

The Functional Morphology of the Anterior Masticatory Apparatus in Tree-Gouging Marmosets (Cebidae, Primates)

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ABSTRACT Although all genera of Callitrichinae feed on tree exudates, marmosets (*Callithrix* and *Cebuella*) use specialized anterior teeth to gouge holes in trees and actively stimulate exudate flow. Behavioral studies demonstrate that marmosets use large jaw gapes but do not appear to generate large bite forces (relative to maximal ability) during gouging. Nonetheless, the anterior teeth of marmosets likely experience different loads during gouging compared to nongouging platyrrhines. We use histological data from sectioned teeth, μ CTs of jaws and teeth, and in vitro tests of symphyseal strength to compare the anterior masticatory apparatus in *Callithrix* to nongouging tamarins (*Saguinus*) and other cebids. We test the hypotheses that (1) marmoset anterior teeth are adapted to accommodate relatively high stresses linked to dissipating gouging forces and (2) the mandibular symphysis does not provide increased load resistance ability compared with closely related nongouging platyrrhines. Differences in decussation between *Callithrix* and *Saguinus* are greatest in the anterior teeth, suggesting an increased load resistance ability specifically in incisor and canine enamel of *Callithrix*. *Callithrix* lower incisor crowns are labiolingually thicker suggesting increased bending resistance in this plane and improved wedging ability compared with *Saguinus*. Anterior tooth roots are larger relative to symphyseal bone volume in *Callithrix*. Anterior tooth root surface areas also are larger in marmosets for their symphyseal volume, but it remains unclear whether this relative increase is an adaptation for dissipating dental stresses versus a growth-related byproduct of relatively elongated incisors. Finally, simulated jaw loading suggests a reduced ability to withstand external forces in the *Callithrix* symphysis. The contrast between increased load resistance ability in the anterior dentition versus relatively reduced symphyseal strength (1) suggests a complex loading environment during gouging, (2) highlights the possibility of distinct loading patterns in the anterior teeth versus the symphysis, and (3) points to a potential mosaic pattern of dentofacial adaptations to tree gouging. *J. Morphol.* 272:833–849, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS: callitrichines; exudativory; stress; teeth; mandible; decussation

INTRODUCTION

Although frugivory and insectivory are essential components of the diet for members of Callitrichinae, exudativory has also emerged as a major dietary strategy within this group of South American monkeys (Kinzey et al., 1975; Ramirez et al., 1977; Sussman and Kinzey, 1984; Rosenberger, 1992). Callitrichine genera consume tree gums and saps to varying degrees. Specifically, marmosets (*Callithrix* and *Cebuella*) emphasize exudativory to a much greater degree than closely related tamarins (*Leontopithecus* and *Saguinus*) and Goeldi's monkeys; *Callimico* (Ramirez et al., 1977; Coimbra-Filho and Mittermeier, 1977; Sussman and Kinzey, 1984; Rosenberger, 1992; Ferrari, 1993; Power and Oftedal, 1996; Kinzey, 1997). Data from behavioral studies show that *Callithrix* and *Cebuella* devote approximately 30–67% of their foraging time to exudates, respectively, as opposed to a maximum of 12% in tamarins (Power and Oftedal, 1996). Indeed, marmosets are known to actively use their lower teeth like a chisel to gouge holes in tree bark to stimulate exudate flow (Kinzey et al., 1975; Ramirez et al., 1977; Sussman and Kinzey, 1984; Rosenberger, 1992). Other callitrichines

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feed on exudates by parasitizing existing wounds (Sussman and Kinzey, 1984; Soini, 1987; Ferrari and Martins, 1992; Ferrari, 1993). Thus, most callitrichines can be viewed as opportunistic exudativores, as opposed to the active exudativory seen in marmosets (Nash, 1986).

Coincident with this tree-gouging behavior, marmosets have modified their masticatory apparatus relative to nongouging callitrichines. Several studies have discussed the functional morphology of the teeth (Kinzey, 1975; Hershkovitz, 1977; Eaglen, 1984; Nogami and Natori, 1986; Rosenberger, 1978, 1992; Propst, 1995; Maas and Dumont, 1999), bony masticatory apparatus (Dumont, 1997; Vinyard et al., 2003; Vinyard and Ryan, 2006; Ryan et al., 2010), temporomandibular joint (TMJ) articular cartilage (Mork et al., 2010), and jaw-muscle architecture (Taylor and Vinyard, 2004; Taylor et al., 2009; Eng et al., 2009) as they correspond to this derived biting behavior. Collectively, these studies suggest that the marmoset masticatory apparatus is designed to facilitate wide jaw gapes but not necessarily to provide improved load resistance abilities. Even though some of these studies have examined the morphology of the anterior mandibular dentition and symphysis, important questions remain about the functional consequences of tooth microstructure and macrostructure for force transmission through the symphysis during gouging, as well as the impact of gouging-related morphology on normal mastication. These issues deserve further consideration given that anterior teeth serve as the point of contact with the tree substrate during gouging, and the symphysis may experience different loads than the rest of the masticatory apparatus (Fig. 1). To further our understanding of the functional morphology of this important masticatory region, we combine analyses of enamel histology, morphometrics, and symphyseal performance in tamarins and marmosets.

Functional Morphology of the Mandibular Incisors and Canines of Marmosets

Marmosets have modified their anterior teeth relative to nongouging callitrichines. Their incisors have relatively heightened crowns and thickened labial enamel but lack lingual enamel (Rosenberger, 1978; Gantt, 1980). This derived enamel morphology has been hypothesized to help these teeth maintain sharp edges through differential wear rates between dentine and labial enamel (Rosenberger, 1978, 1992; Vinyard et al., 2009). Thickened labial enamel may also provide increased load resistance ability and improved resistance to labial wear, allowing us to hypothesize that marmoset incisors might experience elevated loads and/or wear rates versus tamarins (Maas, 1991; Dumont, 1995; Shellis et al., 1998; Martin et al., 2003; Lucas et al.,

2008a,b). Additionally, because enamel is weaker in tension than compression (Currey, 2002), the absence of lingual enamel may prevent enamel's exposure to potentially damaging tensile stresses experienced on the lingual surface of incisors during gouging (Fig. 1). Because dentine is tougher and more resistant to crack propagation compared with enamel, it may be better able to withstand such tensile stresses (Kingery et al., 1976; Xu et al., 1998; Rensberger, 2000; Lucas et al., 2008a; Chai et al., 2009a,b). Marmoset lower canines have also lost the tusk-like appearance seen in other callitrichines, allowing the canines and incisors to function as a single occlusal unit during gouging (Hershkovitz, 1977; Martin, 1990; Rosenberger, 1992; see Fig. 1). Moreover, these teeth are more procumbent in marmosets relative to other callitrichines (Kinzey et al., 1975; Hershkovitz, 1977), which may benefit the angle of force application during gouging (e.g., Ang et al., 2006).

Although prior research has suggested that marmosets may not produce large bite forces during gouging relative to their maximum biting ability (Vinyard et al., 2009), these derived dental features suggest that tree gouging nonetheless places unique functional demands on the anterior masticatory apparatus of *Callithrix* and *Cebuella*. We examine three morphological features of the anterior mandibular dentition in marmosets and nongouging platyrrhines to explore the potential functional consequences for tree gouging: (1) enamel microstructure, (2) labiolingual incisor thickness, and (3) tooth root surface area.

Enamel microstructure. Enamel prisms are basic microstructural units of mammalian enamel, each one representing a more or less cylindrical bundle of enamel crystallites (reviews: Boyde, 1989; Risnes, 1998). Over their course from the enamel-dentine junction (EDJ) to the tooth surface, individual prisms can take a direct path, called radial enamel, or can crisscross one another, undulate, and/or travel in bundles with alternating orientations known as Hunter-Schreger bands (Boyde, 1989; Maas and Dumont, 1999; Rensberger, 2000). We classify these latter three options as decussating enamel. Compared with radial enamel, decussating enamel hinders cracking by increasing the energy necessary for crack propagation (Pfretzschner, 1988; Risnes, 1998; Rensberger, 2000; Popowicz et al., 2004; Lucas et al., 2008a).

Previous surveys of platyrrhines suggest that marmoset teeth exhibit more developed Hunter-Schreger bands than those of other small platyrrhines such as *Saguinus*, potentially linking increased decussation to gouging (Kawai, 1955; Shellis and Poole, 1977; Nogami and Natori, 1986; Martin et al., 1988; Propst, 1995; Maas and Dumont, 1999; Hogg, 2010). More recently, Lucas et al. (2008a) have stressed the importance of assessing regional variation in tooth microstruc-

