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TOOTH WEAR IN CAPTIVE GIRAFFES (*GIRAFFA CAMELOPARDALIS*): MESOWEAR ANALYSIS CLASSIFIES FREE-RANGING SPECIMENS AS BROWSERS BUT CAPTIVE ONES AS GRAZERS

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Abstract: Captive giraffe (*Giraffa camelopardalis*) mostly do not attain the longevity possible for this species and frequently have problems associated with low energy intake and fat storage mobilization. Abnormal tooth wear has been among the causes suggested as an underlying problem. This study utilizes a tooth wear scoring method (''mesowear'') primarily used in paleobiology. This scoring method was applied to museum specimens of free-ranging (n = 20) and captive (n = 41) giraffes. The scoring system allows for the differentiation between attrition- (typical for browsers, as browse contains little abrasive silica) and abrasion- (typical for grazers, as grass contains abrasive silica) dominated tooth wear. The dental wear pattern of the free-ranging population is dominated by attrition, resembles that previously published for free-ranging giraffe, and clusters within browsing herbivores in comparative analysis. In contrast, the wear pattern of the captive population is dominated by abrasion and clusters among grazing herbivores in comparative analyses. A potential explanation for this difference in tooth wear is likely related to the content of abrasive elements in zoo diets. Silica content (measured as acid insoluble ash) is low in browse and alfalfa. However, grass hay and the majority of pelleted compound feeds contain higher amounts of silica. It can be speculated that the abnormal wear pattern in captivity compromises tooth function in captive giraffe, with deleterious long-term consequences.

Key words: Giraffe, *Giraffa camelopardalis*, nutrition, tooth wear, acid insoluble ash, silica, browse, alfalfa, grass, pelleted compound feed.

INTRODUCTION

Giraffes are presumably strict browsers that preferably ingest *Acacia* spp. in the wild.[10] In captivity, giraffe are usually fed a diet of alfalfa hay and pelleted compound feeds, with the addition of fruits, vegetables, grain products, and browse. Grass hay is also used. It has been observed that giraffe do not ingest grass hay or alfalfa hay, if fed this food alone, in quantities that one would expect for a ruminant of this size.[15,24] A potential inadequacy of hays offered has been suspected to be a major contributing cause to the difficulties experienced in giraffe feeding.[7] One of the major health issues in captive giraffe is the phenomenon of animals dying of unknown causes, often having serous fat atrophy at necropsy (formerly termed ''peracute mortality syndrome'').[17,30,38,41] In other ruminants, fat atrophy is often associated with irregular tooth wear.[38] Correspondingly, a comparison of skulls from six captive and 15 free-ranging giraffes consistently showed moderate to severe dental wear in the captive specimens. In contrast, dental wear was mostly absent, or if present, was considered mild, for the free-ranging specimens.[12] In addition, of concern is the fact that on average, captive giraffe rarely reach their maximum life span of 26–30 yr[37] but rather for the most part die much earlier, at approximately 15 yr in age.[8] In a study comparing enamel defects in teeth of free-ranging and captive giraffes, Franz-Odedaal et al.[18] found defects in three of the four captive individuals investigated, when compared to four out of nine free-ranging individuals. While enamel defects are not indicative of dental health, they may indicate a general systemic stress in particular situations—such as during weaning, puberty, or pregnancy—or a poor nutritional status.

It has been suggested[5] that excessive tooth wear is a particularly limiting factor in the husbandry of captive browsing species. Whereas grazers consistently have high-crowned (hypsodont) teeth, which

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is interpreted as a protection against the abrasive silica contained in grass material, browsers usually have low-crowned (brachydont) teeth because their natural forage contains little or no abrasive components.[29] It has been postulated that free-ranging moose (*Alces alces*) select against an abrasive diet[26] and that the diet selected by free-ranging roe deer (*Capreolus capreolus*) contains less silica than the average forage available in their environment.[49] Even though alfalfa, the staple roughage diet item for captive giraffe, as well as browse contain little silica (acid insoluble ash),[6] the additional use of grass hay, fresh grass, and the inclusion of grass products in pelleted compound feeds could be hypothesized to lead to a different, more excessive tooth wear, one dominated by abrasion, in captive animals compared with free-ranging giraffe. In order to test this hypothesis quantitatively, we compared the dental ''mesowear'' patterns in museum specimens of free-ranging and captive giraffes.

The mesowear method of Fortelius and Solounias[16] has proved to be a powerful tool for reconstructing the dietary traits of herbivorous ungulates.[33] This method is based on facet development of cheek tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food-to-tooth contact (abrasion). Attrition creates facets while abrasion obliterates them. In general, the mesowear profile of browsers is dominated by attrition, whereas that of grazers is dominated by abrasion. Mesowear is evaluated at the cutting edges of cheek tooth enamel surfaces, where the buccal wall meets the opposing occlusal surface. To date, analysis has focused on several upper and lower tooth positions. Upper second molars were originally employed,[16,33,47] but the tooth model has been further extended to upper and lower molars and fourth premolars in equids[31,32] and to both upper second and third molars in ruminants.[19]

MATERIALS AND METHODS

Material

Museum specimens from seven German and one Danish zoological museums were investigated; the sample comprised 20 individuals (which died between 1865 and 1962) from the wild and 41 individuals (which died between 1911 and 1999) from captivity. Animals whose origin was not stated in the museum records were not included in the study. Information contained in museum records on the origin, sex, age, and date of death were noted. Museum specimens were carefully cleaned, and a negative mold of one upper premolar–molar tooth row was made using PROVIL novo Putty regular set (Heraeus Kulzer, Hanau, Germany) polysiloxane dental molding putty. Subsequently, positive casts of the teeth rows were produced by filling the molds with the epoxy resin Injektionsharz EP (Reckli-Chemiewerkstoff, Herne, Germany). The use of molds is a prerogative for such a study in order to have continuous access to tooth forms and to be able to investigate tooth forms from different locations under standardized conditions.

