The Functional Correlates of Jaw-Muscle Fiber Architecture in Tree-Gouging and Nongouging Callitrichid Monkeys

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ABSTRACT Common (*Callithrix jacchus*) and pygmy (*Cebuella pygmaea*) marmosets and cotton-top tamarins (*Saguinus oedipus*) share broadly similar diets of fruits, insects, and tree exudates. Marmosets, however, differ from tamarins in actively gouging trees with their anterior dentition to elicit tree exudates flow. Tree gouging in common marmosets involves the generation of relatively wide jaw gapes, but not necessarily relatively large bite forces. We compared fiber architecture of the masseter and temporalis muscles in *C. jacchus* (N = 18), *C. pygmaea* (N = 5), and *S. oedipus* (N = 13). We tested the hypothesis that tree-gouging marmosets would exhibit relatively longer fibers and other architectural variables that facilitate muscle stretch. As an architectural trade-off between maximizing muscle excursion/contraction velocity and muscle force, we also tested the hypothesis that marmosets would exhibit relatively less pinnate fibers, smaller physiologic cross-sectional areas (PCSA), and lower priority indices (I) for force. As predicted, marmosets display relatively longer-fibered muscles, a higher ratio of fiber length to muscle mass, and a relatively greater potential excursion of the distal tendon attachments, all of which favor muscle stretch. Marmosets further display relatively smaller PCSAs and other features that reflect a reduced capacity for force generation. The longer fibers and attendant higher contraction velocities likely facilitate the production of relatively wide jaw gapes and the capacity to generate more power from their jaw muscles during gouging. The observed functional trade-off between muscle excursion/contraction velocity and muscle force suggests that primate jaw-muscle architecture reflects evolutionary changes related to jaw movements as one of a number of functional demands imposed on the masticatory apparatus. Am J Phys Anthropol 139:353–367, 2009.

Muscle fiber architecture plays a crucial role in creating jaw movements and forces during feeding. Yet, despite the mechanical role of the jaw muscles in feeding performance (Herrel et al., 1999, 2005; Taylor and Vinyard, 2004, 2008; van der Meij and Bout, 2004), studies of primate jaw muscles are limited. Typically, previous studies of jaw muscles in mammals, including primates, report weights (Schumacher, 1961; Turnbull, 1970; Cachel, 1978), while only a handful evaluate fiber architecture (Bouvier and Tsang, 1990; Van Eijden et al., 1997; Antón, 1999, 2000). Despite the lack of study, we argue there are important insights to be gained from examining jaw-muscle fiber architecture that can further our understanding of masticatory function and feeding adaptations in primates. Here, we compare jaw-muscle architecture in representative tree-gouging and nongouging callitrichids as a case study exploring the functional role(s) that jaw-muscle architecture plays in primate feeding.

Fiber architecture refers to the internal arrangement of skeletal muscle fibers (see Lieber, 2002). Two critical architectural determinants of muscle function are the length of the individual muscle fibers (L_f) and a muscle's physiologic cross-sectional area (PCSA). The fundamental unit of muscle contraction is the sarcomere, which comprises overlapping actin and myosin filaments. The distance per unit time through which a muscle fiber shortens is a function of its absolute length, which is determined by the number of sarcomeres in series (Gans, 1982). Thus, fiber length is theoretically proportional to a muscle's maximum excursion and velocity of contraction (Lieber, 2002). Physiologic cross-sectional area theoretically represents the sum of the cross-sectional areas of all muscle fibers within a given muscle,

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and has been empirically demonstrated to be directly proportional to the maximum force that a muscle can generate (Gans and Bock, 1965; Powell et al., 1984).

The structural arrangement of muscle fibers varies within a muscle, between muscles in the same individual, and among individuals as well as species for a particular muscle (Turnbull, 1970; Gans, 1982; Roy et al., 1991; Anapol and Barry, 1996). Because muscle fibers rarely run the entire length of a muscle (Lieber, 2002), whole muscle length does not appear to be a good substitute for fiber length. Similarly, muscle mass can be a questionable proxy for PCSA as these two variables are often poorly correlated (Lieber, 2002). Therefore, estimating functionally important parameters, such as the maximum amount of force a muscle is capable of generating or the maximum distance over which a muscle can shorten (or lengthen), requires detailed study of muscle fiber architecture.

Behavioral ecology and functional morphology of feeding in callitrichids: A natural experiment comparing tree-gouging and nongouging callitrichids

All species of callitrichids observed in the wild feed on exudates, an energy-rich, high-calorie food (Coimbra-Filho and Mittermeier, 1977; Garber, 1984; Sussman and Kinzey, 1984; Stevenson and Rylands, 1988; Ferrari, 1993). The significance of exudativory in callitrichids is underscored by the suite of behavioral and morphological specializations that are attributed to exploiting this food source (Kinzey et al., 1975; Hershkovitz, 1977; Rosenberger, 1978; Coimbra-Filho et al., 1980; Garber, 1980; Nash, 1986; Martin, 1990; Garber, 1992; Rosenberger, 1992; Hamrick, 1998; Vinyard et al., 2003; Taylor and Vinyard, 2004, 2008).

Marmosets actively stimulate exudate flow by anchoring their upper dentition in a tree and using the lower dentition to gouge holes in the bark (Coimbra-Filho and Mittermeier, 1976, 1977). These animals return to scrape and/or lick the exuded gums and saps. Among callitrichids, marmosets display additional specializations of the lower anterior dentition that have been adaptively linked to tree gouging. These include enlargement of the incisors and extreme thinning of the lingual enamel. Both help create a sharp wedge at the tip of these teeth (Rosenberger, 1978). Furthermore, the canines have become incisiform while the incisors have elongated to the height of the canines (Coimbra-Filho and Mittermeier, 1977). These changes in dental form yield a single integrated dental unit used in gouging (Coimbra-Filho and Mittermeier, 1976, 1977; Muskin, 1984; Sussman and Kinzey, 1984; Nash, 1986; Garber, 1992; Rosenberger, 1992). Tamarins, by contrast, do not gouge trees. They rely on exudates that have been released through insect damage or other injury to trees (e.g., Soini, 1987; Peres, 1989; Ferrari, 1993). Thus, marmosets and tamarins represent two closely related callitrichid groups with broadly similar diets, but divergent feeding behaviors. This interesting natural experiment affords us the opportunity to compare differences in jaw-muscle architecture between these groups and correlate observed differences to their functional role in tree gouging.

Several investigators hypothesize that tree gouging requires generating relatively large bite forces (Szalay and Seligsohn, 1977; Rosenberger, 1992; Dumont, 1997; Spencer, 1999; Vinyard, 1999; Williams and Wall, 1999). In vivo data (e.g., Vinyard et al., 2001, unpublished data), however, reveal that common marmosets can generate bite forces that significantly exceed the forces routinely used when gouging substrates in a simulated lab setting. Contrary to the above hypothesis, these data suggest that tree gouging does not require generating relatively large bite forces (Vinyard et al., 2001, unpublished data). Consistent with the in vivo data, morphological evidence suggests that the skulls of tree-gouging marmosets provide little to no leverage advantage for increasing bite force production or improvement in load resistance abilities compared with nongouging forms (Vinyard et al., 2003; Vinyard and Ryan, 2006).

While generating relatively large bite forces may not be required during tree gouging, marmosets do produce relatively wide jaw gapes during this behavior. Vinyard et al. (2001, 2004, unpublished data) show that common marmosets use relatively large maximum jaw gapes during gouging in the lab and wild. Notably, common marmosets gouge with gapes that approach their maximum structural capacity for jaw opening (Vinyard et al., 2001, unpublished data), suggesting that generating wide jaw gapes during tree gouging is functionally significant and may impact the morphology of the marmoset masticatory apparatus.

In an earlier morphological study, Vinyard et al. (2003) found that common marmosets exhibit bony features of the masticatory apparatus that facilitate the production of large jaw gapes compared with tamarins. These features include relatively anteroposteriorly elongated condyles and temporal articular surfaces that allow for increased mandibular rotation. Additionally, marmosets have low condylar heights relative to the mandibular occlusal plane and higher masseter origin-insertion ratios that reduce masseter stretch and hence facilitate wide gapes (Herring and Herring, 1974).

To initially assess the functional consequences of jaw-muscle fiber architecture for tree gouging, Taylor and Vinyard (2004) compared fiber architecture of the superficial masseter in common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*). They found that compared with tamarins, common marmosets have relatively longer superficial masseter fibers which, along with other features, indicate a muscle architecturally organized to maximize muscle stretch, rather than muscle force (Taylor and Vinyard, 2004). Therefore, they tentatively linked the relatively longer masseter fibers in common marmosets to the generation of wide jaw gapes during tree gouging. Collectively, both muscular and osteological results support the interpretation that the marmoset masticatory apparatus facilitates the generation of wide jaw gapes during gouging.