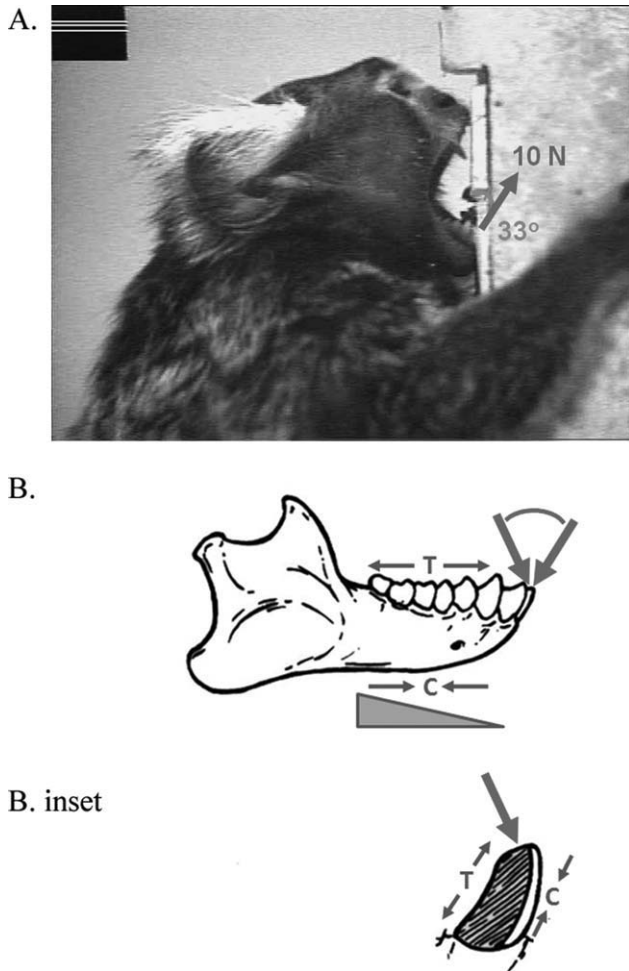


Fig. 1. Forces experienced by the anterior teeth and mandible during tree gouging. **A:** Common marmoset gouging a simulated tree substrate. On average, external forces at the anterior dentition peak at ~10 N during a gouging cycle and are oriented at 33° relative to the substrate during peak force production (arrow; Vinyard, unpublished data). **B:** Throughout the gouging cycle, we estimate the external forces will bend or compress (i.e., when the external force is directed parallel to the tooth axis) each contacting tooth (arrows). Bending will likely tense (T) the lingual and compress (C) the labial surface of the tooth (B inset). The external force will likely bend the entire mandible resulting in compression (C) along the inferior corpus and tension (T) along the alveolar border of the corpus. Corporal bending loads will increase posteriorly (triangle) suggesting that vertical bending forces at the symphysis will be relatively small. (Note: Point locations and directions of arrows in 1B, representing idealized force vectors and are positioned somewhat arbitrarily as we do not know the exact point of external force application). Figure 1B adapted from Fleagle, 1999.

ture. To date, regional variation for callitrichines has not been addressed. Because marmoset incisors and canines may experience elevated loads during gouging compared with those of tamarins, hypothesis 1 tests whether marmosets show greater decussation at the internal enamel margin (i.e., EDJ), the external enamel surface, and cusp tip relative to *Saguinus*. Given the functional divisions of labor across the tooth row, such regional

assessments may also provide insight into microstructural differences across tooth types. Therefore, hypothesis 2 tests whether marmosets exhibit more complex enamel decussation in the anterior versus posterior teeth when compared with similar regional assessments in tamarins.

Labiolingual incisor thickness. The formation of a crack within tree bark during gouging will initially depend in part on the sharpness of the incisor and/or canine cutting surface. Once initiated, continued crack propagation will be directly proportional to the labiolingual thickness of the tooth at the depth where an initial crack begins to grow. This relationship occurs because the tooth functions like a wedge pushing the bark apart (Hoagland et al., 1972; Lucas, 2004; Ang et al., 2006). Therefore, hypothesis 3 suggests that to improve wedging ability during gouging, mandibular incisors of *Callithrix* will be wider in the labiolingual direction relative to those of *Saguinus*. As cracks in tree bark will likely begin to propagate at different crack lengths depending on the tree part (e.g., outer bark, inner barks, or sapwoods) and species, we measure incisor thickness at multiple distances from the cutting tip of the tooth.

Tooth root surface area. Load resistance ability in the tooth root is proportional to the surface area of the root as the contacting surface between tooth and alveolar bone (Sicher and Dubrul, 1975; Kovacs, 1979; Spencer, 2003). Larger roots should transmit the increased loads into alveolar bone more efficiently by increasing the surface area available for transmission and in turn should lessen the risk for structural failure in gougers. Based on these expectations, hypothesis 4 suggests that marmosets will have relatively larger tooth root surface areas for dissipating occlusal loads during tree gouging versus nongouging platyrrhines.

Functional Morphology of the Anterior Mandibular Corpus in Marmosets

Marmosets have transversely narrower and more horizontally inclined symphyses than their close relatives (Kinzey et al., 1975; Hershkovitz, 1977; Rosenberger, 1978, 1992). Their symphyses may also reflect correlated changes required to house their derived anterior dentition. The morphological rearrangement and possible enlargement of tooth roots may incur a reduced load resistance ability in the marmoset symphysis during gouging and/or mastication. Alternatively, changes in symphyseal morphology may reflect improved load-resisting ability linked to novel loads experienced during gouging. Prior morphological analyses, however, contradict this latter scenario as marmosets and tamarins showed little difference in external dimensions (Vinyard et al., 2003) or cross-sectional bone distribution in the symphysis (Vinyard and Ryan, 2006).

TABLE 1. Summary of enamel decussation patterns in *Callithrix* and *Saguinus*

Tooth	Species (n)	Labial decussation ^a	Lingual decussation	Cusp tip decussation	HSB at EDJ	HSB at surface	Source
<i>I</i> ₁	<i>C. jacchus</i> (n = 4)	Y	N/A	Y	Y	Y	
	<i>S. oedipus</i> (n = 1)	N	N	N	N	N	
	<i>Saguinus</i> sp. (n = 1)	N	N	N	N	N	
	<i>S. bicolor</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. fuscicollis</i> (n = 1)	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. imperator</i> (n = 1) ^b	Y	—	—	—	N	Nogami and Natori (1986)
	<i>S. leucopus</i> (n = 1) ^b	Y	—	—	N	N	Nogami and Natori (1986)
	<i>S. midas</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. mystax</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. oedipus</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
<i>I</i> ₂	<i>C. jacchus</i> (n = 4)	Y	N/A	Y	Y	Y	
	<i>S. oedipus</i> (n = 1)	N	N	N	N	N	
C (man)	<i>C. jacchus</i> (n = 1)	Y	—	Y	Y	Y	
	<i>C. humeralifer</i> (n = 1)	Y	—	Y	Y	Y	
	<i>S. oedipus</i> (n = 1)	Y	N	Y	N	N	
	<i>S. fuscicollis</i> (n = 1)	N	N	N	N	N	
	<i>S. bicolor</i> (n = 1) ^b	Y	—	—	—	—	Nogami and Natori (1986)
<i>P</i> ₄	<i>S. oedipus</i> (n = 1) ^b	Y	N	Y	Y	N	Hogg (2010)
<i>M</i> ₁	<i>C. jacchus</i> (n = 1) ^b	Y	—	Y	Y	N	Hogg (2010)
	<i>S. oedipus</i> (n = 1)	—	N	Y	N	N	
<i>I</i> ¹	<i>C. jacchus</i> (n = 4)	Y	Y	Y	Y	Y	
	<i>S. oedipus</i> (n = 1)	—	N	—	—	—	
	<i>S. inustus</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. labiatus</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
	<i>S. oedipus</i> (n = 1) ^b	N	—	—	N	N	Nogami and Natori (1986)
<i>I</i> ²	<i>C. jacchus</i> (n = 5)	Y	Y (4 of 5)	Y	Y	Y	
	<i>S. oedipus</i> (n = 2)	Y	Y	Y	Y	Y	

^a“Y” indicates the presence of decussation and/or Hunter-Schreger Bands (HSB) in a region. “N” indicates their absence. An empty cell (—) indicates it was not possible to make a positive determination because of insufficient anatomical information. “N/A” indicates no enamel is present in this region.

^bIndicates data drawn from the literature in order to augment the data available from the present sample (source given in last column).

Symphyseal load resisting performance. To address the competing explanations for the observed shifts in symphyseal morphology, we assess symphyseal performance during in vitro application of idealized loading regimes in marmosets and nongouging platyrrhines. We focus on wishboning (i.e., lateral transverse bending) and dorsoventral (DV) shear, loading regimes that likely occur during mastication (Hylander, 1984; Hylander et al., 2000) rather than gouging. These loading regimes likely stress the symphysis more than the vertical bending experienced during gouging (Hylander, 1984; see also Fig. 1). Based on previous morphological comparisons, hypothesis 5 suggests that symphyseal strength will not differ between marmosets and other platyrrhines when loaded in simulated wishboning and DV shear.

MATERIALS AND METHODS

This study consists of three datasets analyzed separately by the authors: (1) dental microanatomy (RT Hogg); (2) μ CT of the anterior corpus for studying dental dimensions and proportions of dental versus bone tissues in the symphysis (TM Ryan and CJ Vinyard); and (3) macroscale assessment of symphyseal strength during in vitro loading (MJ Ravosa and CJ Vinyard).

Dental Histology and Enamel Microstructure

Mandibular and maxillary incisors and canines from six *Callithrix* and four *Saguinus* individuals, as well as a *S. oedipus*

*M*₁, were extracted from their alveoli and cleaned of organic debris via incubation in a 5% enzyme detergent solution at 50°C for 1 week, with daily solution changes. Overall, 34 teeth from 11 individuals were examined, with 32 teeth imaged using scanning electron microscopy (SEM) and 2 teeth imaged using transmitted light microscopy due to their availability (see below for details). Between 1 and 8 teeth were examined for each individual (see Table 1 for further details).

For electron microscopy, teeth from five *C. jacchus*, two *S. oedipus*, and one *Saguinus* sp. were ground along a labiolingual plane using a graded series of emery papers, etched for 10 s per tooth using a 5% hydrochloric acid solution, rinsed with distilled water, and dried. These teeth were imaged using an FEI Quanta 600F environmental SEM (FEI Company, Hillsboro, OR), at low vacuum.