Mesowear scoring

Only upper postcanine dentitions were investigated, because to date there has been no consistent comparative data set available for lower premolars and modes. The mesowear signal allows a reasonable scoring of dietary preference when the sample size is 10 dental specimens or greater,[16,33] and a statistically stable dietary signal can be expected when the sample size is 20–30 individuals. Only permanent teeth were scored, and these represented giraffes older than 1 yr of age. Unworn teeth and teeth in early wear (occlusal surface not yet entirely exposed to wear) were excluded from this study, because when too little wear is involved, no stable mesowear equilibrium can be established for the early stages of tooth wear. Also, dental specimens in late advanced wear were excluded, as suggested by Fortelius and Solounias.[16] After excluding unworn teeth, specimens in earliest and latest wear, and those with secondarily broken cusp apices, the available upper postcanine sample comprised 93 individual teeth in the zoo sample and 233 individual teeth in the wild sample. In order to gain a reasonably accurate classification of the samples used in this study, third molars were included in the analysis, following feasibility tests on three extant ruminant species.[19] Only the sharpest of the two cusps of a cheek tooth was scored in order to be consistent with the comparative data of Fortelius and Solounias.[16] Mesowear scoring (Fig. 1) included the scoring of the occlusal relief (''high'' or ''low'') and of the cusp shape (''sharp,'' ''round,'' or ''blunt'').

Statistical analysis

Fourteen data sets were generated, which represent subpopulations of the total dental sample (premolars 2–4 [P2–P4]; molars 1–3 [M1–M3]; and M2+M3 combined, of the zoo and the free-ranging individuals), and mesowear parameter frequencies on each of these subpopulations were calculated. Axum 6.0 software (MathSoft Inc., Needham, Massachusetts 02492, USA) was used to compute Chi-square corresponding probabilities for each com-

