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Morphology is not Destiny: Discrepancy between Form, Function and Dietary Adaptation in Bovid Cheek Teeth

Juan Pablo Gailer[1] · Ivan Calandra[2] · Ellen Schulz-Kornas[1,3] ·
Thomas M. Kaiser[1]

Abstract Mammal teeth have evolved morphologies that allow for the efficient mechanical processing of different foods, therefore increasing dietary energy uptake for maintenance of high metabolic demands. However, individuals masticate foods with biomechanical properties at odds with the optimal function of a given tooth morphology. Here, we investigate tooth form and function using two quantitative 3D methods at different scales on the same individuals of nine bovid species. Dental topometry quantifies the gross morphology, and therefore, reflects evolutionary adaptive patterns. Surface texture analysis infers mechanical occlusal events, which reflect the actual tooth function, and is free from the influence of morphology. We found that tough foods can be satisfactorily exploited by grazing species with enamel ridge morphologies not more complex than those found in intermediate feeders and browsers. Thus, the evolution of enamel complexity is likely determined by a balance between adaptation and constraints. Wider enamel ridges seem to be a common functional trait in bovids to compensate for severe wear from abrasive foods and/or chipping from hard foods. Our results demonstrate that supposedly essential functional adaptations in tooth morphology may not be required to process food efficiently. This emphasizes the large plasticity between "optimal" morphology and the potential function of the tooth, and underscores the need to appreciate (apparently) maladaptive structures in mammalian evolution as nevertheless effective functioning units.

✉ Juan Pablo Gailer
juan.pablo.gailer@uni-hamburg.de

1   Center of Natural History, University of Hamburg,
     Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

2   GEGENAA – EA 3795, University of Reims Champagne-Ardenne,
     CREA – 2 esplanade Roland Garros, 51100 Reims, France

3   Max Planck Institute for Evolutionary Anthropology, Max Planck
     Weizmann Center for Integrative Archaeology and Anthropology,
     Deutscher Platz 6, 04103 Leipzig, Germany

Introduction

Teeth play a central role in achieving efficient energy uptake from the environment by mammals. Mammalian craniodental diversity has been studied widely with the aim of understanding the morphological adaptations that reflect comminution mechanics to different kinds of diets (e.g., Rensberger 1973; Hiiemae and Crompton 1985; Pérez-Barbería and Gordon 1999, 2001; Evans et al. 2007). It has been shown that there is a correspondence between tooth morphology and the biomechanical properties of food (Fortelius 1985; Archer and Sanson 2002; Lucas 2004; Sanson 2006; Clauss et al. 2008).

The main product of mastication is thought to be the increase of the surface-volume ratio of food particles so that enzymes can act more efficiently in the post-oral digestive system to extract as many nutrients as possible (Pond et al. 1984; Bjorndal et al. 1990; Pérez-Barbería and Gordon 1998). In turn, tooth form also relates to mastication mechanics (Turnbull 1970; Greaves 1991; Pérez-Barbería and Gordon 1999; Gailer and Kaiser 2014).

As a mechanical interface with the environment, teeth need to resist mechanical loads (strain/stress) without fracturing. Loads and possibly induced fractures depend on the shape

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and physical properties of both dental tissues and food particles (Lucas et al. 2000, 2008; Lucas 2004; Strait et al. 2013). Mammals rely on durable dentitions because they possess only two sets of teeth (diphyodont) as opposed to all other vertebrates (Hillson 2005). In summary, this comes down to mammalian teeth are shaped to be effective and efficient for years. This is why mammalian teeth are expected to show a high degree of adaptation related to the biomechanical properties of food items and to the overall physical composition of the diet, for both efficient processing and resistance to fracture.

However, tooth morphology is not only the result of functional adaptations: developmental and phylogenetic constraints also influence the outcome of tooth shape (Butler 1939; McKitrick 1993; Salazar-Ciudad et al. 2003; Salazar-Ciudad and Jernvall 2004; Kavanagh et al. 2007). Because of this, it is crucial to assess tooth function separately from tooth form in order to disentangle the influences of these factors on the evolution of teeth. Moreover, individuals may change their dietary preferences over their lifetime, yet morphology takes many generations to change as a response to selective dietary pressures. Thus, morphological indicators of diet reflect what individuals are capable of eating, but not necessarily what each of them actually eats. Is a given morphology really engaged in providing the function for which it is thought to be best designed? Or is a given morphology the best compromise between what is possible in terms of deep-time, developmental constraints, and functional adaptations? Are there discrepancies between expected and observed tooth function? If yes, where do they come from? These are examples of questions that need to be addressed in any evolutionary study of morphology.

In order to address these questions, we analyzed nine bovid species and included representatives from different herbivorous dietary preferences: frugivory, leaf-browsing, intermediate feeding, and grazing (Hofmann and Stewart 1972; Heywood 2010). We combined two 3D methods addressing different scales of occlusal surface data and applied them to the molars of the same individuals. Dental 3D occlusal topometry relates to the large-scale (centimeter) occlusal morphology of the teeth (Gailer and Kaiser 2014). We expected to find signals in tooth form that relate to current as well as to past functional adaptations. The second method employed was the 3D surface texture analysis (Schulz et al. 2010; Calandra et al. 2012). This method provides a tool set for understanding how occlusal facets are contacting each other and with foods at the micrometer scale. The surface texture pattern represents a traceological snapshot that allows inferences to be made regarding actual function in relation to the physical properties of a given diet. This signal can be considered independent of large-scale tooth morphology and underlying phylogenetic affinity (Schulz et al. 2013b), at least within a given bauplan (Mihlbachler et al. 2015).

Hence, the combination of these methods has the potential to discriminate the contributions of function, history, and dietary adaptation on tooth morphology. It also illustrates some aspects of the complex relationships between tooth form and function.

Material and Methods

Specimen Selection and Preparation

Upper second molars (M2) of nine species of the Bovidae (Artiodactyla, Mammalia) were investigated: *Aepyceros melampus*, *Capra ibex*, *Cephalophus silvicultor*, *Connochaetes taurinus*, *Hippotragus equinus*, *Kobus ellipsiprymnus*, *Ovibos moschatus*, *Taurotragus oryx*, and *Tragelaphus strepsiceros*. These species have diets spanning the herbivorous spectrum from fruit-browser, to general browser, to intermediate feeder, and to grazer (Fig. 1, Table 1). Specimens included in this study were adult wild-caught individuals (Online Resource 1). The sample size ranged between five and eight individuals per species. Only molars from tooth rows of individuals in functional wear stages, i.e., with entirely erupted permanent dentitions with internal enamel structures of the first molar to erupt (M1) still exposed, and with the last erupted molar (M3) already showing wear, were included in our sample. This corresponds to the adult individual dental age stage (IDAS 3) of Anders et al. (2011). First molars of two individuals of *C. taurinus* were sampled. This allowed us to increase the sample size for this species; otherwise, material meeting quality requirements to allow application of both methods (3D topometry and 3D surface texture) would not have been available. In order to avoid acquisition of distorted 3D occlusal surface data, all molars had to be in perfect condition with no broken cusps and/or ectolophs. Enamel facets also had to be free from microscopic surface adherences. Thus, all surfaces were thoroughly cleaned prior to moulding following the protocol by Schulz et al. (2010).

Molds were made from the cleaned occlusal molar surface following Kaiser and Brinkmann (2006). Silicone molds were then reversed with epoxy resin (Injektionsharz EP, Reckli-Chemiewerkstoff, Herne, Germany). Enamel facets of upper second molars were individually molded from these castings using the high impression material again to allow precise and repeatable orientation of a single wear facet (Schulz et al. 2010). If available, the originals were molded instead of casts (Online Resource 1).

