Journal of Human Evolution 55 (2008) 1118–1137

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

# Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals

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ARTICLE INFO

*Article history:*
Received 22 January 2008
Accepted 13 August 2008

*Keywords:*
μCT
Functional morphology
Laser scan
Primate evolution
Shearing quotient
Teeth
Lemurs

ABSTRACT

This study describes and tests a new method of calculating a shape metric known as the relief index (RFI) on lower second molars of extant euarchontan mammals, including scandentians (treeshrews), dermopterans (flying lemurs), and prosimian primates (strepsirhines and tarsiers). RFI is the ratio of the tooth crown three-dimensional area to two-dimensional planar area. It essentially expresses hypsodonty and complexity of tooth shape. Like other measurements of complexity, RFI ignores taxon-specific features, such as certain cusps and crests, which are usually considered in more traditional studies of tooth function. Traditional statistical analyses of the study sample show that RFI distinguishes taxa with differing amounts of structural carbohydrates in their diets, with frugivore/gramnivores being significantly lower in RFI than omnivores, and insectivores/folivores being significantly higher in RFI than the other two. Information on absolute size, or body mass, is needed to reliably parse out insectivores and folivores; however, if the study sample is limited to Primates, RFI alone distinguishes many folivores (lower) from insectivores (higher). Finally, phylogenetically independent contrasts of RFI and dietary preference are strongly correlated with one another, indicating that variance in RFI is better explained by dietary diversity than phylogenetic affinity in this sample. Because of the accuracy and phylogenetic insensitivity of the RFI among Euarchonta, this method can be applied to fossil primates and stem-primates (plesiadapiforms) and used to elucidate and compare their dietary preferences. Such comparisons are important for developing a more detailed view of primate evolution.

## Introduction

The goals of the current study are (1) to establish a new method for creating digital tooth-crown models from which to analyze the relationship between variance in tooth form and differences in dietary preference, and (2) to evaluate the utility of one particular tooth-shape metric in reconstruction of basic aspects of diet in euarchontans. Euarchonta is a supraordinal grouping that includes Dermoptera, Scandentia, and Primates as its extant members, as well as fossil plesiadapiforms (probable stem-primates; Bloch et al., 2007) and various other extinct taxa (Silcox et al., 2005). Because Euarchonta includes the closest living and fossil relatives of Primates, an understanding of the relationship between skeletal morphology, function, and ecology in this group is critical for understanding evolutionary origins of the order to which humans belong (Bloch et al., 2007; Sargis et al., 2007).

Dietary preference in fossil mammals has been a focus of investigations by paleontologists and paleoanthropologists because it is a primary ecological parameter, and thus relevant to understanding evolutionary histories (e.g., Gregory, 1922; Gingerich, 1974a,b; Kay and Cartmill, 1977; Grine, 1986). It is recognized that aspects of teeth should be salient reflectors of diet, because they are responsible for harvesting food resources and preparing them for digestion (e.g., Simpson, 1936; Kay and Hiemae, 1974; Ungar, 1994; Lucas, 2004). Ungar (2002) reviewed two types of tooth features that reflect diet: “adaptive” features—morphology that has a genetic basis and which can therefore be a target of natural selection, and “non-adaptive” features—morphology and properties that result from the interaction of the tooth with its’ environment during the lifetime of the animal. This study focuses on potentially-adaptive morphology (tooth-crown shape), because ultimately the influence of ecology on morphological evolution through natural selection must be elucidated from an understanding of such form-function relationships (Evans et al., 2007b). “Non-adaptive” features of teeth that relate to diet include macrowear (e.g., Butler, 1973; Meikle, 1977; Seligsohn and Szalay, 1978; Janis, 1984), mesowear (e.g., Fortelius and Solounias, 2000), microwear (e.g., Rensberger, 1978; Teaford and Walker, 1984; Strait, 1993c; Ungar, 1996; Godfrey et al., 2004; Semprebon et al., 2004), and stable isotope signatures (e.g., MacFadden and Cerling, 1996; Cerling et al., 1997).

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doi:10.1016/j.jhevol.2008.08.002

It has long been recognized that differences in tooth form (shape and size) reflect differences in dietary preference. Kay (1975) summarized an early documentation of such observations by Aristotle and subsequent historic developments in the study of dental functional morphology. It is generally thought that particular tooth forms are suited to processing essential food items of respectively particular forms and material properties (Kay, 1975; Lucas, 1979, 2004). At the same time, mammalian teeth/dentitions are often unique taxonomic identifiers (e.g., Szalay and Delson, 1979; Rose, 1981; Hillson, 1990). Thus, it is recognized that studies of the ecological significance of tooth form must take into account taxonomic/phylogenetic systematic sources of variance and vice versa (e.g., Kay, 1975). Studies that examine adaptive and non-adaptive parameters simultaneously are useful because they may reveal phylogenetic differences in the correspondence between diet and aspects of tooth form, inasmuch as the ecological correspondence between features, such as microwear and diet, are constant (Ungar et al., 2004). However, even so-called "non-adaptive" morphology is a function of the material properties of dental tissues, which are under genetic control to a potentially important degree (Maas and Dumont, 1999).

