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Masticatory Muscle Anatomy and Feeding Efficiency of the American Beaver, *Castor canadensis* (Rodentia, Castoridae)

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Abstract Beavers are well-known for their ability to fell large trees through gnawing. Yet, despite this impressive behavior, little information exists on their masticatory musculature or the biomechanics of their jaw movements. It was hypothesized that beavers would have a highly efficient arrangement of the masticatory apparatus, and that gnawing efficiency would be maintained at large gape. The head of an American beaver, Castor canadensis, was dissected to reveal the masticatory musculature. Muscle origins and insertions were noted, the muscles were weighed and fiber lengths measured. Physiological cross-sectional areas were determined, and along with the muscle vectors, were used to calculate the length of the muscle moment arms, the maximum incisor bite force, and the proportion of the bite force projected along the long axis of the lower incisor, at occlusion and 30° gape. Compared to other sciuromorph rodents, the American beaver was found to have large superficial masseter and temporalis muscles, but a relatively smaller anterior deep masseter. The incisor bite force calculated for the beaver (550-740 N) was much higher than would be predicted from body mass or incisor dimensions. This is not a result of the mechanical advantage of the muscles, which is lower than most other sciuromorphs, but is likely related to the very high percentage (>96 %) of bite force directed along the lower incisor long

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axis. The morphology of the skull, mandible and jaw-closing muscles enable the beaver to produce a very effective and efficient bite, which has permitted beavers to become highly successful ecosystem engineers.

Keywords Beaver \cdot Dissection \cdot Masticatory muscles \cdot Bite force \cdot Rodent

Introduction

Beavers are well-known semi-aquatic rodent species, distinctive for their large size (second only to the capybara among extant rodents; Müller-Schwarze 2011), broad paddle-like tail (Jenkins and Busher 1979), and their spectacular engineering abilities. Beavers are renowned for their ability to fell trees, which they use both as food and construction material for dams and lodges (Nowak 1999). Such trees can be of considerable size, with the largest recorded beaver-felled tree in North America measuring 117 cm in diameter (Rosell et al. 2005). The large impact of beavers on an environment has led to them being termed both 'keystone species' (Naiman et al. 1986) and 'ecosystem engineers' (Wright et al. 2002; Müller-Schwarze 2011). The slowing of river currents and the creation of ponds by beaver dam-building has an important effect on aquatic animals and vegetation, and breach of dams following abandonment of beaver ponds leads to the creation of meadow habitats that can resist invasion by woody plants for several decades (Terwilliger and Pastor 1999). Such meadows have been shown to have greatly elevated soil moisture and temperature levels, and increased levels of soil nutrients such as nitrogen and phosphorus (Naiman et al. 1994). Tree felling also leads to increased light penetration and reduced competition for soil nutrients, thus causing the replacement of deciduous vegetation with shrub zones (Johnston and Naiman 1990).

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Despite the enormous effects that their masticatory behavior can have on an ecosystem, few studies have been undertaken on the masticatory apparatus of beavers. As stated above, beavers are rodents (of the family Castoridae) and as such possess a single pair of enlarged, ever-growing incisors in the upper and lower jaws. The incisors are curved in shape with enamel restricted to the labial surface, and dentine to the lingual surface. This distribution of materials ensures that, as dentine will wear away more quickly than enamel, a sharp incisor tip is constantly maintained (Osborn 1969; Druzinsky 2015). This, combined with the continual growth of the incisors from the root, mitigates the substantial wear caused by gnawing through large trees. The action of gnawing is accomplished by movement of the lower jaw against the skull by the muscles of mastication. The configuration of the jaw-closing muscles has long been used to classify rodents. Brandt (1855), following Waterhouse (1839), first divided the rodents into the Sciuromorpha (squirrel-like rodents), Myomorpha (mouselike rodents), and Hystricomorpha (porcupine-like rodents), based on the morphology of the masseter muscle on the rostrum. To these three groups, Wood (1965) added the concept of 'protrogomorphy' - the ancestral rodent condition in which no part of the masseter attaches to the rostrum. Beavers show an anterior extension of the middle layer of the masseter (the deep, or lateral, masseter) underneath the zygomatic arch to take an origin on the rostrum in front of the orbit (Tullberg 1899). Thus, beavers were placed in the Sciuromorpha alongside the squirrels (Sciuridae), pocket gophers (Geomyidae), and kangaroo rats (Heteromyidae) in many classifications (e.g., Simpson 1945). By the time of Wood (1965), it was becoming clear that the arrangement of the masticatory muscles did not accurately reflect the evolutionary relationships of rodents, and recent molecular phylogenetic work has confirmed that the Sciuridae and Castoridae are only distantly related (e.g., Blanga-Kanfi et al. 2009; Fabre et al. 2012). However, a close association between the Castoridae, Geomyidae, and Heteromyidae has been retained in a clade now termed 'Castorimorpha,' which sits in the larger 'mouse-related clade' with muroids, dipodids, pedetids, and anomalurids (Fabre et al. 2012). Within the Castoridae, there are just two extant species: the American beaver (Castor canadensis) and the European beaver (C. fiber). However, the family was historically much more diverse comprising almost 30 genera since it arose in the early Eocene (Korth 2002). Both the wood-cutting and swimming behaviors are thought to have evolved once within the Castoridae, in the same lineage around 24 million years ago (Rybczynski 2007).