3D Surface Texture Analysis

The mesial enamel facet of the metacone on the upper second (M2) or first (M1) molar was molded following the procedure of Schulz et al. (2010). Surface scans of enamel facets were obtained using the 3D disc-scanning confocal microscope
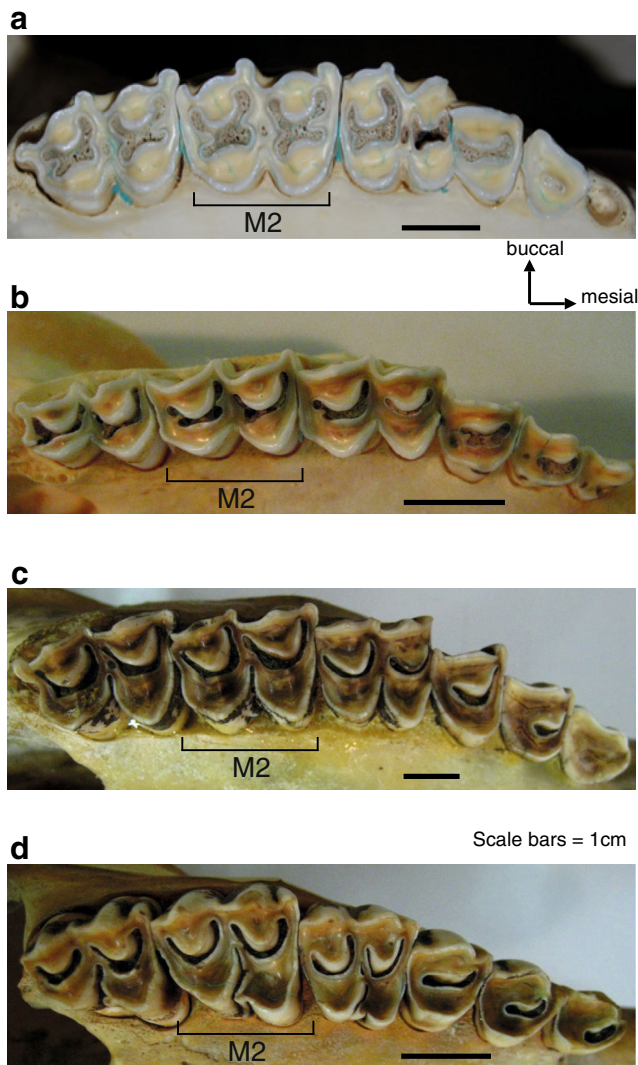
Fig. 1 Photographs of the upper postcanine tooth rows of four species representing the dietary categories studied. **a**, grazer (*Connochaetes taurinus*, ZMH-6774); **b**, intermediate feeder (*Aepyceros melampus*, ZMH-6765); **c**, browser (*Tragelaphus strepsiceros*, ZMH-4527); **d**, frugivore (*Cephalophus silvicultor*, ZMH-4535); M2, second molar. The most anterior tooth shown to the right is the second premolar (P2) and the most posterior tooth shown to the left is third molar (M3). ZMH, Zoologisches Museum Hamburg. See Online Resource 1

μsurf custom (NanoFocus AG, Oberhausen, Germany) with resolution x, $y = 0.16$ μm and $z = 0.06$ μm. Surface areas with defects or adherent dirt were rejected, as well as measurements with less than 94 % surface points recorded or a vertical displacement range δz > 40 μm. Three or four non-overlapping measurements per facet were scanned for each specimen.

Measurements were prepared in batch using a template in μsoft Analysis Premium v. 5.1 (NanoFocus AG; a derivative of MountainsMap® Analysis software by Digital Surf, Besançon, France). This template (1) mirrors all the surfaces in z (measurements were scanned from the molds directly, i.e.,

from an inverted representation of the facet, so that the measurements first had to be inverted) and the surfaces from right molars in x (to have the same orientation for all teeth), (2) levels them (least square plane by subtraction), (3) fills the <6 % of unrecorded points, (4) filters the surface (spatial filtering using denoising median 5 × 5 and Gaussian 3 × 3 filter, default cut offs), (5) removes the form alterations (second order polynomial), and (6) quantifies the surface with 30 ISO 25178–2 parameters (International Organization for Standardization 2010). ISO parameters describe the basic geometric properties of surface textures. We focused on two parameters that can be readily interpreted in terms of food properties: the Root mean square height (Sq) relates to the height difference between the highest and lowest points of the surface, and the Material volume of core (Vmc) corresponds to the volume below the surface between the material ratio p and q (Table 2; see Fig. 2 in Kaiser et al. 2016 for a schematic representation and formula of the parameters).

3D Occlusal Topometry

Subsequent to the data acquisition for 3D surface texture analysis, the high-resolution dental castings were whitened with ammonium chloride powder in order to minimize light reflectance on occlusal surfaces. The optical topometric digitization system (smart*SCAN*³ᴰ, Breuckmann, Meersburg, Germany) was employed to digitalize the teeth according to Gailer and Kaiser (2014). All scans were taken at the maximum output resolution of x, $y = 50$ μm and $z = 1$ μm. The acquired 3D models from the scanning process were subsequently imported as STL files (polygonal models) in the IMEdit module of the metrology software PolyWorks v. 11 (InnovMetric Software Inc., Québec, Canada). Enamel and dentin of the 3D occlusal surface were interactively separated. The 3D length of the resulting polygonal models of enamel structures, and the 3D area of both enamel and dentin surface models, were then quantified following the procedure in Gailer and Kaiser (2014). The occlusal shape parameters (Table 2), Indentation Index D (Schmidt-Kittler 2002; Gailer and Kaiser 2014), and Relative Width of Inner Enamel Ridges EW (Fig. 2) were then calculated based on the measured 3D enamel structures lengths and 3D enamel and dentin areas. The use of 3D data to calculate shape descriptors like D and EW renders more precise information about geometrical attributes of the occlusal surface than the 2D data formerly employed to assess bovid occlusal shape variation among dietary preferences.

The D parameter describes the degree of folding of enamel ridges on a worn occlusal surface, i.e., enamel complexity (Table 2). Higher enamel complexity means more occlusal contacts acting as breaking sites, thus increasing occlusal shearing efficiency. The calculation and functional significance of this parameter for bovid cheek teeth are thoroughly

Table 1   Dietary information on species investigated in this study

| Species	Feeding strategy	Annual dietary variability	References
Aepyceros melampus	Intermediate feeder	Grass > 90 % Browse up to 80 % Fruit (average) 10 %	Estes (1991); Gagnon and Chew (2000); Kingdon (2001); Cerling et al. (2003); Sponheimer et al. (2003)
Capra ibex	Intermediate feeder	Grass up to 76 % Browse (average) 47 % Fruit 0 %	Houte de Lange (1978); Pérez-Barbería et al. (2004)
Cephalophus silvicultor	Frugivore	Grass (average) 1 % Browse (average) 28 % Fruit (average) 71 %	Gagnon and Chew (2000); Kingdon (2001); Cerling et al. (2003)
Connochaetes taurinus	Grazer	Grass up to 100 % Browse (average) 12 % Fruit (average) 0.5 %	Skinner and Smithers (1990); Estes (1991); Gagnon and Chew (2000); Kingdon (2001)
Hippotragus equinus	Grazer	Grass up to 100 % Browse (average) 10 % Fruit (average) 5 %	Skinner and Smithers (1990); Estes (1991); Gagnon and Chew (2000); Kingdon (2001); Pérez-Barbería et al. (2004)
Kobus ellipsiprymnus	Grazer	Grass (average) 92 % Browse (average) 15 % Fruit (average) 1 %	Skinner and Smithers (1990); Estes (1991); Gagnon and Chew (2000); Kingdon (2001); Pérez-Barbería et al. (2004)
Ovibos moschatus	Intermediate feeder	Graminoids, forbs, willows, mosses, lichens	Lent (1988); Oakes et al. (1992)
Taurotragus oryx	Intermediate feeder	Grass (average) 50 % Browse (average) 45 % Fruit (average) 5 %	Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003)
Tragelaphus strepsiceros	Browser	Grass (average) 15 % Browse (average) 55 % Fruit (average) 30 %	Jarman (1971, 1974); Gagnon and Chew (2000); Cerling et al. (2003); Sponheimer et al. (2003)

described and explained in previous work (Gailer and Kaiser 2014: figs. 2 and 3).

