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Craniodental biomechanics and dietary toughness in the genus *Cebus*

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Abstract

The tufted capuchin (*Cebus apella*) has been used in a number of comparative studies to represent a primate with craniofacial morphology indicative of hard-object feeding. Researchers have specifically referred to the tufted capuchin as a seed predator. Craniofacial features exhibited by the tufted capuchin, such as thick cortical bone in the mandibular corpus and symphysis, and a broad face associated with large masticatory muscles, permit the production and dissipation of relatively high masticatory forces. These morphologies, however, cannot distinguish between the tufted capuchin's propensity to exert higher forces when opening food with its anterior dentition or with its cheek teeth. It is also unclear whether these are adaptations for biting or chewing foods. This study uses a constrained lever model to compare the masticatory adaptations of *C. apella* to other cebids and atelids. Results show that the temporalis and masseter muscles in *C. apella* and *C. olivaceus* are more anteriorly positioned relative to nine other platyrrhine taxa. This condition, which appears to be ancestral among the Cebinae, increases force production at the incisors and canines while compromising third molar function. *Cebus apella*, has exaggerated this pattern. Field data on dietary toughness show that both capuchins typically select foods of low toughness, but on occasion, *C. apella* ingests food items of exceptional toughness. Thus, *C. apella* appears to maintain these biomechanical relationships by producing particularly high but relatively infrequent bite forces, particularly at the incisors and canines. However, adaptations for anterior dental use do not tightly constrain the diet of *Cebus apella*. This approach can be used to clarify the dietary adaptations of fossil taxa.

Keywords: constrained lever model; dietary toughness; food processing; biological role; Platyrrhini

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Introduction

A major goal of functional morphology and paleobiology is to identify clear associations between ecology and morphology. Attempts to relate masticatory morphology to diet in primates have compared variation in mandibular or tooth morphology with the percentage of different food types in the diet (Kay, 1975, 1981; Smith, 1983; Smith et al., 1983; Peters, 1987; Anapol and Lee, 1994). A major improvement to this traditional approach has been the investigation of plant tissue mechanics and their relationship to tooth form (Lucas and Luke, 1984; Kinzey and Norconk, 1990; Hill and Lucas, 1996; Yamashita, 1996). It has been argued from these analyses that certain craniodental features indicate the ingestion of relatively high proportions or particular types of food. These studies fulfill part of Bock and von Wahlert's (1965) criteria for studies of adaptation by identifying the biological role(s) of morphological faculties (i.e., features + functions).

Relationships between masticatory morphology and the mechanical properties of food are mediated by processing behavior (Rosenberger, 1992; Ungar, 1992, 1999; Ungar and Teaford, 1996; Lauder, 1996). Processing behavior shapes the stresses that a primate's jaws and teeth must endure. For example, a fruit may be breached by applying enough bite force to produce catastrophic failure of its hardest external tissues, a method that has been suggested for the tufted capuchin (Terborgh, 1983). Fruit, however, may also be breached by using the incisors as a wedge to separate plant fibers depending on the mechanical properties of exocarp tissues. The procumbent incisors of pitheciines have been argued to play such a role (van Roosmalen et al., 1988; Kinzey, 1992).

Few studies have focused on the relationship between the leverage of the jaw adductor and details of food processing behavior in primates and mammals (Spencer and Demes, 1993; Anapol and Lee, 1994; Spencer, 1998, 1999; Dumont and Herrel, 2003; Thompson et al., 2003). The aim of this study is to examine the relationship between food processing behavior and craniofacial morphology. This study focuses on members of the genus *Cebus*, particularly the tufted capuchin (*Cebus apella*) because it has been widely cited as an avatar of hard-object feeding (Kinzey, 1974; Kay, 1981; Masterson, 1996). The presence of thick molar enamel, relatively large temporalis and masseter muscles, wide and deep mandibular corpora and symphyses, and thick cortical bone in the corpus and symphysis of the mandible in all observed *C. apella* have been argued to be causally associated with the exploitation of such foods (Kay, 1981; Cole, 1992; Daegling, 1992; Masterson, 1996).

The present study uses the approach initially developed by Greaves (1978) in a study of selenodont artiodactyls, and further refined by Spencer and Demes (1993) in a study of archaic and modern hominins. This approach allows evaluation of four central questions:

1) Is the mechanical advantage of the masticatory muscles greater in the genus *Cebus* than in other platyrrhines?
2) Is the mechanical advantage of the masticatory muscles greater in *Cebus apella* than in *C. olivaceus*?
3) Does increased leverage for the jaw adductors account for third molar reduction and agenesis in *Cebus* given predictions derived from the constrained lever model of masticatory function?
4) Are changes in anterior dental loading associated with differences in the toughness of foods processed with the anterior and postcanine dentition?

Answers to these questions help clarify important functional differences between two closely related primates (Masterson, 1996) and suggest the agents that may have selected for the derived craniodental complex exhibited by *C. apella*. This study offers an approach that will help refine our understanding of the food processing behavior of fossil primates.

Background

Cebus trait polarity

It is necessary to identify the polarity of craniodental features within *Cebus* in order to