}\text{O}$
602 values across all taxa, and 39 % using $\delta^{18}\text{O}_{\text{ew}}$ values. By contrast, inverse modeling recovers a
603 significant portion of this variation. Using serial M₂ and M₃ measurements from the chamois,
604 which have the lowest measured enamel $\delta^{18}\text{O}$ range, we reconstruct ingested water $\delta^{18}\text{O}$
605 values ranging from -10.3 to 0.8 ‰ across all individuals. Even from a single chamois M₂, we
606 recover a range of 9.5 ‰, or 96 % of the average yearly variation found in Thonon-les-Bains
607 precipitation (Figure 5, Figures S1 and S2). Reconstructions from the mouflons, which are
608 known to migrate across altitudes seasonally, reproduce an even greater proportion of local

609 isotopic and hydrological variation: average reconstructed mouflon $\delta^{18}\text{O}$ ranges across all four
610 teeth are 12.93 ‰. Across all teeth from all taxa sampled isotopically in this study, we
611 estimate average annual oscillations of 9.7 ± 4.5 ‰, a result strikingly similar to the average
612 annual precipitation range of 9.9 ‰ observed at Thonon-les-Bains (Table 5, Figure 5, Figure
613 S1 and S2).

614 It is possible that our modeling parameters may under- or overestimate
615 reconstructed seasonal $\delta^{18}\text{O}$ variability. We hold ingested carbohydrate $\delta^{18}\text{O}$ values
616 contributing to metabolic water production as constant, while these values probably shift by
617 several permil or more over the course of the growing season, or may vary with altitude
618 during the migration of the mouflons. In this case, reconstructed water $\delta^{18}\text{O}$ may vary more in
619 model outcomes to account for measured enamel $\delta^{18}\text{O}$ compositions. Alternatively, we may
620 under- or overestimate the fraction of body water oxygen derived from liquid water, which
621 would tend to amplify or dampen, respectively, reconstructed ingested water $\delta^{18}\text{O}$
622 compositions. Importantly, the mineralization model that we use for reconstruction of
623 seasonal patterns is empirical and based upon mineralization observations in a population of
624 sheep. The cervids analyzed here have less hypsodont molars, and in the case of roe deer form
625 very quickly. One result of this rapid tooth formation process is that uncertainty in our
626 reconstructed $\delta^{18}\text{O}$ inputs for roe deer are high at the end of our reconstruction interval (SI
627 text, Fig. S2). Though our inverse method attempts to account for possible taxonomic
628 variability (SI text), it is possible that differences in cervid mineralization may impact our
629 results, for instance by overestimating input $\delta^{18}\text{O}$ variability if roe deer enamel maturation
630 occurred more rapidly than expected. Lastly, we observe that inverse modeling is highly
631 sensitive to individual values: reconstructions from the M_3 of one roe deer, CC 2653, are
632 based on a very high cuspal value, and produce an estimated isotopic range of 20.7 ‰, very
633 possibly a ringing artifact that is common during inverse modeling (Figure S2). Even in this

634 case however, inverse model estimates of blood $\delta^{18}\text{O}$ change only amount to 7–9 ‰, a result
635 directly measured in experimental sheep when they consumed some quantity of snow (Green
636 *et al.*, 2018a). Inverse modeling does appear robust in several respects. Reconstructed values
637 are not overly sensitive to variation in estimated tooth wear, with more or less wear producing
638 inversion results within 1 ‰ of one another. Ecological patterns observed in raw enamel
639 carbonate $\delta^{18}\text{O}$ measurements are replicated by inverse modeling, where for instance $\delta^{18}\text{O}$
640 variation is reduced in the chamois, and amplified in the mouflons. Reconstructed water $\delta^{18}\text{O}$
641 compositions produced by individual teeth recover nearly the whole range of $\delta^{18}\text{O}$ variation
642 observed in nearby precipitation, suggesting that this method may be a powerful tool for
643 reconstructing past seasonality in contexts where precipitation $\delta^{18}\text{O}$ are not available.

644

646 Table 5. Summary of ecological data and ecological inferences made based on dental proxies of the sympatric ruminants of the BNRP, France.

Taxon	Ecological data *		Interpretations of dental ecological proxies		
	Diet (late summer to early winter)	Habitat use	$\delta^{13}\text{C} - \Delta^{13}\text{C}$	$\delta^{18}\text{O} - \Delta^{18}\text{O}$	DMTA on shearing molar facets
<i>Capreolus capreolus</i> (Roe deer)	Selective browser -mostly browse on leaves -fruits and seeds < 6 % -herbaceous monocots < 6 %	-low altitude -mostly below 1200 m	-C ₃ diet -forested habitats	-varied water inputs -variability not clearly seasonal	-tough foliage-dominated browsing habits -low variations in food resources at (small) home range scale -high inter-individual variations indicating disparity in food resources between (small) home ranges
<i>Cervus elaphus</i> (Red deer)	Mixed feeder -fruits 20% - herbaceous monocots ≈ 40 % <u>In summer**:</u> -herb. monocots 50-60 % -herb. dicots 20 %	-low altitude -mostly below 1200 m -move seasonally at higher altitudes than the roe deer	-C ₃ diet -mixed habitats -low altitudinal range	-apparently annual seasonality -intermediate ecology	-grazing habits -low inter-individual variations reflecting gregarious behavior and access to foods similar to most individuals
<i>Ovis gmelini musimon</i> (Mouflon)	Mixed feeder -herb. monocots 32-40 % -mostly browse on deciduous/evergreen trees and shrubs	-high altitude -mostly above 1200 m -move seasonally at lower altitudes than the chamois	-C ₃ diet -mixed habitats -high altitudinal range	-varied water inputs -interstitial niche exploitation	-mixed feeding habits -diet richer in lignified tissues than deer ones -diet less rich in herbaceous monocots than the red deer and the chamois diets
<i>Rupicapra rupicapra</i> (Chamois)	Mixed feeder -herb. monocots 42-50 % -mostly browse on forbs, evergreen trees and shrubs	-high altitude -mostly above 1200 m	-C ₃ diet -open habitats -low altitudinal range	-limited water inputs -apparently annual seasonality	-mixed feeding habits -diet richer in lignified tissues than deer ones -diet likely richer in herbaceous monocots than the mouflons diet

647 * Both habitat use and dietary data (stomach content analysis) are from Redjadj et al. (2014) – Although they also come from BNRP, the present
648 study was not conducted on the very same individuals as the ones studied by Redjadj et al. (2014).

649 ** data from Suter et al. (2004). This paper summarizes the variations of summer diet of red deer *Cervus elaphus* in the eastern Swiss Alps. The
650 authors concluded that the herbaceous monocots content is maximal in summer. The dietary difference, and notably the amount of herbaceous
651 monocots and dicots between summer and fall for red deer is essential to be emphasized here because due to the dental microwear turnover
652 (much lower than stomach content), DMTA of red deer shot in September and October does not track fall but summer diet.

653 **5. Conclusions**

654 This study provides insights into the feeding ecology of a modern sympatric
655 ruminant community in a C₃ plant ecosystem providing a comparative stable isotope and
656 dental wear dataset (see summary in Table 5), which could serve as a model to interpret past
657 mammalian herbivore communities. For instance, the contrasting $\delta^{13}\text{C}$ values of the roe deer
658 and the chamois mirror their different habitats whereas the red deer and the mouflons show
659 intermediate values, with the latter showing the highest intra-tooth amplitude reflecting its
660 altitudinal seasonal displacements. Dental microwear textures detect some significant
661 differences in diet between species. The two bovids plot as mixed feeding species displaying
662 both intermediate complexity and anisotropy, which is expected for species that ingest less
663 than 50 % herbaceous monocots. This contrasts with the apparent discrepancy between dental
664 proxies and stomach content analysis found for the mixed feeding red deer, where low
665 microwear complexity together with high anisotropy may reflect a summer diet bias towards
666 more grazing habits. Based on comparisons with earlier works on present-day populations of
667 ruminants and experimental controlled food testing on domesticated sheep used as a model for
668 ruminants, the red deer at the BNRP is supposed to be more engaged in grazing than
669 suggested earlier by stomach content analyses. Regarding the roe deer, both mean and inter-
670 individual dispersion of complexity and its anisotropy mirrors stomach content analysis which
671 attests to browsing habits with a low amount of fruits.

672 Variation in enamel $\delta^{18}\text{O}$ compositions appears to reflect the complexity of landscape use in
673 all animals except the roe deer, whose enriched M₂ values likely reflect early life milk
674 consumption. While $\delta^{18}\text{O}$ variability is reduced in enamel compared to regional precipitation,
675 inverse modeling appears to fully recover annual $\delta^{18}\text{O}$ ranges, while preserving inter-species
676 differences in migratory behavior. Altogether, despite some temporal biases introduced by the
677 timing of enamel deposition or wear, in most cases isotopic and microwear proxies

678 successfully recover ecological niche spaces occupied by all four ruminants in this alpine
679 setting. These results highlight the potential of combined proxies and modeling for
680 reconstructing different ecological aspects (diet, habitat tree cover, home range, seasonal
681 displacement, social behaviors) using dental remains.

682

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SUPPLEMENTARY INFORMATION

**Tooth tales told by dental diet proxies: an alpine community of sympatric ruminants as
a model to decipher the ecology of fossil fauna**

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8

9 **1. Material and methods**

10 *1.1. Material*

11 *1.1.1. The Bauges Natural Regional Park (BNRP) and the sympatric ruminants*

12 The Bauges Natural Regional Park (BNRP; 45.69°N, 6.14°E, Figure 1) is a typical
13 subalpine massif of ≈90,000 ha located in the northern French Alps. Altitudes range from 250
14 m to 2217 m. The climate is cold and humid: at 590 meters in altitude, the Météo-France
15 weather station has recorded annual mean temperatures of 9.2 °C, where the coldest month
16 mean is -0.14 °C in January and the warmest month mean 18.5 °C in July. The same station
17 records annual mean rainfall to be 1369 mm. Snow covers the ground from November to April
18 in subalpine pastures (≈1,630 m) with frost lasting in average 123 days per year (Thuiller et al.,
19 2018). More than 70 % of the BNRP has a high tree cover up to 1,500 m. The tree species of
20 European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) represent about 50 % of forest
21 cover. The non-forested habitats, mostly at the highest altitudes, are composed of open pastures,
22 screes and cliffs. The study area also encompasses a National Game and Wildlife Reserve
23 (NGWR; 5,205 ha; Figure 1), comprising the highest part of the massif.

24 Several studies have investigated multiple aspects of behavioral ecology of the four wild
25 ruminant species (chamois, red deer, roe deer and mouflon) inhabiting the BNRP. Among them,
26 Redjadj et al. (2014; Table S1) made a comparative analysis of the feeding ecology of these
27 four large herbivores through a gender-balanced stomach content analysis covering late summer
28 until early winter period from 2003 to 2008. It is worth mention that none of stomach contents
29 from the specimens in the present study have been analyzed. Also, with the exception of the
30 mouflons, most of the specimens were shot in early fall (late September and October; Appendix
31 2); we therefore expect dental microwear textures to reflect the summer diet, since these reflect
32 dietary habits of the last few weeks to months of life (Teaford et al., 2017; Teaford and Oyen,
33 1989; Winkler et al., this volume). Redjadj et al. (2014) have shown a clear spatial distribution
34 between cervids and bovids, the latter, and notably the chamois, occupying the highest areas.
35 Among cervids the red deer goes least frequently to higher altitudes (Redjadj et al., 2014).

36

37

38 The largest ruminant (adult males: 151 kg; adult females: 98 kg) at the BNRP, the red
39 deer *Cervus elaphus*, is a mixed-feeding species (including both monocots and dicots) with
40 spatial variation in its diet. Grasses account for about 30 % of the annual diet in many regions
41 through Europe but can surpass 80 % in Mediterranean habitats (Azorit et al., 2012; Bugalho
42 and Milne, 2003; Gebert and Verheyden-Tixier, 2001). At the BNRP, Redjadj et al. (2014)
43 found out that during late summer and early fall (the period during which most of the
44 specimens were shot), herbaceous monocots and forbs represent about 40 and 6 %,
45 respectively, of the stomach content as dry matter weight. Fruits, mainly apples and to a lesser
46 extent acorns (Redjadj et al., 2014) may account for up to 20 %. Foliages from various
47 evergreen and deciduous trees and shrubs (cumulative proportions reaching 23.6 %),
48 dominated by evergreen shrubs, notably brambles (*Rubus fruticosus*; Table S1), also form a
49 major fraction of the diet. It is worth noting that Suter et al. (2004) indicates that herbaceous
50 monocots represent between 50 and 60 % of summer diet of red deer in the Alps, which is
51 complemented with herbaceous dicots (forbs) that could represent up to 20 %. Although
52 comparisons between the two studies are difficult as the sampling methods differ, the seasonal
53 shift from graze to browse from summer to winter are reported for many Alpine populations
54 (Suter et al., 2004).

55 The second cervid, the roe deer *Capreolus capreolus* (adult males: 22.8 kg; adult
56 females: 21.4 kg), is a selective browser (Cibien, 1984; Cornelis et al., 1999; Cransac et al.,
57 2001; Storms et al., 2008; Tixier et al., 1997). Its diet mostly includes dicot foliage, mosses,
58 mushrooms, fruits including seeds. Herbaceous monocots barely reach 10 % of its diet; this
59 occurs, however, only in spring. In late summer and early fall, roe deer from the BNRP mainly
60 focus on evergreen shrubs (bramble leaves) and forbs at about 44 and 25% of the stomach
61 content expressed as dry matter weight, respectively. Evergreen shrubs reach almost 60%, and
62 forbs surpass 10 % in late fall and winter. What is surprising at the BNRP is the very low
63 amount of fruits in the roe deer diet for the two periods (3.4 and 5.8 % of the diet, respectively)
64 compared to the greater fruit intake among red deer at BNRP, (Redjadj et al., 2014), and to roe
65 deer populations in other locations (Tixier and Duncan, 1996). As expected, grasses represent
66 less than 6% of the roe deer diet for each of the two seasons at the BNRP (Table S1).

67 The mouflons, *Ovis gmelini musimon* (adult males: 42.8 kg; adult females: 31.3 kg) is a
68 mixed-feeding species. Marchand et al. (2013) reviewed the feeding ecology of this wild sheep.
69 Although grasses are the major food type, foliages from shrubs and herbaceous dicots are the
70 secondarily preferred food resources. At the BNRP, grasses represent 42 and 29 % (expressed

71 as percentage of dry matter weight) of their diet for each of the two investigated periods
 72 (Redjadj et al., 2014). Evergreen shrubs (16.2 %) and forbs (15.7 %) are the secondarily
 73 preferred foods in late summer and early fall. In late fall and winter, evergreen trees (mostly
 74 conifer foliages; 28.1 %) counterbalance the drop in proportions of both forbs and grass
 75 component compared to the first period (Table S1; Redjadj et al., 2014).

76 The chamois *Rupicapra rupicapra* (adult males: 34.5 kg; adult females: 29.7 kg) is a
 77 mixed feeder grazing and browsing depending resources availabilities and energetic
 78 requirements (Pérez-Barberia et al., 1997). For instance, recent studies show that the chamois
 79 in Pyrenees may include less than 20 % grasses in its summer and fall diets (Espunyes et al.,
 80 2019). Besides, grasses represent 44 % and more than 50 % in summer and fall, respectively,
 81 of its diet at the BNRP (Table S1; Redjadj et al., 2014). Forbs (22.4 %) and evergreen shrubs
 82 (19.6 %) complement the diet for the first period whereas the drop in forbs is counterbalanced
 83 with evergreen trees (17.5 %) composing the secondary food items (Table S1).

84 **Table S1.** Mean percentage of the main food resource of the ruminants from the Bauges NRP
 85 in late summer/early fall and late fall and winter (for more details, see Redjadj et al., 2014).

Species	N*	Period 1 (early September-mid November)							Period 2 (mid November-late January)						
		Fr	Gr	Fo	DS	ES	DT	ET	Fr	Gr	Fo	DS	ES	DT	ET
<i>C. capreolus</i>	104	3.44	5.08	25.1	2.41	44.3	5.7	0.8	5.83	5.52	10.4	1	58.6	0.61	10.2
<i>C. elaphus</i>	158	19.5	39.8	6.17	1.94	13.5	4.12	4.02	12.5	33.4	1.84	0.96	26.1	1.54	15.7
<i>O. gmelini</i>	86	5.18	41.8	15.7	4.12	16.2	5.81	1.45	4.43	29	3.71	1.32	17.3	2.36	28.1
<i>R. rupicapra</i>	148	1.29	44.4	22.4	0.67	19.6	0.79	0.42	1.48	50.5	9	0.81	16.2	0.48	17.5

86 *N: number of stomach contents; Fr: fruits; Gr: grasses and herbaceous monocots; Fo: forbs; DS: deciduous
 87 shrubs; ES: evergreen shrubs; DT: deciduous trees; ES: evergreen trees.
 88

89 1.1.2 Selection of BNRP specimens

90 Our study was based on tooth samples collected from animals shot during the legal
 91 hunting season both within and outside the NGWR (Fig. 1). All samples come from animals
 92 tagged with official annual hunting quotas delivered by the county prefects in agreement with
 93 the environmental code (Art. R425-2 to 425-141 13). No animals were harvested solely for the
 94 purpose of this study.

95 Mandibles were collected from early September to end of March during three hunting
 96 seasons (2008/2009, 2014/2015 and 2015/2016). A total of 11 and 82 adult specimens (with
 97 erupted and worn second molars) were used for enamel stable isotope and dental microwear
 98 texture analyses, respectively. Five red deer, two roe deer, two chamois and two mouflon molars

99 were serially sampled for enamel stable isotope analyses (Appendix 1). Eighteen roe deer, 21
100 red deer, 22 mouflons, and 21 chamois compose the sample for DMTA, which was performed
101 on second molars (Appendix 2).

102

103 2. Methods

104 2. 1. Enamel carbon and oxygen stable isotope analyses

105 Stable carbon isotopes ($^{13}\text{C}/^{12}\text{C}$ ratio expressed as $\delta^{13}\text{C}$ value) in enamel reflect the $\delta^{13}\text{C}$
106 values of the ingested food resources that are mainly controlled by the photosynthetic pathway
107 used by plants. The C_3 or Calvin-Benson-Bassham cycle results in more fractionation of ^{12}C
108 and therefore lower $\delta^{13}\text{C}$ values, while the C_4 or Hatch-Slack cycle results in less fractionation
109 of ^{12}C and therefore higher $\delta^{13}\text{C}$ values. Vegetation type and plant physiology can further
110 control herbivore enamel $\delta^{13}\text{C}$ values: C_3 plants tend to be trees or shrubs and herbaceous dicots
111 and monocots from either high altitudes or latitudes, whereas C_4 plants tend to be monocots,
112 notably grasses. Even in a pure C_3 ecosystem, the degree of vegetation cover can be observed
113 isotopically, where dense forest cover results in lower $\delta^{13}\text{C}$ values, and open environments
114 result in higher $\delta^{13}\text{C}$ due to increased rates of evapotranspiration and stomatal conductance in
115 leaves (Bonafini et al., 2013; Drucker and Bocherens, 2009). Given these considerations we
116 expect enamel $\delta^{13}\text{C}$ values to be lower in the forest-dwelling roe deer and higher in the chamois,
117 which occupies the most open Alpine habitat within this C_3 plant ecosystem (Redjadj et al.,
118 2014 and citations therein).

119 About 100 μg of enamel powder per sample were serially extracted with a hand-held
120 microdrill, sampled along the crown from apex to cervix on the third lower molars (M_3) of red
121 deer, and on the second (M_2) and third (M_3) lower molars of mouflons, chamois, and roe deer.
122 Six to 16 enamel samples per tooth were analyzed for roe deer and mouflon, respectively
123 (Figures 1 and 2; Table 1; Appendix 1). The spatial location of sample positions on each tooth
124 was recorded to within 0.1 mm precision. No bleach treatment was applied.

125 Isotope analyses of structural carbonate in tooth enamel samples were performed on a
126 Thermo DeltaV mass spectrometer coupled to a Gasbench II gas preparation unit in which a
127 cold trap system at liquid nitrogen temperature is integrated. The system is set up as outlined in
128 Fiebig et al. (2005). With this technique, smaller than usual samples can be analyzed: in this
129 study <200 microgram of non-pre-treated tooth enamel powder. Digestion of enamel powder

130 took place in >99 % H₃PO₄, at a temperature of 70 °C. The sample digestion time between
131 acidification and CO₂ sample transfer to the cold trap was ~90 minutes. Isotope data are
132 calculated by direct comparison to a total of ≈20 replicates of at least two isotopically distinct
133 CaCO₃ isotope standards analyzed in each run of 55 samples. A logarithmic fit through the
134 isotope ratios versus peak size data of the standard replicates is used to remove fractionation
135 effects due to sample size. The reproducibility of standards after these corrections typically is
136 better than 0.3 ‰ for both δ¹⁸O and δ¹³C (1SD). This is a slightly higher uncertainty in
137 comparison to the analysis, on the same equipment, of larger samples that do not require use of
138 the cold trap (Breitenbach and Bernasconi, 2011; Spötl and Vennemann, 2003). For the
139 precision requirements in this study, we believe the slightly higher uncertainty does not
140 outweigh the benefits of achieving high-resolution growth incremental series by analysing the
141 smaller amounts. We routinely analyzed a modern tooth enamel standard of an African elephant
142 (AG-Lox, Gehler et al., 2012) in the runs as well, to verify that this enamel standard (i.e.
143 structurally bound carbonate in bioapatite) has a similar reproducibility to pure carbonate
144 standards. Daily averages of the the AG-Lox standard as measured with this technique yield a
145 δ¹³C_{enamel} value of -11.49 ± 0.11 ‰ (1SD) and a δ¹⁸O_{enamel} value of -1.50 ± 0.19 ‰ (1SD).
146 These precisions are slightly better than sample to sample uncertainties, as they are based on
147 daily averages of multiple analyses of this standard. We observe that the AG-Lox isotope values
148 reported for this technique compare, within error, to the values we find if we run larger amounts
149 of AG-Lox on the same Gasbench system without using the cold trap. Another relevant
150 observation is that the δ¹⁸O_{enamel} values for AG-Lox on this system differ significantly from
151 previous published values, obtained on a fundamentally different IRMS system (Wacker et al
152 2016). Interlaboratory differences for tooth enamel δ¹⁸O_{enamel} values occur frequently, and are
153 believed to relate to analytical conditions like digestion temperature and acid type (e. g.,
154 Demény et al., 2019). Reporting isotope values for tooth enamel standards like AG-Lox enables
155 a better comparison of isotope data from different laboratories. The interlaboratory differences
156 for tooth enamel δ¹³C_{enamel} values tend to be much smaller, and would be insignificant for the
157 δ¹³C_{enamel} variation described in this study.

158 2.2 Modeling ruminant isotope ecology

159 Kierdorf and Kierdorf (2000) report that for the roe deer, enamel formation
160 (amelogenesis) of M₂ begins *in utero* and terminates around 4 months of age. The roe deer M₃
161 is estimated to form between 4–9 months of age. For the red deer, the second molar begins

162 forming prior to 3 months of age and completes formation around 9 months of age; the third
163 molar begins forming at 9 months of age and completes prior to 26 months. Here, we consider
164 only M_3 of red deer. Depending on the breed, sheep second molars may mineralize over a 10–
165 15 months period, and third molars over 10–15 months or more (Milhaud and Nezit, 1991).
166 Assuming that caprine bovids have similar enamel growth rate and that chamois molars are
167 smaller than those of mouflons, we consider it plausible that chamois second and third molars
168 form over slightly less time than those of mouflons (see also Kierdorf et al., 2012).

169 Using a bodymass-dependent equation calibrated specifically for foregut mammals
170 (Tejada-Lara et al., 2018; Table S1; Appendix 1), we calculate ϵ an estimation of the carbon
171 stable isotope composition of the food resources ($\delta^{13}C_{\text{diet}}$) exploited by the ruminants.

172 $\epsilon^* = 2.34 + 0.05 (\text{BM})$; Bodymass expressed need to be ln-transformed, and then ϵ^* needs
173 to be inverted (e^x) to obtain the ‰ value to be applied for each species. We consider bodymass
174 (intermediate value between male and female bodymass) measured on specimens sampled over
175 several years in BNRP: 125 kg for the red deer, 22 kg for the roe deer, 32 kg for the chamois
176 and 37 kg for the mouflon (see Table 1 and Appendix 1). The isolated high $\delta^{13}C_{\text{enamel}}$ value, if
177 not an analytical artefact, is either due the high intake of alpine CAM plants or the few native
178 C_4 plants at high altitudes and mid-to-high latitudinal biomes (Osmond et al., 1975; Pyankov et
179 al., 2010) which can have variable $\delta^{13}C$ values, depending on local and seasonal conditions, or
180 due to the consumption of cultivated maize in valleys. Also, mouflons are known to perform
181 seasonal altitudinal movements (Darmon et al., 2014) and as there are a few areas of cultivated
182 maize in the valleys and the possible existence of some places where hunters spread maize for
183 preventing damages caused by wild boar, we cannot firmly exclude a high consumption of
184 maize for short period.

185 In parallel to carbon isotope analysis of tooth enamel, food remains stuck between cusps
186 and teeth in the jaw were sampled also for carbon isotope analysis to directly assess the $\delta^{13}C$
187 values of ingested food plants. Dried plant samples were homogenized in 2 ml Eppendorf vials
188 using a Retsch ball mill. About 700 μg of plant powder were weight into a 3.3 x 5 mm tin
189 capsule and tightly folded. Each plant sample was analyzed in triplicate for its carbon isotope
190 composition using a Vario EL elemental analyzer (EA) coupled to a Finnigan MAT 253 isotope
191 ratio mass spectrometer in continuous flow mode. Carbon isotope data ($^{13}C/^{12}C$ expressed as
192 $\delta^{13}C$ value) are reported in the δ -notation in per mil (‰), relative to the international isotope
193 reference standard Vienna Pee Dee Belemnite (VPDB). Sample $\delta^{13}C$ values were calibrated

194 against the two international glutamic acid standard reference materials USGS 40 and 41. The
 195 analytical precision of $\delta^{13}\text{C}$ values was better than $\pm 0.1 \text{ ‰}$ (1 SD). The $\delta^{13}\text{C}$ values of these
 196 plant remains were measured from which an expected enamel $\delta^{13}\text{C}_{\text{enamel}}$ value is calculated
 197 according to the equation for foregut fermenting mammals from Tejada-Lara et al. (2018; Table
 198 S2). This hypothetical $\delta^{13}\text{C}_{\text{enamel}}$ is not compared with the mean $\delta^{13}\text{C}$ values of the serial enamel
 199 samples along the tooth crown that would represent a long time span but with the measured
 200 $\delta^{13}\text{C}_{\text{enamel}}$ value of the very last sample to mineralize on the M₃, meaning next to the cervix.
 201 Both, food remains from the teeth/jaw and $\delta^{13}\text{C}_{\text{enamel}}$, represent an unknown interval of time
 202 (even when the enamel is serially sampled). However, the carbon isotope composition of the
 203 enamel was incorporated when it was mineralized at least weeks if not months before food
 204 items were stuck in dental arches. Moreover, we may also argue the plant remains stuck in teeth
 205 is an epiphenomenon meaning the direct comparisons of these data should be done with high
 206 caution. In any case, the $\delta^{13}\text{C}_{\text{enamel}}$ value of the very last sample to mineralize on the M₃ is the
 207 most appropriate value to be compared with $\delta^{13}\text{C}$ measured from food remains lodged between
 208 cusps and teeth.

209

210 **Table S2.** Carbon stable isotope compositions of the food stuck between cuspids and teeth of
 211 different individuals of the ruminants from the Bauges NRP. Estimations of carbon stable
 212 isotope composition of the enamel (based on Tejada et al., 2018) that would have
 213 incorporated carbon atoms from a dietary bolus with a carbon stable isotope composition
 214 similar to the one of the food stuck are calculated compared with the carbon stable isotope
 215 composition of the very last sample on the third molar.

taxon	specimen	$\delta^{13}\text{C}$ vegetation	sd*	$\delta^{13}\text{C}_{\text{enamel}}$ estimation	$\delta^{13}\text{C}_{\text{enamel}}$ M ₃ Last sample	$\Delta^{13}\text{C}_{\text{diet-enamel}}$
<i>Cervus elaphus</i>	CE 4821	-28.27	1.79	-15.30	-14.51	-0.79
<i>Cervus elaphus</i>	CEF 7104	-29.86	0.11	-16.88	-15.83	-1.05
<i>Cervus elaphus</i>	CEM 2616	-29.19	0.10	-16.21	-16.67	0.46
<i>Cervus elaphus</i>	CE 4951	-29.94	0.07	-16.96	-16.00	-0.96
<i>Cervus elaphus</i>	CE 0104	-30.06	0.43	-17.08	-16.89	-0.19
<i>Capreolus capreolus</i>	CC 2613	-28.36	0.04	-16.18	-16.30	0.12
<i>Capreolus capreolus</i>	CC 2653	-28.94	0.04	-16.76	-18.70	1.94
<i>Rupicapra rupicapra</i>	RR 8952	-28.58	0.05	-16.31	-14.50	-1.81
<i>Rupicapra rupicapra</i>	RR 8932	-27.23	0.06	-14.95	-14.43	-0.52
<i>Ovis gmelini</i>	OG 8843	-27.55	0.04	-15.44	-14.57	-0.87
<i>Ovis gmelini</i>	OG 8847	-27.65	0.01	-15.54	-15.54	0.00

216 * Standard deviation

217 In addition, we expect the enamel oxygen isotopic composition ($^{18}\text{O}/^{16}\text{O}$ ratio expressed
218 as $\delta^{18}\text{O}$ value) to primarily reflect the $\delta^{18}\text{O}$ values of the ingested water, including drinking
219 and/or leaf water. The $\delta^{18}\text{O}$ values of precipitation should be lower at low temperatures and
220 high altitudes, and should vary across winter and summer seasons (Dansgaard, 1964; Rozanski
221 et al., 1993; Gat, 1996; Bowen, 2010). Therefore, the altitudinal distribution of the species and
222 their distinct spatial and temporal feeding behaviors can potentially be inferred from enamel
223 $\delta^{18}\text{O}$ values. Additionally, enamel $\delta^{18}\text{O}$ values may reflect differences in feeding ecology and
224 plant physiology. Compared to grazers, browsers gain most of their body water from the
225 vegetation itself, where leaf water and plant structural carbohydrates are significantly ^{18}O -
226 enriched relative to meteoric water (Farquhar and Lloyd, 1993; Farquhar and Gan, 2003; Song
227 et al., 2013). Herbivores produce a portion of their body water from the metabolism of these
228 carbohydrates and the inspiration of atmospheric oxygen (Gretebeck et al., 1997; Podlesak et
229 al., 2008). Lastly, herbivore physiology itself may impact body water and enamel $\delta^{18}\text{O}$
230 compositions, as individuals increased loss of lose body water to the environment through
231 panting and cutaneous evaporation have ^{18}O -enriched body water pools (Kohn et al., 1996;
232 Green et al., 2018a).

233 Based on the enamel oxygen isotope composition, we propose an estimation of the
234 oxygen isotope composition of the environmental water ($\delta^{18}\text{O}_{\text{ew}}$) ingested by the ruminants
235 from the BNRP following the regression between enamel (i.e. structurally bound carbonate in
236 the bioapatite) and ingested water of Iacumin et al. (1996):

$$237 \delta^{18}\text{O}_{\text{enamel}} = 0.998 \times \delta^{18}\text{O}_{\text{ew}} + 33.63$$

238 We also consider the niche breadth B_A (Levins, 1968) and the ecological overlapping
239 O_{Bauges} (Pianka, 1973), based on both $\delta^{18}\text{O}_{\text{ew}}$ and $\delta^{13}\text{C}_{\text{diet}}$ (see also Dantas et al., 2017). These
240 two ecological indexes are computed with the relative proportions of individuals plotting within
241 pre-defined isotopic bins (Table 2). Here, the full range of $\delta^{18}\text{O}_{\text{ew}}$ and $\delta^{13}\text{C}_{\text{diet}}$ based on intra
242 tooth ranges of M_3 (we exclude M_2 data as these might potentially represent a mix of post- and
243 pre-weaning information) are used to define the range of isotopic bins. Seven one-per-mil-
244 intervals from -25.0 ‰ to -32.0 ‰ are then defined for the carbon isotope composition of the
245 diet. Here, we did not consider the single unexpected high enamel $\delta^{13}\text{C}$ value of -6.9 ‰ on
246 mouflons M_2 (MO8843), which might reflect either an undetected analytical error or a
247 significant fraction of C_4 plant in the diet ($\delta^{13}\text{C}_{\text{diet}} = -19.29$ ‰), most likely maize from
248 cultivated fields at low altitudes. We consider this value as non-representative of the mouflon

249 ecology in an Alpine native ecosystem in Europe. In addition, seven one-per-mil-intervals from
250 -16.0‰ to -9.0‰ are defined for the oxygen isotope composition of the environmental water
251 (Table 2).

252

253 *2.3 Estimating oxygen isotope seasonality through inverse modeling*

254 Lastly, we use Bayesian inference inverse modeling to better infer potential seasonal
255 variations in environmental $\delta^{18}\text{O}$ values that contribute to measured spatial variations in tooth
256 $\delta^{18}\text{O}$. As described previously (Green et al., 2018b), we combine our chamois, mouflons, roe
257 and red deer tooth $\delta^{18}\text{O}$ measurements with a synchrotron-based empirical model of ruminant
258 molar enamel formation, originally derived from a population of domesticated sheep. Through
259 forward modeling, these measurements and model predict tooth isotope compositions for any
260 hypothetical history of seasonal $\delta^{18}\text{O}$ ingestion (see Passey and Cerling, 2002; Passey et al.,
261 2005). We iteratively propose seasonal drinking water histories, comparing resulting forward
262 modeled enamel $\delta^{18}\text{O}$ compositions with actual $\delta^{18}\text{O}$ data, until differences between modeled
263 and real enamel $\delta^{18}\text{O}$ compositions are minimized (Green et al., 2018b).

264 Sequential isotopic measurements from enamel are generally intended to reconstruct
265 past seasonal patterns related to an animal's behavior, physiology and environmental
266 chemistry. This is possible because teeth form incrementally, and during formation, enamel
267 increments mineralize at equilibrium with body chemistry, which itself fluctuates over time
268 with changes in diet, physiology or the environment. Sequential samples measured from a
269 tooth do not however directly record either environmental or body chemistry. First,
270 environmental signals are altered as they enter the blood stream on the basis of physiological
271 and molecular discrimination. Because the body has one or several reservoirs with unique
272 turnover times for each ingested constituent, environmental signals tend to be prolonged and
273 dampened. Second, enamel mineralizes in multiple stages with timing and geometry that
274 changes across the tooth crown. For this reason, changes in body chemistry over time, already
275 an indirect reflection of environmental chemistry, are further attenuated and distorted when
276 reflected as spatial variations in enamel chemistry across the length of a tooth.