The enamel width (*EW*) parameter is introduced in the present study as a morphological descriptor in dental topography that is useful in inferring tooth durability and resistance to different kinds of mechanical stresses. It is calculated as the proportional width of the inner enamel ridges relative to the overall proportional width of all occlusal enamel ridges (Fig. 2, Table 2). *EW* has been developed in this study based on the fact that differentiation of occlusal morphologies

Table 2   Description and meaning of the 3D dental parameters

Name	Parameter	Description	Example
Topometry			
Indentation Index (occlusal complexity)	*D*	Structural density of an occlusal pattern defined as a quotient of two areas: the numerator is determined by the area of the circle whose perimeter equals the total measured 3D-length of the enamel structures; the denominator corresponds to the measured 3D-area of the occlusal surface (Gailer and Kaiser 2014: fig. 3).	An occlusal pattern characterized by long, infolded enamel ridges will have high *D* values.
Relative width of inner enamel Ridges	*EW*	Width of the internal enamel structures relative to the overall width of occlusal enamel, which is calculated as a quotient where the area-length ratio of inner enamel is divided by the area-length ratio of total occlusal enamel (Fig. 1).	An occlusal surface in which proportionally wider enamel structures build up the inner enamel ridges will have larger *EW* values.
Microtexture			
Root mean square height of the scale limited surface	*Sq*	Standard deviation of the height distribution or of the amplitudes of the surface (height parameter). Parameter units: μm (Kaiser et al. 2016: fig. 2).	A surface with high peaks and/or deep valleys will have a high *Sq* value.
Material volume of core	*Vmc*	Volume below the surface when the 10 % highest and 20 % lowest points are removed. Parameter units: $\mu m^3 / \mu m^2$ (Kaiser et al. 2016: fig. 2).	A surface with wide and/or deep valleys will have a high *Vmc* value.
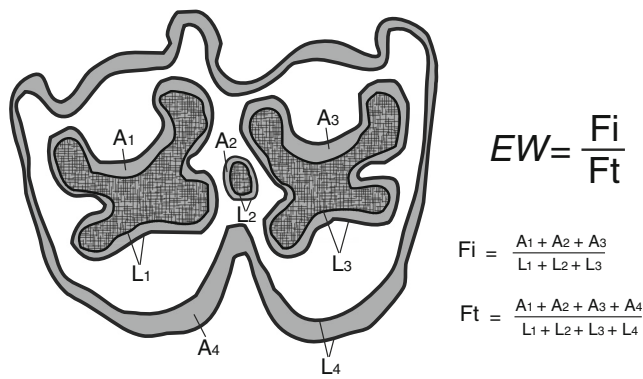
Fig. 2 Schematic representation of an occlusal surface of a bovid upper molar showing how the relative inner enamel width (*EW*) is calculated. *EW* is the quotient of two area-length ratios, where the area to length ratio of the inner enamel (Fi) is divided by the area to length ratio of the total enamel (Ft). Deviations from the effect that long enamel band boundaries tend to enclose thin enamel areas is controlled for by using the area:length ratios of each enamel structure. The enamel length for each enamel structure is therefore calculated as the sum of both inner and outer boundaries. A, area; L, length; black, enamel borders; grey, enamel; white, dentin; hatched, cementum (central cavity)

among bovids with different dietary preferences largely results from variation of the inner enamel structures; i.e., in occlusal view, the band-like enamel ridges (inner enamel) that are discontinuous with the surrounding, tooth crown-delimiting enamel ridge (outer enamel) (Fig. 1; Archer and Sanson 2002; Bibi 2007a; Heywood 2010). There is a very strong correlation (percentage bend correlation coefficient = 0.916)

between the area-length ratios of the inner and of the total occlusal enamel ridges indicating that variations in occlusal enamel are indeed due to differences in the inner enamel ridges (Online Resource 2). This implies that *EW* quantifies the most important part of the variation in enamel width on the occlusal surface.

Statistics

The complete statistical procedure was carried out with the open-source software R 2.12.2 (R Development Core Team 2010). The following R packages were used for data mining: doBy (Højsgaard et al. 2010), R.utils (Bengtsson 2010), RSvgDevice (Luciani 2009), and xlsReadWrite (Suter 2010). The statistic tests themselves were applied with the functions written by Rand R. Wilcox (Wilcox 2005) and included in the package WRS (Wilcox and Schönbrodt 2010).

The median of the ISO parameters derived from the several (three or four) surface texture measurements taken from a single facet was calculated (Schulz et al. 2010; Calandra et al. 2012) and subsequently used for further statistical analysis.

We tested for differences between species' means using one-way analyses of variance (ANOVA). Because our data were not normally distributed and homoscedastic (Online Resources 3–4), we followed the method of Wilcox (2003, 2005) and applied the robust Welch-Yuen heteroscedastic omnibus test (Welch 1938; Yuen 1974) coupled with a heteroscedastic pair-wise comparison test analogous to Dunnett's T3 test (Dunnett
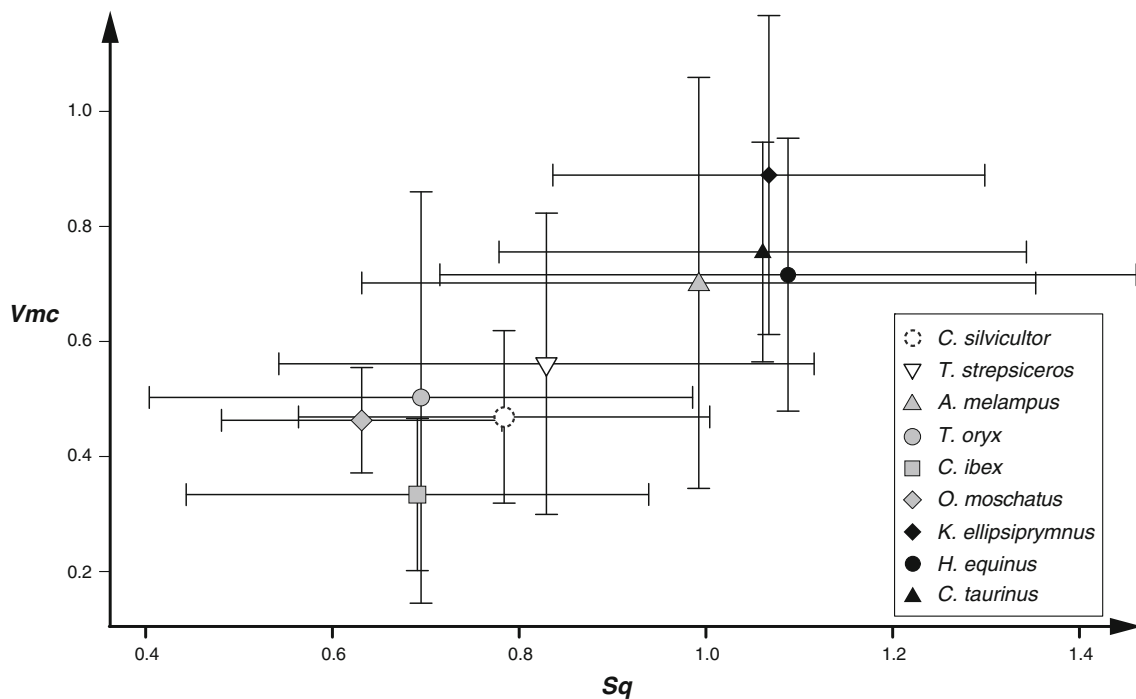
Fig. 3 Bivariate plot of the surface texture parameters Root mean square height (*Sq*) vs. Material volume of core (*Vmc*). Symbols indicate the means and error bars represent the standard deviation for both parameters for each species. Black, grazer; grey, intermediate feeder; white, browser; hatched outline, frugivore

1980) to locate the source of significant differences among all species. In addition to these robust tests, we applied a 15 % symmetrical trimming on means to cope with non-normality (i.e., 15 % of the data was removed from each side of the distribution). This approach was found to perform better than the standard F-test in the case of heteroscedasticity and/or non-normality and equally well in the case of coupled homoscedasticity and normality (Wilcox et al. 1986; Moser et al. 1989; Wilcox 2003). A more detailed description of the procedure applied here can be found in the supplementary material of Calandra et al. (2012).