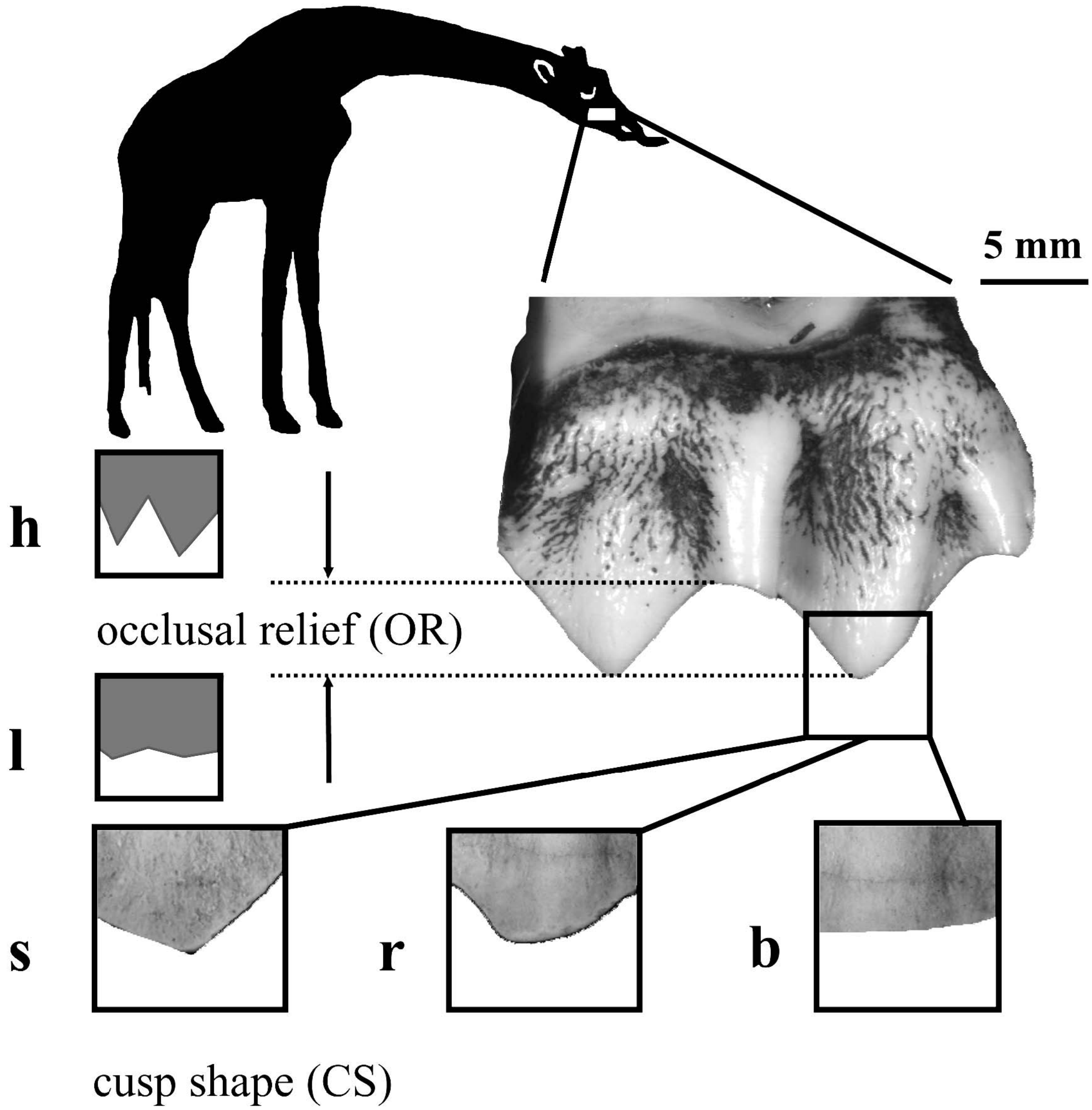

Figure 1. The mesowear variables[16] of a brachydont giraffid cheek tooth (upper right M2; captive male ZMH-2202). The occlusal relief (OR) may be scored ''high'' (h) or ''low'' (l); the cusp shape (CS) is classified as ''sharp'' (s), ''round'' (r), and ''blunt'' (b). Scale bar: 5 mm.

bination of data sets (i.e., P2 zoo vs. P2 free range, P3 zoo vs. P3 free range, etc.).

In order to test the clustering of the two giraffe populations of this study in relation to published mesowear data for other ungulate species, two different analyses were performed, using the record of 27 extant mammalian ungulate species (by Fortelius and Solounias[16]) for comparison. First, a cluster statistics was performed for the M2+M3 data set, as suggested for ruminants by Franz-Odendaal and Kaiser,[19] using Systat 11.0 (SYSTAT Software, Inc., San Jose, California 95110, USA) software (licensed to TMK) and using default settings. Hierarchical cluster analysis with complete linkage (furthest neighbors) was applied following the standard hierarchical amalgamation method of Hartigan.[23] The algorithm of Gruvaeus and Weiner[20] was then used to order the cluster tree using the three cusp shape variables (% high, % sharp, and % blunt). The resulting trees demonstrate the relationship of the data sets by joining them in clusters. The closer the data are, the smaller is the normalized Euclid-

Figure 2. Occlusal relief of a free-ranging giraffe (ZSM 1911/2446). Note the missing lower first molar, an indication of progressed age, and the high relief in the upper molars.

ean distance at the branching point. The exact sequence and direction of species arrangement in the diagram, however, may not be interpreted as an expression of sequential differences, because clusters may flip. Additionally, a principal components analysis (PCA) on mesowear parameters (% high, % sharp, and % blunt) was performed on the M2+M3 data set using Systat 11.0 software.

RESULTS

When handling the museum specimens, there was a subjective impression that free-ranging giraffes, even old individuals, had a high occlusal relief (Fig. 2), in contrast to several captive animals (Fig. 3).

In both the captive and the free-ranging populations, high occlusal reliefs prevailed in the data set (Table 1; Fig. 4), with the exception of the first molar in the zoo population. In the zoo population, at least 18% of respective teeth had low reliefs (P4), with a maximum of 56% low reliefs in M1. In contrast, no low reliefs were scored in three tooth positions in the free-ranging population (P4, M2, M1), and a maximum of only 14% low-relief scoring was reached in P2. In both populations, the percentage of low reliefs followed the pattern M1 > P2 > P3 > P4. In the free-ranging population, it continued as P4 = M2 = M3, while in the zoo population, it continued as P2 > M2 > P3 = M3 > P4.

Round cusp shapes prevailed in the zoo population for all tooth positions, with the exception of M1, in which blunt cusps comprised 49% (Fig. 5). Sharp cusps ranged consistently between 16% and 19% in the zoo population. In the free-ranging population, sharp cusps were most prevalent (75%) in M3 and least frequent, with 14%, in M1. Round

