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Traces of chewing bark and wood? – A microwear study of *Castor fiber* (Rodentia: Castoridae)

Stopy po žvýkání kůry a dřeva? – Mikroskopická studie obrusu u bobra evropského (*Castor fiber*) (Rodentia: Castoridae)

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Abstract. Tooth microwear analysis has been used repeatedly in the last decades to reconstruct diets of fossil mammals in comparison to recent ones and works well if the modern analogue has a characteristic miocrowear pattern. Here the microwear pattern of cheek teeth in several enamel bands of 20 specimens of the Eurasian beaver (*Castor fiber*) have been studied and were compared to data of mixed feeders and browsers from the literature as well as to nutria (*Myocastor coypus*) and muskrat (*Ondatra zibethicus*). The wear and microwear of incisors is only qualitatively described and consists of parallel broad scratches and few irregular pits and gauges on the lingual dentine facet, as well as irregularly distributed fine scratches on the enamel side. The microwear of the cheek teeth of beavers is dominated by fine scratches and shows few pits and gauges. The variability in the amount of scratches, pits and gauges is very high between individuals, different teeth and different enamel bands. Significant statistical differences in the occurrence of some microwear features were observed between p4/m1, p4/m2, p4/m3 and between P4/M3. Some significant differences between anterior and anterior hypoflexus were observed, but as none occurred in mandibular teeth are difficult to explain. The microwear pattern in *Ondatra* and *Myocastor* is similar but shows fewer scratches and relatively more pits. Comparable data for microwear of *Myocastor* obtained with a different method shows overall slightly more scratches, pits and gauges, which could indicate that the method used here underestimates the features by a certain small amount. This raises the question about comparability of microwear data found with different methods. Compared to the microwear signal of average pits versus average scratches in ungulate browsers, grazers and mixed feeders obtained with the same methodology used here, beavers show few pits and a moderate number of scratches and fall at the lower range of mixed feeders and the edge of the range of grazers. Muskrats and nutria are separated from beavers by the amount of average scratches and fall at the lower range of mixed feeders and at the edge of browsers compared to ungulates studied. However, no differentiation of the three species was obtained in discriminant analyses using all microwear features.

Key words. Beaver, cheek teeth, nutria, muskrat, browser, grazer, mixed feeder.

INTRODUCTION

Teeth are morphologically adapted to their use on all levels, from overall gross morphology (Starck 1982) to the arrangement of prisms in the enamel (e.g. Koenigswald 1997, Koenigswald & Sander 1997, Lucas 1979, Resnberger 1992, 1997, Resnberger & Stefen 2006). Usually sharp cutting blades are associated with carnivores, and piercing cusps indicate a diet of insects.

Within the last decades, especially with the works by Walker et al. (1978) and Teaford (1988, 1991), the study of tooth microwear and additional mesowear (Kaiser & Solounias 2003) has become another important tool to reconstruct diets of extinct mammals in comparison to recent mammals or to compare animals under wild and captive conditions (e. g. Clauss et al. 2007, Kaiser et al. 2009). Dental abrasion works on the order of days, and so microwear patterns are indicative of the diets prior to the death of the animal only.

In microwear analyses the microscopic features like scratches that form on the tooth's surface from use are studied. Many studies deal with primates and ungulates (e.g. Walker 1981, Solounias & Hayek 1993, Solounias et al. 1988, Solounias & Semprebon 2002, Ungar et al. 2006), but there are also analyses of moles (Silcox & Teaford 2002), some squirrels (Nelson et al. 2005) and caviomorph rodents (Townsend & Croft 2008a).

Beavers are the largest rodents in the Northern hemisphere, and two species are generally distinguished: the Canadian beaver *Castor canadensis* Kuhl, 1820 and the European beaver *Castor fiber* Linnaues, 1758. Both differ in the number of chromosomes (Lavrov & Orlov 1973, Jenkins & Busher 1979) but otherwise are nearly alike and are also ecological equivalents. Beavers are herbivores and well known for their ability to cut trees and build dams. They

Fig. 1. Stomach content of *Castor fiber* showing rests of bark and wood.
Obr. 1. Obsah žaludku bobra evropského (*Castor fiber*) ukazující zbytky kůry a dřeva.

feed on a series of herbs, water plants, even *Equisetum*, the leaves of trees and shrubs, and particularly the bark of twigs and smaller branches. However, they prefer soft wood species like aspen, poplar, and willow. If these species are not available also British oak, maple-species, ash, alder or elm are used, but other tree species are also taken. They also feed on several fruits and agricultural plants like apples and maize (see HINZE 1950, DJOSHKIN & SAFONOW 1972, or BUSHER 1996). Part of the leaves as well as smaller branches and twigs and part of the bark of felled trees are eaten immediately. Felling of trees usually occurs in autumn when beavers start to cache food for the winter. Beavers peel off the bark off branches to get to the nutritious cambium, but they also chew on bark and pieces of wood as is indicated by rests of these in their feces and stomach content (Fig. 1).

The question whether the diet with a high percentage of bark and wood shows a particular microwear pattern on the teeth has only been addressed briefly (STEFEN 2006). Here, the microwear of *Castor fiber* cheek teeth is dealt with in more detail, with a larger sample of specimens' statistical analysis and a comparison to different ungulate browsers, grazers and mixed feeders (SOLOUNIAS & SEMPREBON 2002), as well as to fruit-, fruit-seed and fruit-grass feeding caviomorph rodents (TOWENSEND & CROFT 2008a). The focus is on cheek teeth, as they are used in mastication, and incisors are only briefly considered. Microwear studies have been used to estimate diets of fossil taxa (e.g. KAISER & RÖSSNER 2007, PUECH et al. 2006, VAN VALKENBURGH et al. 1990). So one of the aims of this study was to see if the microwear diet of extant beavers would be characteristic enough in comparison to some other herbivorous mammals to predict a similar diet using bark and cutting of trees in fossil beavers.

