



## Membrane–plate transition in leaves as an influence on dietary selectivity and tooth form



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### ABSTRACT

Primates need accurate sensory signals about food quality to forage efficiently. Current evidence suggests that they target leaf foods based on color at long-range, reinforcing this with post-ingestive sensations relating to leaf toughness evoked during chewing. Selection against tough leaves effectively selects against high fiber content, which in turn gives a greater opportunity of acquiring protein. Here we consider a novel intermediate mechanical factor that could aid a folivore: leaves may transform mechanically from membranes (sheets that cannot maintain their shape under gravitational loads and thus 'flop') early on in development into plates (that can maintain their shape) as they mature. This transformation can be detected visually. Mechanical tests on two species of leaf eaten by southern muriqui monkeys (*Brachyteles arachnoides*) in Southern Atlantic Forest, Brazil, support a membrane-to-plate shift in turgid leaves during their development. A measure of this mechanical transition, termed lambda ( $\lambda$ ), was found to correlate with both leaf color and toughness, thus supporting a potential role in leaf selection. Muriquis appear to select membranous leaves, but they also eat leaves that are plate-like. We attribute this to the degree of cresting of their molar teeth. A dietary choice restricted to membranous leaves might typify the type of 'fallback' leaf that even frugivorous primates will target because membranes of low toughness are relatively easily chewed. This may be relevant to the diets of hominins because these lack the bladed postcanine teeth seen in mammals with a specialized folivorous diet. We suggest that mammals with such dental adaptations can consume tougher leaf 'plates' than others.

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### 1. Introduction

Food selection by animals is thought to be based on a chain of sensations that act from long to close range, drawing an individual towards potential food items and progressively differentiating them from surrounding scenery (Dominy et al., 2008c). Utilizing such a series of sensory cues increases the probability that an animal can ingest items with desirable nutrient content (Dominy et al., 2001). For leaves, color is thought to be an important long-distance foraging cue, particularly the red–green signal that trichromatic primates are capable of differentiating (Dominy and

Lucas, 2001; Frey et al., 2011). Such prior information at longer range can be reinforced by the textural assessment of toughness that an animal obtains during ingestion and fracturing of a leaf. This is a signal of great importance for both vertebrate and invertebrate herbivores in a much broader ecological context (Onoda et al., 2011): toughness is positively correlated with fiber content (Choong et al., 1992; Hill and Lucas, 1996; Lucas et al., 2000), but negatively with leaf protein content (Dominy and Lucas, 2001). A common assumption in the literature is that leaf choice by primates, and many other herbivores, involves the selection of 'young' leaves because of their high protein-to-fiber ratio (Milton, 1979; Chapman et al., 2002). However, this is clearly behavioral short-hand because there is no evidence that a primate or any other animal monitors leaf cohorts in terms of an age criterion.

Time is of the essence because the developmental period of leaf expansion in the tropics is so short. Depending on the species, the

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entire period of expansion ranges from 7 to 21 days, while average leaf lifespan, in contrast, is 3 years (Coley and Barone, 1996). So, without considering phenology, perhaps only 1% of the vegetation that forms the visual background in a forest might be classifiable as 'young.' This percentage covers leaves of virtually all developmental states. At some stages, 'young' leaves may be highly chemically-defended (Coley, 1983) and, thus, not considered as potential food by primates. Some may be bereft of nutrients because tropical leaves often delay the activation of their photosynthetic apparatus until full expansion (Kursar and Coley, 1992). At full expansion, a tough venous network has been developed, at which point chemical defenses seem to diminish (Choong, 1996; Coley and Barone, 1996). Thus, the window of feeding opportunity for an herbivore may be much smaller than the term 'young' suggests. The window may open at the point when chemical building blocks are being transported into the leaf to build up the cell walls, but unless a mammalian herbivore has the dentition to deal with rapidly increasing toughness, it may close quickly (Lucas et al., 1998). If a primate can learn a series of sensory cues leading it to leaves within this window, then it must have a competitive advantage. Toughness is a mechanical cue that helps during actual feeding because young leaves have low toughness and, thus, fracture more easily (Coley, 1983). Leaf color and toughness are linked in developing leaves, although the actual color depends on whether a species has a 'red' phase, which many tropical leaves possess (Lucas et al., 1998; Dominy, 2004). However, toughness is only detectable after a leaf has been fractured with the teeth, thus leaving a large time gap between visual and textural assessments.