In this study, we extend our preliminary analysis to more comprehensively evaluate how jaw-muscle fiber architecture functionally relates to tree gouging in marmosets. We evaluate the fiber architecture of both the superficial masseter and temporalis muscles because their orientation and position suggest that both muscles affect maximum jaw gape and bite forces in these primates (Herring and Herring, 1974). To overcome methodological concerns associated with drawing comparisons between only two taxa (Garland and Adolph, 1994), we compare fiber architecture of two tree gougers (*Callithrix jacchus* and *Cebuella pygmaea*) with a nongouging tamarin (*Saguinus oedipus*). All three species are

Callitrichinae, enabling us to retain a narrow phylogenetic framework for our comparisons. We address whether tree-gouging callitrichids have superficial masseter and temporalis muscles that are architecturally well suited to facilitate the production of wide maximum jaw gapes compared with the nongouging tamarin.

Lastly, and in contrast to Taylor and Vinyard (2004, 2008), we normalize fiber length to a standard sarcomere length. The use of a standard sarcomere length to normalize fiber length has been empirically validated as a means of eliminating the natural variation in fiber length that occurs when joints have been fixed at various angles (in this case, varying degrees of jaw gape) (Felder et al., 2005). We use this opportunity to compare results from both raw and normalized fiber architecture data. If similar results are observed using both methods, then this would help validate the study of cadavers fixed in standardized joint postures when normalization is impossible (e.g., poor tissue preservation).

Hypotheses to be tested

We address two hypotheses relating the functional consequences of jaw-muscle architecture to jaw movements and bite force production during callitrichid feeding behaviors.

Hypothesis 1. Longer fibers are functionally advantageous for promoting increased maximum muscle excursion (Lieber, 2002). For the jaw-closing muscles, this likely translates into wider maximum jaw gapes. Therefore, Hypothesis 1 predicts that tree-gouging marmosets will exhibit relatively longer masseter and temporalis fibers as well as other architectural features designed to maximize muscle stretch, compared with nongouging cotton-top tamarins.

Hypothesis 2. For a given muscle volume, fibers oriented at an angle relative to the force-generating axis of the muscle tend to be shorter, in contrast to longer, more fusiform fibers, which tend to be aligned in parallel relative to the axis of force generation (Lieber, 2002). Pinnate-fibered muscles are able to increase PCSA by packing more fibers parallel to each other in a given space (Gans, 1982; Lieber, 2002). Therefore, as an architectural trade off of their relatively long fibers, Hypothesis 2 predicts that marmosets will exhibit both relatively lower pinnation angles and relatively lower PCSAs compared with the cotton-top tamarin. We have no basis for predicting that cotton-top tamarins generate relatively greater maximum jaw-muscle forces compared with tree-gouging marmosets. Thus, we would initially interpret a relatively greater PCSA in *S. oedipus* as an architectural consequence of their relatively shorter, more pinnate fibers compared with marmosets.

MATERIALS AND METHODS

Samples

We analyzed the superficial masseter and temporalis muscles in a maximum of 18 *Callithrix jacchus*, five *Cebuella pygmaea*, and 13 *Saguinus oedipus*.[1] All specimens were adults based on patterns of tooth eruption and wear as well as husbandry records. Cadavers were provided by courtesy of the Wisconsin National Primate Research Center, New England Primate Research Center, and Southwest National Primate Research Center.

[1]Not all specimens preserved both the masseter and temporalis muscles.

Data collection

The skin and superficial fascia overlying the jaw muscles were removed. We then measured muscle belly length (l_b) on intact muscles using digital calipers (0.01 mm). Superficial masseter muscle length was estimated as the distance from the anterior proximal attachment on the zygomatic arch to the distal attachment on the angle of the mandible. We measured temporalis muscle length from the posterior-most attachment on the calvaria to the anterior-most attachment at the coronoid process and anterior margin of the ramus. Muscles then were dissected free from their bony attachments, trimmed of excess fascia, blotted dry, and weighed to the nearest 0.0001 g. We measured jaw length to the nearest 0.01 mm from the posterior edge of the condyle to infradentale.

Fiber length and pinnation angle were measured for both muscles following Taylor and Vinyard (2004, 2008). We bisected the masseter along its length to produce a superior and inferior portion (Fig. 1a). The inferior portion was analyzed to avoid the deep masseter, which maintains a different fiber orientation and muscle action than the superficial masseter (Hylander et al., 2000; Vinyard et al., 2007). We sectioned the temporalis muscle into anterior and posterior portions and analyzed the anterior portion (Fig. 1b). We oriented each segment to view fibers in cross section, pinned the segment to a styrofoam block, and visualized the proximal and distal attachments of individual fibers to tendon with the use of a 5 diopter (2.25×) magnifer light. To enhance viewing of the extremely small muscles of *Cebuella*, we additionally employed a pair of Zeiss (2.3×) binocular glasses during data collection. We selected anterior and posterior sampling sites for measurements along the length of the superficial masseter (Fig. 2a), and proximal and distal sampling sites for the anterior temporalis muscle (Fig. 2b).

We measured up to six adjacent fascicles (myofiber bundles) at each sampling site. For each fiber, we measured the following: (1) fiber length, between the proximal and distal myotendinous junctions (L_f); (2) the perpendicular distance from the tendon of insertion to the proximal attachment of the fiber (a); (3) the length of tendon from the proximal bony attachment to the proximal myotendinous junction (t_p); and (4) the length of tendon from the distal bony attachment to the distal myotendinous junction (t_d) (Table 1 and Fig. 3). We calculated the angle of pinnation (θ) as the arcsine of a/L_f (Anapol and Barry, 1996) (Table 1; Fig. 3). Tendon length and pinnation angle were computed for each fiber and then averaged across all fibers measured in a given muscle.

Depending on the position of the jaws at the time of fixation, muscle fibers may be either elongated or contracted relative to their resting length. Thus, jaw position at fixation will have an effect on whole muscle and individual fiber lengths and, by extension, all variables that involve fiber length. Previously, Taylor and Vinyard (2004, 2008) addressed this concern by including only specimens whose jaws were fixed in a standardized jaw posture with the incisors in tip-to-tip occlusion. However,

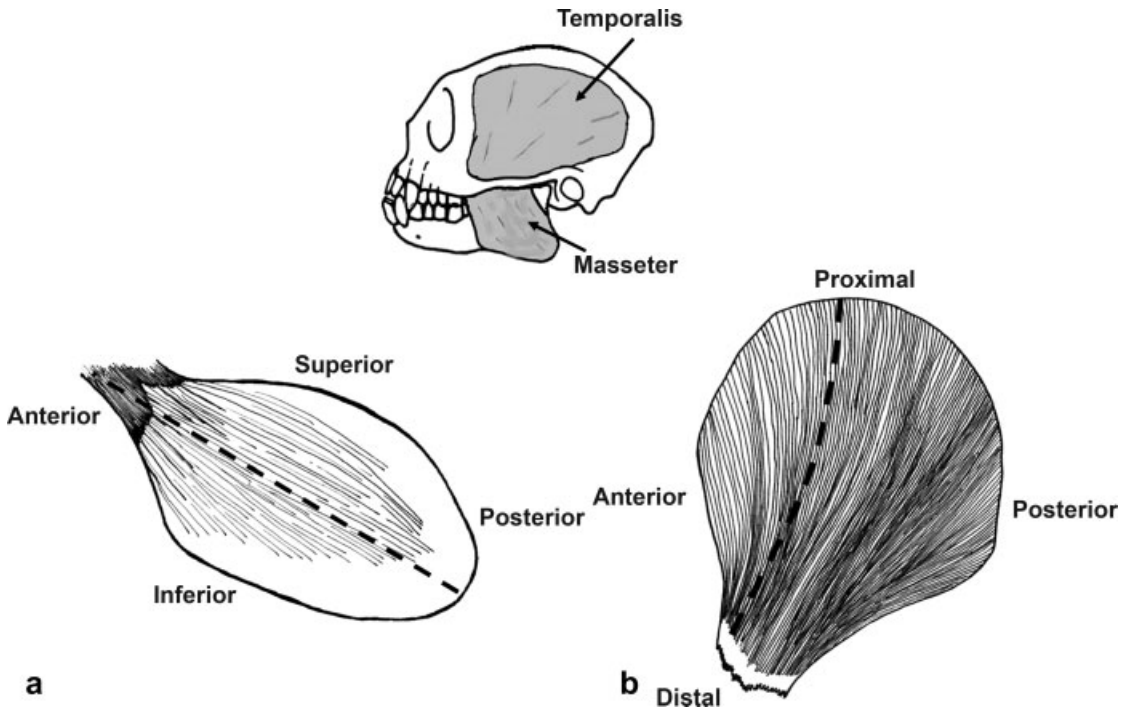

Fig. 1. Schematic representation of a common marmoset skull in lateral view and left (**a**) masseter and (**b**) temporalis. The masseter was bisected mid-belly, along the length of the muscle (see dotted line), into superior and inferior portions, and the inferior portion analyzed. The temporalis was bisected into anterior and posterior portions (see dotted line), and the anterior portion was analyzed.

