Journal of Mammalogy, 97(2):619–630, 2016
DOI:10.1093/jmammal/gyv209
Published online January 21, 2016

Biomechanical aspects of incisor action of beavers (*Castor fiber* L.)

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Beavers are known for their gnawing performance, e.g., felling trees. Even though this is well known, the biomechanics of it are not, and so this is the focus of this study. The lower incisors work as main cutting tools so that their technical parameters were studied. There are 3 angles (adding to 90°) of importance in cutting: 1) the wedge angle, the angle of the incisor tip; 2) the clearance angle between tooth and material (tree trunk); and 3) the chip angle between incisor tip and the perpendicular to the surface of the trunk. Cutting is usually oblique to the wood fibers. For technical wood cutting tools, an optimal wedge angle of 27° is known under certain conditions, and for the incisor of *Castor fiber* the wedge angle was determined using micro-Computed Tomography (µCT) scans to be 26.95°. Potential cutting forces of beavers were estimated for wood chips (2 mm in thickness) of 3 sample tree species. For plum trees hardness forces ranged from 246 to 328 N, and for maples from 190 to 254 N. Finite element analyses were performed to determine stresses in the incisor under different loads on the incisor tip. Three hypotheses concerning gnawing were posed and are supported by the data: 1) The shape of the cutting blade of the incisor determines the geometry of wood chips and ultimately the maximum wood hardness that can be cut. 2) Clearance angle and maximum gape determine the maximum diameter of a tree that can be cut (if rough bark is neglected). 3) Functionally most importantly the lower incisors are optimized in shape and supporting tissue for compression stress with all forces being transmitted along the locations of the center of gravity in theoretical cross sections within the tooth, so that only compression occurs under load.

Key words: collagen fibers, cutting force, finite element model, form of incisors, gnawing of trees, histology, mechanical stressing, periodontal ligament, tooth enamel, wood chips

Beavers, Castoridae, including the 2 extant species *Castor canadensis* Kuhl, 1820 the Canadian beaver, and *Castor fiber* Linné, 1758 the European or Eurasian beaver, are well-known rodents of the northern hemisphere. They differ in number of chromosomes (Lavrov and Orlov 1973) but otherwise are nearly alike and can be considered ecological equivalents. Their main behavioral characteristics are the cutting of trees and use of wood to build lodges and dams to regulate the water table in aquatic systems. As they have the ability to modify ecosystems (Rosell et al. 2005), they are considered as ecosystem engineers (Raffel et al. 2009) or landscape architects. This behavior is well known (e.g., Morgan 1868; Martin 1892; Dugmore 1914; Hinze 1950). For example, Shadle and Austin (1939) documented the work of 2 beavers during 1 year and counted 116 cut trees in diameter from 2.5 to 33 cm and 2 dams constructed 215 m in total length.

Aims and scope.—Even though tree cutting is an important and well-known ability of beavers, the biomechanical details are poorly known. Thus, the focus of this paper is to describe biomechanical details of incisor action in *C. fiber* and to interpret the anatomy of incisors and mandible in functional anatomical terms. Three hypotheses form the baseline of the study:

Hypothesis 1.— The form of the cutting blade of the incisor determines the initial cutting force and the maximal wood hardness that can be cut. It also determines the geometry of the wood chips. In this context wood chips and shape of incisors are studied, and the wedge angle of the lower incisors used as cutting tool is determined.

Hypothesis 2.— The clearance angle at the incisor cutting blade and the maximal gape are constraints that influence the maximum tree diameter that can be gnawed. For this purpose, cutting forces are calculated and compared to experimental data.

Hypothesis 3.— The incisors are optimized in regard to compression stress in a sense of light-weight construction with a maximum of stability. Thus, all forces acting on the cutting blade of the incisors are transmitted along the locations of the centers of gravity of all cross sections or neutral axis (plane running down the middle completely unstressed in either tension or compression. In objects with a density "that does not vary from point to point, the geometric centroid and the center of mass coincide" (Ruina and Partap 2015). In objects consisting of different materials like rodent incisors the center of gravity does not coincide with the geometric center). Under load only compression stress occurs: there is no tensile stress and only low shear stress on dentin, enamel and cementum. In this context, histology of the periodontal ligament holding the incisor in place is studied and Finite Element Analyses (FEAs) are performed to determine the stress distribution in one incisor and in a simplified 3D model of the mandible.

Review of relevant beaver feeding ecology.—Beavers use trees for food: parts of leaves, as well as smaller branches and twigs, and parts of the living bark of felled trees are eaten immediately. In autumn, when most trees are felled, beavers cache food for the winter (Busher 1996, 2003; Dzięciołowski and Misiukiewicz 2002; Hartman and Axelsson 2004). In Europe, *Populus* sp. and *Salix* sp. are preferred. In North America, *Populus* and *Carpinus* (hornbeam, hardwood) made up 57% of felled trees and *Populus*, *Carpinus*, *Amelanchier* (serviceberry trees), *Salix* (willow), *Acer* (maple trees), *Betula* birch, and *Prunus* accounted for 93% of cut trees in Allegany State Park, New York (Shadle et al. 1943). Usually softwood species (here in the sense of wood density) are used more often than hardwood species. But, beech (*Fagus sylvatica*—Fuchs et al. 2009) and oak (*Quercus robur*) are also sometimes cut. At least 86 woody plant species and 149 herbs have been recorded as food plants of beavers (Heidecke 1988). Although woody plants dominate, they also use several fruits and agricultural plants like apples and maize.

Traces of cutting: trees cut.—Trees cut by beavers varied greatly in circumference, from about 8 cm to 135.72 cm (Shadle et al. 1943; Samways et al. 2004). Most commonly, trees with a diameter of about 20 cm are cut (Warren 1927; Hinze 1950), but there are noteworthy exceptions, e.g., a cottonwood tree of 117 cm diameter in North America (Warren 1927).

Traces of cutting: wood chips.—Trees cut and wood chips are well-known signs of beaver activity and have been described by Shadle (1957). He distinguished 2 types of chips: those mainly composed of bark and those entirely or almost entirely composed of wood. The former are clearly longer than the latter type, but both vary considerably in length from 5.1 to 15.56 cm with an average of 7.66 cm. Width ranged from 1.27 to 4.4 cm and thickness from 0.32 to 1.43 cm (Shadle 1957). Hinze (1950) found chips to be up to 10 cm long and 3 cm wide, depending on the type of wood.