It is hypothesized that, given their impressive tree-felling abilities, beavers must have a powerful and efficient masticatory apparatus. However, to date, there are no values for bite force in beavers, estimated or experimentally determined, in the published literature, barring an anecdotal value of 80 kg (around 785 N) that appears unreferenced on many natural history websites and in Caspari (2003). Druzinsky (2010a, b) studied the masticatory musculature of a number of aplodontid, sciurid, and geomyid rodents and concluded that sciuromorphy is more efficient at producing incisor bites than is protrogomorphy, the proposed ancestral condition of rodent jaw-closing muscles. Specifically, Druzinsky (2010b) noted that the mean mechanical advantage of the adductor muscles is larger in sciuromorph rodents, and that sciuromorphs have a greater bite force relative to input muscle force. However, beavers were not included in Druzinsky's study. This analysis seeks to fill that gap by investigating the masticatory muscle morphology and bite force capabilities of the American beaver, C. canadensis, and comparing the results to the sciuromorphs studied by Druzinsky (2010a, b). It is hypothesized that beavers will have a masticatory system of greater efficiency of bite force production at the incisors than that of other sciuromorphs. Furthermore, given the large diameter of the trees that beavers are able to fell, it is hypothesized that the efficiency of the beaver incisor bite will be maintained or even improved at wide gape.

Materials and Methods

Dissection

A frozen head of C. canadensis (specimen number GH 75.13) was obtained from the collections of National Museums Scotland. Total length of the beaver specimen was 940 mm and condylobasal cranial length was measured to be 115 mm. The specimen was dissected to reveal the masticatory musculature with photographs taken of each muscle layer. As each muscle was removed, it was weighed and then stored in ethanol. After careful dissection of all the masticatory muscles, the skull and mandible were transferred to a colony of hide beetles (Dermestes maculatus) housed at the University of Hull for removal of all remaining soft tissues. The results of the dissections were compared with published descriptions of the masticatory muscles of other sciuromorphous and protrogomorphous rodents including: Ball and Roth (1995: Glaucomys, Microsciurus, Sciurillus, Sciurus, Tamias, Tamiasciurus); Cox and Jeffery (2011: Sciurus); Druzinsky (2010a: Aplodontia, Cynomys, Marmota, Ratufa, Sciurus, Tamias, Thomomys); Thorington and Darrow (1996: Aplodontia, Atlantoxerus, Callosciurus, Funambulus, Funisciurus, Heliosciurus, Myosciurus, Paraxerus, Protoxerus, Ratufa, Tamiops, Xerus); and Turnbull (1970: Sciurus).

Fiber Length Measurement

Each muscle was removed from the ethanol and submerged in a 30 % solution of nitric acid for 24 h in order to dissolve the connective tissue (following Herrel et al. 1999). The resulting muscle fascicles were then transferred to glycerol and placed under a dissecting microscope. The fascicles were separated with a blunt needle and then photographed using a Canon PowerShot SX50 HS digital camera. The length of 8-10 fascicles from each muscle were measured from the photographs using the ImageJ software (Schneider et al. 2012), and a mean length was calculated for each masticatory muscle. Mean fascicle length was assumed to provide a good estimate of mean fiber length, following Druzinsky (2010b).