For comparison, also the similarly semiaquatic rodents nutria, *Myocastor coypus* (Molina, 1782), and muskrat, *Ondatra zibethicus* (Linnaeus, 1766), were studied. Nutria feeds on rhizomes, leaves and saplings of several water plants, e.g. *Carex*, *Thypha*, or *Nymphea*. They also eat saplings and, especially in hard winters, trees or woody plants are peeled like *Alnus*, *Salix*, *Crataegus monogyna*, or *Hedera helix*. Like beavers they also use agricultural crops, e.g. potato, beet, carrots, maize and cereals (STUBBE 1982). TOWNSEND & CROFT (2008a) assigned *Myocastor* to a fruit-leaf dietary class. Muskrats are herbivorous and mainly feed on the roots of water plants like *Typha*, *Cirpus*, *Potamogetum*, *Nymphaea* etc. Usually they prefer one or two species, *Thypha* and *Sparganium*. Usually only the leaves and basal parts of the stalk are used, and, in winter, the rhizomes. Grasses, green cereal plants, vegetables, fruits, twigs, and bark of willows are also eaten (PIETSCH 1982).

MATERIAL AND METHODS

The dentitions of 20 specimens of *Castor fiber* from the Elbe in Germany were used. Material came from the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde Dresden (MTD: B 15082, B 15083, B 15085, B 15087, B 15092, B 15982, B 16613, B 17479, B 19041, B 19098) and from the Zoology Department at the Institute of Biology of the Martin-Luther-Universität Halle-Wittenberg (95/45, 94/90, 94/104, 94/105, 94/107, 94/120, 94/157, 94/190, 94/192, 94/19). For comparison, seven specimens of *Myocastor coypus* (MTD B 14222, B 14233, B 1881, B 9315, B 9315, B 9876, B 9876) and five specimens of *Ondatra zibethicus* (MTD B 16123, B 17004, B 17004, B 17017, B 17018) were also studied.

Microwear analyses has been done originally using scanning electron microscopy (WALKER et al. 1978, RENSBERGER 1978, TEAFORD 1988). SOLOUNIAS & SEMPREBON (2002) described a method using low resolution light microscopy to quantify wear patterns. This method has been shown to be effective in primates (SEMPREBON et al. 2004). In other studies this method has been further modified, particularly using computer programs to analyze the microwear features (e.g. MERCERON et al. 2005, SCOTT et al. 2006).

Here the method of Solounias & Semprebon (2002) is used and briefly described in the following. The teeth are cleaned with cotton swabs and alcohol. After drying (at least for 30 minutes) molds are made of the dentitions to be studied using a high resolution molding material, President Plus Jet Regular Body by Colthene Whaledent. The first mold is usually used for further cleaning the tooth's surface. The second mold is surrounded by lab putty (silicone) by hand to form a wall around the mold and thus to create a basin that can be filled with resin. The cast is then made using the high resolution clear epoxy resin (Epo-kwick Bühler). Special care has to be taken to eliminate air bubbles from the epoxy during or, rather, before hardening. The resin is poured into the prepared basins very carefully, starting in one corner and slowly covering the mold surface so that all small features can be filled with resin and no air is trapped. Casts can be studied by light microscopy with light shining obliquely on and "into" the cast and in this way making the surface microwear structures well visible.

The microwear features were analyzed by light microscopy as mentioned above and were counted at a magnification of 35× in a 0.4×0.4 mm standard square area. The differentiation of the microwear features followed Solounias & Semprebon (2002: 11–13): small pits "are very regular in appearance with sharp,

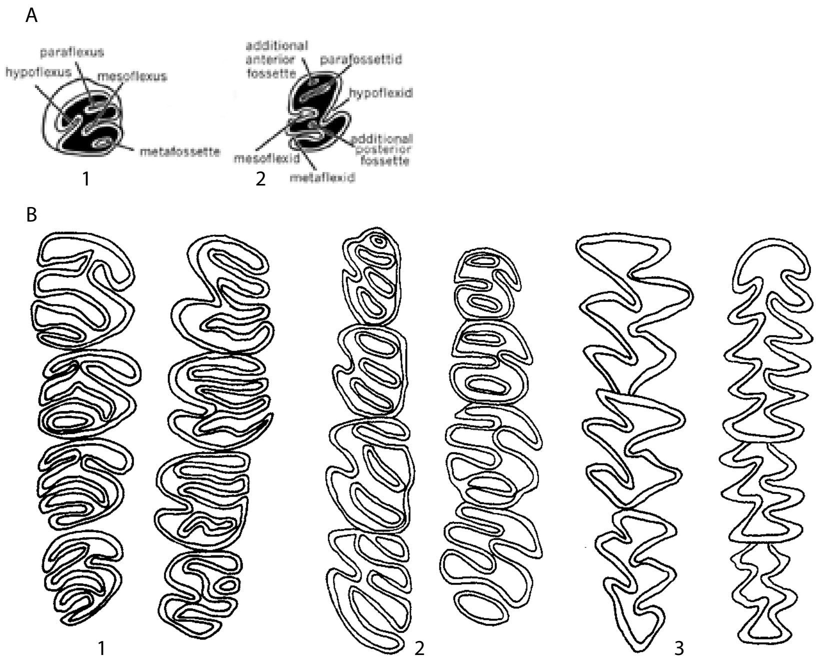

Fig. 2. Schematic illustration of (A) beaver teeth and nomenclature of enamel folds and (B) comparative dentitions of *Castor fiber*, *Myocastor coypus* and *Ondatra zibethica* not to scale. Anterior is to the top. (A) Nomenclature of enamel bands in upper (1) and lower (2) cheek teeth of Castoridae adapted after Stirton (1935). (B) Right maxillary dentition and left mandibular dentition of *Castor fiber*, *Myocastor coypus* and *Ondatra zibethicus*. Here the squares indicate the enamel.
Obr. 2. (A) schematický obrázek bobřích zubů a nomenklatury záhybů skloviny horních (1) a spodních (2) stoliček čeledi bobrovitých (Castoridae) podle Stirtona (1935) (přední strana je nahoře). (B) schematický obrázek porovnávající (pravé horní a levé spodní) stoličky bobra evropského (*Castor fiber*), nutrie (*Myocastor coypus*) a ondatry (*Ondatra zibethica*) (nikoli ve shodném měřítku).

distinct borders, being circular in nature and, very refractive or shiny ...”; “large pits are deeper, less refractive ... and often have less regular outlines than do small pits but are still generally circular.”; coarse scratches are relatively wide and deep and thus are refractive; fine scratches are much narrower; gauges “have ragged, irregular edges, and are much larger”, about 2–3 times the size of pits.