Cutting technique.—The way in which beavers cut trees and branches of different size has been described and illustrated, for example, by Hinze (1950), Göhre (1954), and Rybczynski (2008) and is shown in at least 1 film (Arendt and Schweiger 1986). In general, rodents need an edge on the material to serve as abutment for gnawing, and the upper incisors are used mainly as an anchor (Wilsson 1971; Maul 2003). Also Zhijiang et al. (2003) showed that the upper incisors moved only slightly during incising wood. When the upper incisors are fixed at an anchor point, the lower incisors can perform gnawing movements similar to a planer and in this way create more or less parallel corrugations in the wood. Because rodents can move their lower jaw laterally to some degree, they can create adjacent furrows with the upper incisors in the same position (Maul 2003). Alternatively, as described by Göhre (1954:83), the lower incisors can cut into the wood up to a depth of about 1–2 cm and then the upper ones cut abruptly and obliquely into the wood fibers. The bite extends until upper and lower incisors meet so that hardly an edge remains. Also Hinze (1950) indicated a similar use of lower and upper incisors. Rybczynski (2008, figure 6) observed cutting of twigs by *C. canadensis*: the edge of the tip of 1 upper incisor was placed at the stick and the corresponding lower incisor was used for cutting. This method leaves characteristic cut marks: concave marks that are formed by the anterior surface of the lower incisor at the tree and convex marks that are formed by the lingual (posterior) side, the wear facet of the lower incisor on the chip.

When cutting a tree, the beaver holds its head obliquely and cuts the wood at varying angles to the long axis of the wood fibers. When cutting larger trees, beavers do not use a single position to fell the tree. The different directions the lower incisors acted in can be traced on the tree. Small trees can be cut on 1 side only, while larger trees are cut on 2 sides or around the trunk. In the latter case, the shape of the gnawed stem is a rotational hyperboloid.

Technical aspects of cutting.—In wood machining, 3 main cutting direction radians can be distinguished: A) the sectioning plane is perpendicular to the wood grain (rip sawing); B) the sectioning plane and the movement of the sectioning tool are parallel to the wood grain (planing); and C) the sectioning plane is parallel to the wood grain, and the movement of the cutting tool, however, is perpendicular to it (veneer cutting). Depending on the direction to the growth rings, 2 modes are distinguished (Fig. 1; after Kivimaa 1952; Cristóvão et al. 2012; Cristóvão 2013). These differences are important in wood machining. This is due to the high heterogeneity and anisotropy of the wood influenced by the annual growth rings with varying densities. When a beaver cuts a large tree, different cutting direction radians are used, partially veneer cutting in mode II (Fig. 1), oblique rip saw cutting, and thus will in some orientations be affected by the annual growth rings.

Cutting force depends on several factors, including cutting geometry, cutting angles, mechanical properties (of tool and wood), chip thickness, feed speed of the tool, wood species, wood density, and moisture content (Cristóvão 2013). The efficiency of cutting depends on the clearance angle α, cutting wedge angle β, and chip angle γ and thus on the tool shape (Fig. 2). The cutting force has 3 components: main cutting force F_c, normal force F_n (Fig. 2) and the lateral force F_l (not indicated; after Cristóvão 2013; Porankiewicz 2014). The lateral force is not considered here further.

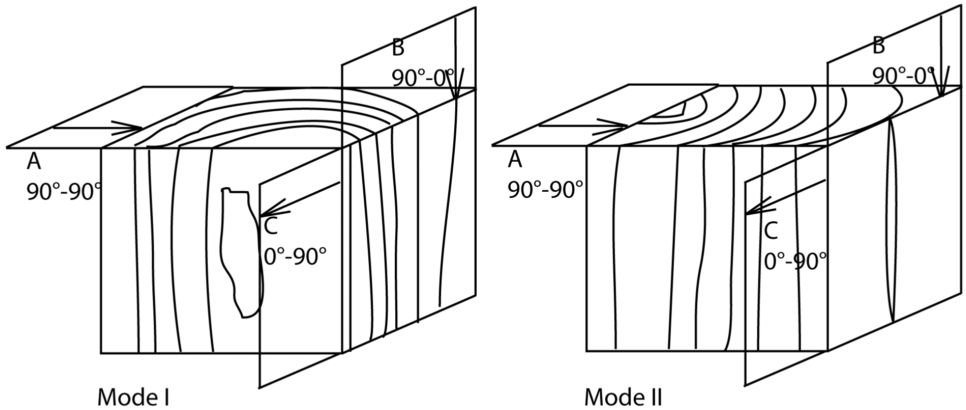

Fig. 1.—Cutting directions or rather cutting direction radians of wood adapted according to Kivimaa 1952 and Cristóvão 2013. Kivimaa (1950) differentiated between the orientation of the cutting edge (indicated by the fist given degree number) and the movement of the cutting tool (given in the 2nd number of degree) in relation to the wood grain or fibers. For each direction, 2 modes exist depending on the direction of the annual rings. Particularly, veneer cutting, C, is strongly affected by varying densities in mode I and therefore in research on wood cutting of this type mode II is used.

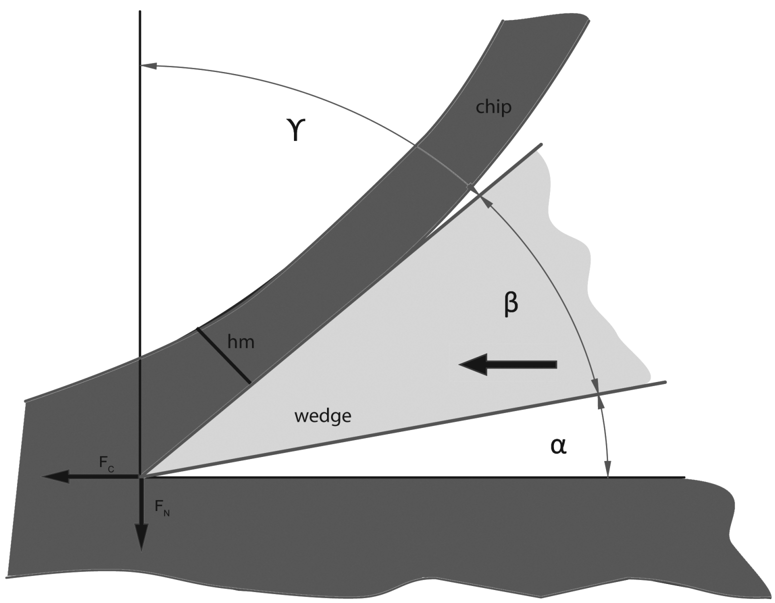

Fig. 2.—Schematic illustration of the cutting geometry with the angles and forces important in cutting (after Kivimaa 1950 and Porankiewicz 2014). The arrow in the wedge indicates the direction of cutting. The angles are α—clearance angle between wedge and material, β—wedge or bevel angle, and γ—rake angle or chip angle. The sum of these angles is 90°. If the clearance angle equals 0, no cutting is possible. F_C: main (cutting) force, F_N: normal force.

Cutting resistance decreases with smaller wedge angles to an optimal β_{opt} = 27° (under certain conditions: chip thickness 0.2 mm and α = 10°—Kivimaa 1952; Ettelt and Gittle 2004). The optimal wedge angle to minimize cutting resistance also depends on the material of the wedge (in this case, carbon steel), its sharpness (wear changes cutting force), and clearance angle α. Smaller wedge angles of 10° to 20° would require an even lower cutting force but would be too prone to blunting. The more stable wedge angle of technical cutting tools is commonly β_{tech} = 35° (Ettelt and Gittel 2004) because this provides more resistance to abrasion and breaking. However, breaking of the enamel tip of incisors in rodents leads to the self-sharpening of the wedge. This effect occurs if the wear of dentin leads to the loss of support for the enamel layer by the dentin. Research in progress indicates that in rodents, breaking of enamel at the cutting edge of the incisors takes place at an angle of about 25° and thus the angle of the tip is maintained (Fig. 3B). In a future paper, we will try to verify this assumption.

