

Differential mesowear in the maxillary and mandibular cheek dentition of some ruminants (Artiodactyla)

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The mesowear method assesses the dietary regime of herbivorous mammals based on the attrition/abrasion equilibrium by evaluating cusp shape and relief of upper second molars. The method has recently been extended to include four tooth positions, upper P4–M3, in equids. In this study we determine whether the method can be extended in ruminants by applying it to maxillary and mandibular dentitions of a browser, the giraffe (*Giraffa camelopardalis*) and two mixed feeders, the oribi (*Ourebia ourebi*) and the musk ox (*Ovibos moschatus*). We find that including the upper third molar in addition to the upper second molar provides consistent mesowear classifications in these species. Lower dentitions of mixed feeders score significantly differently in terms of mesowear as compared with upper dentitions. We infer that adaptive optimization in differential anisodonty is related to the composition of the diet and should be mirrored in differential mesowear signals of adjoining upper and lower molars. Our results suggest that in mixed feeders, sharpness is maximized in upper teeth, whereas in specialized feeders this is not the case.

Introduction

Artiodactyla and some Perissodactyla have certain biomechanical adaptations of their dentition in common, which are closely related to their particular herbivorous diets. In all these animals, occlusal surfaces of opposing teeth (left and right) are inclined toward each other in a tectiform fashion. This allows a one-phase upward-inward occlusal stroke, which produces a buccolingually straight occlusal surface. Our approach here is restricted to forms with transverse chew-

ing, as the method applied here, the mesowear method, cannot as yet be applied to animals with chewing strokes parallel to the tooth row (such as in elephants). A basic requirement for transitory chewing is anisodonty, the differential width of occluding teeth that allows one tooth row to move across the other while maintaining occlusal contact. That anisodonty is clearly related to chewing dynamics is shown by the fact that it has a strong relationship to the spacing of the tooth rows or anisognathly. Anisodonty and anisognathly are strongly correlated in forms

with a two-phase occlusal morphology, whereas in forms with a single-phase morphology, such as hypsodont equids, the precise relationship disappears although anisodonty itself remains (*see* detailed discussion in Fortelius 1985: p. 53). Anisodonty is a general feature of mammals with transitory chewing and is invariably positive, upper teeth being wider than lowers.

Wear in hypsodont molars has two sources, abrasion (tooth-to-food contact) and attrition (tooth-to-tooth contact). While abrasion is the result of grinding action that takes place when food inclusions, such as phytoliths or grit that remove softer dental tissues, contact the occlusal surface under pressure, attrition is the result of immediate tooth-to-tooth contact. Mesowear analysis is a relatively new technique used to assess the dietary regime of herbivorous mammals based on the attrition/abrasion equilibrium (Fortelius & Solounias 2000). The method evaluates cusp shape and cusp relief of upper second molars (txM2) and is able to correctly classify species into expected feeding groups. Mesowear analysis has been applied to fossil and extant Equidae (Bernor *et al.* 1999, Kaiser *et al.* 2000a, 2000b, Kaiser 2001, Kaiser & Bernor 2001a, 2001b, Kaiser 2003, Kaiser *et al.* 2003, Kaiser & Fortelius 2003; T. M. Kaiser & T. A. Franz-Ondendaal unpubl. data) to fossil Cervidae (Kaiser & Croitor 2002; T. M. Kaiser & R. Croitor unpubl. data) as well as fossil giraffids (Franz-Ondendaal 2002). Recently Kaiser and co-authors (Kaiser & Fortelius 2003, Kaiser & Solounias 2003) have extended the mesowear method to include the upper tooth positions P4–M3 for equids only.

In this study, we apply the mesowear method to the rest of the upper dentition and to the second molar of some ruminants in order to determine whether the method can be extended to include other tooth positions in these animals. We test taxa from each of the major trophic groups — a browser (giraffe, *Giraffa camelopardalis*, Gc) and two mixed feeders (musk ox, *Ovibos moschatus*, Om, and oribi, *Ourebia ourebi*, Oo) — and compare differences with grazers (*Equus burchelli*, Eb) for which the method has already been extended (Kaiser & Fortelius 2003, Kaiser & Solounias 2003). Extending the mesowear method is important if fossil assemblages with limited

tooth specimens are to be analysed in the future.

A second focus of this paper is to assess whether a difference in the mesowear signal is found if upper and lower dentitions are compared. Kaiser and Fortelius (2003) have observed that after a certain amount of wear in both zebras (*Equus burchelli*) and in the extinct Miocene hipparionine horse (*Hippotherium primigenium*), cusp apices of upper and lower molars show obvious differences in their distinctness and sharpness. These differences appear to be highly consistent, at least in hypsodont equids. No other ungulates however, have so far been investigated.

According to Kaiser and Fortelius (2003), gravity, which will always ensure that unloaded food will more frequently contact the lower than the upper teeth, is a major factor responsible for differences observed in the mesowear signature of upper and lower dentitions. Another factor these authors consider is occlusal geometry. They expect occlusal geometry to result in different loading patterns on the cutting edges of upper and lower teeth, for example towards versus away from the supporting dentine (Fortelius 1985: p. 59). In this context, adaptive optimisation of enamel ultrastructure is considered a possible source of differential wear control (Rensberger & von Koenigswald 1980, Fortelius 1985, von Koenigswald & Sander 1997). It seems plausible that a general explanation of positive anisodonty (upper teeth wider than lower teeth) could be derived from basic relationships imposed by position and geometry. Kaiser and Fortelius (2003) suggest that food polishing acts on lower teeth when the teeth are not in occlusion and might explain why the polarity of the anisodonty is initially set as positive. They propose the hypothesis that an arrangement maximising sharpness in upper teeth would be superior to one that maximises sharpness in lowers, since lowers are more influenced by food abrasion between occlusal events.

In summary, this study addresses the following questions:

- Can the mesowear model be extended to include more upper teeth in ruminants?
- What is the difference in mesowear scorings for upper and lower cheek teeth in ruminant

artiodactyls?

- How do these relate to differential anisodonty with regard to the composition of the diet?

Materials and methods

We investigate three assemblages of extant ruminants — *Ovibos moschatus*, *Ourebia ourebi* and *Giraffa camelopardalis*. Datasets of *Equus burchelli* from Kaiser and Fortelius (2003) are incorporated in this study for comparative purposes only.

All specimens investigated are wild shot animals. The sample of *Giraffa camelopardalis* (giraffe) comprises 91 upper premolars and molars and 17 lower second molars. These specimens are housed at the Museum für Naturkunde, Berlin (Germany). The sample of *Ovibos moschatus* (musk ox) consists of 238 upper molars and premolars and 32 lower second molars. This population is derived from Greenland and is curated at the Zoological Museum of the University of Copenhagen (Denmark). The sample of *Ourebia ourebi* (oribi) is from the Museum für Naturkunde, Berlin (Germany) and consists of 152 upper premolars and molars and 29 lower second molars. In total, over 500 teeth were analysed (*see* the appendix for accession numbers).

We compare mesowear signatures of upper (tx) and lower (tm) second molars in these three populations of ungulates. In addition, we test combinations of all six upper tooth positions (txP2–M3) for their consistency in correctly classifying species as compared with the model tooth position (txM2) on which the original mesowear method of Fortelius and Solounias (2000) was based. In this study, we follow the methodology by Kaiser and Solounias (2003). In order to extend the mesowear model to more than one tooth position in ruminant populations, we test two extended models. The four-tooth model (txP4 + txM1 + txM2 + txM3), which is the “extended” model proposed for hypsodont equids (Kaiser & Solounias 2003), and a two-tooth model (txM2 + M3), which we find to show high consistency in mesowear classifications of the three ruminant species investigated. We refer to these two models as tx(P4–M3) and tx(M2 + M3), respectively. As comparison data we use

the mesowear data for 28 extant species from Fortelius and Solounias (2000) as well as the data provided by Kaiser and Fortelius (2003) for 41 upper and 42 lower second molars of *Equus burchelli*. The extant species from Fortelius and Solounias (2000) consist of 27 “typical” species, which they found to cluster in expected categories based on known diets, as well as one “neutral” species, *Ourebia ourebi*.

