STRETCHING THE LIMITS: JAW-MUSCLE ARCHITECTURE IN TREE-GOUGING AND NONGOUGING CALLITRICHIDS

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Purpose/Objectives:

Gummivory is an important part of callitrichid behavioral ecology. Some callitrichids are opportunistic gum feeders, while others actively gouge trees to elicit the flow of exudates. Tree gougers differ from nongouging callitrichids in exhibiting a uniform cutting edge of the lower dentition and thinning of lingual enamel, and low condyle heights relative to the occlusal plane (Coimbra-Filho & Mittermeier, 1977; Rosenberger, 1978; Vinyard et al., 2003; Fig. 1a). Some investigators have linked skull form differences between tree-gouging and nongouging taxa to the expectation of high jaw forces during gouging behaviors (e.g., Dumont, 1997), while others have theoretically argued and empirically demonstrated that tree gouging involves the production of wide jaw gapes (Fig. 1b-c) but at surprisingly low jaw forces (Vinyard et al., 2001). Thus, structural modifications of the masticatory apparatus that facilitate the generation of wide jaw gapes should be advantageous to tree gougers.

Previously, Taylor & Vinyard (2004) demonstrated that masseter muscle in tree-gouging common marmosets (*Callithrix jacchus*) has relatively longer fibers and other architectural features related to facilitating muscle stretch, compared to the nongouging cotton-top tamarin (*Saguinus oedipus*). Taylor & Vinyard (2004) argued that the relatively longer fibers were functionally and/or adaptively linked to facilitating the production of wide jaw gapes during tree gouging.

Here we continue to evaluate the muscular correlates of tree gouging by comparing temporalis fiber architecture of tree-gouging common (*C. jacchus*) and pygmy marmosets (*Cebuella pygmaea*) with that of nongouging tamarins (*S. oedipus*). We argue that the temporalis, like the masseter muscle, may be an important limiting factor to achieving wide maximum gapes. Therefore, we predict that tree-gouging marmosets will exhibit relatively longer temporalis fibers and associated architectural parameters that make the muscle well-suited to facilitating wide jaw gapes during tree gouging.

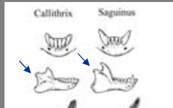


Fig. 1a

Fig 1b

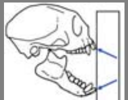


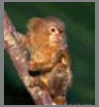
Fig. 1c

Samples:

1. Temporalis muscles of *Callithrix jacchus*, *Cebuella pygmaea* and *Saguinus oedipus* were dissected, cleaned of fascia and extra tendon, blotted dry, and weighed to the nearest 0.0000g. Animals were included in this study only if their jaws were fixed in the same jaw posture (upper and lower incisors in tip-to-tip contact).

Callithrix jacchus (n = 14)

Cebuella pygmaea (n = 5)



Saguinus oedipus (n = 9)

Measurements:

2. The muscle was bisected along the line of action, oriented on its perpendicular to expose the fibers, and pinned to a styrofoam block to facilitate fiber measurement (Fig. 2a).
3. Measurements were taken on a maximum of six fibers at a maximum of two sampling sites on each muscle (Fig. 2b). Measurements included: fiber length (l_f); 2) proximal tendon length (t_p); 3) distal tendon length (t_d); and the perpendicular distance from the tendon of insertion to the proximal attachment of the fiber (a), which was used to calculate the angle of pinnation (θ = arcsine a/l_f).
4. Pinnation angle was calculated for each fiber and the average used for data analysis. Fiber length, physiological cross-sectional area (PCSA), the ratio of mass to maximum tetanic tension (M/Po), and maximum distal tendon excursion (h), were computed with values averaged from all fibers across both sites.

Fig. 2a

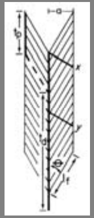


Fig. 2b

Results:

Means, standard deviations (in parentheses), and results of Mann-Whitney U-tests are presented below (Table 1). As predicted, *Callithrix jacchus* has relatively longer fibers (Fig. 3a), a greater ratio of mass to effective maximal tetanic tension (M/Po), and relatively greater maximum potential excursion of the distal tendon of attachment (h/l_b), compared to *Saguinus oedipus*. By contrast, PCSA is relatively greater in *S. oedipus* (Fig. 3b). *Cebuella pygmaea* and *S. oedipus* do not differ in absolute or relative fiber lengths, although the relative difference approaches significance. *C. pygmaea* has a relatively greater potential maximum excursion of the distal tendon (h/l_b). *C. pygmaea* does have significantly ($p < 0.01$) longer fibers relative to both temporalis muscle weight and length compared to *S. oedipus* (not shown). *S. oedipus* has significantly greater absolute and relative PSCA than *C. pygmaea*. The two species do not differ in pinnation angle and M/Po, although the difference in M/Po approaches significance.