Materials and Methods

Specimens.—Dry skulls of *C. fiber* were studied in the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde (MTD), and in the collection Witzel, Biomechanik, Ruhr Universität Bochum. Two skulls of partially prepared and frozen specimens at the MTD were used for coarse sectioning of the mandible. One jaw (MTD B 27697) was stripped of musculature and fixed in 10% formalin solution and sent to Morphisto GmbH in Frankfurt for preparation for histological studies (see below). One mandible was donated by Th. Moers, State National History Museum (SNHM) Stockholm, to U. Witzel and the REM analyses of the incisor surface were done by J. Schemme under supervision of L. Gerke and M. Pohl, Institut für Werkstoffe der Ruhr Universität Bochum.

Wedge angle and µCT scans of beaver incisor.—The wedge angle of the lower incisors was determined using lateral photos of the teeth under the assumption that a tangent to the enamel face is perpendicular to the enamel surface (Fig. 3A). As this cannot be an exact measurement, micro-Computed Tomography (µCT) scans of the tip of 1 lower incisor (MTD B 27546) were obtained. The µCT scan was performed with a Nanotom (Phoenix GE, GE Sensing & Inspection, Wunstorf, Germany) in the tomography Lab (Geocenter/Senckenberg Frankfurt) with 90 kV and 80µA tube settings. The lower incisor was cut below the wear facet, 37 mm below the tip perpendicular to the long axis. The incisor tip was mounted on a 95-mm-long aluminum tube in such a way that the cutting edge was exactly horizontal and thus strictly parallel in relation to the xy-plane of the final 3D-CT volume. This mounting ensured a rotation of 360° within the X-ray center beam of only about 10 mm width when the specimen was fixed in the tomography (z-)axis of rotation. These elaborate preparations provided a much higher quality of the reconstructed 3D dataset compared to an in situ scan of teeth still in the jaw by avoiding excentric movements of the specimen from the center beam. All projection data were very close to the rotational (z-) axis which enabled high resolution and high geometric accuracy. During fitting of the tooth tip in the µCT scanner, several 2D scans at 90° rotation and corresponding readjustments were used to ensure that the mesial and distal enamel edges were projected nearly on top of each other. In this way, the labial (frontal) tooth plane is exactly defined by the laterally limiting enamel edges for very precise measurements in the 3D dataset.

To determine the angle at the cutting edge of the 3D dataset, the 4-point angle measuring tool of the 3D software VGStudio MAX Version 2.2 (Volume Graphics, Heidelberg, Germany; was used. Measurements were taken at 6 equidistant points along the cutting edge in a labio-lingual direction. Depending on wear features and the degree of wear, the (cutting) wedge angle between the enamel front (labial) surface and the enamel back (lingual) surface was measured or alternatively, in some cases, enamel was attrited between the enamel front and the dentin back surfaces.

Gape.—The theoretical maximal gape has been determined for dry skulls with the lower jaw opened until interaction of mandibular and maxillary bones prevented further movement. This gape is larger than would be possible in living beavers with intact musculature. The maximal theoretical gape was measured as the angle between a line from the articulation between the mandibular condyle to the glenoid on the squamosal to the tip of the maxillary and mandibular incisors, respectively. The maximal opening of the mouth was measured as the linear distance between maxillary and mandibular incisor tips.

Procumbency shape of incisor tip.—Procumbency of upper and lower incisors was measured according to Lessa and Thaeler (1989). They used 2 lines: 1 from the anterior alveolar rim of P4/p4 (A) and the distal rim of the alveolus of the incisor (B) and 1 from this latter point to the tip of the incisor (C) in the upper and lower jaws, respectively. The procumbency angle is the angle between these lines.

Histology of incisor periodontal ligament.—A broken dried skull and mandible of *C. fiber* (MTD B15088) and a 2nd

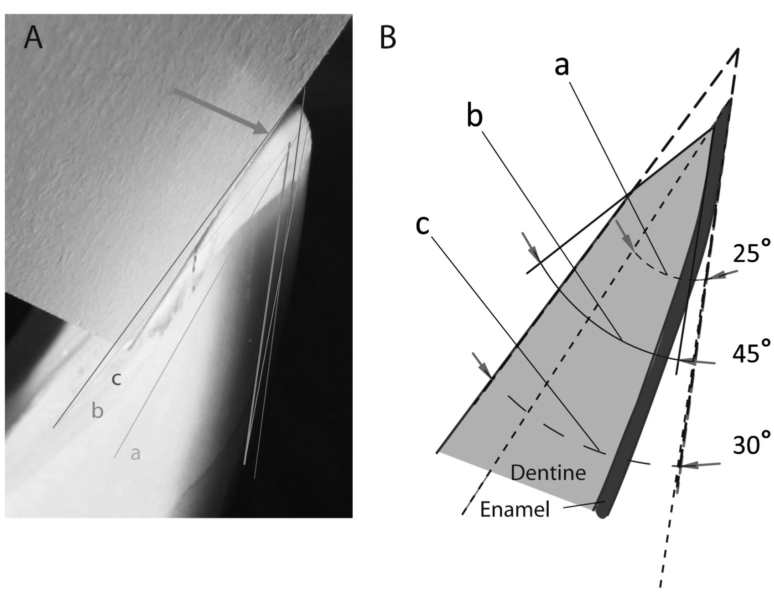

Fig. 3.—Illustration of the measurement of the wedge angle of the lower incisors of *Castor fiber*. A) Photo of lower incisor in lateral view used to measure the wedge angle in an idealized longitudinal section as indicated in B. B) Schematic longitudinal section perpendicular to the enamel surface of the lower incisor of beaver. a) indicates the active cutting wedge angle of a used incisor about 25°; b) indicates the angle of the worn dentin tip supporting the enamel, angle about 45°; and c) indicates the wedge angle of dentin with an angle of 30°.

uncatalogued specimen were used for macroscopic analyses. A 3rd fresh mandible was used for crude sections using a Bühler isomet 4000 linear precision saw in different orientations. These sections were analyzed with a binocular dissecting scope (Nikon SMZ 1500). The mandible of *C. fiber* (MTD B 27697) was sent to Morphisto GmbH Frankfurt (www.morphisto.de) for processing. Sections were photographed and analyzed in the Anatomical Institute of the Ruhr University Bochum, the MTD with a Nikon Eclipse 90i, and in the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie (MMG) using a Leica DM 5500 B microscope.

Wood chips.—Cut marks on trees and twigs as well as associated wood chips produced by *C. fiber* were studied from the Elbe river embankment in Dresden and different locations in the Dübener Heide, Saxony, and Brandenburg. Wood chips were collected and are now stored at the MTD. Wood chips from *Salix* sp. were used to measure a) maximal length of chip, b) the maximal width perpendicular to the long axis of the chip, c) thickness or depth of the chip using a ruler (Fig. 4), and d) number of cuts made on one or both sides and approximate angles of cut marks to woody fibers. Only chips from willow trees were used as this is one of the preferred food species of beavers. No systematic study of wood chips from different tree species or beavers of different ages was within the scope of the study; only some basic measurements were needed.