Scanning and Reconstruction

The beetle-cleaned skull and mandible were CT scanned at The York Hospital with voxel dimensions of $0.42 \times 0.42 \times$ 0.5 mm. The number of slices was 312 and 263 for the skull and mandible, respectively. Virtual 3D reconstructions of the beaver skull and mandible were created in Avizo 8.0 (FEI, Hillsboro, OR, USA) using the automatic threshold function. The lower jaw reconstruction was translated and rotated to align it with the skull in incisor occlusion.

Mechanical Calculations

Muscle physiological cross-sectional areas (PCSA) were calculated by dividing the mass of each muscle by its mean fiber length and a value of muscle density (1.0564 g/cm³; Murphy and Beardsley 1974). PCSAs were converted to forces by multiplying by an intrinsic muscle stress value of 0.3 N/mm² (van Spronsen et al. 1989). Muscle lines of action were recorded from 3D landmark co-ordinates representing the centroid of the origin and insertion placed on the reconstruction of the skull and mandible. In muscles in which the fiber direction varied substantially, two or three lines of action were calculated (anteriormost, posteriormost, and, in the case of three lines, a midline) and the force was divided equally between them. The vertical and horizontal components of each muscle vector were calculated by measuring the angle of the line of action to the occlusal and coronal planes. The occlusal plane was defined as the plane containing the points defining the left and right temporo-mandibular joints and the cranial end of the wear facet on the upper right incisor. The coronal plane was defined as the plane perpendicular to the occlusal plane containing the points defining the left and right temporomandibular joints. The long axis of the lower incisor was defined as the line passing through the straightest portion of the center of the wear facet on the lingual tooth surface (Druzinsky 2010b).

Using the muscle forces and lines of action, and 3D coordinates representing the incisor bite point and the temporomandibular joint on each side, we were able to calculate the length of the muscle moment arms, the maximum incisor bite force of the beaver, and the proportion of the bite force projected along the long axis of the incisor. As the goal of this study was to compare the American beaver with the sciuromorph rodents studied by Druzinsky (2010b), the methods of calculating moment arms, bite force and tooth angle outlined in Appendix 1 of that article were followed as closely as possible, although in 3D rather than 2D. Moment arm lengths were calculated as the perpendicular distance from the jaw joint to each muscle force vector. The bite force was calculated assuming: 1) static equilibrium conditions; 2) the jaw joint resists only vertical forces; 3) the entire anteroposterior component is resisted by the bite point; and 4) the muscles are bilaterally activated and thus any medio-lateral components are cancelled out. The biomechanical metrics were initially calculated with the mandible in incisor occlusion, and then recalculated to simulate a gape of 30° by transforming the co-ordinates of the muscle insertions by a rotation matrix acting around a vector running between the two jaw joints. The metrics were also recalculated without the anterior deep masseter and without the superficial masseter to assess the effect of these two important muscles on biting efficiency. The superficial masseter was chosen for further analysis because it is the largest of the adductor muscles, and the anterior deep masseter was investigated more closely because it is the muscle that defines sciuromorphy and was shown by Druzinsky (2010b) to be a major contributor to gnawing efficiency in other sciuromorph rodents. Further details of how the metrics were calculated are given in Online Resource 1.

For comparison, the bite force (BF) of the beaver was also estimated from body size and from the dimensions of the lower incisor using the two regression equations formulated by Freeman and Lemen (2008):

$$log_{10}BF = 0.430 \ log_{10}BM + 0.416$$

$$log_{10}BF = 0.566 \ log_{10}Z_i + 1.432$$

where BM is body mass and Z_i is the strength of the section modulus of the incisor and is calculated

$$Z_i = \frac{(anteroposterior \ length)^2 \times (mediolateral \ width)}{6}$$

Anteroposterior length and mediolateral width refer to the cross-section of the incisor at the level of the dorsalmost margin of the alveolus. The orientation of anteroposterior length was defined to be perpendicular to a tangent to the incisor curvature. The body mass at death of the beaver specimen was pathologically low, but its total length (940 mm) suggests a large individual, so 25 kg was estimated as the healthy body mass, as this is the top end of the mass range reported by Jenkins and Busher (1979) and Nowak (1999).