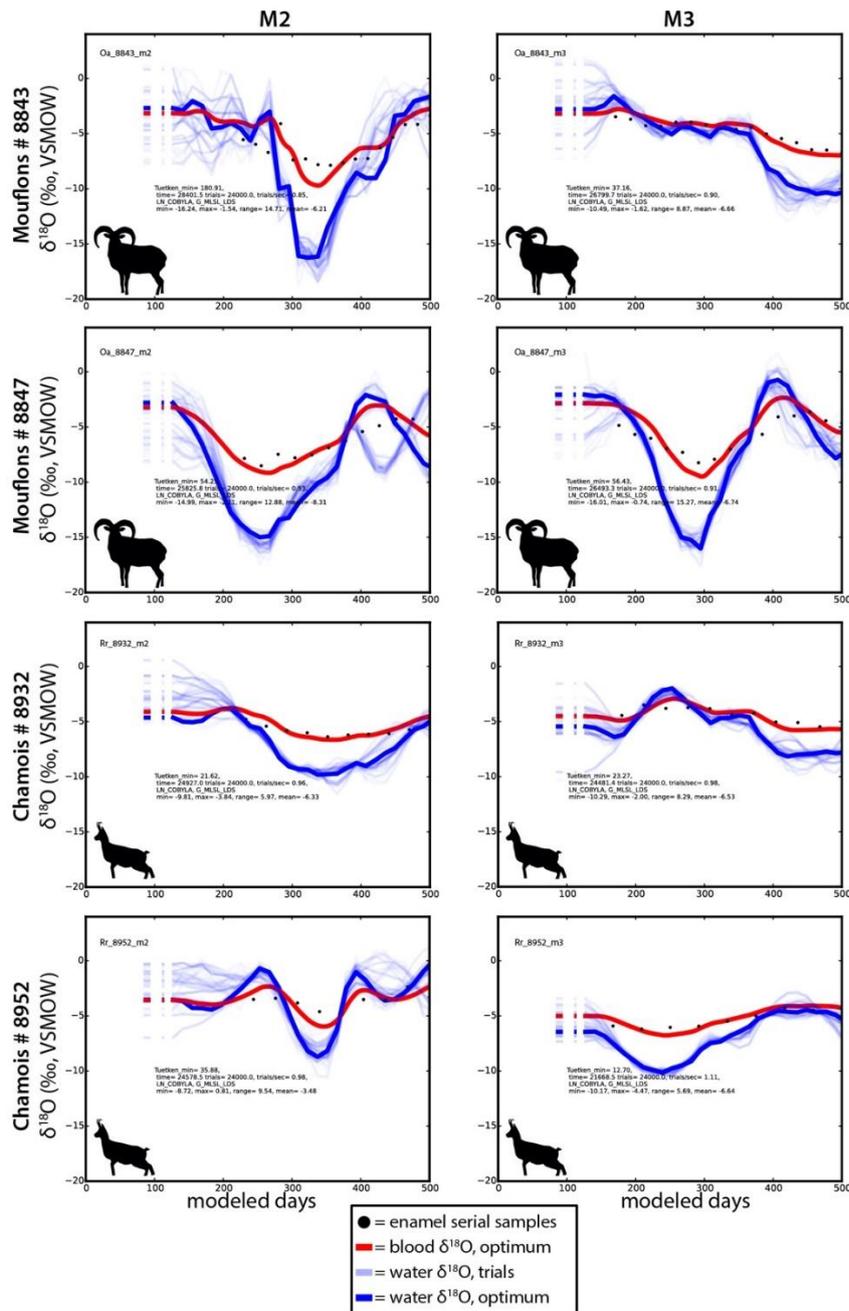
277 We attempt to use enamel isotopic measurements made from ruminants in the Bauges
278 Regional Natural Park, to reconstruct their original seasonal ingested drinking waters through
279 inverse modeling. To do this we must first propose forward models that estimate how body
280 chemistry changes over time given changes in environmental chemistry, and then use forward

281 models that estimate how enamel chemistry is determined given these estimates of body water
282 chemistry (Passey and Cerling, 2002; Passey et al., 2005). Here, we use equations adapted by
283 Gretebeck et al. (1997) to estimate blood water $\delta^{18}\text{O}$ compositions from air ($\delta^{18}\text{O} = 23.5 \text{ ‰}$
284 globally), drinking water, and feed, which we here treat as pure carbohydrate for simplicity
285 (Podlesak et al., 2008), and to which we give an invariant value of $\delta^{18}\text{O} = 25 \text{ ‰}$, comparable to
286 other measured northern hemisphere feed $\delta^{18}\text{O}$ compositions ranging from 23–26.1 ‰
287 (Gretebeck et al., 1997; Podlesak et al., 2008; Green et al., 2018a). We assume a single body
288 oxygen turnover pool (Cerling et al., 2007) in ruminants of seven days, given measured water
289 turnover rates ranging from 3–13 days in living ruminants, and recognizing that the highest and
290 lowest values in this range are found among either physiological specialists or domesticated
291 animals, respectively (Macfarlane et al., 1971). We set the ratio of oxygen ingested as drinking
292 water compared to that consumed as both feed and air to 1:1, within the range of values
293 observed in humans, rodents and sheep (Gretebeck et al., 1997; Podlesak et al., 2008; Green et
294 al., 2018a), and set the amount of water lost evaporatively to 40 %. Under this rubric we assume
295 that half of animal body water is derived from water ingested directly from streams and snow,
296 or contained within vegetation; we model the remainder of body water as deriving from
297 metabolic water production from atmospheric oxygen ($\delta^{18}\text{O} = 23.5 \text{ ‰}$) and plant carbohydrate
298 ($\delta^{18}\text{O}$ estimated at 25 ‰). While we recognize that carbohydrate, protein and fat resources
299 within plants all contribute to ruminant metabolic water production, for the sake of simplicity
300 we here consider only carbohydrate metabolism, and treat carbohydrate $\delta^{18}\text{O}$ compositions as
301 seasonally invariant (Podlesak et al., 2008).

302 Given these estimates of the behavioral, environmental and physiological values and
303 processes, from a given proposed history of seasonal drinking water $\delta^{18}\text{O}$ over time, derived
304 either from snow, liquid water or from water within plant tissues, we can estimate body water
305 $\delta^{18}\text{O}$ compositions over time. These compositions are then used to calculate modeled tooth
306 enamel $\delta^{18}\text{O}$ values. Given a model of ruminant enamel formation (Green et al., 2017), we
307 estimate that the value of any given location xy in a tooth on day d of formation, is equal to
308 the sum of blood $\delta^{18}\text{O}$ compositions for all of i days from the initiation (init) of enamel
309 formation until day d , multiplied by the fractional daily mineral density increases $\rho\Delta_i$ relative
310 to cumulative mineral densities ρ_{td} at that location for all of i days until day d : $\delta^{18}\text{O}_{xy,d} = \sum_i$
311 $\delta^{18}\text{O}_i \times \rho\Delta_i / \rho_{td}$. A value of 19.1 ‰ taken from Puc at et al. (2010) is added to account for
312 the offset between blood water and mineral phosphate.

313 Following Green et al. (2018b), inverse seasonal blood and water $\delta^{18}\text{O}$ modeling was
314 conducted using Python 2.7, and with the aid of optimization algorithms hosted by the python
315 non-linear optimization module (NLOpt, Johnson, 2017). For each optimization, water $\delta^{18}\text{O}$
316 parameter values were proposed at 14-day intervals. Local searches were conducted using
317 constrained optimization by linear approximation (COBYLA; Powell, 1998), and global
318 searches were conducted using the quasi-Monte Carlo multi-level single linkage algorithm
319 (MLSL) (Rinnooy Kan and Timmer, 1987; Kucherenko and Sytsko, 2005). Parameter
320 goodness of fit was evaluated using a likelihood framework comparing modeled tooth $\delta^{18}\text{O}$
321 values resulting from hypothetical drinking water $\delta^{18}\text{O}$ parameters to measured enamel $\delta^{18}\text{O}$
322 values. In addition to accounting for measurement error, modeled enamel $\delta^{18}\text{O}$ uncertainty
323 incorporates 10 estimates of within-population variation in mineralization trajectory per
324 sampled location within the enamel, and three estimates of potential between-population or
325 between-species variation in enamel formation rates (Green et al., 2018b). Each optimization
326 trial shown is the result of 24,000 trials, with increasingly relaxed d_{rate} priors used to increase
327 both accuracy and precision of the result.

328 During modelling, we assume that 50 % of tooth crown height has been lost in second
329 molars (M_{2s}), and 25 % of tooth crown height lost in third molars (M_{3s}), prior to sampling.
330 Sensitivity testing indicates that altering the total estimated crown wear does not dramatically
331 shift reconstructed drinking water $\delta^{18}\text{O}$ values. Because most chamois, mouflons and red deer
332 M_{2s} and M_{3s} appear to form over a period of up to or beyond one year, we model their
333 extension (growth along the cuspal-cervical axis) as equivalent to measured rates in a
334 domesticated sheep second molar, completing within 14 months. For the roe deer, we estimate
335 that extension completes more quickly: within 7 months, though mineralization may continue
336 briefly afterwards (Milhaud and Nezeit, 1991; Kierdorf and Kierdorf, 2000; Green et al., 2017;
337 Witzel et al., 2018). Measured enamel carbonate $\delta^{18}\text{O}$ values in VPDB (Vienna PeeDee
338 Belemnite) scale were converted to VSMOW (Vienna Standard Mean Ocean Water) using the
339 equation $\delta^{18}\text{O}_{\text{VSMOW}} = 1.030911 \times \delta^{18}\text{O}_{\text{VPDB}} + 30.91$. Estimated equivalent enamel phosphate
340 $\delta^{18}\text{O}$ values in teeth were estimated by subtracting 8 ‰ from each carbonate measurement.

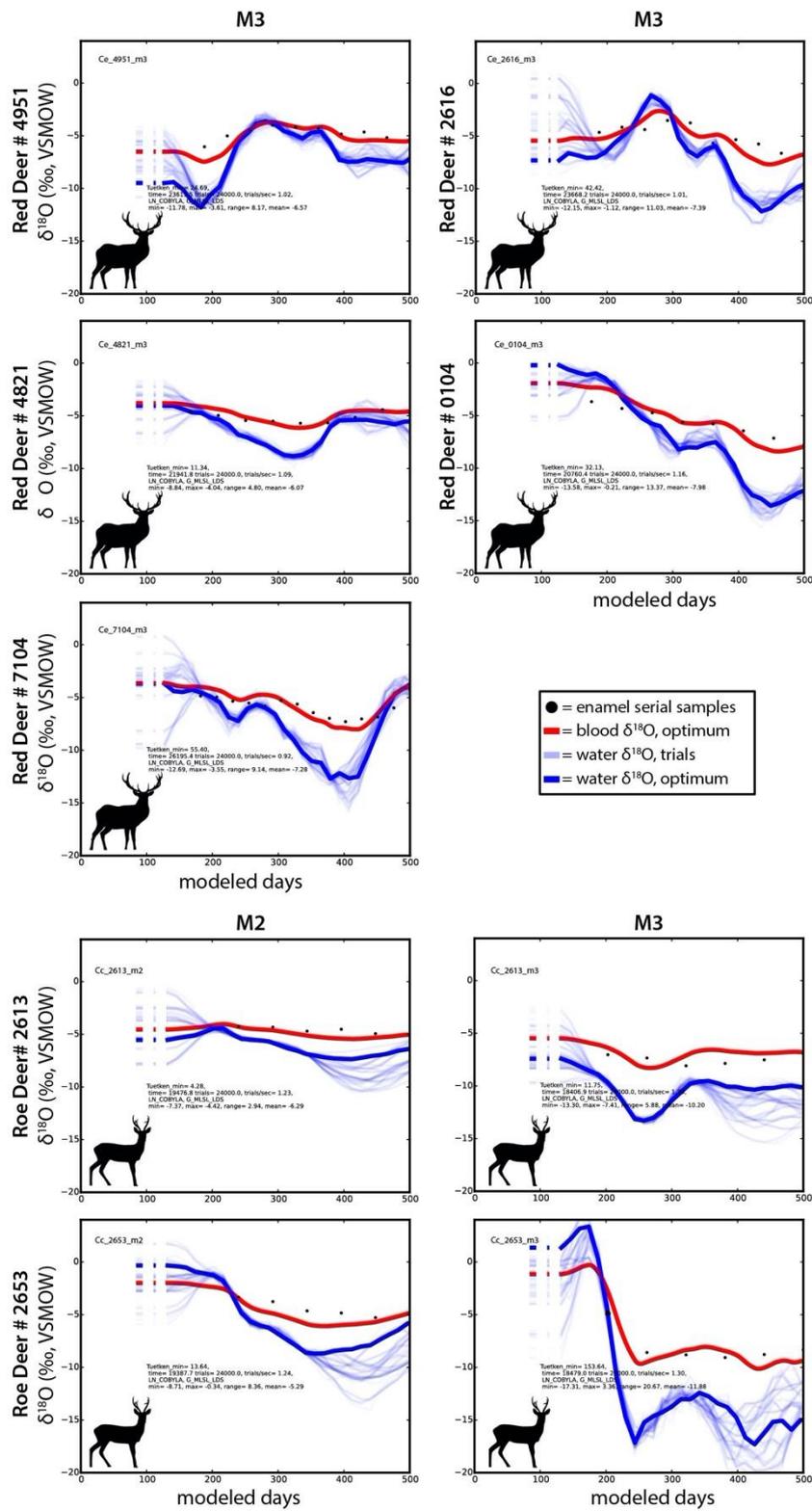


341

342 **Figure S1.** Inverse oxygen isotope input reconstructions for mouflons and chamois
 343 specimens. Measurements of enamel oxygen isotope compositions ($\delta^{18}\text{O}$ ‰, here shown as
 344 phosphate $\delta^{18}\text{O}$ -equivalent on the VSMOW scale, with an estimated PO_4 -water offset of 19.1
 345 ‰ subtracted from each measurement) are made serially down the tooth crown (black
 346 circles). These measurements are combined with a model of tooth formation to infer likely
 347 (light blue) and best guess (dark blue) histories of ingested seasonal $\delta^{18}\text{O}$ compositions in
 348 environmental and plant water. The $\delta^{18}\text{O}$ of blood water over time (red) is also estimated.
 349 Periods of uncertainty resulting from significant tooth wear or limitations in the synchrotron-
 350 based model of enamel formation are affect the earliest and latest days of reconstruction.
 351 Uncertainty also increases towards the end of the tooth, when enamel growth slows and
 352 incorporates ever greater periods of time into smaller spatial increments. Details of inverse
 353 model outcomes including minimum, maximum, and mean oxygen isotope compositions are
 354 listed as text on each reconstruction plot.

355

356



357

358 **Figure S2.** Inverse oxygen isotope input reconstructions for red deer and roe deer specimens.
359 Further details are as described above for Figure S1.

360 2. 4. *Dental microwear texture analysis*

361 The analysis was performed on second lower molars of adult specimens with erupted
362 and worn last third molar and thus the second molar being fully operational. This strict selection
363 of specimens allows us to target adult individuals. Following standard procedures, replicas of
364 the dental facet (disto-buccal facet of the protoconid) were produced with a silicone (medium
365 consistency) polyvinylsiloxane (Coltène Whaledent, President Regular Body, ISO 4823). Scans
366 (320×280 μm) were produced on replicas using the surface profilometer confocal DCM8 Leica
367 Microsystems "TRIDENT" with a 100× lens (Leica Microsystems; Numerical Aperture=0.90;
368 working distance=0.9 mm) at the Paleovoprim lab, CNRS and University of Poitiers, France (see
369 details in Merceron et al., 2016). Lateral resolution is 0.129 μm and vertical spacing is 0.002
370 μm. A 200×200 μm was cropped from the original scans and saved as .Plμ files (Appendix 3
371 provides photosimulations and false color altitudinal maps for every scan analyzed in the
372 present study).

373 After treating surfaces (see supplementary information in Merceron et al., 2016), the
374 Dental Microwear Texture Analysis (DMTA) was performed using the Scale-Sensitive Fractal
375 Analysis using Toothfrax and Sfrax software (Surfract, <http://www.surfract.com>) following
376 Scott et al. (2006). Four variables were extracted from the surface: complexity (Asfc),
377 anisotropy (epLsar), heterogeneity of complexity (HASfc calculated with a 9-cell mesh) and
378 Textural fill volume (Tfv; Table 3; Appendix 2). Complexity (Asfc or Area-scale fractal
379 complexity) is a measure of the roughness at a given scale. Anisotropy (epLsar or exact
380 proportion of length-scale anisotropy of relief) measures the orientation concentration of
381 surface roughness. Heterogeneity of complexity (HASfc or heterogeneity of area-scale fractal
382 complexity), quantifies the variation of complexity of the scanned surface area. These textural
383 parameters are dimensionless. Textural fill volume (Tfv) measures the volume of surface
384 roughness and is expressed in μm³. Dispersion of the values are calculated following Plavcan
385 and Cope (2001) Levene equations as follows:

$$386 \text{Disp-X} = \sum (| \ln(X_i) - (\text{Med}_{1 \rightarrow n}(\ln(X_i))) |)$$

387 where X_i is the value i of the variable X ; Med is the median.

388

389

390

391 **Table S3.** Analyses of variances on the box-cox transformed variables and pairwise
 392 differences for microwear texture parameters (disp-Asfc, epLsar and HASfc_{9-cells}) between
 393 species of ruminants from the Bauges NRP.

Asfc	dof	SS	MS	F	p
Intercept	1	34.19026	34.19026	1648.236	0.000000
Taxa	3	0.11929	0.03976	1.917	0.133718
Residuals	78	1.61800	0.02074		
Total	81	1.73728			
epLsar		SS	MS	F	p
Intercept	1	49715.15	49715.15	527.8888	0.000000
Taxa	3	1420.54	473.51	5.0279	0.003079
Residuals	78	7345.83	94.18		
Total	81	8766.37			
HASfc _{9-cells}		SS	MS	F	p
Intercept	1	3.348500	3.348500	1590.020	0.000000
Taxa	3	0.018368	0.006123	2.907	0.039842
Residuals	78	0.164264	0.002106		
Total	81	0.182632			
Tfv		SS	MS	F	p
Intercept	1	3.888671E+11	3.888671E+11	472.1923	0.000000
Taxa	3	3.281385E+08	1.093795E+08	0.1328	0.940249
Residuals	78	6.423576E+10	8.235354E+08		
Total	81	6.456390E+10			
disp-Asfc		SS	MS	F	p
Intercept	1	1.944057	1.944057	247.0138	0.000000
Taxa	3	0.065820	0.021940	2.7877	0.046121
Residuals	78	0.613878	0.007870		
Total	81	0.679698			
disp epLsar		SS	MS	F	p
Intercept	1	3.407464	3.407464	156.4401	0.000000
Taxa	3	0.051163	0.017054	0.7830	0.506987
Residuals	78	1.698939	0.021781		
Total	81	1.750102			
disp-HASfc _{9-cells}		SS	MS	F	p
Intercept	1	0.286799	0.286799	158.8392	0.000000
Taxa	3	0.003448	0.001149	0.6366	0.593660
Residuals	78	0.140836	0.001806		
Total	81	0.144285			
disp Tfv		SS	MS	F	p
Intercept	1	1.823465	1.823465	163.1278	0.000000
Taxa	3	0.027674	0.009225	0.8252	0.483894
Residuals	78	0.871894	0.011178		
Total	81	0.899568			

394 dof: degree of freedom. SS: sum of squares. MS: mean of squares; F: statistic F; p: probability p.

395

	<i>C. capreolus</i>	<i>C. elaphus</i>	<i>O. gmelini</i>	<i>R. rupicapra</i>
<i>C. capreolus</i>		disp-Asfc (+)	epLsar(+)	
<i>C. elaphus</i>	HASfc (+), disp-Asfc (-)		epLsar (+), HASfc (+)	
<i>O. gmelini</i>	epLsar (-)	epLsar (-), HASfc (-)		
<i>R. rupicapra</i>	epLsar (-), disp-Asfc (-)	epLsar (-), HASfc (-)		

396 Significance at $p < .05$ is indicated below the diagonal for Fisher's LSD tests and above the diagonal for both
 397 Tukey's HSD and Fisher's LSD tests (+ and - indicate how is the value found for the species in row compared to
 398 the one in column)

399

400 After box-cox transformations, one-way analyses of variance (ANOVAs) were
 401 performed for each texture parameter (Table S3). For each significant parameter, pairwise
 402 comparisons were performed using the combination of Tukey’s HSD (Honest Significant
 403 Difference) and the less conservative Fisher’s LSD test (Least Significant Difference; Figure 6;
 404 Table S3). Furthermore, seasonal variations in DMTA are explored on the mouflons as 10 of
 405 them were sampled in late summer/early fall 2015 and 12 others during winter 2009. Seasonal
 406 variations cannot be assessed for the other species as they were not seasonally-balanced
 407 sampled. Values were also box-cox transformed before applying a t-test of Student (Table S4).

408

409 **Table S4.** T test on the box-cox transformed variables from the Dental Microwear Textural
 410 Analysis on the mouflon samples from the Bauges NRP comparing the samples with
 411 specimens sampled at different seasons.

Variable	Group #1: late summer/early fall 2015 Group #2: early winter 2009 & late fall 2009										
	Mean (# 1)	Mean (# 2)	t	dof	p	n (# 1)	n (# 2)	sd (# 1)	sd (# 2)	F-ratio Variances	p Variances
Asfc	1.20	1.22	-0.13	20	0.896	10	12	0.45	0.32	2.04	0.26
epLsar	4.76	4.41	0.69	20	0.494	10	12	1.28	1.09	1.38	0.60
HAsfc	0.27	0.31	-1.16	20	0.258	10	12	0.08	0.08	1.09	0.90
Tfv	87236.3	53578.7	2.97	20	0.007	10	12	21811.7	29626.5	1.84	0.36

412 dof: degree of freedom, t: Statistic t, sd: standard deviation, n: number of individuals, F: Statistic F, p:
 413 probability p, n: sample size.

414

415

416

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Appendix 1. Intra-tooth carbon and oxygen stable isotope compositions of analyzed specimens.

<i>Taxon</i>	specimen	tooth	sample position on tooth	crown height (mm)	distance from apex (mm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
<i>Cervus elaphus</i>	CEM2616	M3	1	27.4	1.2	-16.33	-7.90
			2		3.5	-15.98	-7.43
			3		5.5	-16.37	-7.66
			4		7.7	-15.78	-6.81
			5		9.7	-15.82	-7.04
			6		12.9	-15.45	-8.91
			7		15.8	-15.98	-8.59
			8		18.8	-16.46	-8.99
			9		21.5	-16.24	-9.84
			10		24.0	-16.67	-10.11
	CE0104	M3	1	24.3	1.0	-16.40	-6.98
			2		2.9	-16.27	-7.61
			3		5.6	-16.22	-8.00
			4		9.3	-15.97	-8.88
			5		11.9	-16.09	-9.03
			6		15.3	-16.58	-9.66
			7		18.7	-16.48	-10.35
			8		21.6	-16.89	-10.95
	CE4951	M3	1	21.4	0.0	-16.20	-9.27
			2		1.8	-15.93	-8.27
			3		3.6	-15.36	-7.74
			4		5.7	-15.62	-7.30
			5		8.0	-15.75	-7.46
			6		10.2	-15.50	-7.57
			7		12.5	-15.47	-8.10
			8		14.8	-15.45	-7.91
			9		17.1	-15.74	-8.42
			10		19.3	-16.00	-8.67
	CEF7104	M3	1	28.0	0.8	-16.22	-8.11
			2		2.7	-16.64	-8.22
			3		4.7	-16.22	-8.60
			4		6.6	-16.18	-8.77
			5		8.8	-16.46	-9.05
			6		10.6	-15.77	-8.54
			7		12.6	-15.60	-8.87
			8		14.5	-15.53	-9.66
			9		16.5	-15.91	-10.17
			10		18.7	-15.68	-10.48
			11		20.6	-15.95	-10.23
			12		22.8	-15.71	-10.05
			13		24.7	-16.03	-9.21
			14		26.7	-15.83	-7.54
	CE4821	M3	1	23.5	0.9	-15.74	-7.87
			2		3.0	-15.98	-8.23
			3		5.3	-16.14	-8.70
			4		7.9	-15.89	-8.75
5			10.4		-15.75	-8.95	
6			13.0		-16.19	-8.91	
7			15.7		-16.20	-8.40	
8			18.6		-15.71	-7.69	
9			20.5		-15.57	-8.05	

Appendix 1. continued

Taxon	specimen	tooth	sample position on tooth	crown height (mm)	distance from apex (mm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$		
<i>Ovis arnon</i>	15MO8847	M3	1	40.3	0.6	-15.38	-8.12		
			2		2.8	-15.72	-8.92		
			3		4.6	-16.05	-9.26		
			4		6.7	-16.69	-10.16		
			6		11.5	-16.23	-10.49		
			8		15.9	-16.48	-11.40		
			9		18.0	-17.13	-11.10		
			10		20.5	-16.79	-10.22		
			11		23.1	-16.28	-9.69		
			12		25.4	-16.07	-8.91		
			13		28.0	-15.30	-7.37		
			14		30.7	-14.99	-7.29		
			15		33.4	-15.30	-6.92		
			16		36.2	-15.26	-7.72		
			17		38.9	-15.17	-7.91		
			M2		1	32.6	1.2	-17.34	-11.02
					2		3.1	-17.53	-11.67
		3		5.4	-17.47		-10.67		
		4		8.0	-17.32		-10.97		
		5		10.5	-17.14		-10.72		
		6		12.7	-16.57		-10.10		
		7		15.6	-16.10		-9.48		
		8		17.9	-15.28		-8.67		
		9		20.7	-15.44		-8.15		
	10	22.9		-15.30	-7.56				
	11	25.5		-15.21	-7.57				
	12	28.2		-15.42	-8.94				
	15MO8843	M3	1	36.8	2.5	-14.70	-6.78		
			2		4.4	-14.72	-7.00		
			3		6.8	-15.08	-7.57		
			4		8.8	-14.87	-7.62		
			5		10.6	-14.83	-7.27		
			6		12.4	-15.06	-7.27		
			7		14.4	-15.43	-7.51		
			8		16.3	-15.85	-7.83		
			9		18.6	-16.06	-7.90		
			10		20.4	-16.44	-7.72		
			11		22.6	-16.49	-8.30		
			12		24.9	-16.53	-8.71		
			13		27.3	-16.59	-9.06		
			14		29.4	-16.59	-9.68		
			15		31.8	-16.35	-9.71		
			16		34.1	-15.25	-9.96		
		M2	1	36.8	0.4	-16.54	-8.80		
			2		2.1	-16.63	-9.21		
			3		4.3	-16.59	-9.92		
			4		6.8	-6.85	-7.39		
			5		9.3	-16.96	-10.58		
6			11.9		-16.43	-10.49			
7			14.2		-17.09	-10.99			
8			16.4		-17.16	-11.05			
9			18.9		-16.64	-10.82			
10			20.8		-16.45	-10.50			
11			23.3		-16.70	-10.46			
12			25.3		-16.54	-9.51			
13			27.5		-16.15	-8.59			
14			29.9		-15.90	-7.47			
15			32.2		-15.14	-7.45			
16			34.7		-14.54	-6.68			

Appendix 1. *continued*

<i>Taxon</i>	specimen	tooth	sample position on tooth	crown height (mm)	distance from apex (mm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
<i>Rupicapra rupicapra</i>	15IS8952	M3	1	22.8	1.2	-13.91	-9.15
			2		4.3	-14.54	-9.42
			3		6.6	-14.63	-9.27
			4		8.7	-14.73	-9.17
			5		10.9	-14.63	-8.74
			6		12.9	-14.57	-8.28
			7		15.2	-14.31	-7.58
			8		17.9	-13.84	-7.76
			9		20.4	-14.02	-7.50
		M2	1	20.3	1.0	-14.38	-6.81
			2		3.3	-14.47	-6.72
			3		5.2	-13.95	-7.12
			4		7.5	-14.42	-7.88
			5		9.9	-14.76	-7.92
			6		12.2	-14.42	-6.82
			7		14.3	-14.39	-6.86
			8		16.3	-14.21	-5.71
			9		18.7	-14.62	-6.62
	15IS8932	M3	1	26.6	0.5	-13.68	-7.72
			2		2.5	-13.79	-6.81
			3		4.9	-14.00	-7.10
			4		7.2	-14.00	-7.03
			5		9.7	-14.25	-7.12
			6		12.0	-14.46	-7.66
			7		14.5	-14.39	-7.51
			8		16.7	-14.69	-8.29
			9		19.2	-14.60	-8.35
			10		21.3	-14.70	-8.72
			11		23.6	-14.40	-8.91
		M2	1	26.0	1.5	-14.13	-8.05
2	3.7		-14.77		-8.65		
3	6.2		-14.72		-9.03		
4	8.7		-14.97		-9.24		
5	10.9		-15.17		-9.59		
6	13.3		-14.90		-9.42		
7	15.3		-15.24		-9.36		
8	17.8		-15.23		-9.30		
9	19.7		-14.96		-8.96		
10	22.2	-14.44	-7.98				

Appendix 1. *continued*

<i>Taxon</i>	specimen	tooth	sample position on tooth	crown height (mm)	distance from apex (mm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
<i>Capreolus capreolus</i>	CC2653	M3	1	12.0	0.8	-14.69	-8.17
			2		2.2	-18.69	-11.74
			3		3.8	-18.69	-11.96
			4		5.2	-18.71	-12.21
			5		6.9	-18.63	-11.92
			6		8.7	-18.77	-11.49
		M2	1	11.3	1.1	-18.49	-6.66
			2		2.9	-18.27	-7.06
			3		4.7	-18.10	-7.91
			4		6.5	-18.25	-8.10
			5		8.2	-18.37	-8.53
			6		9.8	-18.70	-9.00
	CC2613	M3	1	10.4	0.7	-17.63	-10.24
			2		2.0	-18.12	-10.54
			3		3.7	-18.65	-11.26
			4		5.3	-18.22	-11.03
			5		6.8	-18.91	-10.70
			6		8.7	-18.70	-10.15
		M2	1	10.4	0.5	-17.04	-7.56
			2		1.7	-16.95	-7.61
			3		3.2	-16.57	-7.98
			4		5.4	-16.31	-7.80
			5		7.3	-16.18	-8.21
			6		9.0	-16.31	-8.31

Appendix 2. List of 82 specimens with individuals values of the dental microwear texture parameters. All analyses were associated with $r^2 > 0.97$, which guarantees the robustness of the complexity calculation. M: male; F: female. DMTA was done on disto-buccal enamel facet of protoconid or hypoconid if the former facet was damaged.

Taxa	Specimen	Sex	Date (d/m/y)	Asfc	epLsar	HAsfc	Tfv	disp Asfc	disp epLsar	disp HAsfc	disp- Tfv2
<i>C. capreolus</i>	CC2611	F	19/9/15	7.58	0.00053	0.41	65541.5	1.15	2.48	0.02	0.56
	CC2183	F	23/9/15	1.74	0.00459	0.57	44994.0	0.01	0.32	0.12	0.18
	CC2637	M	27/9/15	0.90	0.00738	0.53	45588.3	0.35	0.15	0.10	0.19
	CC8624	F	27/9/15	1.67	0.00735	0.50	64059.5	0.01	0.15	0.08	0.53
	CC8640	M	27/9/15	3.49	0.00346	0.44	33042.4	0.51	0.60	0.04	0.13
	CC2184	F	30/9/15	2.23	0.00619	0.30	3624.0	0.17	0.02	0.06	2.34
	CC7122	M	3/10/15	0.41	0.00540	0.32	0.0	0.65	0.16	0.05	10.53
	CC2613	M	4/10/15	2.75	0.00519	0.54	37524.2	0.33	0.20	0.11	0.00
	CC0741	M	11/10/15	9.47	0.00282	0.17	52070.3	1.35	0.81	0.16	0.33
	CC2538	M	18/10/14	1.97	0.00648	0.07	26758.6	0.09	0.02	0.25	0.34
	CC0642	M	20/10/15	1.27	0.00723	0.42	46146.8	0.18	0.13	0.02	0.21
	CC0742	M	24/10/15	1.06	0.00897	0.36	33255.6	0.27	0.35	0.02	0.12
	CC7124	F	31/10/15	1.45	0.00511	0.43	43440.8	0.10	0.21	0.03	0.15
	CC0259	F	22/11/15	1.09	0.00738	0.41	1598.8	0.26	0.15	0.02	3.16
	CC0017	M	29/11/15	5.32	0.00776	0.24	40779.0	0.85	0.20	0.11	0.08
	CC0258	F	16/1/16	0.45	0.00750	0.19	37402.9	0.63	0.17	0.15	0.00
	CC0262	M	17/1/16	0.95	0.01055	0.36	26035.5	0.33	0.51	0.02	0.37
CC0001	M	16/2/16	3.25	0.00508	0.17	48888.4	0.45	0.22	0.17	0.26	
<i>C. elaphus</i>	CE4525	F	4/10/15	1.21	0.00574	0.39	28787.4	0.00	0.01	0.00	0.32
	CE4687	F	11/10/15	1.69	0.00834	0.38	42898.9	0.19	0.37	0.01	0.08
	CE3732	F	17/10/15	1.55	0.00708	0.86	47363.7	0.14	0.20	0.29	0.18
	CE0106	M	18/10/15	0.49	0.00195	0.55	27926.2	0.39	1.09	0.11	0.35
	CE4691	F	22/10/15	1.54	0.00989	0.65	42382.8	0.14	0.54	0.17	0.07
	CE4820	F	22/10/15	1.24	0.00782	0.52	53617.2	0.01	0.30	0.08	0.30
	CE4821	F	22/10/15	1.21	0.00465	0.62	39634.9	0.00	0.22	0.15	0.00
	CE4825	F	22/10/15	0.90	0.00586	0.68	34551.1	0.15	0.01	0.19	0.14
	CE4929	F	22/10/15	1.02	0.00573	0.37	52437.9	0.09	0.01	0.02	0.28
	CE2655	M	24/10/15	0.94	0.00806	0.28	24835.1	0.13	0.33	0.09	0.47
	CE2616	M	26/10/15	2.04	0.00292	0.23	38476.6	0.32	0.68	0.13	0.03
	CE0104	F	31/10/15	0.89	0.00537	0.40	30946.8	0.16	0.07	0.00	0.25
	CE7104	F	31/10/15	1.62	0.00238	2.54	30463.3	0.17	0.89	0.93	0.26
	CE5002	F	5/11/15	2.71	0.00848	0.42	45048.0	0.52	0.38	0.02	0.13
	CE4526	F	8/11/15	1.03	0.00257	0.39	26323.7	0.09	0.81	0.00	0.41
	CE5616	M	12/11/15	1.96	0.00554	0.33	42387.0	0.29	0.04	0.05	0.07
	CE5837	M	15/11/15	0.87	0.00915	0.36	42479.9	0.17	0.46	0.02	0.07
CE2620	M	22/11/15	1.35	0.00826	0.22	41100.1	0.06	0.36	0.13	0.04	
CE4951	F	22/11/15	2.56	0.00110	0.56	42542.5	0.48	1.66	0.11	0.07	
CE0141	F	5/12/15	0.85	0.00578	0.54	13323.6	0.18	0.00	0.10	1.09	
CE4819	F	1/10/15	0.99	0.00920	0.28	27184.6	0.10	0.47	0.09	0.38	
<i>O. gmelini</i>	MO8837	M	11/9/15	2.82	0.00280	0.35	31520.0	0.28	0.02	0.01	0.09
	MO8832	M	21/9/15	2.50	0.00223	0.26	52733.6	0.19	0.25	0.05	0.43
	MO8841	M	21/9/15	1.75	0.00549	0.50	43273.9	0.05	0.65	0.12	0.23
	MO8847	M	22/9/15	3.20	0.00286	0.38	49720.7	0.37	0.00	0.04	0.37
	MO8857	F	25/9/15	1.13	0.00505	0.33	34747.8	0.31	0.57	0.00	0.01
	MO8845	F	9/10/15	1.02	0.00878	0.18	41925.9	0.36	1.12	0.12	0.20
	MO8851	F	9/10/15	0.72	0.00279	0.27	33061.6	0.52	0.02	0.05	0.04
	MO8849	F	28/10/15	1.01	0.00994	0.15	62871.9	0.37	1.25	0.14	0.60
	MO8833	M	30/10/15	3.77	0.00218	0.30	45893.7	0.50	0.27	0.03	0.29
MO8843	M	30/10/15	2.36	0.00065	0.30	35142.6	0.15	1.48	0.03	0.02	