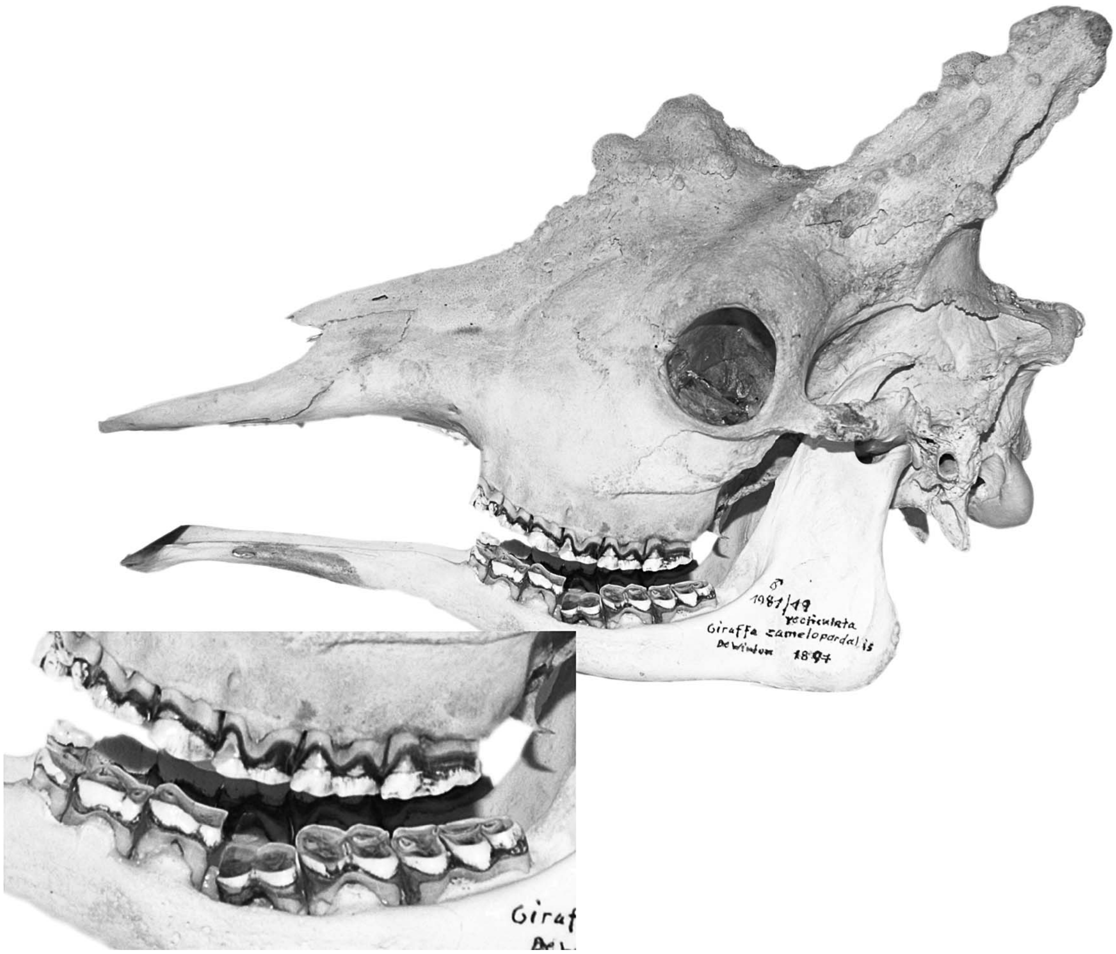

Figure 3. Occlusal relief of a captive giraffe (ZSM 1981/19). Note the missing lower first molar, an indication of progressed age, and the low relief in the upper molars.

cusps ranged between 25% (M3) and 86% (M1). There were no blunt cusps in the free-ranging population. In the zoo population, the percentage of blunt cusps followed the pattern M1 > P2 > P3 = M2 > P4 = M3. In the free-ranging population, the percentage of round cusps followed the pattern M1 > P2 > P3 > P4 = M2 > M3.

Chi-square analysis comparing the combined mesowear signal for M2+M3 indicates a significant difference between the free-ranging and the zoo populations ($P = 0.0023$). If the isolated tooth positions are compared between the populations, *P*-values decrease from 0.98 (no difference between P2 mesowear signals) to 0.69 (P3), 0.26 (P4), 0.15 (M1), 0.06 (M2), and 0.02 (M3), indicating an increasing dissimilarity in the mesowear signal between the populations with more posterior tooth position.

Applying cluster analysis to the reference data set of Fortelius and Solounias[16] and the combined M2+M3 mesowear signal of the zoo and free-ranging populations results in a distinct separation of the two study populations: whereas the free-ranging population clusters among the browsers, similar to the data for giraffe from the reference data set, the zoo population of giraffe clusters among the grazers, close to the wildebeest (*Connochaetes taurinus*) and the hartebeest (*Alcelaphus buselaphus*) (Fig. 6).

In the PCA, the free-ranging giraffe population of this study is placed between the browsers and the mixed feeders, but it is still close to the giraffe from the reference data set. In contrast, the zoo giraffe population of this study is placed among the grazers, again, close to the wildebeest and hartebeest (Fig. 7).

Table 1. Mesowear scoring of premolars 2–4 (P2–P4) and molars 1–3 (M1–M3) in populations of free-ranging and zoo giraffes. For an explanation of scoring parameters, see Figure 1. Occlusal relief parameters: l = low, h = high; cusp shape parameters: s = sharp, r = round, and b = blunt.

		Mesowear scoring									
		Proportion in population					Absolute numbers				
		Occlusal relief		Cusp shape			Occlusal relief		Cusp shape		
Population	Tooth	%l	%h	%s	%r	%b	l	h	s	r	b
Free-ranging	P2	14	86	25	75	0	2	12	3	9	0
	P3	7	93	33	67	0	1	13	4	8	0
	P4	0	100	50	50	0	0	14	5	5	0
	M1	6	94	14	86	0	1	16	1	6	0
	M2	0	100	50	50	0	0	19	4	4	0
	M3	0	100	75	25	0	0	15	6	2	0
Zoo	P2	41	59	16	50	34	16	23	6	19	13
	P3	23	77	16	62	22	9	30	6	23	8
	P4	18	82	19	62	19	7	32	7	23	7
	M1	56	44	19	32	49	22	17	7	12	18
	M2	31	69	18	61	21	12	27	7	23	8
	M3	24	76	18	64	18	9	29	6	21	6
Free-ranging	M2+M3	0	100	63	38	0	0	34	10	6	0
Zoo	M2+M3	27	73	18	62	20	21	56	13	44	14

DISCUSSION

This study demonstrates a significant difference in the tooth wear pattern between the free-ranging population and a sample population of zoo giraffes. In both populations (free-ranging and zoo), the M1 has the most abrasion-dominated mesowear signal (most blunt cusps in the zoo sample and most round cusps in the wild sample) of all single tooth positions. Along the tooth row, the transition between round and blunt shows the same gradient in the zoo population, as does the transition between sharp and round cusps in the free-ranging population. In the zoo population, there is a constant of 19% sharp cusps regardless of the tooth positions. The distribution pattern of occlusal relief parameters along the tooth row is, again, equivalent in both populations, with consistently higher relief in the free-ranging population. The Chi-square test *P*-values for the pairwise comparisons of the individual tooth positions between the populations consistently decrease along the tooth row from anterior to posterior and approach the benchmark of 0.05 in the M2. The difference in mesowear signatures between the two populations increases the more posterior the tooth position. When compared to mesowear signals in other free-ranging herbivore species, the captive giraffe population clearly clusters with those animals whose wear pattern is abrasion dominated, that is, the grazers.