Only few casts of incisors of *Castor fiber* were studied by a Zeiss EVO 50 scanning electron microscope (SEM) to describe the microwear qualitatively. To do so they were sputter coated with a palladium/gold alloy for 120 seconds in a Polaron sputter coater.

Statistical analyses were computed using SPSS (Statistical Package for the Social Sciences, SPSS Inc, Chicago) 16. As the data are not all of normal distribution the nonparametric Mann-Whitney-Test was used to test for statistical significance between samples. For each species it was tested whether differences between right and left, between teeth or between enamel bands in mandibular or maxillary teeth could be found in the data. This test was also used to test between the species in the microwear features summed over all teeth.

Discriminant analyses (DAs) were used to see if the microwear features would separate between taxa. DAs were performed using Wilk’s lamda statistic, entry of all variables at once rather than stepwise, with equal prior probabilities of group membership, based on the pooled within-group covariance matrix.

Naming of enamel bands in *Castor fiber* follows Stirton (1935), see Fig. 2A. Microwear features were counted on the anterior and posterior enamel band of teeth, anterior and posterior enamel band of the hypoflexid/flexus, and the anterior enamel band of the mesoflexid/flexus. In *Myocastor* and *Ondatra* the anterior and posterior enamel band of the teeth and the anterior and posterior enamel band of the second triangle were used for counting the microwear features (fig 2b).

RESULTS

Incisors

The wear and microwear of incisors is mainly described qualitatively. In *Castor fiber*, upper and lower incisors show different macroscopic wear: usually the lower ones have a longer wear facet tapering gradually to the end, whereas the upper ones have a shorter wear facet ending in steps. Microwear on the dentin facet below the tip is similar in upper and lower incisors and is characterized by long, broad, parallel scratches of similar depth (Fig. 3). There are only few fine scratches of different direction. About 5 mm below the enamel edge more irregular large pits occur on lower incisors. The enamel front close to the tip shows fine scratches of different length, depth and direction (Fig. 3). The enamel edge of the incisor is fairly sharp and straight but shows several defects. Depending on the light, the two zones in the enamel characteristic for many rodents including beavers can be seen (Koenigswald & Mörs 2001).

In *Ondatra zibethicus* and *Myocastor coypus* the wear is also different in upper and lower incisors, and the overall wear pattern is similar to that of *Castor fiber*.

Cheek teeth

A marked relief between high enamel ridges and low dentine areas is characteristic of the cheek teeth of all three species. In *Castor fiber* the relief often decreases from anterior to posterior cheek teeth. In many cases the enamel bands are not flat on the occlusal surface but quite rounded. Microwear features can be seen on the enamel and dentine. With light optical means the overall direction of scratches can be seen to be about 20-30° labio-lingually to the long axis of the dentition.

In the beaver, scratches, particularly fine ones, dominate the microwear features, whereas pits are rare.

Four patterns of distribution of the highest amount of microwear patterns can be detected on the basis of individual mandibular dentitions: (a) in p4, (b) in m3, (c) in p4 and m3 and (d) in m1 and m2.