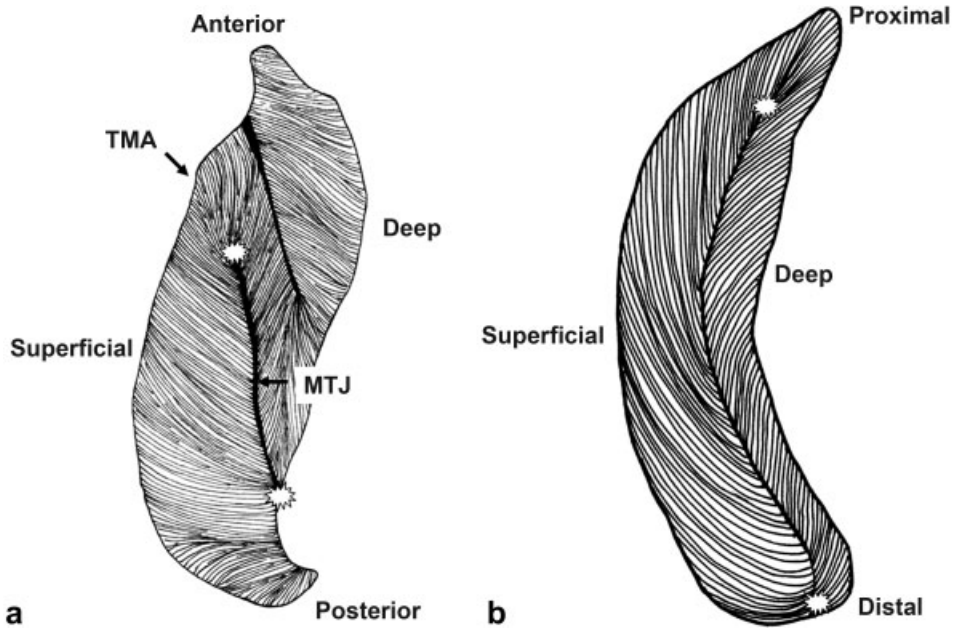

Fig. 2. Schematic representation of the internal configuration of the (**a**) inferior portion of the masseter muscle, and (**b**) anterior portion of the temporalis muscle. Fiber measurements were sampled from anterior and posterior sites along the length of the superficial masseter, and from proximal and distal sites along the length of anterior temporalis muscle. The stars at the (a) anterior and posterior regions of the MTJ, and (b) proximal and distal regions, mark the sampling sites for masseter and temporalis fibers, respectively.

even this standardized jaw posture may involve a small amount of variation in muscle stretch due to differences in tooth size and wear. Therefore, to address the potential influence of jaw posture on fiber length, we normalized muscle fiber length to a standard sarcomere length (Felder et al., 2005).

TABLE 1. Species means ± standard deviations and between species comparisons of masseter and temporalis measurements and jaw length

Variable	*Callithrix jacchus*	*Cebuella pygmaea*	*Saguinus oedipus*	Two-sample *t*-test[a]		
				Cj vs. *So*[b]	*Cp* vs. *So*	*Cj* vs. *Cp*
Masseter muscle						
Muscle length (mm)	19.14 ± 1.24	12.38 ± 1.45	19.71 ± 1.22	NS	0.0018	0.0013
Mass (g)	1.10 ± 0.18	0.23 ± 0.03	1.29 ± 0.32	NS	0.0016	0.0014
NL_f (mm)[c]	7.46 ± 1.22	5.01 ± 0.56	5.12 ± 1.20	0.0004	NS	0.0019
Fiber length (L_f) (mm)	6.20 ± 0.6	4.61 ± 0.49	4.85 ± 0.95	0.0009	NS	0.0019
NPCSA (cm^2)[c]	1.31 ± 0.30	0.41 ± 0.08	2.19 ± 0.55	0.0003	0.0018	0.0014
PCSA (cm^2)	1.50 ± 0.30	0.44 ± 0.08	2.07 ± 0.32	0.0007	0.0018	0.0014
Pinnation angle (°)	27.81 ± 6.78	18.67 ± 2.71	33.78 ± 11.59	NS	0.0018	0.0120
Temporalis muscle						
Muscle length (mm)	23.51 ± 2.90	19.28 ± 2.62	30.48 ± 2.93	0.0001	0.0027	0.0117
Mass (g)	1.53 ± 0.22	0.30 ± 0.06	1.79 ± 0.51	0.0362	0.0027	0.0010
NL_f (mm)[c]	9.06 ± 2.02	6.17 ± 1.42	6.52 ± 0.73	0.0040	NS	NS
Fiber length (L_f) (mm)	7.71 ± 1.19	5.07 ± 0.65	5.38 ± 0.61	0.0003	NS	0.0022
NPCSA (cm^2)[c]	1.60 ± 0.35	0.40 ± 0.08	2.72 ± 0.44	0.0001	0.0034	0.0010
PCSA (cm^2)	1.82 ± 0.34	0.54 ± 0.06	2.93 ± 0.61	0.0010	0.0027	0.0010
Pinnation angle (°)	17.32 ± 5.38	13.75 ± 3.7	17.81 ± 3.80	NS	NS	NS
Jaw length (mm)	31.21 ± 2.00	23.42 ± 1.65	32.05 ± 1.76	NS	0.0014	0.0008

[a] *P*-values for two-sample Mann-Whitney *U*-tests between species. Because we are not testing specific predictions in these comparisons, all tests are two-tailed and a multiple test correction is not applied. NS, nonsignificant with $P > 0.05$.
[b] *Cj*, *C. jacchus*; *So*, *S. oedipus*; *Cp*, *C. pygmaea*.
[c] Data normalized to a given sarcomere length (N) are listed in this row; raw data are presented in the next row.

Briefly, we chemically digested the masseter and temporalis muscles in 30% HNO_3 to facilitate isolating fiber bundles. Digestion time varied depending on the size of the muscle and tissue preservation. The muscles then were immediately placed in 1× PBS, and dissection of small fiber bundles continued under a dissecting microscope (10–20× magnification). From each muscle, we isolated five to ten fiber bundles, which then were mounted on slides, cover slipped with mounting medium, and allowed to air dry. We used laser diffraction (Lieber et al., 1994) to measure sarcomere length. Laser diffraction relies on the use of coherent laser light to pass through the uniform muscle-banding pattern formed by the arrangement of A-bands and I-bands within the sarcomere. Light diffracts through the I-band region, and the diffraction pattern can be converted to an estimate of sarcomere length. We obtained at least two sarcomere length measurements at two different points along each mounted bundle or, when this was not possible, at least three sarcomere length measurements from three different bundles taken from the same muscle region. We used the equation $NL_f = L_f'L_s/L_s'$, where NL_f is the normalized fiber length, L_f' is the measured fiber length, L_s is the standard sarcomere length (μm), and Ls' the measured sarcomere length obtained from the measured fiber length (μm). Raw fiber lengths were normalized to a resting fiber length (NL_f) by dividing by a standard sarcomere length of 2.41 μm, calculated as optimal sarcomere length in macaque limb muscles (Walker and Schrodt, 1974).

Variables

Using the aforementioned fiber measurements, we computed average fiber lengths and PCSAs for the superficial masseter and temporalis muscles for each species.[2]

PCSA (cm^2) was calculated using the equation:

$$\frac{\text{muscle mass (gm)} * \cos\theta}{\text{fiber length (cm)} * 1.0564\ (\text{gm/cm}^3)},$$

where θ is the pinnation angle and 1.0564 represents the specific density of muscle (Mendez and Keys, 1960; Murphy and Beardsley, 1974).

We also calculated several composite variables designed to address whether jaw muscle architecture facilitates excursion/contraction velocity versus force production:

Muscle mass/predicted effective maximal tetanic tension. Muscle mass/predicted effective maximal tetanic tension (M/P_0) estimates how much of a muscle's

[2]We also calculated mean fiber lengths for the anterior and posterior portions of the superficial masseter, respectively, for common marmosets and cotton-top tamarins. We could not make similar calculations in *C. pygmaea* because their small masseter muscles made it difficult to reasonably discriminate two sets of fibers. Previous studies in rats (Nordstrom and Yemm, 1972) and pigs (Herring et al., 1979) show that anterior masseter fibers are longer than posterior fibers in these taxa suggesting the possibility of functionally significant variation within the masseter muscle. We found that when restored to putative resting lengths, there were no significant differences between anterior and posterior fiber lengths either in common marmosets (paired samples *t*-test, df = 23, $P = 0.212$) or cotton-top tamarins (paired samples *t*-test, df = 10, $P = 0.939$). The pattern of statistical results between common marmosets and cotton-top tamarins did not differ when using combined masseter data versus specific comparisons of anterior or posterior fibers. Therefore, we only report comparisons of the combined fiber length data for the superficial masseter.