We used Axum 6 software (licensed to TMK) to compute Chi-square statistics and to test for significance of differences observed between individual data sets. Chi-square “corresponding probabilities” (p) are computed for each of the 62 combinations of single and multiple upper tooth positions and the txM2 in order to test whether incorporating one or more tooth positions into the mesowear model influences the mesowear classification. The resulting matrices are sorted in descending order according to the p value for each combination. The closer a single model is to the txM2, the more similar is the distribution pattern of the mesowear variables. The txM2, which is acting as the reference of these Chi-square analyses, has the p value 1, while the p values of all the other matrix columns (tooth combinations) are smaller than or equal to 1. The closer a column is to the p value of 1, the higher is the probability that the distribution of the mesowear variables of that particular model of tooth combinations is not different from the reference position, txM2.

Chi-square statistics is further used to test for significance of differences observed between upper and lower M2’s in the individual species tested. The absolute frequencies of mesowear variables (high, sharp, and round) were tested and p values were plotted. Hierarchical cluster analysis with complete linkage (furthest neighbors) is applied following the standard hierarchical amalgamation method of Hartigan (1975). The algorithm of Gruvaeus and Weiner (1972) was used to order the tree. We analyze the three mesowear variables (% high, % sharp and % blunt). For this analysis we use Fortelius and Solounias’ (2000) original data set, the data set of *Equus burchelli* from Kaiser and Fortelius (2003) and data sets of *Ovibos moschatus*, *Ourebia ourebi* and *Giraffa camelopardalis* presented in this study.

Results

Comparing upper and lower second molars

In *Ovibos moschatus* (Om), there are no differences in either occlusal relief scorings or in cusp shape scorings of “blunt” (Table 1) between upper and lower second molars. However cusp shape scorings of “sharp” are significantly more prevalent in upper M2’s (46%) than in lower M2’s, which are dominated by round cusps (97%) ($p = 0.029$; since relief scorings are identical, this p value reflects the difference in sharp and round scorings). In *Ourebia ourebi* (Oo) the distribution pattern seen in Om for sharp and round scorings is even more pronounced. Cusp shape scorings of “sharp” are 58% in upper M2’s versus 4% in lower M2’s ($p = 0.0001$) while “blunt” cusps are not present in either upper or lower teeth. In *Giraffa camelopardalis* (Gc) the distribution pattern shows an intermediate position between the two mixed feeders described above. Sharp cusps are more common in the upper second molars than in the lower ones (73% in txM2 versus 24% in tmM2, $p = 0.029$). Occlusal relief is high in *G. camelopardalis*.

Taken together, in all three species, occlusal relief variables are not different in upper and

lower second molars, while a significantly different mesowear pattern is observed for the cusp shape variables “sharp” and “round”. Typically, cusps of lower second molars tend to be less frequently sharp as compared with the upper M2’s. Kaiser and Fortelius (2003) observed a similar trend in *E. burchelli*. It therefore appears from these preliminary results, that all three feeding groups (grazers, browsers and mixed feeders) show this pattern. Corresponding probabilities indicate that mesowear signatures in upper and lower second molars are less likely to be different in both the browser, *G. camelopardalis* ($p = 0.029$) and the grazer, *Equus burchelli* ($p = 0.021$) and more likely to be different in the two mixed feeders investigated (Om, $p = 0.0003$ and Oo, $p = 0.0001$) (Fig. 1). Put another way, the difference between uppers and lowers is more pronounced in the two mixed feeders than in the more specialised taxa, *Giraffa* and *Equus*.

Chi-square ranking matrices

In the sample of *G. camelopardalis*, the corresponding probability (p) of all isolated tooth positions and of any combination of tooth positions ranges between $p = 1$ for only the txM2, the model position of Fortelius and Solounias

Table 1. Distribution of mesowear variables in upper (tx) and lower (tm) second molars of *Giraffa camelopardalis* (Gc), *Ourebia ourebi* (Oo), *Ovibos moschatus* (Om) and *Equus burchelli* (Eb) (*Equus* data are from Kaiser & Fortelius 2003). n = number of specimens available, tm = mandibular tooth, tx = maxillary tooth; Mesowear variables: l = absolute scorings low, h = absolute scorings high, s = absolute scorings sharp, r = absolute scorings round, b = absolute scorings blunt; % l = percent low occlusal relief, % h = percent high occlusal relief, % s = percent sharp cusps, % r = percent rounded cusps, % b = percent blunt cusps. Chi-squared statistics are shown for mesowear variables h, s and r, comparing the upper and lower second molars.

Population	n	l	h	s	r	b	% l	% h	% s	% r	% b
Gc(txM2)	17	0	17	8	3	0	0	100	73	27	0
Gc(tmM2)	17	0	17	4	13	0	0	100	24	76	0
Oo(txM2)	30	0	30	15	11	0	0	100	58	42	0
Oo(tmM2)	29	0	29	1	27	0	0	100	4	96	0
Om(txM2)	43	0	43	19	22	0	0	100	46	54	0
Om(tmM2)	32	0	32	1	30	0	0	100	3	97	0
Eb(txM2)	41	8	33	15	22	1	20	80	39	58	3
Eb(tmM2)	42	16	26	4	30	8	38	62	10	71	19

Gc(tx/tm) h, s, r	$\chi^2 = 7.069$,	df = 2,	$p = 0.029$
Oo(tx/tm) h, s, r	$\chi^2 = 18.996$,	df = 2,	$p = 0.0001$
Om(tx/tm) h, s, r	$\chi^2 = 16.378$,	df = 2,	$p = 0.0003$
Eb(tx/tm) h, s, r	$\chi^2 = 7.706$,	df = 2,	$p = 0.021$

(2000), and $p = 0.075$ for txP2 + M1. Using all tooth positions (txP2–M3) gives a p value of 0.6 (Fig. 2) indicating that this combination has a low probability of giving different dietary results for the species as compared with using txM2 alone. The txM2 + M3 model for Gc classifies less consistently with the classical model (txM2) than with the “extended model” (txP4–M3) formulated for hypsodont equids (Kaiser & Solounias 2003) (Fig. 2).

In the two mixed feeders, *Ourebia ourebi* and *Ovibos moschatus*, the corresponding probability (p) of all isolated tooth positions and of any combination of tooth position ranges between $p = 1$ for txM2 and $p < 0.0001$ for txP2 (Figs. 3 and 4). The use of all cheek tooth positions (txP2–M3) in both species is likely to classify the species differently to the reference position, txM2, as p values are less than 0.05 (0.014 for *Ovibos* and 0.029 for *Ourebia*). The “extended model” for hypsodont equids (Kaiser & Solounias 2003) using txP4–M3 is however likely to correctly classify these species as p values are 0.327 and 0.682, respectively, for the musk ox and oribi. In both mixed feeders the combination of using the two most proximal tooth positions, txM2 + M3, consistently classifies the species closer to the reference model (using txM2 only) than any other combination of tooth positions.

As a concluding result, we find a larger degree of inconsistency in the individual upper tooth positions in the mixed feeders (*Ourebi* and *Ovibos*) than in the browser (*Giraffa*). Both the four- and two-tooth models were therefore tested further using cluster analyses.

Cluster analysis

The cluster diagrams computed show relations of datasets by joining them in the same clusters. The closer the data are the smaller is the normalized Euclidean distance (NED) at the branching point (root-mean-squared difference). Cluster analysis polarizes the entire set of 28 recent species and the populations of *G. camelopardalis*, *O. ourebi*, *O. moschatus* and *E. burchelli* into a pattern with grazers and browsers at the extremes and with mixed feeders in between (Figs. 5 and 6). There are generally four main clusters, one containing

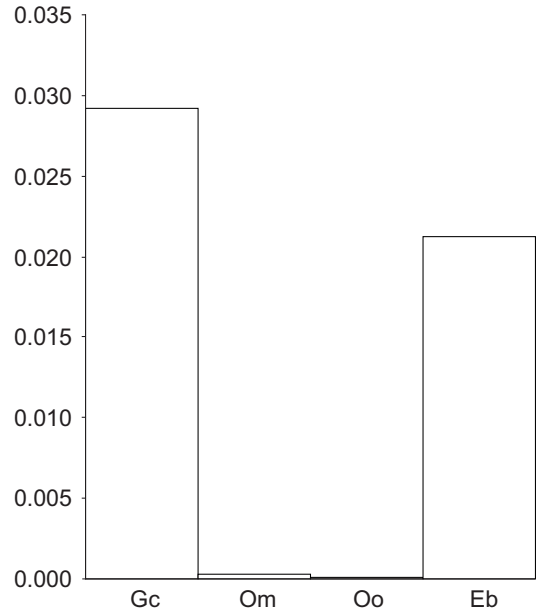


Fig. 1. Chi-square corresponding probabilities testing absolute mesowear scorings in upper versus lower second molars. Mesowear variables high, sharp and round were tested (see Table 1). Gc = *Giraffa camelopardalis*, Om = *Ovibos moschatus*, Oo = *Ourebia ourebi*, Eb = *Equus burchelli*.

the most abrasion dominated grazers, one containing the remaining grazers, one containing the mixed feeders and one the browsers.

