Impact of Ecology on the Teeth of Extant Lemurs:

A Review of Dental Adaptations, Function, and Life History

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INTRODUCTION

Lemur dental morphology has been characterized by a number of workers (e.g., Godfrey et al., 2004a; Kay et al., 1978; Milton, 1978; Sauther et al., 2001; Schwartz and Tattersall, 1985; Seligsohn, 1977; e.g., Seligsohn and Szalay, 1974, 1978; Strait, 1993; Tattersall, 1982; Yamashita, 1998a,b) who have investigated these teeth from descriptive, functional, developmental, and ecological perspectives. In this chapter, we discuss how the external environment leaves an imprint on lemur dentitions, either through adaptations to the physical requirements of specific environments or through environmental effects during the lifetime of the animal. We also discuss the patterns of intraspecific dental variation in selected lemurs, and comment on the role of this variability in lemur taxonomy.

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In addition, we briefly review the relationship between dental microstructure, growth and development, and ecology.

The chapter begins with an introductory section describing the major issues that concern us from functional and ecological perspectives, including a brief review of dental development and microstructure. We then discuss anterior and posterior teeth in separate sections, each describing basic morphology, functional morphology, and indicators of dental health. Throughout this chapter, we refer to examples from the lemur community at the Beza Mahafaly Special Reserve, southern Madagascar (see Sussman and Rakotozafy, 1994, for a description of the reserve at Beza Mahafaly), a location at which each of us has conducted long-term research.

Diet and Tooth Morphology

Primates, like most mammals, possess heterodont dentitions, with virtually all taxa having incisors, canines, premolars, and molars (see reviews in Martin, 1990; Swindler, 2002; Tattersall, 1982). Living lemurs also share the derived tooth-comb with other members of the Strepsirhini (the aye-aye [*Daubentonia madagascariensis*] is the one exception [e.g., Martin, 1990; Swindler, 2002; Tattersall, 1982]). Despite sharing a common heritage likely resulting from a single ancestral colonization of Madagascar (e.g., Karanth et al., 2005; Yoder, 1994), the Malagasy lemurs display considerable variation in dental morphology across their radiation. In addition to expected differences in gross morphology and topography of the teeth, there are differences in tooth formulae. As seen in Table 1, the maximum primate dental formula of $I_2^2 C_1^1 P_3^3 M_3^3$, a derivation of the ancestral placental mammal condition, is present in most lemurs, with secondary reductions in the indriids, *Lepilemur*, and *Daubentonia* (Martin, 1990).

In any discussion of functional relationships between diet and tooth form, the physical properties of foods play an important role. The primary function of teeth is to reduce food particle size for further digestion in the gut. This physical interaction occurs between foods of varying compositions and teeth that have designs suitable for efficiently breaking down those foods. Relationships between tooth morphology and the physical parameters of foods in primates have been well documented (Happel, 1988; Hiiemae and Crompton, 1985; e.g., Hylander, 1975; Kay, 1975, 1977, 1978; Kinzey and Norconk, 1990; Lucas, 1979, 2004; Maier, 1984; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Strait, 1993; Wright, 2003; Yamashita, 1998b).

How a food fragments depends on its composition. Physical properties of foods include external properties, such as size and shape, and internal properties that are related to material composition (see Lucas, 2004, and Strait, 1997, for extended discussions). Fragmentation depends on the ability of the consumer to initiate and continue runaway crack formation in foods with particular mechanical properties. Tough foods are able to deform considerably before failing and

Table 1. Dental formulae for extant lemurs

Taxon	Dental formula[a]	Total number of teeth
Lemuridae		
Eulemur	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Lemur	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Hapalemur	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Varecia	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Cheirogaleidae		
Cheirogaleus	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Microcebus	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Phaner	$I^2 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	36
Lepilemuridae		
Lepilemur	$I^0 \, C^1 \, P^3 \, M^3 / I_2 \, C_1 \, P_3 \, M_3$	32
Indriidae		
Propithecus	$I^2 \, C^1 \, P^2 \, M^3 / I_2 \, C_0 \, P_2 \, M_3$	30
Indri	$I^2 \, C^1 \, P^2 \, M^3 / I_2 \, C_0 \, P_2 \, M_3$	30
Avahi	$I^2 \, C^1 \, P^2 \, M^3 / I_2 \, C_0 \, P_2 \, M_3$	30
Daubentonidae		
Daubentonia	$I^1 \, C^0 \, P^1 \, M^3 / I_1 \, C_0 \, P_0 \, M_3$	18