In addition to specimens examined in SEM, we also examined thin sections using light microscopy. A single mandibular canine of *Callithrix humeralifer* (AMNH 94926) and *Saguinus fuscicollis* (AMNH 1829421) was dehydrated under vacuum using a graded series of ethanol/water solutions and was then embedded in an acrylic resin (polymethyl methacrylate; for detailed embedding protocol, see Hogg, 2010). Thin sections were cut along the labiolingual plane of the teeth using a slow-speed diamond wafering saw (Buehler, Inc., Lake Bluff, IL) and mounted to glass slides using a methacrylate-based adhesive. Sections were ground and polished to a thickness of ~100 μ m using graded emery papers and finally a 1- μ m diamond polish (in water suspension) (Buehler, Inc., Lake Bluff, IL). Both teeth were imaged using a Leica-Leitz DMRX/E Universal Microscope, configured with a Marzhauser motorized stage, phase contrast, and circularly polarizing filters (CPL) (Leica Microsystems, Bannockburn, IL). All CPL images were acquired via Syncoptics Montage Explorer (Synoptics, Ltd., Cambridge, UK), using a JVC KYF55B color video camera (JVC Professional Products Company, Wayne, NJ).

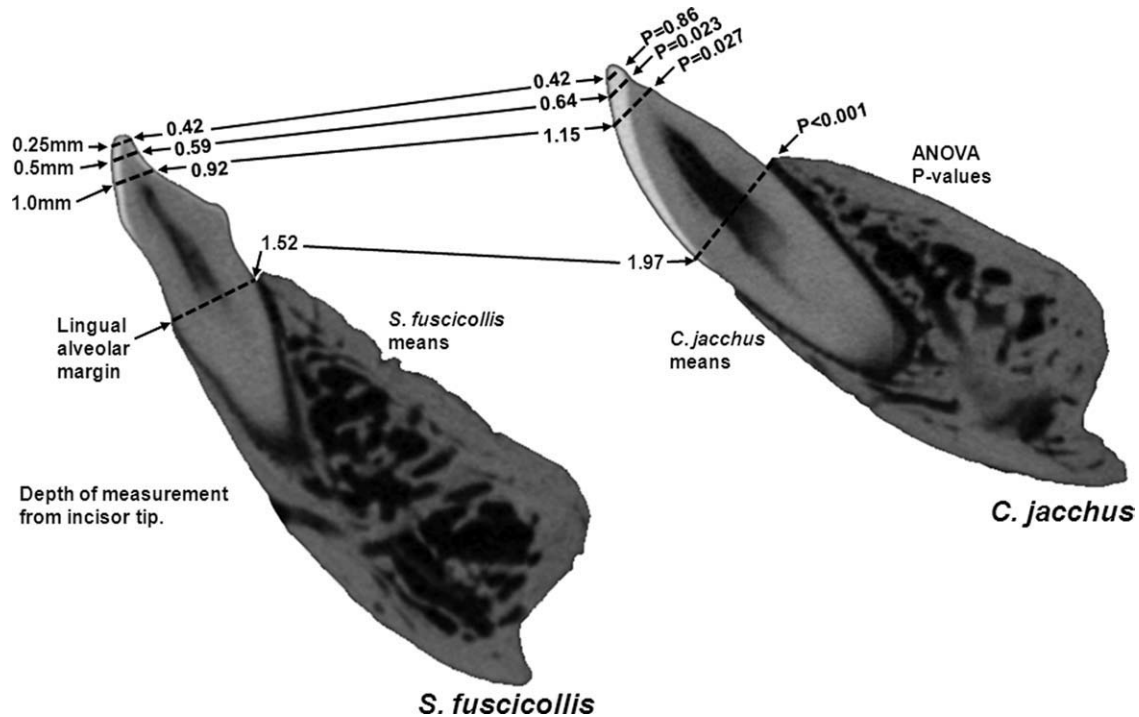


Fig. 2. Comparison of central incisor widths in common marmosets (*Callitrix jacchus*) and saddle-back tamarins (*Saguinus fuscicollis*). Widths were measured from CT scans at 0.25, 0.5, and 1.0 mm from the incisor tip and at the lingual alveolar margin in common marmosets ($n = 5$) and saddle-back tamarins ($n = 5$). Marmosets have significantly wider incisors (one-way ANOVA, $P < 0.05$) starting at 0.5 mm from the tip and continuing proximally.

See Hogg (2010) for further details on the use of CPL and enamel imaging.

To test hypotheses 1 and 2, we combined SEM and CPL images from our 10 marmosets and tamarins to qualitatively assess the presence of decussating or radial prisms in specific tooth regions, as is standard for enamel microstructure studies (e.g., Maas and Dumont, 1999; Martin et al., 2003; Lucas et al., 2008a,b; see Table 1). Where Hunter-Schreger bands were present, we noted whether banding was seen in deep and/or surface enamel. For SEM images, prisms paths were observed directly, whereas in CPL images we compared patterns of color variation in tooth images. The data collected here were supplemented with additional data on anterior and posterior teeth drawn from Nogami and Natori (1986) and Hogg (2010).

μCT Scanning

Mandibles from five *Callitrix jacchus*, five *Saguinus fuscicollis*, and two *Saimiri sciureus* were scanned in the high-resolution X-ray computed tomography facility at the University of Texas at Austin (Vinyard and Ryan, 2006; Ryan et al., in press). All specimens were wild caught and assumed to have dietary behaviors typically described for the species. Scan resolutions ranged from 0.02067 to 0.0237 mm slice thickness and between 0.0195 and 0.0224 mm x,y pixel size. Between 1400 and 1788 ct slices were collected for each jaw during scanning. Raw scan data were reconstructed as 1024 × 1024 16-bit TIFF images for analysis (see Vinyard and Ryan, 2006 and Ryan et al., 2010 for details).

We calculated labiolingual widths of the central incisors in *C. jacchus* and *S. fuscicollis* from midline μCT scan reconstructions. Widths were measured at 0.25, 0.5, and 1.0 mm from the incisor tip and at the lingual alveolar margin using SigmaScan Pro 5.0 (Systat Software, San Jose, CA) (Fig. 2). To test hypothesis 3, we compared marmoset and tamarin incisor widths

using a one-way ANOVA ($\alpha = 0.05$). Because wedging ability depends on absolute width, we did not compare incisal shapes between callitrichine species.

We used Avizo 6.0 (Visualization Sciences Group, Burlington, MA) to define and quantify symphyseal bone volume as well as surface area and volume of the anterior tooth roots. Incisors and canines were initially segmented using a combination of manual and automatic tools in Avizo 6.0. The outline of each tooth was selected using the 3D magic wand ensuring that no surrounding bone was selected. Regions representing the teeth were set to zero and all other voxels in the dataset were set to one. This binary, segmented dataset was multiplied by the original to produce a new dataset in which all the anterior teeth were removed (i.e., set to zero).

To operationalize the symphyseal region for measurement, we first created a line perpendicular to the sagittal plane, connecting the lingual junction of the P_4 and M_1 on the right and left sides of the mandible using a 3D isosurface reconstruction in Avizo 6.0 (Fig. 3). We then created rays emanating from the midpoint of this cross-mandibular line to transect the buccal junction of the canine and P_2 on both sides of the jaw. The volumetric region between these two rays was defined as the symphysis. (Note: in cases where only a hemimandible was scanned, we used the midline ray in Figure 3 to define the symphysis on one side of the jaw and doubled relevant variables to estimate overall symphyseal dimensions.) We cropped the CT dataset along these rays, segmented these cropped images for bone and calculated symphyseal bone volume in Avizo 6.0. The threshold for bone was calculated separately for each of the 12 specimens using an iterative algorithm (Ridler and Calvard, 1978; Trussell, 1979). We calculated root surface areas and volumes for incisors and canines by finding the CT slice nearest the cuspal surface that included mandibular bone and calculated values for the root lying below that level (i.e., within the alveolus of the tooth). For comparisons, root surface areas and volumes were summed for each of the 12 individuals across all 6 anterior teeth.

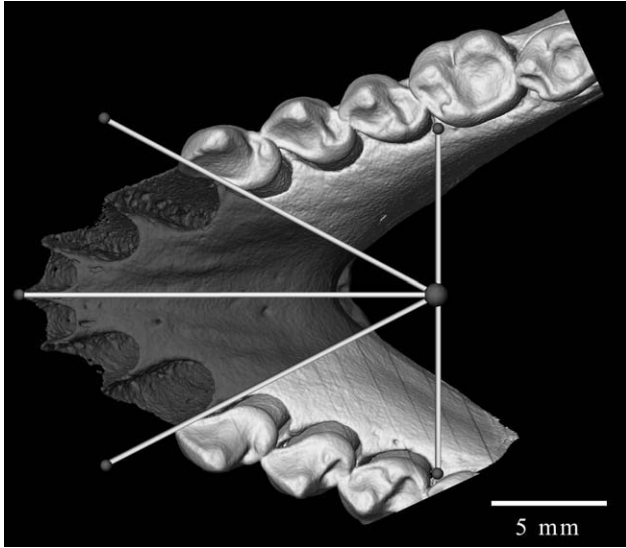


Fig. 3. We used a three-dimensional isosurface to operationalize the symphysis as the region enclosed by two rays passing between the canine and P₂ on each side of the mandible and intersecting the midpoint of a transverse line drawn between the P₄ and M₁ on each side of the mandible (dark gray area). For scans including only hemimandibles, we used the midline ray to define one-half of the symphysis and multiplied all variables by two.