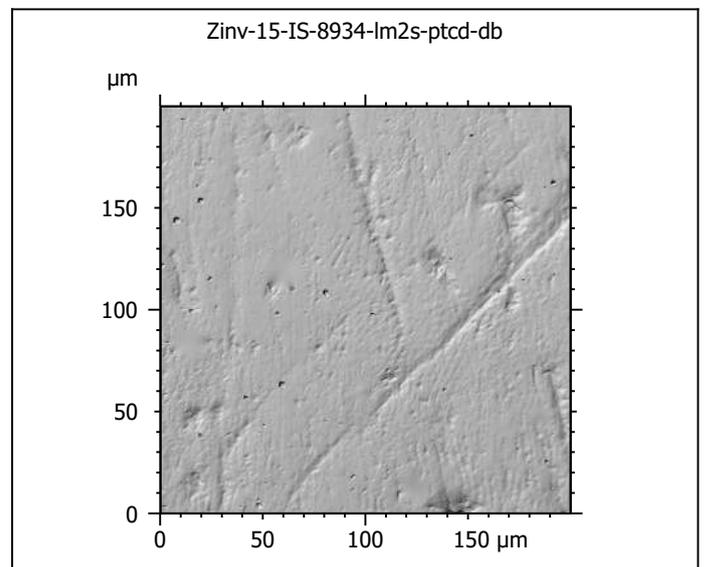
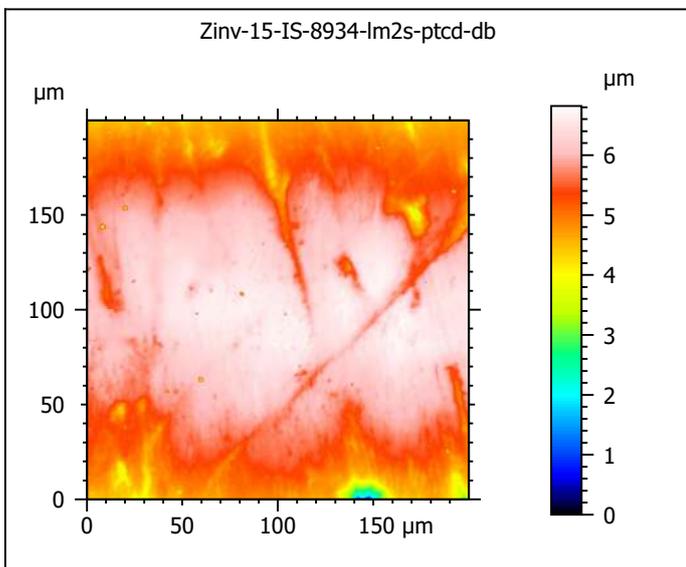
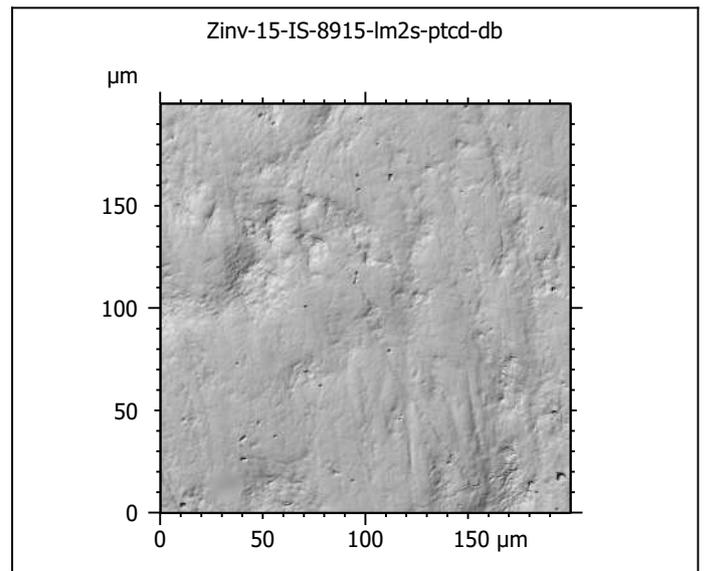
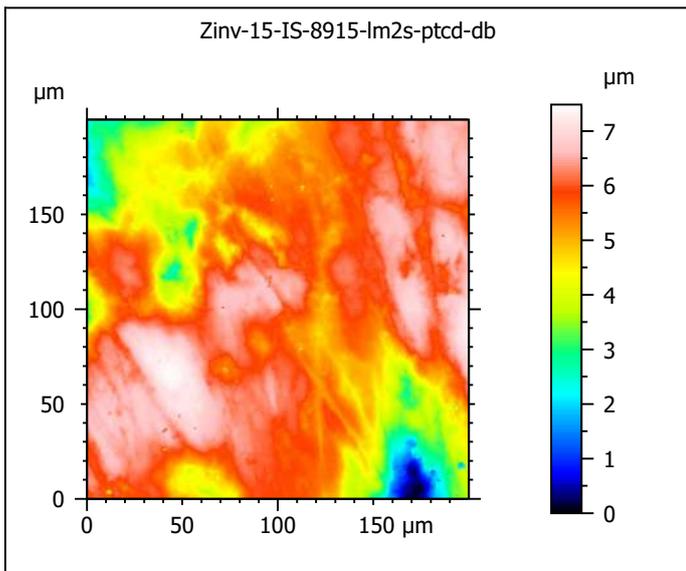
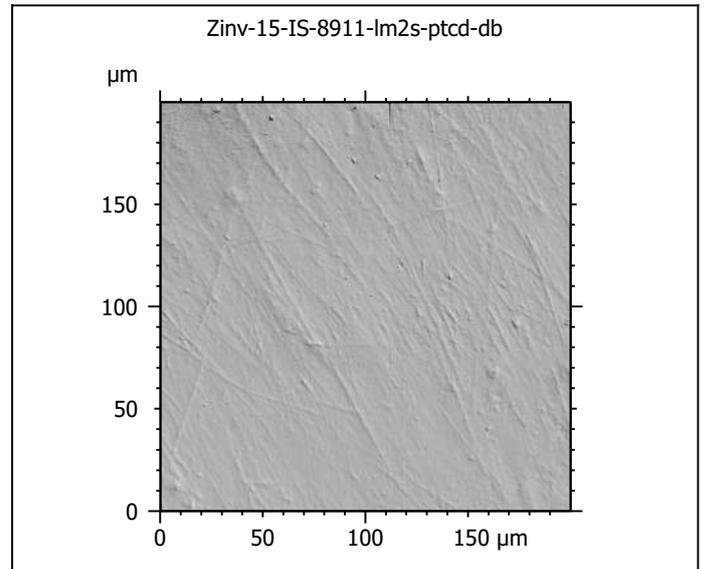
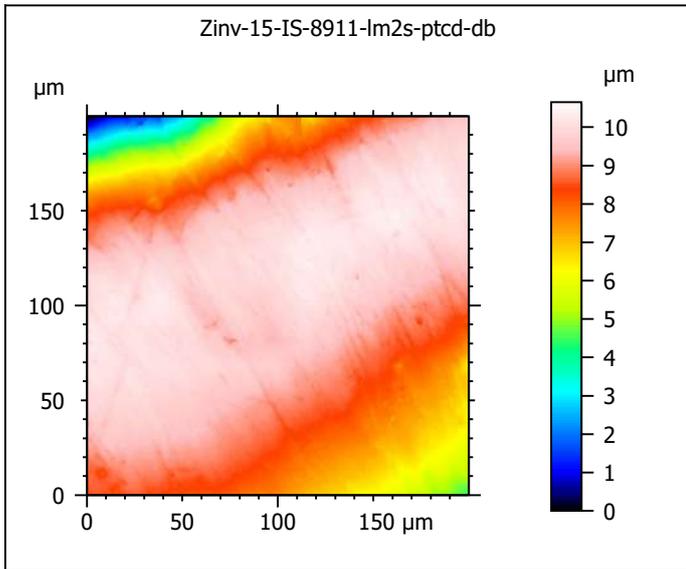
Taxa	Specimen	Sex	Date (d/m/y)	Asfc	epLsar	HAsfc	Tfv	disp Asfc	disp epLsar	disp HAsfc	disp- Tfv2
<i>O. gmelini</i>	MO0007	M	8/1/09	2.01	0.00117	0.50	34291.8	0.04	0.89	0.12	0.00
	MO0013	F	9/2/09	1.50	0.00736	0.19	15881.7	0.14	0.95	0.12	0.77
	MO0008	F	15/1/09	3.35	0.00314	0.34	25049.6	0.41	0.10	0.00	0.32
	MO0015	M	14/2/09	2.83	0.00520	0.50	27146.2	0.28	0.60	0.12	0.24
	MO0017	F	16/2/09	2.62	0.00096	0.40	55256.3	0.22	1.09	0.05	0.47
	MO0018	M	19/2/09	2.77	0.00275	0.27	36637.5	0.26	0.04	0.05	0.06
	MO0010	M	24/1/09	1.78	0.00284	0.21	1065.9	0.04	0.01	0.10	3.47
	MO0020	F	11/3/09	1.57	0.00285	0.38	31646.3	0.12	0.00	0.04	0.08
	MO0021	F	11/3/09	2.03	0.00118	0.36	31841.6	0.05	0.88	0.02	0.08
	MO0022	F	12/3/09	1.53	0.00419	0.39	6715.1	0.13	0.38	0.05	1.63
	MO0024	F	16/3/09	1.32	0.00169	0.43	34534.7	0.22	0.52	0.07	0.00
	MO0025	F	27/3/09	0.81	0.00664	0.26	25048.3	0.47	0.84	0.05	0.32
<i>R. rupicapra</i>	IS8911	M	3/9/15	0.79	0.00518	0.39	38168.2	0.37	0.19	0.06	0.02
	IS8915	M	10/9/15	1.59	0.00381	0.30	33961.0	0.00	0.11	0.01	0.13
	IS8934	M	11/9/15	1.29	0.00264	0.19	41859.5	0.12	0.48	0.09	0.08
	IS8621	M	16/9/15	1.70	0.00671	0.15	38371.4	0.04	0.45	0.13	0.01
	IS8944	M	21/9/15	1.82	0.00444	0.21	10125.9	0.08	0.04	0.08	1.34
	IS8929	F	21/9/15	1.33	0.00175	0.31	38788.5	0.11	0.89	0.00	0.00
	IS8932	M	21/9/15	2.32	0.00079	0.26	38832.5	0.25	1.68	0.04	0.00
	IS8943	M	21/9/15	3.43	0.00412	0.61	43862.2	0.54	0.03	0.21	0.12
	IS8884	F	25/9/15	1.01	0.00683	0.33	47498.2	0.25	0.47	0.01	0.20
	IS8891	F	25/9/15	1.67	0.00458	0.21	47669.3	0.03	0.07	0.08	0.21
	IS8892	F	25/9/15	1.12	0.00728	0.23	52005.5	0.20	0.54	0.06	0.29
	IS8940	F	1/10/15	0.65	0.00564	1.04	26647.1	0.45	0.28	0.44	0.38
	IS8878	F	9/10/15	1.53	0.00427	0.27	45365.9	0.02	0.00	0.03	0.16
	IS8939	F	9/10/15	1.85	0.00398	0.33	8846.8	0.10	0.07	0.02	1.48
	IS8638	M	24/10/15	3.38	0.00386	0.41	35336.9	0.53	0.10	0.08	0.09
	IS8913	F	9/11/15	1.62	0.00510	0.50	49291.0	0.01	0.18	0.14	0.24
	IS8885	M	10/11/15	2.49	0.00426	0.27	37838.9	0.30	0.00	0.03	0.02
	IS8960	F	10/11/15	4.55	0.00051	0.88	39707.6	0.76	2.12	0.36	0.02
	IS2643	F	2/12/15	1.38	0.00370	0.55	52855.0	0.08	0.14	0.17	0.31
	IS2647	F	19/12/15	0.85	0.00419	0.40	32509.5	0.34	0.02	0.07	0.18
IS0001	M	15/3/09	1.27	0.00588	0.31	10019.3	0.13	0.32	0.00	1.35	

Appendix 3. Photosimulations and false color elevation map of the dental surfaces scanned on the disto-buccal facets of the protoconid or hypoconid on the second lower molars of roe deer, red deer, chamois and mouflons.

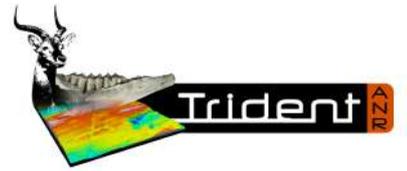
Photosimulations and false color elevation maps of scanned molar facets
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Park, France
scanned at the PALEVOPRIM lab by G. Merceron , CNRS and University of
Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



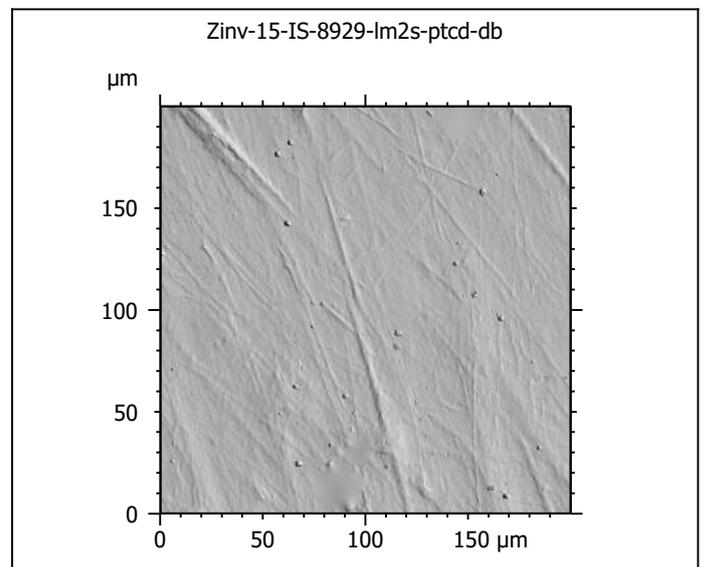
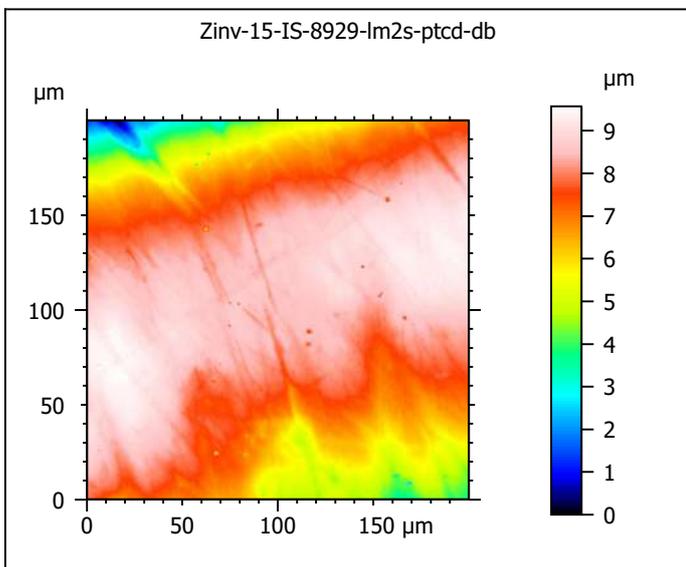
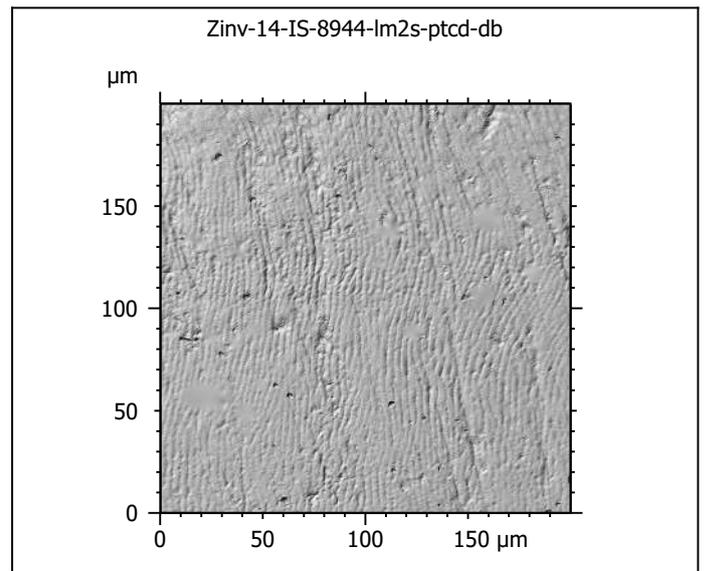
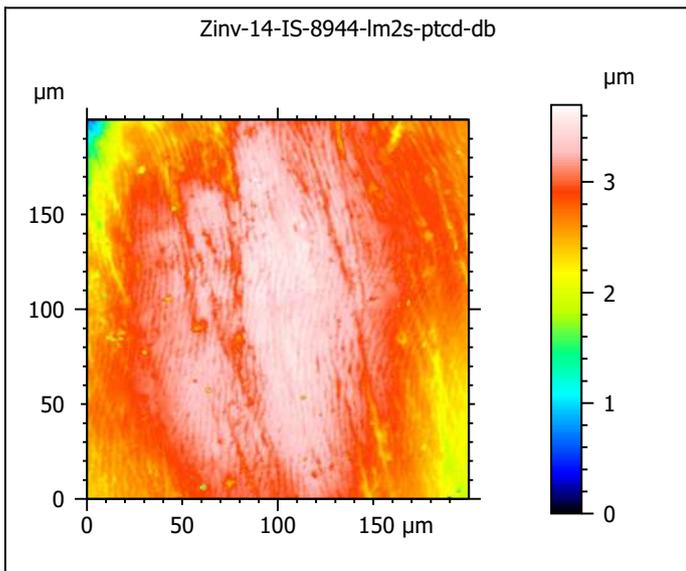
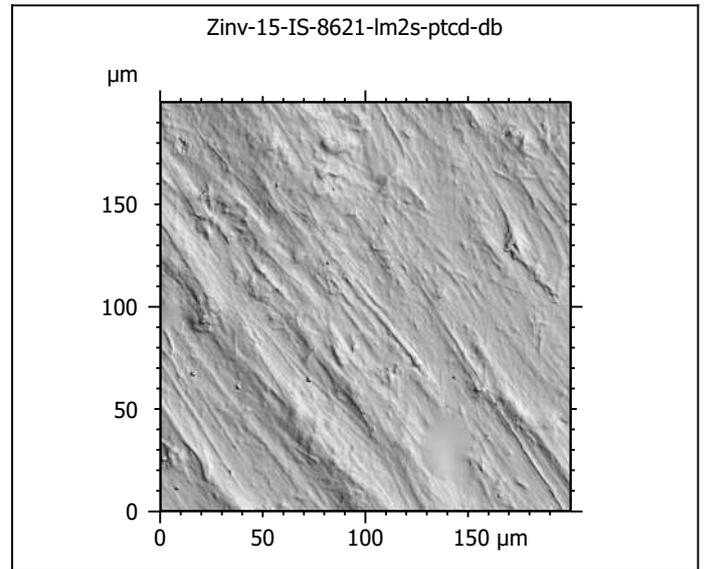
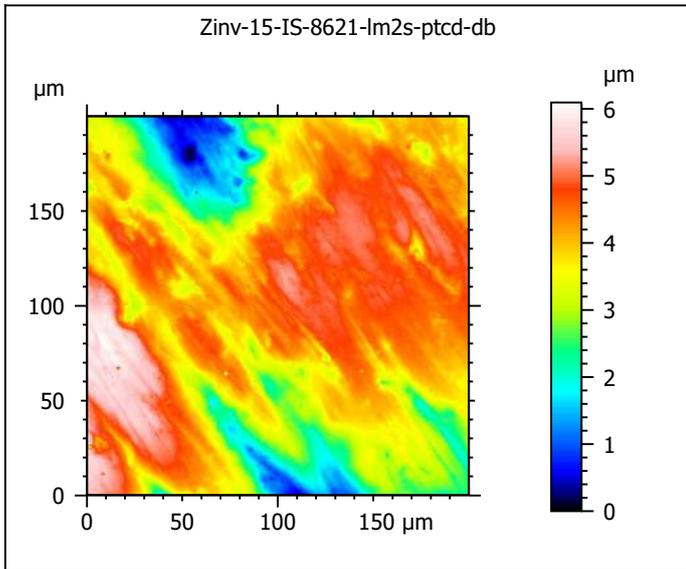
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the chamois (*Rupicapra rupicapra*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



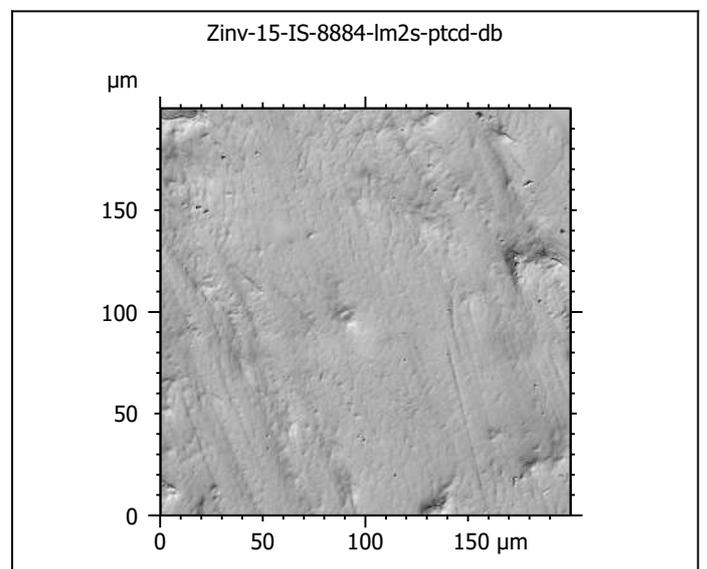
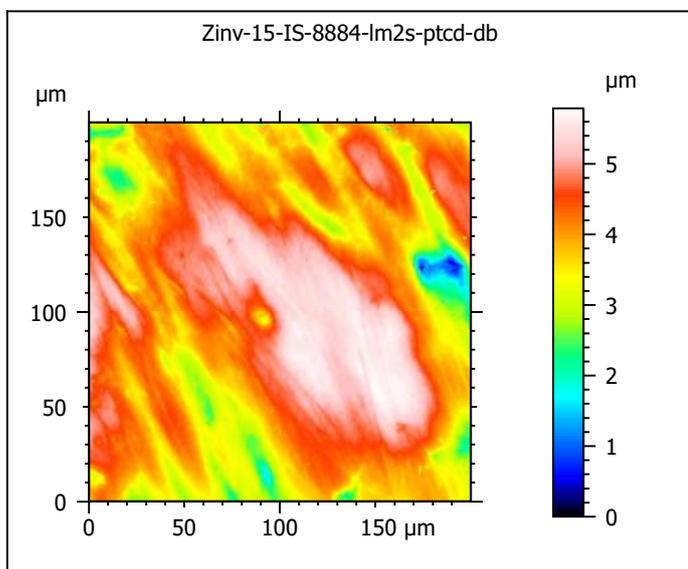
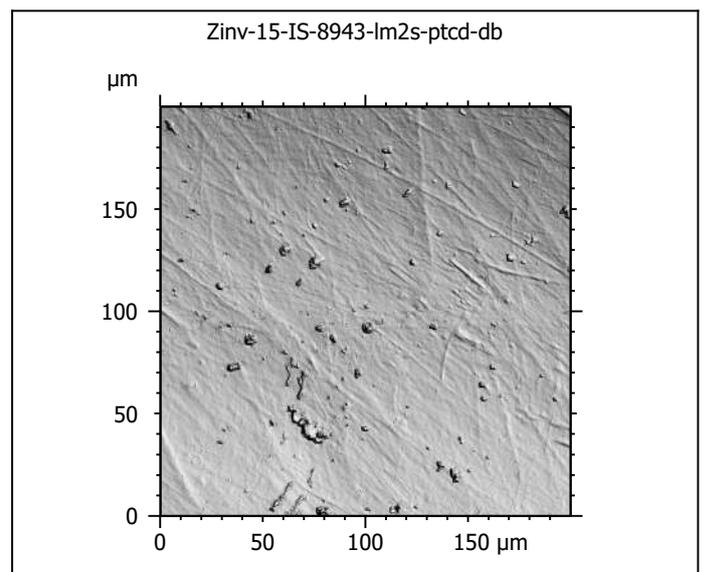
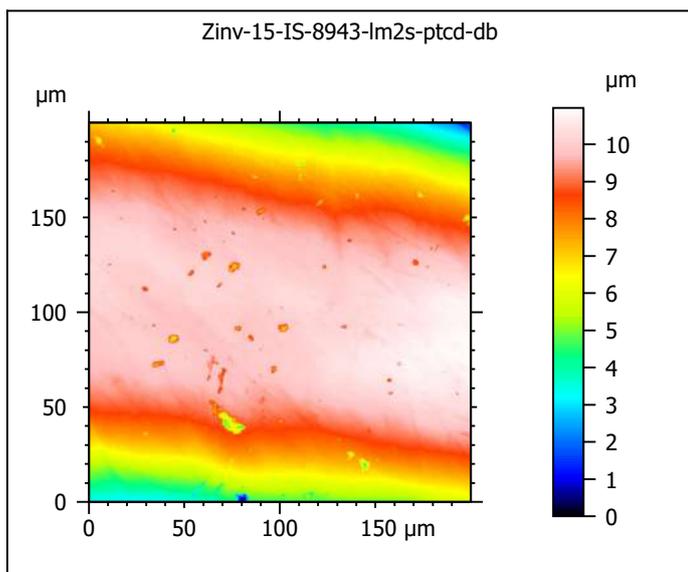
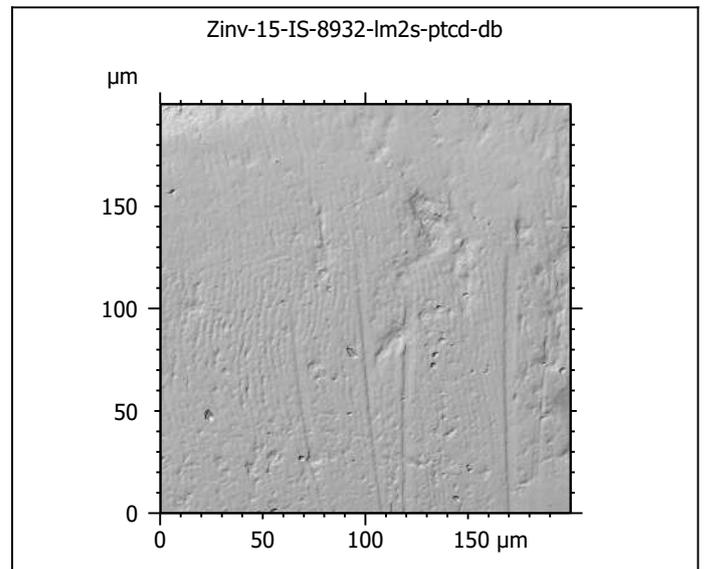
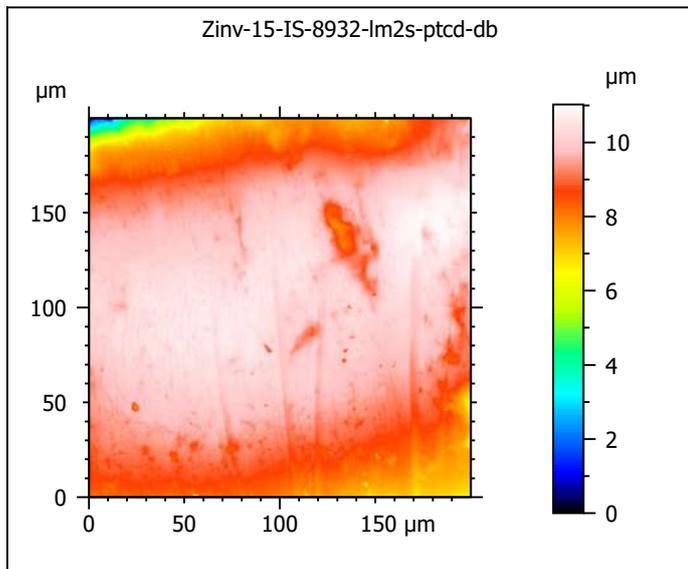
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the chamois (*Rupicapra rupicapra*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



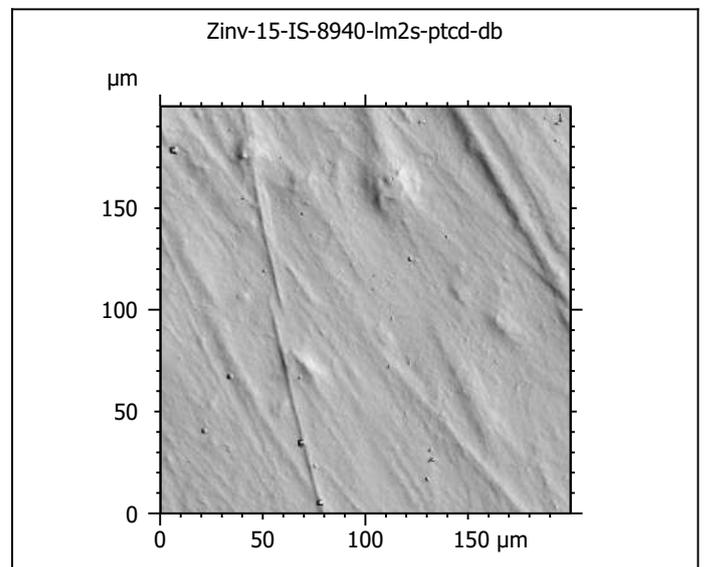
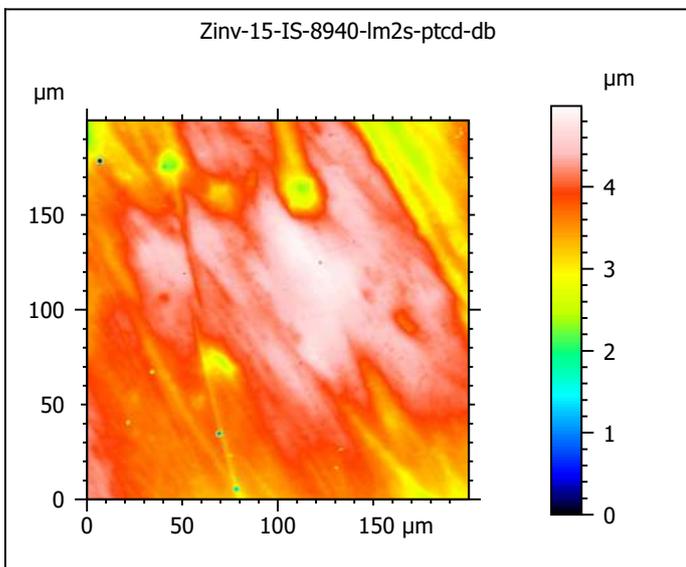
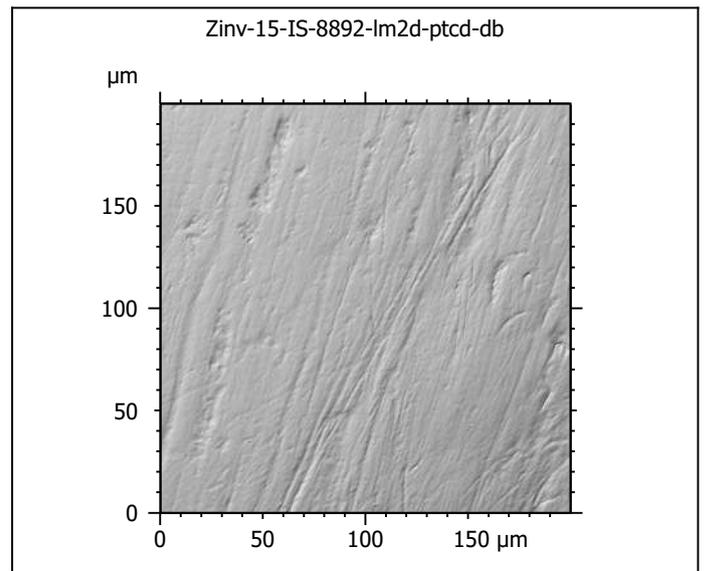
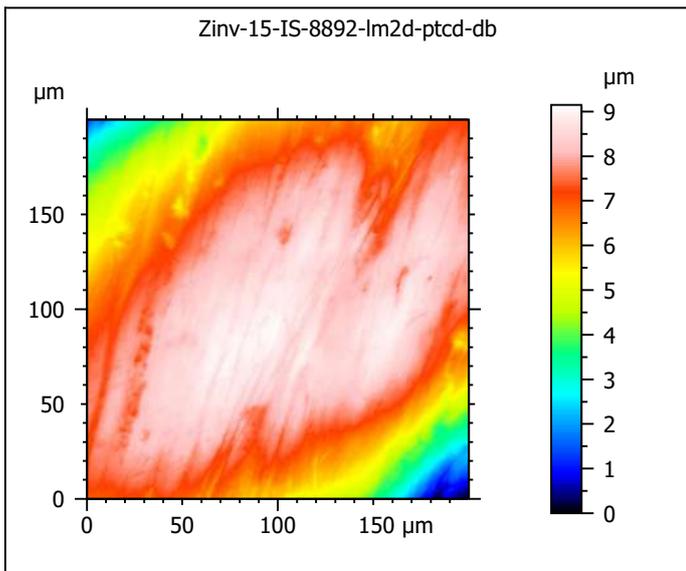
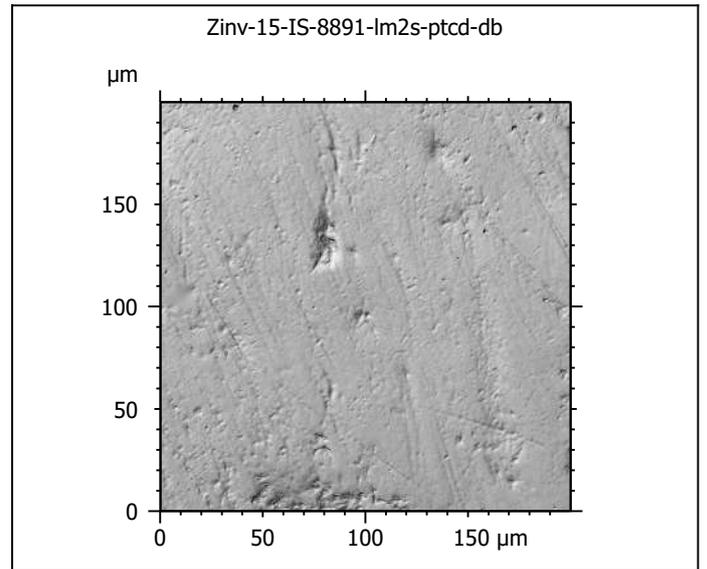
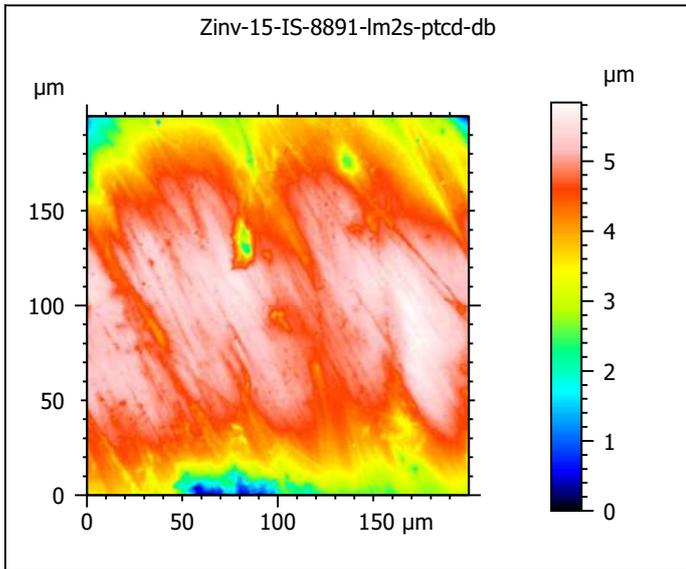
ANR-13-JSV7-0008-01, PI: G. Merceron