[a] Data compiled from Martin (1990), Swindler (2002), Tattersall (1982).

are good at arresting cracks once they start. Brittle foods are the opposite; they propagate cracks readily once they are initiated. Elastic modulus is a measure of stiffness or resistance to bending. Hardness is resistance to indentation. The relationship between toughness (R) and elastic modulus (E) describes how plants mount mechanical defenses against herbivory (Agrawal et al., 1998; Lucas, 2004; Lucas et al., 2000). Stress-limited foods ($\sqrt{ER}$) are brittle and shatter when sufficient stress levels are reached. A plant that invests in this type of defense relies on herbivores being unable to generate the required force to fragment it. Displacement-limited defenses ($\sqrt{R/E}$) depend on predators being unable to strain the plant part to failure (Agrawal et al., 1998). Thin materials, such as leaves, tend to rely solely on toughness as a defense.

In order for herbivores to overcome physical plant defenses, it would be advantageous for them to possess morphologies that are suitable for fragmenting plant parts with distinct mechanical properties. Tough foods should require bladed features to initiate and guide crack formation since they do not easily propagate cracks. The carnassial teeth of carnivores represent a bladed system for fracturing soft, tough foods. Flat, tough foods such as leaves also require crests, though in a configuration that resembles a "milling machine" (Hiiemae and Crompton, 1985). Hard/brittle foods are best fractured with blunt cusps that can tolerate the high stresses involved in overcoming stress-limited defenses. In addition, fine reduction of hard foods would be made easier with a loose occlusal fit between a cusp and basin to locate weak areas in the food (Lucas, 1979). In this chapter, we examine this relationship between tooth form and diet in the varied dentition of lemurs.

Dental Development and Microstructure

In addition to variation in tooth form and function, lemurs display a wide variety of dental developmental patterns. In fact, lemur dental development often does not "play by the rules" with the quickest pace of tooth formation and eruption sometimes occurring among the largest forms, a pattern which contrasts with the general pattern seen in anthropoid primates (e.g., Godfrey et al., 2005, this volume; Schwartz and Godfrey, 2003; Schwartz et al., 2002). Of note, patterns of dental development appear linked to phylogeny, with extinct, large-bodied relatives of smaller living forms (e.g., *Propithecus* and *Palaeopropithecus*) sharing similar patterns of development, despite significant differences in body size (e.g., Godfrey et al., this volume; Schwartz and Godfrey, 2003; Schwartz et al., 2002). Dental development also corresponds to diet and feeding ecology, with noticeable differences between sympatric folivorous and more frugivorous and/or omnivorous lemurs, for example *Propithecus v. verreauxi* and *Lemur catta*, in terms of the pace of dental eruption (e.g., Eaglen, 1985; Godfrey et al., 2001, 2004a). In fact, specialized folivores such as *Propithecus* display early and rapid dental eruption, often possessing a number of erupted deciduous teeth at birth (Eaglen, 1985; Godfrey et al., 2001, 2004a; Schwartz et al., 2002, 2005).

As with morphology and dental development, dental microstructure reflects the feeding ecology of extant (and fossil) lemurs. When compared to anthropoids, lemurs (and extant prosimians in general) possess relatively thin dental enamel (e.g., Godfrey et al., 2005; Martin et al., 2003; Shellis et al., 1998). Because enamel thickness generally corresponds to diet among primates (although not a perfect relationship [e.g., Maas and Dumont, 1999; Martin et al., 2003]), Shellis et al. (1998) argued that, given their thicker enamel, the diet of anthropoids likely consists of a higher proportion of tough foods than does that of prosimians. As seen in Table 2, only highly derived forms such as extant *Daubentonia* and the large, subfossil *Archaeolemur*, both of which are quite specialized in their dietary adaptations, possess thick enamel, comparable to well-known hard-object feeders, for example the extant New World capuchins (*Cebus*) (e.g., Godfrey et al., 2005) and the fossil hominid *Paranthropus* (e.g., Teaford and Ungar, 2000). Maas (1994) suggested that thin enamel is the primitive condition for lemurs. The rarity of thick-enameled lemurs supports this suggestion.