To assess differences in relative root surface area (hypothesis 4), we used a one-way ANOVA ($\alpha = 0.05$) to compare *Callithrix* ($n = 5$) to nongouging *Saguinus* ($n = 5$) and *Saimiri* ($n = 2$; Table 2). We examined tooth root area^{0.5} relative to jaw length, symphyseal volume^{0.333}, and central incisor length. Jaw length was measured in the midline from incisor alveolus to the back of the condyle, whereas central incisor length was measured from the occlusal tip to the inferior extent of the root. We also compared the percent of tooth root volume relative to root + symphyseal volume between gouging and nongouging taxa using a one-way ANOVA ($\alpha = 0.05$). Finally, relative symphyseal volume^{0.333}/jaw length was compared using ANOVA between gouging and nongouging taxa to assess relative symphysis size.

Symphyseal Performance during In Vitro Loading

We estimated the strength of formalin-fixed, articulated mandibular symphyses from 22 adult platyrrhine cadavers in either wishboning or DV shear (Table 3). The anthropoid symphysis is thought to experience both loading regimes during unilateral mastication (Hylander, 1984; Hylander et al., 2000). We chose these two masticatory loading regimes because they likely stress the symphysis more than the vertical bending experienced during gouging. The 22 harvested symphyses were attached to a Universal Testing Machine (Instron, Norwood, MA) and loaded to structural failure in either loading regime at a constant rate of 2.54 cm/min. Depending on the size of the specimen, either a 45.3 kg (100 lbs) or 90.7 kg (200 lbs) load cell was used to load each symphysis. To simulate wishboning, we wrapped stiff wires around both sides of the jaw just behind the symphysis (to minimize the bending moment arm), attached the ends of the wire to either the load cell or stationary grip, and pulled the symphysis to structural failure in tension. To estimate symphyseal strength in DV shear, we firmly affixed one hemimandible to the base grip behind the last premolar using an adjustable beveled acrylic plate. The specimen was oriented so that the occlusal plane was in line with a metal post attached to the load cell. This post was positioned just behind

TABLE 2. Comparisons of symphyseal volume, anterior tooth root volumes, and root surface areas in tree gouging *Callithrix* versus nongouging *Saguinus* and *Saimiri*

Species and groups	Symphyseal volume (mm ³)	Anterior tooth root volume (mm ³)	% Tooth root/(root + symphysis)	Symphyseal volume ^{0.333} /jaw Length	Anterior tooth root surface area (mm ²)		Tooth root area ^{0.5} /jaw length	Tooth root area ^{0.5} /incisor length	Tooth root area ^{0.5} /symphyseal volume ^{0.333}
					Surface area	Surface area			
<i>Callithrix jacchus</i> ($n = 5$)	47.47 (4.73) ^a	43.64 (10.25)	47.50 (8.70)	0.13 (0.01)	182.92 (18.41)	182.92 (18.41)	0.50 (0.04)	1.93 (0.18)	3.69 (0.33)
<i>Saguinus fuscicollis</i> ($n = 5$)	86.07 (14.36)	42.73 (6.38)	33.35 (3.61)	0.15 (0.01)	164.06 (13.25)	164.06 (13.25)	0.45 (0.02)	2.18 (0.20)	2.92 (0.24)
<i>Saimiri sciureus</i> ($n = 2$)	185.74 (11.82)	93.45 (2.64)	33.49 (0.79)	0.17 (0.01)	272.48 (14.61)	272.48 (14.61)	0.49 (0.03)	—	2.90 (0.02)
Nongougers average ^b	—	—	33.39 (2.97)	0.16 (0.01)	—	—	0.46 (0.03)	2.18 (0.20)	2.92 (0.20)
ANOVA: gougers vs. nongougers ^c	—	—	$F = 16.3$ $P = 0.003$	$F = 17.6$ $P = 0.002$	—	—	$F = 5.0$ $P = 0.05$	$F = 4.4$ $P = 0.07$	$F = 26.7$ $P < 0.001$
			(G > NG)	(G < NG)			(G > NG)	(G ≤ NG)	(G > NG)

^aMean followed by standard deviation (in parentheses).

^bNongouger averages are only reported for dimensionless variables that are used in interspecific comparisons.

^cANOVA refers to one-way ANOVA comparing gouging *Callithrix* (G) to nongouging (NG) *Saguinus* and *Saimiri*.

TABLE 3. Symphyseal performance during in vitro loading in platyrrhines

Species and groups	Wishboning			DV Shear		
	n	Load at failure (N) ^a	Stress (N/mm ⁴) ^b	n	Load at failure (N)	Stress (N/mm ²)
<i>Callithrix jacchus</i>	6	76.11 (11.24) ^c	0.106 (0.030)	5	100.7 (17.31)	3.08 (0.34)
<i>Aotus trivirgatus</i>	3	173.59 (34.14)	0.149 (0.021)	—	—	—
<i>Saguinus oedipus</i>	1	112.20 (—)	0.131 (—)	—	—	—
<i>Saimiri sciureus</i>	4	128.50 (30.10)	0.143 (0.035)	3	166.95 (37.09)	4.16 (0.91)
Nongougers average ^d	8	—	0.144 (0.026)	3	—	4.16 (0.91)
ANOVA: gougers vs. nongougers ^e		—	<i>F</i> = 6.09 <i>P</i> = 0.03 (<i>G</i> < <i>NG</i>)		—	<i>F</i> = 6.12 <i>P</i> = 0.048 (<i>G</i> < <i>NG</i>)

^aN = Newtons.

^bStress at failure in wishboning is estimating by dividing load (N) by an estimate of the second moment of area for resisting wishboning (mm⁴). For DV shear, stress at failure is estimated by dividing load at failure by the approximation of symphyseal cross-sectional area (mm²). These estimates provide a means of comparing values across the range of species included here, but do not fully account for variation in symphyseal bone distribution, position of the neutral axis or curvature of the symphysis in estimating stress (Hylander, 1985; Vinyard and Ravosa, 1998; Daegling and McGraw, 2009). As such, this estimate should be viewed as a first approximation of stress at failure in these specimens.

^cMean followed by standard deviation (in parentheses).

^dNongouger averages are only reported for dimensionless variables that are used in interspecific comparisons.

^eANOVA refers to one-way ANOVA comparing gouging *Callithrix* to nongouging species.

the central incisor on the unsupported hemimandible. The mandible was loaded in compression as the symphysis was sheared inferiorly to structural failure (Vinyard et al., 2006). We recorded the force required for structural failure in Newtons (N) for both quasi-static tests. In all 22 specimens, fracture location was recorded to determine whether marmoset symphyses tended to fail at different locations than other nongouging platyrrhines.

To adjust for variation in symphyseal size and size-related variation in bone distribution across the interspecific sample, we measured symphyseal length and width and estimated the area moment of inertia for resisting wishboning (*I_{yy}*) and symphyseal cross-sectional area. Both were estimated as an elliptical approximation. We divided force at failure (N) by our *I_{yy}* estimate for wishboning and by symphyseal cross-sectional area (mm²) for DV shear to estimate stress at failure. Because of the small sample sizes within several nongouging species, we combined these stress estimates to compare marmosets and nongouging platyrrhines using a one-way ANOVA ($\alpha = 0.05$).

RESULTS

Enamel Microstructure

Hypothesis 1 predicts that the anterior teeth of *Callithrix* will show greater decussation than *Saguinus* throughout their enamel. SEM and CPL micrographs reveal that this is the case (see Table 1; Figs. 4 and 5). All *Callithrix* incisors and canines exhibited highly regular, densely packed Hunter-Schreger bands in their imbricational enamel with these bands extending from the EDJ to the enamel surface. *Callithrix* anterior tooth cusps also exhibited either Hunter-Schreger bands or irregular patterns of decussation. Clearly visible Hunter-Schreger bands, however, did not extend into the cusp tips of the upper incisors. Both upper and lower *Saguinus* incisors exhibited radial enamel. However, because some *Saguinus* teeth were highly worn (especially upper incisors), it is possible that some decussation near the cusp surface may have been missed. Therefore, we also considered data from images from the work done by Nogami and Natori (1986; Table 1),

which show no Hunter-Schreger banding in *Saguinus* incisors (though some slight decussation was seen in two *Saguinus* species). In our study, an *S. oedipus* upper canine did exhibit Hunter-Schreger bands (Fig. 4d) extending from the EDJ to the enamel surface, whereas the lower canine exhibited some slight prism deviation. The lower canine of *S. fuscicollis* also did not exhibit Hunter-Schreger banding (Fig. 5b). Results suggest that *Saguinus* canines are somewhat variably decussated among different individuals/species; however, they are generally more decussated than *Saguinus* incisors (see also Nogami and Natori, 1986).

Hypothesis 2 suggests that because the anterior teeth of marmosets and tamarins may be subject to a greater functional difference in use relative to the posterior dentition (which should undergo a similar masticatory regime; see Sussman and Kinzey, 1984; Rosenberger, 1992), marmosets should exhibit relatively more complex enamel decussation patterns in the anterior versus posterior teeth compared with similar regional assessments in tamarins. In *Callithrix*, both anterior and posterior teeth exhibit strong Hunter-Schreger banding (see Table 1). However, these regions differ in that Hunter-Schreger bands of posterior teeth start at the EDJ but do not always reach the tooth surface (Hogg, 2010; Table 1). *Saguinus* incisors exhibit the least decussation of all teeth examined. Their canines, however, often possess Hunter-Schreger bands, as do their postcanine teeth (Maas and Dumont, 1999; Hogg, 2010). Therefore, the hypothesis is corroborated in that: (1) *Callithrix* teeth are universally banded, with this character seeing its “greatest” expression in the anterior teeth, whereas; (2) *Saguinus* teeth are more heterogeneous in their level of decussation, with incisors showing the “least” expression of the character.