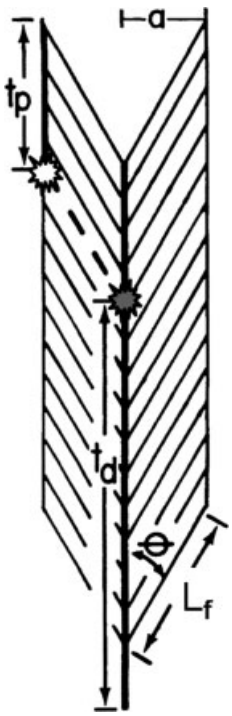

Fig. 3. Schematic of the internal configuration of a muscle. At each sampling site, a maximum of six adjacent fibers was measured. For each fiber of interest (as represented by the dashed line), (1) fiber length (L_f) was measured from the central tendon (gray star) to the distal tendon of insertion (white star); (2) the perpendicular distance from the tendon of insertion to the proximal attachment of a fiber was measured (a) and used to calculate the angle of pinnation (θ); (3) proximal tendon length was measured as the length of tendon running from the proximal bony attachment to the proximal myotendinous junction (t_p); and 4) distal tendon length was measured as the length of tendon from the distal bony attachment to the distal myotendinous junction (t_d) (Table 1 and Fig. 3). Total tendon length ($t_p + t_d$) and pinnation angle (arcsin of a/L_f) were computed for each individual fiber and averaged across the 12 fibers. Figure from Anapol and Barry (1996).

mass is due to longer fibers, and hence dedication to excursion, versus the amount of mass due to the number of fibers in parallel, and hence dedication to force production (Sacks and Roy, 1982; Anapol and Barry, 1996):

$$M/P_0 = \text{muscle mass (g)}/22.5\ \text{N cm}^{-2} \times \text{PCSA (cm}^2),$$

To calculate M/P_0, the specific tension of muscle is estimated to be ~22.5 N cm^{-2} (Powell et al., 1984).[3] A higher M/P_0 ratio suggests that relative to its mass a muscle is facilitating excursion/contraction velocity over force production.

***Estimated maximum excursion (h)* of the distal tendons of attachment.** The variable h considers both fiber length and pinnation angle to estimate the excursion of a whole muscle during contraction:

$$h = L_f(\cos\theta - \sqrt{\cos\theta^2 + n^2 - 1}),$$

(adapted from Benninghoff and Rollhäuser, 1952). Here (n) is the coefficient of contraction or fiber length after contraction/resting fiber length. Following Anapol and Gray (2003), we used the refined value of $n = 0.767$ for pinnate fibers (see also Gans and Bock, 1965; Muhl, 1982). To adjust for size, h was divided by overall muscle length (l_b) (Anapol and Gray, 2003) (h/l_b).

Total tendon length per muscle fiber + tendon length. The ratio of tendon to fiber plus tendon length reflects the relative cost of applying force through muscle contraction and provides an estimate of the relative amount of active neural control during excursion. The ratio of total tendon length per muscle fiber + tendon length ($l_t/L_f + l_t$) was computed for each fiber and then averaged for each muscle (Anapol and Barry, 1996). Total tendon length (l_t) was computed as proximal (t_p) + distal (t_d) lengths.

Priority index for force. For muscles of equal volume, the muscle with shorter, more pinnate fibers will enhance force at the expense of excursion, while a muscle with longer, parallel fibers will increase excursion over force. We computed priority index for force (I) as $PCSA/V^{2/3}$, where V = wet muscle weight (Woittiez et al., 1986; Weijs et al., 1987; Van Eijden et al., 1997). Higher ratios reflect muscles facilitating force production at the expense of excursion.

Data analysis

We used one-tailed Mann-Whitney U-tests to test the hypotheses that tree-gouging marmosets exhibit architectural features of the masseter and temporalis muscles that facilitate muscle excursion (Hypothesis 1) and reduced force production through an architectural tradeoff (Hypothesis 2). Marmosets are predicted to have relatively longer muscle fibers (L_f) as well as higher ratios for M/P_0 and h/l_b compared with nongouging cotton-top tamarins. By contrast, we predict that pinnation angle (θ), relative PCSA, $l_t/L_f + l_{t,}$ and I, will be significantly smaller in marmosets. Because of the variation in size among these three species, we calculated ratios of L_f and $PCSA^{0.5}$ by dividing by jaw length (Taylor and Vinyard, 2004, 2008). We also adjusted fiber length by dividing by the cube root of muscle weight (L_f/MW) (Lieber and Blevins, 1989) as a second relevant denominator. In both cases, more parallel-fibered muscles should exhibit higher ratios. While we provide statistical results for both raw data and values adjusted to a normalized sarcomere length, we focus our hypothesis tests on normalized data. Although not part of the explicit hypothesis tests, we compared fiber architecture between common and pygmy marmosets using two-tailed Mann-Whitney U-tests.

We evaluated four predictions for each hypothesis, for each pairwise species comparison, separately for the superficial masseter and temporalis. Because of these multiple statistical comparisons, we applied a sequential Bonferroni technique to set a pairwise significance level of $\alpha = 0.05$ for all statistical comparisons involving a gouging and nongouging species on a per muscle basis (Rice, 1989). Initial analysis indicated no significant sex differences (paired t-tests; $P > 0.05$). Therefore, males and females were combined in all analyses. All statistical tests were performed using Systat 11.0.

[3]We report the specific tension in N cm^{-2} (Powell et al., 1984) rather than in kg/cm^2 (Sacks and Roy, 1982), where force N = mass x gravity.

RESULTS

Muscle morphology

The gross morphology of the masseter and temporalis muscles is similar among these three taxa. Both muscles are bipinnate with superficial and deep portions characterized by relatively simple internal configurations (Figs. 1 and 2). Within the superficial masseter, there is a central tendon (myotendinous junction; MTJ) extending from the aponeurosis of insertion at the gonial region anteriorly toward the aponeurosis of origin along the zygomatic arch (TMA) (Fig. 1b). The central tendon (MTJ) terminates prior to the tendon of insertion (TMA). The temporalis likewise consists of a central tendon separating the superficial and deep parts of the muscle (Fig. 2b). The central tendon extends from the superior aspect of the muscle to the coronoid process and continues distally to its attachment on the inferior mandible. In both muscles, the longest and most parallel fibers are positioned at the proximal attachment sites and fibers become progressively shorter and more pinnate toward the distal attachment sites.

Functional architecture of the masseter and temporalis muscles

Absolute comparisons. As might be expected based on differences in body mass (Smith and Jungers, 1997), *S. oedipus* (416 g) has absolutely larger muscles masses, greater muscle lengths, and a longer jaw than the two marmosets (Table 1). *C. pygmaea* (116 g) is smallest in these dimensions making *C. jacchus* (321 g) intermediate (Table 1). The temporalis and masseter muscles show roughly comparable patterns of difference. *C. pygmaea* is absolutely smaller than both *C. jacchus* and *S. oedipus* for most dimensions (Table 1).

Common marmosets have significantly greater masseter and temporalis fiber lengths compared with cotton-top tamarins and pygmy marmosets (Table 1 and Fig. 4). Alternatively, *C. pygmaea* and *S. oedipus* show no statistical difference in fiber lengths. Average measured sarcomere lengths for the masseter and temporalis muscles, respectively, are 2.02 and 2.06 μm for *C. jacchus*, 2.23 and 1.97 μm for *C. pygmaea*, and 2.19 and 2.05 μm for *S. oedipus*. Normalization of fibers to a standard sarcomere length demonstrates that initial fiber length estimates were shorter than the normalized lengths by approximately 9–20% for the masseter and between 17.5 and 22% for the temporalis (Table 1 and Fig. 4). Both the percentage difference between species and the variance tended to increase slightly with normalization of fiber length estimates (Table 1 and Fig. 4). Nevertheless, significant differences in raw architectural variables remained significant following sarcomere-length normalization.

Masseter and temporalis PCSAs are significantly larger in *S. oedipus* compared with both marmosets, while *C. jacchus* has significantly larger PCSAs than *C. pygmaea* (Table 1). Given that normalization to a standard sarcomere length results in greater fiber length estimates, it is not surprising that PCSA estimates are smaller after normalization. Similar to fiber length estimates, interspecific differences in PCSAs remain significant after normalization.

Pinnation angles increase progressively with increase in size from *C. pygmaea* to *S. oedipus*. However, there are no significant pairwise differences in pinnation angle for the temporalis, and no significant difference between *S. oedipus* and *C. jacchus* for masseter pinnation (Table 1). Normalizing to a standard sarcomere length results in lower pinnation angle estimates for both muscles in all the three species (Table 2). Furthermore, following normalization, pinnation angle is significantly smaller in *C. pygmaea* compared with *S. oedipus* for the temporalis.