Results

Muscle Morphology

The muscles of mastication of *C. canadensis* are described below and illustrated in Fig. 1. Attachment sites on the skull and mandible are shown in Fig. 2. The nomenclature followed is that of Ball and Roth (1995) and Thorington and Darrow (1996) in which the three layers of the masseter are named the superficial masseter, deep masseter, and zygomaticomandibularis. These are equivalent to the superficial, lateral, and medial masseters of Wood (1965) and Woods (1972). Muscle masses and mean fiber lengths are given in Table 1 alongside the calculated PCSAs and maximum muscle forces.

Superficial Masseter

The superficial masseter is a very large muscle in the beaver, forming 29 % of the total masticatory muscle mass. The muscle has two distinct origin sites on the skull (Figs. 1a, 2a). Anteriorly, the superficial masseter originates via a tendon on a bony projection on the ridge forming the anterior limit of the masseteric fossa on the rostral part of the maxilla,

Fig. 1 Masticatory muscles of the American beaver, *C. canadensis.* **a**, superficial masseter (*light blue*); **b**, anterior (*light purple*) and posterior (*dark purple*) parts of the deep masseter; **c**, zygomaticomandibularis (*green*) and posterior masseter (*brown*); **d**, temporalis (*red*) immediately caudal to the infraorbital foramen. Posteriorly, the muscle originates, again via a tendon, from the ventral surface of the zygomatic arch. This attachment sites runs across both the zygomatic portion of the maxilla and the jugal bone. The muscle fibers arising from these tendons run posteroventrally, coming together to insert on the ventral margin of the angular process of the mandible (Fig. 3). Despite their disconnected origins, the two parts of the superficial masseter are indistinguishable as they insert on the mandible, and impossible to separate into anterior and posterior parts with any degree of confidence. No fibers of the superficial masseter were found to wrap around the mandibular margin to form a pars reflexa as in many hystricomorph rodents (Fig. 2b).

Deep Masseter

The deep masseter is split very clearly into anterior and posterior parts, composing 11 % and 6 % of the total adductor muscle mass respectively. The anterior portion originates directly from the bone in the masseteric fossa on the rostrum formed by the zygomatic plate of the maxilla, the posteriormost part of the premaxilla, and the bony ridge on the lateral margin of the infraorbital foramen (Fig. 1b). Its fibers run ventrally to insert, via a tendon, on the lateral surface of the mandible ventral to the first and second molars. The tendon inserts at its anteriormost point midway between the ventral margin and the molar alveolus, and runs down to the ventral mandibular margin posteriorly. The posterior portion originates as an aponeurosis from the ventral surface of the jugal medial to the superficial masseter origin. The muscle



Fig. 2 Attachment sites of the masticatory muscles of the American beaver shown on: a, lateral aspects of the skull and mandible; b, lateral and medial aspects of the mandible; c, ventral aspect of the skull. Crosshatching represents tendinous attachments. Colors: red, temporalis; light blue, superficial masseter; light purple, anterior deep masseter; dark purple, posterior deep masseter; green, zygomatico-mandibularis; brown, posterior masseter; orange, medial pterygoid; yellow, lateral pterygoid



fibers insert along the dorsal margin of the ridge forming the ventral border of the angular process of the mandible (Fig. 2b). The posterior part of the deep masseter is completely covered in lateral view by the superficial masseter, but the anterior part

Zygomatico-Mandibularis

masseter.

Forming around 14 % of the jaw-closing muscle mass, the zygomatico-mandibularis originates widely from the medial surface of the zygomatic arch, from the zygomatic plate of the maxilla anteriorly, across the jugal to the jugo-squamosal suture posteriorly (Figs. 1c, 2c). Indeed, the anteriormost part of the muscle pushes anterodorsally into the orbital

is exposed by the discontinuity in the origin of the superficial

Table 1 Absolute and relative

masses, mean fiber lengths, PCSAs and maximum forces of the masticatory muscles of C. canadensis

region, almost resembling a nascent infraorbital part of the zygomatico-mandibularis as seen in myomorph and hystricomorph rodents. From this wide origin, the muscle fibers converge on the relatively narrow lateral surface of the coronoid process, thus forming a fan-shaped muscle.

Posterior Masseter

This small muscle, just 1.5 % of the adductor muscle mass, is located immediately posterior to the zygomaticomandibularis. The muscle originates from the posteriormost part of the ventral surface of the zygomatic arch formed by the jugal bone, immediately lateral to the glenoid fossa. Its fibers run anteroventrally to a deep semicircular fossa on the ramus of the mandible ventral to the coronoid process (Fig. 1c).