In addition to enamel thickness, the structure and organization of enamel also reflects dietary adaptations. Along with their thin enamel, extant lemurids exhibit significant enamel decussation (i.e., differentially oriented enamel prisms [Janis and Fortelius, 1988]), with up to 90% of the enamel in *Varecia*, *L. catta*, and *Eulemur macacao* consisting of these prisms (Maas, 1994). Enamel decussation is thought to provide resistance to crack propagation, and often correlates with diets dominated by hard foods (Godfrey et al., 2005; Maas and Dumont, 1999; Martin et al., 2003). Despite the dietary variability exhibited by extant lemurids, the presence of noticeable decussation in this group suggests an adaptation to hard foods

Table 2.   Relative enamel thickness (R.E.T.) of extant lemurs compared with other primates

Taxon[a]	Mean R.E.T.[b,c]
Varecia variegata†	5.7
Lemur catta†	7.3
Gorilla gorilla	10.0
Pan troglodytes	10.1
Propithecus verreauxi†	10.7
Hylobates lar	11.0
Paleopropithecus ingens† (extinct)	11.3
Propithecus diadema†	13.0
Hadropithecus stenognathus† (extinct)	14.4
Papio cynocephalus	15.4
Theropithecus gelada	15.6
Pongo pygmaeus	15.9
Cebus apella	19.2
Daubentonia madagascariensis†	21.7
Homo sapiens	22.4
Archaeolemur majori† (extinct)	28.3

[a] † = Malagasy lemurs.
[b] Data from Godfrey et al. (2005).
[c] See Godfrey et al. (2005) for a review of calculating R.E.T.

(at least some time in the past), as seen in its extreme condition in extinct archaeolemurids (e.g., Godfrey et al., 2005, this volume).

Dental Health, Feeding Ecology, and Behavior

Mammalian teeth, in addition to providing a record of both growth and development and evolutionary relationships (e.g., Schwartz and Dean, 2000), also reflect an individual's life experience or life story (e.g., Morbeck, 1997). Even among humans, diet and behavior leave a record of life on the teeth (e.g., Molnar, 1971). Despite the hardness of dental enamel (e.g., Maas and Dumont, 1999) and its assumed resistance to damage and crack propagation, tooth wear is common across the mammalian radiation (e.g., Hillson, 1986, 2005). Tooth damage, including severe wear, breakage, and pathology, is also common throughout the primate order (e.g., Schultz, 1935). However, to date data on patterns of dental health in lemurs are limited when compared to anthropoid primates, especially hominoids (e.g., Kilgore, 1989; Lovell, 1990). Patterns of dental damage often correlate with behavior in anthropoids, for example the high frequency of tooth loss resulting from breakage among male howler monkeys, which is often a result of intermale aggression (Smith et al., 1977). A similar pattern likely exists in

African apes (Lovell, 1990). Among ring-tailed lemurs, tooth damage most often occurs in the anterior teeth, which likely results from their use in both grooming and feeding, as well as aggression, especially among males (e.g., Cuozzo and Sauther, 2006; Sauther et al., 2002).

ANTERIOR TEETH: INCISORS AND CANINES

Lemur anterior teeth function to aid the cheek teeth in reducing food particle size, but are also involved in food procurement. In addition, the mandibular toothcomb is often used for grooming. With the exception of the mandibular toothcomb, the anterior teeth are relatively little studied.

Basic Morphology

Maxillary incisors range within and among Malagasy lemurs from entirely absent (*Lepilemur*) or reduced (lemurids, *Avahi*) to relatively prominent (cheirogaleids, indriids) (see Table 1) (Martin, 1972; Tattersall, 1982). Maxillary canine size varies considerably among lemurs, with some taxa exhibiting very large (i.e., high) canines, relative to first molar size (see Table 3 in Godfrey et al., this volume). *Daubentonia* has no permanent canines (Swindler, 2002; Tattersall, 1982). In *Hapalemur*, the maxillary canine is comparatively short and robust, especially so in *H. simus* (Milton, 1978). In contrast, *Lemur catta* displays large, prominent maxillary canines (Figure 1). Although Malagasy strepsirhines are generally viewed as dentally monomorphic (e.g., Kappeler, 1996), a view supported in numerous studies (e.g., Lawler et al., 2005), some taxa do exhibit significant sexual dimorphism in favor of either males or females (e.g., Kappeler, 1996). For example, a recent study of brown lemurs (*Eulemur*) (Johnson et al., 2005) indicates a contrast in maxillary canine height between *E. albocollaris* and *E. fulvus rufus*, with *E. albocollaris* displaying significant male-biased canine height dimorphism. However, the patterns of sexual dimorphism seen among lemurs are not consistent with those in anthropoid primates, as to date, hypotheses concerning intermale competition, female dominance, and mating system do not display a clear correspondence among lemurs (Kappeler, 1996). In addition to their large, projecting canines, ring-tailed lemurs exhibit a high degree of metric variability in both canine length (e.g., Cuozzo and Sauther, 2004a; Sauther et al., 2001) and height (e.g., Kappeler, 1996). Metric variability in anterior teeth (when compared to the postcanine dentition) can indicate sexual dimorphism in primates, including fossil forms (e.g., Gingerich, 1995). Given the large canines and intense intermale aggression seen in ring-tailed lemurs, significant (anthropoid-like) canine dimorphism would not be unexpected, as suggested by Kappeler's (1996) work. Preliminary data from the ring-tailed lemurs at Beza Mahafaly indicate