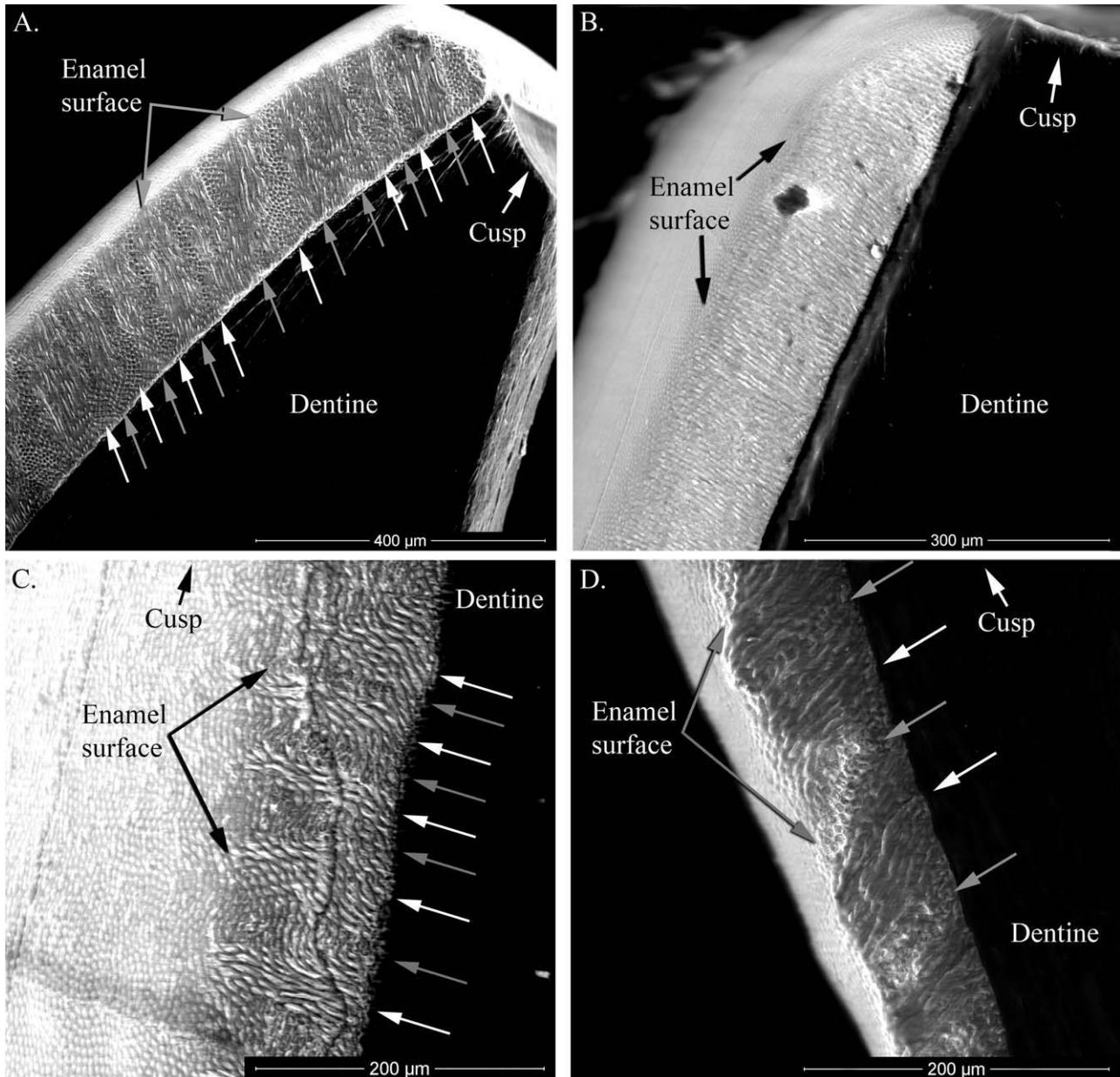


Fig. 4. Scanning electron micrographs of enamel in *Callithrix* and *Saguinus*. Gray and white arrows indicate alternating prism orientations in successive Hunter-Schreger bands. **A** and **B**: Comparison of labial enamel, near the cusp tip, of a *C. jacchus* I₁ (**A**) and a *Saguinus* sp. I₁ (**B**). *C. jacchus* exhibits Hunter-Schreger bands extending to the cusp tip, while *Saguinus* exhibits radial enamel. **C** and **D**: Images from mid-crown labial enamel in the maxillary canines of *C. jacchus* (**C**) and *S. oedipus* (**D**) representing the greatest morphological similarity across teeth seen in this study between the two genera. Hunter-Schreger banding is similar in these images, although *Saguinus* exhibits a less regular pattern (cf. Maas and Dumont, 1999). Cuspal direction is toward the top of the page in all four images; "enamel surface" indicates the intersection between the longitudinal plane of section and the plane of the tooth surface.

Labiolingual Incisor Thickness

Hypothesis 3 suggests that *Callithrix* will exhibit labiolingually wider mandibular incisors to improve wedging ability during gouging compared with closely related *Saguinus*. Marmosets have significantly wider incisors starting at 0.5 mm from the tip (ANOVA; $F = 7.9$, $P = 0.027$, $df = 9$) to 1.0 mm from the tip (ANOVA; $F = 7.3$, $P = 0.27$, $df = 9$) and

continuing proximally through the crown to the alveolar margin (ANOVA; $F = 26.9$, $P < 0.001$, $df = 9$) supporting hypothesis 3 (Fig. 2).

Tooth Root Surface Area and Symphyseal Volume

Hypothesis 4 suggests that marmosets will have relatively larger tooth root surface areas for dissi-

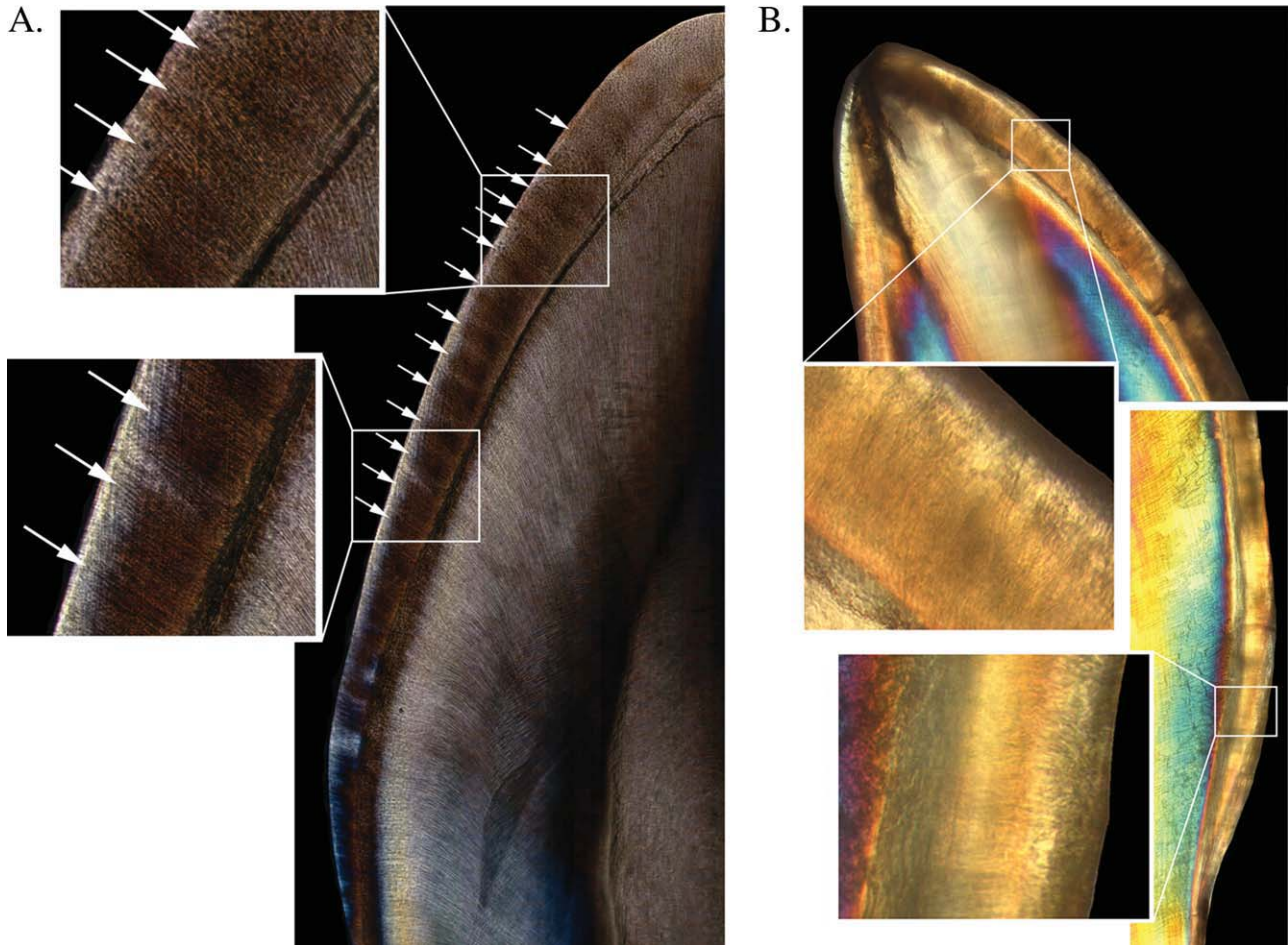


Fig. 5. **A:** Numerous distinct Hunter-Schreger bands are visible as alternating brown and light-colored bands (indicated by white arrows) in CPL images of the lingual side of a *Callithrix humeralifer* mandibular canine. These bands extend through most of the crown; however, they become much less apparent toward the cusp tip, where enamel decussation is most likely irregular (based on comparisons with SEM micrographs). (Field width = 1,336 μm , top inset = 380 μm , bottom inset = 384 μm). **B.:** Circular-polarizing filter images demonstrating a lack of organized Hunter-Schreger banding in the enamel of a *Saguinus fuscicollis* mandibular canine. The upper image and its inset depict cuspal and upper imbricational enamel (lingual is to the right). The lower right image and its inset depict cervical and lower imbricational enamel (both lingual side). The lack of banding is apparent throughout the tooth crown. Dark regions in upper image are preparation artifacts. (Upper image field width = 1,236 μm , inset = 160 μm . Lower image field width = 381 μm , inset = 160 μm).