	Absolute mass (g)	Relative mass (%)	Mean fiber length (mm)	PCSA (cm ²)	Force (N)
Superficial masseter	21.04	29.1	28.1	7.08	212.3
Anterior deep masseter	7.79	10.8	39.0	1.89	56.8
Posterior deep masseter	4.43	6.1	16.1	2.61	78.3
Zygomatico-mandibularis	10.19	14.1	21.2	4.56	136.8
Posterior masseter	1.05	1.5	20.4	0.49	14.6
Temporalis	19.35	26.8	31.1	5.89	176.6
Medial pterygoid	5.61	7.8	20.0	2.66	79.7
Lateral pterygoid	2.79	3.9	11.7	2.25	67.5
Total	72.25	100		27.42	822.7



Fig. 3 Skinned head of American beaver, *C. canadensis* in right lateral view, showing anterior and posterior origins of superficial masseter. Abbreviations: *ADM* anterior deep masseter, *O* orbit, *SM* superficial masseter, *T* temporalis, *ZA* zygomatic arch

Temporalis

The temporalis is a large muscle, second only to the superficial masseter in mass, comprising just under 27 % of the total masticatory muscle mass. The muscle originates from the large temporal fossa extending over the entire dorsal surface of the skull behind the orbit, covering the parietal and interparietal bones as well as the dorsal surface of the squamosal (Fig. 1d). A robust temporal fascia attaches to the sagittal crest, the anterior border of the temporal fossa, and the dorsal surface of the zygomatic arch, thus completely covering the temporalis and providing an origin site for some of the dorsalmost fibers of the muscle (Fig. 2a). All fibers of the temporalis converge on a tendon running through the middle of the muscle that then inserts on the dorsal margin of the coronoid process of the mandible. No subdivisions of the temporalis could be separated with any confidence although there were some indications of a suprazygomatic portion originating from the zygomatic process of the temporal bone.

Medial Pterygoid

The medial pterygoid forms 8 % of the jaw-closing muscle mass and originates from deep within the pterygoid fossa of the sphenoid. The fibers fan out laterally to insert widely on the medial surface of the angle of the mandible (Fig. 2b, c).

Lateral Pterygoid

The lateral pterygoid is a small muscle forming almost 4 % of the muscle mass. It originates from the lateral surface of the pterygoid process of the alisphenoid bone. It inserts on a small area of the medial surface of the mandible just ventral to the condyle (Fig. 2b, c).

Biomechanical Calculations

Although, for the sake of completeness, the morphology of the lateral pterygoid muscle has been described above, it will be ignored in all further biomechanical calculations to facilitate more direct comparisons with Druzinsky (2010b) who excluded it from his analysis (presumably because its action tends to open rather than close the jaw).

Muscle Mass and Line of Action

The relative sizes of the PCSAs of the muscles were very similar to their relative masses. The largest discrepancy between the percentage of the total masticatory muscle mass and the percentage of the total PCSA was 5.3 %, seen in the temporalis, which has smaller PCSA than might be predicted from its mass owing to relatively long muscle fibers. All other muscles had a relative PCSA within 5 % of their relative mass. The angle of each muscle's mean line of action to the occlusal and coronal planes at incisor occlusion and 30° gape are given in Table 2. At incisor occlusion, the anterior deep masseter has the most vertical line of pull, approaching 70° to the horizontal. The superficial masseter, posterior deep masseter, and zygomatico-mandibularis also have strongly vertical lines of action (over 50°). As the jaw opens to 30° gape, the actions of the superficial masseter, deep masseter, and medial pterygoid muscles become less vertical, whereas that of the zygomaticomandibularis, temporalis and posterior masseter become more so. The last two muscles also have a strongly posterior pull at incisor occlusion (-40° to the coronal plane), but only the temporalis retains this direction of pull at 30° gape. The superficial masseter and posterior deep masseter have the most strongly anterior lines of actions at both gapes measured in this analysis. The total resultant of adductor muscle forces forms an angle of 70° to the occlusal plane at incisor occlusion and 51° at 30° gape.