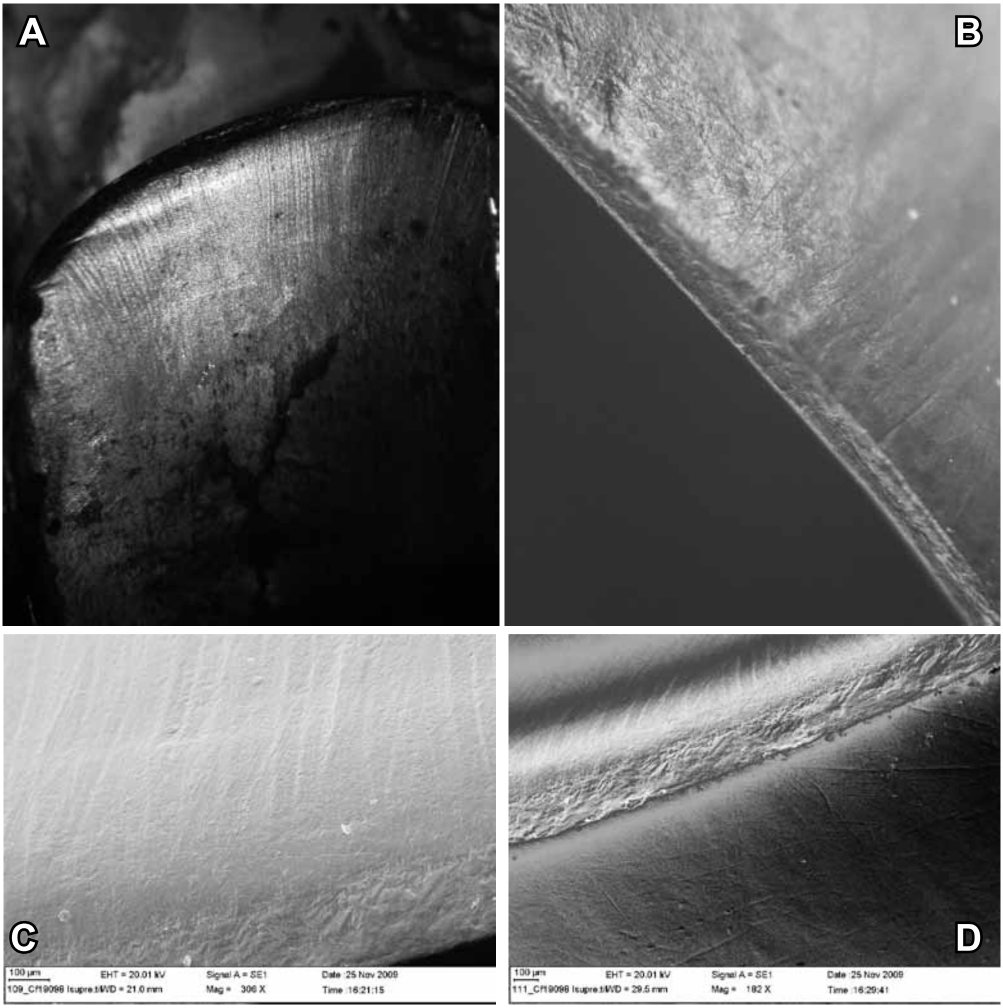

Fig. 3. Microwear on the incisor of *Castor fiber* as seen by light microscopy (A–B) and scanning electron microscopy (C–D). (A) maxillary incisor lingual wear facet, ca. 20×, (B) maxillary incisor microwear on enamel side, ca. 20×, (C) maxillary incisors lingual wear facet, (D) maxillary incisor enamel side.
Obr. 3. Mikroskopické zářezy na řezáku bobra evropského (*Castor fiber*) viditelné ve světelném mikroskopu (A–B) a v řádkovacím elektronomvém mikroskopu (C–D). (A) horní řezák, jazyková obrusová plocha, zvětšení cca 20×, (B) mikroskopický obrus horního řezáku na sklovinové straně, cca 20×, (C) horní řezák, jazyková obrusová plocha, (D) sklovinová strana horního řezáku.

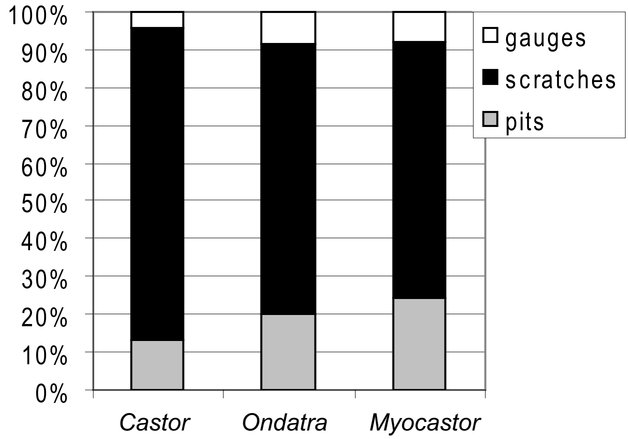

Fig. 4. Percent of average occurrence of microwear features gauges, scratches and pits over all studied cheek teeth in *Castor fiber* (*Castor*), *Ondatra zibethicus* (*Ondatra*) and *Myocastor coypus* (*Myocastor*). No further differentiation of wear features was chosen as comparisons are often based on scratches versus pit data (see Fig. 5).
Obr. 4. Procentuální průměrný výskyt mikroskopických obrusů (gauges – rýh, scratches – škrábanců, pits – důlků) na všech studovaných stoličkách u bobra evropského (*Castor*), ondatry (*Ondatra*) a nutrie (*Myocastor*). Dalšího rozlišování obrusových typů nebylo činěno, jelikož jsou nejčastěji porovnávány škrábance a důlky (viz obr. 5).

Overall, *Castor fiber* showed a higher number of microwear features than *Myocastor coypus* and *Ondatra zibethicus*, in particular fine scratches. In all three taxa the number of pits is about equally sparse (Fig. 4).

Statistics

The descriptive statistics for all microwear features over all teeth and enamel bands, and separated for teeth, is given in appendix 1. The range and variety of all features in *Castor fiber* as well as in *Ondatra zibethicus* and *Myocastor coypus* is quite large.

For *Castor fiber* no statistical significant differences between right and left dentitions (all teeth of each side taken together) were observed. Comparing teeth there are statistically significant differences between p4 and m1 in large and small pits; between p4 and m2 in fine scratches and gauges; and between p4 and m3, as well as between P4 and M3, in gauges and large pits.

In mandibular teeth no differences between the enamel bands were observed; in maxillary teeth there was a difference between anterior enamel and anterior hypoflexus as well as between anterior hypoflexus and posterior enamel in coarse scratches.

Discriminant analyses between teeth or between enamel bands in mandibular or maxillary teeth respectively did not reveal any separation of the groups for *Castor fiber*. For *Myocastor coypus* only statistical significant differences between m1 and M1 were observed for small pits. In maxillary dentitions, significant differences were observed between anterior enamel and anterior mesoflexus, anterior enamel and anterior hypoflexus and anterior enamel and distal