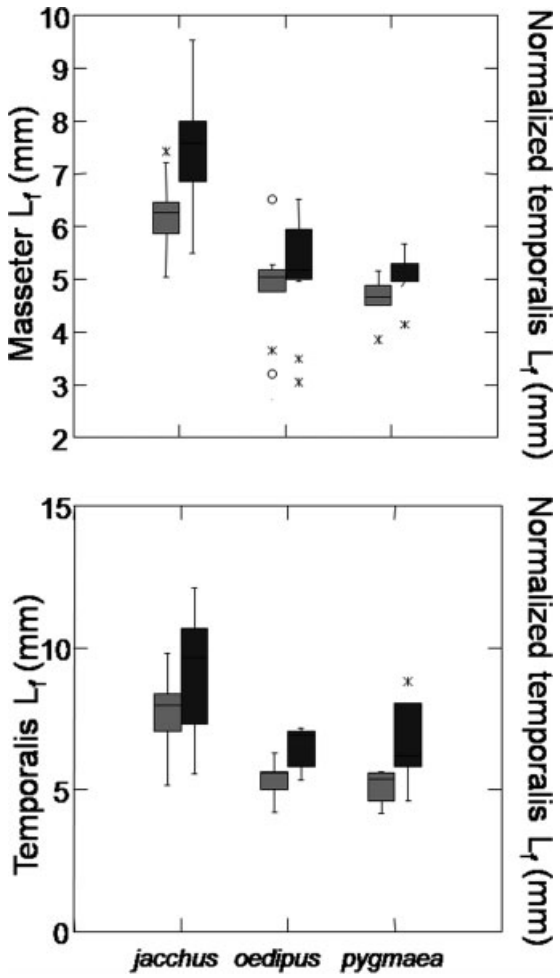

Fig. 4. Box-plot of fiber length differences in the (**a**) masseter and (**b**) temporalis muscles. Raw fiber lengths are grey, normalized fiber lengths are black. Fiber lengths are absolutely longest in common marmosets, and shortest in pygmy marmosets, with and without sarcomere normalization. In this and all subsequent box-plots, the center vertical line marks the median of the sample. The length of each box shows the range within which the central 50% of the values fall. Whiskers indicate 10th and 90th percentiles. Outside values are plotted with asterisks; far outside values are plotted with empty circles.

Hypothesis 1. The first hypothesis predicts that the two marmoset species will exhibit relatively longer masseter and temporalis fibers as well as other architectural features designed to maximize muscle stretch compared with cotton-top tamarins. These architectural features would facilitate wide jaw gapes during tree gouging. Both common and pygmy marmosets demonstrate most of the predicted differences for both the superficial masseter and temporalis including significantly greater fiber lengths scaled for both jaw length (see Fig. 5) and

TABLE 2. Species means ± standard deviations and hypothesis test results for masseter and temporalis architectural variables

Variable	Hypothesis	*Callithrix jacchus*	*Cebuella pygmaea*	*Saguinus oedipus*	Two-sample *t*-test[a]		
					Cj vs. *So*[b]	*Cp* vs. *So*	*Cj* vs. *Cp*
Masseter muscle							
NL_f/Jaw length[c]	Hyp 1	0.24 ± 0.04	0.22 ± 0.03	0.15 ± 0.04	**0.0001**	**0.0054**	NS
L_f/Jaw length		0.20 ± 0.02	0.20 ± 0.03	0.15 ± 0.03	<**0.0000**	**0.0101**	NS
NL_f/MW[d]	Hyp 1	7.25 ± 1.23	8.26 ± 1.04	4.72 ± 1.14	**0.0002**	**0.0009**	NS
L_f/MW		6.03 ± 0.67	7.61 ± 0.92	4.45 ± 0.77	**0.0000**	**0.0009**	**0.0067**
NM/P_o	Hyp 1	0.038 ± <0.01	0.025 ± <0.01	0.027 ± 0.01	**0.0002**	NS	**0.0014**
M/P_o		0.033 ± <0.01	0.023 ± <0.01	0.028 ± <0.01	**0.0110**	**0.0308**	**0.0014**
Nh/l_b	Hyp 1	0.16 ± 0.03	0.17 ± 0.03	0.11 ± 0.02	**0.0001**	**0.0013**	NS
h/l_b		0.13 ± 0.02	0.16 ± 0.03	0.10 ± 0.02	**0.0002**	**0.0019**	NS
NPCSA/Jaw length	Hyp 2	0.04 ± <0.01	0.02 ± <0.01	0.07 ± 0.02	**0.0005**	**0.0009**	**0.0014**
PCSA/Jaw length		0.05 ± <0.01	0.02 ± <0.01	0.06 ± 0.01	**0.0012**	**0.0009**	**0.0014**
NPinnation angle (°)	Hyp 2	21.74 ± 5.81	17.03 ± 2.39	24.75 ± 6.12	NS	**0.0019**	NS
$l_t/Nl_f + l_t$	Hyp 2	0.58 ± 0.07	0.65 ± 0.07	0.74 ± 0.07	<**0.0000**	**0.0136**	NS
$l_t/l_f + l_t$		0.62 ± 0.06	0.67 ± 0.06	0.76 ± 0.06	<**0.0000**	**0.0074**	NS
N*I*	Hyp 2	1.23 ± 0.21	1.10 ± 0.15	1.86 ± 0.44	**0.0001**	**0.0009**	NS
I		1.40 ± 0.19	1.18 ± 0.15	1.76 ± 0.24	**0.0006**	**0.0013**	0.0433
Temporalis muscle							
NL_f/Jaw length	Hyp 1	0.29 ± 0.06	0.32 ± 0.15	0.21 ± 0.02	**0.0013**	**0.0202**	NS
L_f/Jaw length		0.25 ± 0.03	0.22 ± 0.04	0.17 ± 0.02	<**0.0000**	0.0478	NS
NL_f/MW	Hyp 1	7.88 ± 1.70	10.98 ± 3.79	5.26 ± 0.47	**0.0004**	**0.0017**	0.0390
L_f/MW		6.73 ± 1.11	7.60 ± 0.66	4.49 ± 0.19	<**0.0000**	**0.0013**	NS
NM/P_0	Hyp 1	0.044 ± 0.01	0.035 ± 0.01	0.031 ± <0.01	**0.0016**	NS	NS
M/P_0		0.038 ± 0.01	0.025 ± <0.01	0.027 ± <0.01	**0.0001**	NS	**0.0013**
Nh/l_b	Hyp 1	0.16 ± 0.03	0.16 ± 0.06	0.09 ± 0.01	<**0.0000**	**0.0064**	NS
h/l_b		0.14 ± 0.02	0.11 ± 0.03	0.07 ± 0.01	<**0.0000**	**0.0046**	0.0318
NPCSA/Jaw length	Hyp 2	0.05 ± 0.01	0.02 ± <0.01	0.09 ± 0.01	**0.0001**	**0.0017**	**0.0010**
PCSA/Jaw length		0.06 ± 0.01	0.02 ± <0.01	0.09 ± 0.02	**0.0006**	**0.0013**	**0.0010**
NPinnation angle (°)	Hyp 2	14.33 ± 4.39	9.65 ± 2.0	12.05 ± 5.34	NS	NS	0.0166
$l_t/NL_f + l_t$	Hyp 2	0.66 ± 0.06	0.65 ± 0.09	0.79 ± 0.03	**0.0001**	**0.0017**	NS
$l_t/L_f + l_t$		0.69 ± 0.05	0.72 ± 0.05	0.82 ± 0.03	<**0.0001**	**0.0020**	NS
N*I*	Hyp 2	1.22 ± 0.26	0.91 ± 0.26	1.77 ± 0.17	**0.0001**	**0.0017**	0.0390
I		1.37 ± 0.20	1.21 ± 0.11	2.02 ± 0.10	<**0.0001**	**0.0013**	NS

[a] *P*-values based on one-tailed Mann-Whitney *U*-tests for comparisons between tree-gouging marmosets (*Cj* and *Cp*) and the non-gouging tamarin (*So*). *P*-values were adjusted separately for each species comparison and each hypothesis ($\alpha = 0.05/4$). *P*-values based on two-tailed Mann-Whitney *U*-tests for comparisons between *C. jacchus* (*Cj*) and *C. pygmaea* (*Cp*). Because we have no *a priori* functional hypotheses for the two gougers, *P*-values were adjusted for all eight predictions ($\alpha = 0.05/8$). Boldface values indicate that differences are significant at the adjusted α level. Nonboldface values indicate significant differences prior to the adjusted α level. NS, nonsignificant.

[b] *Cj*, *C. jacchus*; *So*, *S. oedipus*; *Cp*, *C. pygmaea*.

[c] N = sacromere adjusted value; L_f = fiber length; l_b = muscle length; MW = muscle weight; M/P_0 = muscle mass/predicted effective maximal tetanic tension; *h* = estimated excursion of distal tendon of attachment; PCSA = physiologic cross-sectional area; l_t = tendon length; $l_t/NL_f + l_t$ = total tendon length per muscle fiber plus tendon length; *I* = priority index for force.

[d] The cube root of muscle mass is used for Nl_f/MW.

muscle weight and a relatively greater maximum excursion (*h*) of the distal tendons of attachment. However, only *C. jacchus* has a significantly larger proportion of longer fibers per muscle mass (NM/P_0) (Table 2). These results support the hypothesis that gouging primates have masseter and temporalis muscles that facilitate wide jaw gapes.