Results

Descriptive statistics for all parameters are presented in Table 3 and boxplots for each parameter are shown in Online Resource 3–4.

3D Surface Texture Analysis

The Sq and Vmc parameters differ significantly ($p = 0.036$ and $p = 0.013$, respectively) among the nine bovid species (Table 4). Pair-wise tests group the three grazers together with the highest Sq and Vmc means (high heights and volumes, respectively) without significant differences in both parameters among these species (Fig. 3, Table 5). Three of the intermediate feeders, C. ibex, O. moschatus, and T. oryx, are characterized by low Sq and Vmc, which do not significantly differ among these species. The remaining intermediate feeder, A. melampus, and the browser, T. strepsiceros, are intermediate in range for both parameters. These two species also show a very large variation in Vmc and Sq, which overlaps with the means of all other species in both parameters (Online Resource 3). There is only one significant difference in Vmc

that discriminates A. melampus from any other species, namely C. ibex (Table 5). The frugivorous species, C. silvicultor, also displays a large Sq variation that does not permit discrimination from any other species (Table 5). However, its Vmc values are significantly lower than in the grazers.

3D Occlusal Topometry

Significant differences are detected for both enamel complexity (D) and enamel width (EW) parameters ($p < 0.001$, Table 4) among the nine bovid species studied. Results of the pair-wise tests (Table 5) reveal that in one species, H. equinus, D is significantly larger than in any of the remaining species (Fig. 4). This species also possesses the largest EW, although not significantly different from K. ellipsiprymnus and C. silvicultor.

The latter two species represent a second group also having an EW significantly higher than the remaining species, but with low to intermediate mean D values. D is also significantly lower in C. silvicultor than in K. ellipsiprymnus.

Table 4 Results from the Welch-Yuen tests with 15 % trimming for the interspecific variation of the dental parameters D, EW, Sq, and Vmc

Parameter	F	p	nu1	nu2
D	8.820	<0.001	8	17.205
EW	34.720	<0.001	8	17.252
Sq	2.784	0.036	8	17.109
Vmc	3.615	0.013	8	16.841

Interspecific differences per parameter are significant when $p <= 0.05$. F, test statistics; nu1 and nu2, 1st and 2nd degree of freedom; p, significance level. Parameters: see Table 2

Table 3 Descriptive statistics. n, number of individuals per species; SD, standard deviation

| Species	n	D Mean	D SD	EW Mean	EW SD	Sq Mean	Sq SD	Vmc Mean	Vmc SD
A. melampus	7	8.118	1.335	0.644	0.034	0.992	0.361	0.702	0.357
C. ibex	6	9.316	1.164	0.699	0.069	0.691	0.247	0.334	0.132
C. silvicultor	8	8.217	0.933	0.908	0.054	0.784	0.220	0.469	0.150
C. taurinus	7	10.564	0.822	0.797	0.064	1.061	0.282	0.756	0.191
H. equinus	8	14.158	3.344	0.955	0.055	1.088	0.373	0.716	0.237
K. ellipsiprymnus	5	9.508	0.883	0.891	0.055	1.067	0.231	0.889	0.277
O. moschatus	6	9.216	1.608	0.811	0.039	0.631	0.150	0.463	0.091
T. oryx	6	9.617	1.416	0.686	0.066	0.695	0.291	0.503	0.357
T. strepsiceros	6	10.123	0.988	0.626	0.049	0.829	0.286	0.561	0.262

Parameters: see Table 2

Table 5 Results from pair-wise Dunnett Tests with 15 % trimming for the interspecific variation of the dental parameters *D*, *EW*, *Sq,* and *Vmc*

		D			*EW*			*Sq*			*Vmc*		
Species 1	Species 2	Test	*p*	df	Test	*p*	df	Test	*p*	df	Test	*p*	df
C. taurinus	*H. equinus*	2.995	**0.029**	5.229	4.843	**0.001**	8.999	0.184	0.858	8.877	0.276	0.789	8.999
C. taurinus	*K. ellipsiprymnus*	2.317	0.065	5.318	3.040	**0.016**	7.933	0.177	0.864	7.898	0.736	0.484	7.465
C. taurinus	*A. melampus*	6.210	**0.001**	5.726	5.753	**0.002**	5.541	0.303	0.770	7.473	0.610	0.560	7.479
C. taurinus	*C. ibex*	2.354	0.056	6.135	2.531	**0.032**	8.891	2.629	**0.029**	8.473	4.064	**0.006**	6.492
C. taurinus	*T. oryx*	1.469	0.194	5.778	2.954	**0.016**	8.961	2.412	**0.039**	8.931	1.567	0.155	8.245
C. taurinus	*O. moschatus*	1.897	0.110	5.607	0.766	0.467	7.523	3.539	**0.012**	6.156	3.078	**0.026**	5.249
C. taurinus	*T. strepsiceros*	0.863	0.418	6.541	5.460	**<0.001**	8.525	1.616	0.141	8.905	1.499	0.168	8.998
C. taurinus	*C. silvicultor*	7.003	**<0.001**	7.521	4.182	**0.003**	7.785	2.007	0.079	8.166	2.789	**0.025**	7.496
H. equinus	*K. ellipsiprymnus*	3.709	**0.009**	6.301	1.770	0.111	8.936	0.038	0.970	8.571	0.946	0.371	8.339
H. equinus	*A. melampus*	4.972	**0.003**	5.986	11.217	**<0.001**	6.501	0.111	0.914	8.797	0.346	0.738	8.356
H. equinus	*C. ibex*	3.777	**0.007**	6.886	6.740	**<0.001**	9.891	2.081	0.068	8.888	3.421	**0.010**	7.484
H. equinus	*T. oryx*	3.391	**0.010**	7.672	7.243	**<0.001**	9.965	1.943	0.082	9.596	1.300	0.226	9.060
H. equinus	*O. moschatus*	3.604	**0.007**	8.278	4.773	**0.001**	8.433	2.710	**0.032**	6.699	2.461	**0.047**	6.252
H. equinus	*T. strepsiceros*	3.163	**0.018**	6.384	10.185	**<0.001**	9.461	1.237	0.246	9.538	1.169	0.269	9.995
H. equinus	*C. silvicultor*	5.073	**0.003**	5.789	1.531	0.161	8.696	1.525	0.163	8.531	2.283	**0.050**	8.482
K. ellipsiprymnus	*A. melampus*	2.602	**0.032**	7.836	9.131	**<0.001**	5.297	0.165	0.874	7.044	1.197	0.266	8.000
K. ellipsiprymnus	*C. ibex*	0.311	0.763	8.954	5.148	**0.001**	8.996	2.606	**0.029**	8.839	4.111	**0.008**	5.499
K. ellipsiprymnus	*T. oryx*	0.155	0.881	8.457	5.619	**<0.001**	8.994	2.367	**0.042**	8.994	2.019	0.074	8.976
K. ellipsiprymnus	*O. moschatus*	0.382	0.713	7.972	2.734	**0.029**	7.066	3.632	**0.009**	6.640	3.295	**0.023**	4.726
K. ellipsiprymnus	*T. strepsiceros*	1.088	0.305	8.927	8.378	**<0.001**	8.134	1.528	0.161	8.999	2.005	0.078	8.432
K. ellipsiprymnus	*C. silvicultor*	2.846	**0.022**	7.897	0.537	0.608	7.325	1.946	0.085	8.630	3.101	**0.020**	6.225
A. melampus	*C. ibex*	1.993	0.079	8.623	1.690	0.140	6.233	1.896	0.099	7.186	2.571	**0.046**	5.510
A. melampus	*T. oryx*	2.186	0.061	7.898	1.330	0.229	6.344	1.774	0.114	7.985	0.928	0.378	8.973
A. melampus	*O. moschatus*	1.442	0.190	7.396	8.626	**<0.001**	8.153	2.476	0.054	5.287	1.684	0.156	4.732
A. melampus	*T. strepsiceros*	3.733	**0.005**	8.973	0.992	0.353	7.297	1.084	0.310	7.911	0.728	0.486	8.448
A. melampus	*C. silvicultor*	0.126	0.903	8.538	13.214	**<0.001**	7.945	1.351	0.220	6.839	1.618	0.155	6.241
C. ibex	*T. oryx*	0.402	0.696	9.640	0.317	0.758	9.979	0.025	0.980	9.750	1.086	0.317	6.339
C. ibex	*O. moschatus*	0.123	0.905	9.112	3.471	**0.009**	7.917	0.505	0.627	8.233	1.972	0.081	8.893
C. ibex	*T. strepsiceros*	1.294	0.225	9.744	2.108	0.064	8.989	0.895	0.392	9.794	1.900	0.097	7.388
C. ibex	*C. silvicultor*	2.172	0.060	8.484	6.362	**<0.001**	8.171	0.758	0.466	9.949	1.395	0.195	9.586
T. oryx	*O. moschatus*	0.458	0.657	9.842	3.986	**0.004**	8.137	0.476	0.648	7.480	0.264	0.801	5.650
T. oryx	*T. strepsiceros*	0.718	0.491	8.939	1.803	0.104	9.204	0.806	0.439	9.998	0.324	0.754	9.166
T. oryx	*C. silvicultor*	2.337	**0.049**	7.551	6.967	**<0.001**	8.398	0.665	0.522	9.501	0.309	0.767	6.993
O. moschatus	*T. strepsiceros*	1.177	0.272	8.307	7.256	**<0.001**	9.560	1.500	0.174	7.547	0.868	0.418	6.199
O. moschatus	*C. silvicultor*	1.555	0.164	7.035	4.152	**0.002**	9.972	1.465	0.179	8.591	0.128	0.901	7.857
T. strepsiceros	*C. silvicultor*	4.026	**0.003**	9.274	10.804	**<0.001**	9.739	0.224	0.828	9.560	0.858	0.415	8.370