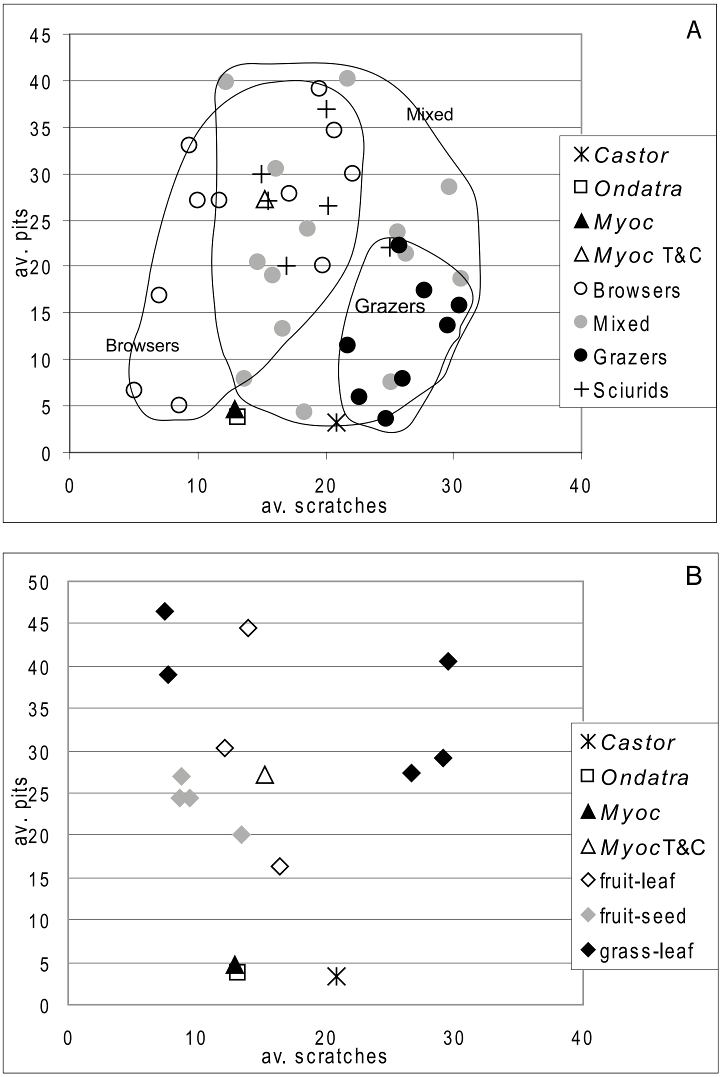

Fig. 5. Scatter diagram of average (av.) number of pits versus average number of scratches *Castor fiber* (*Castor*), *Ondatra zibethicus* (*Ondatra*) and *Myocastor coypus* (*Myoc*). (A) In comparison to typical browsers, mixed feeders (Mixed) and grazers (data from Solounias & Semprebon 2002), as well as to squirrels (data form Nelson et al. 2005). (B) In comparison to fruit-leaf, fruit-seed and grass-leaf feeders (data from Townsend & Croft 2008b [T&C]).

Obr. 5. Porovnání průměrného počtu (av.) důlků průměrného počtu škrábanců u bobra evropského (*Castor*), ondatry (*Ondatra*) a nutrie (*Myoc*); (A) ve srovnání s typickými spásači výhonků (browsers), směsnými spásači (mixed) a spásači travin (grazers) (údaje podle Solouniase & Semprebona 2002), a s veverkami (Sciurids) (údaje podle Nelsona et al. 2005); (B) ve srovnání s požírači plodů a listů (fruit-leaf), plodů a semen (fruit-seed) a trav a listů (grass-leaf) (údaje podle Townsenda & Crofta 2008b [T&C]).

hypoflexus in coarse scratches; in mandibular dentitions, between anterior and distal hypoflexus in coarse scratches. DAs did not result in a differentiation of cheek teeth. For *Ondatra zibethicus* no statistical significant differences between teeth were observed, nor between the anterior or posterior enamel bands (comp. Fig. 2). DAs did not reveal a separation of teeth on the basis of microwear structures. No separation between the three species studied was obtained in DAs using the microwear features of all teeth together.

DISCUSSION

The differentiation between microwear features is subjective to some degree, with the method of Solounias & Semprebon (2002) without computer programs. But the features appear different enough and it seemed adequate enough to use this method. As low magnification is used, not all especially small microwear features might be detected, and thus microwear in general is probably underestimated in this way. Here, main comparisons are made to the taxa studied by Solounias & Semprebon (2002) using the same method, and thus an error of similar magnitude could be assumed. Moreover, Semprebon et al. (2004) showed that this method has a low intra- and interobserver measurement error.

For the rat it had been shown experimentally that the mandibular movement clearly showed a separation in incisor interaction and masticatory activity. In this way, rodents are able to use incisors independently from the oral cavity in gnawing (Hiiemäe & Ardran 1968). Two types of incisor interaction can be noticed in beavers: gnawing with the mandibular incisors moving upwards and sliding along the lingual side of the maxillary incisors (movement described by Weijs (1994: 306); and tooth sharpening, or thegosis (Shadle 1936, Every 1975), when the lower incisors are in a position anterior to the lower incisors (Druzinsky 1995). In beavers the mandibular incisors slide along the maxillary incisors until the cheek teeth reach occlusion, and at this level the maxillary incisor shows a sharp ledge (Stefen et al. 2011). Whether sharpening of the teeth observed by Shadle (1936: 18) leaves characteristic microwear marks on maxillary incisors of beavers cannot be clarified with this study, as only irregular scratches were observed on the enamel side of the maxillary incisors (Fig. 3) and for tooth-sharpening clear parallel marks would be expected. These parallel scratches seen on the lingual side of the maxillary incisor originate from tooth-food/bark-tooth contact; those on the lingual side of the mandibular incisors from tooth-food/bark contact only. Tooth sharpening would also result in parallel scratches on the lingual enamel of mandibular teeth, but probably it occurs more rarely than gnawing and therefore tooth-food/bark contact is the assumed cause for the microwear here. When incisors interact the movement of the mandibular condyle is restricted and incisors can only move up and down (Stefen et al. 2011), which leaves the parallel scratches in the dentine. As dentine is softer than enamel the scratches are deep and broad.

Mastication in beavers and other rodents involves cheek teeth interaction, in which case the incisors do not get into contact as described above. In cheek teeth of beavers the microwear pattern is mainly formed by fine scratches. The higher an enamel band is elevated in relation to the dentine, the more rounded it is and the microwear features are difficult to focus on. Parallel scratches approximately parallel to each other and in an angle of about 20–30° to the long axis of the dentition dominate the picture. Mastication in beavers involves forward and transverse or mediolateral movement of the mandible, and the mandible is alternately moved to the right and left side (Stefen et al. 2011). Thus the dominant parallel scratches most likely result from this tooth-food-tooth interaction during mastication.