To address this, we describe a mechanical characteristic of leaves that can be detected visually prior to ingestion and that could add a missing link into the behavioral chain. The central idea is that sheet materials under load, such as leaves, may behave either as plates, which can be thought of as laterally-expanded beams that deform via bending that involves tension and compression, or else as membranes that deform only by stretching (Fig. 1A). A considerable amount of theory has been developed to describe the mechanical behavior of such structural elements (Timoshenko and Woinowsky-Krieger, 1959; Ventsel and Krauthammer, 2001), in which the term 'membrane' is equivalent in most respects to a flat 'shell' in mechanical theory. The practical difference between plates and membranes is that the latter can easily be folded or crumpled in a ball; left alone, they cannot retain their shape under gravitational load and flop (Atkins and Mai, 1979; Atkins, 2009). However, if they are thickened or stiffened sufficiently, they bend like plates. The behavior of a single sheet of newsprint versus a whole newspaper illustrates the difference between the two. Floppiness is visually apparent in forest leaves at short distances, sometimes due to wilting, but always as a sign of flushing. Flushing leaves are likely to be membranous because their venation is too undeveloped to maintain leaf position. In contrast, mature leaves of the 'dorsoventral' type have a well developed venation that makes them plate-like, even without any increase in lamina thickness, allowing them to be held at optimum angles for sunlight absorption (Falster and Westoby, 2003). Recent advances in materials testing have led to a novel load relaxation test that distinguishes membranes from plates (Scott et al., 2004; Aherne et al., 2005; Komaragiri et al., 2005; Oyen et al., 2008; Chua and Oyen, 2009). Here, we have modified this test for field research on leaves to help establish our main hypothesis, which is that during development, leaves cross the membrane-plate boundary. However, this paper also focuses on folivory. Although the category is based on leaf-eating, its umbrella encompasses the consumption of many structural parts of plants such as stems, pith, and shoots. These rod-shaped foods behave very differently under load to sheet-like leaves (van Casteren et al., 2016), but they can also be eaten extensively by African great apes (Fossey and Harcourt,

1977; Watts, 1984; Wrangham et al., 1991; Malenky and Wrangham, 1994; Rothman et al., 2007) and by grazing ruminants (Poppi et al., 1981). The large  $C_4/CAM$  plant component of many fossil hominin diets (Cerling et al., 2011, 2013; Lee-Thorp et al., 2012; Wynn et al., 2013) suggests a very different diet to that of great apes that live in  $C_3$ -dominated habitats. Yet with the exception of underground storage organs (Hatley and Kappelman, 1980; Lucas et al., 1985; Laden and Wrangham, 2005; Dominy et al., 2008b; Wrangham et al., 2009), many suggested hominin foods listed in Peters and Vogel (2005) and van der Merwe et al. (2008) could also be classified as a type of 'folivory.'

Mammalian folivores, such as browsing and grazing ungulates (Archer and Sanson, 2002), generally have postcanine teeth with many sharp ridges and crests. Tallies of these features indicate the degree of folivory (Kay, 1978; Kay and Covert, 1984; Lister and Joysey, 1992; Evans et al., 2007), with high counts typifying the teeth of, for example, equids, rhinoceroses, tapirs, elephants, colobine monkeys, and bovids. The teeth of hominins have low scores (Kay, 1985), so it might be doubted that they could have eaten a folivorous diet (Teaford and Ungar, 2000). This seems entirely relevant to the finding that the teeth of some fossil hominins appear poorly adapted to chew foods that microwear and isotopic analyses indicate were prominent in their diets (Grine et al., 2012). However, judgment of such an anatomical-behavioral mismatch must depend greatly on knowledge of the dentition and diet of living primates. The problem at the moment is an imbalance: much more is known about primate teeth (in terms of their shape, size, structure, and mechanical properties) than about equivalent aspects of primate diets. The result is that intricate measurements of tooth form tend to be analyzed in terms of gross dietary classifications that may be irrelevant to the mechanical behavior of foods and thus to the selective pressures ultimately acting on the teeth.

Here, to test the applicability of our mechanical theory, we studied two leaf species consumed by Southern muriqui (*Brachyteles arachnoides*) monkeys. The molar dentition of muriquis has a large 'shearing quotient' (Anthony and Kay, 1993) and could thus be thought of as highly folivorous. To relate this study to previous efforts on sensory aspects of leaf foraging (Dominy and Lucas, 2001; Lucas et al., 2003), we also measured the reflectance spectra of these leaves, in order to construct models of color and toughness. Any correlations between these measures and the membranous state of leaves could support a reinforcing chain of long- to short-range sensory cues for a foraging primate. We also investigated whether the study primate appears to show any mechanical preference for membranes or plates. Our overall aim in initiating this work is to try to understand what it is about the mechanical behavior of leaves to which a dentition needs to adapt, and to establish a behavioral basis for dental-dietary adaptation in generalist feeders like primates. The current investigation is intended as a start towards this.

## 2. Materials and methods

### 2.1. Field site and materials

The study was conducted at the Parque Estadual Carlos Botelho (PECB; 22°44–24°03 S, 47°46–48°40 W) within the long-term study area of fully habituated Southern Muriquis (*B. arachnoides*) in the southern region of São Paulo State (19°48 S, 40°07 W; Talebi and Lee, 2010; Coles et al., 2012). The muriqui diet in the study area is well known. These primates are not primarily folivorous, but they eat significant amounts of leaves when fruits are unavailable (Talebi et al., 2005). Samples of leaves of two tree species that muriquis were consuming at the time of study, *Nectandra oppositifolia* (Lauraceae;  $n = 45$ ) and *Guapira opposita* (Nyctaginaceae;  $n = 49$ ),

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