Values in bold indicate a significant difference ($p \leq 0.05$). Species are sorted in the first column (Species 1) according to amount of grass in the diet, from greatest (top) to lowest (bottom). df, degree of freedom; *p*, significance level; Test, value of the test statistics. Parameters: see Table 2

A third group is characterized by an intermediate *D* and intermediate *EW* and includes the grazer *C. taurinus* and the intermediate feeder *O. moschatus*. Mean *EW* values are significantly lower than in the first and the second group but significantly higher than in the remaining intermediate feeders and the browser. Mean *D* values are not significantly different from *K. ellipsiprymnus*.

A fourth, and last group is characterized by a low to intermediate *D* and low *EW*. It is represented by the intermediate feeders *A. melampus*, *C. ibex*, and *T. oryx*, and by the browser *T. strepsiceros*. Mean *EW* values are significantly lower than in all other groups. Within this group, *D* is significantly different between the lowest mean in *A. melampus* and the highest mean in *T. strepsiceros*. Both *A. melampus* and the
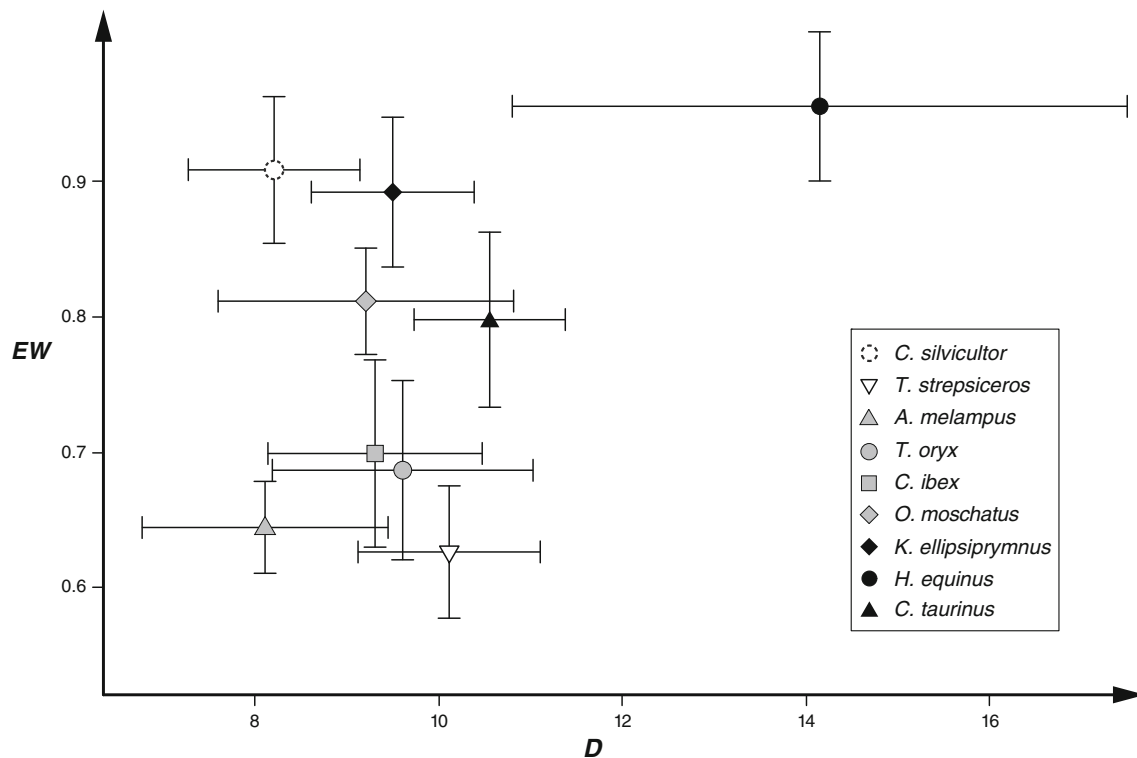
Fig. 4 Bivariate plot of the dental topometry parameters Indentation Index (*D*) vs. Relative Width of Inner Enamel Ridges (*EW*). Symbols indicate the means and error bars represent the standard deviation for both parameters for each species. Black, grazer; grey, intermediate feeder; white, browser; hatched outline, frugivore

frugivore *C. silvicultor* show the lowest *D* among all species, with significantly lower means than in all grazers and the browser (Fig. 4, Table 5).

Discussion

Short-Time Dietary Signal and Evidence of Actual Tooth Function

The 3D surface texture parameters applied in this study reflect geometric characteristics of the tooth surface proposed to distinguish major food sources according to their physical properties (Schulz et al. 2010, 2013a; Calandra et al. 2012; Kaiser et al. 2016). Our results consistently suggest that grazing species consume foods of similar physical character, thus leaving a common surface signature of dietary mechanical impact: the tooth surface is characterized by high height (*Sq*) and volume (*Vmc*; Fig. 3 and Online Resource 3). This reflects the processing of small abrasive particles like phytoliths and grit that heavily wear the enamel surfaces (Calandra et al. 2012). This is consistent with previous studies on ungulates based on ISO 25178 parameters (Schulz et al. 2013a; Winkler et al. 2013).