Comparing upper and lower second molars (Fig. 5)

The upper tooth sample of *G. camelopardalis* (Gc(txM2)) shares the same subcluster within the browser spectrum as the comparison population by Fortelius and Solounias (2000). The lower tooth sample (Gc(tmM2)) however is linked in the mixed feeder spectrum, where it shares a subcluster of NED = 8 with the impala (*Aepyceros melampus*), an abrasion dominated mixed feeder, and the oribi (a “neutral” mixed feeder according to Fortelius and Solounias (2000)). The upper molars of *Ourebia ourebi* (Oo(txM2)) are linked in the mixed feeder spectrum, but are only linked at the level of NED = 23 to the reference population of Fortelius and Solounias (2000). This indicates a considerable difference between the population investigated

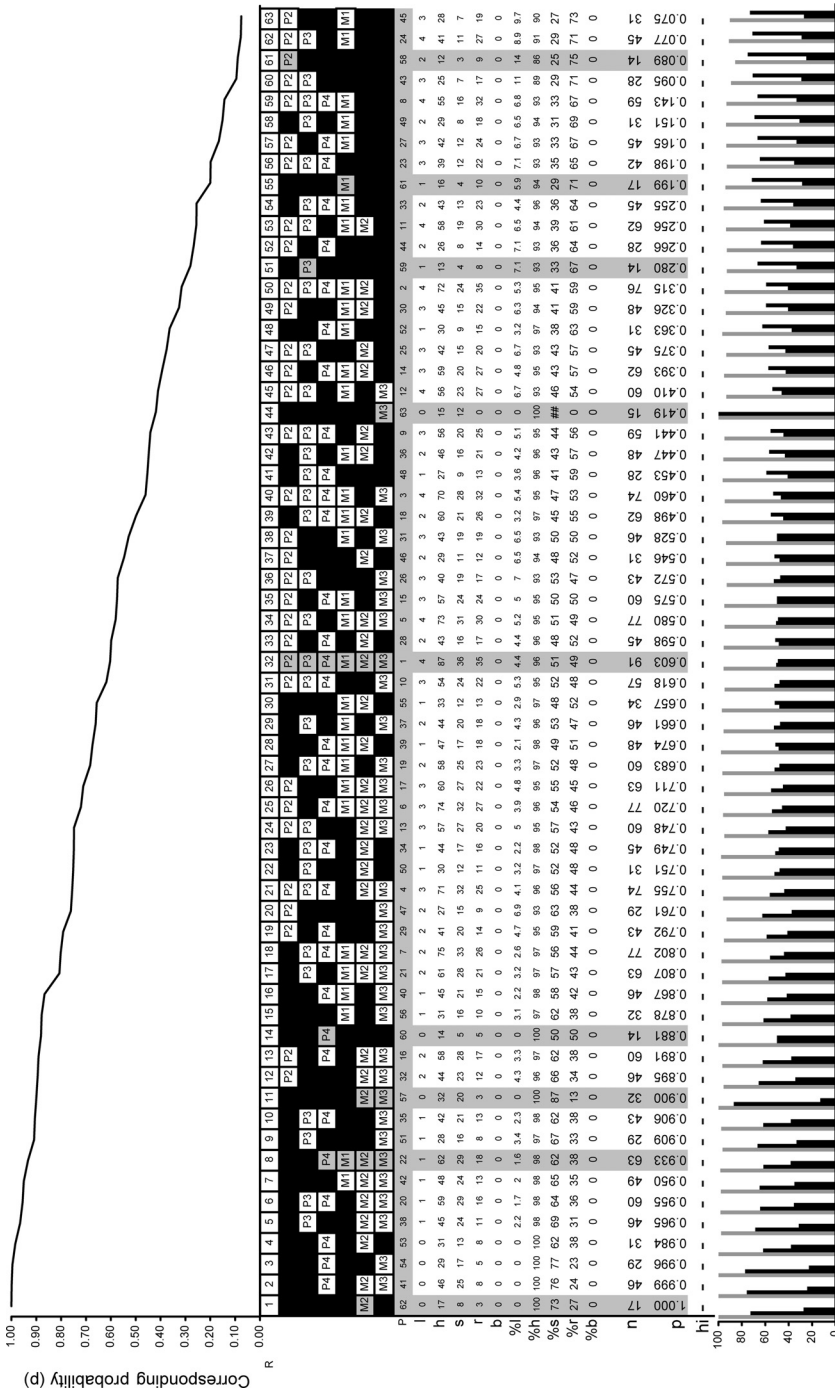


Fig. 2. Chi-square ranking matrix of the absolute frequencies of mesowear variables “low” (l), “high” (h), “sharp” (s), “round” (r) and “blunt” (b) calculated for 63 single and multiple tooth combinations for *Giraffa camelopardalis* from Africa. R = ranking position; P = number of combination of single and multiple tooth positions; l, h, s, r, b = absolute numbers of mesowear scores; % l, % h, % s, % r, and % b = calibrated frequency (percentages) of mesowear variables; n = number of tooth specimens in a certain model; χ^2 = Chi-square corresponding probability. The reference position for each test is the txM2 (far left column of the matrix, P = 62). The columns are sorted by decreasing p values. Large p value (left), small p value (right). TxM2 (R = 1) always has the p value of 1, because this position is the model position of the “original” mesowear method. hi: – (minus) = null-hypotheses of independence should be rejected at an error probability of 0.05; the distribution patterns are likely to be equal; + (plus) null-hypotheses of independence cannot be rejected, the distribution patterns are likely to be different. Grey background: all single tooth positions txP2, txP3, txP4, txM1, txM2 and txM3, the total of all tooth positions (txP2–M3) and the model for the “extended” mesowear method (txP4–M3) after Kaiser and Soloumias (2003). The bar charts to the bottom of each matrix plot indicate the calibrated frequencies (percentages) of mesowear variables for each column of the matrix. Gray = % h, black = % s, % r and % b.