In the mandibular dentitions different patterns of frequency of the microwear features were observed, which cannot be explained, and as no general pattern between the different teeth was obvious it is assumed that these represent individual signs of chewing action or preferences. Differences between p4 and the mandibular molars in *Castor* were small but statistically significant in Mann-Whitney test, and would indicate that molars are used slightly more in chewing than p4. However, the difference was not obvious in maxillary dentitions but between P4 and M3, so it is difficult to argue for clear differences between molars and premolars. Differences in the amount of microwear features between the enamel bands were not obvious in mandibular or maxillary dentitions, and therefore differences between the enamel bands seem negligible. The large variability might partially reflect the fact that microwear pattern is caused by the diet a few days prior to death only, which, due to the large number of food species and seasonal preferences, might change. The anterior enamel band is often broken and not useful for counting, and thus the low number compared to others might have influenced the output for this position. For further studies in Castoridae it is suggested to use the enamel band of the meso- or hypofossette/tid as this is usually present, represent the middle of the crown, remain intact with wear for a long time, and are present in most fossil beavers as well (Stirton 1935). For *Ondatra* the small sample studied here did not show differences, so probably any enamel band could be used. For *Myocstor* the anterior band differed from the anterior mesoflexus/id and anterior and posterior hypoflexus/id so that here also hypo- and mesoflexus/id are best for studying microwear.

The question whether beaver populations from different sites dominated by other food plants might be asked but cannot be answered here. A controlled feeding study would be necessary. On the basis of the obtained results it seems unlikely that the preference of certain food species would be clearly discernible, particularly if beavers are considered in comparison to other herbivores (see below). The average number of fine scratches is the highest with about 20 on average in *Castor*. All other features are rarer and the average is about one to two. This is similar in the studied muskrat and nutria teeth (Fig. 4). In *Myocastor coypus* on average 11.9 (SD=4.9, SD – standard deviation) fine scratches, 2.49 (SD=3.23) small pits and 1.55 (SD=1.61) gauges were found. Townsend & Croft (2008a), however, found on average 15.25 (SD=5.27) scratches, 27.25 (SD=16.02) small pits and 3.88 (SD=2.02) gauges. These differences are difficult to explain but might be related to (a) the large variability in tooth microwear in these species, which might require even larger samples to come to a generalized conclusion and render statements on diets based on few individuals rather difficult (see SD); or (b) to the different methods and magnification used to count the microwear features, which were 35× and "by eye" herein and 70× and computer assisted in Townsend & Croft (2008a). This indicates that microwear data from different methods might be very difficult to compare between studies. For the other species studied herein no comparative data are available, so that it is difficult to judge whether the number of features might be underestimated.

In the analysis of browsers, grazers and mixed feeders of ungulates, browsers showed about 20–60 pits and abound 10 scratches, grazers between 24 and 30 scratches and up to 20 pits, and mixed feeders about 20 scratches and between 20 and 40 pits. Scratches are considered the more distinguishing characteristic with 0 to 17 in browsers and 17.5 to 19.5 in traditional grazers (Solounias & Semprebon, 2002). There is considerable overlap between mixed feeders and grazers, as well as between mixed feeders and browsers (Fig. 5a; Solounias & Semprebon, 2002). Grazing is associated with more scratches in general but also with more large pits; more fine scratches also indicate mixed feeders (Solounias & Semprebon 2002, Townsend & Croft

2008b). The overall average of all scratches puts beavers at the edge of the ranges of mixed feeders and grazers. Nutria and muskrat both fall at the edges of browsers and mixed feeders in comparison to data by Solounias & Semprebon (2002). The data for *Myocastor coypus* by Townsend & Croft (2008a) would place it in the browser category in comparison to the ungulates studied by Solounias & Semprebon (2002) – if such a comparison of data obtained by different methods is valid. The problem with comparing results obtained by different methods has been discussed above. However, the overall result for the dietary group would be expected to be similar. From their known diets, muskrat and nutria are best characterized as browsers and mixed feeders where grass (C4 grasses) probably plays a minor role. Lower amounts of pits indicate low amounts of sand and hard material. The slight difference in the probable assignment of beaver, muskrat and nutria to feeding categories is visible only if the overall averages of scratches and pits is used (Fig. 5); DAs using all microwear features were not able to separate these taxa, so that a very similar diet should be assumed or such a general diet that does not leave enough characteristic features for differentiation.

Townsend & Croft (2008a) used the dietary classes fruit-seed, fruit-leaf and grass-leaf for caviomorph rodents which, however, do not separate clearly on a scatter plot of average pits versus average number of scratches (Fig. 5b). Several – but not all – of the grass-leaf representatives show more than 25 scratches. The number of average pits of all their studied species is more than 15. Considerable overlap between the categories grass-leaf and fruit-leaf is observed, and the group of fruit-seed feeders is so close to the fruit-leaf feeders that a clear separation would need to be corroborated by a larger sample.

The number of microwear features of *Castor fiber*, *Ondatra zibethicus* and *Myocastor coypus* are below the range given in Townsend & Croft (2008a), who used a different methodology. The number of pits might be underestimated herein. Even adjusting for the low number of pits and thus imaginarily shifting the dot up in Fig. 5b would leave *Castor fiber* between the categories of grass-leaf and fruit-leaf feeders in caviomorph rodents. *Myocastor* and *Ondatra* again imaginarily shifted upwards in the graph allowing for the small number of pits would fall within the range of fruit-seed and fruit-leaf feeders of the categories used for caviomorph rodents. Thus, compared to the ungulates and caviomorph rodents, the results obtained herein place *Castor* more towards grazers or grass-leaf eaters than browsers or fruit eaters, thus maybe indicating some more abrasive food.

Based on the wide range of food plants used by beavers this is not surprising. Due to the use of several plant species, including herbs, water plants, leaves of trees and shrubs, *Castor* can be considered a mixed feeder. Beavers use grass (Hinze 1950), but probably only a low amount and not regularly. Still the number of scratches is in the lower range of other species using grass compared to Solounias & Semprebon (2002) as well as to Townsend & Croft (2008a). They are particularly known for the usage of bark of the twigs and branches of several trees. This diet does not leave a microwear pattern clearly distinct from other mixed feeding herbivores.