Figure 1. Projecting maxillary canine (white arrow) in a male *Lemur catta* (Black 240) from Beza Mahafaly (photo courtesy of Michelle Sauther).

significant male-biased canine height dimorphism (Sauther and Cuozzo, unpublished data).

The mandibular anterior teeth of lemurs are elaborated into a toothcomb, which represents a diagnostic character for all strepsirrhines. As such, there are few departures from the basic structure across Malagasy lemur families. The basic morphology involves integration of the two incisors plus the canine from each side to form a procumbent six-tooth comb (Figure 2). There is a loss of one tooth per side in the indriids, which leaves a comb comprised of an incisor and a canine (Schwartz, 1974, 1978) or two incisors (Gingerich, 1977) (Figure 3). In *Daubentonia*, the toothcomb, as well as the maxillary anterior tooth, has been further reduced to a single, continuously growing (hypselodont) tooth that has been identified as an incisor (Swindler, 2002) or a canine (Tattersall, 1982) (Figure 4). The anterior premolar among lemurs is often caniniform (Figure 2) (Swindler, 2002; Tattersall, 1982).

Origin and Function of the Toothcomb

The original function of the toothcomb has been a matter of some debate for many years (e.g., Avis, 1961; Stein, 1936). Depending on the study, the toothcomb

Figure 2.   Six-toothed mandibular toothcomb in *Lemur catta* (USNM 395517) (photo by Frank Cuozzo).

originally functioned as a grooming tool (Rosenberger and Strasser, 1985; Szalay and Seligsohn, 1977), for food procurement (Martin, 1972), or one or both of these scenarios, though there is insufficient evidence to support either hypothesis unequivocally (Asher, 1998; Rose et al., 1981). Martin (1972) argues that the grooming function of the toothcomb is secondary to its tooth-scraping role. The addition of the canine demonstrates that the scraping role of the structure took precedence over the normal piercing role of the canine. In contrast, Szalay and Seligsohn (1977) posit that the inclusion of the canine in the six-toothed comb does not increase the cutting surface of the comb, forming instead an additional interdental space. The resulting comb was used for fur grooming. The more transversely compressed comb of the exudate-feeding *Phaner* and the robust four-toothed indriid structure (Figure 3) are interpreted as derived. Rosenberger and Strasser (1985) suggest that the toothcomb is part of an olfactory complex that follows the reduction of the upper incisors away from a feeding function, which allows a connection of the philtrum with the vomeronasal organ through the resulting interincisal diastema. The toothcomb functions to stimulate and distribute
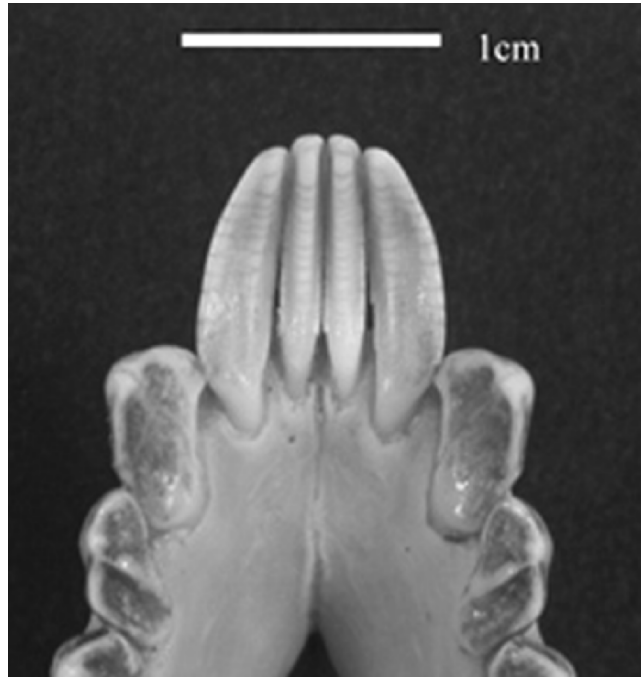
Figure 3. Four-toothed mandibular toothcomb in *Propithecus diadema* (USNM 63349) (photo by Frank Cuozzo).
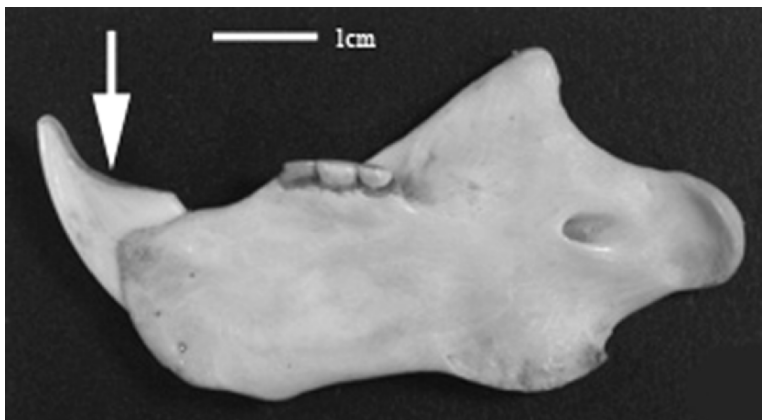