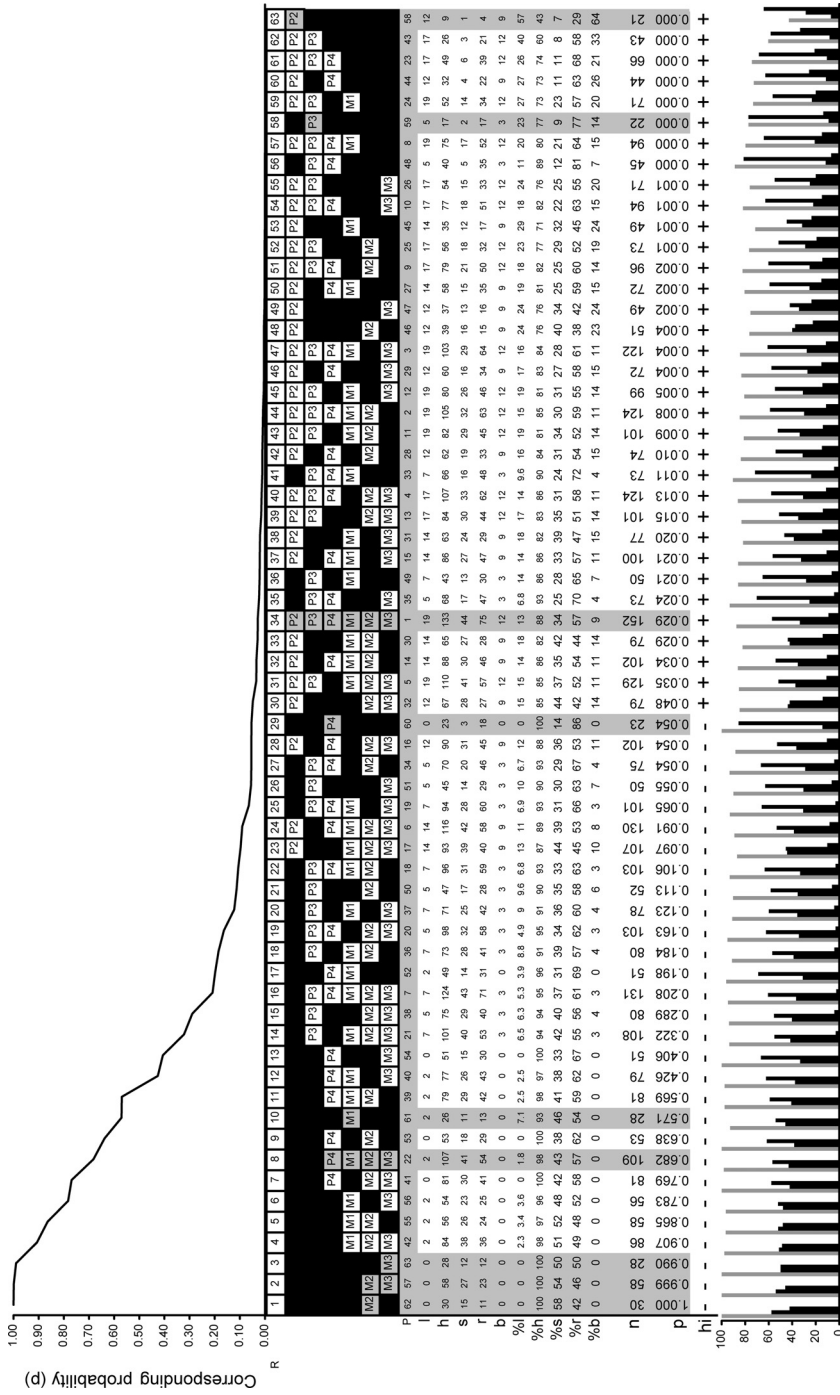


Fig. 3. Chi-square ranking matrix of the absolute frequencies of mesowear variables "low" (l), "high" (h), "sharp" (s), "round" (r) and "blunt" (b) calculated for 63 single and multiple tooth combinations for *Ourebia ourebi* from Africa. See Fig. 2 for details.

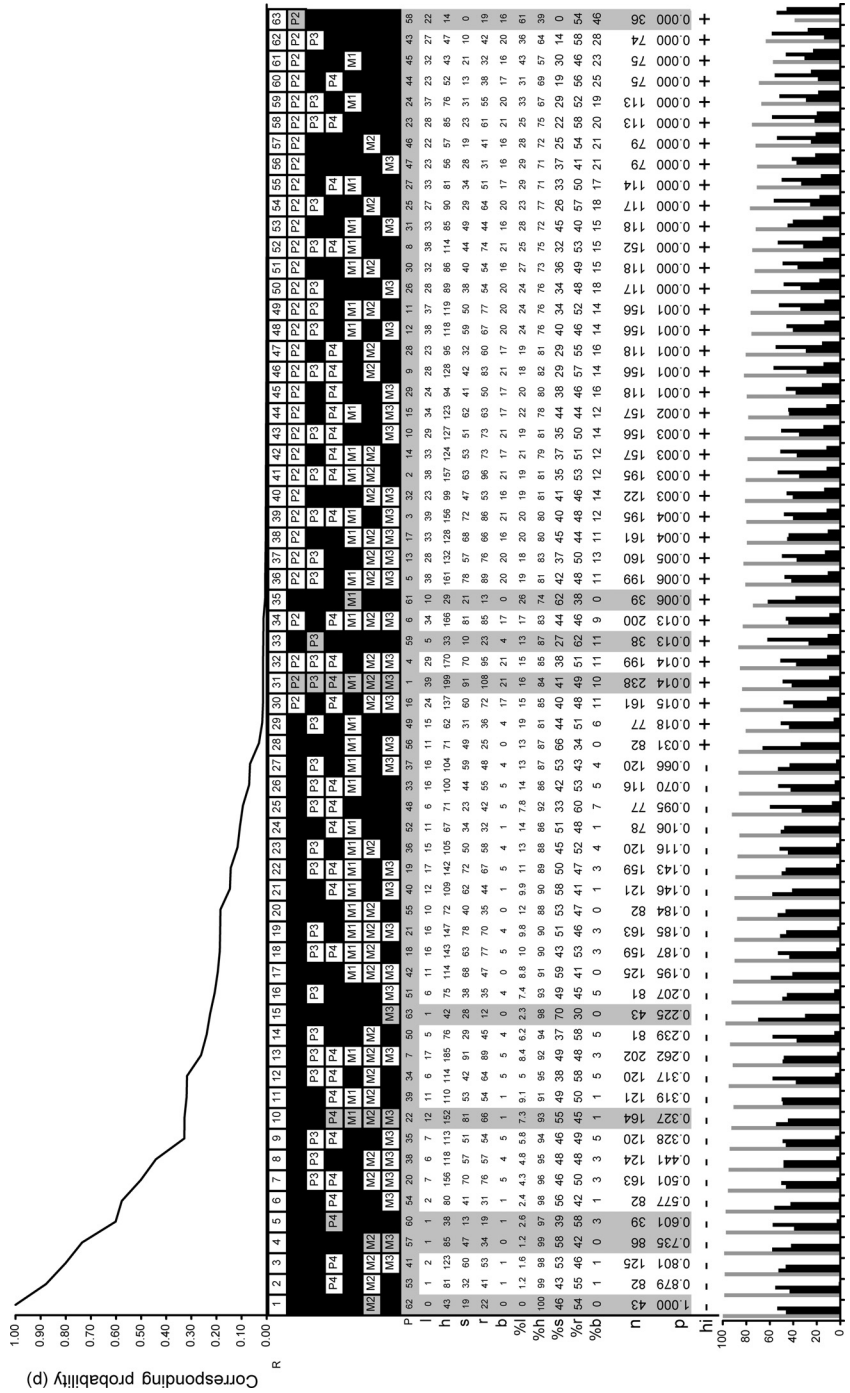


Fig. 4. Chi-square ranking matrix of the absolute frequencies of mesowear variables "low" (l), "high" (h), "sharp" (s), "round" (r) and "blunt" (b) calculated for 63 single and multiple tooth combinations for *Ovibos moschatus* from Greenland. See Fig. 2 for details.

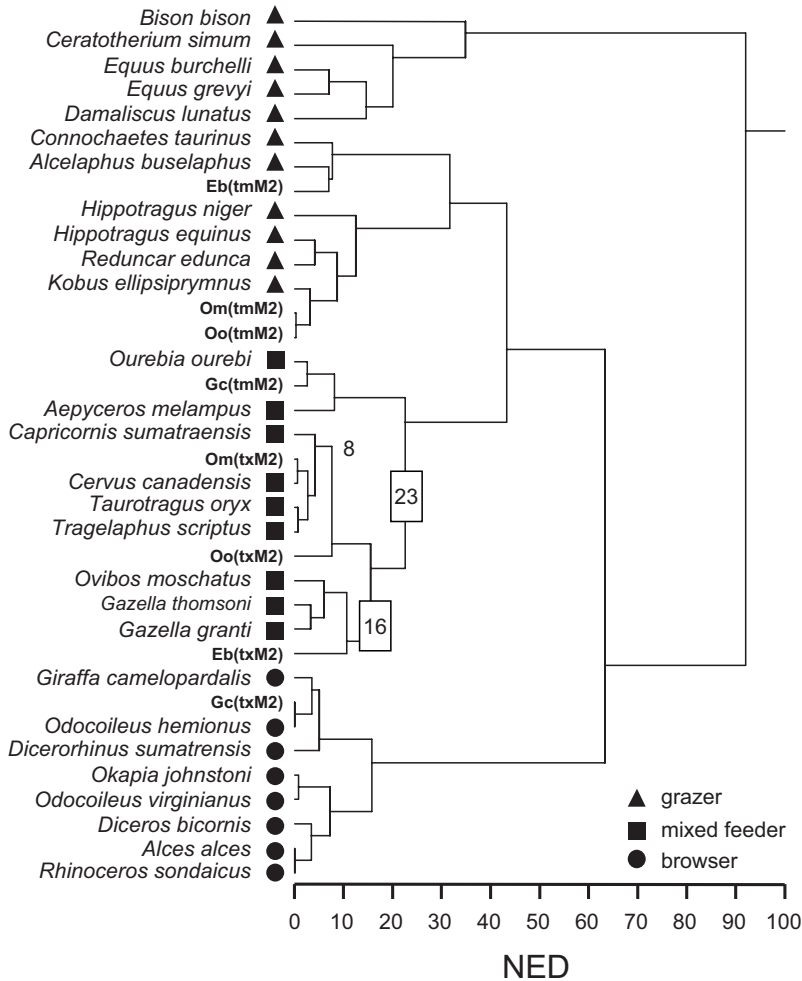


Fig. 5. Hierarchical cluster diagram comparing upper second molars (txM2) and lower second molars (tmM2) of populations of *Giraffa camelopardalis*, *Ovibos moschatus*, *Ourebia ourebi* and *Equus burchelli*, based on a set of “typical” recent species from Fortelius and Solounias (2000). *Ourebia ourebi*, a neutral species after Fortelius and Solounias (2000) is included, for comparative purposes. NED = normalized Euclidean distance (root-mean-squared difference). Oo = *Ourebia ourebi*, Om = *Ovibos moschatus*. Gc = *Giraffa camelopardalis*, Eb = *Equus burchelli*. tx = maxillary tooth, tm = mandibular tooth. tx(P4–M3) = four tooth model comprising upper (maxillary) teeth P4, M1, M2 and M3. This is the “extended” model by Kaiser and Fortelius (2003), tx(M2 + M3) = two-tooth model comprising upper (maxillary) M2 and M3. Data for *E. burchelli* is from Kaiser and Fortelius (2003).