Estimation of cutting force.—To model the cutting force for wood is difficult due to the high anisotropy of the material. Also, wood is characterized by its moisture content; nearly all characteristics are influenced by humidity. These facts and the cellular construction of wood render models to calculate forces very difficult to nearly impossible. In chipping, the actual cutting force can only be measured. But, there are ways to estimate it using coefficients related to the width of the chips because cutting force in planing changes linearly with chip width (Maier 2000). The cutting force can be calculated after e.g., Gottlöber (2014) or Maier (2000) using:

$$F_C = k_{c0.5} b \sqrt{h_m}$$

with $k_{c0.5}$ = cutting factor [N/mm$^{1.5}$], an approximated, artificial value, nearly independent of h_m to describe the material properties in relation to cutting force (Gottlöber, pers comm., TU Dresden), b = chip width [mm] and h_m = average chip thickness [mm].

The cutting factor $k_{c0.5}$ depends on the wood species, its moisture content and gross density ρ (= mass/volume [g/cm^3]), and on the cutting direction radians (Fig. 1) and has to be determined experimentally (Ettelt and Gittel 2004; Wagenführ and Scholz 2008). Published values for the cutting factor vary greatly and are available only for few tree species (i.e., Wagenführ and Scholz 2008; Table 1) and depend on the cutting direction radian (Gottlöber, pers comm., TU Dresden). Kivimaa (1952) showed in measurements with different wood species that cutting force F_c reaches a maximum with a wood moisture content of 10% and decreases steadily to a moisture content of 50%. Due to the high anisotropy of wood, gross density varies within 1 trunk and within 1 wood species from

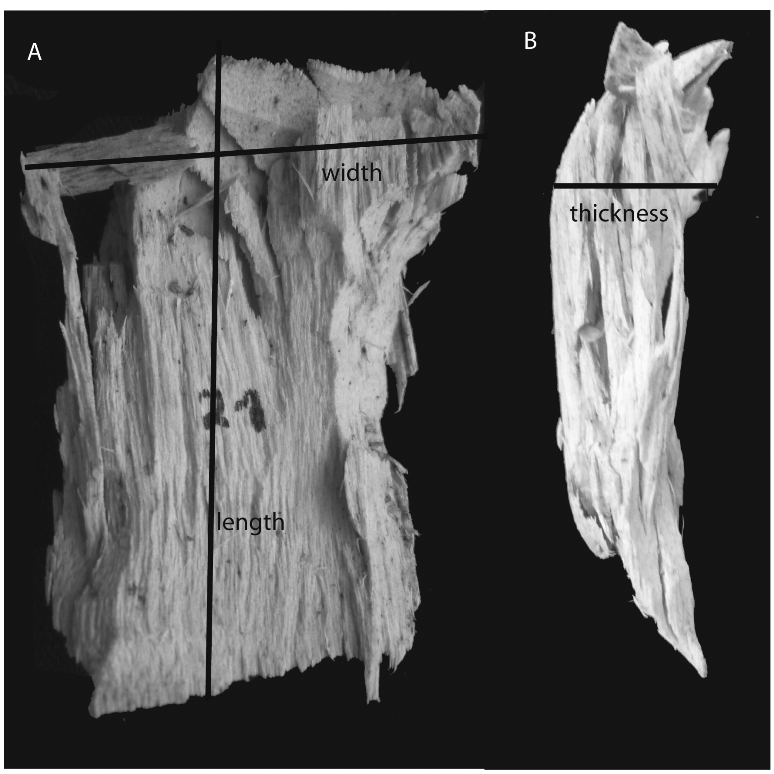

Fig. 4.—Explaining the measurement of wood chips. A) Wood chip lying flat on the surface and length and width are indicated. B) Wood chip is placed on the thinnest side, so that thickness (or breadth) can be measured. No scale is given as it is irrelevant.

Table 1.—Cutting factors for some tree species in relation to the 3 different cutting radians (see Fig. 1) from Wagenführ and Scholz (2008).

Tree species	Cutting direction radians		
	A	B	C
Maple	23 … 35	12	9
Ash	22 … 42	11	7.5
Birch	23 … 35	10	6
Beech	26 … 40	12	7.5

different localities (Maier 2000:89). In solid wood, cutting force and cutting factor are approximately proportional to gross density (Wagenführ and Scholz 2008). And under comparable conditions, known cutting force parameters can be converted and transmitted to another wood species using gross density. Therefore, $k_{c0.52}$ of wood species 2 with a gross density ρ_2 can be estimated when $k_{c0.51}$ of wood species 1 and its gross density ρ_1 are known (Ettelt and Gittel 2004:103):

$$k_{c0.52} = k_{c0.51}\rho_2 / \rho_1$$

Normal gross density is given for normal conditions of 20°C/65% relative humidity (Table 2). Under these conditions, moisture content of wood is about 12% and thus dried wood. Living trees (those cut by beavers and of interest here) have a much higher humidity of more than 30%. When using gross density to estimate the cutting force factor, it is important to consider the same humidity—cutting force factors are given for dried wood (8–12% humidity—Gottlöber, pers comm., TU Dresden). As only these are available, they are used here, knowing that with the higher humidity of living trees the necessary cutting force is lower than the calculated one (see also above).

Finite element analysis.—A 3-dimensional finite element analysis (FEA) was performed to estimate the compression stress distribution in the total volume of an incisor and its supporting tissue in a simplified mandible. This FE model is based on the 3D laser scan of the mandible of the dry skull of *C. fiber* (collection Witzel) and the resultant surface model in the.stl-format (Standard Triangulation Language; Fig. 5). After geometrical simplification, the model of the mandible was imported into the FEA software ANSYS version 12 Ansys Inc. 1994, to determine the distribution of compression stresses within the mandible and the incisor under gnawing conditions. The model consists of 263,000 10-noded tetrahedral finite elements with Young's moduli for bone and dentin $E_{B/D}$= 17 GPa, and for enamel E_E= 60 GPa (Vogel 2003). The Poisson ratio is 0.3.

Results

Wood chips.—Wood chips from willow trees (*Salix* sp.) showed a length range from 1.5 to 12.5 cm (n = 100) with an average of 6.65 cm ± 2.53 *SD*. Chips with bark ranged in size from 4.5 to 12.5 cm with an average of 7.79 ± 2.59 cm (n = 22); those without bark ranged from 1.5 to 10.6 cm with an average of 6.27 ± 2.39 cm (n = 77). The width of all chips ranged from 1.8 to 5 cm with an average of 3.3 ± 0.67 cm (n = 99) and the thickness or depth from 0.2 to 2 cm with an average of 0.96 ± 0.45 cm. Usually, the bark can be stripped off in larger pieces than wood, and so chips with bark are generally longer. At trees with larger diameters, more chips without bark are produced.