Mechanical Advantage

The mechanical advantage of the masticatory muscles ranges from 0.09 in the posterior masseter up to 0.40 in the anterior deep masseter at incisor occlusion (Table 3). When the jaw is opened to 30° gape, the mechanical advantage of the superficial and deep masseter muscles drops considerably (by 0.09 and 0.13, respectively), but the mechanical advantage of the other masticatory muscles is maintained to a much greater degree. Overall, the mean mechanical advantage of all muscles is 0.28 at incisor occlusion and 0.22 at 30° gape. Removal of either the anterior deep masseter or the superficial masseter has almost no impact on the mean mechanical advantage of the adductor muscles (Table 4).
 Table 2
 Orientation of mean line
 of action for masticatory muscles of C. canadensis calculated at incisor occlusion (IO) and 30° gape. Positive angles represent dorsal lines of action with respect to the occlusal plane and anterior lines of action with respect to the coronal plane

	Angle to occlusal plane		Angle to coronal plane	
	ΙΟ	30°	IO	30°
Superficial masseter	51.0	37.7	38.7	52.1
Anterior deep masseter	67.4	55.5	21.4	33.8
Posterior deep masseter	53.3	33.0	35.0	55.1
Zygomatico-mandibularis	50.7	58.6	-1.4	9.9
Posterior masseter	44.6	70.5	-40.3	-7.6
Temporalis	18.6	30.3	-43.2	-41.1
Medial pterygoid	34.8	19.4	22.7	46.3

Bite Force

The total incisor bite force calculated for C. canadensis is 556 N at incisor occlusion and 714 N at 30° gape. As a proportion of the total input muscle force, this equals 37 % and 47 %, respectively. This is much greater than the 202 N bite force estimated from body mass or the 334 N predicted by incisor dimensions, using the regression equations of Freeman and Lemen (2008). When the anterior deep masseter muscle is removed from the calculations, the bite force drops by 12.5 % at both gapes: to 486 N at incisor occlusion and 626 N at 30° gape (Table 4). However, although the decreases in bite force resulting from removal of the anterior deep masseter are quite sizeable, there is only a small reduction in the mechanical efficiency of biting: around 5 % at both gapes. Removal of the superficial masseter leads to a much greater drop in bite force: 353 N and 426 N at incisor occlusion and 30° gape, respectively (equal to approximately a 40 % reduction in both cases); and a decrease in mechanical efficiency of biting of approximately 12 % at incisor occlusion and 17 % at 30° gape for the superficial masseter.

Percentage of Bite Force Projected Along the Incisor Axis

The angle of the lower incisor wear facet to the mandibular occlusal plane was calculated to be 63°. This is very similar to

Table 3 Mean moment arm length and mechanical advantage of the masticatory muscles of C. canadensis calculated at incisor occlusion (IO) and 30° gape

occlusion (70°), and it was calculated that 99.3 % of the bite force is projected along the long axis of the incisor. At 30° gape, there is greater disparity between the tooth angle and the angle of the muscle force resultant (51°). However, a strong incisor bite is still maintained with 95.2 % of bite force projected along the incisor axis. Removal of the anterior deep masseter has very little effect on the angle of the resultant adductor muscle force resulting in a maximum reduction of only 0.5 % in the proportion of bite force directed along the incisor axis. However, removal of the superficial masseter reduces the proportion of bite force projected along the incisor substantially to 77–80 % at both gapes (Table 4).

the angle of the resultant of adductor muscle forces at incisor

Discussion

Masticatory Muscle Morphology

The dissection of the head of C. canadensis shows that the beaver clearly exhibits the sciuromorph morphology (Brandt 1855; Wood 1965), with a large anterior portion of the deep masseter attaching to the rostrum in front of the orbit. However, unlike many other sciuromorphs, the attachment site of the anterior deep masseter in the American beaver takes the form of a distinct fossa immediately anterior to the orbit on

	Moment arm length (mm)		Mechanical advantage		
	ΙΟ	30°	ΙΟ	30°	
Superficial masseter	32.0	23.3	0.34	0.25	
Anterior deep masseter	37.8	25.9	0.40	0.27	
Posterior deep masseter	24.3	19.8	0.26	0.21	
Zygomatico-mandibularis	26.8	24.3	0.28	0.26	
Posterior masseter	8.5	8.3	0.09	0.09	
Temporalis	18.3	16.4	0.19	0.17	
Medial pterygoid	27.7	25.4	0.29	0.27	
Mean	26.2	20.5	0.28	0.22	