Hypothesis 2. The second hypothesis predicts that, primarily as an architectural trade-off of elongated fibers, marmoset jaw muscles will exhibit both relatively smaller PSCAs and less pinnation than cotton-top tamarins. Again, marmoset masseter and temporalis show significant differences for both muscles. Common and pygmy marmoset masseter and anterior temporalis demonstrate significantly smaller relative NPCSAs, lower priority indices of force (*I*), and significantly less tendon ($l_t/NL_f + l_t$), compared with *S. oedipus* (Table 2 and Figs. 6 and 7). Alternatively, pinnation angle does not differ consistently between gougers and nongougers (Table 2). Thus, architectural trade-offs related to gouging appear to primarily involve changes in PCSA (i.e., muscle weight and fiber length) rather than pinnation angle.

Comparisons between marmoset species. Although not part of the hypothesis tests evaluating gougers and nongougers, we also compared jaw-muscle architectural parameters between common and pygmy marmosets (Table 2). No consistent pattern of differences is apparent after Bonferonni adjustment. We can generalize that relative differences largely follow the pattern seen above when comparing absolute jaw-muscle parameters. Compared with *C. jacchus*, *C. pygmaea* exhibit relatively greater masseter and temporalis excursion capabilities (e.g., masseter L_f/MW, and temporalis NL_f/MW prior to Bonferroni adjustment) but relatively less force production abilities (e.g., NPCSA/Jaw length for both muscles, NM/P_0 and *I* for the masseter muscle, and M/P_0 for the temporalis muscle) (Table 2). Thus, *C. pygmaea* generally exhibit relatively greater masseter and temporalis excursion capabilities but relatively less force production abilities (Table 2). These differences suggest that allometric variation in callitrichid jaw muscles may yield a

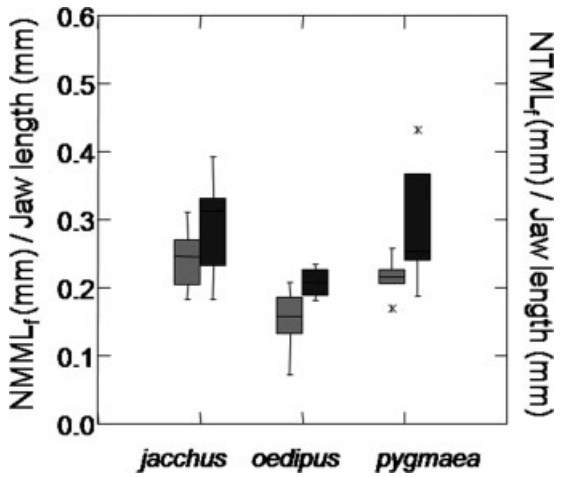

Fig. 5. Box-plot of relative differences in masseter and temporalis fiber lengths normalized for sarcomere length. The masseter muscle ($NMML_f$) is grey, the temporalis muscle ($NTML_f$) black. Tree-gouging common (*C. jacchus*) and pygmy (*C. pygmaea*) marmosets have significantly longer masseter and temporalis fibers relative to jaw length compared with the nongouging cotton-top tamarin (*S. oedipus*). Relatively longer fibers indicate that tree gougers have relatively greater excursion capabilities, and are thus able to generate relatively wider jaw gapes with less stretch of the masseter and temporalis muscles.

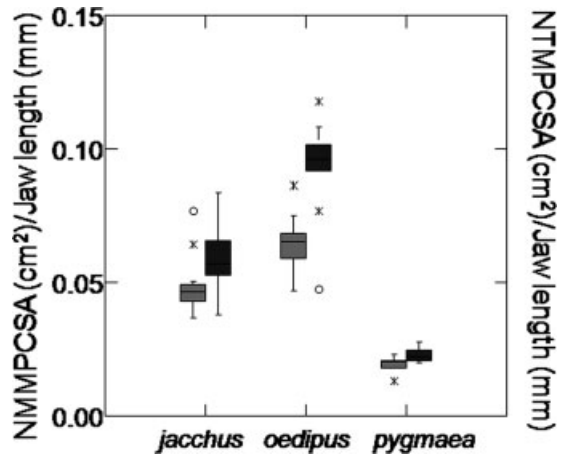

Fig. 6. Box-plot of relative differences in masseter and temporalis PCSA normalized for sarcomere length. The masseter muscle (NMMPCSA) is grey, the temporalis muscle (NTMPCSA) black. Nongouging cotton-top tamarins (*S. oedipus*) have significantly greater masseter and temporalis PCSAs compared with tree-gouging common (*C. jacchus*) and pygmy (*C. pygmaea*) marmosets. Relatively greater PCSAs reflect the capacity of *S. oedipus* to generate relatively greater jaw-muscle and bite forces.

size-related decrease in excursion coupled with an increase in force production capabilities. Alternatively, these differences in jaw-muscle architecture may indicate functional differences in how these two marmoset species gouge trees.

DISCUSSION

The ecological morphology of marmoset jaw-muscle architecture

Tree-gouging common and pygmy marmosets display architectural features of the masseter and temporalis muscles that facilitate relatively greater muscle excursion compared with nongouging tamarins. For masticatory performance, these features facilitate increased whole muscle stretch during jaw opening, and thus, the production of wide jaw gapes. Comparative differences in common marmoset jaw-muscle architecture correspond to differences in muscle position on the skull and skull morphology that also facilitate greater jaw-opening ability (Vinyard et al., 2003). Given field observations that common marmosets use wide jaw gapes during tree gouging (e.g., Vinyard et al., in press), these architectural features can be functionally linked to facilitating these wide gapes during this behavior (i.e., they participate in a biological role sensu Bock and von Wahlert, 1965). These results are consistent with previous studies linking elongated masseter fibers to the production of wide jaw gapes in pigs (Herring and Herring, 1974; Herring et al., 1979) and mice (Satoh and Iwaku, 2006).

We hypothesize that the relatively elongated fibers in marmoset jaw muscles contribute certain performance advantages during gouging. The higher NM/P_0 ratios in common marmoset jaw-closing muscles are consistent with their relatively longer fibers and indicate that common marmosets are capable of generating more excursion, beyond their force-producing capability, compared with the nongouging tamarin (see Sacks and Roy, 1982). The higher estimate of relative muscle excursion (Nh/l_b) suggests that common and pygmy marmosets experience increased whole-muscle excursion during contraction. Both of these architectural differences point to tree-gouging marmosets having jaw muscles geared for increased contraction velocity compared with cotton-top tamarins. Increased contractile velocity may help marmosets generate more power, or the rate at which work

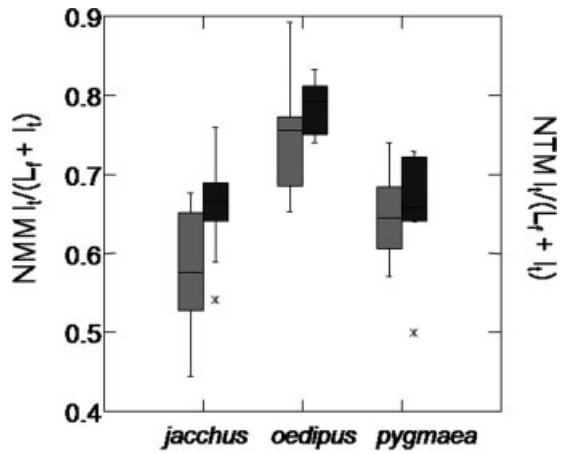

Fig. 7. Box plot of differences in the ratio of tendon length to muscle fiber + tendon length ($l_t/NL_f + l_t$). The masseter muscle (NMM $l_t/(L_f + l_t)$) is grey, the temporalis muscle (NTM $l_t/(L_f + l_t)$) is black. Both common and pygmy marmosets have lower ratios compared with cotton-top tamarins. A lower ratio of $l_t/NL_f + l_t$ indicates that a greater proportion of the range of motion during jaw closing can be achieved through active, likely isotonic, contraction of masseter and temporalis fibers in tree-gouging marmosets. This configuration suggests an enhanced neural control of excursion over this range of motion.

is done, from their jaw muscles during gouging. For a repetitive behavior like tree gouging, increased muscle power may benefit the net gain in nutrient extraction per unit time spent on feeding.

The ratio of tendon length to muscle fiber + tendon length ($l_t/NL_f + l_t$) is lower in marmosets for both the masseter and temporalis (see Fig. 7). This ratio contrasts the active and passive contributions to the total tension generated in a muscle. Active contraction of skeletal muscle is metabolically expensive because it requires the breakdown of adenosine triphosphate, whereas tendon is a viscoelastic structure that passively stores and releases elastic energy (Cavagna et al., 1977; Alexander, 1984; Biewener and Roberts, 2000; Roberts, 2002). Tendons lack the molecular machinery necessary for active contraction (Nordin et al., 2001). Thus, while tendons can reduce energy expenditure, contractile fiber has the potential for increased modulation as it is under neural control. Therefore, a lower $l_t/NL_f + l_t$ indicates that a greater proportion of the range of motion during jaw closing can be achieved through active, likely isotonic, contraction of masseter and temporalis fibers in tree-gouging marmosets. This suggests an enhanced neural control of excursion over this range of motion.