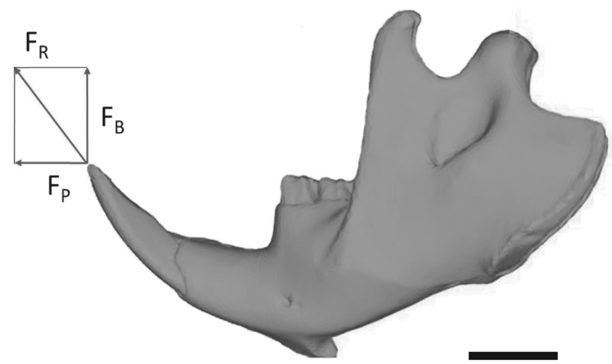

Fig. 5.—3D surface model of the mandible of *Castor fiber* with F_B = biting force, F_P = pressing force, F_R = resultant force as the working force of the incisor. Scale bar = 20 mm.

Chips can also be described as "single-cut" or "multi-cut" chips and the latter can be divided into 1-sided or 2-sided multi-cut chips. Most chips were multi-cut chips. Single-cut chips occurred more frequently at larger trees, where the beaver had to cut deeper into the tree. However, they are much easier to overlook, or multi-cut chips degrade and produce single-cut chips and thus introducing bias into estimates for their occurrence.

Up to 12 cuts have been observed on 1 side of a chip; often 5–6 can be seen. In double-sided chips, the cut marks on both ends are usually divergent and seldom oriented parallel to each other. The cuts are at an angle to the wood fiber direction. The angle varies between 45° and 90° to the fiber direction, most often a range of 60° to 90° was observed with an average of 76°.

Gape and procumbency angle.—The maximum theoretical gape ranged from 32° to 55° in 11 specimens with a mean of 42.38°. The maximum distance between the incisor tips ranged from 5 to 7.8 cm in dry skulls (n = 11) and averaged 6.3 cm. In a beaver of full adult size found dead in Dresden the distance between the incisors was 3 cm when unprepared. The procumbency angle of the lower incisors varied from 115° to 142° with an average of 129.1° (n = 11) and of upper incisors it varied between 79° and 95° with an average of 89.17° (n = 11).

Wedge angle of beaver incisors.—The wedge angle β of 20 lower incisors measured from lateral photos (Fig. 3A) ranged from 23° to 25°. The wedge angle from the CT scan 3D volume was taken from 1 lower incisor using the spatial calibration described above. Measurements were taken at 6 equidistant sections and varied from 25.4° to 29.4°, with a mean of 26.95° (Fig. 6).

Histology.—Scanning electron microscopy of isolated dried incisors does not reveal porosities on the dentin or enamel surface, but the histology of the periodontal ligament of the lower incisor in *C. fiber* indicates a strong fixation of the tooth along the dentin sides of the triangular cross section by Sharpey's fibers. The incisor is fixed by fibers along the complete length within the alveolus. From the anterior margin of the alveolus to the apical end of the incisor, the periodontal ligament shows a very dense arrangement of fibers. The fibers are generally attached to the dentin at approximate right angles and bend after a few µm to an acute angle to the long axis and tip of the incisor. After the bend, the fibers form a dense meshwork, with an apparent dominant direction, but with crossing bundles. Along most of the tooth, fibers are not strongly curled. They are strongly interwoven with the bone; the fibers are inserted into the bone of the alveolus at right angles (Figs. 7 and 8). The enamel side of the tooth is not fixed in this way but supported by a loose connective tissue allowing sliding of the incisor (growth) and giving support.

Cutting force.—Sample estimates of the cutting force of beavers are given in Table 3. Required cutting force depends strongly on the thickness and width of the wood chip and cutting direction radian as indicated in the "Materials and Methods" section above. The lowest forces are required with smaller chips (small thickness and width).

Diameter of the trunk that could be gnawed.—If distance between the incisors is 6.5 cm and the clearance angle α between the enamel tips of the incisors and the trunk is 18°, the maximum diameter of tree or trunk that could be gnawed is 50 cm. At this diameter, the initial clearance angle of 18° ensures, as a precondition, that the angle at the end of the bite is greater than zero.

Finite element analysis.—During cutting, 2 forces are exerted from the cutting edge of each incisor, the biting force (F_B) and the pressing force (F_p) against the tree trunk. The vector sum of these forces is a resultant force (F_R) and represents the cutting force of the incisors, and in the opposite direction the working load of the incisor in opposite direction (Fig. 5). Both components are controlled by the animal using variable chip geometry to calibrate the biting force and using the upper incisors hooked on the trunk as anchors to generate a moment with adjusted pressing forces at the cutting edges of the lower incisors. In the biological sense, this must operate as a reflex arc because the resultant force on each side of the mandible has to pass the location of the center of gravity of each cross section of the incisors to minimize inner bending moments. This is significant because dentin and enamel are adapted mainly to tolerate compression forces, and the anatomy of the anterior mandible would not tolerate bending because the bony lateral wall of the alveolus is extremely thin. The idea of a reflex arch is supported by the presence of Ruffini endings, a type of mechanoreceptors in collagenous tissues, in the lingual periodontal ligament (Jayawardena et al. 2002).