There are several limitations to this study. Although an effect of age was indirectly controlled for by the exclusion of particularly worn teeth—and also by the fact that zoo giraffes do not surpass their free-ranging conspecifics in average life span—an age bias between the two populations cannot be ruled out with absolute certainty. However, general qualitative differences in the mesowear parameters, such as the presence of blunt cusp shapes in the zoo population, contrasted with no blunt cusps in the free-ranging population. In addition, the fact that the proportion of sharp cusps was not influenced by tooth position in the zoo population is indicative of fundamental differences in tooth wear and not only of differences in wear degree due to age. These findings indicate that this difference could be a result of the difference in diets ingested by the two populations.

Another limitation of this study is that individual feeding records for the zoo animals investigated were generally unavailable and that in order to achieve a sufficient sample size, individuals had to be included that had been kept in captivity between 1911 and 1999, (with the majority of these animals comprising the period from 1960 to 1990). Therefore, a direct conclusion for a particular feeding regime cannot be made, and it cannot be stated with certainty whether our findings are representative for giraffe recently or currently maintained in zoological institutions. In this context, a question of major interest would be whether the zoo population investigated in this study represents animals predominantly maintained on grass or on alfalfa hay, be-

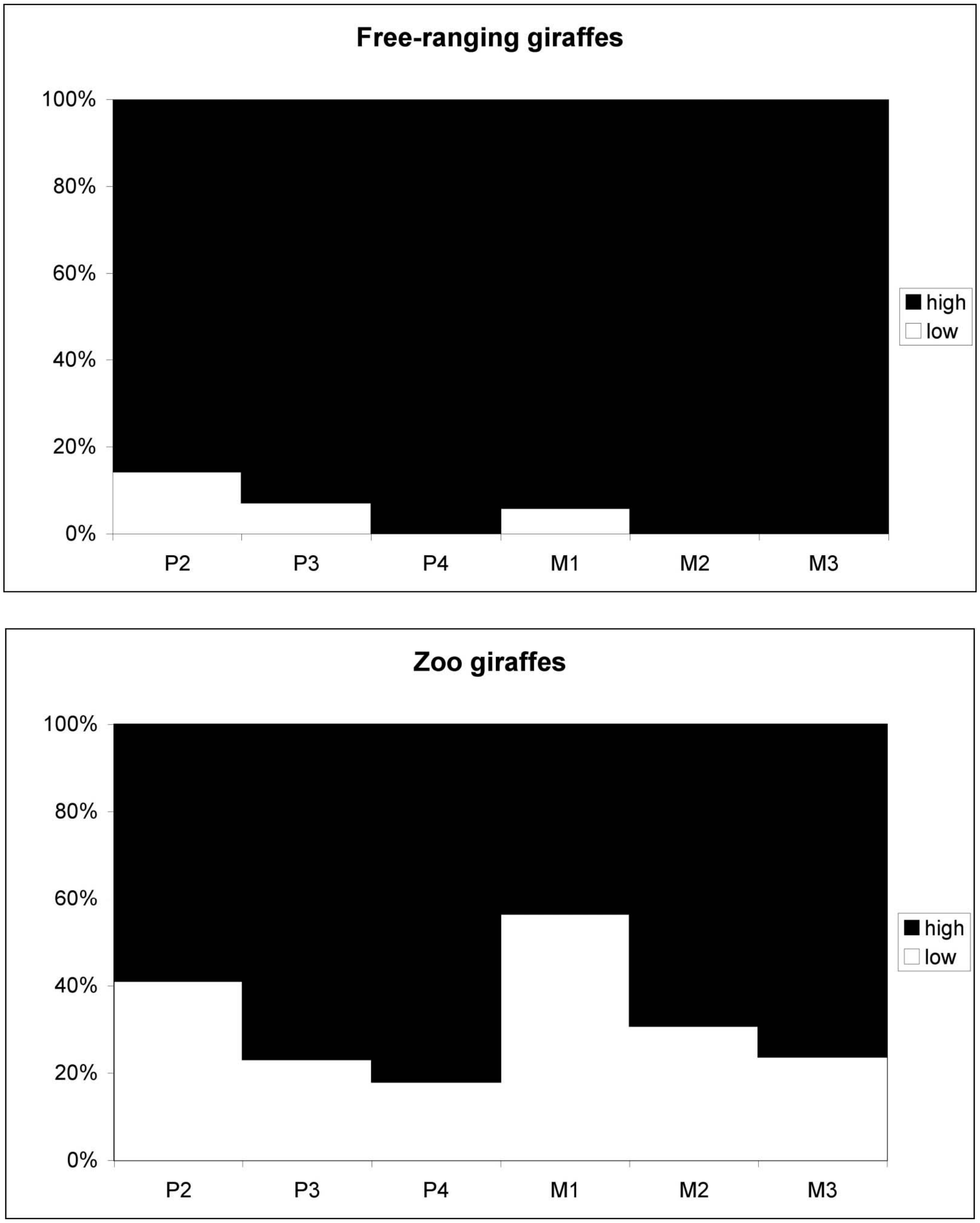

Figure 4. Distribution of occlusal relief mesowear variables along the postcanine tooth row of the study populations of free-ranging and zoo giraffes. Note the similar gradient in both populations, the prevalence of high reliefs in all tooth positions in the free-ranging population, and the peak of low reliefs in M1 in the zoo population.