here and the population investigated by Fortelius and Solounias (2000). Lower molars of *O. ourebi* (Oo(tmM2)) are linked within the grazer spectrum where they are closest to the common waterbuck (*Kobus ellipsiprymnus*). Upper molars of the *Ovibos moschatus* population (Om(txM2)) are linked in the mixed feeder spectrum, where they are linked to the reference population at the level of NED = 16. Lower molars of *O. moschatus* (Om(tmM2)) classify together with lower

molars of *O. ourebi* close to the common waterbuck (*Kobus ellipsiprymnus*) and thus are within the grazer spectrum. The classification of the *E. burchelli* population has already been described by Kaiser and Fortelius (2003) and is displayed to show the relation to the ruminant species investigated in this study (Fig. 5).

In summary, we show that for both the “neutral” (*Ourebia ourebi*) and “typical” (*Ovibos moschatus*) mixed feeders (as reported by

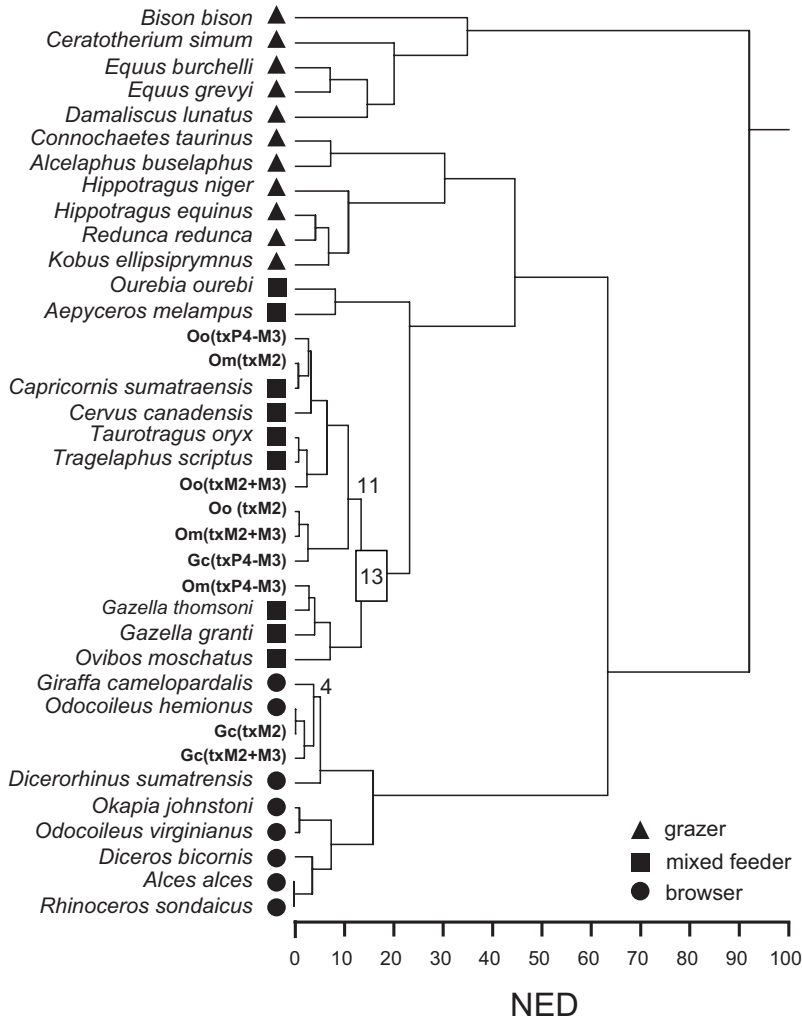


Fig. 6. Hierarchical cluster diagrams comparing the one-tooth model using upper second molars (txM2) only, the two-tooth model using upper second and upper third molars (txM2 + M3) and the four-tooth model (tx(P4-M3)) for populations of *Giraffa camelopardalis*, *Ovibos moschatus*, *Ourebia ourebi* and *Equus burchelli*, based on a set of “typical” recent species from Fortelius and Solounias (2000). See Fig. 5 for details.

Fortelius & Solounias 2000), the upper M2’s score within the mixed feeders while the lower M2’s are classified in the grazer range. For the browser, *G. camelopardalis*, lower M2’s score with the mixed feeders, while the uppers classify as browsers. The grazer population of *E. burchelli* investigated by Kaiser and Fortelius (2003) behaves like a mixed feeder based on upper M2’s and like a grazer based on lowers (for further discussion see Kaiser & Fortelius 2003).

Testing tooth models in ruminants (Fig. 6)

In the giraffe sample, the reference position of the original mesowear method based on the txM2 only is closely linked to the two-tooth model (txM2 + M3). Both share a subcluster of NED = 4 with the reference population of Fortelius and Solounias (2000). For *G. camelopardalis*, the “extended” four-tooth model (i.e. txP4-M3) proposed for hypsodont equids by Kaiser and Solounias (2003) does not classify

the population consistently. Using this model Gc is classified in the mixed feeder spectrum close to the bushbuck (*Tragelaphus scriptus*) and the eland (*Taurotragus oryx*).

The sample of *O. ourebi* second molars (txM2) is linked with both the two-tooth model (txM2 + M3) and the four-tooth model proposed by Kaiser and Solounias (2003) at the level of NED = 11. This cluster is shared with extant mixed feeders like the bushbuck (*Tragelaphus scriptus*), eland (*Taurotragus oryx*) and the wapiti (*Cervus canadensis*). In *O. moschatus*, the second mixed feeder in this study, all three models tested are linked at the level of NED = 13. The original one-tooth model (txM2), however, is more closely linked to the two-tooth model (txM2 + M3) at a distance of NED = 11 than to the four-tooth model (txP4–M3). While the two-tooth model classifies the *Ovibos* sample consistently with the one tooth model (txM2) and together with other mixed feeders (i.e. *Tragelaphus scriptus* and *Cervus canadensis*), the four-tooth model is linked to a different group of mixed feeders, comprising the two gazelles *Gazelle granti* and *Gazelle thomsoni*.

Discussion

Extending the number of model tooth positions available for mesowear evaluation in ruminants would significantly improve the mesowear method especially if fossil assemblages are to be investigated in the future. Most fossil assemblages contain low numbers of tooth specimens and restricting the mesowear method to just one tooth position considerably limits sample sizes. Our preliminary observations indicate that the “extended” four-tooth model suggested by Kaiser and Solounias (2003) for hypsodont equids (tx(P4–M3)) can not be applied to the ruminant species under study, because it does not result in a consistent classification of the species as compared with the one-tooth model of the original mesowear method by Fortelius and Solounias (2000). We observed that in the ruminants we investigated, the differences in mesowear signature between the individual tooth positions is larger than in *E. burchelli* and

the Miocene hipparionine *Hippotherium primigenium* (Kaiser & Solounias 2003) presumably as a result of a much more pronounced heterodonty in the ruminants. These observations, supported by chi-square analysis and cluster diagrams, indicate that a two-tooth model consisting of the upper M2 and M3 is preferred as a preliminary “extended” model for ruminants. This two-tooth model was found to consistently match the dietary classification of the one-tooth (tx(M2)) model. This extended model, incorporating only one additional tooth position (i.e. the upper M3), is likely to take the heterodonty of ruminants into account and should therefore be considered in the future application of the mesowear method to ruminant artiodactyls.