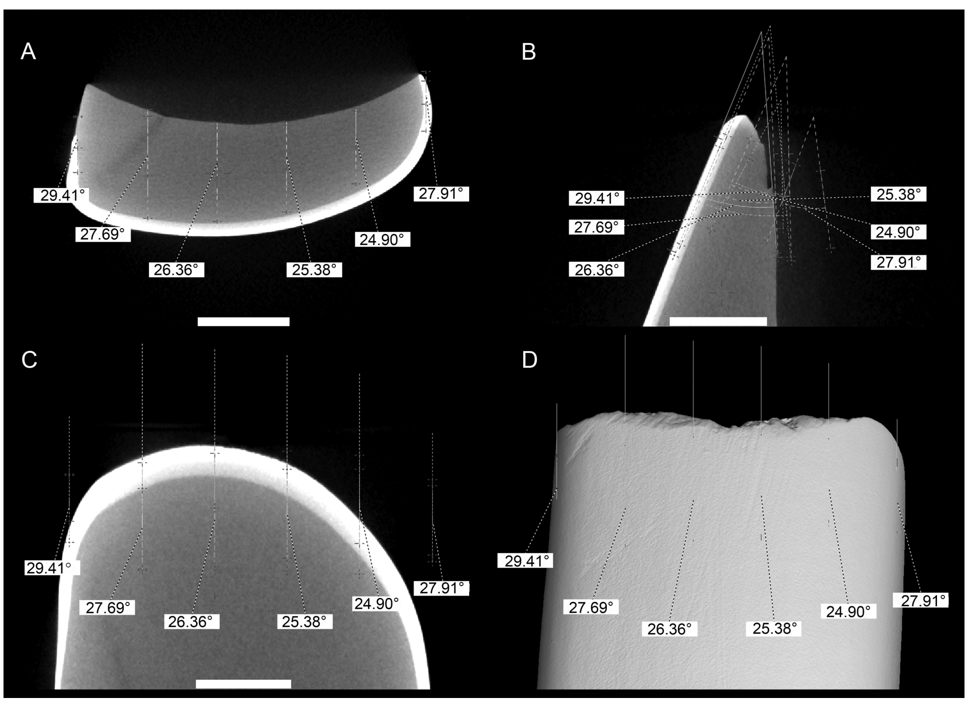

Fig. 6.—CT scans of the lower left incisor of *Castor fiber* (MTD B 27546) indicating precise measurements of the wedge angle. A) Scan slice perpendicular to axial direction, dorsal view, virtual cut below the wear facet. B) Lateral slice cut in a plane corresponding to the 26.36° measurement (lingual view toward the right cross-sectional area) with all 6 measurements of the wedge angle superimposed (solid faint lines = inside slice; dashed faint lines = outside slice). C) Scan slice in frontal direction, view of the mesial enamel surface in frontal view. Note the asymmetric shape of the enamel border caused by the contorted 3D shape of the entire tooth. D) Photorealistic CT 3D model of incisor tip in frontal view with indication of angle measurements partly covered by the outermost enamel layer. The large cross hairs in A–C indicate the common spatial overcrossing point of the respective 3 planes, and the small cross hairs represent the 4 measuring points for each of the angle measurements. All scale bars (horizontal, white) represent 2 mm. MTD = Museum für Tierkunde.

The results of force vector analysis (Fig. 9A) in a semisagittal plane of an incisor and its anchoring in the mandible show the influence of the periodontal ligament. In this case, the resultant force (directed into the incisor, arrow in Fig. 9A) is set at 50 N and the tension of each radial periodontal fiber in the model is calculated to 5.56 N. The pathway of the incisor load runs through the location of neutral fiber for all cross sections.

Our FEA (Fig. 9B) shows 2 remarkable results: first, the very thin anterior position of the alveolus is moderately loaded. The incisor receives exclusively compressive forces, because the periodontal fibers gradually redirect the resulting forces. Second, the compressive stresses along the incisor decrease along its length so that the dentin can be reduced and a rather wide pulp cavity is left open at the apical end of the root. The axial movement in this case is $L_{ax} = 0.0055$ mm (Fig. 9C). If the resultant force F_R (Fig. 5) as working load on the cutting wedge of 1 incisor increases, for example, to 250 N, the axial movement reaches $L_{ax} = 0.03$ mm.

During cutting, beavers do not only load their incisors directly perpendicular to the cutting blade, but certainly sometimes obliquely, or only the lateral edges. These cases were not considered here.

Discussion

Wood chips.—The wood chips of *Salix* sp. measured here are similar in size to those measured by Shadle (1957). He found a width of 1.27–4.45 cm and thickness of 0.32–1.43 cm. The largest width of a chip found here is 5 cm, but most varied from 2 to 4.5 cm. No chip was more than 2 cm in thickness, indicating that 2 cm represents the thickness a beaver can comfortably process. Maximum size might also be dictated by the required cutting force as explained below. Chip lengths vary greatly, and so does the number of cut marks visible on one or both ends of the chip: up to 12. Beavers are able to move the mandible laterally, so that lower incisors can be offset horizontally by as much as about 1 cm from the midline (Stefen et al. 2011). Thus, they are able to make several cuts with upper incisors in the position.

Gape and form of incisors.—The maximal theoretical gape measured on dry skulls varies and is greater than that in living beavers. For 1 dead individual, gape was estimated to be about 20° (Stefen et al. 2011). Thus, theoretical gape exceeds actual gape by 10° to even 30°. The distance between the incisor tips varies from 5 to 7 cm and is 6.3 cm on average in dry skulls. In a freshly dead beaver, it was only about 3 cm, without using force in opening the mouth. This is supported by pictures of dead beavers by Nitsche (pers. comm.).

Wedge angle.—The tip of the lower incisor is used as the main cutting tool and has a small wedge angle. Measurements from photos (n = 20) showed a range from 23° to 25°. The precise measurement of the wedge angle was only possible for 1 incisor, which was prepared and spatially calibrated for CT 3D volumes. These measurements (Fig. 5) gave an average of 26.95°. The values are close to the optimal wedge angle of 27° of a sharp steel wedge under certain conditions. Although variance in the wedge angle estimate cannot be assessed because of the destructive preparation methods needed for the high-resolution CT, our estimate is likely robust because of the high geometrical accuracy obtained through this specially adapted measuring procedure. The wedge angle certainly varies slightly between individuals as well as with the abrasion of the enamel and dentin resulting in differently shaped wear facets forming the supporting bevels of the enamel.

Cutting force.—Due to the specific characteristics of wood, particularly, the high anisotropy, cellular texture, and its physical parameters change with moisture content, modeling cutting forces is very difficult to nearly impossible. We estimate cutting force using approaches from wood machining. With this approach, we can obtain an approximate range

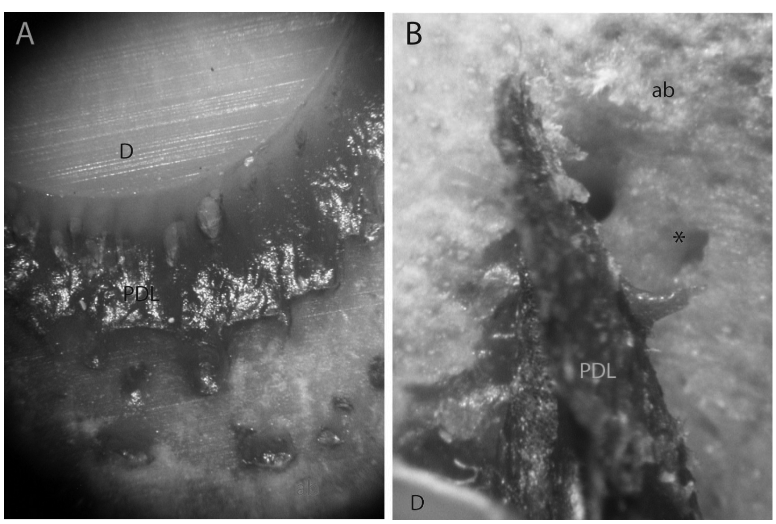

Fig. 7.—Oblique cross section of the right mandible of *Castor fiber* (MTD 27697) cut in the anterior region of the alveole at about the chin process. A) View from the distal in the direction of the tip of the incisor indicating the periodontal ligament (PDL) at the dentin (D) part of the incisor attached to the alveolar bone (ab). B) A detail of the small piece of the PDL loosened from the alveolar bone (ab) showing projections attaching it to the bone at the corresponding pore in the bone (*). MTD = Museum für Tierkunde.