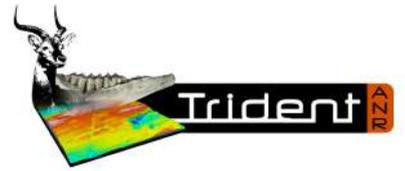
Photosimulations and false color elevation maps of scanned molar facets
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scanned at the PALEVOPRIM lab by G. Merceron , CNRS and University of
Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



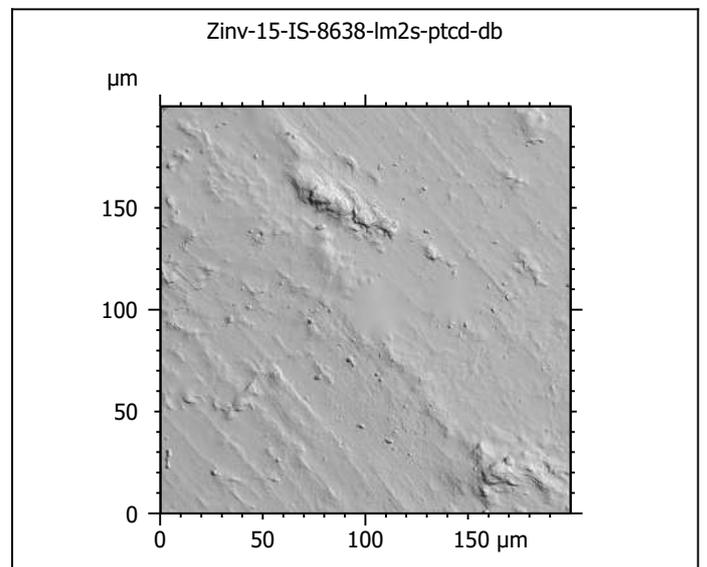
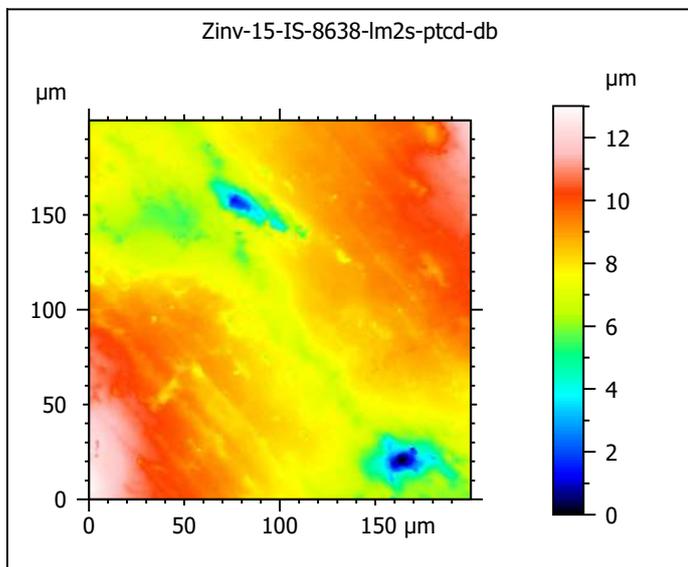
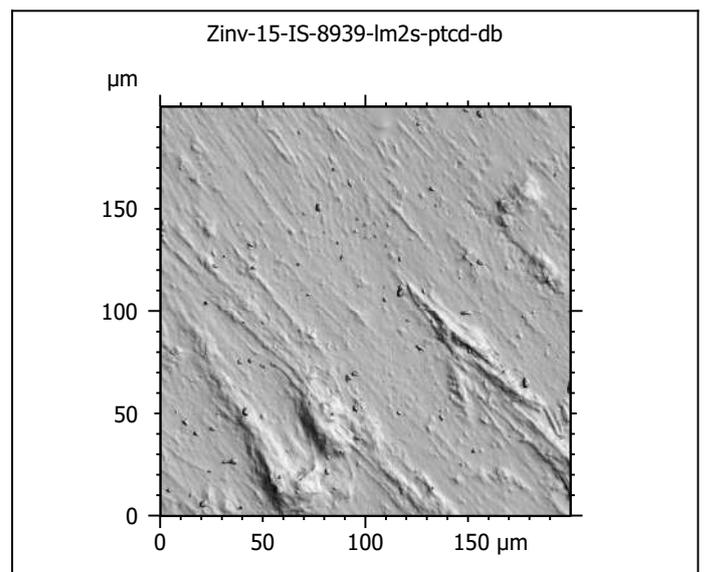
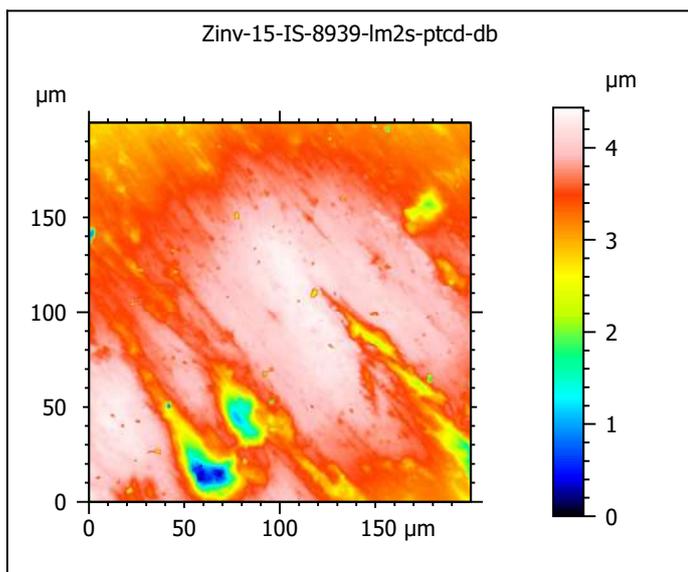
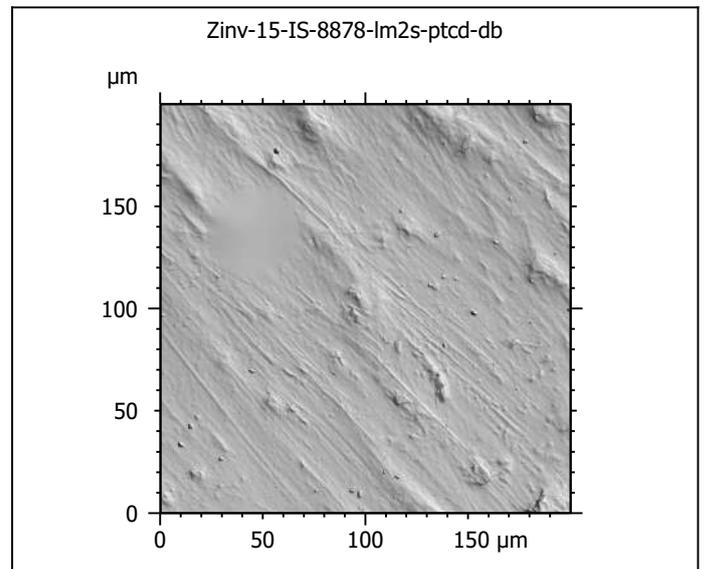
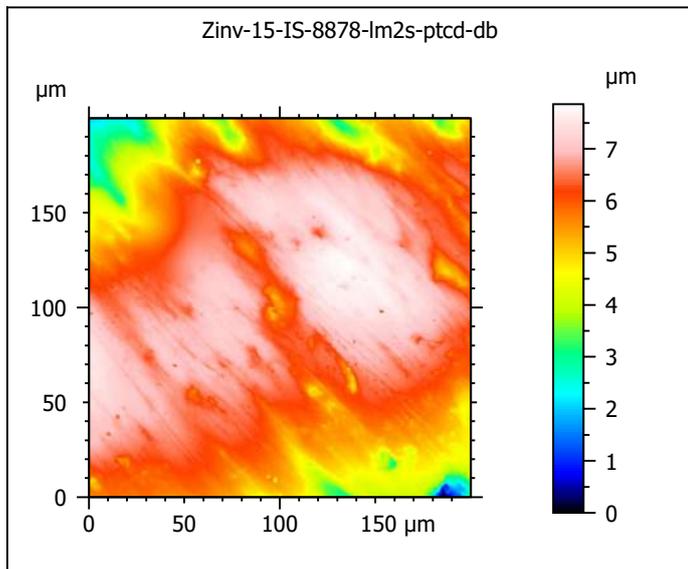
ANR-13-JSV7-0008-01, PI: G. Merceron



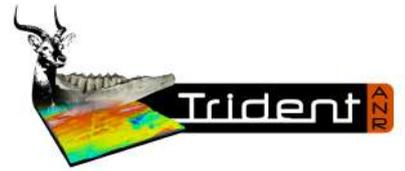
Photosimulations and false color elevation maps of scanned molar facets of the chamois (*Rupicapra rupicapra*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



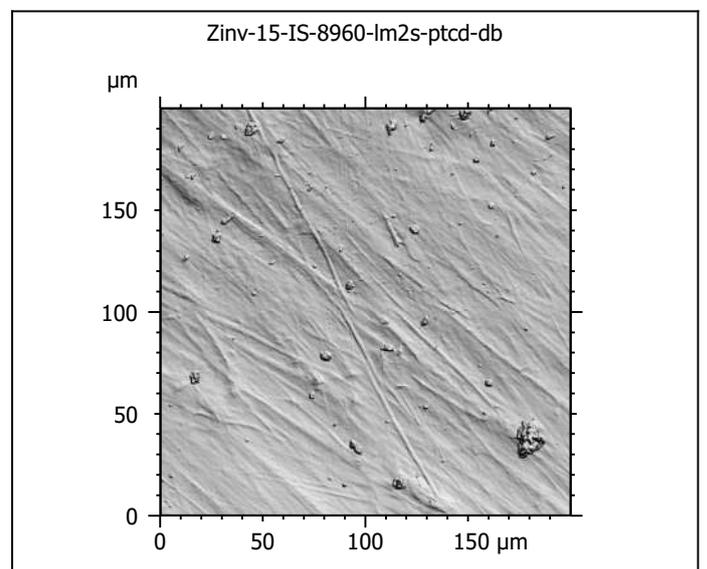
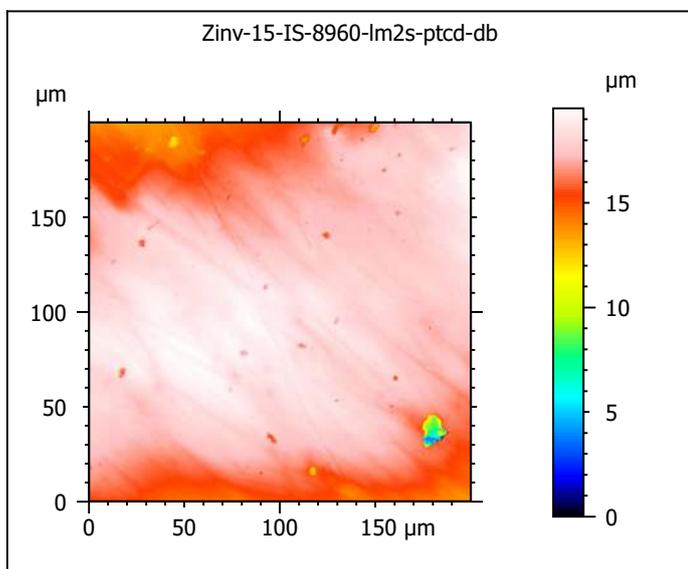
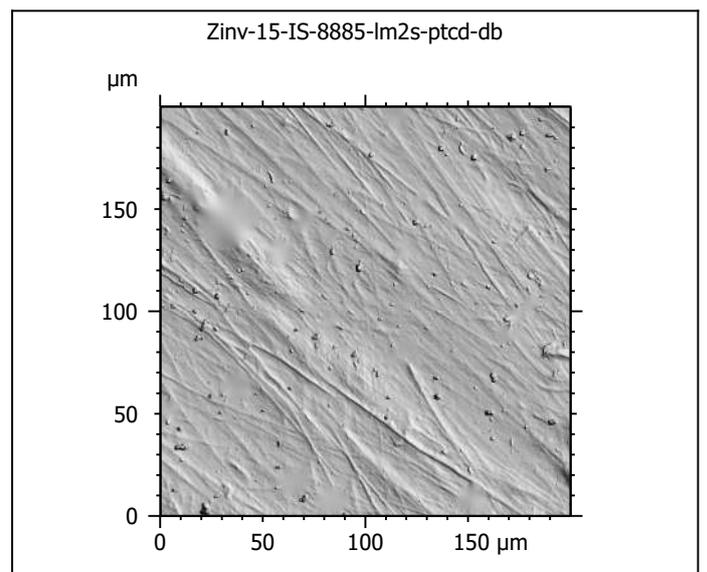
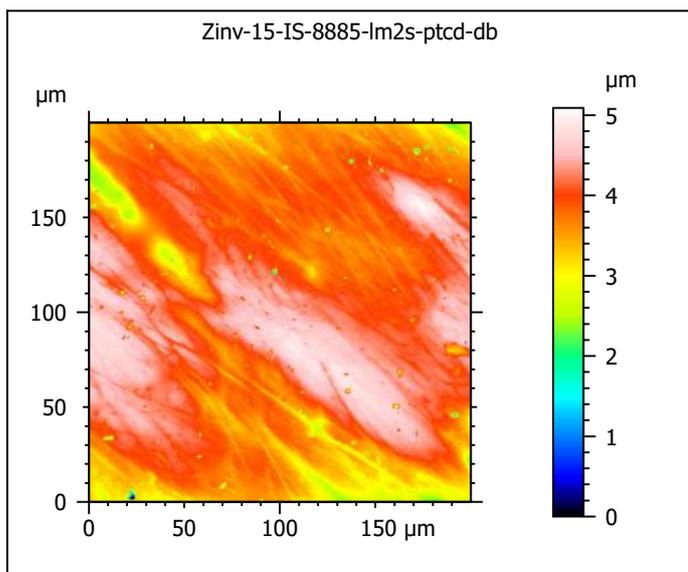
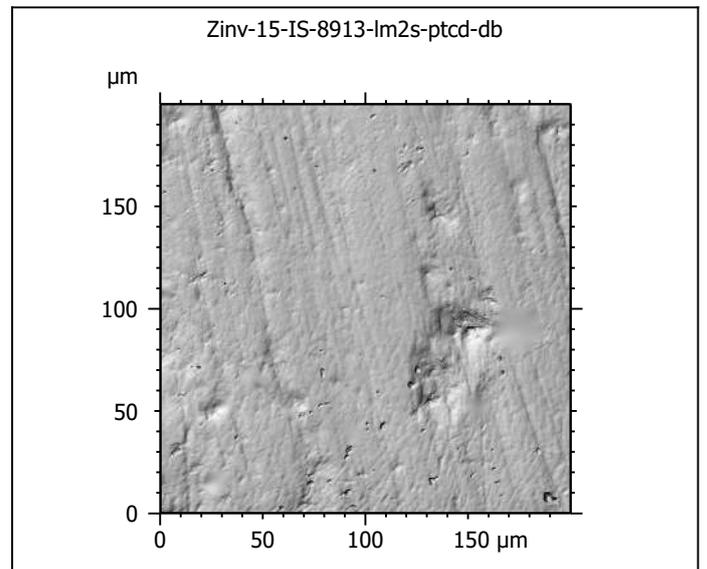
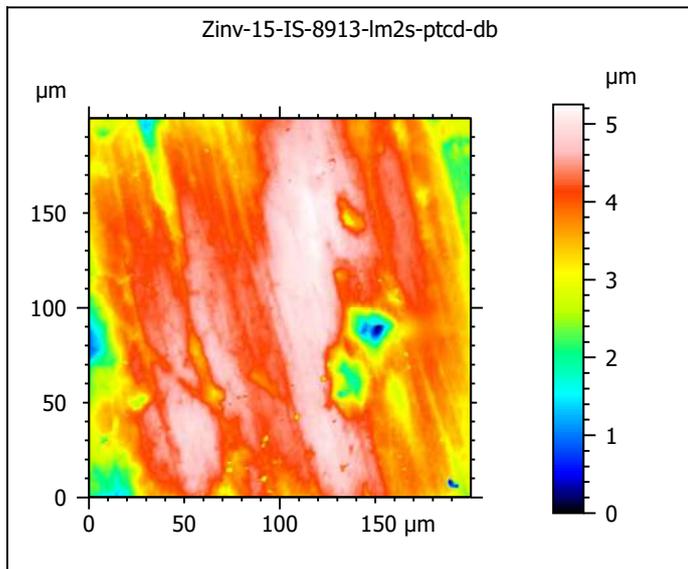
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the chamois (*Rupicapra rupicapra*) from the Bauges Natural Regional Park, France
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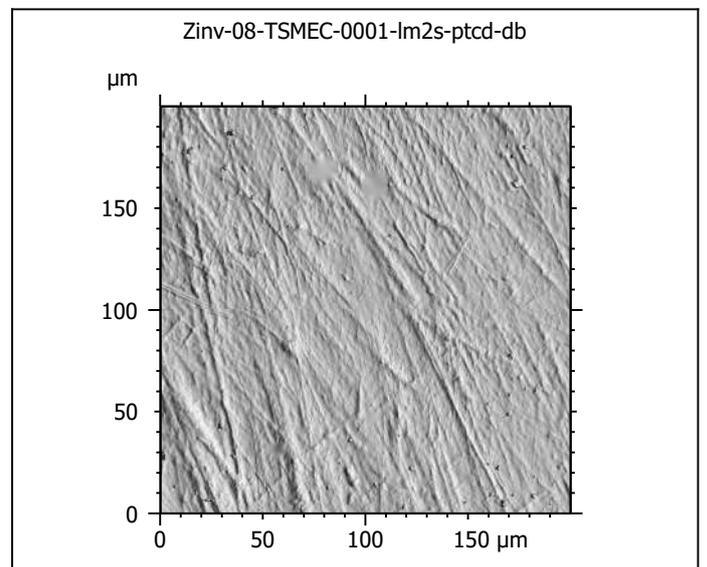
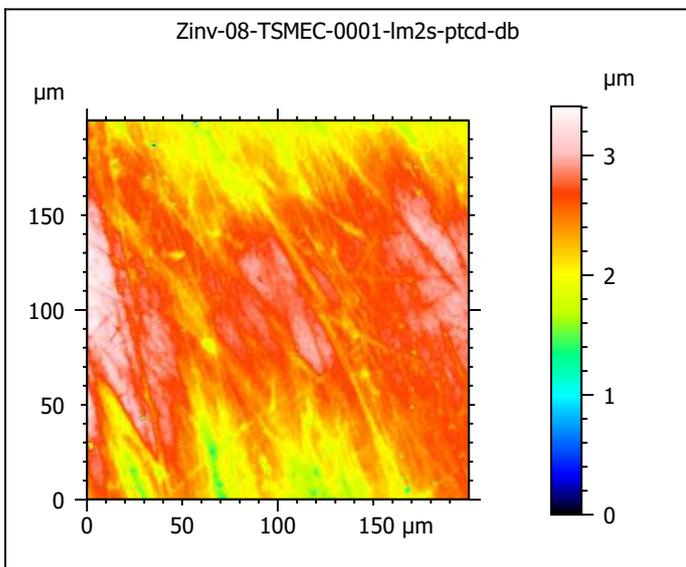
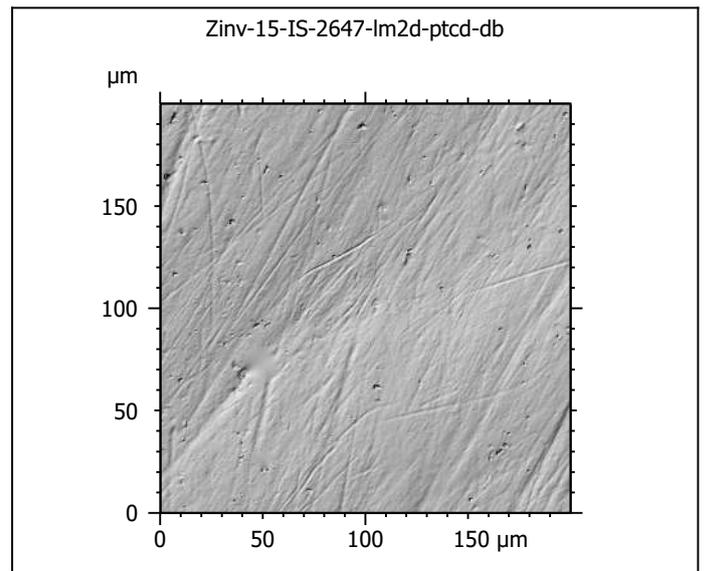
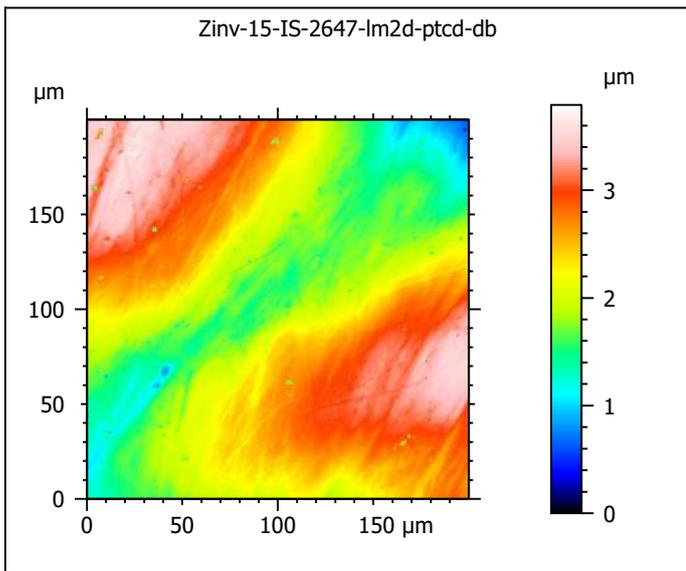
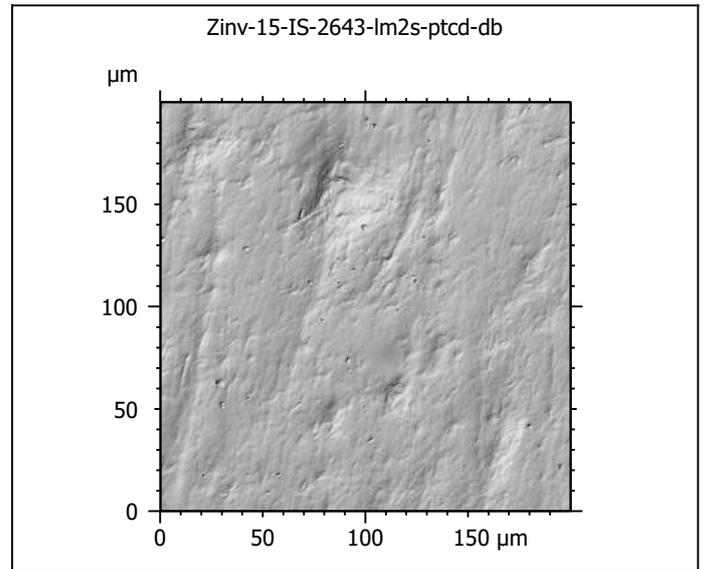
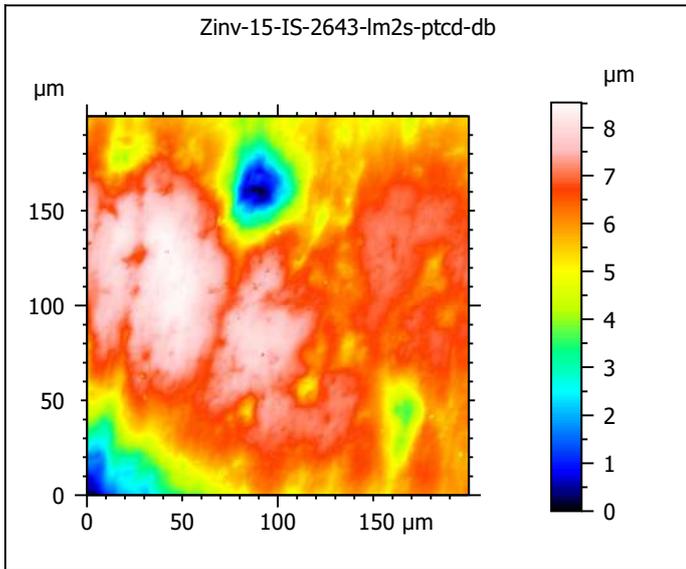
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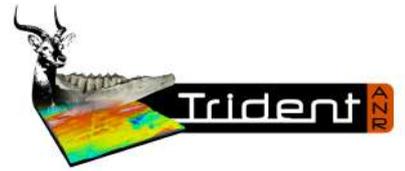
Photosimulations and false color elevation maps of scanned molar facets of the chamois (*Rupicapra rupicapra*) from the Bauges Natural Regional Park, France
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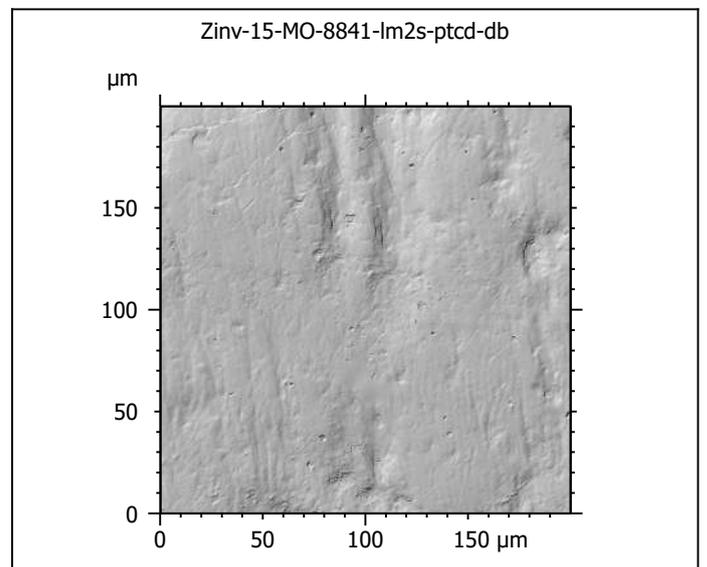
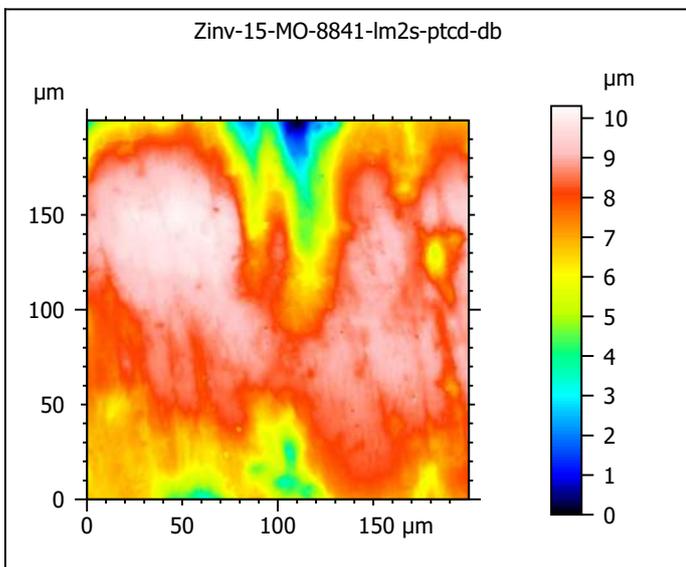
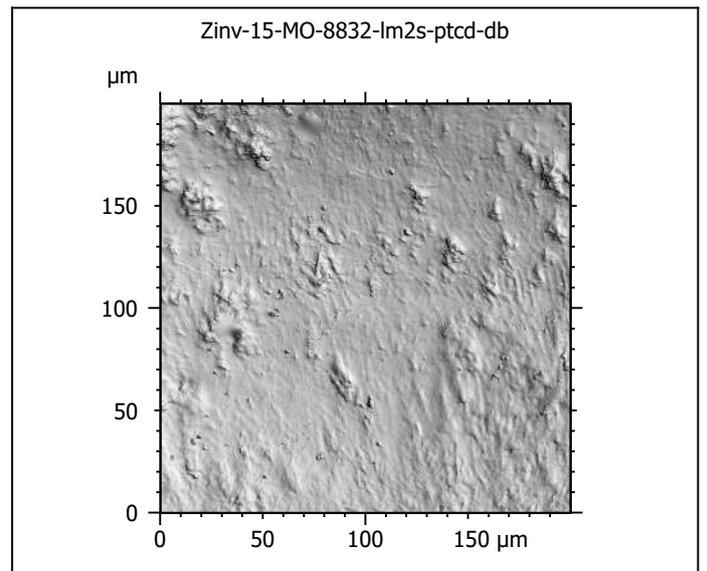
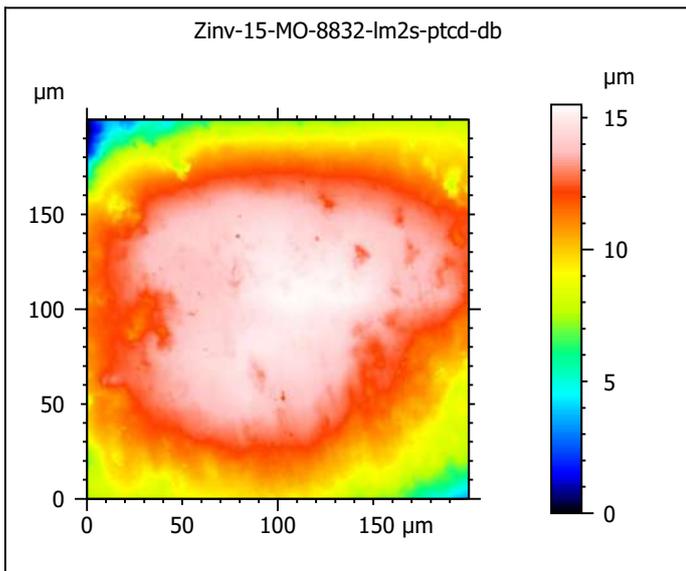
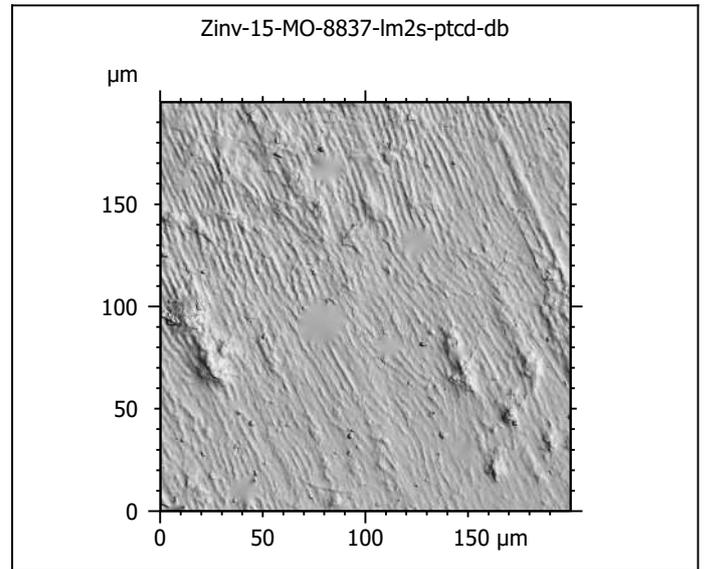
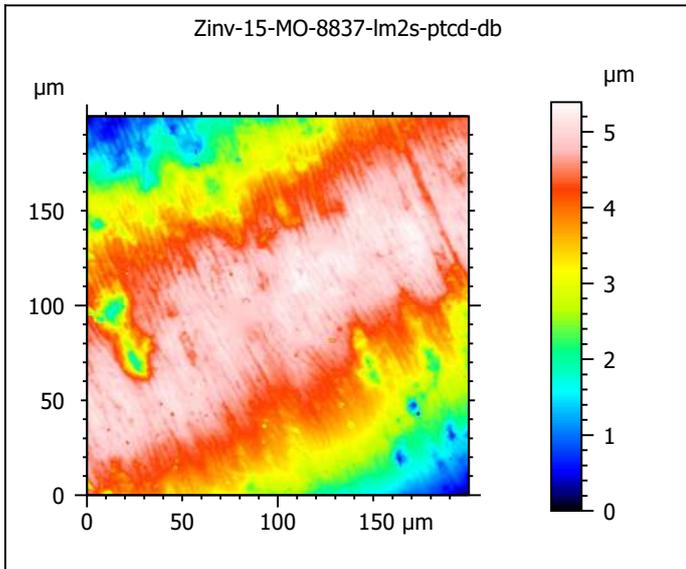
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