In comparing mesowear signatures in upper and lower second molars we make two important observations. Firstly, cusps of lower teeth tend to be less frequently sharp than those of upper molars, and secondly, mesowear signatures for upper and lower molars are more similar in the specialized feeders (the browsing giraffe and the grazing zebra) as compared with those in the mixed feeders (the oribi and musk ox). According to Kaiser and Fortelius (2003), gravity causes more pronounced additional wear in the lower teeth of highly hypsodont dentitions such as those of *Equus burchelli*. This gravitational force will always ensure that unloaded food will much more frequently contact the lower than the upper teeth. The comparatively higher degree of similarity between upper and lower mesowear signatures in *Equus* may therefore be the result of compensative evolutionary effects that reduce differential wear in order not to allow the adjoining tooth antagonists to diverge. We therefore expect adaptive optimization of enamel ultrastructure (Rensberger & von Koenigswald 1980, von Koenigswald & Sander 1997) to be particularly pronounced in *Equus* as compared with some ruminant species. This hypothesis should be further tested and is considered a possible source of differential wear control in grazers.

We find a similar effect in the giraffe, the browser in this comparison. Since both the giraffe and the zebra are specialized feeders, one would expect a similar functional adaptation forcing upper and lower dentitions to remain

similar in terms of mesowear signatures. In the giraffe however, the degree of anisodonty is much less pronounced than in the zebra. The less abrasive food eaten by the giraffe presumably causes far less additional unloaded abrasion to lower cheek teeth than is noted in the zebra. This could explain why the giraffe shows the smallest degree of differential mesowear, a hypothesis that is supported by the comparatively large p value (Table 1 and Fig. 1).

The mixed feeders, on the other hand, are required to cope with a wide variety of food items, including abrasive grass, grit loaded matter and tough foliage. We would therefore expect their lower dentitions to be subjected to a considerable amount of additional unloaded abrasion, which would favor differential wear in upper and lower cheek teeth. It appears as if lower molars “loose” their sharpness, while the uppers are optimized in terms of sharp cutting edges. This optimization is possible because of the lack of gravitational forces (and additional loading) acting on upper teeth. The degree of functional anisodonty is therefore likely to be most pronounced in the mixed feeders. This interpretation is further supported by a study by T. M. Kaiser (unpubl.), which indicates that enamel ridge alignments in ruminant cheek teeth are highly correlated with diet. T. M. Kaiser (unpubl.) finds that compared with browsers and grazers the mixed feeding ruminants have a particularly high proportion of cutting blades oriented at 75°–85° towards chewing direction. This observation is interpreted as reflecting an adaptation to cope with the extreme heterogeneity of plant materials eaten. Depending on body size, grazers and browsers however are found more frequently to have cutting blades oriented parallel or in low angle alignments to chewing direction. In terms of keeping upper teeth sharp, this is further evidence that maintaining sharp cutting blades in upper molars is the most critical adaptation of mixed-feeders, which lack many of the specific adaptations grazers have, but at the same time have to cope with grass as an extremely abrasive and fiber rich component in their diet.

In summary, although the significance of the results presented here with regards to the mesowear method are clear, understanding the processes behind differential wear control in upper

and lower teeth is far more complex. We have attempted to address these based on our preliminary data. Our results seem to suggest that in mixed feeders, sharpness is maximized in upper teeth, whereas in specialized feeders this is not the case to the same extent. Kaiser and Fortelius (2003) observe a similar pattern in mixed feeding horses. No doubt further investigations will shed light on these hypotheses and provide a better understanding of the evolutionary processes involved in differential wear control.

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Appendix

Dental specimens included in this investigation. ZMB = Museum für Naturkunde Berlin (Germany), ZMUK = Zoological Museum, University of Copenhagen (Denmark), tx = maxillary tooth, tm = mandibular tooth, s = left, d = right.

Ourebia ourebi: ZMB-17109 txP2 s, ZMB-20942 txP2 d, ZMB-36759 txP2 s, ZMB-36760 txP2 d, ZMB-40299 txP2 s, ZMB-40301 txP2 d, ZMB-41815 txP2 s, ZMB-4758 txP2 d, ZMB-56878 txP2 d, ZMB-56882 txP2 d, ZMB-56893 txP2 s, ZMB-56894 txP2 d, ZMB-56924 txP2 s, ZMB-56927 txP2 d, ZMB-56931 txP2 s, ZMB-56933 txP2 s, ZMB-56936 txP2 s, ZMB-56943 txP2 d, ZMB-57319 txP2 s, ZMB-57727 txP2 d, ZMB-17109 txP3 s, ZMB-20942 txP3 d, ZMB-36759 txP3 s, ZMB-36760 txP3 d, ZMB-40299 txP3 s, ZMB-40301 txP3 d, ZMB-41815 txP3 s, ZMB-4758 txP3 d, ZMB-56878 txP3 d, ZMB-56882 txP3 d, ZMB-56893 txP3 s, ZMB-56894 txP3 d, ZMB-56924 txP3 s, ZMB-56927 txP3 d, ZMB-56931 txP3 s, ZMB-56933 txP3 s, ZMB-56936 txP3 s, ZMB-56938 txP3 s, ZMB-56943 txP3 d, ZMB-56946 txP3 s, ZMB-57319 txP3 s, ZMB-57727 txP3 d, ZMB-17109 txP4 s, ZMB-20942 txP4 d, ZMB-36759 txP4 s, ZMB-36760 txP4 d, ZMB-40299 txP4 s, ZMB-40301 txP4 d, ZMB-41815 txP4 s, ZMB-4758 txP4 d, ZMB-56878 txP4 d, ZMB-56882 txP4 d, ZMB-56885 txP4 d, ZMB-56893 txP4 s, ZMB-56894 txP4 d, ZMB-56924 txP4 s, ZMB-56927 txP4 d, ZMB-56931 txP4 s, ZMB-56933 txP4 s, ZMB-56936 txP4 s, ZMB-56938 txP4 s, ZMB-56943 txP4 d, ZMB-56946 txP4 s, ZMB-57319 txP4 s, ZMB-57727 txP4 d, ZMB-17109 txM1 s, ZMB-20942 txM1 d, ZMB-36759 txM1 s, ZMB-36760 txM1 d, ZMB-40299 txM1 s, ZMB-40301 txM1 d, ZMB-41815 txM1 s, ZMB-4758 txM1 d, ZMB-56875 txM1 s, ZMB-56878 txM1 d, ZMB-56882 txM1 d, ZMB-56885 txM1 d, ZMB-56893 txM1 s, ZMB-56894 txM1 d, ZMB-56897 txM1 d, ZMB-56927 txM1 d, ZMB-56928 txM1 s, ZMB-56929 txM1 d, ZMB-56930 txM1 s, ZMB-56931 txM1 s, ZMB-56933 txM1 s, ZMB-56934 txM1 s, ZMB-56936 txM1 s, ZMB-56938 txM1 s, ZMB-