Dietary inferences from teeth were historically, and still recently, often done qualitatively (e.g., Gregory, 1922; Szalay, 1968; Gingerich, 1974a,b; Godinot and Mahbouti, 1992): fossil taxa possessing apparently lower-crowned teeth are generally interpreted as having eaten "brittle" foods that require crushing (most fruits and nuts), but not puncturing or slicing. Teeth that have long blades that are reciprocally concave are understood to be effective at fragmenting foods that are tougher, more ductile, or more generally speaking, in which cracks are not self-propagating (leaves and most insects). Teeth with tall cusps are said to allow puncturing of hard carapaces sported by insects, such as beetles (Coleoptera; Kay, 1975; Strait, 1993b; Evans and Sanson, 1998). It has been further recognized that simple dietary categories, such as "frugivore," "folivore," and "insectivore," may not always sufficiently explain functional variation in tooth morphology due to differential and overlapping material properties of different foods eaten by animals in these basic categories (Lucas, 1979; Strait, 1993b; Lucas and Teaford, 1994; Strait, 1997). Indeed, work by Lucas (2004) elegantly outlines the mechanical basis for different tooth forms as a product of the interaction between these forms, their intrinsic material properties, and those of the food resources they process. However, studies have found that among lemurids, tooth form correlates with dietary categories better than food material properties in some cases (Yamashita, 1998). Furthermore, it can be argued that these categories often *do* correspond to distinct differences in food material properties (Kay et al., 1978, 2002). Specifically, diets of "insectivores" and "folivores" are high in structural carbohydrate, which are more ductile than brittle and respond well to shearing (Ungar, 2002).

Kay (1975) ushered in an era of quantifying functional aspects of tooth shape. For instance, he showed that scaling relationships of molar tooth size, as well as lengths of various molar crests, to body mass differed among living primate groups representing different dietary preferences. He further showed that multivariate analyses of various size-standardized tooth measurements effectively discriminate frugivorous from insectivorous and folivorous non-cercopithecoid primates (Kay, 1975; Kay et al., 1978). The most successful and widely-used quantitative method for dietary reconstruction, developed and demonstrated on many groups of primates by Kay and colleagues (e.g., Kay, 1978; Kay and Hylander, 1978; Kay and Covert, 1984; Anthony and Kay, 1993; Kirk and Simons, 2001), is the shearing quotient. Shearing quotients are residuals from a regression of the sum of shearing surface lengths on a given tooth and the mesiodistal length of the same tooth. Living taxa with relatively long shearing crests have positive residuals and tend to be folivorous or insectivorous. Those with shorter blades are omnivores, frugivores, and gramnivores. The shearing quotient is a better discriminator of diet than metrics based on single crest lengths (Kay, 1975), apparently because the total shear surface of a tooth is less affected by phylogenetic differences than lengths of individual crests. It is preferable to principle component/coordinate scores of multivariate methods because the morphological meaning of its' values is more straightforward. Strait (1993a) has demonstrated a similar method to be effective in distinguishing insectivorous bats, marsupials, and primates from their more frugivorous close relatives. She has also argued that "hard object" feeding insectivores have less shearing development than "soft object" feeding insectivores (Strait, 1993b). Furthermore, Hogue (2004) argued that there is a correlation between percentage of dietary structural carbohydrate and shearing quotient in a sample of 65 marsupial taxa. King et al. (2005) showed that shearing surface length is robust to changes in tooth form due to wear in a longitudinally studied population of indriids.

A drawback of the method is that it still appears to be phylogenetically specific compared to multivariate methods (e.g., Kay, 1975; Kay et al., 1978). For example, even though folivorous strepsirhine primates and folivorous hominoids have longer crests than their more omnivorous close relatives (Ungar and Kay, 1995; Kirk and Simons, 2001), as a group, hominoids have longer crests than strepsirhines. As a specific example, if a shearing quotient is calculated with data on *Avahi*, the highly-folivorous woolly lemur, from Kirk and Simons (2001) using the hominoid equation from Ungar and Kay (1995), *Avahi* is shown to have a negative shearing quotient ($-1.1$), like hominoid frugivores. This is in contrast to a highly positive quotient obtained using an equation based off of a sample of strepsirhines (14.73). As another example, the offset increases when one looks to folivorous cercopithecoids that have even relatively longer crests than folivorous hominoids (Kay and Covert, 1984). Likewise, some taxa are poorly predicted by this metric even when the equation is based on their close relatives. *Lepilemur*, which is known to be a committed folivore, has a highly negative residual ($-14.29$) and is reconstructed as a frugivore by the method (Kirk and Simons, 2001). In fact, it is notable that *Lepilemur* and *Avahi* are nearly ecological analogues, but fall out on opposite ends of the shearing quotient spectrum. The most dentally-derived taxon among strepsirhines (*Daubentonia*) actually lacks the necessary measurement landmarks and cannot be formally included in analyses using this method (but see Kay, 1975). Another problem with shearing quotients is that measurement accuracy decreases with tooth wear as landmarks (cusp tips and crests) are eroded away (Teaford, 1981).

New methods using digital imagery of tooth crowns to calculate metrics that describe the occlusal surface as a complex landscape are promising (Reed, 1997; Jernvall and Selanne, 1999; Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; Dennis et al., 2004). For example, Ungar and M'Kirera (2003) presented data on variables, such as angularity and average slope of the occlusal surface. These studies have focused on identifying shape parameters that are maintained in spite of progressive tooth wear (Dennis et al., 2004). Additionally, M'Kirera and Ungar (2003) showed that a relief index—the ratio of the surface area of the enamel crown to the area of the crown's projection into an occlusal plane (measured from laser scan data) —distinguished *Gorilla gorilla* (a more folivorous taxon) from a closely-related less folivorous taxon, *Pan troglodytes*. They explained that a tooth that has a tall crown, long crests, and/or tall cusps has more crown area relative to its planometric occlusal area, and thus, a higher relief index than teeth that are shorter and flatter (Fig. 1). Ungar (2004) compared these data to a sample of *Australopithecus afarensis* and early *Homo* in order to comment on dietary diversity in fossil hominids.