We speculate that tree gouging may be a highly modulated behavior that would benefit from greater, more deliberate neural control of muscle stretch as a means of minimizing the risk of injury to the masticatory apparatus. Generating bite forces at wide jaw gapes during tree gouging may place marmosets at risk for stretch-related injuries of their jaw-closing muscles and masticatory apparatus (e.g., Isacsson et al., 1989). Embedded muscle spindles mediate rapid reflex adjustments when a muscle is stretched (Purves et al., 2004). All else being equal, a relative increase in muscle tissue at the expense of tendon would provide for a greater number of muscle spindles which may be important in monitoring length changes in the jaw-closing muscles during tree gouging.

In addition to a musculoskeletal configuration that facilitates increased gapes, the jaw-muscle architecture of tree-gouging marmosets may allow these animals to generate relatively larger bite forces at these wide gapes. When opening the mouth widely marmosets and tamarins are likely stretching their jaw-closing muscles beyond their resting length (i.e., the plateau region of the length-tension curve) (Eng et al., 2007). Bite forces diminish as jaw muscle fibers are stretched beyond this resting length (Dechow and Carlson, 1982, 1986, 1990). Furthermore, stretch-related decreases in bite force with increasing gape are exacerbated by the relatively inefficient jaw leverage for producing bite forces at the anterior teeth. Eng et al. (2007) modeled the sarcomere operating ranges of motion for the masseter and temporalis muscles in common marmosets and cotton-top tamarins, and found that common marmoset jaw muscles operate at a more favorable position on the length-tension curve at wider jaw gapes. This relatively improved location on the length-tension curve suggests that tree-gouging common marmosets maintain an advantage for generating bite forces specifically at wide jaw gapes compared with tamarins. This finding does not contradict the observation that tamarins have relatively greater muscle PCSAs, and thus the potential to generate relatively greater maximum muscle forces compared with marmosets. Rather, it suggests that common marmosets have the advantage over tamarins when it comes to generating muscle forces at wide jaw gapes, while tamarins have the advantage when it comes to generating muscle forces at optimal muscle length.

Gape and bite force: Trade-offs in muscle architecture

The architectural features of the jaw muscles that facilitate greater excursion and increased contraction velocity entail a cost for tree-gouging marmosets. Marmosets possess relatively smaller physiological cross-sectional areas (NPCSA) compared with nongouging tamarins (Table 2) suggesting a relatively smaller maximum bite force at an optimal sarcomere length. Additionally, several composite measures of muscle architecture indicate that tree-gouging marmosets have emphasized excursion over force production (e.g., index priority of force) by having longer jaw-muscle fibers (Nh/l_b) but fewer ones in parallel (NM/P_0). Because fiber length is inversely related to PCSA, we argue that the relatively reduced muscle force reflects an architectural trade-off of increased excursion and contraction velocity given that both architectural features cannot be augmented simultaneously (Gans, 1982; Taylor and Vinyard, 2004, 2008; Fig. 8). It is also possible that longer jaw-muscle fibers allow marmosets to produce relatively greater bite forces at wide gapes during gouging (Eng et al., 2007).

The relatively smaller force-generating capabilities of marmoset jaw muscles correspond to observations that common marmosets do not produce relatively large bite forces during gouging, compared with the bite forces they are capable of generating (Vinyard et al., 2001, in press, unpublished data). Furthermore, common marmoset skull shapes do not facilitate the generation of relatively large bite forces or increased load resistance compared with nongouging tamarins (Vinyard et al., 2003; Vinyard and Ryan, 2007). Based on these results, arguments that tree gouging in marmosets involves relatively large bite forces likely misrepresent the behavior. We offer the alternative hypothesis that marmosets only need to score the tree bark during gouging to elicit exudate flow as part of the tree's defense response (Vinyard et al., in press). As previously argued (Vinyard et al., in press), these observations linking morphological changes to wide jaw gapes during tree gouging provide one of the few examples where jaw movements, rather than bite forces, appear to be the target of functional and potentially evolutionary adaptations related to a biting behavior.

Most studies of primate jaw-muscle architecture have focused on variation in force- producing ability (e.g., Antón, 2000; Anapol et al., 2008; Perry and Wall, 2008). The observation that marmosets may have increased fiber lengths at the cost of force production raises the possibility that jaw-muscle architecture in some primates reflects evolutionary changes related to jaw movements over bite force. This functional trade-off between excursion/contraction velocity and bite force raises concern for hypotheses tests focusing on single functional attributes, particularly those involving interspecific scaling approaches (e.g., Gould, 1966; Fleagle, 1985). Following Lucas (2004), recent efforts have focused on characterizing scaling patterns of jaw-muscle PCSA and fiber length across primates to test models related to bite force production and fracture mechanics (Lucas, 2004; Taylor and Vinyard, 2007; Anapol et al. 2008; Perry and Wall, 2008). By including species that potentially experience differing relative demands on jaw-muscle architec-

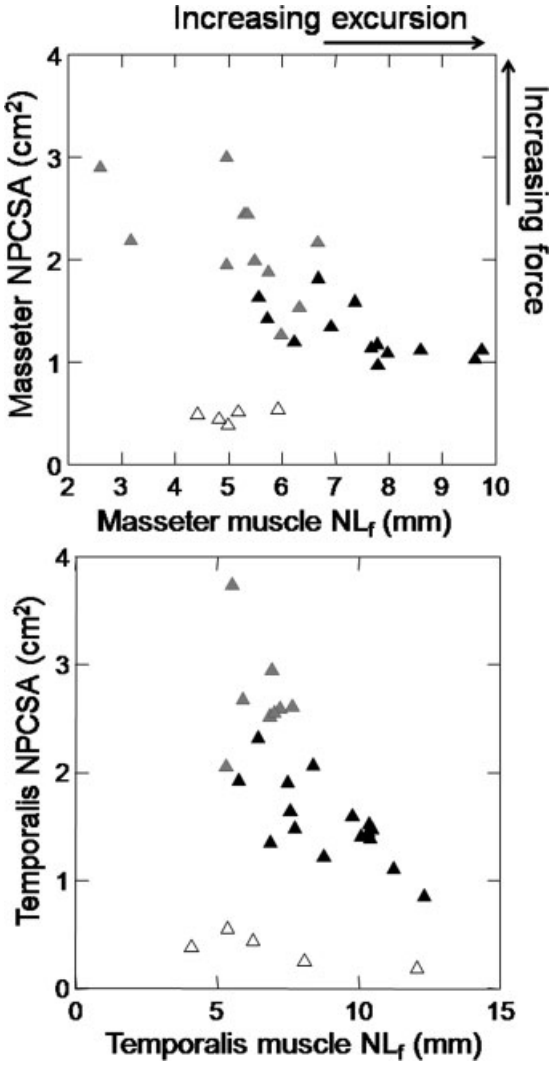

Fig. 8. Bivariate plot demonstrating that for a given muscle volume, there is an architectural trade-off between absolute muscle force (NPCSA) and muscle excursion (fiber length; NL_f). Cotton-top tamarins are represented by grey triangles, common marmosets by solid black triangles, pygmy marmosets by open triangles. There is some overlap between common marmosets and cotton-top tamarins, but the longer fibered masseter and temporalis muscles in common marmosets are suited for muscle excursion and the production of relatively wide jaw gapes. By contrast, cotton-top tamarins have shorter fibers and larger PCSAs and are thus better suited for generating larger muscle forces with smaller excursions. Pygmy marmosets fall outside the size range of common marmosets and cotton-top tamarins because their muscle volumes are five to six times smaller than those of the other two taxa. However, their fiber lengths are comparable to cotton-top tamarins at 25% of their body weight (Smith and Jungers, 1997), indicating that pygmy marmosets have long fibers best suited to large excursions. The architectural trade-offs are significant ($P < 0.05$) in all cases with the exception of the masseter muscle for pygmy marmosets.

ture, these interspecific analyses most reliably test the hypothesis that entire clades follow a predicted functional relationship. Hypothesis tests for individual species may require additional comparisons involving sister taxa or closely-related forms as performed here.