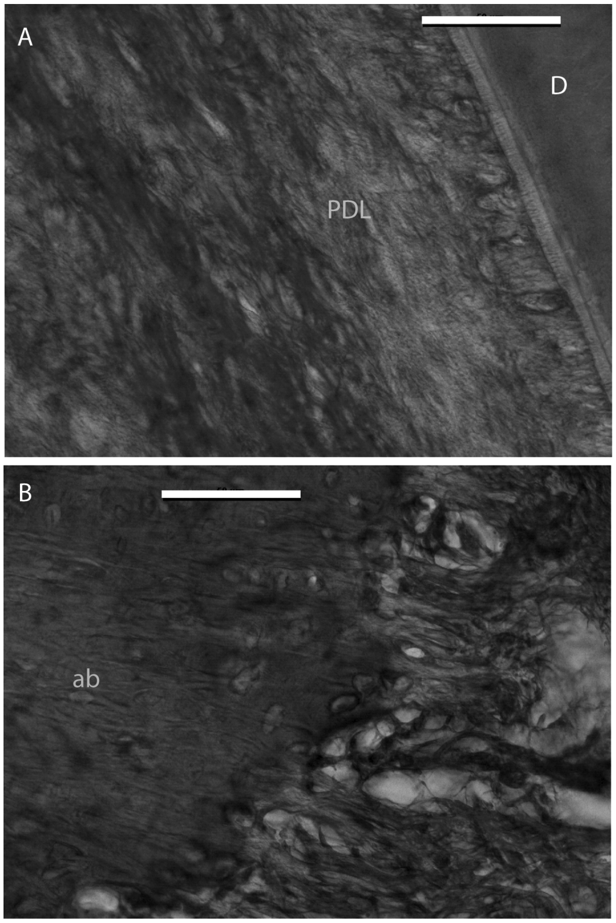

Fig. 8.—Section of mandible of *Castor fiber* at the anterior region of the alveole viewed by light microscopy, Azan Blue dying after Geideies. The tip of the incisor is to the lower right corner. A) Periodontal ligament (PDL) close to the dentin. B) PDL attached to the alveolar bone (ab).

of forces required by beavers when cutting tress. These estimations were calculated using normal moisture content which is lower than in living trees (where it would be more than 30%). Because cutting force is usually minimal at wood moisture content of 50% (Kivimaa 1952, see above), the forces estimated here are higher than those needed by beavers for living trees. For larger trees, beavers change the direction in which they cut, and so steadily varying the cutting direction median slightly and therefore the needed cutting force as well.

Göhre (1954) was probably the first to estimate cutting forces needed by incising beavers for different tree species, experimentally using fresh trees producing similar wood chips. He determined the average force of each cut for European maple (considered as hardwood) to be 117 kg and for willow (considered as softwood) to be 88 kg. An average for 6 tree species was 109 kg. The work required to cut 1 kg of wood was 1,310 mkg or 12.85 kNm for maple, 1,002 mkg or 9.83 kNm for willow, and 1,530 mkg or 15 kNm as an average of 6 tree species. The sample of the cutting force for beaver given here differs from those of by Göhre (1954) by 1.7% for common spruce and

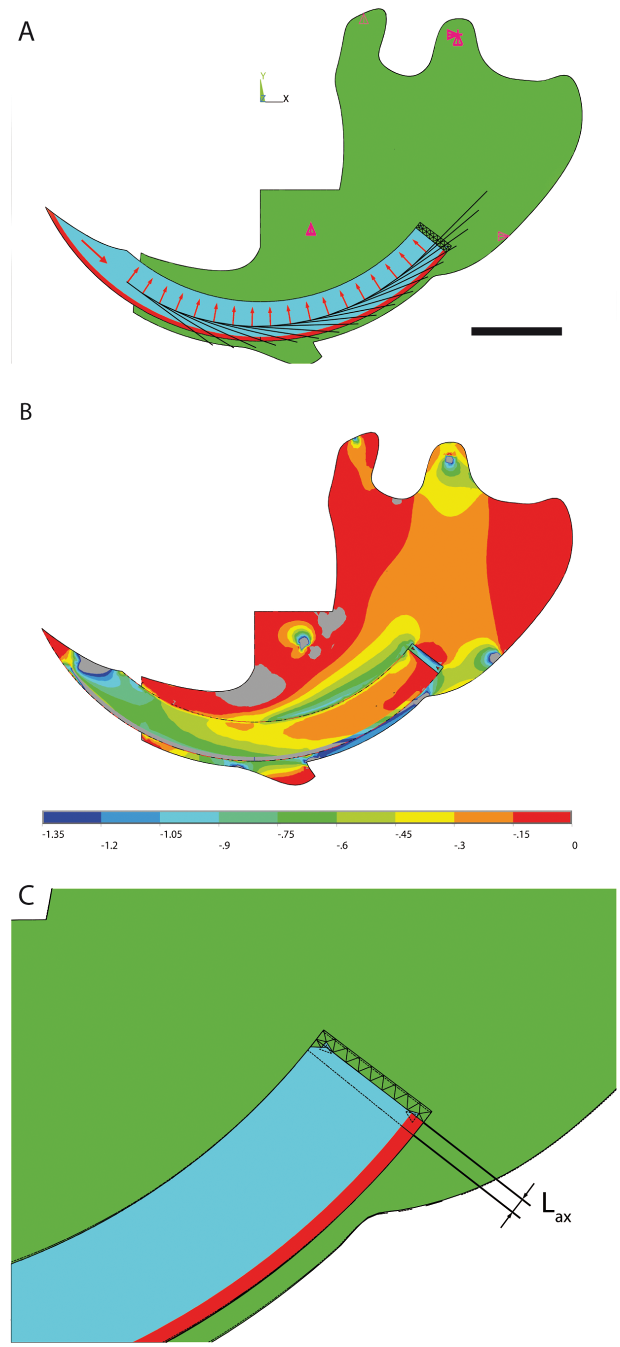

Fig. 9.—Finite element analysis. A) Load plan with resultant force as the acting load on the incisor and a number of periodontal fibers holding the incisor in place. Visible is the influence of periodontal fibers rotating the acting load along the circular line of notional centers of gravity of the incisor. Scale bar = 20 mm. B) Compression stress distribution in a semisagittal plain of an incisor. The reduction of compressive stress in the apical half of the tooth corresponds exactly to the apically increasing width of the pulp cavity in the tooth. C) Axial movement of the incisor under load.

1.9% for maple (calculations not shown both cut in the direction of the wood fibers).

Zhijiang et al. (2005) also used an experimental approach to determine cutting force used by beavers for a tulip tree

(*Liriodendron tulipifera*) with different cutting directions and wood with and without annular growth rings. They found an average cutting force of 740 N and noted that "cutting resistance was increased due to the change of cutting angles from cutting direction '0–90' to '90–90.'"(Zhijiang et al. 2005:25). Direct comparison is difficult, as different cutting direction radians were used.

Histology.—Incisors grow continuously, and thus growth, eruption, and wear occur simultaneously. For *C. canadensis,* seasonal growth rates of the lower incisors have been documented and vary from 0.74 to 1.06 mm/day (Rinaldi and Cole 2004). A very similar growth rate of 0.75 mm/day was estimated by Stuart-Williams and Schwarcz (1997). Growth rates of upper and lower incisors do not necessarily correspond to each other on any given day (Rinaldi and Cole 2004:298). Osborn (1969) assumed that "the mandibular incisors erupt slightly more quickly and may be presumed to be abraded more quickly than the maxillary incisors." As with the basic gnawing technique detailed here, lower incisors are more often used as chisels and are thus likely susceptible to greater wear than upper incisors. Rinaldi and Cole (2004:298) also observed that upper and lower incisors show different growth patterns during the year: for uppers, they observed "a marked decline in growth rate during the late summer and early fall," whereas for lower incisors, only a weak seasonal trend was observed, with the period of fastest growth continues throughout fall and early winter. This supports the assumption of Osborn (1969) and agrees with the pattern of tooth use. Beavers cut most trees during fall and early winter, when they cache food (e.g., Busher 1996, 2003).