pating occlusal loads during tree gouging compared with nongouging platyrrhines. Comparisons of relative tooth root surface areas for the anterior teeth between *Callithrix* and nongouging platyrrhines yield mixed results (Table 2). Relative to jaw length, *Callithrix* exhibits larger surface areas as predicted by hypothesis 4 (ANOVA; $F = 5.0$, $P = 0.05$, $df = 11$; Table 2; Fig. 6a). Moreover, *Callithrix* also has more root surface area relative to symphyseal bone volume than nongougers (ANOVA; $F = 26.7$, $P < 0.001$, $df = 11$; Table 2; Fig. 6b). Alternatively, when assessed relative to central incisor length, marmosets exhibit smaller root surface areas on average. This difference in means, however, is not statistically significant as it only approaches significance (ANOVA; $F = 4.4$, $P = 0.07$, $df = 9$; Table 2; Fig. 6c). Unfortunately, the appropriate mechanical scalar for anterior tooth loading

during gouging is unclear. At present, these results suggest that marmosets have larger tooth root surface areas relative to their biting load arm (and potentially overall size); however, based on the observed difference in means noted above, we do not think it appropriate to rule out the possibility that the increased surface area may also reflect in part their relatively elongated anterior teeth.

The relatively large anterior dentition of marmosets is further demonstrated by their significantly higher percentage of tooth root volume relative to symphyseal + tooth root volume versus nongouging platyrrhines (ANOVA; $F = 16.3$, $P = 0.003$, $df = 11$; Table 2; Fig. 7a). Nearly one-half of the symphysis is taken up by the anterior dentition in marmosets compared with approximately one-third in the nongouging species. The impact of their relatively large tooth root volume is further exacerbated by the fact

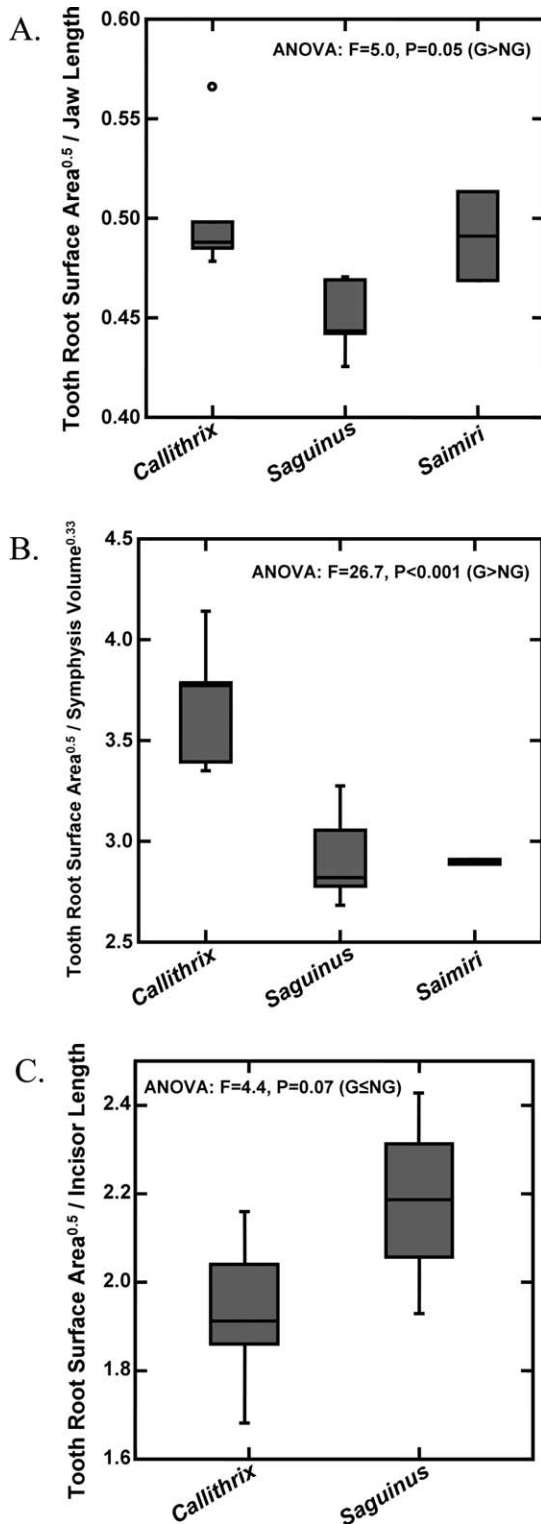


Fig. 6. Boxplots comparing the **A** ratio of tooth root surface area^{0.5} to jaw length, **B** ratio of tooth root surface area^{0.5} to symphyseal bone volume^{0.33}, and **C** ratio of tooth root surface area^{0.5} to incisor length in *Callithrix* and the nongouging *Saguinus* and *Saimiri*. These comparisons provide mixed results as common marmosets exhibit relatively greater surface areas in some comparisons (A and B) but not others (C). (Incisor lengths were not available for *S. sciureus*).

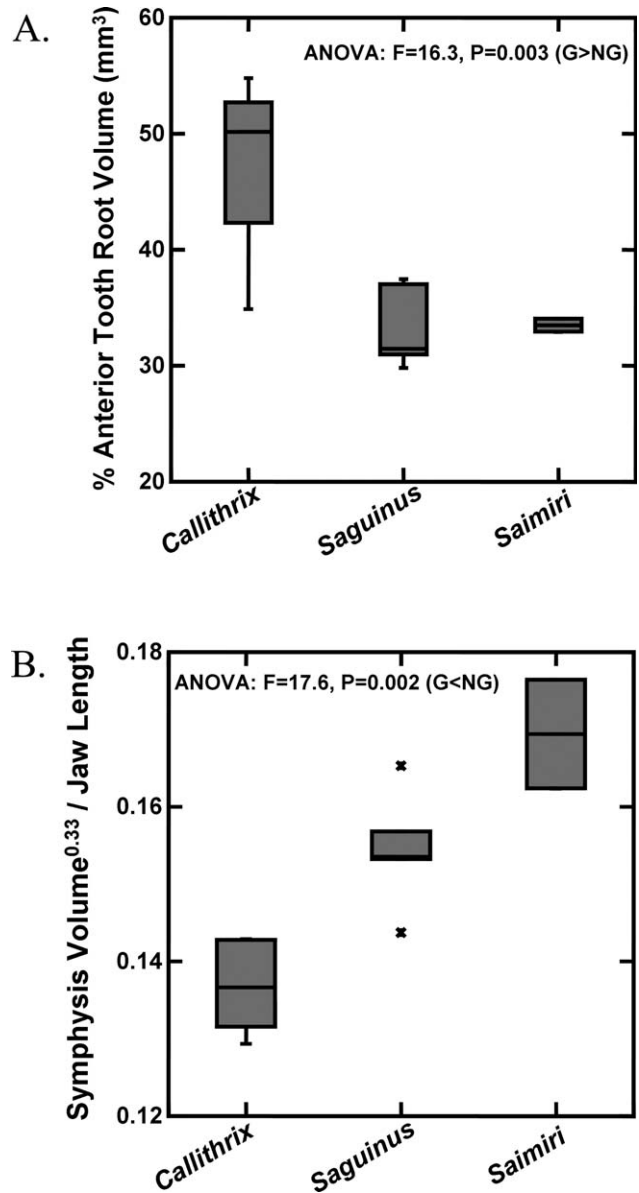


Fig. 7. Boxplots comparing the **(A)** percentage of anterior tooth root volume (relative to tooth root + symphyseal volume) and **(B)** the ratio of symphyseal volume^{0.33} to jaw length in *Callithrix*, *Saguinus*, and *Saimiri*. *Callithrix* exhibits relatively larger anterior tooth root percentages in a relatively smaller symphysis.

that marmosets have significantly smaller symphyseal bone volumes relative to jaw length versus tamarins and squirrel monkeys (ANOVA; $F = 17.6$, $P = 0.002$, $df = 11$; Table 2; Fig. 7b).