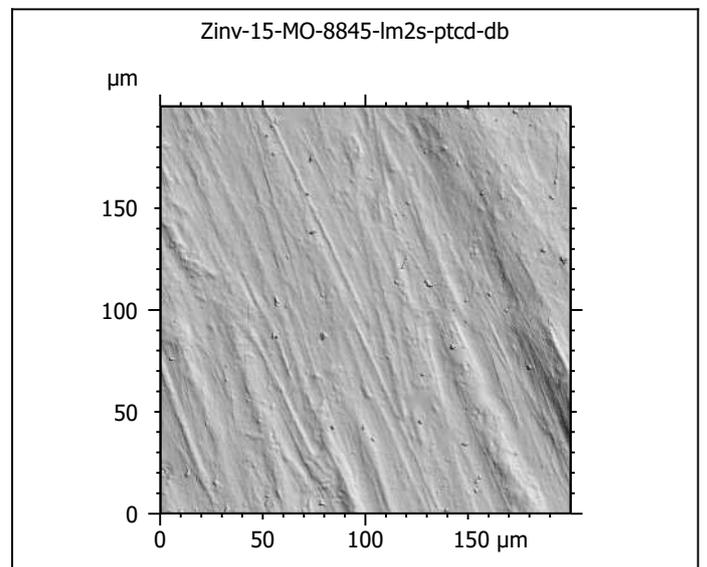
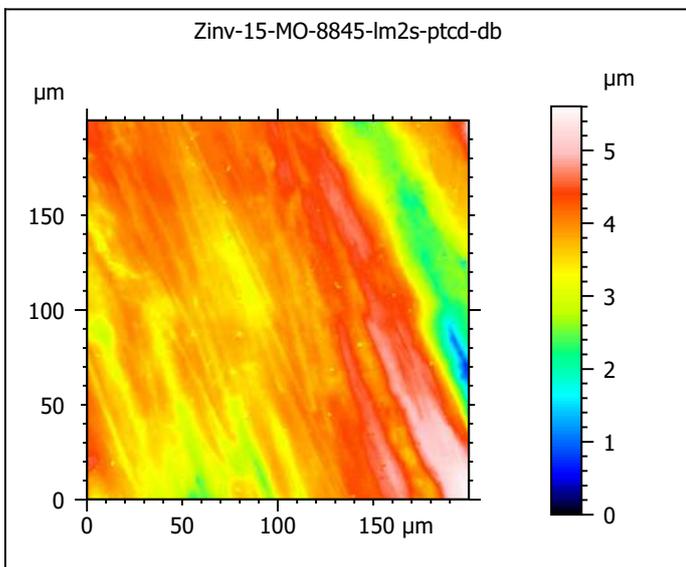
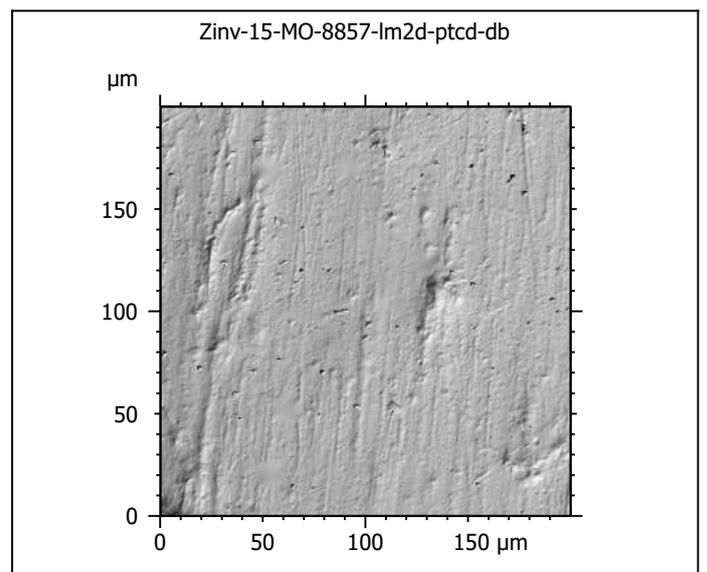
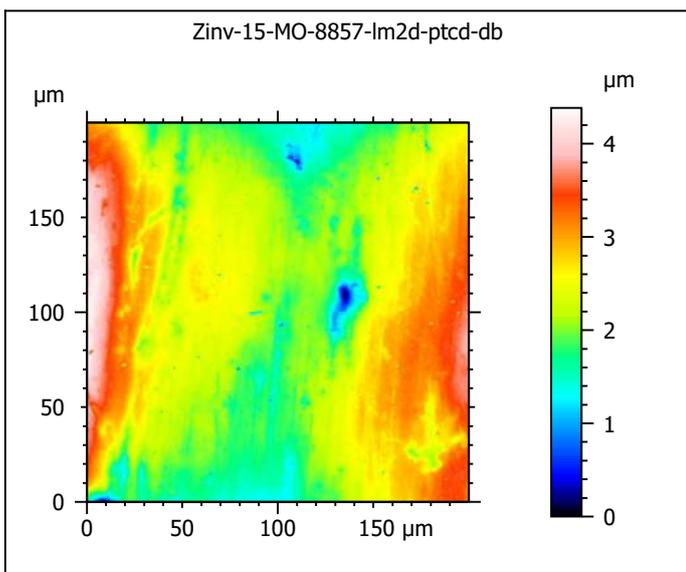
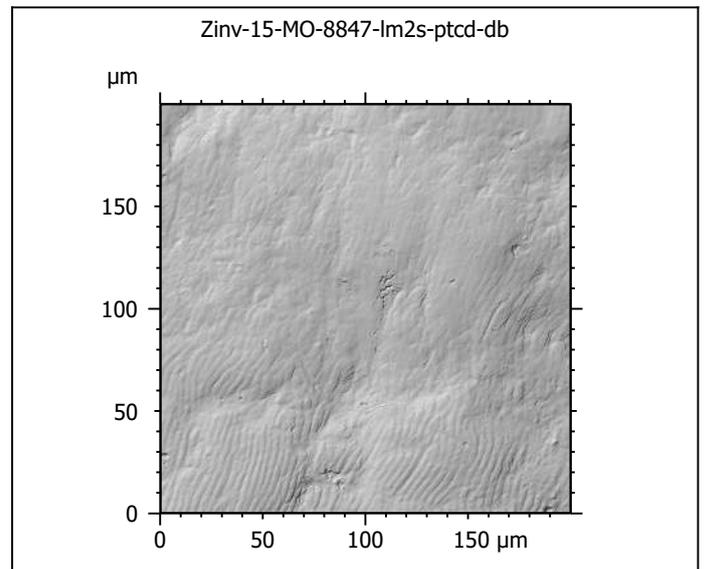
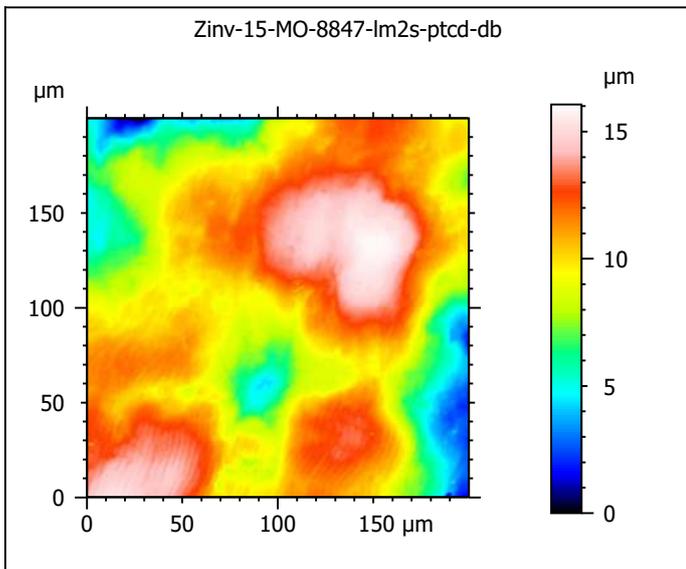
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets
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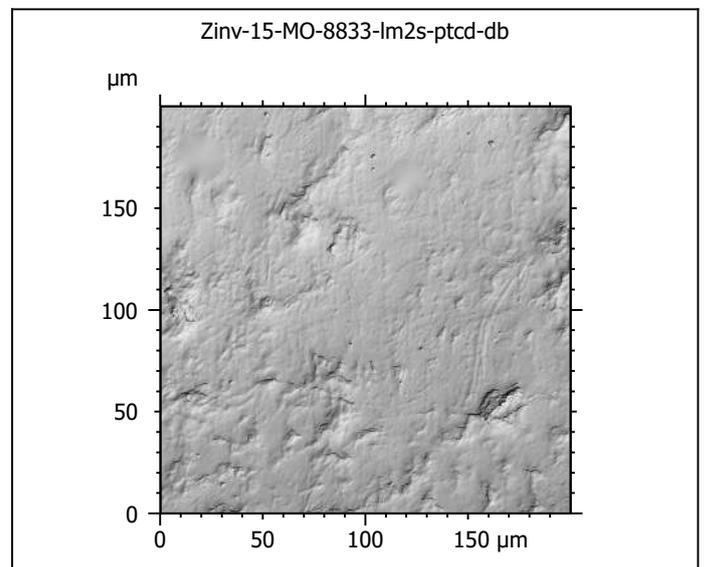
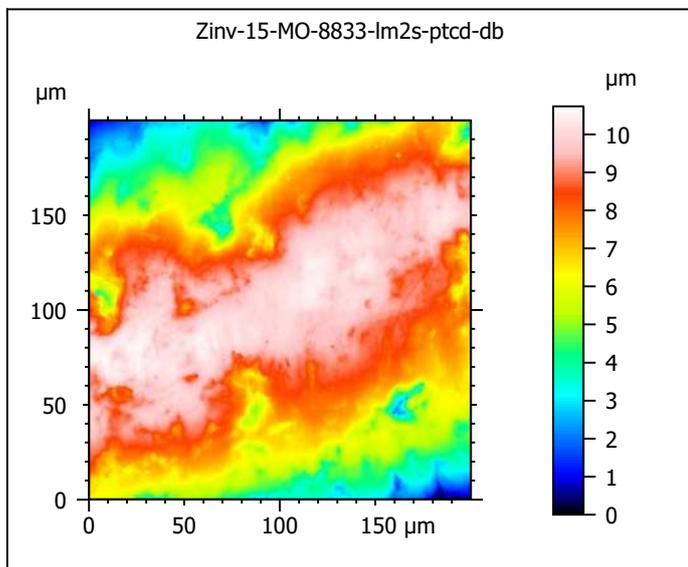
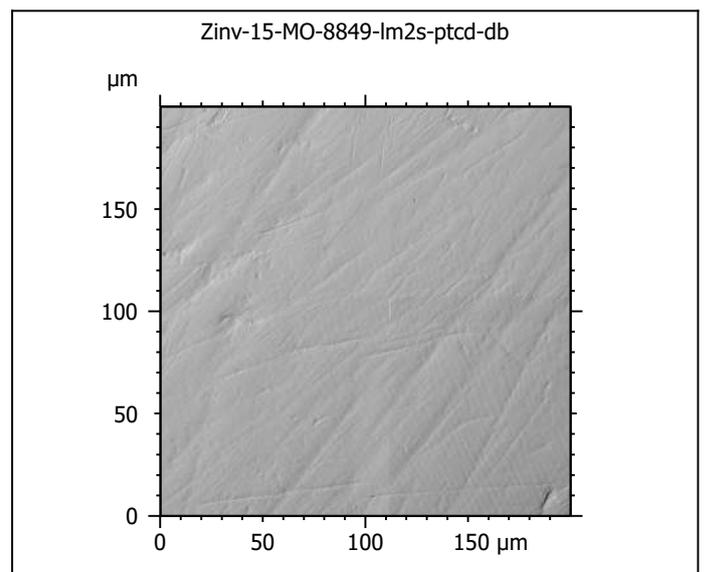
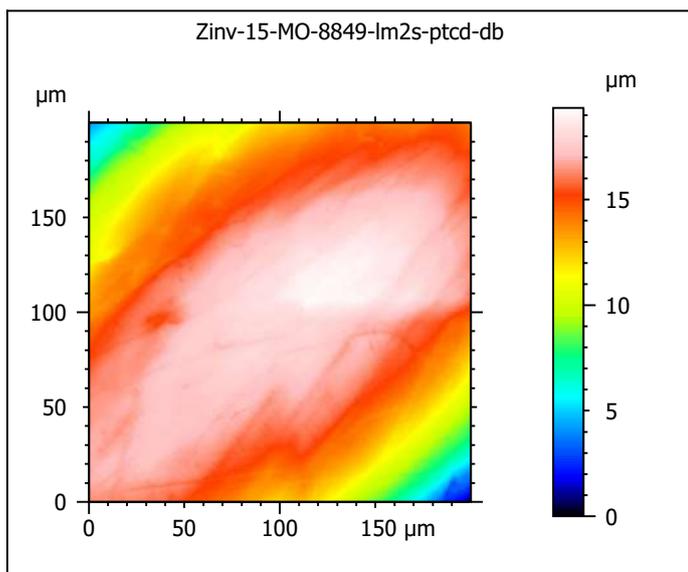
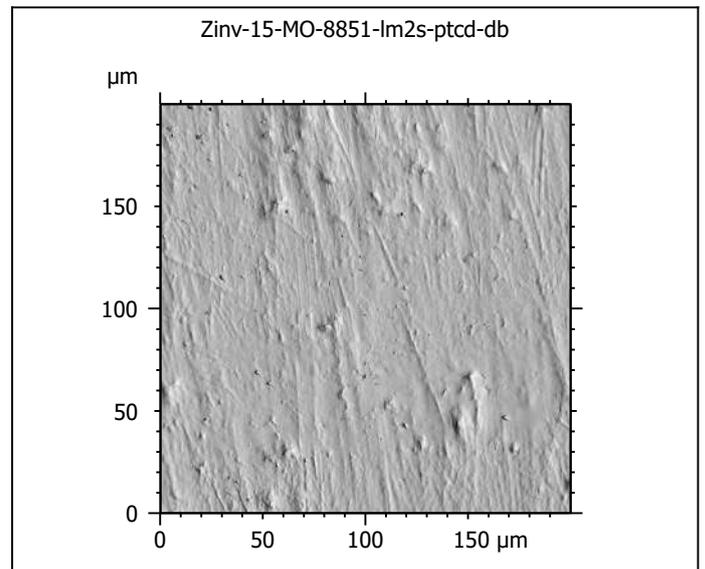
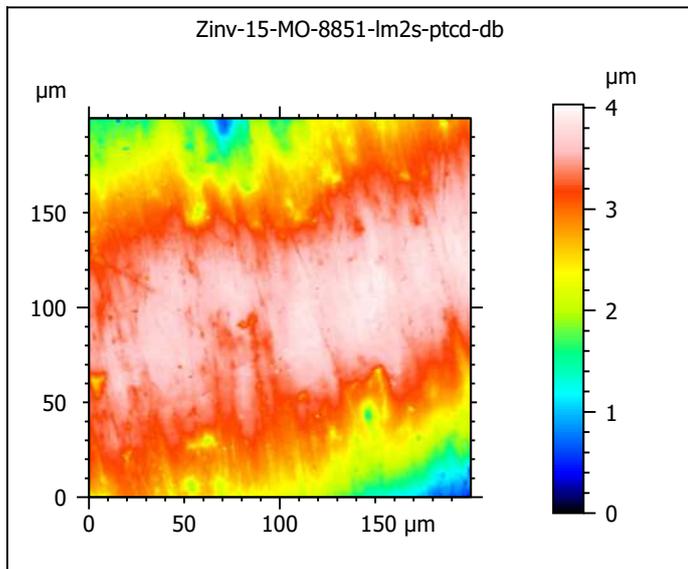
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



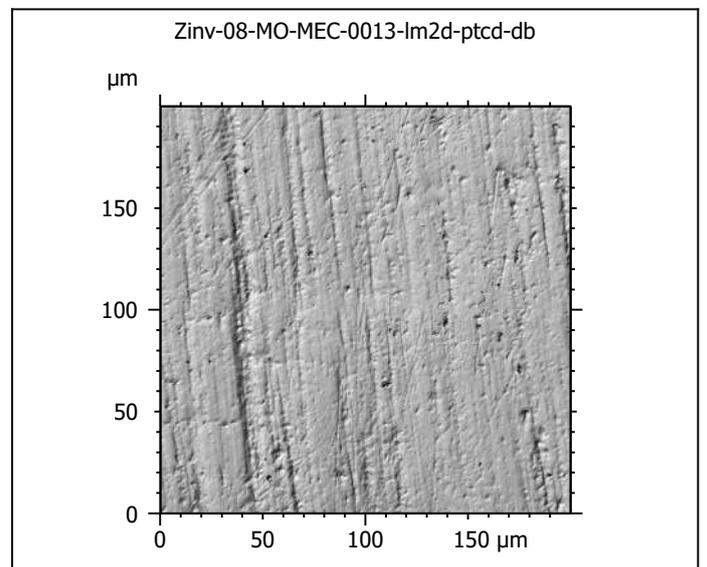
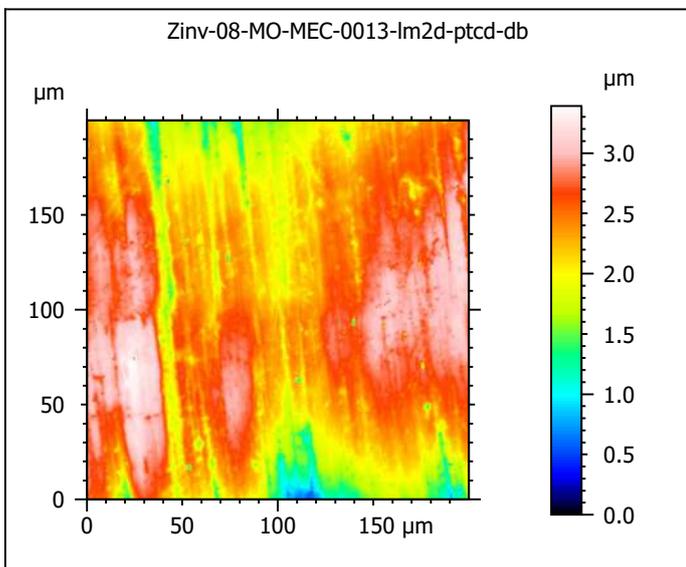
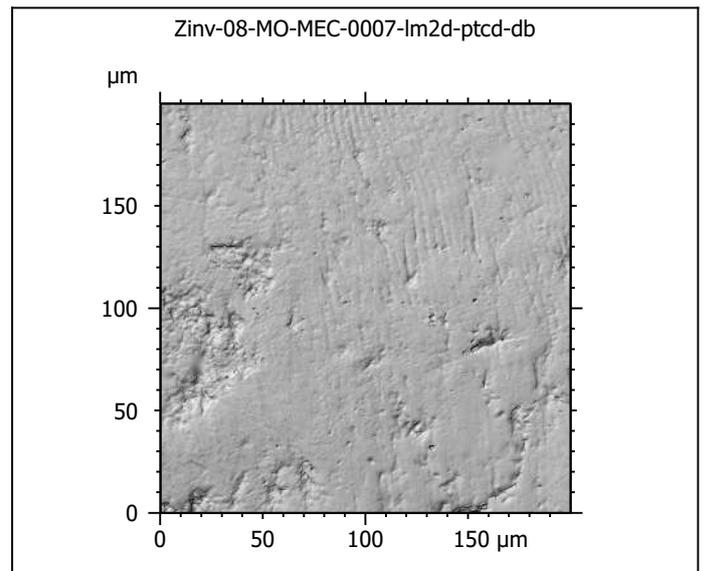
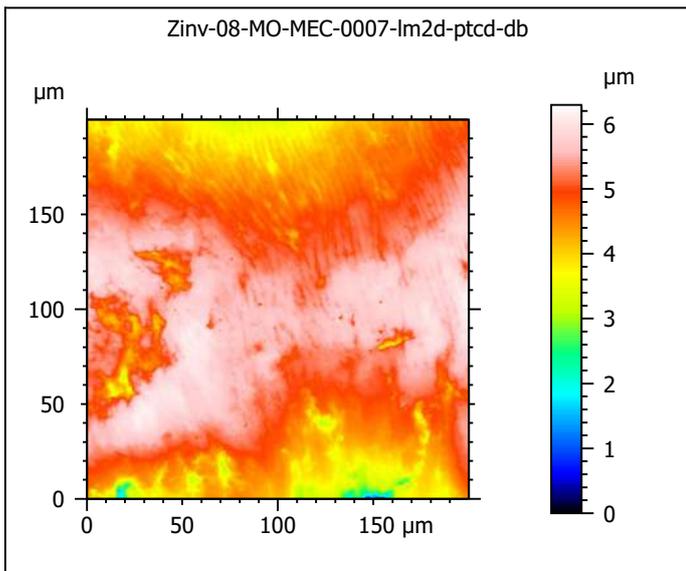
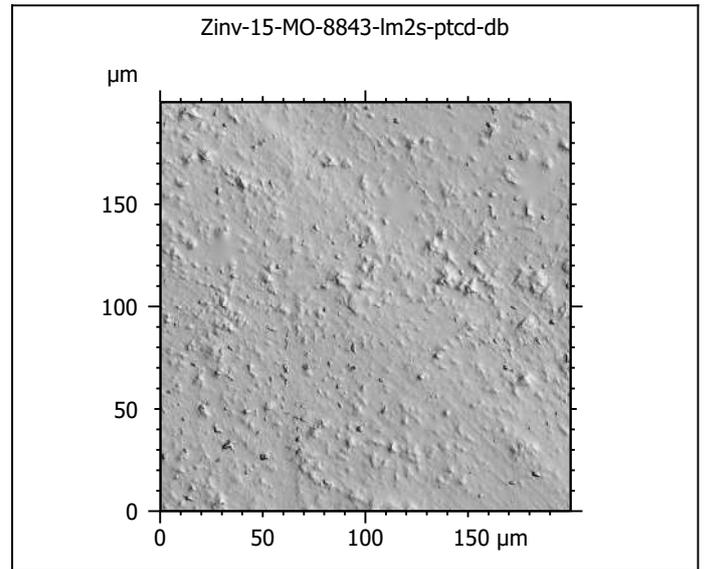
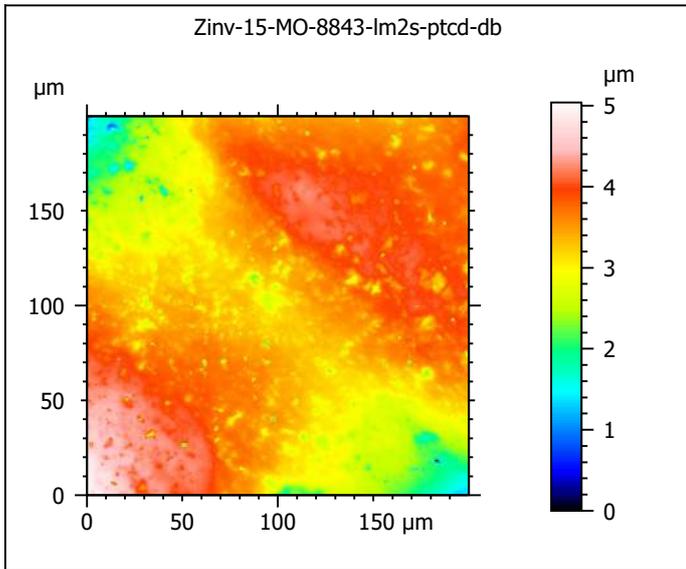
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Photosimulations and false color elevation maps of scanned molar facets
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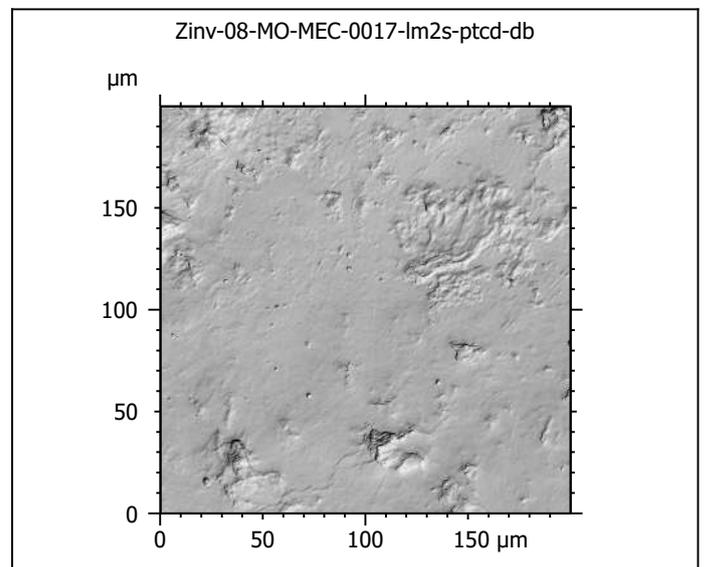
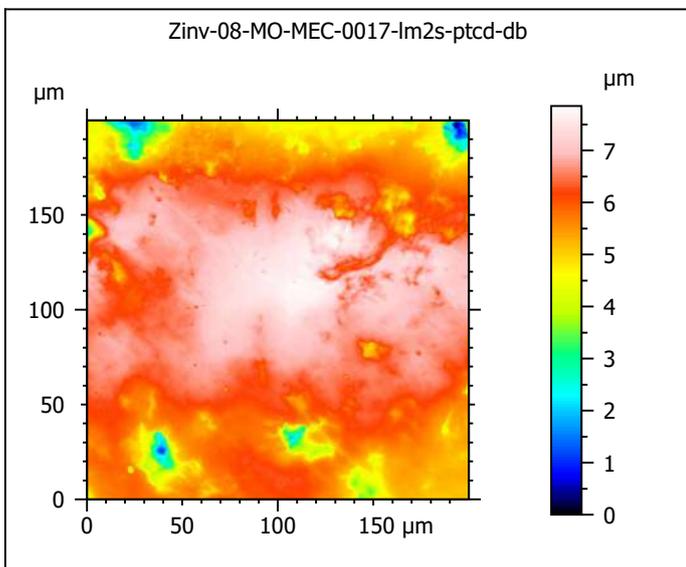
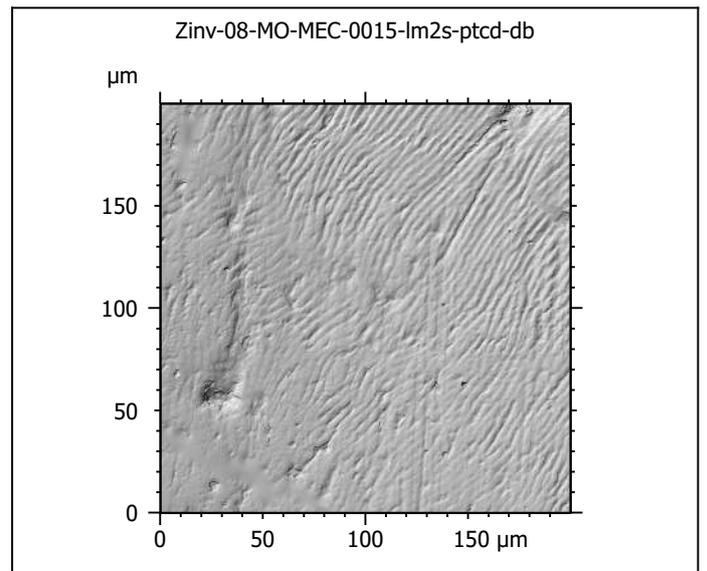
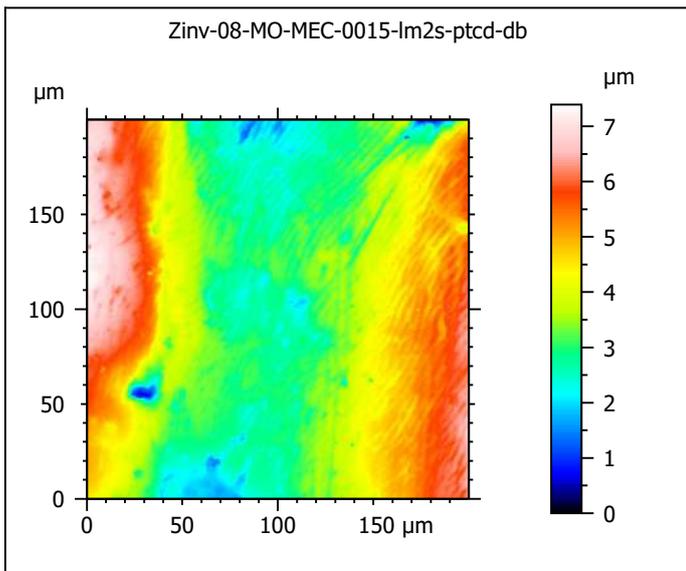
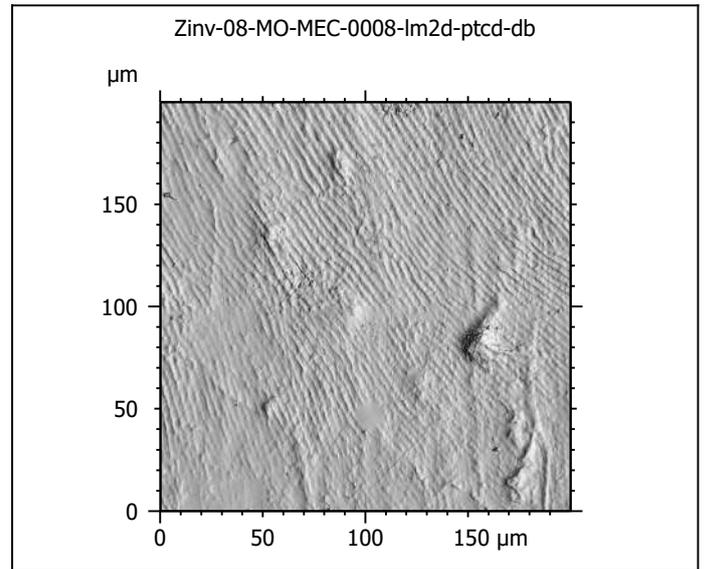
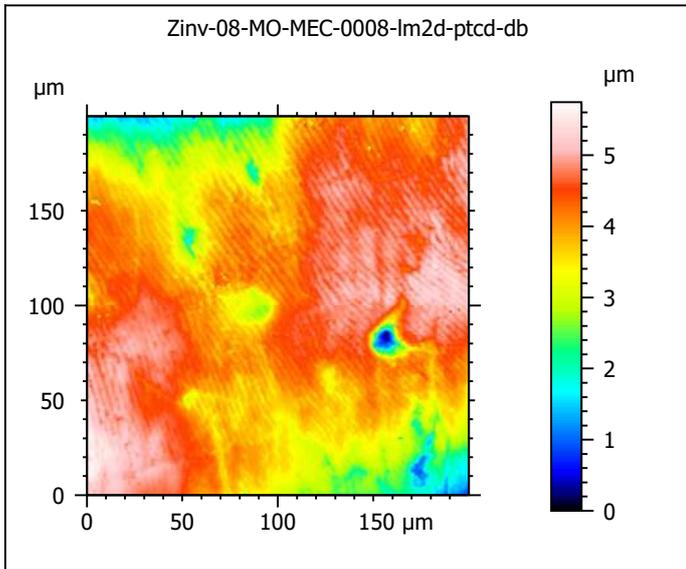
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