Lower *Sq* and *Vmc* values indicate that, except for *A. melampus*, intermediate feeding species suffer less surface abrasion than grazers. Less hard and/or lower abundance of small indenting abrasive particles in their mixed diets conform to their lower values for both texture parameters. We argue that the surface texture signal of these intermediate feeders is more likely reflecting a less frequent processing of plant material comprising similar kinds of abrasive particles. We are not aware of significant interspecific variation in phytolith hardness among angiosperms, but there are variations in relative abundance between taxa, for instance between dicot and monocot species (Richmond and Sussman 2003; Hodson et al. 2005; Currie and Perry 2007). Also, it is not known whether differences in the hardness of exogenous abrasive particles (dust and grit) are correlated with different kinds of feeding strategies. However, it is hypothesized that abundant ingestion of exogenous abrasive particles is strongly associated with food intake close to ground level and in dry environments (Janis 1988; Damuth and Janis 2011; Jardine et al. 2012), and therefore to a large extent with grazing feeding strategies. Thus, less frequent consumption of abrasive particles in intermediate feeders is due to their regional, seasonal and/or opportunistic switching between browsing and grazing (Jarman 1971, 1974; Estes 1991; Kingdon 2001; Cerling et al. 2003; Sponheimer et al. 2003). The textures of these species rather indicate that their teeth were used to process browse of lower phytolith content, and, most likely, at feeding heights above grass level.

Contrary to the rest of the intermediate feeding species, the surface texture of *A. melampus* reveals that this species may partly consume diets of similar abrasiveness to grazers. This is very likely depicting the distinctive seasonal and regional variation (Estes 1991; Kingdon 2001) coupled with the extremely wide range of dietary fluctuation (with up to 90 % grass; Sponheimer et al. 2003) of this species. Some of the specimens sampled here must be representative of populations collected in grass-dominated seasons and/or habitats.

In a similar way, the browser *T. strepsiceros* seems to comminute foods with abrasive properties that considerably overlap with those of the grazers' diets. The comparatively middle range values of both surface texture parameters in this species indicate a consumption of grass too high to agree with the dietary composition characteristic of a browser (Hofmann and Stewart 1972). Browsing dicot plant material far above the ground by large bovid species like *T. strepsiceros* would minimize ingestion of extrinsic and intrinsic abrasives. Surface texture patterns would then appear flatter than in intermediate feeders and grazers because surface textures would have lower peaks (low *Sq*) and shallower and narrower valleys (low *Vmc*). In summary, comparatively lowest *Sq* and *Vmc* values would characterize the surface textures of a typical leaf-browsing species. That *T. strepsiceros* is not depicted here as a typical browser is consistent with its more recent recognition as a generalist species based on another type of surface texture analysis (Scale sensitive fractal analysis; Scott 2012) and with its seasonal variability inferred from field observations (Jarman 1971, 1974).

The surface texture pattern of the frugivorous species, *C. silvicultor*, does not fully differentiate it from any other species (*Sq*) and it rather resembles those of intermediate feeding species (*Vmc*). This is not surprising since, although fruit objects are biomechanically different (i.e., harder; Lucas 2004) than the plant foliage (such as grass leafs), surface textures reflect readily the abrasive effect of consumed microscopic particles associated with a specific food type with a given biomechanical property, but not the biomechanical nature of the foods themselves (Strait et al. 2013). Hard fruit objects with large radii (e.g., seed shells) would not be recorded by surface texture analyses because indentation with a large radius on the enamel surface will fracture the tooth crown causing enamel chipping before inducing microwear features (Strait et al. 2013). In contrast, hard (microscopic) particles with radii < 50 µm (e.g., phytoliths, dust; Lucas et al. 2008) affect enamel surfaces causing microwear features before inducing cracks (Strait et al. 2013). Thus, the observed surface texture pattern could be missing information about the processing of hard, relatively large fruit objects in the diet of these animals. However, Calandra et al. (2012) suggest that high values of surface texture features like *Sq* reveal the consumption of large hard particles like fruit seeds among primates. We cannot confirm such conclusions from our bovid sample, but our results do not contradict this either. Processing of large objects in primates occurs mainly by crushing, as opposed to the predominantly bucco-lingual chewing motion in bovids, thus leading to fragmentation of foods by shear-cutting. We propose that this difference between chewing dynamics could explain that the consumption of large hard particles is much better recorded in the surface texture features in primates than in bovids. Large object crushing produces chipping by induction of cone cracks that result in deep features on the enamel (Lucas et al. 2008). The depth of such features in the thick enamel of primates can contribute to high surface texture reliefs. On the other hand, bucco-lingual chewing of large objects in bovids would induce crack formation in a more perpendicular manner to the sagittal plane. Enamel chipping might then result in flatter and wider features that are hardly recorded as surface texture signals.

The surface texture signal displayed by *C. silvicultor* is likely indicating that small hard particles are consumed to a lesser extent than in grazing diets but within the range of intermediate feeders.

Deep-Time Legacy and Expected Functional Adaptation in Morphology

Complexity (*D*) and relative width (*EW*) of enamel structures represent two different functional performances of the chewing topography. Teeth with more complex occlusal patterns are more likely to render increased fragmentation efficiency (Evans et al. 2007) due to abundant enamel-enamel contact sites spread throughout the occlusal stroke (Schmidt-Kittler 2002; Gailer and Kaiser 2014). This should in turn facilitate the processing of tough food components at low Young's modulus (modulus of elasticity; Lucas 2004). Thus, highly anisotropic plant materials rich in fiber and of relatively small dimension like grass may only be efficiently comminuted with multi bladed "shear-cutting" and grinding occlusal topographies (Schmidt-Kittler 2002; Kaiser et al. 2010). We therefore expect the *D* parameter to reflect adaptations related to food toughness.

Teeth with relatively wide enamel ridges are prone to withstand higher wear rates because masticatory loads are distributed onto a larger area. There is always a constant loss of small quantities of dental tissues due to microscopic intrinsic and/or extrinsic abrasives (phytoliths, grit, and/or dust; Williams and Kay 2001). Dietary wear may result in tooth fracture or chipping leading to sudden loss of dental tissue as the consequence of local overload when biting on relative hard, large food objects (Strait et al. 2013). In primates, thick enamel is seen as an adaptation to resist wear in both such circumstances (e.g., Pampush et al. 2013). In selenodont dentitions, enamel thickness is represented by the width of occlusal enamel ridges (Archer and Sanson 2002). The latter measure,

however, is not independent of the proportion of occlusal enamel, because of spatial limitations (Schmidt-Kittler 1984). A complex pattern of thin enamel ridges may occupy the same area on the occlusal surface as a simple pattern of wide ridges (Fig. 2, Table 2). Thus, we may assume that relative wider enamel ridges are better adapted to resist wear, regardless of the mechanism and kind of abrasive agent inducing loss of dental tissue. *EW* should therefore reflect adaptations to tooth wear.

Adaptation to Food Toughness

We expected to find a gradient of decreasing occlusal enamel complexities (*D*) from grazers to mixed feeders, to browsers and to frugivores, reflecting the decreasing need for efficient processing of fibrous, tough plant material like grass. However, *D* reveals that increased grass consumption results in adaptation toward higher enamel complexity in only one of the grazing species, *H. equinus*. Although the other two grazers, *C. taurinus* and *K. ellipsiprymnus*, suffer equal dietary wear impact as *H. equinus*, which is confirmed by the texture signals (Fig. 3 and Online Resource 3) and in accordance with diet data from the literature (Table 1), their enamel occlusal patterns are not more complex than in intermediate feeders, which consume substantial amounts of browse material. The reason for the high values in *H. equinus* might be related to evolutionary history (see below).