Symphyseal Performance during In Vitro Loading

Hypothesis 5 suggests that marmosets will not differ from other platyrrhines in relative symphyseal strength. *Callithrix* demonstrated significantly lower stress values at failure during wish-boning (ANOVA; $F = 6.09$, $P = 0.03$, $df = 13$) and

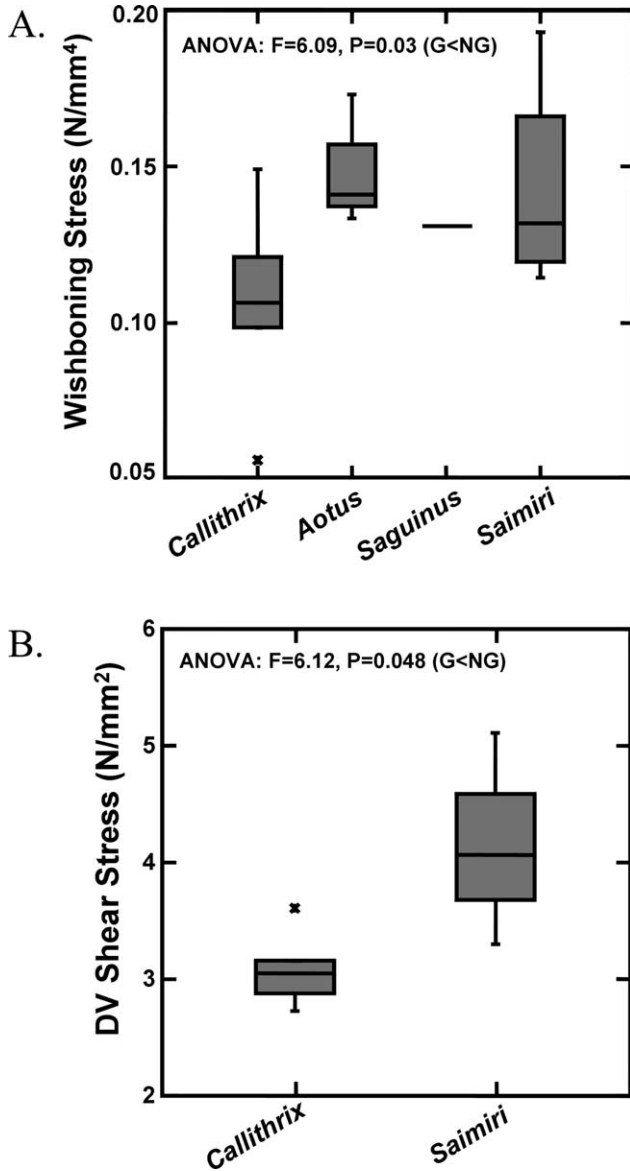


Fig. 8. Boxplots comparing stress at failure during (A) wishboning and (B) DV shear in the symphyses of *Callithrix* and several nongouging platyrrhines. *Callithrix* specimens failed at significantly lower stress levels than nongouging taxa in both in vitro loading regimes.

DV shear (ANOVA; $F = 6.12$, $P = 0.048$, $df = 7$) compared with nongouging platyrrhines (Table 3; Fig. 8). Although these results fail to support the hypothesized similarity in relative symphyseal strength, they corroborate previous morphological comparisons suggesting that marmosets do not possess robust symphyses (Vinyard et al., 2003; Vinyard and Ryan, 2006).

DISCUSSION

Enamel Microstructure and Loading during Tree Gouging in Marmosets

Our findings support prior studies arguing that *Callithrix* has increased its degree of dental enamel

decussation relative to nongouging callitrichines (Kawai, 1955; Shellis and Poole, 1977; Nogami and Natori, 1986; Martin et al., 1988; Propst, 1995; Maas and Dumont, 1999). Although true, we demonstrate that enamel complexity has not increased uniformly across the dentition. When comparing *Callithrix* and *Saguinus*, we observed the largest difference in decussation between the incisors when assessed relative to other tooth types in these callitrichines. We argue that this difference in anterior tooth microstructure is related to the functional role of the anterior dentition during tree gouging in *Callithrix*.

Increased decussation, as observed in marmoset anterior teeth, is argued to protect enamel from fracture by blunting crack propagation (Pfretzschner, 1988; Risnes, 1998; Rensberger, 2000; Popowics et al., 2004; Lucas et al. 2008a,b). Specifically, decussated enamel may require up to a four-fold increase in force to fracture compared with radial enamel (Lucas et al., 2008b). Theoretically, the enhanced enamel organization and extensive Hunter-Schreger banding of marmoset lower incisors and canines should provide increased resistance to elevated internal forces and increased cyclic loads during gouging. In fact, these anterior teeth more closely resemble the highly decussated enamel of hard-object feeding capuchins (*Cebus*; Nogami and Yoneda, 1983; Maas and Dumont, 1999; Hogg, 2010) than nongouging callitrichines. The relatively thickened labial enamel (Hershkovitz, 1977; Rosenberger, 1978, 1992; Gantt, 1980; Nogami and Natori, 1986) and labiolingually thicker incisors of marmosets also likely enhance the load-resisting ability of these teeth.

It is interesting to speculate on the type(s) of internal forces that may compromise anterior dental integrity during tree gouging given that the external bite forces during this behavior do not approach the structural capacity for biting in marmosets (Vinyard et al., 2009). Following recent theoretical work on enamel fracture by Lucas et al. (2008a,b), we argue that gouging large diameter substrates will tend to initiate radial fractures in the enamel near the EDJ at the tooth surface and/or along the imbricational enamel, rather than at the contact point between tooth and substrate. Using Eqs. 2 and 3 in Lucas et al. (2008b), we estimate that the force required to initiate cracks (P_i) at the incisor EDJ as ~ 12 N, whereas forces reaching 678 N are required to propagate cracks through the enamel (P_f). More specifically, $P_i = C_2 \sigma_f t^2 / \log(E_E/E_D)$ and $P_f = C_3 (E_E R)^{0.5} t^{1.5} / \log(E_E/E_d)$ where constants $C_2 = 2$ and $C_3 = 60$, $\sigma_f = 30$ is the fracture stress of enamel, $t = 0.36$ is a minimum estimate of marmoset enamel thickness at the cusp, $E_E = 90$ is the elastic modulus of enamel, $E_D = 20$ is the elastic modulus of dentine, and $R = 13 \text{ Jm}^{-2}$ estimates the toughness of enamel (see Lucas et al., 2008b,c for further discussion of equations and variables). Given maximum bite forces of 35 N during gouging (Vinyard et al., 2009), we predict that marmoset incisors should exhibit arrested cracks

radiating from the EDJ. Because maximum gouging forces are much less than the predicted force for enamel failure (P_f), we argue that decussation and thickened labial enamel in lower incisors likely provide increased fracture resistance to cyclic but not necessarily large magnitude bite forces during gouging.

A second potentially significant loading regime involves bending of the tooth crown during gouging (Fig. 1). Using a standard equation for estimating bending stress (σ_B) in a section, we estimate the maximum bending stress during gouging to approach 38 MPa. Specifically, we apply the equation $\sigma_B = FMaY/I_{xx}$ where $F = 13.7$ as the estimated vertical component of bite force at a maximum gouging force of 35 N, $Ma = 4.03$ mm is the bending moment arm along the incisor crown, $Y = 0.93$ mm is the distance to the neutral axis, and $I_{xx} = 1.33$ mm⁴ is the area moment of inertia for parasagittal bending of the incisor (see Hylander, 1979 for more details). This σ_B estimate exceeds published fracture stress values for enamel ($\sigma_f = 30$ MPa) (Waters, 1980), suggesting that our value is an overestimate (most likely due to our uncertainty in determining the vertical component of the bite force vector during gouging). The proximity of our estimate to the fracture stress of enamel suggests that bending of the crown during gouging is a potentially significant loading regime impacting anterior tooth form. Following on models of Lucas et al. (2008a,b), these bending loads may help explain the extension of Hunter-Schreger bands to the enamel surface. During bending, the moment acting on the alveolar border of the incisor is increased by the elongated crown height coupled with the procumbent incisors of marmosets (Natori and Shigehara, 1992; Rosenberger, 1992; Swindler, 2002). Collectively, the increased labiolingual thickness of the incisor, thickened labial enamel and increased enamel decussation may improve resistance to this localized bending loading regime during gouging.

We also observed enamel decussation extending to the cusp tips in the lower incisors of marmosets. We should clarify that all lower incisor samples for marmosets exhibited some wear at the cusp tips forcing us to speculate that decussation extended the final few millimeters to the unworn cusp tip. We did observe unworn cusp tips in the canines and upper incisors of *Callithrix* and each exhibited complex, irregular decussation. Because radial enamel is argued to resist abrasive wear better than decussating enamel (Rensberger, 2000), the decussation at the cusp tip suggests an increased rate of occlusal wear. We speculate that the decussated enamel promotes increased wear (as well as resists loading) and perhaps helps maintain the geometry of the functional cutting edge with the more rapidly wearing dentine throughout the lifetime of the tooth (see also Rosenberger, 1978). Alternatively, thickened labial enamel in *Callithrix* may also serve to limit the effects of ab-

rasive wear in the incisors while the extensive decussation benefits load resistance ability.

The distinct anterior-posterior patterns in microstructural complexity distinguishing *Callithrix* from *Saguinus* imply that the developmental controls governing enamel microstructure are not constrained along the developing toothrow. Rather, there appears to be varying levels of modularity allowing anterior and posterior teeth to develop with differing degrees and types of enamel complexity. This level of heterogeneity in microstructure along the toothrow is common for many mammals; however, primates have been described as unusually homogenous across their dentitions (Maas and Dumont, 1999). Comparisons of *Saguinus* and *Callithrix* suggest that primates may also "fine-tune" their enamel microstructure according to the differing functional roles performed by specific tooth types.

The relative increase in decussation in the lower anterior teeth of *Callithrix* compared with both their posterior teeth and the anterior teeth of *Saguinus* argues against the hypothesis that increased decussation in marmosets represents a phylogenetic retention from a larger ancestor (Propst, 1995; Maas and Dumont, 1999). Alternatively, the similarity in enamel microstructure in the postcanine teeth of *Callithrix* and *Saguinus* may represent the primitive condition in callitrichines and/or may be linked to the similar mechanical demands related to breaking down the insect chitin of tough-shelled arthropods (Sussman and Kinzey, 1984; Hogg, 2010). Support for the functional hypothesis is provided by research demonstrating that differences in insect exoskeleton toughness and hardness are related to enamel thickness in insectivorous primates and bats (Freeman, 1979; Dumont, 1995; Strait and Vincent, 1998; Evans and Sanson, 2005).