cause of the difference in abrasive phytolith content between grass (phytoliths present) and legumes (no phytoliths). From as early as 1964[9] onwards, it is documented that within the United States, giraffe diets contain alfalfa hay as the main fiber source. Already prior to 1977, alfalfa or clover hays were in use for giraffes in the United States, the U.K., and Switzerland.[3,11,17,22,51] German recommendations for giraffe husbandry from 1976[35] advocate the use of grass and legume hay and browse, and in 1989,[42] only the use of alfalfa was advocated. Therefore, it appears unlikely that the results for the zoo popu-

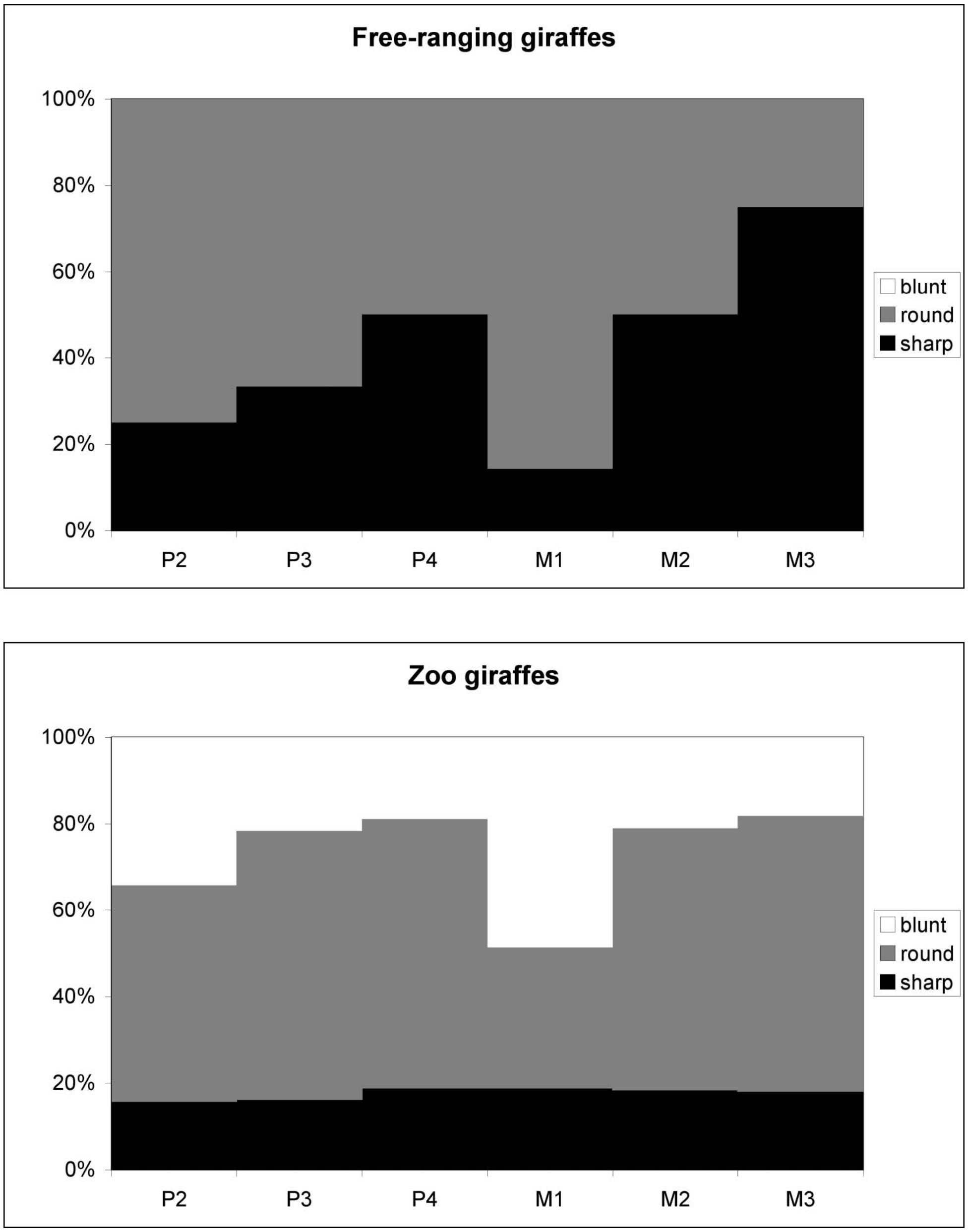

Figure 5. Distribution of cusp shape mesowear variables along the postcanine tooth row of the study populations of free-ranging and zoo giraffes. Note the similar gradient in both populations, the lack of blunt cusps in the free-ranging population, and the peak of blunt cusps in M1 in the zoo population. Also note that the frequency of sharp cusps is not sensitive to tooth position in the zoo population.

lation in this study represent a general feeding regime without alfalfa hay. Current feeding recommendations for giraffe advocate diets based on alfalfa,[36,48] although the inclusion of grass hay has been proposed for behavioral enrichment.[2] In a survey in European facilities that maintain giraffe, 36% of 70 respondents indicated that they were offering grass hay regularly (in addition to alfalfa hay) to their giraffe. In two facilities, grass hay was the only roughage used.[27] Although grass hay cannot be regarded as the sole culprit for the increased dental wear documented in this study, its use is to