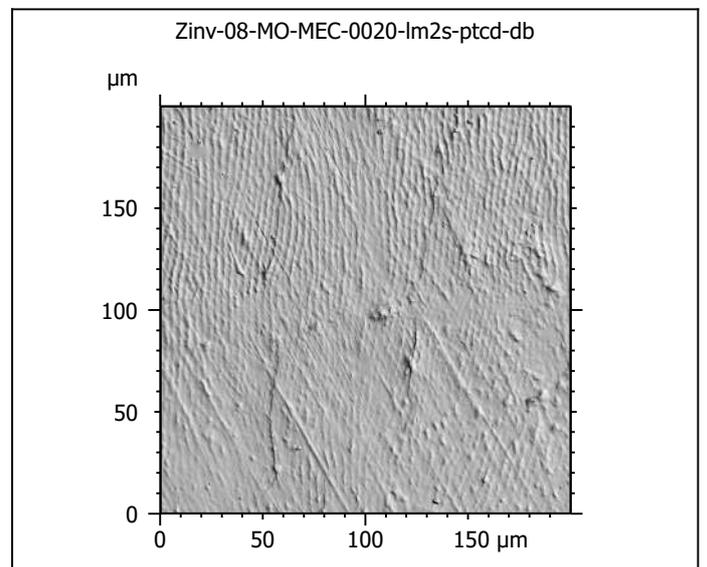
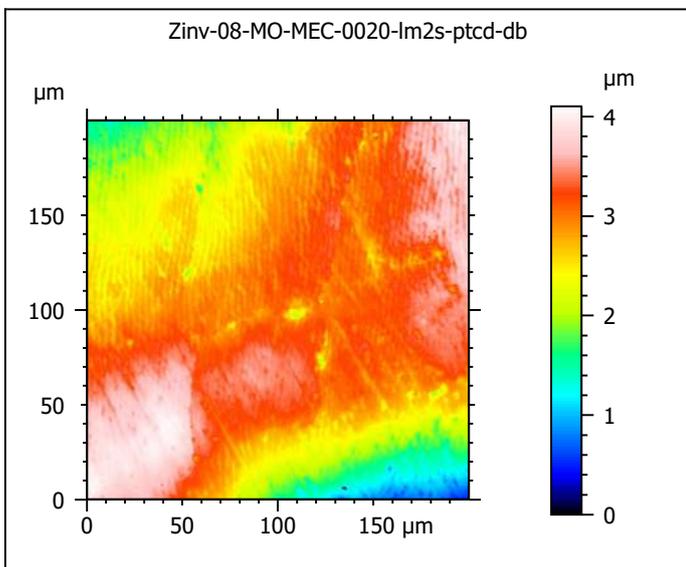
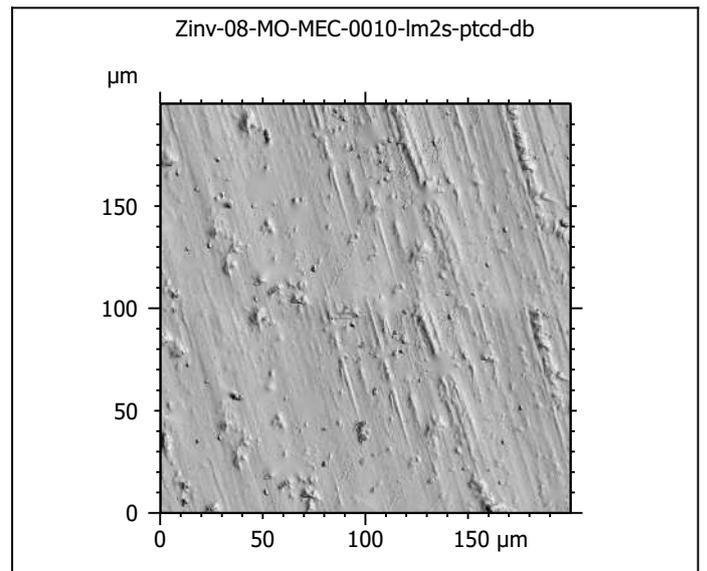
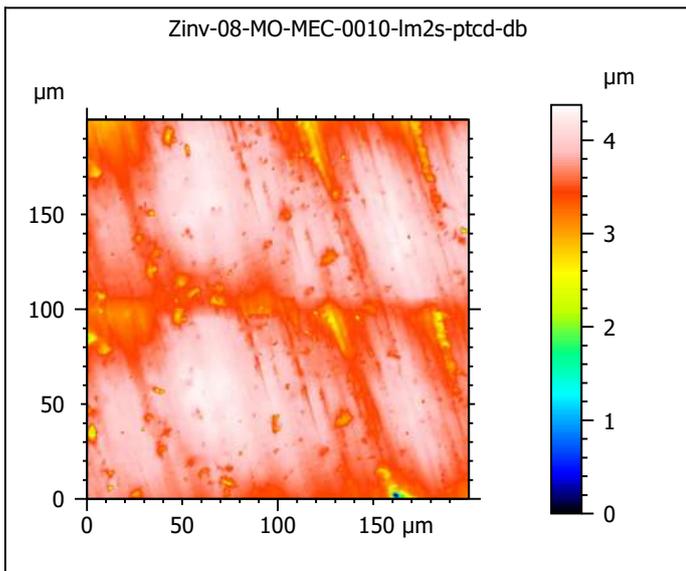
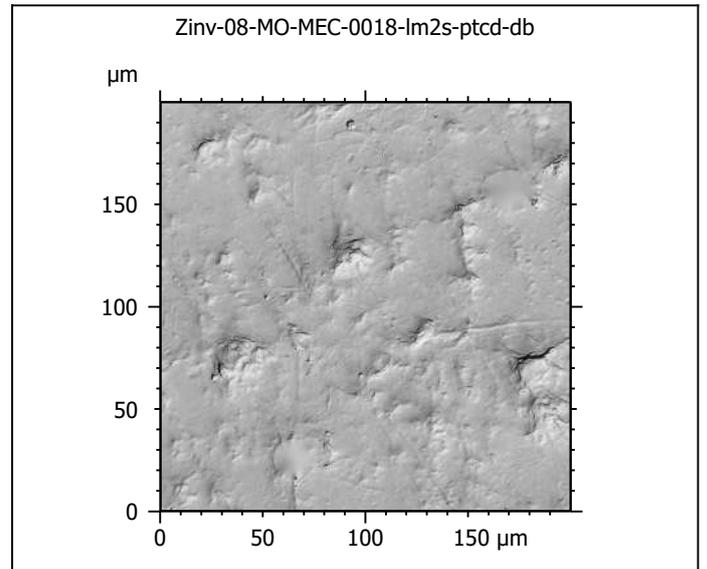
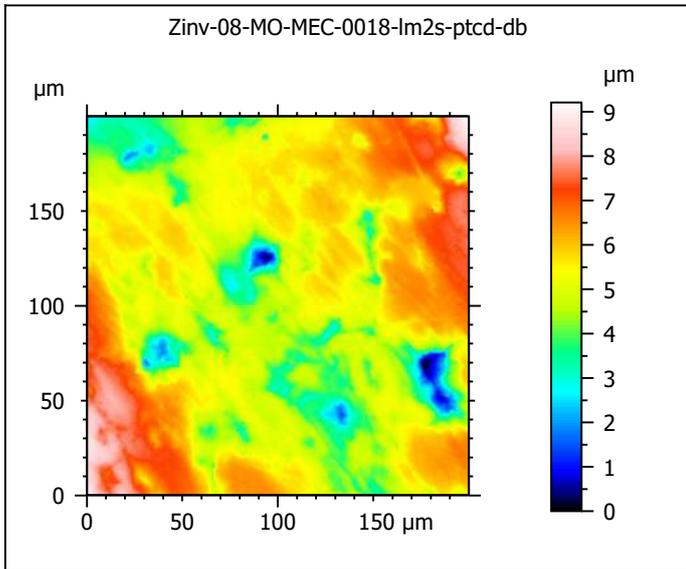
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
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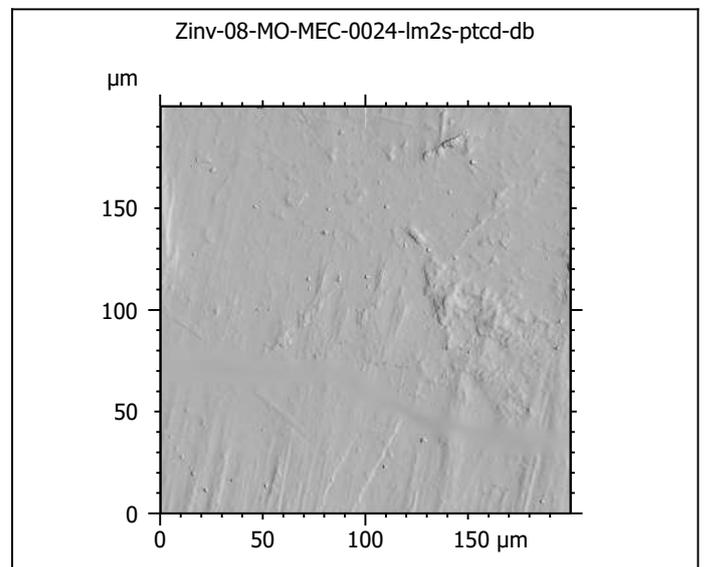
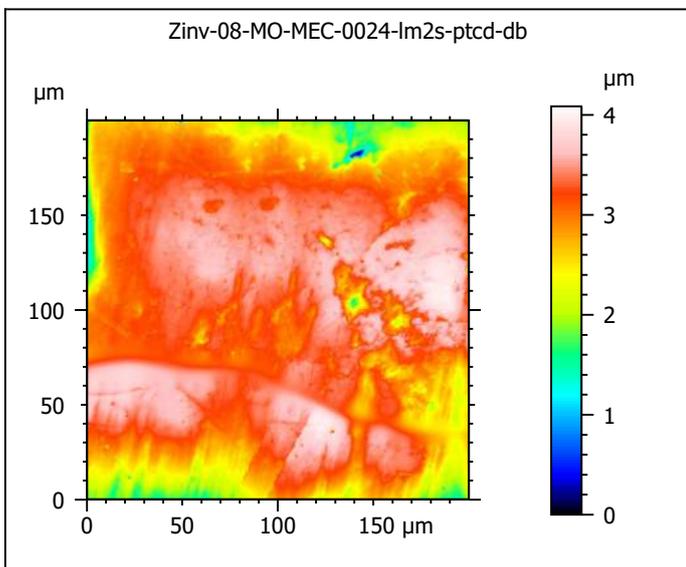
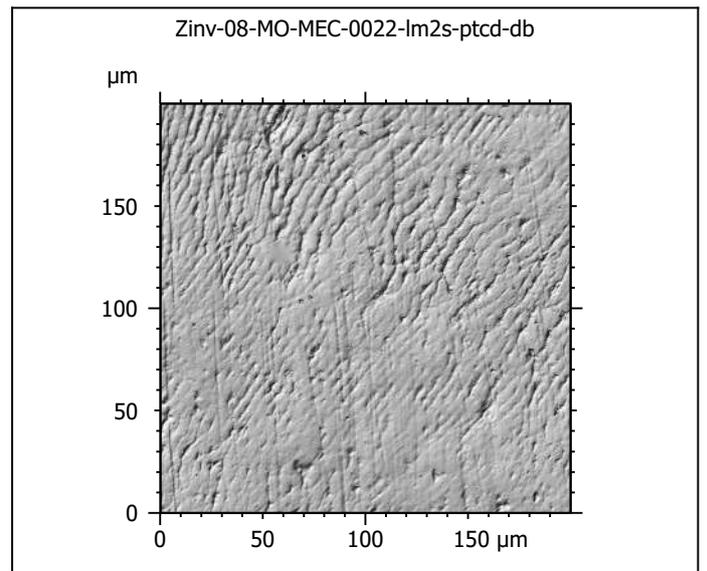
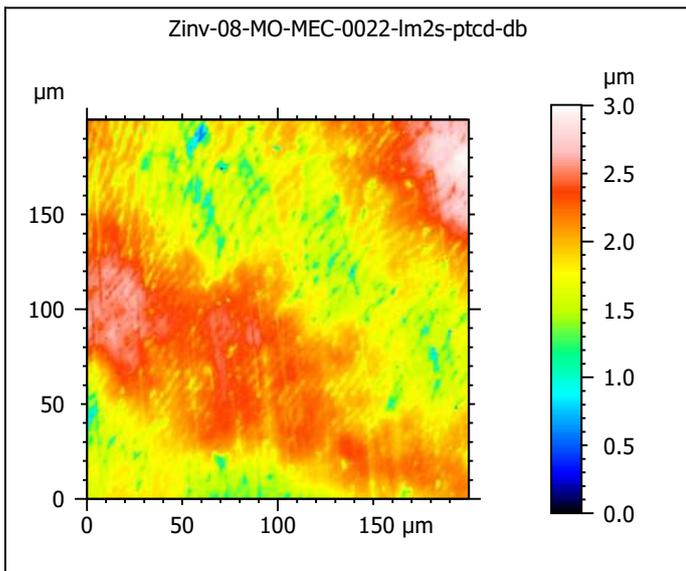
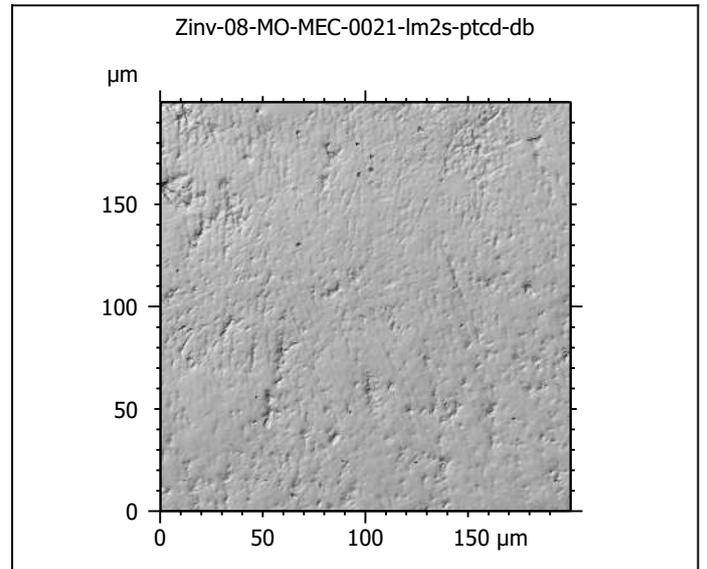
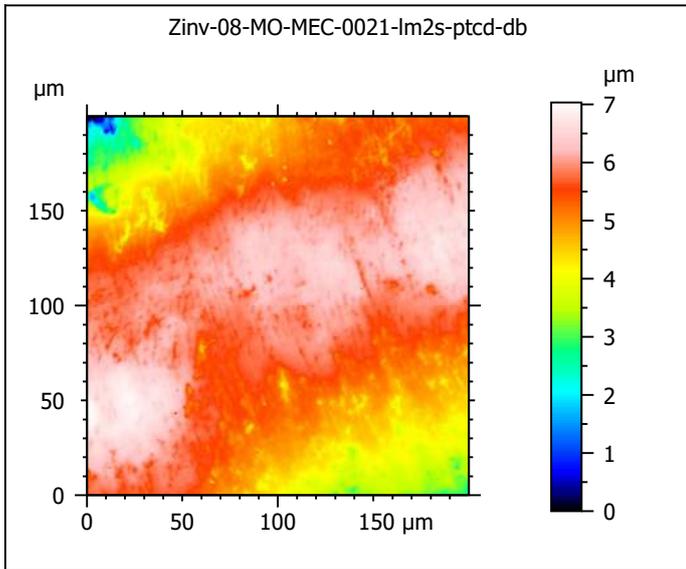
ANR-13-JSV7-0008-01, PI: G. Merceron



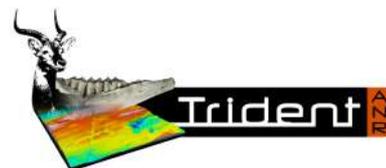
Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



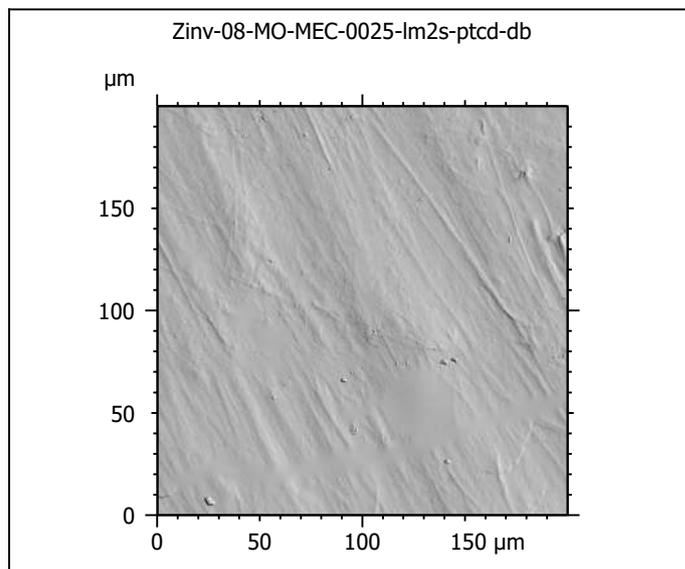
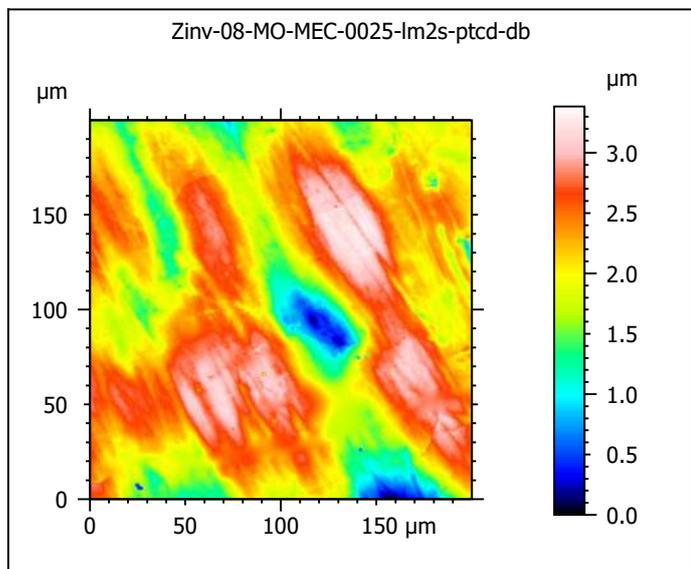
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the mouflon (*Ovis gmelini musimon*) from the Bauges Natural Regional Park, France
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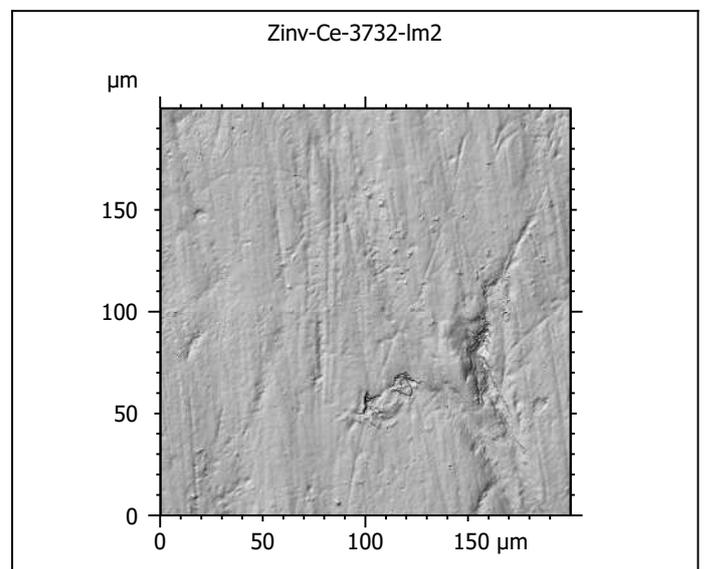
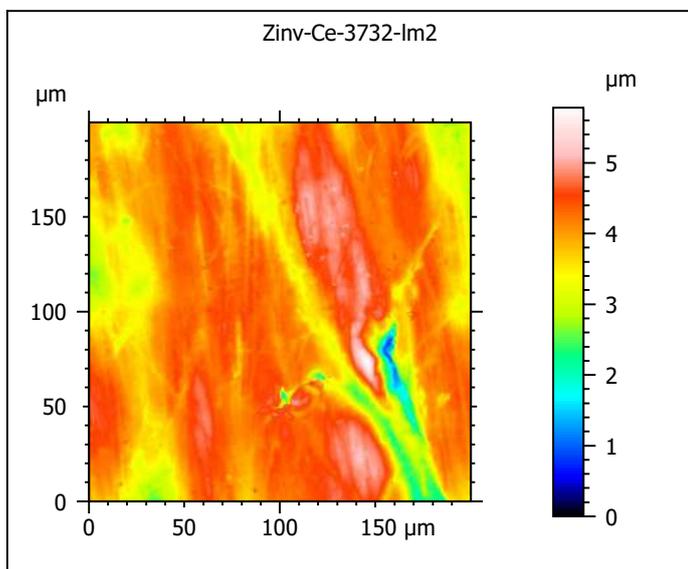
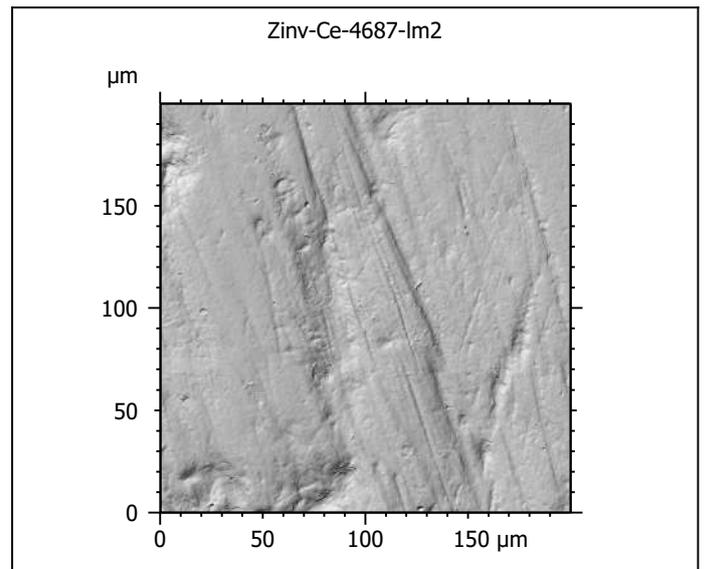
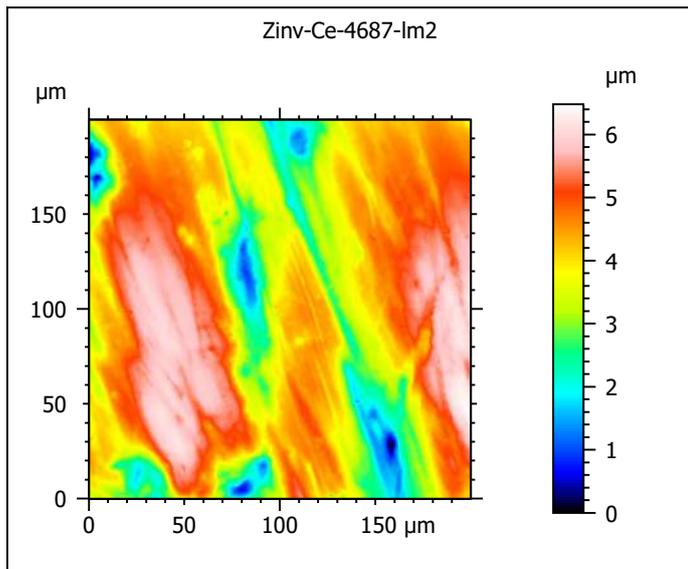
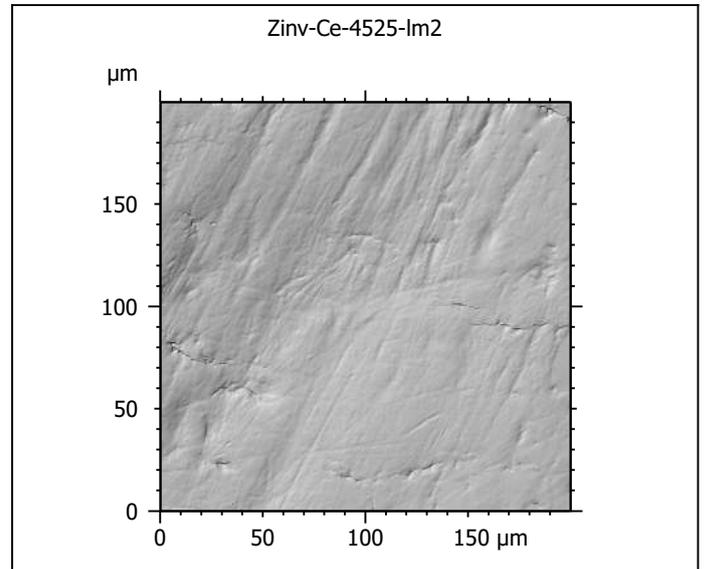
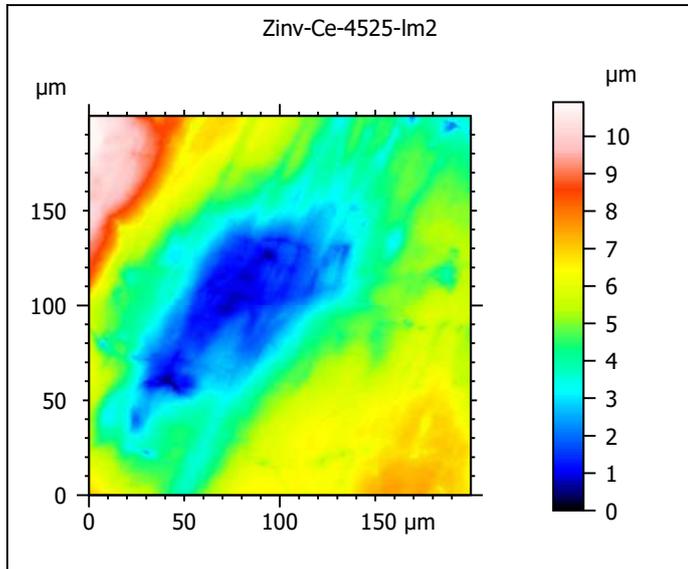
ANR-13-JSV7-0008-01, PI: G. Merceron



Photosimulations and false color elevation maps of scanned molar facets of the red deer (*Cervus elaphus*) from the Bauges Natural Regional Park, France scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



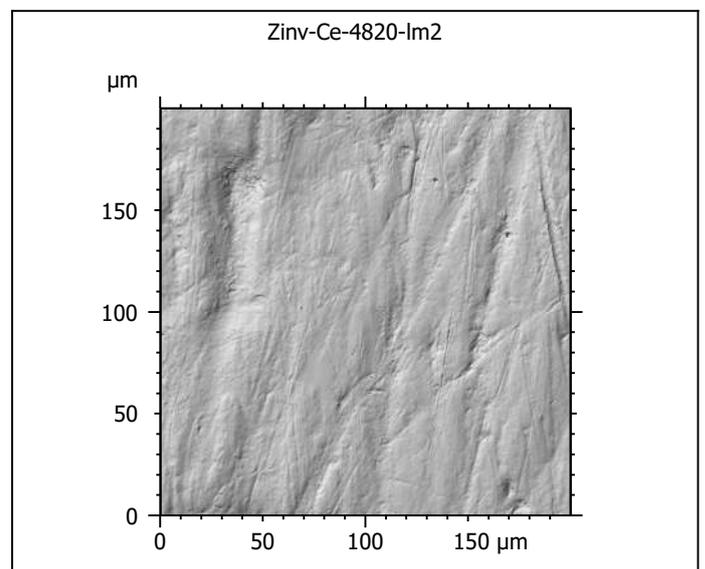
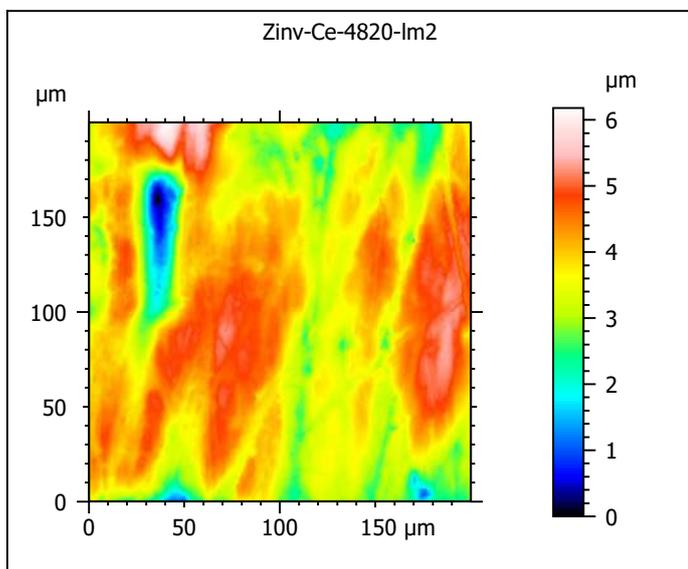
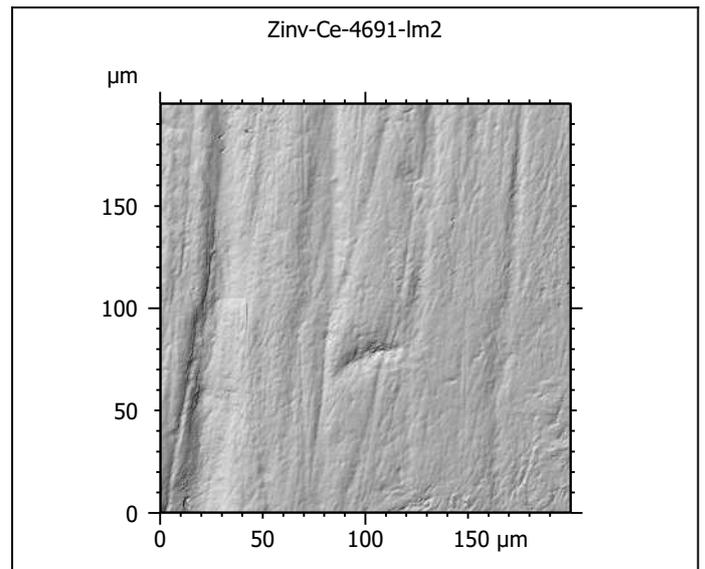
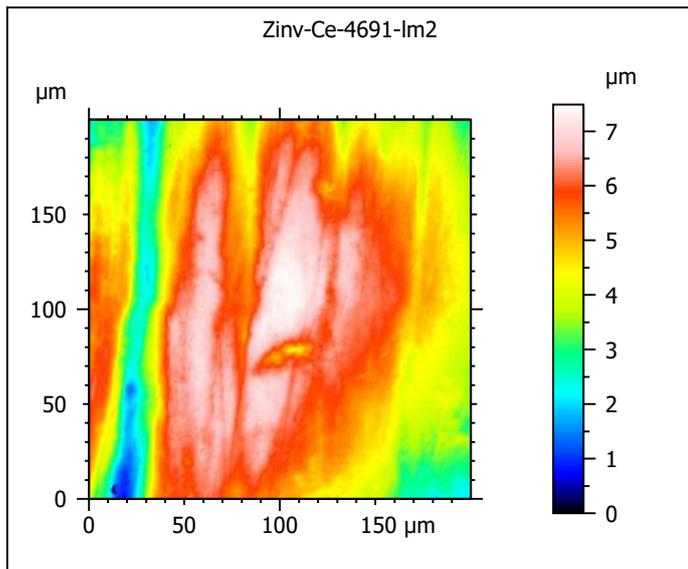
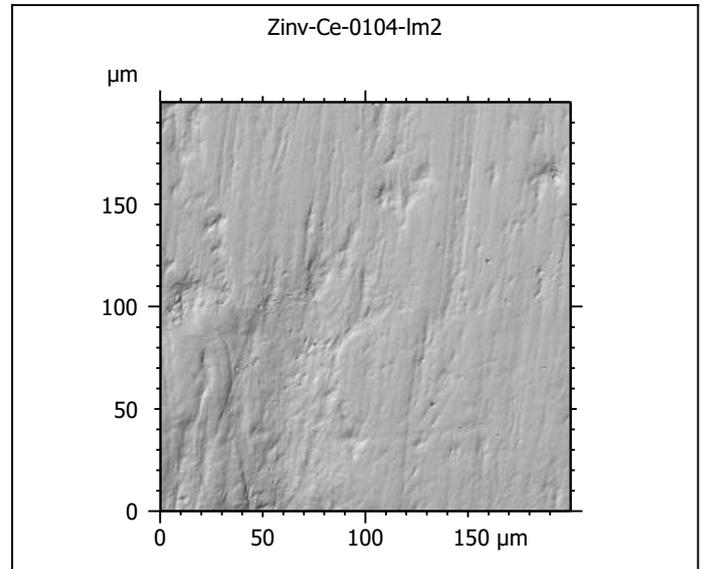
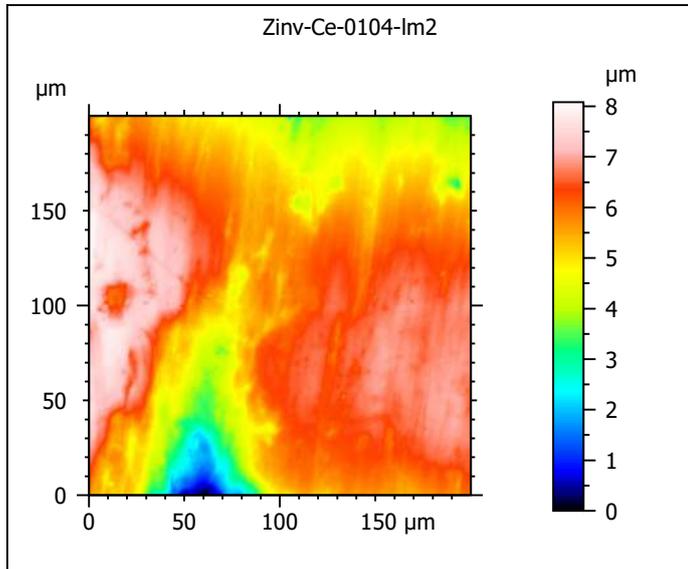
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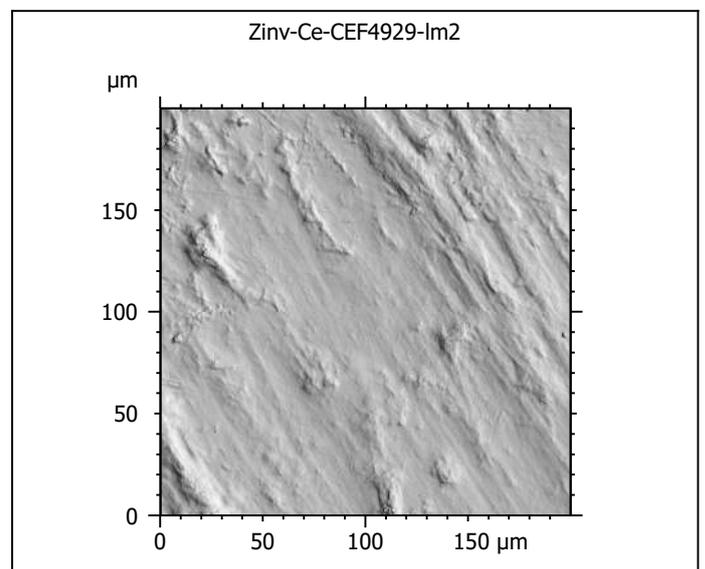
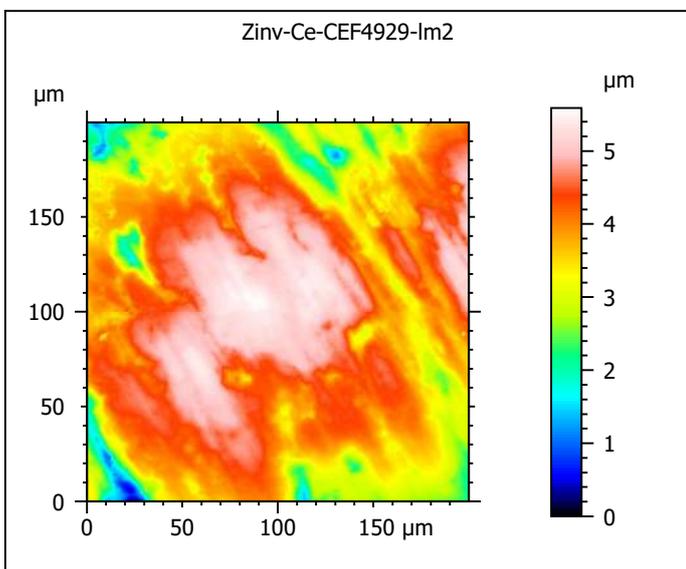
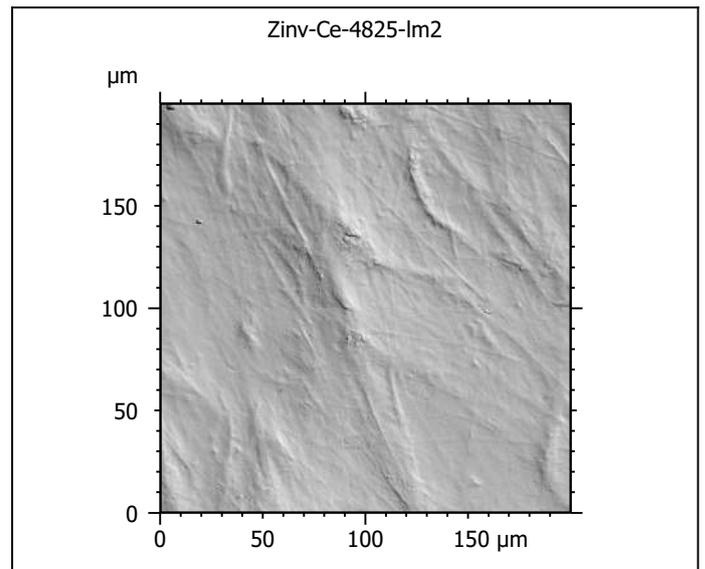
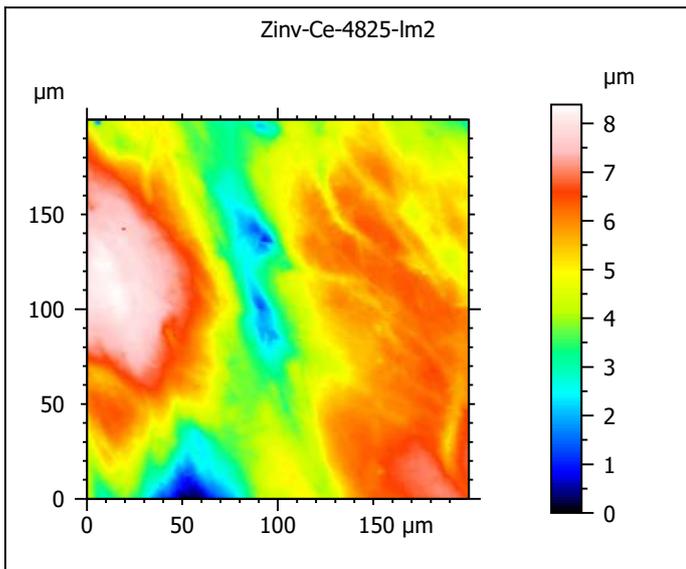
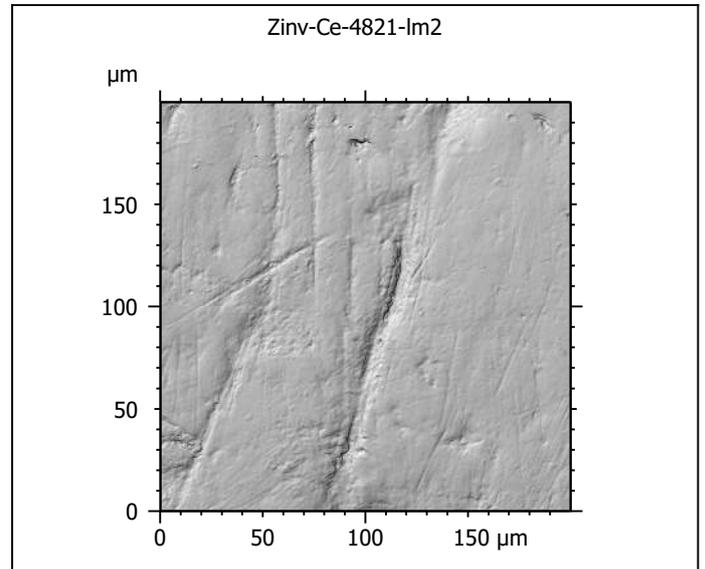
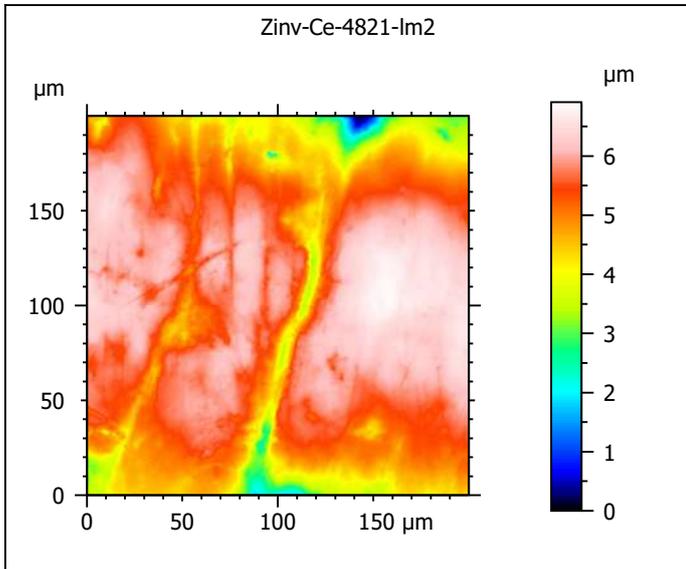
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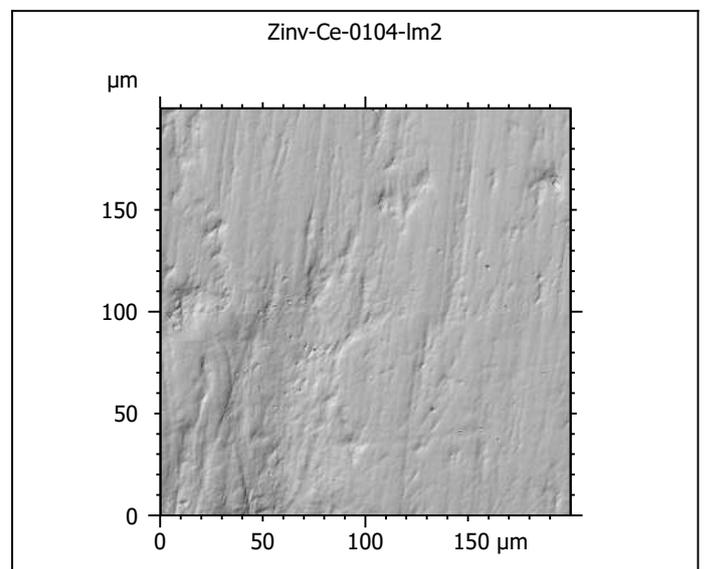
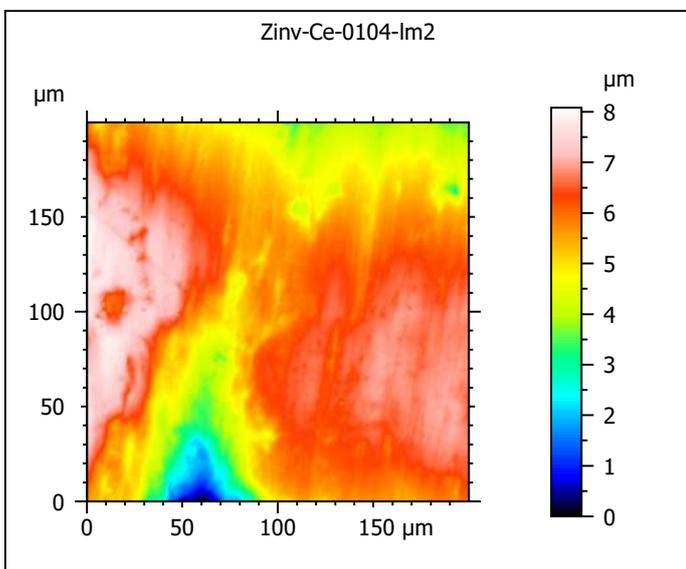
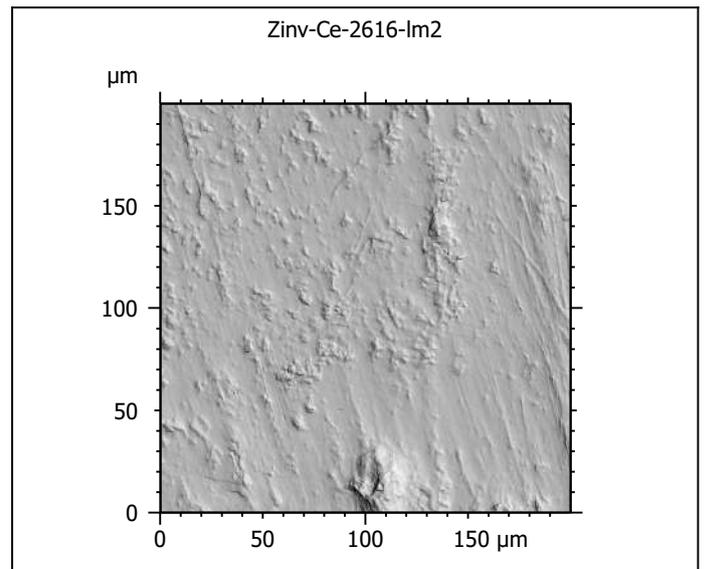
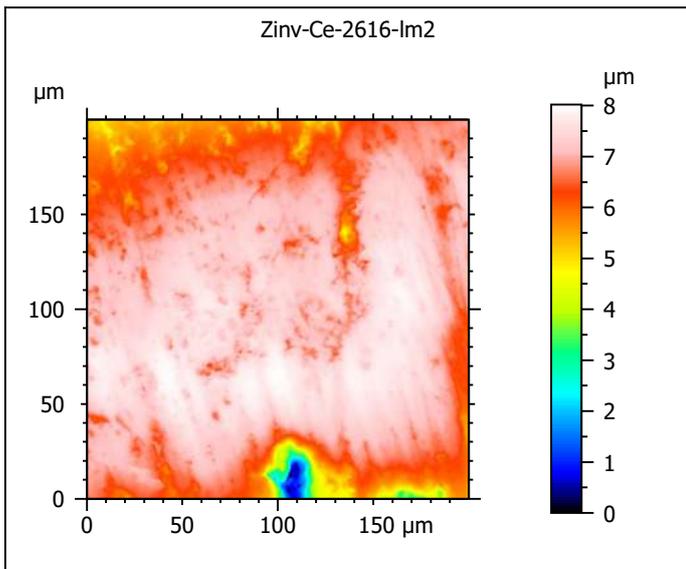
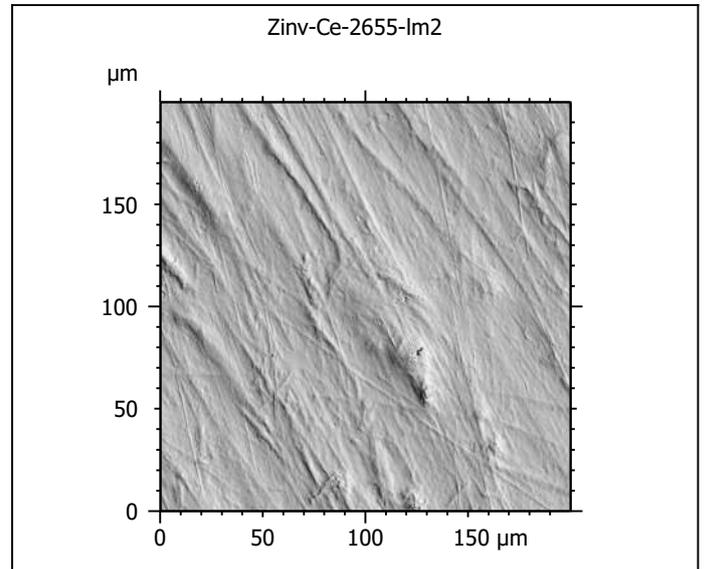
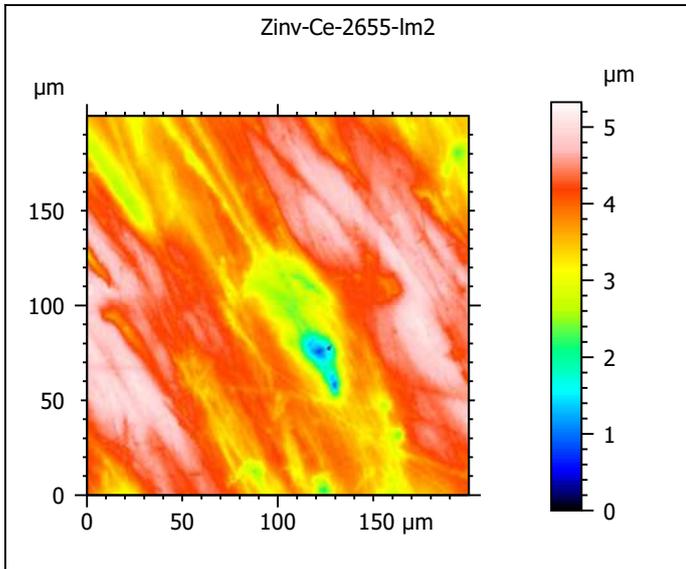
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Photosimulations and false color elevation maps of scanned molar facets of the red deer (*Cervus elaphus*) from the Bauges Natural Regional Park, France scanned at the PALEVOPRIM lab by G. Merceron , CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