Squirrels studied also show between 15 and 25 scratches but more than 20 pits on average (Neslon et al. 2005; Fig. 5a). Moles showed a microwear pattern with very numerous fine scratches and few pits, a pattern that "seems consistent with a diet that forces teeth to shear against soil while processing food" (Silcox & Teaford 2002: 810). It had been assumed previously that hard objects increased the number of pits (Teaford & Walker 1984) and soil would be expected to include small sand grains which would lead to the expectancy of more pits in moles.

The numbers of scratches and pits are much higher in moles than in beavers. In moles, the high occurrence of small, narrow scratches indicates soil particles on the food (Silcocx & Teaford

2002). In beavers, soil particles play a negligible role in producing microwear, as the animals often feed in the water or keep branches in water, thus washing away soil particles. Although including tubers in the diet might increase the number of wider scratches (King et al. 1999), this effect might also be reduced by feeding in water. Even compared to most ungulate mixed feeders, beavers have few microwear features on the cheek teeth, and no clearly distinctive ones. Thus, based on microwear features alone, it would be very difficult to give a clear diet description for the beaver.

When microwear patterns of fossil teeth are studied the aim is to assign them to a feeding category or to describe important parts of the diet. This is only possible in relation to a well known and characteristic modern analogue. As extant beavers do not show a clear pattern, one would not be able to detect wood-cutting and the use of bark in fossil beavers. Whether fossil castorids, particularly fossorial palaeocastorids of North America (Martin & Bennett 1977, Martin 1987), might show a different diet could still be tested. From the fossil specimens which were to be included in this study (few palaeocastorine beavers and the upper Miocene European *Chalicomys jaegeri* Kaup, 1832 (Stefen 2009)), only casts which did not reveal microwear details were obtained, although teeth were well-cleaned. The reason for that was not obvious but the issue cannot be addressed further here.

SOUHRN

Mikroanalysa zubního obrusu byla opakovaně používána v posledních dekádách k rekonstrukci potravy fossilních savců v porovnání se současnými a je užitečná, pokud současné analogie mají typické znaky mikrozářezů. V předložené práci byly studovány znaky mikrozářezů stoliček na několika pásech skloviny u 20 jedinců bobra evropského (*Castor fiber*) a srovnány s údaji o spásačích výhonků a směsných spásačích z literatury a ze studia zubů nutrie (*Myocastor coypus*) a ondatry (*Ondatra zibethicus*). Obrus a mikroobrus řezáků je pouze kvalitativně popsán a sestává z rovnoběžných pásů škrábanců a nemnoha nepravidelných důlků a rýh na jazykové ploše zuboviny a nepravidelně rozmístěných jemných škrábanců na sklovinové straně. Mikroobrus na stoličkách bobra převažují jemné škrábance a ukazují se nepočetné důlky a rýhy. Proměnlivost v počtu škrábanců, rýh a důlků je velmi vysoká mei jedinci, jednotlivými zuby a jednotlivými pásy skloviny. Statisticky významné rozdíly ve výskytu některých mikroobrusových typů byly pozorovány mezi dvojicemi zůbů p4/m1, p4/m2, p4/m3 a P4/M3. Určité významné rozdíly byly zaznamenány mezi předním a zadním hypoflexem, ovšem proč se obrus nevyskytuje na spodních stoličkách je obtížné vysvětlit. Mikroobrus u ondatry a nutrie je obdobný, avšak vykazuje méně rýh a poměrně více důlků. Srovnatelné údaje o mikroobrusu nutrie získané různými methodami ukazují celkově lehce méně rýh, důlků a škrábanců, což může naznačovat, že methoda zde užitá podhodnotila v malé míře některé typy. Vyvstává tedy otázka, zda jsou srovnatelné údaje o mikroobrusu získané různými methodami. Ve srovnání s mírou mikroobrusu (průměrný počet důlků versus průměrný počet rýh) u kopytníků – spásačů výhonků, travin a smíšených spásačů získané stejnou methodikou jak zde, bobři vykazují méně důlků a mírný počet rýh a blíží se dolní hranici počtu u smíšených spásačů a okraji rozpětí spásačů travin. Ondatry a nutrie se liší od bobra průměrnými počty rýh a spadají na dolní okraj rozpětí kopytníků – směsných spásačů. Žádné rozdíly mezi třemi zkoumanými druhy však nebyly potvrzeny diskriminační analysou všech mikroobrusových typů.

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APPENDIX 1

Descriptive statistics of the microwear features in all teeth of *Castor fiber* and of *Myocastor coypus* and *Ondatra zibethicus* over all teeth together only;
Legend: n – number, SE – standard error of mean, SD – standard deviation, var. – variance.

descriptive statistics *Castor fiber* all teeth

	n	range	min	max	mean	SE	SD	var
scratches broad	787	9	0	9	1.07	0.054	1.508	2.275
scratches fine	787	43	0	43	19.74	0.280	7.865	61.863
gauges	786	11	0	11	1.13	0.056	1.568	2.458
pits large	787	39	0	39	2.21	0.150	4.198	17.626
pits small	787	35	0	35	1.11	0.105	2.953	8.719
microwear total	786	72	4	76	25.26	0.314	8.796	77.360
scratches all	787	46	0	46	20.81	0.288	8.068	65.095
pits all	787	52	0	52	3.32	0.200	5.590	31.246

descriptive statistics *Castor fiber* p4

	n	range	min	max	mean	SE	SD	var
scratches broad	97	9	0	9	1.04	0.163	1.607	2.582
scratches fine	97	39	0	39	17.06	0.792	7.801	60.850
gauges	96	7	0	7	1.41	0.159	1.560	2.433
pits large	97	19	0	19	2.68	0.369	3.633	13.199
pits small	97	24	0	24	2.38	0.477	4.700	22.093
microwear total	96	56	6	62	24.55	0.994	9.734	94.755
scratches all	97	39	0	39	18.10	0.798	7.861	61.802
pits all	97	30	0	30	5.06	0.632	6.223	38.725