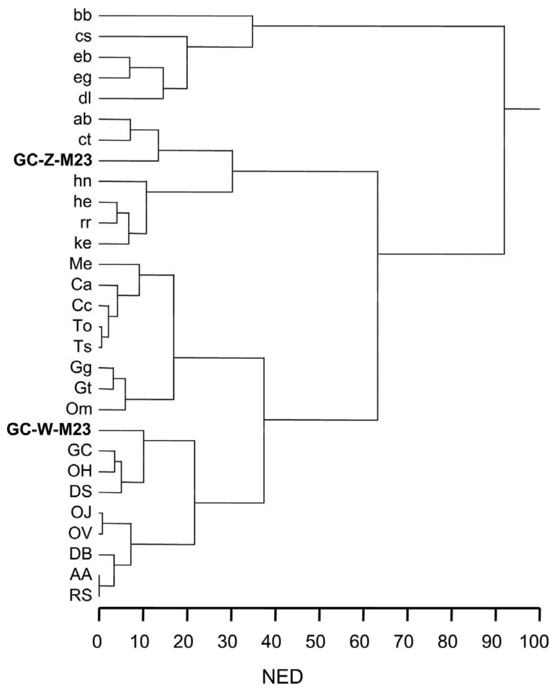

Figure 6. Hierarchical cluster diagram based on a set of 27 "typical" species from Fortelius and Solounias.[16] Giraffe populations from this study are in bold, with mesowear scorings based on the upper second and third molar (M2+M3), according to Franz-Odendaal and Kaiser.[19] Distances are Euclidean distances. **Browsers**: AA = *Alces alces*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*. **Grazers**: ab = *Alcelaphus buselaphus*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchellii*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*. **Mixed feeders**: Ca = *Capricornis sumatraensis*, Cc = *Cervus canadensis*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Me = *Aepyceros melampus*, Om = *Ovibos moschatus*, To = *Taurotragus oryx*, Ts = *Tragelaphus scriptus*.

be discouraged with respect to the potentially detrimental effect of tooth wear related to this hay.

Whereas silicate levels (measured as acid insoluble ash) are low in alfalfa and dicot foliage, they are considerably higher in grass products as well as in pelleted compound feeds used in captive giraffe and other zoo herbivores (Table 2).

To our knowledge, no studies exist on the potential to reduce silicate/acid insoluble ash levels in compound feeds. However, we believe that a reduction of the abrasive elements in pelleted feed compounds could represent a relevant contribution to the prevention of the increased wear patterns of captive giraffe.

The dental health status of zoo animals is an indicator of their general well-being.[52] Since the comprehensive work of Colyer in 1936,[39] few studies have been performed on the comparative dental health of captive versus free-ranging animals; as is the case in this work, the conclusion has typically been that free-ranging mammals are in better oral/dental health than their captive counterparts.[34,43,44,46] Hungerford et al.[28] found a higher incidence of periodontal disease and caries in raccoons living in a recreational park than in animals from an agricultural area. Sainsbury et al.[45] found a distinctively lower incidence of oral disease in free-ranging squirrels (*Sciurus vulgaris*) than that reported for captive specimens. Wenker et al.[53] compared the dental pathology of free-ranging and captive brown bears (*Ursus arctos*) and reported that captive specimens had a higher incidence of dental calculus, a frequent finding in captive carnivores and primates, usually explained by the low abrasiveness of the diets fed to these animals.[13,14,21,50,54] In a survey on the occurrence of irregular or excessive tooth wear in necropsy reports of ruminants in one zoological facility, Martin Jurado et al.[38] noted that the problem did not predominantly occur in senile animals but rather in animals that were within 25–75% of their reported maximum life span; the authors concluded that dental problems can reduce the longevity of captive animals. In order to confirm this assumption for giraffes, experimental data, such as feeding trials involving both free-living and captive giraffes, would have to be obtained in large numbers in order to test for reduced digestive efficiency or food intake in the captive animals. In a study on red deer, increased tooth wear was correlated with lower voluntary food intake and less effective food communition; therefore, even if digestibility itself was not affected, digestible energy intake decreased.[40] In the long run, this would lead to a poor body condition.

In their study of zoo ruminants, Martin Jurado et al.[38] identified the feeding on sandy grounds, without the use of troughs or racks, as one major factor contributing to the problem of excessive dental wear. In sheep it has been shown that tooth wear is a direct function of the amount of soil ingested.[25] Thus, both the use of artificial diets with too few abrasive elements and the use of diet components of an abrasiveness exceeding that to which a species is naturally adapted can cause serious dental abnormalities in captive wildlife. The high incidence of dental problems in the controlled captive