Table 2.—Normal gross densities given for normal climate of 20°C/65% relative humidity and variation coefficient (if known) for some deciduous wood species from Niemz (1993) and 1 from Lohmann (2003). Under the normal climate condition, the wood humidity is about 12% and thus it is dried wood. The humidity of living trees is higher (see text).

Species	ρ [kg/m³]	Variation coefficient
Maple *Acer pseudoplantanus*	610	
Birch *Betula verrucosa*	650	6.2
Beech *Fagus sylvatica*	890	6.0
Ash *Fraxinus excelsior*	690	9.3
Hornbeam *Carpinus betulus*	770	
Plum *Prunus domestica*	800	(from Lohmann 2003)

Biomechanical analysis.—The lower incisors of beavers exhibit a wedge angle that is close to the optimal wedge angle of sharp steel cutting tools (under certain conditions, it varies e.g., with given the clearance angle and cutting direction radians [Kivimaa 1952]). Cutting a large tree, beavers change their position often and thus clearance angle and cutting direction radian vary steadily. This would require different optimal wedge angles, which a beaver cannot provide. Therefore, it can be assumed, that under the changing conditions the wedge angle of about 23° to 27° is optimal for beavers and is similar to the optimal wedge angle of sharp steel cutting tools. The upper incisors have a slightly larger wedge angle, consistent with their general use as anchors during cutting.

The wood chips produced by beavers usually do not exceed 5 cm in width and 2 cm in thickness (Fig. 3), indicating a maximum comfortable working gape and distance between the incisors. The calculated cutting forces indicate that the lowest forces are needed when veneer cutting in mode II (Fig. 1.), tangentially to the growth rings and perpendicular to the wood fibers, is used (Table 3) and the size of the wood chip of each cut is 15 mm in width and 2 mm in thickness (Table 3). This is the maximum thickness of wood chips found supporting the 1st hypothesis.

The idealized circular tree diameter with a smooth surface that can be cut by beavers can be estimated from the maximum distance between the incisor tips and the clearance angle and is about 50 cm. This estimate supports the 2nd hypothesis. That larger trees cut by beavers have been recorded (e.g., 117 cm diameter cottonwood or a poplar 2 m diameter poplar [Friedrich 1907 in Hinze 1950]) may be due to the fact that trees in nature have a rough bark rather than a smooth surface and are not necessarily clearly circular in cross section, providing beavers a possible starting point for gnawing.

The FEA revealed that no other than compressive forces act along the incisor. This analysis also revealed the mechanism by which the resulting forces are redirected by the fibers of the periodontal apparatus. Redirection of force applied to an element was first observed by Preuschoft (1970) for curved phalanges of apes. Dentin and enamel of the incisor are adapted to compression stress, and the anterior position of the alveolus is not developed to tolerate bending moments, because there is an extremely thin bony layer on the enamel side. Therefore, the resultant force of the working load of the incisor has to pass through the location of center of gravity for all cross sections or neutral axis. That requirement must be satisfied for the free part

Table 3.—Examples of estimated cutting forces [F_c in Newton, N (kgm/s²)] needed to be used by beavers in wood cutting with different cutting direction (dir) radians (B, C, see Fig. 1) and 3 possible thicknesses of wood chips (h_m, see Fig. 4) and a chip width of 15 mm (determined by the width across both lower incisors of an adult beaver). The lowest cutting forces of both cutting direction radians (B and C) are marked in bold. b = chip width [mm] and h_m = average chip thickness [mm].

Tree species	Cutting dir radian and $k_{0.5}$ [N/mm$^{1.5}$]	b [mm]	h_m = 8 mm	h_m = 5 mm	h_m = 2 mm
Plum	B: $k_{0.5\,B}$ = 15.48	15	657	520	**328**
Plum	C: $k_{0.5\,C}$ = 11.61	15	493	389	**246**
Maple	B: $k_{0.5\,B}$ = 12	15	509	403	**254**
Maple	C: $k_{0.5\,C}$ = 9	15	382	302	**190**
Ash	B: $k_{0.5\,B}$ = 13.57	15	576	456	**287**
Ash	C: $k_{0.5\,C}$ = 10.18	15	432	342	**215**

of the incisor and the proximal distal portion within the alveolus. This principle results in minimized bending and is accomplished by the pressing force (Fig. 4B) and an arrangement of radial fibers of the periodontal ligament (Figs. 6 and 9A) acting as multiplex passive tension chords (Witzel and Preuschoft 2005). Tension chords are crucial because they reduce or eliminate bending stress. If bending is removed from a bony structure and from teeth, they are loaded only by compressive forces (Fig. 9B). This principle serves to reduce material and weight (Witzel et al. 2011). Axial forces under load between the incisor and the alveolus are taken over by the periodontal ligament as well. Axial or semiaxial fibers assume this function (Fig. 6). This supports the 3rd hypothesis. Thus, the results of the biomechanical analysis support all 3 postulated hypotheses.

Concluding it can be summarized that particularly the lower incisors are well adapted to their cutting function and thus well enable beavers the cutting of trees, even of hardwood species. The incisor tip is optimized in the wedge angle comparable with the optimal wedge angle of sharp steel technical cutting tools and self-sharpening. With the common thickness of wood chips produced cutting forces in relation to tool hardness and thus wood species are relatively minimized (Table 1). And the incisors are optimized in shape and supporting tissue for compression stress with all forces being transmitted along the locations of the center of gravity in theoretical cross sections within the tooth. Bending moments would not be tolerated by the system.

Acknowledgements

Thanks are due to W. Sykora (deceased), Bad Düben, Germany, for several wood chips and information on beavers, and K.-A. Nitsche, Dessau, Germany, who allowed study of musculature of Bavarian beaver skulls. Several people helped the microscopy: R. Dermietzel and N. Prochnow, Anatomical Institute of the Ruhr University; A. Weck-Heimann and L. Kunzmann, both Senckenberg Nathurhistorische Sammlungen Dresden. M. Siemund, Senckenberg Research Institute Frankfurt, Germany, helped with the CT studies, and B. Krückhans, Ruhr University of Bochum, Germany, who executed numerous calculations and gave his creative assistance in biomechanics. A. Hardwick, Ipswich, England, commented on the English and wrote the abstract; W. Z. Lidicker, University of California, Berkeley, discussed some aspects and corrected the English; and C. Gottlöber, Technical University Dresden, answered several questions on wood machining. The helpful comments of the editor and reviewers helped to improve the manuscript and are gratefully acknowledged.

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Submitted 19 January 2015. Accepted 15 December 2015.

Journal Editor was John Scheibe.