descriptive statistics *Castor fiber* m1

	n	range	min	max	mean	SE	SD	var
scratches broad	105	8	0	8	1.30	0.165	1.692	2.864
scratches fine	105	38	0	38	19.74	0.764	7.831	61.327
gauges	105	11	0	11	1.15	0.185	1.895	3.592
pits large	105	30	0	30	2.41	0.493	5.053	25.533
pits small	105	10	0	10	081	0.185	1.892	3.579
microwear total	105	44	6	50	25.41	0.886	9.081	82.456
scratches all	105	43	0	43	21.04	0.816	8.361	69.902
pits all	105	30	0	30	3.22	0.533	5.457	29.769

descriptive statistics *Castor fiber* m2

	n	range	min	max	mean	SE	SD	var
scratches broad	102	6	0	6	1.12	0151	1.524	2.323
scratches fine	102	42	0	42	20.49	0840	8.481	71.936
gauges	102	8	0	8	1.08	0160	1.615	2.608
pits large	102	33	0	33	2.31	0.430	4.342	18.851
pits small	102	13	0	13	1.21	0.263	2.660	7.076
microwear total	102	63	5	68	26.21	0.943	9.522	90.660
scratches all	102	46	0	46	21.61	0.889	8.973	80.518
pits all	102	34	0	34	3.52	0.560	5.660	32.034

descriptive statistics *Castor fiber* m3

	n	range	min	max	mean	SE	SD	var
scratches broad	100	5	0	5	1.09	0.136	1.364	1.861
scratches fine	100	35	7	42	21.01	0.790	7.898	62.374
gauges	100	5	0	5	0.78	0.120	1.203	1.446
pits large	100	17	0	17	1.53	0.256	2.564	6.575
pits small	100	15	0	15	0.93	0.233	2.328	5.419
microwear total	100	46	7	53	25.34	0.866	8.658	74.954
scratches all	100	36	7	43	22.10	0.812	8.122	65.970
pits all	100	32	0	32	2.46	0.415	4.152	17.241

descriptive statistics *Castor fiber* P4

	n	range	min	max	mean	SE	SD	var
scratches broad	99	8	0	8	0.92	0.154	1.536	2.361
scratches fine	99	43	0	43	20.14	0.791	7.874	62.000
gauges	99	9	0	9	1.25	0.181	1.798	3.231
pits large	99	35	0	35	2.76	0.523	5.202	27.063
pits small	99	35	0	35	1.26	0.420	4.176	17.441
microwear total	99	72	4	76	26.33	0.976	9.707	94.224
scratches all	99	43	0	43	21.06	0.770	7.657	58.629
pits all	99	52	0	52	4.02	0.793	7.886	62.183

descriptive statistics *Castor fiber* M1

	n	range	min	max	mean	SE	SD	var
scratches broad	97	4	0	4	0.88	0.123	1.210	1.464
scratches fine	97	36	6	42	20.38	0.735	7.236	52.363
gauges	97	5	0	5	0.90	0.123	1.212	1.468
pits large	97	39	0	39	2.26	0.515	5.073	25.735
pits small	97	16	0	16	1.09	0.282	2.773	7.689
microwear total	97	56	11	67	25.51	0.871	8.581	73.628
scratches all	97	37	6	43	21.26	0.758	7.461	55.672
pits all	97	39	0	39	3.35	0.601	5.921	35.063

descriptive statistics *Castor fiber* M2

	n	range	min	max	mean	SE	SD	var
scratches broad	96	7	0	7	1.20	0.167	1.639	2.687
scratches fine	96	38	0	38	19.10	0.853	8.357	69.842
gauges	96	11	0	11	1.29	0.176	1.729	2.988
pits large	96	23	0	23	2.16	0.395	3.870	14.975
pits small	96	9	0	9	0.57	0.157	1.541	2.374
microwear total	96	32	10	42	24.33	0.780	7.837	61.425
scratches all	96	39	0	39	20.30	0.852	8.352	69.750
pits all	96	23	0	23	2.73	0.440	4.315	18.621

descriptive statistics *Castor fiber* M3

	n	range	min	max	mean	SE	SD	var
scratches broad	91	5	0	5	0.99	0.149	1.426	2.033
scratches fine	91	41	0	41	19.89	0.717	6.843	46.832
gauges	91	5	0	5	1.18	0.134	1.279	1.635
pits large	91	16	0	16	1.55	0.290	2.766	7.650
pits small	91	7	0	7	0.64	0.162	1.546	2.389
microwear total	91	38	1	49	24.24	0.699	6.664	44.408
scratches all	91	42	0	42	20.88	0.748	7.137	50.930
pits all	91	16	0	16	2.19	0.350	3.336	11.131

descriptive statistics *Myocastor coypus* all teeth

	n	range	min	max	mean	SE	SD	var
scratches broad	112	19	0	19	1.08	0.236	2.501	6.255
scratches fine	112	24	0	24	11.90	0.465	4.923	24.234
gauges	112	7	0	7	1.55	0.152	1.610	2.592
pits large	112	12	0	12	2.23	0.239	2.529	6.396
pits small	112	15	0	15	2.49	0.305	3.227	10.414
microwear total	112	32	4	36	19.26	0.528	5.586	31.203
scratches all	112	24	0	24	12.98	0.433	4.584	21.009
pits all	112	16	0	16	4.72	0.375	3.967	15.734

descriptive statistics *Ondatra zibethica* all teeth

	n	range	min	max	mean	SE	SD	var
scratches broad	56	6	0	6	0.95	0.193	1.445	2.088
scratches fine	56	18	6	24	12.29	0.491	3.672	13.481
gauges	56	4	0	4	1.54	0.184	1.375	1.890
pits large	56	18	0	18	2.07	0.358	2.682	7.195
pits small	56	9	0	9	1.64	0.297	2.219	4.925
microwear total	56	26	8	34	18.48	0.709	5.309	28.181
scratches all	56	22	6	28	13.23	0.565	4.225	17.854
pits all	56	18	0	18	3.71	0.466	3.489	12.171