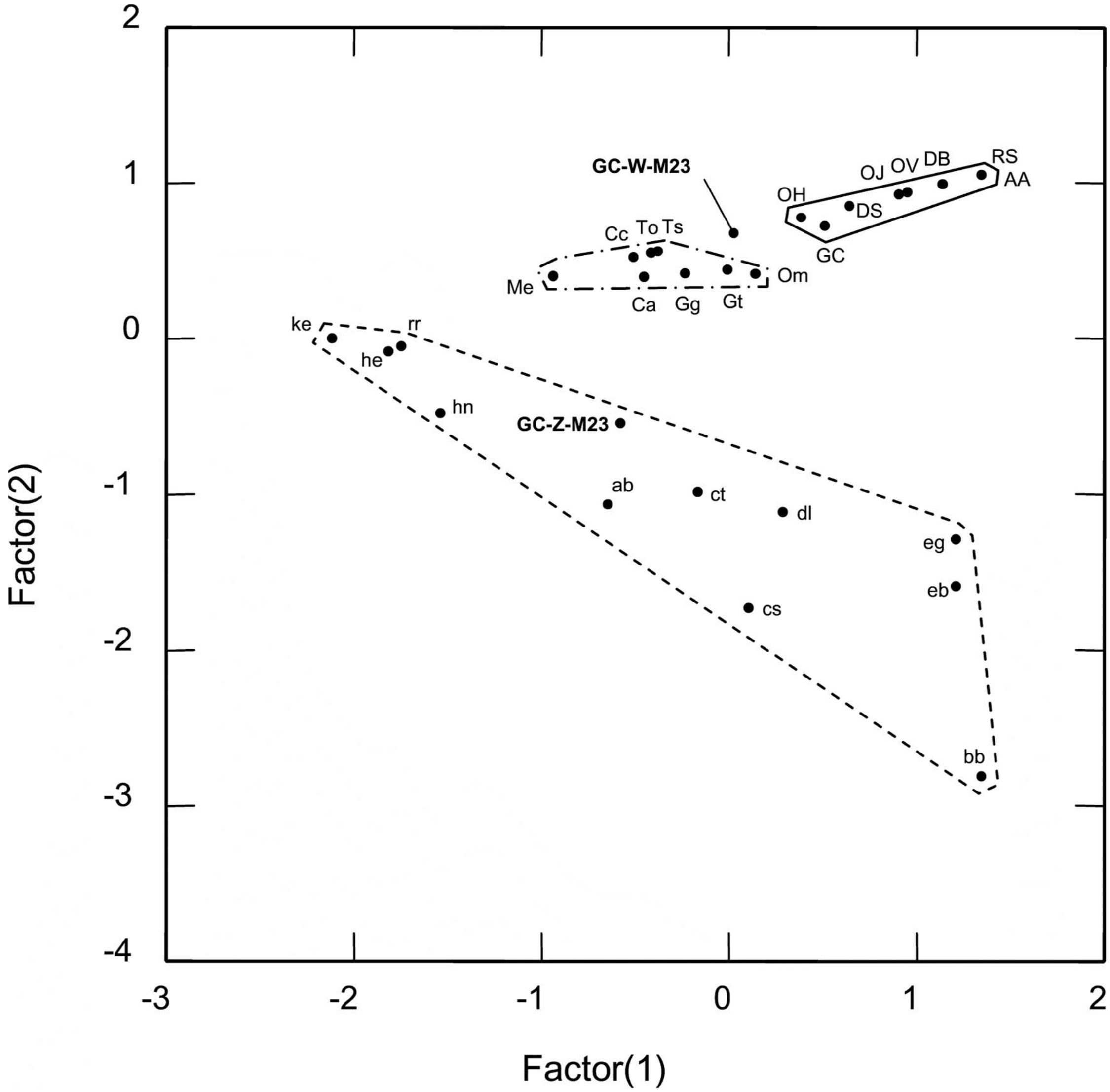

Figure 7. Principal component analysis based on a set of 27 "typical" species from Fortelius and Solounias.[16] Giraffe populations from this study are in bold, with mesowear scorings based on the upper second and third molar (M2+M3), according to Franz-Odendaal and Kaiser.[19] **Browsers**: AA = *Alces alces*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*. **Grazers**: ab = *Alcelaphus buselaphus*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchellii*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*. **Mixed feeders**: Ca = *Capricornis sumatraensis*, Cc = *Cervus canadensis*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Me = *Aepyceros melampus*, Om = *Ovibos moschatus*, To = *Taurotragus oryx*, Ts = *Tragelaphus scriptus*.

environment could possibly be reduced by requesting that zoo managers alter dietary ingredients.

CONCLUSIONS

The general trend of an increased dental pathology in captive versus free-ranging individuals of a species and the specific trend of an excessive dental wear pattern in captive versus free-ranging giraffes, outlined by Enqvist et al.,[12] was quantitatively confirmed in this study. Giraffe dental wear patterns, dominated by an attrition-dominated wear signal in free-ranging individuals (as typical for browsing species), have an abrasion-dominated wear signal (as typical for grazing species) in captivity. This

Table 2. Acid insoluble ash (AIA, % dry matter [DM]) contents (as a surrogate measure for the abrasiveness of the diet) of different feed items used in giraffe husbandry. Note the low AIA content in browse and alfalfa products, as opposed to grass products and most pelleted compound feeds.

Food item	*n*	AIA (%DM) Mean	AIA (%DM) Range	Source
Temperate browse	1	0.0	—	Clauss et al.[6]
	6	0.2	0.0–0.4	Castell[4]
Alfalfa hay	1	0.2	—	Baer et al.[1]
	1	0.2	—	Clauss et al.[6]
	9	0.3	0.0–0.7	Castell[4]
Alfalfa meal pellet	1	0.5	—	Castell[4]
Grass hay	13	2.0	0.3–5.1	Castell[4]
Fresh grass	2	2.0	1.8–2.2	Castell[4]
Grass meal pellet[a]	1	6.4	—	Castell[4]
Pelleted compound feed	2	0.9	0.2–1.5	Baer et al.[1]
	3	0.8	0.7–1.0	Clauss et al.[6]
	24	1.5	0.5–3.1	Castell[4]

[a] Young grass cut low, dried artificially, ground and pelleted.

finding indicates that captive diets are overly abrasive in relation to the giraffe's dentition, which could play a role in the reduced average longevity in this species. In particular, grass products and abrasive elements in pelleted compound feeds should be reduced. Given the higher abrasiveness of grass hay or many pelleted compound feeds, compared with dicotyledonous browse material, it could be hypothesized that browsing species in general, characterized by a low-crowned (brachydont) dentition, may be more susceptible to excessive tooth wear in captivity, in contrast to grazing species. In order to test this hypothesis, comparative data from a larger range of species would be required.

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