56943 txM1 d, ZMB-56946 txM1 s, ZMB-57127 txM1 s, ZMB-57319 txM1 s, ZMB-57727 txM1 d, ZMB-17109 txM2 s, ZMB-20942 txM2 d, ZMB-36759 txM2 s, ZMB-36760 txM2 d, ZMB-40299 txM2 s, ZMB-40301 txM2 d, ZMB-41815 txM2 s, ZMB-4758 txM2 d, ZMB-56875 txM2 s, ZMB-56878 txM2 d, ZMB-56882 txM2 d, ZMB-56885 txM2 d, ZMB-56893 txM2 s, ZMB-56894 txM2 d, ZMB-56897 txM2 d, ZMB-56924 txM2 s, ZMB-56927 txM2 d, ZMB-56928 txM2 s, ZMB-56929 txM2 d, ZMB-56930 txM2 s, ZMB-56931 txM2 s, ZMB-56933 txM2 s, ZMB-56934 txM2 s, ZMB-56936 txM2 s, ZMB-56938 txM2 s, ZMB-56943 txM2 d, ZMB-56946 txM2 s, ZMB-57127 txM2 s, ZMB-57319 txM2 s, ZMB-57727 txM2 d, ZMB-17109 txM3 s, ZMB-20942 txM3 d, ZMB-36759 txM3 s, ZMB-36760 txM3 d, ZMB-40299 txM3 s, ZMB-40301 txM3 d, ZMB-41815 txM3 s, ZMB-4758 txM3 d, ZMB-56875 txM3 s, ZMB-56878 txM3 d, ZMB-56882 txM3 d, ZMB-56885 txM3 d, ZMB-56893 txM3 s, ZMB-56894 txM3 d, ZMB-56924 txM3 s, ZMB-56927 txM3 d, ZMB-56928 txM3 s, ZMB-56929 txM3 d, ZMB-56930 txM3 s, ZMB-56931 txM3 s, ZMB-56933 txM3 s, ZMB-56936 txM3 s, ZMB-56938 txM3 s, ZMB-56943 txM3 d, ZMB-56946 txM3 s, ZMB-57127 txM3 s, ZMB-57319 txM3 s, ZMB-57727 txM3 d, ZMB-17109 tmM2 s, ZMB-20942 tmM2 d, ZMB-36759 tmM2 s, ZMB-36760 tmM2 d, ZMB-40299 tmM2 s, ZMB-40301 tmM2 d, ZMB-41815 tmM2 s, ZMB-4758 tmM2 d, ZMB-56875 tmM2 s, ZMB-56878 tmM2 d, ZMB-56882 tmM2 d, ZMB-56885 tmM2 d, ZMB-56893 tmM2 s, ZMB-56893 tmM2 d, ZMB-56894 tmM2 d, ZMB-56924 tmM2 s, ZMB-56927 tmM2 d, ZMB-56928 tmM2 s, ZMB-56929 tmM2 d, ZMB-56930 tmM2 s, ZMB-56931 tmM2 s, ZMB-56933 tmM2 s, ZMB-56936 tmM2 s, ZMB-56938 tmM2 s, ZMB-56943 tmM2 d, ZMB-56946 tmM2 s, ZMB-57127 tmM2 s, ZMB-57319 tmM2 s, ZMB-57727 tmM2 d.

Ovibos moschatus: ZMUK-R-1725 txP2 d, ZMUK-R-1726 txP2 s, ZMUK-R-1732 txP2 d, ZMUK-R-1734 txP2 d, ZMUK-R-1736 txP2 s, ZMUK-R-1737 txP2 s, ZMUK-R-2412 txP2 s, ZMUK-R-2414 txP2 s, ZMUK-R-2416 txP2 s, ZMUK-R-2419 txP2 s, ZMUK-R-2423 txP2 d, ZMUK-R-2430 txP2 s, ZMUK-R-2431 txP2 s, ZMUK-R-3012 txP2 s, ZMUK-R-3015 txP2 d, ZMUK-R-3471 txP2 s, ZMUK-R-3472 txP2 s, ZMUK-R-3472 txP2 d, ZMUK-R-3479 txP2 s, ZMUK-R-3607 txP2 d, ZMUK-R-3608 txP2 d, ZMUK-R-3610 txP2 d, ZMUK-R-3614 txP2 s, ZMUK-R-3615 txP2 s, ZMUK-R-3617 txP2 d, ZMUK-R-3619 txP2 d, ZMUK-R-3707 txP2 s, ZMUK-R-3708 txP2 s, ZMUK-R-3762 txP2 s, ZMUK-R-3769 txP2 s, ZMUK-R-3772 txP2 s, ZMUK-R-3777 txP2 s, ZMUK-R-3778 txP2 s, ZMUK-R-779 txP2 d, ZMUK-R-997 txP2 s, ZMUK-R-998 txP2 d, ZMUK-R-1725 txP3 d, ZMUK-R-1726 txP3 s, ZMUK-R-1727 txP3 s, ZMUK-R-1727 txP3 s, ZMUK-R-1732 txP3 d, ZMUK-R-1734 txP3 d, ZMUK-R-1736 txP3 s, ZMUK-R-1737 txP3 s, ZMUK-R-2412 txP3 s, ZMUK-R-2414 txP3 s, ZMUK-R-2416 txP3 s, ZMUK-R-2419 txP3 s, ZMUK-R-2423 txP3 d, ZMUK-R-2430 txP3 s, ZMUK-R-2431 txP3 s, ZMUK-R-3012 txP3 s, ZMUK-R-3015 txP3 d, ZMUK-R-3471 txP3 s, ZMUK-R-3472 txP3 s, ZMUK-R-3472 txP3 d, ZMUK-R-3479 txP3 s, ZMUK-R-3607 txP3 d, ZMUK-R-3608 txP3 d, ZMUK-R-3610 txP3 d, ZMUK-R-3614 txP3 s, ZMUK-R-3615 txP3 s, ZMUK-R-3617 txP3 d, ZMUK-R-3619 txP3 d, ZMUK-R-3707 txP3 s, ZMUK-R-3708 txP3 s, ZMUK-R-3762 txP3 s, ZMUK-R-3769 txP3 s, ZMUK-R-3772 txP3 s, ZMUK-R-3777 txP3 s, ZMUK-R-3778 txP3 s, ZMUK-R-779 txP3 d, ZMUK-R-997 txP3 s, ZMUK-R-998 txP3 d, ZMUK-R-1725 txP4 d, ZMUK-R-1726 txP4 s, ZMUK-R-1727 txP4 s, ZMUK-R-1727 txP4 s, ZMUK-R-1732 txP4 d, ZMUK-R-1734 txP4 d, ZMUK-R-1736 txP4 s, ZMUK-R-1737 txP4 s, ZMUK-R-2412 txP4 s, ZMUK-R-2414 txP4 s, ZMUK-R-2416 txP4 s, ZMUK-R-2419 txP4 s, ZMUK-R-2423 txP4 d, ZMUK-R-2430 txP4 s, ZMUK-R-2431 txP4 s, ZMUK-R-3012 txP4 s, ZMUK-R-3015 txP4 d, ZMUK-R-3471 txP4 s, ZMUK-R-3472 txP4 s, ZMUK-R-3472 txP4 d, ZMUK-R-3479 txP4 s, ZMUK-R-3607 txP4 d, ZMUK-R-3608 txP4 d, ZMUK-R-3610 txP4 d, ZMUK-R-3614 txP4 s, ZMUK-R-3615 txP4 s, ZMUK-R-3617 txP4 d, ZMUK-R-3619 txP4 d, ZMUK-R-3707 txP4 s, ZMUK-R-3708 txP4 s, ZMUK-R-3762 txP4 s, ZMUK-R-3769 txP4 s, ZMUK-R-3772 txP4 s, ZMUK-R-3777 txP4 s, ZMUK-R-3778 txP4 s, ZMUK-R-777 txP4 d, ZMUK-R-779 txP4 d, ZMUK-R-997 txP4 s, ZMUK-R-998 txP4 d, ZMUK-R-1725 txM1 d, ZMUK-R-1726 txM1 s, ZMUK-R-1727 txM1 s, ZMUK-R-1727 txM1 s, ZMUK-R-1732 txM1 d, ZMUK-R-1734