As we expected, none of the intermediate feeders showed any remarkably high occlusal complexity. The latter do not vary considerably among them either. The intermediate feeders investigated ingest different proportions of grass and browse (Table 1). This shows that a common morphological trait such as the enamel occlusal complexity in intermediate feeders is able to yield a large range of functional tolerance. Thus, it can be used to process effectively, although probably not most efficiently, biomechanically distinctive foods (i.e., from grass at the one end and browse at the other of the continuum of toughness and brittleness of plant material properties). It is of great interest that enamel complexity in *T. oryx*, *C. ibex*, and *O. moschatus* is not different from that of two of the grazing species, *C. taurinus* and *K. ellipsiprymnus* (Fig. 4 and Online Resource 4). This is in discordance with Heywood's (2010) conclusions that "grazer-like" occlusal morphologies in bovids are only attained if grass is consumed all year round; the results presented here show that similarities between grazer-like and non grazer-like occlusal morphologies might depend on the specific trait from which tooth adaptation is being inferred. In terms of efficiency to comminute tougher food items like grass, intermediate feeders exhibit occlusal enamel complexities as "adapted" as some grazers do. However, other occlusal traits of functional significance to cope with an all year round grazing behaviour might be

relatively poorly adapted (see *EW* below). In accordance with the surface texture signals, the morphology of the browser *T. strepsiceros* seems to be in fact adapted for processing foods with the same biomechanical properties as those eaten by intermediate feeders and some grazers. Its enamel complexity equals that of intermediate feeders and even that of two of the grazers. This may help to explain why, despite preferring browse (Table 1), it is not detrimental for this species to extend its dietary range to (occasionally) feed on grass (Jarman 1971, 1974; Cerling et al. 2003). Moreover, the fact that *T. strepsiceros* is not depicted here as an exclusively leaf-browsing species not only conforms to Scott's (2012) interpretation as a generalist, but also to the interpretation of enamel complexity patterns along its postcanine dentition as adapted to intermediate feeding strategies (Gailer and Kaiser 2014).

We found that the frugivorous species present a very low enamel complexity and link this to the low toughness and high hardness, which characterizes frugivory among various herbivorous diets in mammals (Lucas et al. 2008), although the surface textures do not reflect this aspect (see above).

Adaptation to Tooth Wear

Relatively wider enamel ridges (higher *EW*) should more effectively resist both fracture and chipping due to ingestion of hard, large indenting particles, as well as the progressive, long term removal of dental tissue induced by small indenting particles (Lucas et al. 2009; Strait et al. 2013). Wide enamel ridges result in large areas of contact, and hence low local occlusal pressure (Rensberger 1973; Gailer and Kaiser 2014). Large enamel contact sites sliding across each other during the chewing stroke enable large bite forces to be applied while maintaining local occlusal pressure comparatively low. Hence, the risk of sudden loss of dental tissue by the action of hard, relative large abrasive agents (for instance grit particles > 50 μm; Lucas et al. 2008) is reduced. Larger enamel contact areas also result in increased resistance to wear by means of the same mechanism.

All grazers investigated show wider enamel than intermediate feeders (except for *O. moschatus*) and the single browser (Fig. 4, Table 5 and Online Resource 4). The very wide enamel ridges of *H. equinus* and *K. ellipsiprymnus* match well with the higher abrasive effect of grass diets on the enamel surface as indicated by their surface textures. Increased dental wear rates are strongly associated with grazing because of two major reasons: (1) higher phytolith content in monocots than dicots (Richmond and Sussman 2003; Hodson et al. 2005) and (2) grit contamination of ingesta collected close to the ground and/ or in drier environments (Mendoza and Palmqvist 2008; Damuth and Janis 2011). In the third grazer, *C. taurinus*,

enamel ridges are significantly narrower than in *H. equinus* and *K. ellipsiprymnus*. Yet, there is no difference in the texture signals among all grazers. *Connachaetes taurinus* forage is short, but fresh grass (Gagnon and Chew 2000; Kingdon 2001), which is considered less abrasive than the taller grass eaten by the other two grazers. This is likely due to the increased phytolith content in tall and dry grasses (Kaufman et al. 1981). On the other hand, we expect that feeding short grass closer to the ground would drive selection towards the acquisition of wider enamel ridges because of increased rates of grit ingestion. Evidently, occlusal morphology in *C. taurinus* did not respond to this kind of dietary abrasiveness in such way. We suggest this could be explained by two non-exclusive reasons: either hypsodonty is the major evolutionary response and effective enough to counteract this source of dietary abrasion, and/or the fresh short grass consumed by this species is substantially washed from grit and other extraneous abrasives because it mainly occurs in drained landscapes (Kingdon 2001). Wide enamel ridges along with high Sq and Vmc values in all grazers investigated however suggest that all-year-round grass diets indeed exert selective pressure to acquire wider enamel as morphological adaptation to dental wear.

Lent (1988) and Oakes et al. (1992) suggested that *O. moschatus* is best classified as opportunistic mixed feeder that switches among grasses, woody plants, lichens, mosses and artic willows on both a regional and temporal basis. It is generally obligated to feed at low feeding heights, very close to the ground, in a treeless environment like the tundra (Skinner and Smithers 1990). In terms of surface texture, *O. moschatus* displays the signature of an intermediate feeder, characterized by low Sq and Vmc values. It is thus surprising to find this species within the EW range of grazers, close to *C. taurinus*. Its surface texture signature however is clearly different from that of a typical grazer. Regardless of foraging grass or less abrasive dicot plant material, its diet is probably characterized by the frequent ingestion of large amounts of exogenous hard particles when food sources above ground level are scarce. This could explain why such wider enamel became positively selected in this intermediate feeding species. However, exaptation (i.e., pre-adaptation, sensu Gould and Vrba 1982) cannot be ruled out. If ancestors along this lineage were grass feeders and recent taxa changed feeding habit, then recent species from this lineage could still maintain these adaptations. The same has been observed with hypsodonty, which is not reduced even when species returned to browsing (hypsodont browsers; Bernor and Armour-Chelu 1999; Kaiser and Fortelius 2003). The second member of the Caprinae studied here, *C. ibex*, however does not share this morphology with *O. moschatus*. We argue that *O. moschatus* is more likely adapted to high abrasion due to its species-specific and peculiar habitat-related demanding diet. The capability of this species to exploit various but commonly high abrasive foods without sacrificing subordinate functions of its intermediate feeding behaviour illustrates here

one example of the fallback food hypothesis; derived morphologies allow for the efficient consumption of specific food sources (in this case ones with exceptional abrasiveness) whenever otherwise abundant or preferred foods are not available (Liem 1980; Robinson and Wilson 1998; Ungar et al. 2008).

Among the remaining intermediate feeders, *C. ibex* and *T. oryx* display thinner enamel than the grazers and *O. moschatus*. Surface texture shows that these species indeed process less abrasive foods. This is congruent with data from the literature indicating mixed feeding strategies for these species (Table 1). This match between morphology and function confirms our expectation that there is a general association between enamel ridge width and dietary abrasiveness. However, the thin enamel ridges of the intermediate feeder *A. melampus* and the browser *T. strepsiceros* contrast with the consumption of highly abrasive diets as indicated by their texture signals. For instance, Sq and Vmc mean values in *A. melampus* are closer to grazers than to any other intermediate feeder (Fig. 3). These two species do not exhibit the wide enamel ridges that are expected with feeding behaviours similar in dietary abrasiveness to grazing feeding strategies. This mismatch between form and function shall be discussed in the next section.

Cephalophus silvicultor confirms our hypothesis that the consumption of hard, large fruit items like seeds, which have the potential to fracture and chip enamel surfaces, induces selective pressures toward high EW. Indeed, wide enamel ridges result in larger indenter radii (site of enamel contact) to crack more efficiently hard food objects (Lucas et al. 2009; Strait et al. 2013). This facilitates the initiation of cracks, which is the most determinant factor in comminuting hard and brittle food items (Lucas 2004; Lucas et al. 2008). In turn, by distributing stress over a larger area, wide enamel ridges are advantageous to prevent the severe and sudden loss of dental tissue imposed by hard, large foods when high biting forces are necessary to crack them open (Lucas 2004; Lucas et al. 2008). Thus, frugivores are adapted to this diet by developing large indenter areas at each contact site. As *C. silvicultor* also displays low enamel complexity (D; Fig. 4), the question then arises: does complexity have to be reduced at the expense of increasing enamel width? The very wide and complex enamel ridges of *H. equinus* suggest this should not be a mechanical constraint in the selenodont tooth-bauplan; the development of wider ridges might be decoupled, at least to some extent, from reducing complexity. In frugivores, a large area of contact is needed but complexity is probably not critical. Indeed, in comparison to the seed shells, the softer fruit flesh does not represent a substantial mechanical resistance, so that its role in the adaptation of occlusal complexity is negligible. Hence, we argue that *C. silvicultor* is a morphologically well-adapted hard object-feeder capable of efficiently fragmenting large items and at the same time capable of resisting high abrasion rates. It is thus not surprising that surface texture signals do not differentiate the frugivore in terms

of increased abrasion rates from the rest of the species because of the potential macroscopic wear effect of such large hard objects (see above).