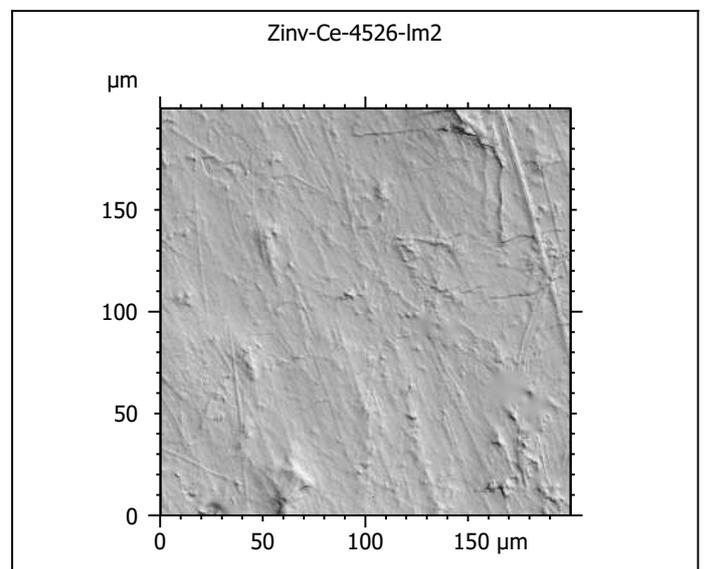
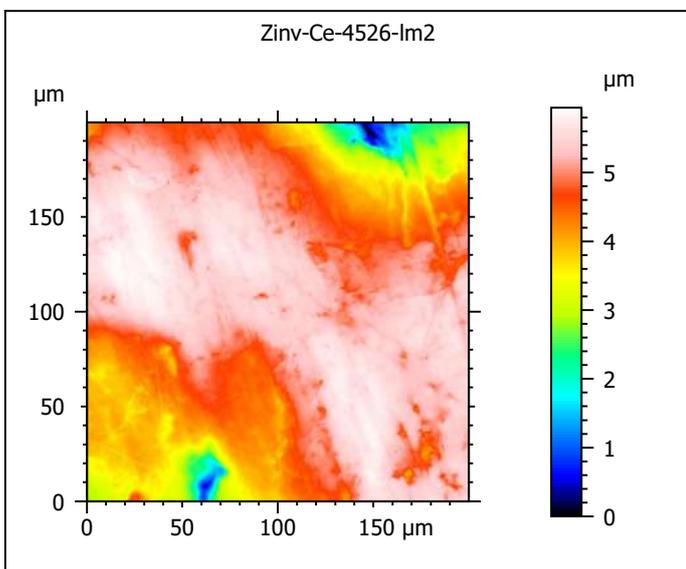
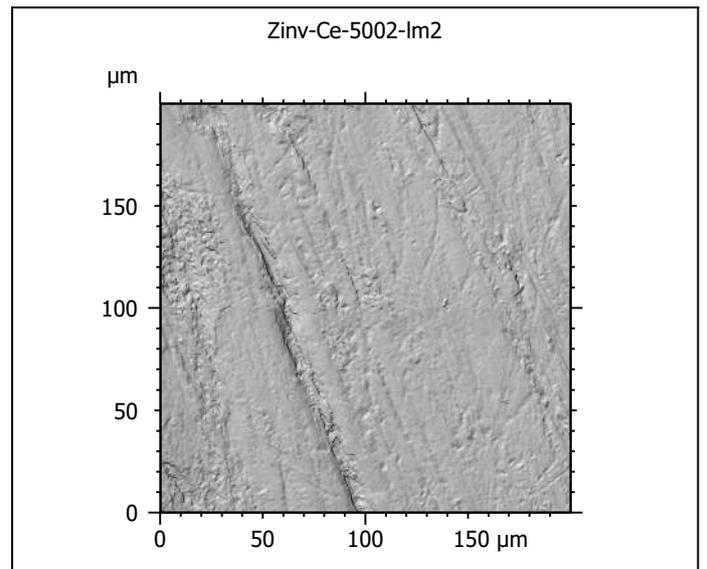
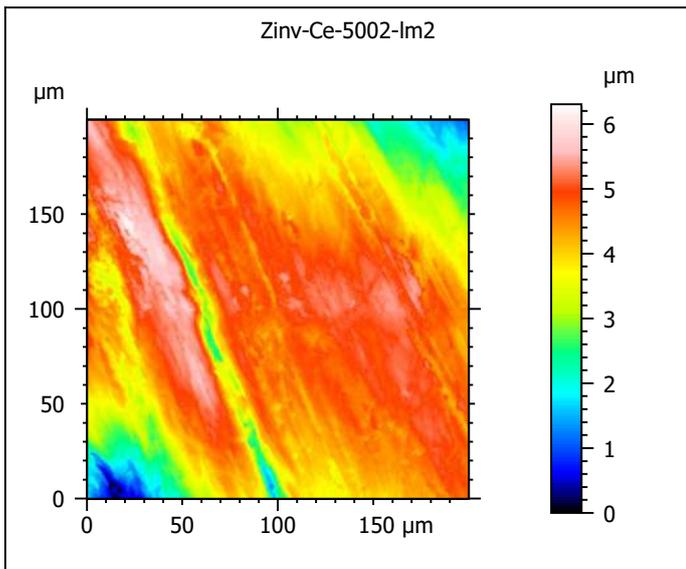
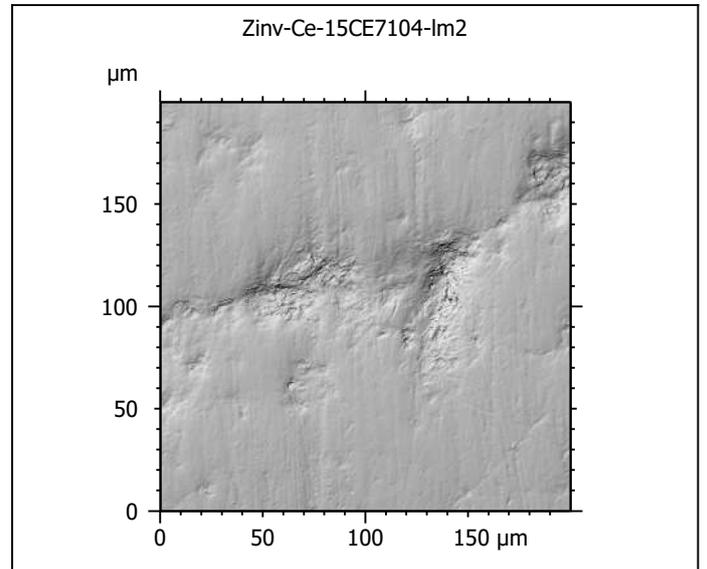
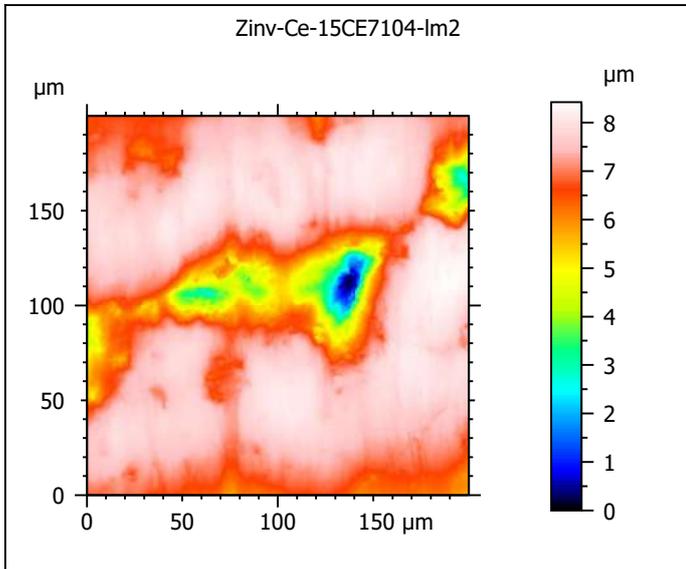
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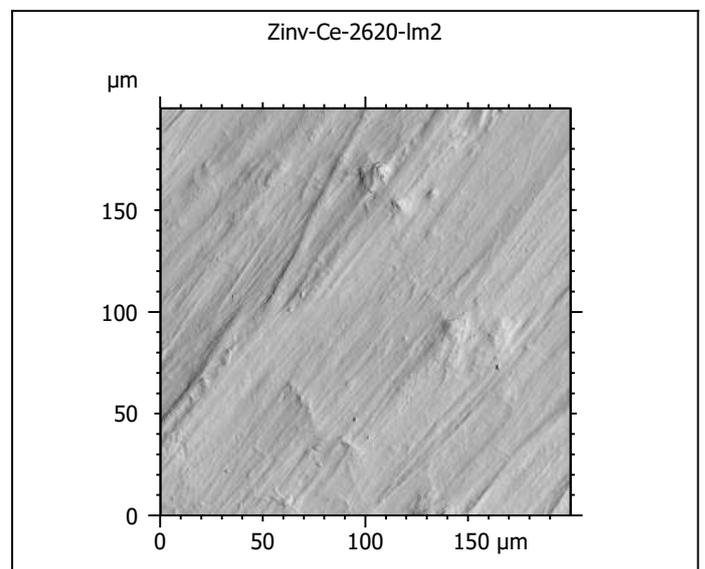
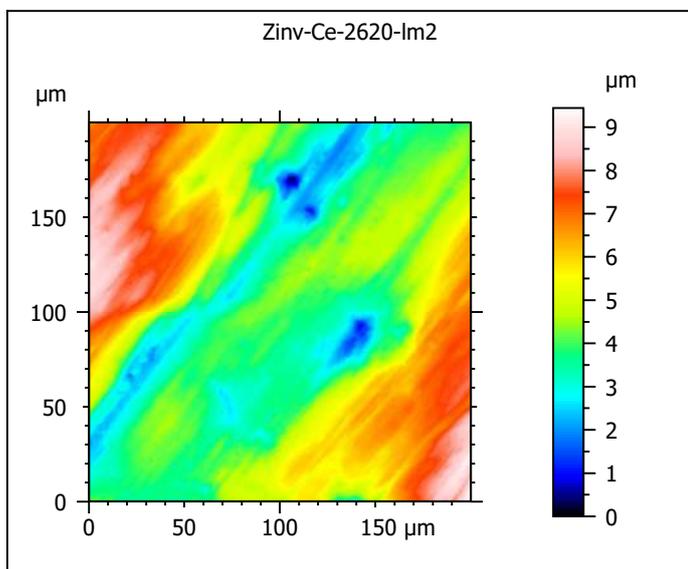
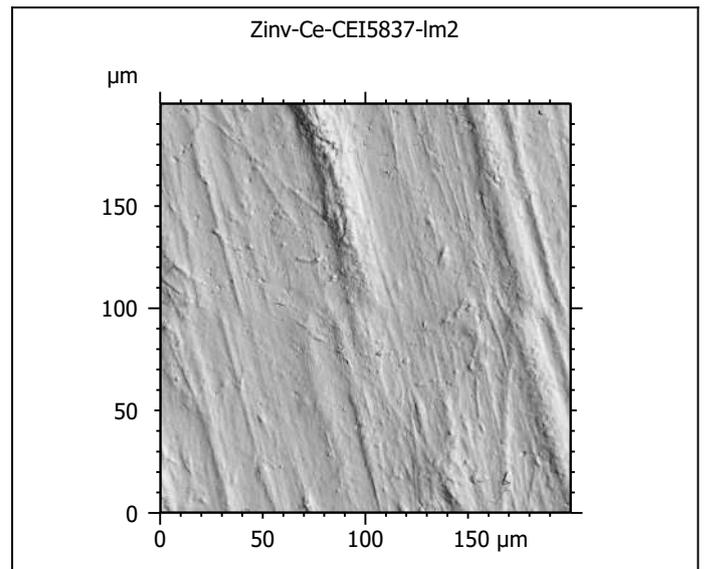
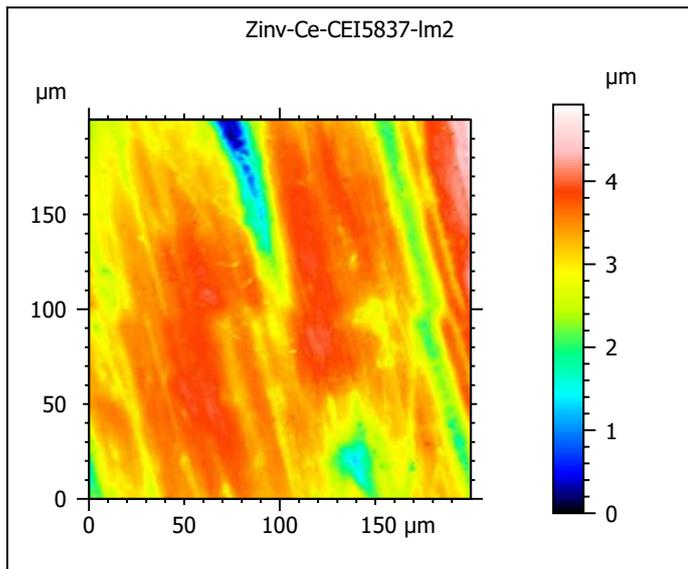
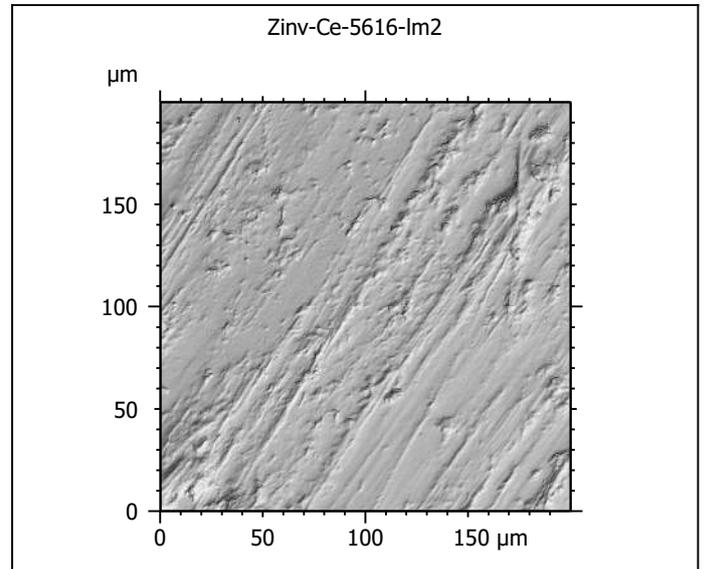
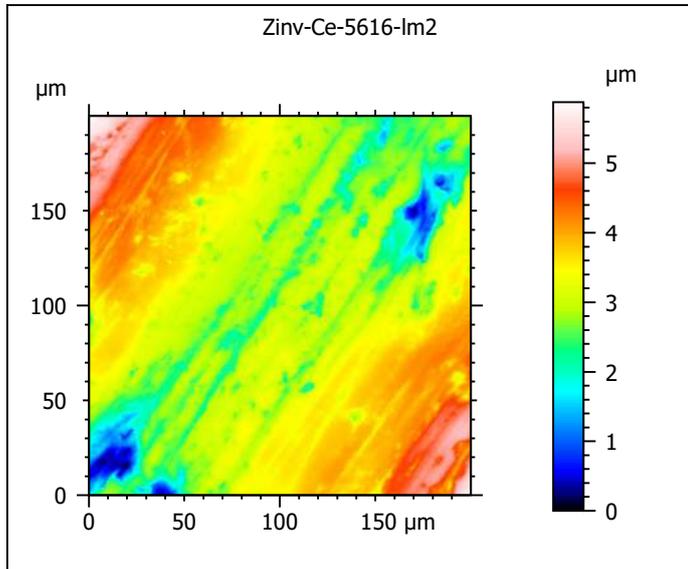
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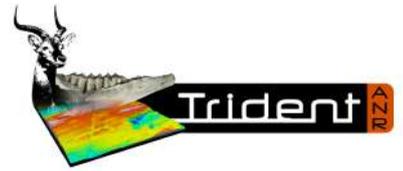
Photosimulations and false color elevation maps of scanned molar facets of the red deer (*Cervus elaphus*) from the Bauges Natural Regional Park, France scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



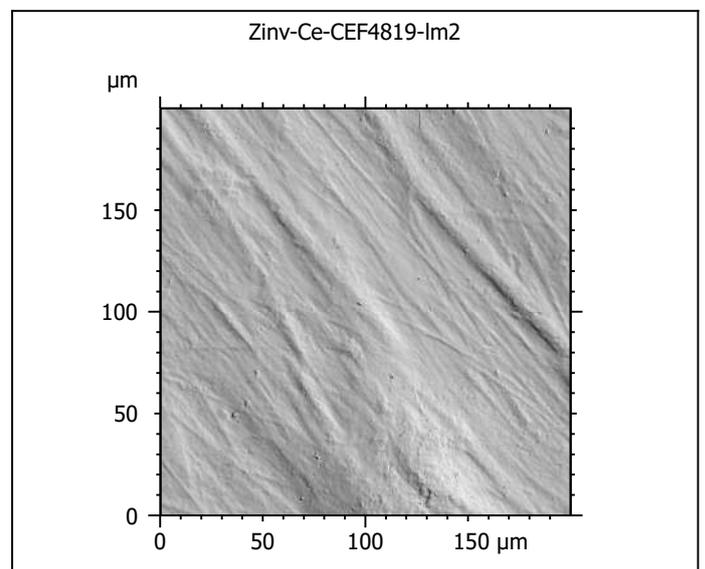
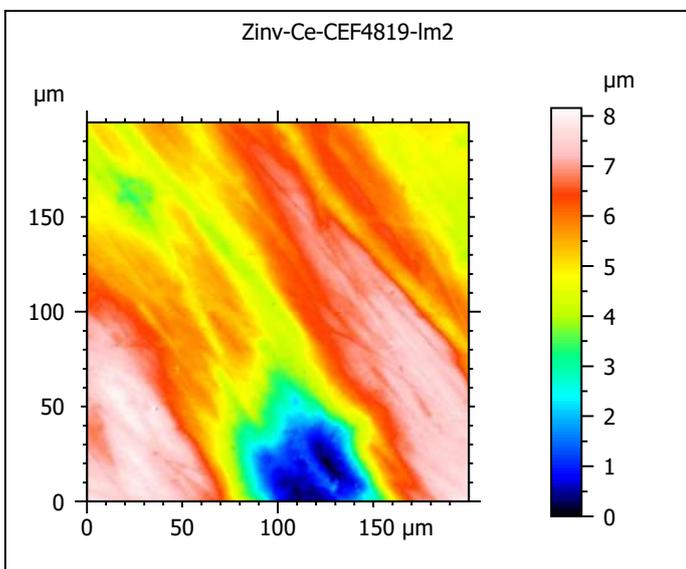
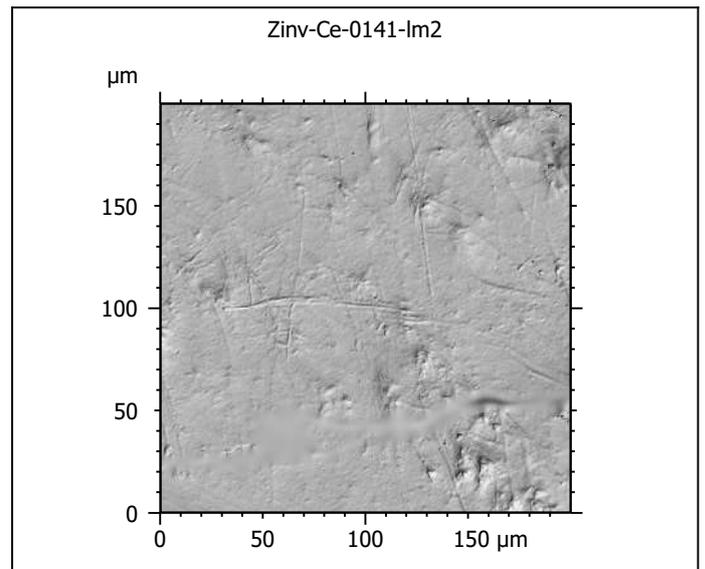
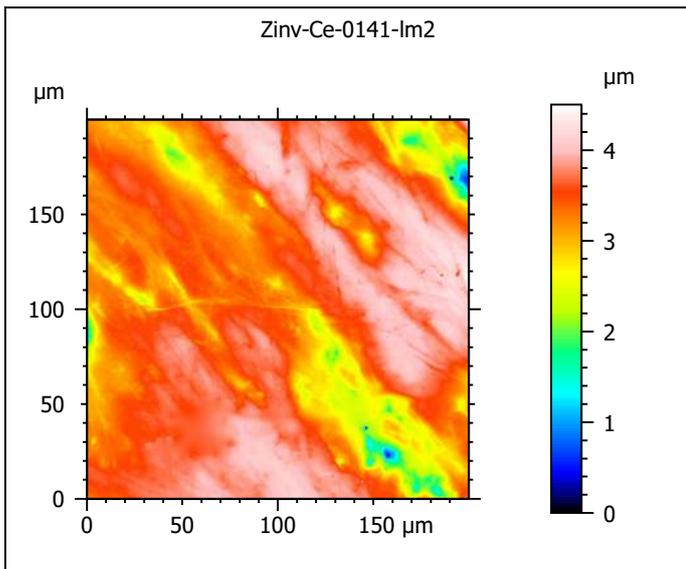
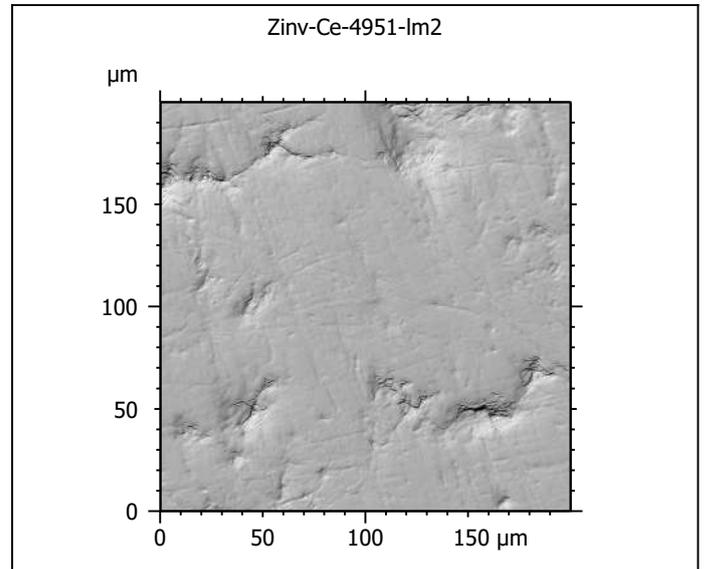
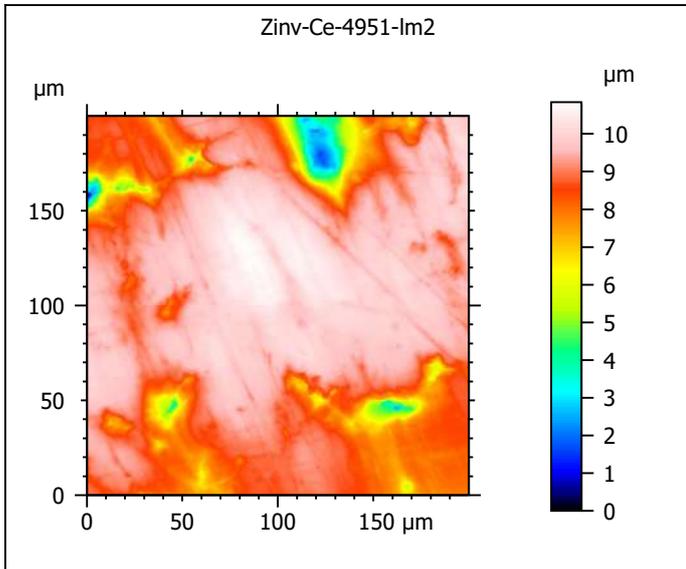
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Photosimulations and false color elevation maps of scanned molar facets of the red deer (*Cervus elaphus*) from the Bauges Natural Regional Park, France scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



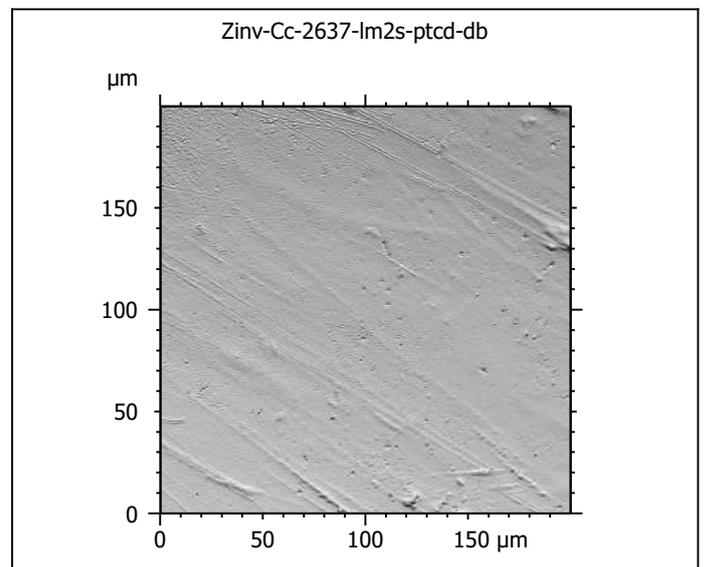
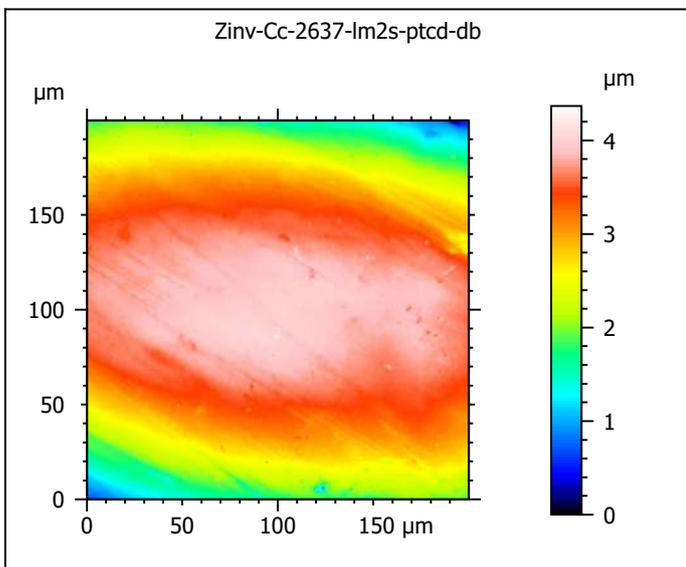
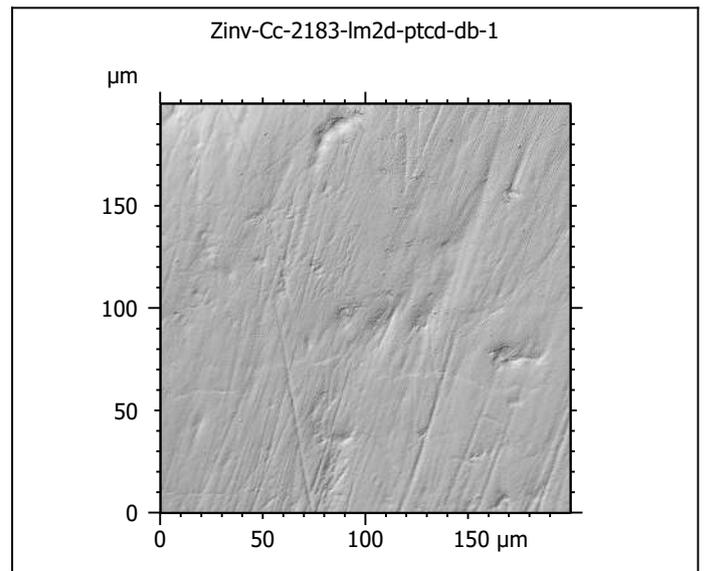
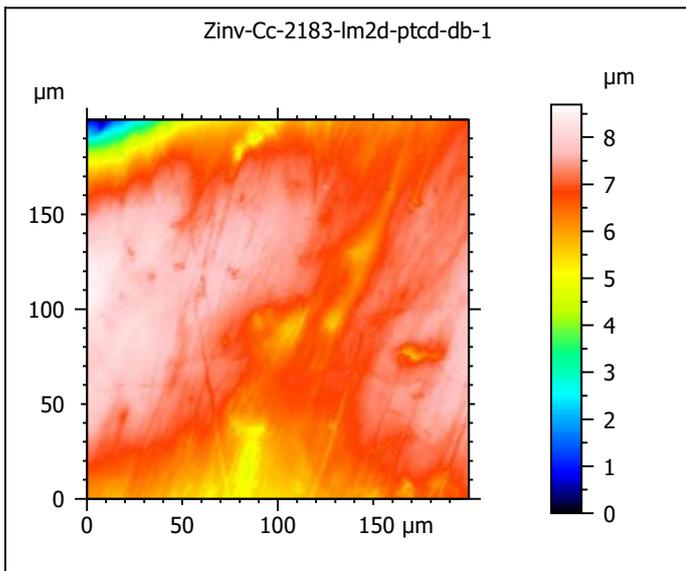
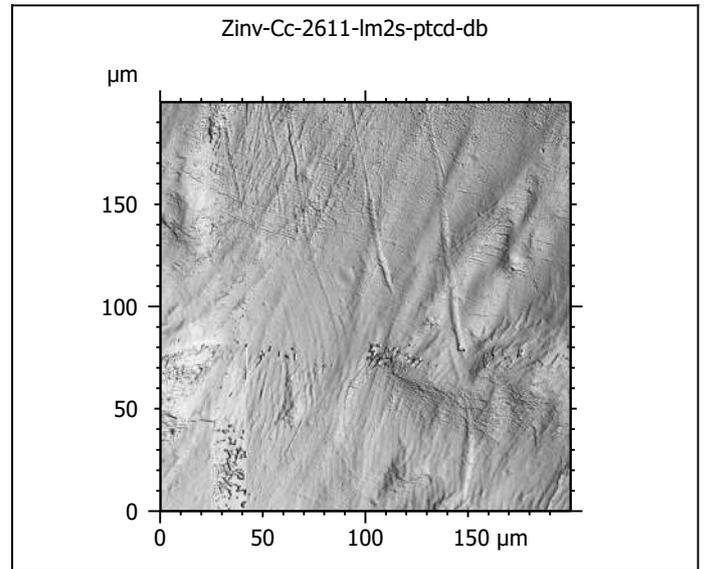
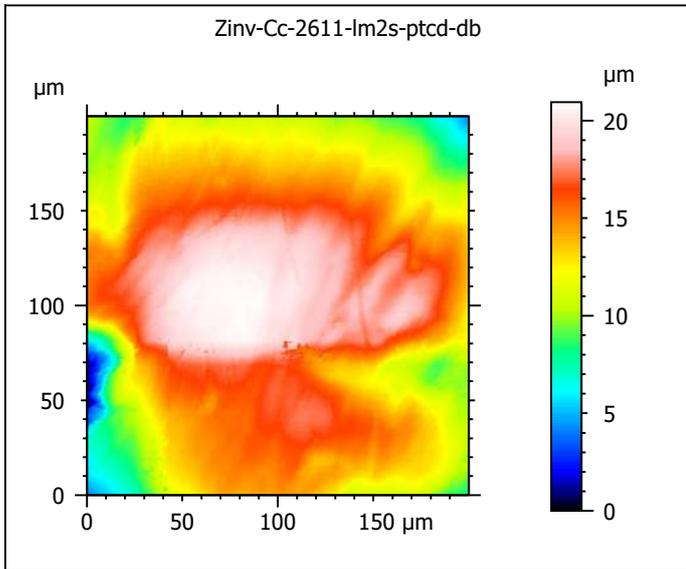
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Photosimulations and false color elevation maps of scanned molar facets of the roe deer (*Capreolus capreolus*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