	Incisor occlusion			30° gape		
	All muscles	Minus ADM	Minus SM	All muscles	Minus ADM	Minus SM
Mean mechanical advantage	0.28	0.26	0.26	0.23	0.22	0.22
Total bite force (N)	556	486	353	714	626	426
Biting efficiency (%)	36.8	34.8	32.5	47.3	44.8	39.2
% bite force projected along incisor	99.3	98.8	80.2	95.2	94.8	77.4

 Table 4
 Biomechanical parameters (mean mechanical advantage, bite force, mechanical efficiency of biting, percentage of bite force directed along incisor long axis) in *C. canadensis*, calculated with all muscles, without the anterior deep masseter (ADM), and without the superficial masseter (SM)

the rostrum. This fossa is formed by the zygomatic plate of the maxilla and the bony protrusion forming the lateral margin of the infraorbital foramen. The anterior deep masseter has been shown to be important in the generation of bite force at the incisors (Druzinsky 2010b). However, despite the beaver's well-documented impressive gnawing abilities (Rosell et al. 2005), the anterior deep masseter is relatively small compared to other sciuromorphs, forming just 11 % of the total adductor muscle mass.

Within the masseter of the beaver, there seems to be a much greater emphasis on the superficial masseter and zygomaticomandibularis than the deep masseter. The morphology of the superficial masseter is particularly unusual, with its two distinct origin sites. It was initially thought that the origin on the zygomatic arch was in fact that of the posterior deep masseter (e.g., as seen in Funisciurus pyrropus figured in Thorington and Darrow 1996: 149), but the presence of a completely separate layer below this muscle attaching to the zygomatic arch that must itself be the posterior deep masseter, plus the near impossibility of separating the two parts of the superficial masseter as their fibers converged on the mandible, convinced us that this was not the case. The zygomaticomandibularis is almost equivalent in mass to the deep masseter in C. canadensis, which is unusually large compared to other sciuromorphs (Druzinsky 2010a). The anterior extremity of its origin pushes far forward into the orbital region, ventral to the eye, a trait also seen in Old World squirrels (Thorington and Darrow 1996).

A posterior masseter muscle has been described in a number of hystricomorph rodent species (Woods 1972; Woods and Howland 1979; Woods and Hermanson 1985; Offermans and De Vree 1989) and was also noted in *Aplondontia rufa* and several sciuromorphs by Druzinsky (2010b). However, a posterior masseter was not described in the sciuromorphs studied by Turnbull (1970), Ball and Roth (1995) or Thorington and Darrow (1996). A posterior masseter is described here for the beaver as, although its position might suggest that it is a posterior part of the zygomatico-mandibularis, as it is clearly separated from that muscle with a discrete origin on the zygomatic arch and a distinct insertion in a fossa on the ascending ramus of the mandible. The relative sizes of the masseter, temporalis, and pterygoid muscles (approximately 61, 27 and 12 % of total adductor muscle mass, respectively) are broadly similar to those reported for other sciuromorph rodents (Turnbull 1970; Ball and Roth 1995; Druzinsky 2010a). The temporalis appears to be large in *C. canadensis* compared to many sciurid species, but it is still relatively smaller than the temporalis of *Marmota monax* measured by Druzinsky (2010a), and similar to that of *Glaucomys volans* reported in Ball and Roth (1995). Despite its large size, the temporalis was not clearly divided into medial and lateral portions as in many sciurids (Ball and Roth 1995; Thorington and Darrow 1996).

Masticatory Biomechanics

The bite force calculated for the American beaver is very large for a rodent - 556 N rising to 714 N at 30° gape. These values are much larger than was predicted from body mass (202 N) or from incisor dimensions (334 N) using the equations of Freeman and Lemen (2008), but are consistent with an anecdotal value of 80 kg (approximately 785 N) that appears in some sources (e.g., Caspari 2003). The discrepancy between the calculations in this study and the predictions based on body and tooth size may be because both regression equations were determined based on smaller rodents (<1 kg) and thus it may not be justified to extrapolate to larger sized rodents. However, it is also likely that beavers are able to produce relatively higher bite forces than most other rodents in order to accomplish the tree-felling behavior that is necessary for constructing their habitat (Jenkins and Busher 1979; Nowak 1999).