Figure 4. Lingual view of the single anterior tooth (white arrow) in *Daubentonia madagascariensis* (USNM 199694) (photo by Frank Cuozzo).

olfactory secretions throughout the body and brings secretions up to the vomeronasal organ. Whatever its original function, the incisiform canine represents an unusual addition to the toothcomb, especially since the anterior premolar subsequently became caniniform in many taxa (Martin, 1972; Swindler, 2002; Tattersall, 1982).

Among extant lemurs, the toothcomb is used as both a grooming and a feeding tool (e.g., Richard, 1978; Sauther et al., 2002). In addition to numerous field accounts of such usage, Rose et al. (1981) demonstrated via SEM that the interstitial facet of the central incisor had grooves and scratches consistent with hair grooming, and Asher (1998) found that the interincisal gap is wider in gregarious taxa, which presumably groom socially. In indriids, *Daubentonia*, and *Phaner*, the toothcomb has a more derived adult morphology, which is probably related to its use in food procurement in these taxa. Food ingestion in *L. catta* and *P. v. verreauxi* takes place both anteriorly in the mouth and on the postcanines, depending on the size of the fruit or leaf (Yamashita, 2003). Initial food placement is related to food size more than to a material property such as toughness, as seen in the processing of large tamarind fruit (*Tamarindus indica*) by *L. catta* (Cuozzo and Sauther, 2006, in press).

Functional Morphology of Anterior Teeth

Few fruits with peels occur in Madagascar forests, so the correlation between incisor morphology and fruit preparation in anthropoids observed by Hylander (1975) is not found to the same extent in lemurs. Though some folivorous lemurs have reduced upper incisors, the largest incisors are found in exudate feeders, not frugivores.

The upper incisors are reduced or absent in folivorous lemurs (with the exception of the indriids) to form a complex with the mandibular toothcomb that resembles an ungulatelike browsing pad (Avis, 1961). In *Phaner* and *Allocebus* the incisors are enlarged, presumably to work in concert with the toothcomb for exudate feeding (Martin, 1972). This condition is further elaborated in *Daubentonia*, where the upper and lower anterior teeth have been reduced to a single tooth on each side (Figure 4). Aye-ayes use these teeth to scrape off resistant fruit pulp and gouge dead wood in their search for insect larvae (Erickson, 1994; Iwano and Iwakawa, 1988; Kitko et al., 1996).

In the *Hapalemur* species, the canine is shorter and more robust than in other lemurids. This, coupled with the short P^2, is probably related to the stereotypical harvesting behavior that these species employ when feeding on bamboo shoots, in which a shoot is pulled across the mouth behind the canines to liberate it from its sheath (Milton, 1978). *H. simus* also uses its stout upper canine to puncture bamboo culm preparatory to stripping it (Yamashita et al., 2004). This tooth is often worn in older individuals (NY, personal observation).