Discrepancies Between Expected and Observed Tooth Form and Function

Some results from two 3D multi scale analyses (Dental Topometry and Surface Texture) on the same bovid dataset seem to challenge our understanding of functional morphology. We found cases among grazers, intermediate feeders, and browsers where tooth function (Sq and Vmc) contradicts morphology and its supposed adaptations (D and EW).

Although all grazers' teeth in this study seem to serve the same function, there are significant differences in the enamel complexity among them. This might be related to two complementary aspects. First, it seems that a very high enamel complexity (as displayed by *H. equinus*) is not essential to process grass efficiently. This might be because all grasses probably do not have exactly the same biomechanical properties (toughness variations) and/or because a further increase in enamel complexity may not lead to a more efficient processing of grass. Second, the very high complexity observed in *H. equinus* might be also related to different courses of evolutionary adaptation towards more grass-dominated diets among different lineages in the Bovidae. As bovines (e.g., cattle, bison, and African buffalo; not included in this study) represent the earliest and progressively specialized grazers, hippotragines convergently developed increased infolding of the enamel (higher complexity) making it difficult to differentiate between these two "innate" grazing bovid groups on such morphological aspects (Bibi 2007b). On the other hand, grazers from the tribe Reduncini (like *K. ellipsiprymnus*) never attained the high degree of occlusal complexity seen in bovines and hippotragines (Bibi 2007a). *Connochaetes taurinus* belongs to the alcelaphines, which is the sister group of hippotragines (Hernandez Fernandez and Vrba 2005; Hassanin et al. 2012). The proximity in occlusal complexity between *C. taurinus* and *H. equinus* among the grazers may be reflecting a closer phylogenetic relationship between these two taxa. In summary, we conclude that not having exceptionally increased enamel complexity does not seem to be a barrier for feeding on a permanent grass-based diet. Significant differences of enamel complexity among grazing taxa are determined most likely by a balance between functional adaptation and phylogenetic affinity.

The case of *A. melampus* displays a broad discordance between observed function and tooth morphology. This species displays great variations in both surface texture parameters (Fig. 3 and Online Resource 3). Surface texture data thus indicate ingestion of foods of abrasive faculty (and probably biomechanical properties) much like those eaten by grazing species. The large overlap of high Vmc and Sq values between grazers and *A. melampus* in fact indicates that the latter consumes great amounts of grass, at least on a regional and/or seasonal basis (see Vmc and Sq variations in Online Resource 3). This is congruent with carbon isotope data reflecting great dietary variability for this species with some individuals consuming more than 90 % and other less than 20 % of grass (Table 1; Cerling et al. 2003; Sponheimer et al. 2003). In contrast, we found that *A. melampus* presents the lowest enamel complexity among all sampled species and the thinnest enamel among all intermediate feeders. One possible explanation for this divergence between form and function is that this species has recently undergone a dietary transition in its adaptational history, from a browsing diet to a more frequent grazing feeding strategy. In fact, browsing aepycerotines seem to be quite common among bovid faunas at least until the late Pliocene, when the extant species had become dominant (Harris et al. 2003; Le Fur et al. 2009). *Aepyceros melampus* thus illustrates the fact that "anatomy is not destiny," where structure may well be "suboptimal" in design, but still good enough, because there must be a vast tolerance range between "optimal" design and dysfunction of a given trait. The limits to this tolerance remain to be tested. Nevertheless, it appears that taxa, which are "not adapted" to process tough plant material, are indeed able to extract enough stored nutrients from such vegetation in order to subsist. The discrepancy between the peculiar morphology less adapted to tough foods in highly abrasive diets and the large dietary flexibility of *A. melampus* underscores the need to appreciate (apparently) maladaptive structures as nevertheless effective functioning units.

Similarly, *T. strepsiceros* shows large flexibility in its dietary behavior (Fig. 3 and Online Resource 3). This agrees with the various feeding preferences coupled to seasonal behavior documented for this species (Table 1). Although abrasion here seems to be less than in *A. melampus*, it is higher than in all other intermediate feeders and the surface texture signature also largely overlaps with those of all grazers (Fig. 3 and Online Resource 3). This contradicts the fact that *T. strepsiceros* presents the thinnest enamel among all species. This mismatch between tooth function on high abrasive diets and poorly adapted occlusal shape demonstrates that there is a large plasticity between expected, "optimal" morphology and the potential function of the tooth. This further illustrates the case among the bovids we sampled that morphology does not necessarily means destiny.

The present work has implications in paleoecology where diets are often inferred from gross tooth morphology. Indeed, our results demonstrate that morphology can be an ambiguous proxy for diet. Therefore, dietary proxies independent of tooth morphology, such as wear or isotope analyses, should always be considered in addition to morphology in order to get a more precise picture of the paleobiology and evolution of fossil taxa.

Conclusion

We investigated the extent to which adaptational value of dental morphology reflect real tooth function in extant bovid species with different feeding behaviours. We combined 3D occlusal topometry with 3D surface texture analyses to test whether adaptations for more efficient food processing and increased resistance to dietary wear matched the dietary physical demands the tooth must actually cope with. Implementing a multi-scale approach on each specimen of our data sample enables us to align information about what the individual is capable of processing with its teeth (topometry) to what it has in fact been eating, i.e., the actual tooth function (surface texture). The enamel width (*EW*) parameter is introduced in the present study as a morphological descriptor in bovid dental topography, but it also represents a promising tool in many wear-induced occlusal patterns across a wide taxonomic diversity (e.g., rodents, artiodactyls, perissodactyls, proboscideans, etc.) in both fossil and modern taxa.

What is thought to be determinant in the evolution of bovid tooth morphology to cope with the biomechanical dietary demands of a given feeding strategy does not seem essential to be able to process foods efficiently enough and to achieve the necessary nutrient extraction. For instance, tough plant material is satisfactory exploited by grazing species with occlusal enamel that is not more complex (similar *D* values) than in intermediate feeding species. On the other hand, adaptations of occlusal morphology to diet-induced tooth wear tend to be more consistent with abrasion levels associated with the consumed food objects. Wide enamel ridges (high *EW*) are used to cope with high abrasion rates of year-round grass diets, or of the processing of hard, large fruit items in frugivores. Thus, the evolution of wider enamel is a common adaptation to counteract high potential occlusal wear in selenodont teeth. Nevertheless, there are also cases in which occlusal shape is incongruent with its function in terms of durability. These cases illustrate the variation of a morphological trait that greatly deviates from its "optimum" state to serve a given function; but this, however, does not mean absolute constraint to still fulfil that function (at least in terms of guaranteeing survival).

We suggest a two-tier process where the large differences in occlusal morphology between diets is first dependent on adaptations that increase efficiency of the comminution of plant material, and where the smaller differences within a given dietary category are likely the result of ancestral legacy. This implies that teeth can still efficiently operate despite not being "optimally" designed for the function they are actually being used for.

In summary, inferring tooth function from two different but complementary scales on the occlusal surface of bovid teeth allowed us to separate the adaptational value of the tooth's shape from the actual functioning of the tooth, thus widening our understanding about the complex relationship between form and function, i.e., what is possible from what is done with the tooth as the only mechanical instrument of the mammalian digestive system.

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