Functional partitioning of jaw-closing musculature

Marmosets and tamarins retain the primitive mammalian pattern of having temporalis muscles that are larger than the masseter and pterygoid muscles (Turnbull, 1970). Because PCSA is heavily influenced by muscle mass, all three species have temporalis muscles with larger maximum force-generating capacities relative to their masseters (Table 2). Both muscles are powerful jaw closers. However, intra- and inter-muscular differences in connective tissue morphology, fiber types, and fiber architecture, can serve to enhance functional partitioning of muscles and thus broaden the functional range of a muscle group for a given behavior (e.g., Herring et al., 1979; Anapol and Jungers, 1982, 1986; Anapol and Barry, 1996). In our study, we observed no species differences in connective tissue morphology. However, by considering the temporalis and masseter as part of a larger functional muscle group involved in feeding, we can examine whether there are differences in the relative contributions of these two muscles to the overall force- and excursion-producing capabilities of the jaw adductors (i.e., "a division of labor" sensu Anapol and Jungers, 1982).[4]

Expression of NPCSA for each muscle as a percentage of total NPCSA for both muscles reveals less difference in NPCSA between the masseter and temporalis in tree-gouging marmosets compared with tamarins (see Fig. 9). While all three taxa exhibit significant intermuscular diversity ($P < 0.05$), the disparity in %NPCSA is more pronounced in *S. oedipus*, suggesting the nongouging species has a greater capacity for functional partitioning of these jaw muscles. We speculate that the derived gape requirements for tree gouging constrain this intermuscular partitioning in marmosets compared with tamarins. These observations should be regarded as preliminary, however, both because data for the pterygoids are lacking, and the masticatory muscles are architecturally complex containing regionally differentiated, task-specific segments (Herring et al., 1979; Weijs and Dantuma, 1981; Van Eijden et al., 1993; van Eijden and Turkawski, 2001), only some of which have been evaluated here.

Controlling for mandibular position in the study of jaw-muscle architecture

We also address a methodological issue in this study by comparing muscle architecture among callitrichids using two different procedures for estimating fiber lengths. We observe similar relative differences among species in jaw-muscle architecture using fiber measures taken from jaws fixed in a standardized position (i.e.,

[4]We acknowledge that a complete assessment of how the jaw-closing muscles are differentially dedicated to generating muscle excursion/velocity of contraction and muscle force requires evaluation of the pterygoid muscles. We do not include the pterygoid muscles because their location and attachments would require mandibular resection which was not allowed for these samples. Herring and Herring (1974) theoretically argue that the medial pterygoid muscle is unlikely to impose a significant restriction on gape in mammals because of its spatial position and orientation. Empirically, we can also note that the medial pterygoid, with its relatively short, pinnate fibers, suggests its gape-limiting and force generating capabilities are considerably less than those of either the masseter or temporalis muscles.

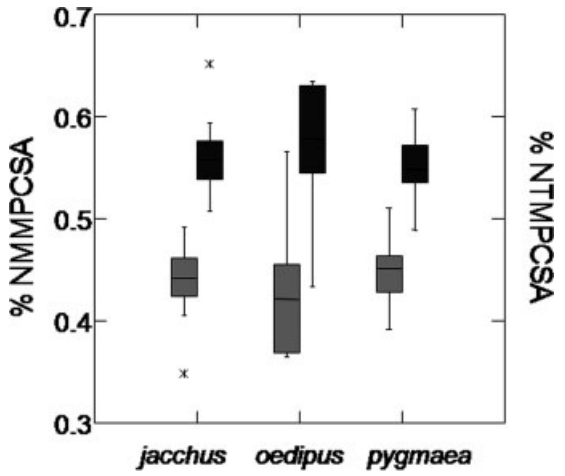

Fig. 9. Box plot demonstrating the percentage contribution of the masseter and temporalis muscles separately to the combined cross-sectional area of the two muscles. The masseter muscle (%NMMPCSA) is grey, the temporalis muscle (%NTMPCSA) black. In all species, the temporalis muscle contributes a relatively greater percentage than the masseter to the total PCSA of the two muscles. However, the intermuscular disparity in %NPCSA is more pronounced in *S. oedipus*, suggesting the nongouging species has a greater capacity for functional partitioning of these jaw-closing muscles.

tip-to-tip incisor occlusion) versus the same measures normalized to a given sarcomere length (Table 2). The similar pattern of results is encouraging. However, similarity in this analysis should not be taken as evidence that other comparisons would yield similar results.

The decision on how to account for jaw position at fixation when measuring fiber lengths will depend primarily on the goals of a study. Normalization to a resting sarcomere length will be critical if a study requires absolute measures of fiber dimensions at their resting lengths given that fiber length estimates were shortened by 20–22% prior to this sarcomere length adjustment (Table 1). Our results raise two immediate concerns with using these normalized fiber lengths. First, this method assumes that resting sarcomere length is conserved among species in a study. Unfortunately, resting sarcomere lengths are poorly known among primates (e.g., Walker and Schrodt, 1974), although estimates in mammals are fairly conserved, ranging from 2.3 to 2.8 μm (Huxley, 1972). Second, normalization may increase the variance in fiber length estimates at a given jaw posture within a species, as observed in this study (see Fig. 5). Several factors potentially contribute to this increased variance. First, the quality of the diffraction signal varies across muscles (e.g., Burkholder et al., 1994; Felder et al., 2005). Secondly, the addition of another source of measurement error from calculating sarcomere lengths in muscle preparations will also tend to increase the variance in a sample. There are two reasons we have confidence in our measured sarcomeres. First, our average measured masseter sarcomere lengths obtained from heads with jaws fixed in incisor occlusion fall within the range obtained from the masseters of rats whose heads were fixed in a similar jaw posture (2.00–2.23 μm; Nordstrom and Yemm, 1972). Secondly, our average measured sarcomere lengths for both jaw-closing muscles fall well within the physiologic range of mouse skeletal muscles maximally contracted and extended (Goulding et al., 1997).

For studies comparing jaw-muscle architecture among individuals and/or species, analyses of relative differences in fiber dimensions fixed to a standardized posture (e.g., tip-to-tip incisor occlusion) may be adequate. The advantages of this approach are simplicity and the potential for reduced variance tied to measurement error. Using a standardized posture does, however, involve certain assumptions and limitations. First, there is no reason to expect that a specific posture remains functionally homologous across species. In other words, we must assume that the standardized posture retains the same relationship to resting sarcomere length across the sample. Second, some postures will be difficult to standardize. For example, incisor wear and incisal open/closed bites may influence the standardized posture and hence fiber length measures. Finally, the use of a standardized posture may reduce sample sizes when jaw position at fixation cannot be determined by the researcher (e.g., in museum specimens).

Evolutionary adaptation and plasticity of muscle architecture

In this study, we have functionally linked architectural features of the jaw-closing muscles in marmosets to the specific biological role (e.g., Bock and von Wahlert, 1965) of generating relatively wide jaw gapes during gouging. Observed craniodental specializations in marmosets support an hypothesis that these animals have undergone selection to improve tree-gouging performance. Similarly, selection may have favored the evolution of relatively longer fibers to improve gouging ability. This evolutionary adaptive hypothesis is arguably challenged by the observation that skeletal muscle is a highly plastic tissue (Botticelli and Reggiani, 2006). In fact, several thousand sarcomeres can be serially added to an existing fiber in a matter of days with muscle stretch, or stretch combined with electrical stimulation (Williams et al., 1986). In addition to the observed phenotypic plasticity of muscle, this evolutionary adaptive hypothesis is further challenged by our essential ignorance of the genetic basis of fiber architecture in skeletal muscle.

The heritability of muscle fiber architecture has important implications for the evolution of behavioral performance in humans and other primates. While some studies have estimated fiber type heritabilities in humans (e.g., Simoneau and Bouchard, 1995) and other mammals/mice (e.g., Nakamura et al., 1993; Suwa et al., 1996), there are no published studies to our knowledge estimating heritabilities of muscle fiber architecture. Unfortunately, it is difficult to estimate genetic aspects of fiber architecture, such as heritabilities, in a primate model. Preliminary research using an inbred mouse model (Taylor et al., 2008) demonstrates significant genetic variation in both masseter fiber lengths and PCSA. Furthermore, this heritable variation in fiber length may contribute to variation in maximum jaw opening in these mice. While further studies are needed to solidify this initial finding, these preliminary results provide the necessary foundation for hypotheses of evolutionary adaptation in jaw-muscle architecture of marmosets and other primates.

CONCLUSION

In this study, we evaluated and compared fiber architecture of the masseter and temporalis muscles in tree-gouging and nongouging callitrichids. As predicted,

tree-gouging common and pygmy marmosets exhibit relatively elongated muscle fibers, higher ratios of fiber length to muscle mass and greater tendon excursion abilities compared with nongouging tamarins. We hypothesize that the relatively elongated fibers improve feeding performance in marmosets by facilitating the production of relatively large jaw gapes and more power during tree gouging. As a consequence of the functional trade-off between maximizing muscle excursion/contraction velocity and muscle force, tree-gouging marmosets display relatively smaller muscle PCSAs and lower priority indices for force, indicating the potential for relatively less force production compared with cotton-top tamarins. These relative architectural differences are substantiated in muscles obtained from specimens whose jaws were fixed in a standardized jaw posture (tip-to-tip occlusion of the incisors) and in specimens normalized for sarcomere length. These findings suggest that standardizing by jaw posture may be a suitable method of controlling for fiber length differences when sarcomere-length normalization is not possible. Finally, the observed architectural trade-off between fiber length and force production highlights the important possibility that jaw-muscle architecture in some primates reflects evolutionary changes related to jaw movements, as but one of the many functional demands placed on the masticatory apparatus. These results have important implications for interspecific scaling studies emphasizing force production, and underscore the need for comparisons between closely related forms to further elucidate adaptive differences.

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