Druzinsky (2010b) concluded that the sciuromorph masticatory apparatus was more efficient for incisor biting than the protrogomorph condition owing to the greater mechanical advantage of the resultant of adductor muscle forces. However, this does not seem to hold true for the beaver. The mean mechanical advantage of adductor muscles was found to be 0.28 at incisor occlusion and 0.23 at 30° gape in *C. canadensis*, which is at the low end of the range for the sciuromorph rodents measured by Druzinsky (2010b) and similar to that of the protrogomorphous mountain beaver. Instead, this study indicates that one of the major contributors to the high bite forces produced by the beavers is the mechanical efficiency of their masticatory system. At incisor occlusion, 37 % of the force generated by the muscles is converted to bite force and this rises to 47 % at 30° gape. This exceeds the efficiency of any of the sciuromorphs studied by Druzinsky (2010b) or any of the rodents modelled by Cox et al. (2012, 2013). The increase in efficiency at 30° gape compared to incisor occlusion is particularly important as some of the trees felled by beavers can be very large (over a meter in diameter has been observed; Nowak 1999; Rosell et al. 2005), and would thus require the beaver to gnaw at a wide gape.

The other aspect of the masticatory system that enables such effective gnawing is the close alignment of the long axis of the lower incisor and the bite force resultant. In the American beaver, the long axis of the incisor is oriented at 63° to the occlusal plane and, at incisor occlusion the bite force resultant is angled at 70°. This results in 99 % of the bite force being projected along the incisor axis. At 30° gape, the alignment is not so close – the bite force is at 51° to the occlusal plane. However, the percentage of bite force projected along the incisor axis is still high at 95 %. This alignment between the tooth axis and the bite force resultant is important as it facilitates the effective penetration of an object by the incisor. Compared to other sciuromorphs (Druzinsky 2010b), the beaver projects a greater percentage of its bite force along the incisor axis and is thus likely able to gnaw more efficiently.

Given that the presence of the anterior deep masseter on the rostrum is the diagnostic feature of sciuromorph rodents, it was hypothesized that this muscle may be an important contributor to the efficiency of the masticatory system in beavers, as it is in other sciuromorphs (Druzinsky 2010b). However, this does not seem to be the case. Although the anterior deep masseter accounts for approximately 12.5 % of the total bite force, this is no more than would be expected on the basis of the proportion it forms of the total adductor muscle mass. Moreover, removal of the anterior deep masseter does not have any substantial impact on the overall efficiency of the system or the percentage of bite force that is directed along the long axis of the incisor, either at incisor occlusion or 30° gape. Instead, it was found that the superficial masseter has a greater impact on masticatory efficiency. Removal of the superficial masseter leads to a 40 % reduction in bite force at both incisor occlusion and 30° gape – a greater reduction than can simply be attributed to the large size of the muscle. Even more significantly, removal of the superficial led to a 20 % decrease in the percentage of the bite force that was projected along the incisor axis. Thus, it appears that the superficial masseter is a particularly important muscle for effective penetration of the incisors into objects such as tree trunks. Without the superficial masseter, the efficacy of the beaver's gnawing action is substantially reduced.

As might be predicted from its behavior, the beaver appears to be producing a much larger bite force relative to its size than other sciuromorph rodents. It achieves this large bite force with a combination of high masticatory efficiency (a large percentage of muscle force converted into bite force) and a very close alignment of the bite force resultant and the long axis of the lower incisor. This latter trait can be at least partly attributed to the superficial masseter muscle, which forms a very large proportion of the total adductor muscle mass in beavers. Overall, beavers have evolved a highly efficient gnawing apparatus that, combined with specialized behaviors such as unilateral gnawing (Rybczynski 2008), has enabled the extremely effective wood-cutting and tree-felling behaviors for which they are so famed.

Conclusions

The masticatory musculature of the American beaver, *C. canadensis*, conforms to the general sciuromorphous arrangement, albeit with a relatively larger superficial masseter and zygomatico-mandibularis, and reduced deep masseter. The masticatory apparatus is capable of producing very high bite forces at the incisors: 556 N at incisor occlusion and 714 N at 30° gape, which are concluded to be a result of the close alignment between the long axis of the incisor and the orientation of the bite force resultant. The superficial masseter was shown to be a particularly important muscle for gnawing efficacy. Overall, the efficiency of the beaver masticatory system is much greater than that of other sciuromorphs or indeed other rodents, thus enabling the impressive tree-felling behavior that characterizes this species and is so important for the construction of its environment.

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