Tooth Size and Shape and Loading during Gouging in Marmosets

We also observed a relative increase in the labiolingual width of the lower incisors of marmosets compared with tamarins. This relatively greater width has two potential functional consequences. As noted above, it provides increased resistance to bending of the incisors during gouging. Second, the increased width may improve wedging ability as the tooth functions like a wedge pushing the bark apart (Hoagland et al., 1972; Vincent et al., 1991; Lucas, 2004; Ang et al., 2006). For gouging, the width of the incisor, along with the coefficient of friction between tooth and substrate, angle of tooth relative to the substrate and size of the substrate combine to affect the external work to fracture (Hoagland et al., 1972; Vincent et al., 1991; Ang et al., 2006). In many of the interactions among these variables, increasing the incisor

labiolingual width can act to reduce the external work required to propagate a crack through a material. By reducing the work to fracture, internal loads throughout the jaw are potentially decreased as the required bite force is reduced. Sharper incisor tips may also help reduce internal loads as they focus the stress on a small region of the substrate during crack initiation. Although purely anecdotal, the increased labiolingual width of marmoset incisors may help them function analogously to chisels that maintain a high bevel angle. For example, scraping chisels are recommended to maintain bevel angles greater than 70° (Lee, 1995) to provide increased control and avoid inadvertent gouging into wood. For marmosets increased control would likely help protect their incisors from unanticipated bending loads during tree gouging.

The tooth roots of *Callithrix* are larger than those of *Saguinus* and *Saimiri* relative to both symphyseal volume and mandibular length. The increase in relative surface area supports the hypothesis that the lower incisors of *Callithrix* provide increased ability to dissipate occlusal forces during gouging (and other behaviors). The interpretation that relatively large incisor roots provide increased load dissipation fit similar interpretations that enamel microstructure and relatively thick incisors provide increased load resistance ability for marmosets.

Alternatively, when considered relative to incisor length, marmoset incisor roots are smaller on average but the *p*-value of 0.07 does not reach statistical significance compared to other platyrrhines. Because of our small sample sizes and potential developmental associations (see below), we take a conservative interpretation in this case by not ruling out a potential influence of overall incisor length on root surface area. If valid, this observation may contradict the interpretation of relatively increased load dissipation given that incisor length can estimate the incisal bending moment arm. These potentially conflicting results make it difficult to interpret the mechanical significance of tooth root morphology in marmosets. First, in vivo observations (Vinyard et al., 2009) suggest that marmoset incisors are bent during gouging. Although bending forces in the tooth will likely be maximized near the alveolar margin, we anticipate that increased bending will be correlated with an overall increase in stress between the tooth root and alveolus. Thus, we are left evaluating the relative importance of the incisal bending moment arm (i.e., incisor length) versus the masticatory load arm during biting (i.e., jaw length) in relation to stress dissipation ability. Given the lack of in vivo data on tooth loading and confounding mechanical variables not considered here, we cannot reasonably choose between these alternatives. The question of the functional significance of marmoset incisor root morphology deserves further consideration and may be appropriate for

both FEA modeling of tooth loading and the tooth-periodontal ligament-bone interface during gouging (e.g., Jeon et al., 1999; Reddy and Vandana, 2005) as well as comparative study of the organization and composition of incisor periodontal ligaments.

A potential alternative interpretation focuses on the developmental consequences of changes in tooth crown morphology for root form. It is possible that the relatively tall crowns in *Callithrix* evolved as adaptations for increased mechanical efficiency during gouging and/or to reduce the impact of tooth wear throughout life (Rosenberger, 1978, 1992; Garber, 1992). Larger roots relative to symphyseal volume could follow as a developmental byproduct of relatively elongated incisors in *Callithrix*. Classical genetic work demonstrates correlations between root and crown phenotypes (Gruneberg, 1951, 1965). Moreover, changes in both crown and root morphology have been observed during manipulation of specific genes in the developing tooth, such as *eda* (Miard et al., 1999; Charles et al., 2009; Tummers and Thesleff, 2009) as well as altered expression of endocrine factors, such as growth hormone (Smid et al., 2007). In particular, recent work has identified regulatory pathways that modulate labial and lingual enamel expression, which are derived in marmosets, and can also impact the size of the crown and root (Tummers and Thesleff, 2009). Similar dental developmental studies do not exist for primates, but interspecific comparisons in primates suggest that root and crown sizes are correlated across species (Kupczik et al., 2009). Although these developmental studies may challenge the hypothesis that selection acted directly to augment root morphology for dissipating loads during gouging, they do not alter the functional consequence for load dissipation.

Symphyseal Morphology and Loading during Gouging

In contrast to the greater load resistance ability seen in several dental features, the mandibular symphysis of marmosets is relatively smaller than that of tamarins, and the incisors occupy a significantly larger percentage of the symphysis. The relatively smaller size and reduced percentage of cortical bone in the marmoset symphysis translate into relatively reduced strength in resisting wish-boning and DV shear. These two loading regimes are hypothesized to generate significant stress in the anthropoid mandibular symphysis during mastication (Hylander, 1984, 1985; Hylander et al., 1998, 2000, 2005). Our morphological comparisons support previous arguments that the marmoset symphysis does not provide increased load resistance compared with nongouging tamarins (Vinyard et al., 2003; Vinyard and Ryan, 2006). The in vitro comparisons of symphyseal strength extend these morphological observations to suggest that

the marmoset symphysis exhibits reduced performance in resisting loads during mastication.

At least two derived features of the marmoset jaw may contribute to their reduced symphyseal strength. First, the relative increase in incisor volume may negatively impact symphyseal strength. A similar argument has been made to explain symphyseal fusion in camelids, which possess large, procumbent incisors that fill the symphysis (Williams et al., 2008). A second potential factor contributing to the relative reduction in strength is the derived "v-shaped" symphysis of marmosets. The increase in symphyseal curvature is argued to assist in effective orientation of the anterior teeth for gouging (see Kinzey et al., 1975; Rosenberger, 1978, 1992). If marmosets experience lateral transverse bending during mastication, then increased symphyseal curvature will result in a higher strain gradient and elevated stress concentrations along the lingual symphysis (Hylander, 1985). When loaded to structural failure in wishboning, the intensification of midline stresses would increase the likelihood that the symphysis fails along the midline at a lower external force. We observed this result during the *in vitro* wishboning tests as most of the marmoset jaws failed at the midline (five of six specimens), whereas only one of the nongouging samples failed at the symphyseal midline (one of eight specimens).

The contrast of reduced symphyseal strength versus the derived features of the anterior dentition and increased symphyseal curvature suggest that the marmoset symphysis has experienced a functional tradeoff. Regardless of whether the changes in marmoset incisor morphology, such as enlarged roots, are adaptations for increased load resistance, the resulting reduction in symphyseal strength persists. Additionally, the reduction of symphyseal bone in marmosets has the functional consequence of reducing symphyseal bone mass and helping to offset the larger, denser incisors (Driessens and Verbeek, 1990) by reducing the muscle force needed to accelerate the jaw during gouging (all other factors being equal).

The spatial juxtaposition of enhanced dental robusticity and depleted symphyseal strength raise the question of how dental loads are transmitted to the symphysis. Multiple studies show that teeth transmit stresses into the surrounding alveolar bone via the periodontal ligaments (Daegling et al., 1992, 2008; Enlow and Hans, 1996; Daegling and Hotzman 2003). The transmitted loads, however, can vary markedly from largely localized to the adjacent alveolar bone to a broader effect on strain patterns throughout a corporal section (Daegling et al., 1992, 2008; Daegling and Hylander, 2000). Thus, it is possible that stresses arising in the dentition may be largely limited to the adjacent alveolar bone,

which could account for the comparative differences in marmoset incisor robusticity versus relatively weak symphyses. Given the behavioral significance of tree gouging for marmosets, the tradeoff in functional capabilities between anterior teeth and symphysis suggests that external forces in the jaw during gouging are not sufficient to demand increased load resistance in the symphysis (Vinyard et al., 2003, 2009; Vinyard and Ryan, 2006). The fact that marmosets' symphyses are relatively weaker than nongougers in loads typically associated with mastication suggests that external forces during mastication have not placed significant demands on symphyseal form versus nongouging platyrrhines.

Mosaic Evolution of the Marmoset Masticatory Apparatus Related to Tree Gouging

Based on the dental microstructural and gross morphological changes, marmoset lower anterior teeth provide increased load-resisting ability compared with tamarins. Given that tree gouging is the primary difference in feeding behaviors between marmosets and tamarins, these results support the hypothesis that marmoset lower anterior teeth are evolutionarily adapted to resist elevated dental loads (or increased number of cyclic loads) during tree gouging. A recent comparative analysis of the articular cartilage in the TMJ identified the anterior glenoid as a second region in the masticatory apparatus that provides increased load resistance ability during gouging (Mork et al., 2010). Alternatively, several previous morphological comparisons have indicated a number of musculoskeletal changes throughout the remainder of the masticatory apparatus that facilitate increased jaw excursion during gouging often at an expense to force generation or load resistance (Vinyard et al., 2003, Taylor and Vinyard, 2004; Vinyard and Ryan, 2006; Taylor et al., 2009; Eng et al., 2009; Ryan et al., 2010). The relatively reduced symphyseal strength during *in vitro* loading in marmosets follow this general trend observed throughout the marmoset jaw.

The contrasting functional capabilities identified in different regions of the marmoset masticatory apparatus point to the potential for varying patterns of loads during tree gouging. Moreover, these varying functional consequences highlight the possibility that the marmoset masticatory apparatus represents a mosaic pattern of adaptive responses to tree gouging. The mosaicism in potential masticatory adaptations along with the functional tradeoffs, such as those observed in the anterior masticatory apparatus, highlight the complexity of evolutionary changes in the masticatory apparatus related to the derived tree-gouging behavior.

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