Table 1. Comparisons of temporalis fiber architecture between gouging & nongouging callitrichids.

Variable	*C. jacchus*	*C. pygmaea*	*S. oedipus*	*Cj* vs. *So*	*Cp* vs. *So*
Temporalis weight (gm)	1.53 (0.22)	0.30 (0.06)	1.80 (0.44)	**0.0440**	**0.0015**
Jaw length (mm)	30.72 (1.87)	23.42 (1.65)	31.31 (1.81)	NS	**0.0015**
Temporalis length (t_b) (mm)	23.26 (2.81)	19.28 (2.62)	30.48 (2.93)	**0.0000**	**0.0015**
Fiber length (mm)	7.51 (1.10)	5.07 (0.65)	5.48 (0.44)	**0.0005**	NS
Fiber length / jaw length	0.24 (0.03)	0.22 (0.04)	0.18 (0.01)	**0.0000**	0.0625
PCSA (cm²)	1.86 (0.33)	0.54 (0.05)	2.95 (0.58)	**0.0005**	**0.0015**
PCSA / jaw length	0.06 (0.01)	0.02 (0.00)	0.10 (0.02)	**0.001**	**0.0015**
M/Po	3.63 (0.45)	2.40 (0.32)	2.64 (0.24)	**0.0000**	0.0810
Potential excursion (h)	3.09 (0.45)	2.09 (0.27)	2.25 (0.18)	**0.0005**	NS
h / l_b	0.13 (0.02)	0.11 (0.03)	0.07 (0.008)	**0.0000**	**0.0045**
Angle of pinnation (degrees)	17.51 (5.55)	13.55 (3.53)	16.62 (3.37)	NS	NS

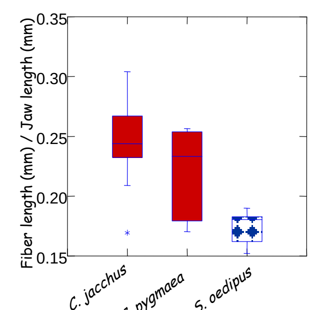


Fig. 3a

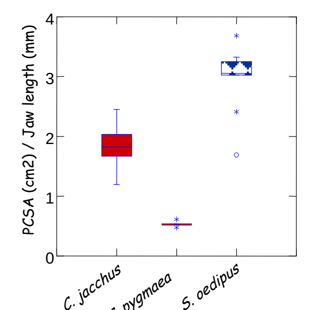


Fig. 3b

Conclusion:

Results demonstrate that common marmoset temporalis fibers are configured for achieving a greater range of motion compared to *Saguinus oedipus*, as reflected in their relatively longer fibers, greater distal tendon excursion (h), and higher ratio of M/Po. *Cebuella pygmaea* has longer fibers relative to muscle weight, muscle length, and potentially jaw length (the latter is not statistically significant) and a relatively greater distal tendon excursion (h/l_b), suggesting that their temporalis fibers may be similarly configured for achieving greater range of motion. These results strongly suggest that temporalis fiber architecture in tree-gouging common and pygmy marmosets facilitates increased stretching during jaw opening and, therefore, the production of wide jaw gapes during tree gouging. Results also support previous hypotheses linking masseter fiber length to maximum jaw gape (Herring et al., 1979; Taylor & Vinyard, 2004). Given the absence of differences in pinnation angle between gougers and nongougers, the greater PCSA in *S. oedipus* is largely a function of their greater muscle weight coupled with shorter fibers. Finally, our results are consistent with previous theoretical and empirical work demonstrating the difficulties of simultaneously maximizing muscle excursion and muscle force (Fig. 4). Thus, *C. jacchus* temporalis provides relatively greater muscle excursion compared to *S. oedipus*, but this increase in excursion is at the expense of relative force production.

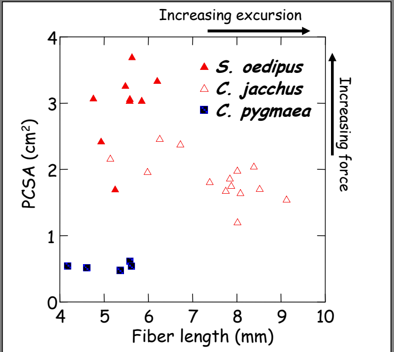


Fig. 4. Bivariate plot demonstrating the architectural trade-off between muscle force (PCSA) and muscle excursion (fiber length). There is some overlap between *S. oedipus* and *C. jacchus*, but in general, marmoset temporalis, with its relatively long fibers and low PCSA, is suited more for muscle excursion (i.e., production of wide gapes), while *S. oedipus* temporalis, with its relatively greater PCSA and shorter fibers, is better suited for generating larger muscle force with smaller excursions.

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