txM1 d, ZMUK-R-1736 txM1 s, ZMUK-R-1737 txM1 s, ZMUK-R-2412 txM1 s, ZMUK-R-2414 txM1 s, ZMUK-R-2416 txM1 s, ZMUK-R-2419 txM1 s, ZMUK-R-2423 txM1 d, ZMUK-R-2430 txM1 s, ZMUK-R-2431 txM1 s, ZMUK-R-3012 txM1 s, ZMUK-R-3015 txM1 d, ZMUK-R-3471 txM1 s, ZMUK-R-3472 txM1 s, ZMUK-R-3472 txM1 d, ZMUK-R-3479 txM1 s, ZMUK-R-3607 txM1 d, ZMUK-R-3608 txM1 d, ZMUK-R-3610 txM1 d, ZMUK-R-3614 txM1 s, ZMUK-R-3615 txM1 s, ZMUK-R-3617 txM1 d, ZMUK-R-3619 txM1 d, ZMUK-R-3707 txM1 s, ZMUK-R-3708 txM1 s, ZMUK-R-3762 txM1 s, ZMUK-R-3769 txM1 s, ZMUK-R-3772 txM1 s, ZMUK-R-3777 txM1 s, ZMUK-R-3778 txM1 s, ZMUK-R-777 txM1 d, ZMUK-R-779 txM1 d, ZMUK-R-997 txM1 s, ZMUK-R-998 txM1 d, ZMUK-R-1725 txM2 d, ZMUK-R-1726 txM2 s, ZMUK-R-1727 txM2 s, ZMUK-R-1727 txM2 s, ZMUK-R-1732 txM2 d, ZMUK-R-1734 txM2 d, ZMUK-R-1736 txM2 s, ZMUK-R-1737 txM2 s, ZMUK-R-2412 txM2 s, ZMUK-R-2414 txM2 s, ZMUK-R-2416 txM2 s, ZMUK-R-2419 txM2 s, ZMUK-R-2423 txM2 d, ZMUK-R-2430 txM2 s, ZMUK-R-2431 txM2 s, ZMUK-R-3012 txM2 s, ZMUK-R-3015 txM2 d, ZMUK-R-3471 txM2 s, ZMUK-R-3472 txM2 s, ZMUK-R-3472 txM2 d, ZMUK-R-3476 txM2 d, ZMUK-R-3479 txM2 s, ZMUK-R-3607 txM2 d, ZMUK-R-3608 txM2 d, ZMUK-R-3610 txM2 d, ZMUK-R-3614 txM2 s, ZMUK-R-3615 txM2 s, ZMUK-R-3617 txM2 d, ZMUK-R-3619 txM2 d, ZMUK-R-3707 txM2 s, ZMUK-R-3708 txM2 s, ZMUK-R-3762 txM2 s, ZMUK-R-3767 txM2 d, ZMUK-R-3769 txM2 s, ZMUK-R-3772 txM2 s, ZMUK-R-3777 txM2 s, ZMUK-R-3778 txM2 s, ZMUK-R-777 txM2 d, ZMUK-R-779 txM2 d, ZMUK-R-992 txM2 d, ZMUK-R-996 txM2 s, ZMUK-R-997 txM2 s, ZMUK-R-998 txM2 d, ZMUK-R-1725 txM3 d, ZMUK-R-1726 txM3 s, ZMUK-R-1727 txM3 s, ZMUK-R-1727 txM3 s, ZMUK-R-1732 txM3 d, ZMUK-R-1734 txM3 d, ZMUK-R-1736 txM3 s, ZMUK-R-1737 txM3 s, ZMUK-R-2412 txM3 s, ZMUK-R-2414 txM3 s, ZMUK-R-2416 txM3 s, ZMUK-R-2419 txM3 s, ZMUK-R-2423 txM3 d, ZMUK-R-2430 txM3 s, ZMUK-R-2431 txM3 s, ZMUK-R-3012 txM3 s, ZMUK-R-3015 txM3 d, ZMUK-R-3471 txM3 s, ZMUK-R-3472 txM3 s, ZMUK-R-3472 txM3 d, ZMUK-R-3476 txM3 d, ZMUK-R-3479 txM3 s, ZMUK-R-3607 txM3 d, ZMUK-R-3608 txM3 d, ZMUK-R-3610 txM3 d, ZMUK-R-3614 txM3 s, ZMUK-R-3615 txM3 s, ZMUK-R-3617 txM3 d, ZMUK-R-3619 txM3 d, ZMUK-R-3707 txM3 s, ZMUK-R-3708 txM3 s, ZMUK-R-3762 txM3 s, ZMUK-R-3767 txM3 d, ZMUK-R-3769 txM3 s, ZMUK-R-3772 txM3 s, ZMUK-R-3777 txM3 s, ZMUK-R-3778 txM3 s, ZMUK-R-777 txM3 d, ZMUK-R-779 txM3 d, ZMUK-R-992 txM3 d, ZMUK-R-996 txM3 s, ZMUK-R-997 txM3 s, ZMUK-R-998 txM3 d, ZMUK-R-1725 tmM2 s, ZMUK-R-1726 tmM2 s, ZMUK-R-1727 tmM2 s, ZMUK-R-1732 tmM2 s, ZMUK-R-1734 tmM2 d, ZMUK-R-1736 tmM2 s, ZMUK-R-2412 tmM2 s, ZMUK-R-2414 tmM2 s, ZMUK-R-2416 tmM2 s, ZMUK-R-2419 tmM2 s, ZMUK-R-2423 tmM2 s, ZMUK-R-2423 tmM2 d, ZMUK-R-2430 tmM2 s, ZMUK-R-2431 tmM2 s, ZMUK-R-3012 tmM2 s, ZMUK-R-3471 tmM2 s, ZMUK-R-3471 tmM2 d, ZMUK-R-3472 tmM2 s, ZMUK-R-3479 tmM2 s, ZMUK-R-3707 tmM2 s, ZMUK-R-3708 tmM2 s, ZMUK-R-3762 tmM2 s, ZMUK-R-3769 tmM2 s, ZMUK-R-3772 tmM2 s, ZMUK-R-3777 tmM2 s, ZMUK-R-3778 tmM2 s, ZMUK-R-775 tmM2 s, ZMUK-R-777 tmM2 d, ZMUK-R-779 tmM2 d, ZMUK-R-993 tmM2 s, ZMUK-R-997 tmM2 s, ZMUK-R-998 tmM2 d.

Giraffa camelopardalis: ZMB-15552 txP2 s, ZMB-17391 txP2 d, ZMB-20997 txP2 s, ZMB-31781 txP2 d, ZMB-32236 txP2 d, ZMB-32372 txP2 s, ZMB-32373 txP2 d, ZMB-42103 txP2 d, ZMB-48440 txP2 d, ZMB-84923 txP2 s, ZMB-84954 txP2 d, ZMB-84955 txP2 s, ZMB-84962 txP2 s, ZMB-84967 txP2 d, ZMB-15552 txP3 s, ZMB-17391 txP3 d, ZMB-20997 txP3 s, ZMB-31781 txP3 d, ZMB-32236 txP3 d, ZMB-32372 txP3 s, ZMB-32373 txP3 d, ZMB-42103 txP3 d, ZMB-48440 txP3 d, ZMB-84923 txP3 s, ZMB-84954 txP3 d, ZMB-84955 txP3 s, ZMB-84962 txP3 s, ZMB-84967 txP3 d, ZMB-15552 txP4 s, ZMB-17391 txP4 d, ZMB-20997 txP4 s, ZMB-31781 txP4 d, ZMB-32236 txP4 d, ZMB-32372 txP4 s, ZMB-32373 txP4 d, ZMB-42103 txP4 d, ZMB-48440 txP4 d, ZMB-84923 txP4 s, ZMB-84954 txP4 d, ZMB-84955 txP4 s, ZMB-84962 txP4 s, ZMB-84967 txP4 d, ZMB-15552 txM1 s, ZMB-17391 txM1 d, ZMB-20997 txM1 s, ZMB-31393 txM1 d, ZMB-31781 txM1 d, ZMB-32236 txM1 d, ZMB-32372 txM1 s, ZMB-32373 txM1 d, ZMB-42103 txM1 d,

ZMB-48440 txM1 d, ZMB-84923 txM1 s, ZMB-84942 txM1 d, ZMB-84954 txM1 d, ZMB-84955 txM1 s, ZMB-84961 txM1 d, ZMB-84962 txM1 s, ZMB-84967 txM1 d, ZMB-15552 txM2 s, ZMB-17391 txM2 d, ZMB-20997 txM2 s, ZMB-31393 txM2 d, ZMB-31781 txM2 d, ZMB-32236 txM2 d, ZMB-32372 txM2 s, ZMB-32373 txM2 d, ZMB-42103 txM2 d, ZMB-48440 txM2 d, ZMB-84923 txM2 s, ZMB-84942 txM2 d, ZMB-84954 txM2 d, ZMB-84955 txM2 s, ZMB-84961 txM2 d, ZMB-84962 txM2 s, ZMB-84967 txM2 d, ZMB-15552 txM3 s, ZMB-17391 txM3 d, ZMB-20997 txM3 s, ZMB-31781 txM3 d, ZMB-32236 txM3 d, ZMB-32372 txM3 s, ZMB-32373 txM3 d, ZMB-42103 txM3 d, ZMB-48440 txM3 d, ZMB-84923 txM3 s, ZMB-84942 txM3 d, ZMB-84954 txM3 d, ZMB-84955 txM3 s, ZMB-84962 txM3 s, ZMB-84967 txM3 d, ZMB-15552 tmM2 s, ZMB-17391 tmM2 d, ZMB-20997 tmM2 s, ZMB-31393 tmM2 d, ZMB-31781 tmM2 d, ZMB-32236 tmM2 d, ZMB-32372 tmM2 s, ZMB-32373 tmM2 d, ZMB-42103 tmM2 d, ZMB-48440 tmM2 d, ZMB-84923 tmM2 s.