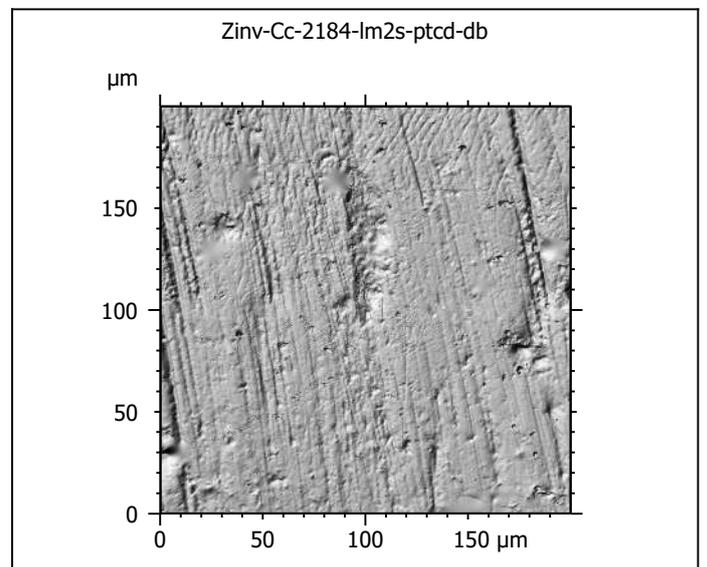
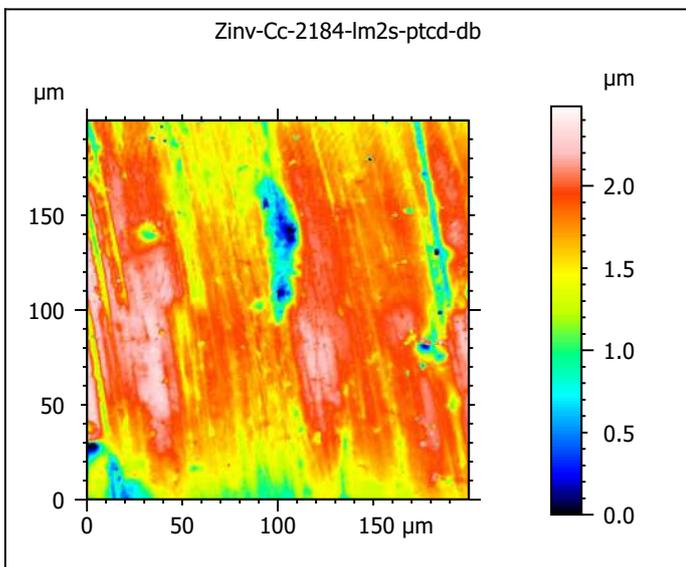
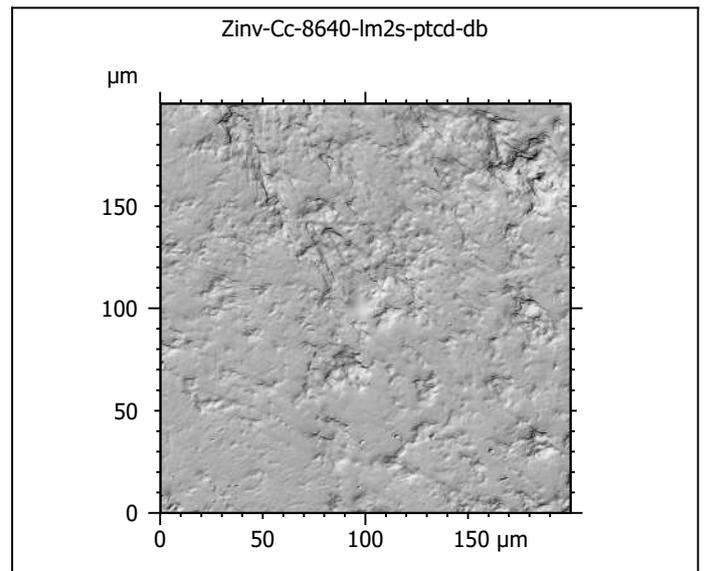
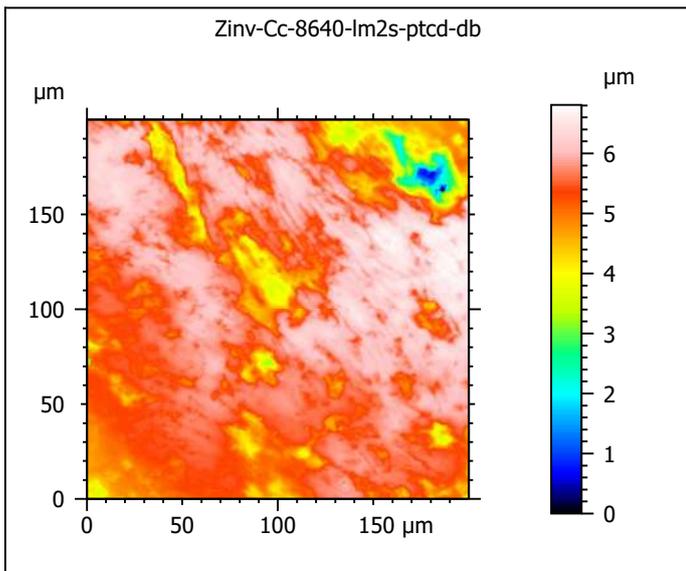
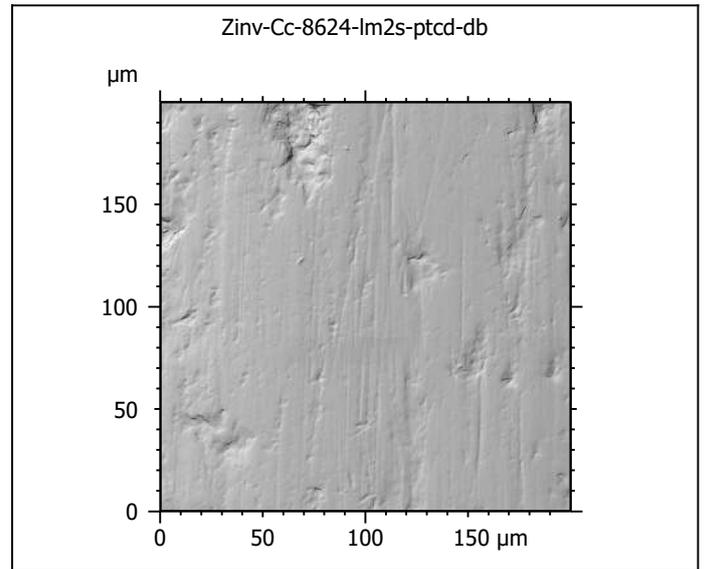
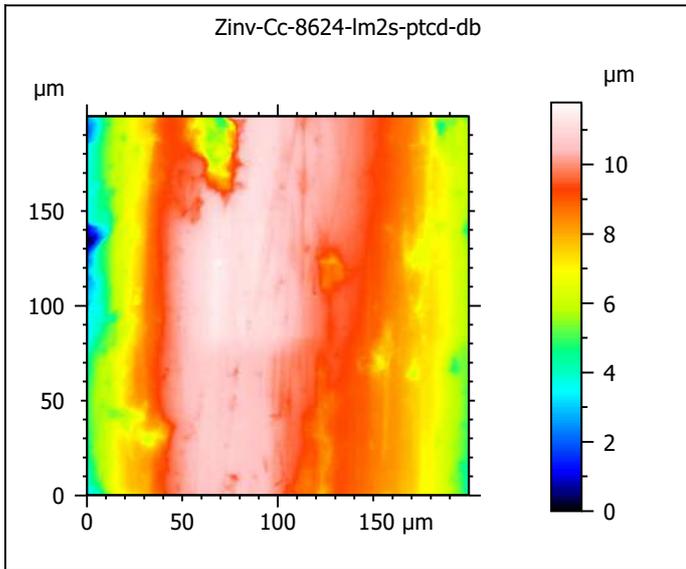
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Photosimulations and false color elevation maps of scanned molar facets of the roe deer (*Capreolus capreolus*) from the Bauges Natural Regional Park, France
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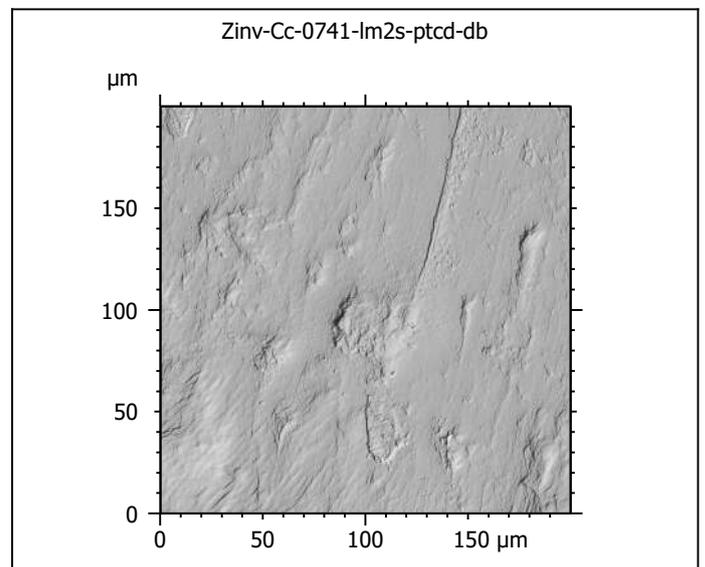
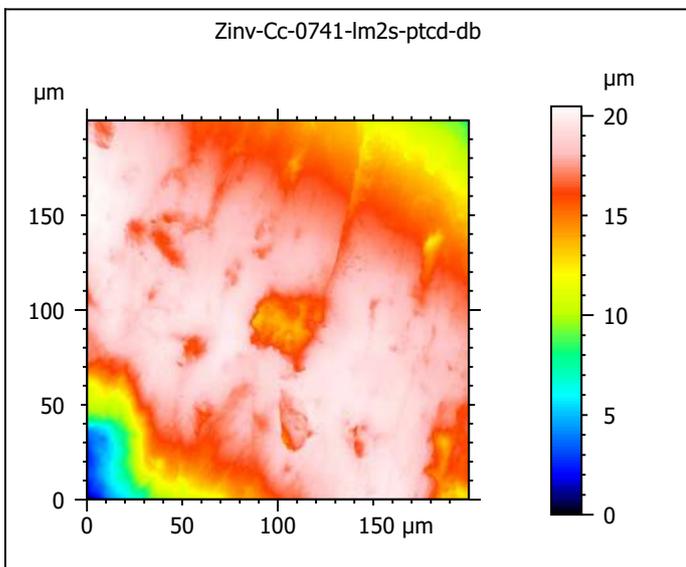
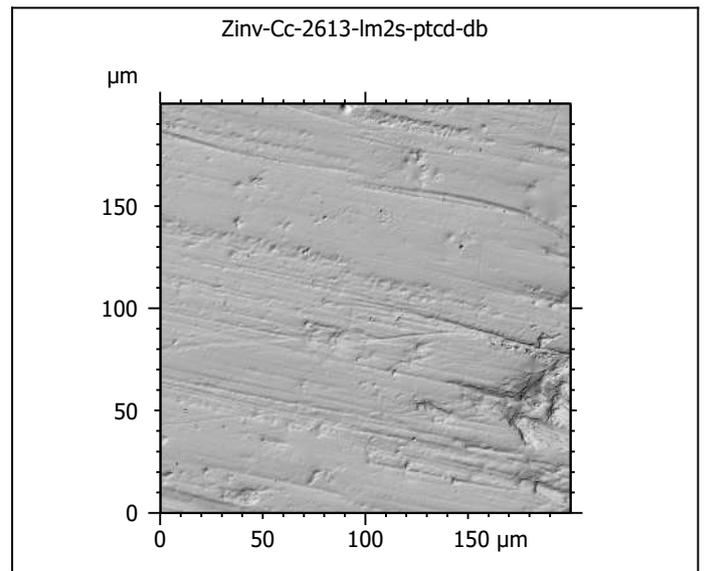
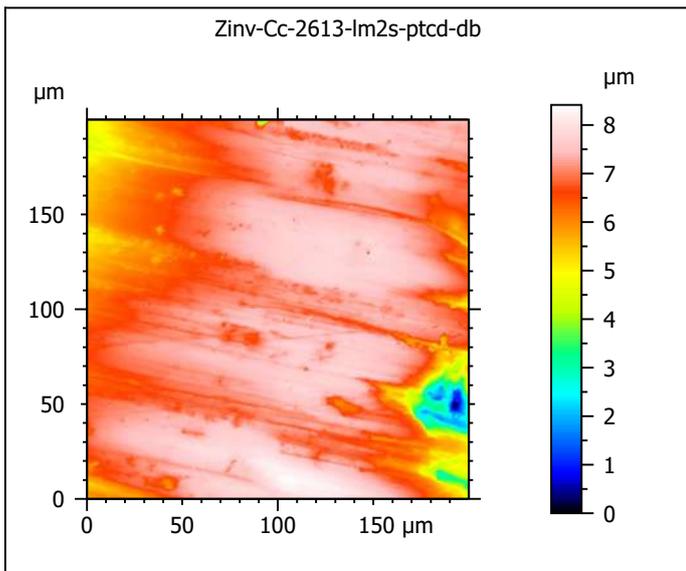
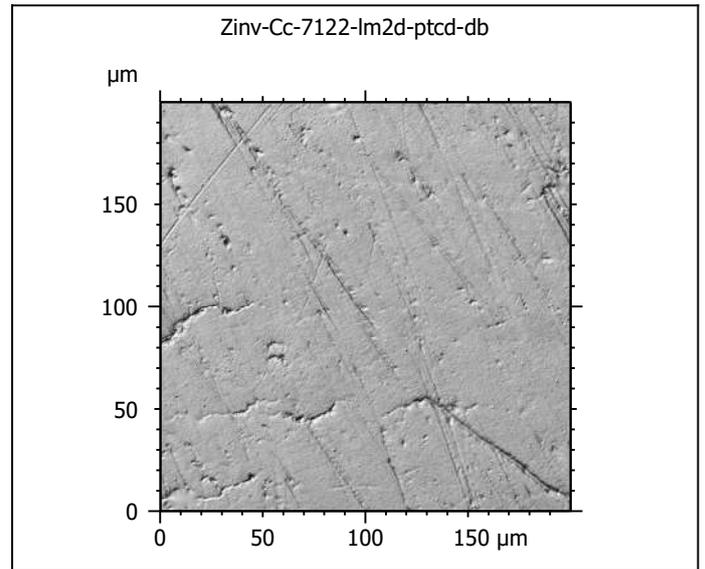
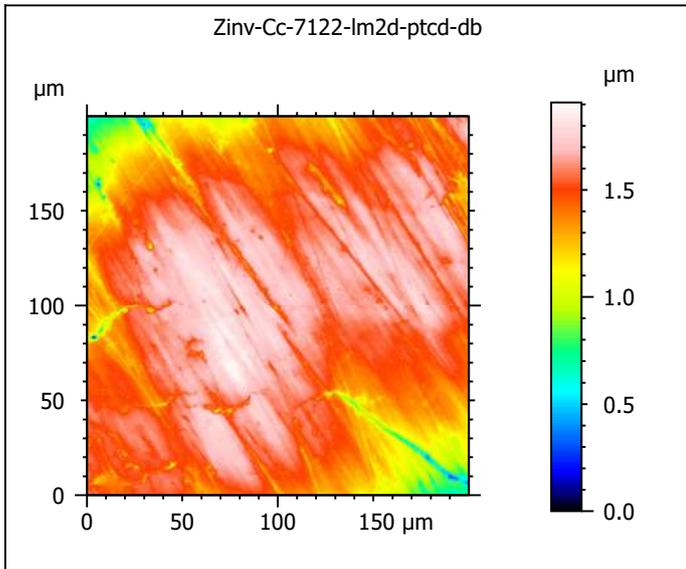
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Photosimulations and false color elevation maps of scanned molar facets of the roe deer (*Capreolus capreolus*) from the Bauges Natural Regional Park, France
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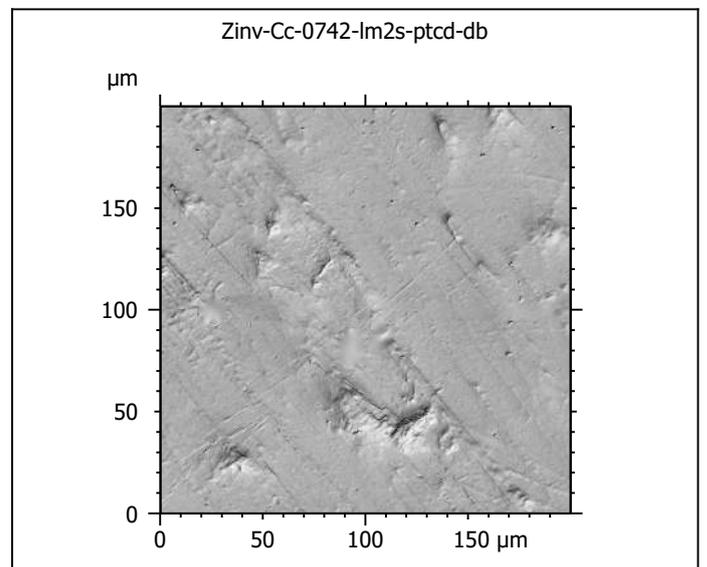
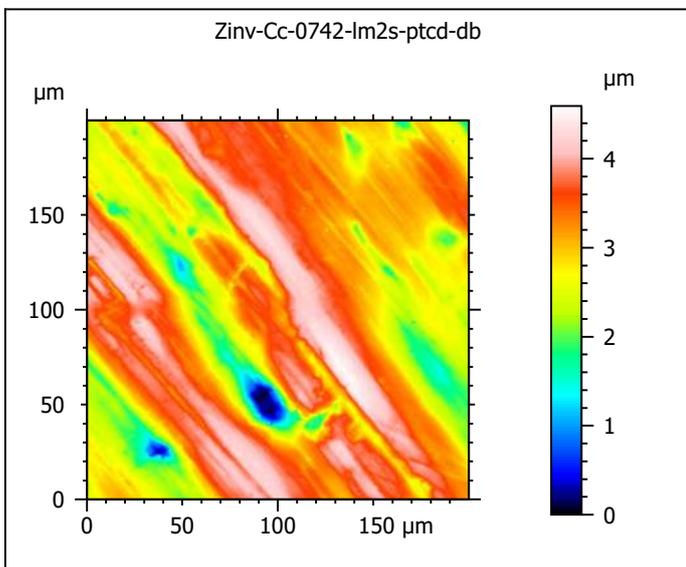
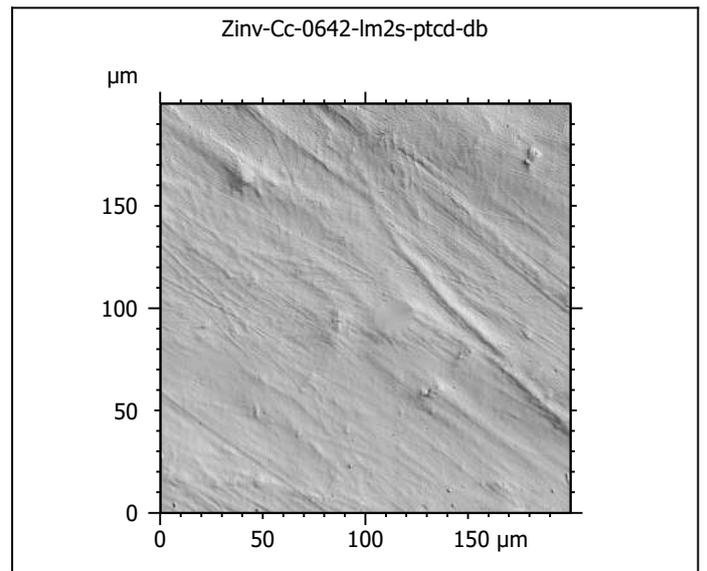
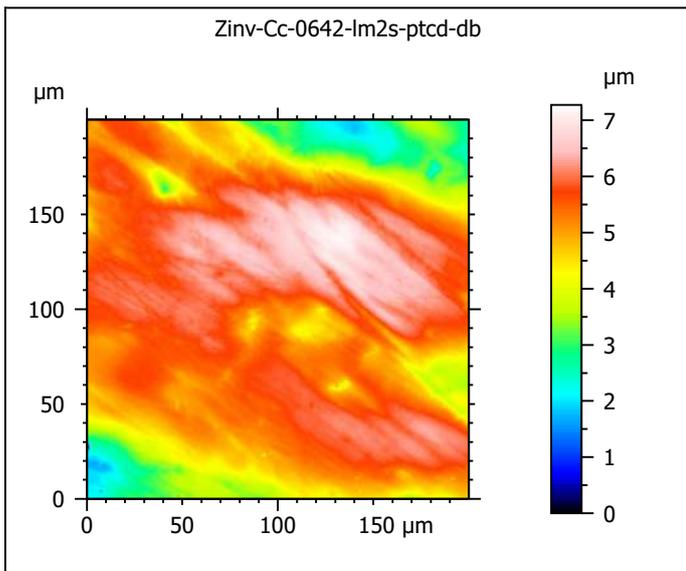
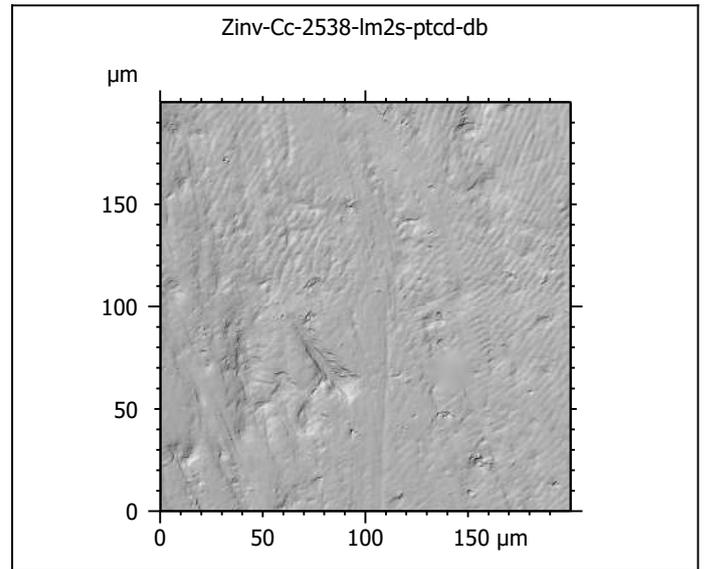
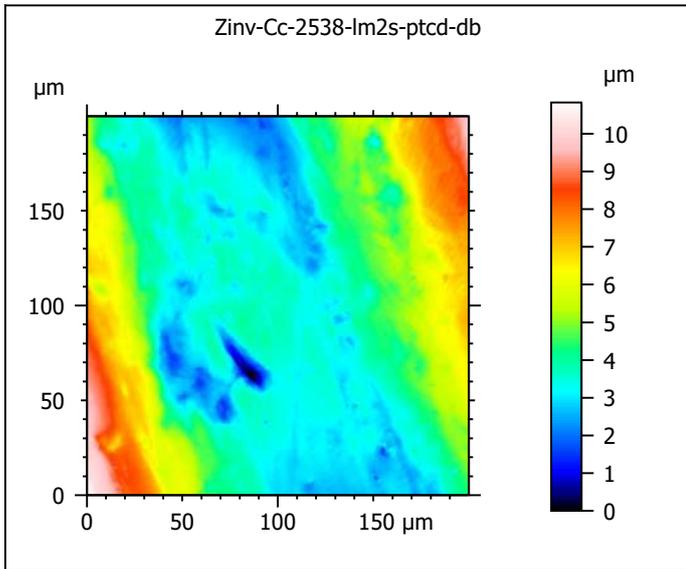
ANR-13-JSV7-0008-01, PI: G. Merceron



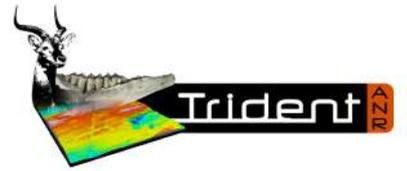
Photosimulations and false color elevation maps of scanned molar facets of the roe deer (*Capreolus capreolus*) from the Bauges Natural Regional Park, France
scanned at the PALEVOPRIM lab by G. Merceron, CNRS and University of Poitiers, France with "TRIDENT", white light confocal microscope Leica DCM8



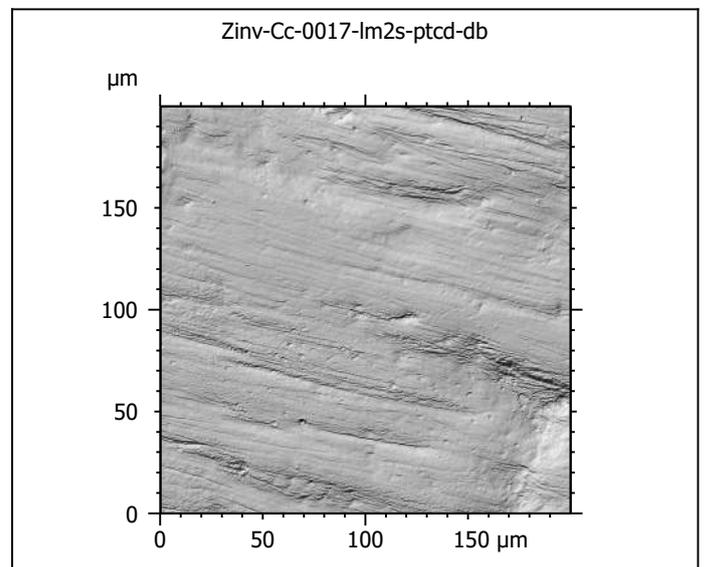
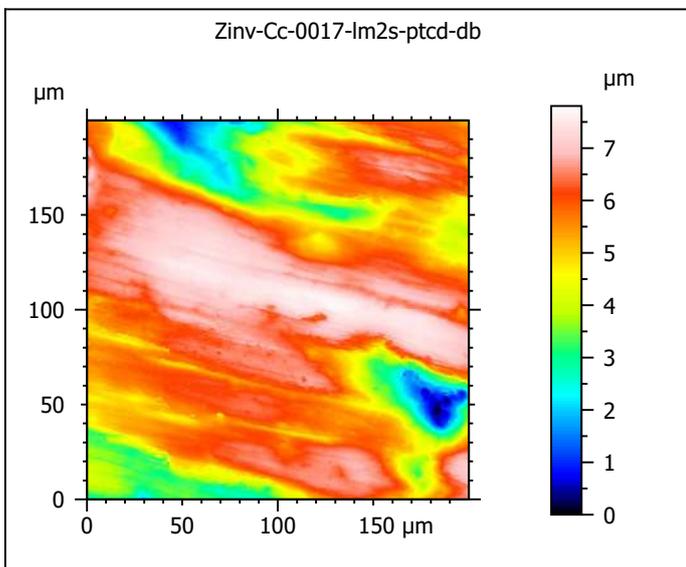
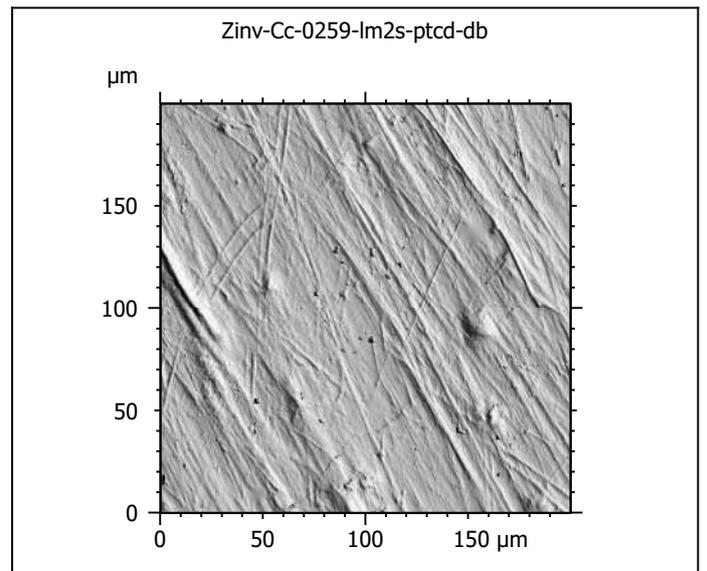
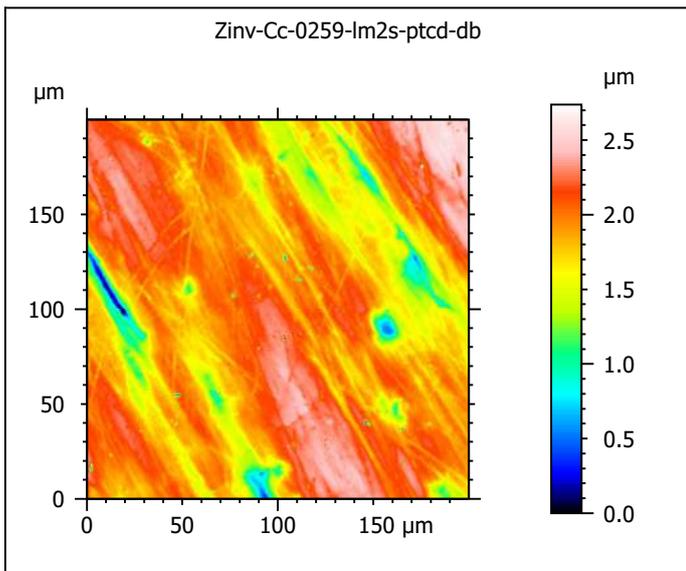
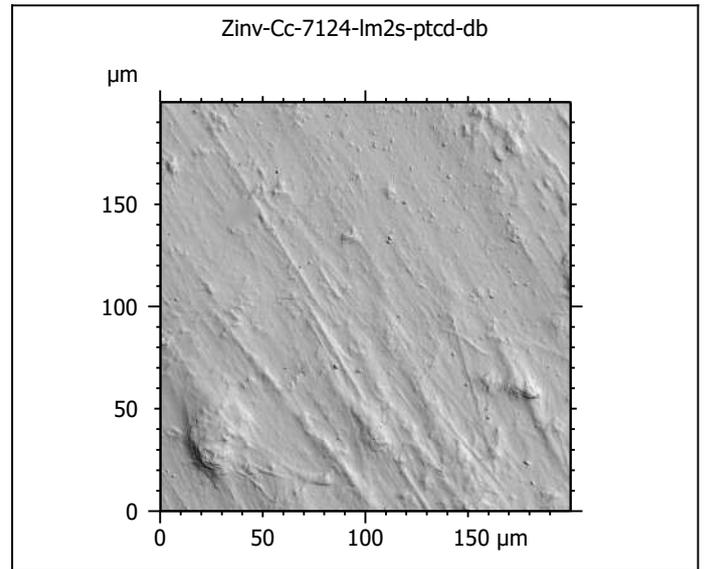
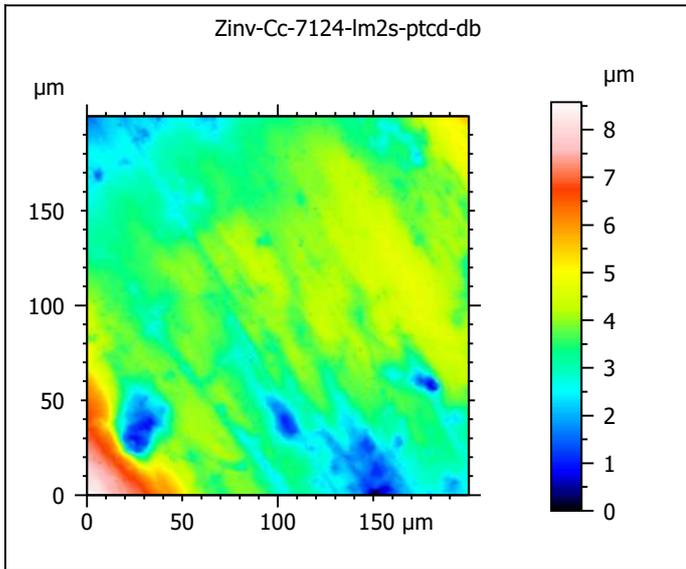
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