Indicators of Dental Health

Data on primate dental health primarily come from anthropoids (e.g., Lovell, 1990; Schultz, 1935; Smith et al., 1977), and only recently have data been published for lemurs. Lemur dental health (e.g., wear, pathology, and antemortem tooth loss) reflects many variables, including age, diet, habitat, life history, and even human impact (e.g., Cuozzo and Sauther, 2004a, 2006, in press; Sauther et al., 2006). *L. catta* at Beza Mahafaly often display excessive damage to the toothcomb, with a number of individuals having toothcombs worn more than 50% (Figure 5) (Cuozzo and Sauther, 2006; Cuozzo et al., unpublished data; Sauther et al., 2002).

In addition, the teeth of ring-tailed lemur toothcombs are often broken, chipped, and even missing (Cuozzo and Sauther, 2004a, in press; Sauther et al., 2002), with the majority of dental damage in *L. catta* occurring in the anterior teeth (e.g., Cuozzo & Sauther, 2006; Cuozzo et al., 2004; Sauther et al., 2002). It is likely that the excessive damage seen in ring-tailed lemur anterior teeth results from the use of the toothcomb in both feeding and grooming (e.g., Sauther et al., 2002; Yamashita, 2003). The frequency of severe wear and antemortem loss of the maxillary incisors in ring-tailed lemurs is also a result of the dual function of anterior tooth use (e.g., Cuozzo and Sauther, 2006, in press). It is important to note that individuals can and do survive for a number of years with anterior tooth

Figure 5. Severe toothcomb wear in an adult ring-tailed lemur (Yellow 195) from Beza Mahafaly: compare with the unworn toothcomb in Figure 2. Also note the severe wear on right P_2 (white arrow) (photo courtesy of Michelle Sauther).

damage, and even missing teeth in the toothcomb (e.g., Cuozzo and Sauther, 2004a, in press; Sauther et al., 2002). Also among ring-tailed lemurs, abscessed maxillary canines, which present as open wounds on the muzzle in living individuals, are a regular occurrence at Beza Mahafaly (Cuozzo et al., 2004; Sauther et al., 2006). Their presence corresponds to areas of human impact, and may reflect an increased consumption of nonnative foods in these areas (Cuozzo et al., 2004; Sauther et al., 2006). Decayed and possibly abscessed canines have also been noted among ring-tailed lemurs at Berenty Reserve in southeastern Madagascar (Crawford, personal communication; see Cuozzo and Sauther, in press), an area also impacted by human activity.

POSTCANINES: PREMOLARS AND MOLARS

The cheek teeth are the primary chewing teeth, and as such, are more subject to selection by the physical properties of the foods they masticate. Molar tooth form approximates designs that are best suited for inducing and continuing fragmentation in the foods they contact, especially in more specialized forms such as folivorous *Propithecus* or insectivorous *Daubentonia*. However, in more generalized taxa, especially those with a wide geographic range that inhabit a variety of environments (e.g., *L. catta*), the relationship between tooth morphology and diet becomes less distinct. In this section, we review the basic morphology of postcanine teeth and then discuss correlates between individual tooth features and the mechanical properties of the diets the lemurs eat. Finally, we discuss patterns of postcanine dental health with respect to their ecological and environmental contexts.

Basic Morphology

Indriids have reduced the number of premolars from the standard number of three to two (Table 1), and *Daubentonia* has a single, peglike upper premolar. The upper premolars vary among the families. In cheirogaleids the first two premolars are bladelike. Among the lemurids and cheirogaleids, P^4 has a well-developed protocone, though it is not molariform except in *Hapalemur* (and *Lepilemur*; Tattersall, 1982). This tooth in *L. catta* is also broad and molarlike, although with some individual variation, for example the presence of accessory cusps (FC, personal observation). The two indriid premolars are not molariform. The lower anterior premolar is caniniform in all lemurs (Swindler, 2002; Tatersall, 1982). In *Hapalemur*, P_4 is molariform and possesses two distinct basins (Tattersall, 1982).

The mammalian tribosphenic molar pattern has not been greatly modified in the primates as a whole. In the Malagasy lemurs, the lemurids retain the original pattern of three cusps (paracone, metacone, protocone) that surround the trigon basin in the first two maxillary molars (Figure 6). A lingual cingulum is variably present with an anterior protostyle. M^3 is reduced but less so in *Hapalemur*
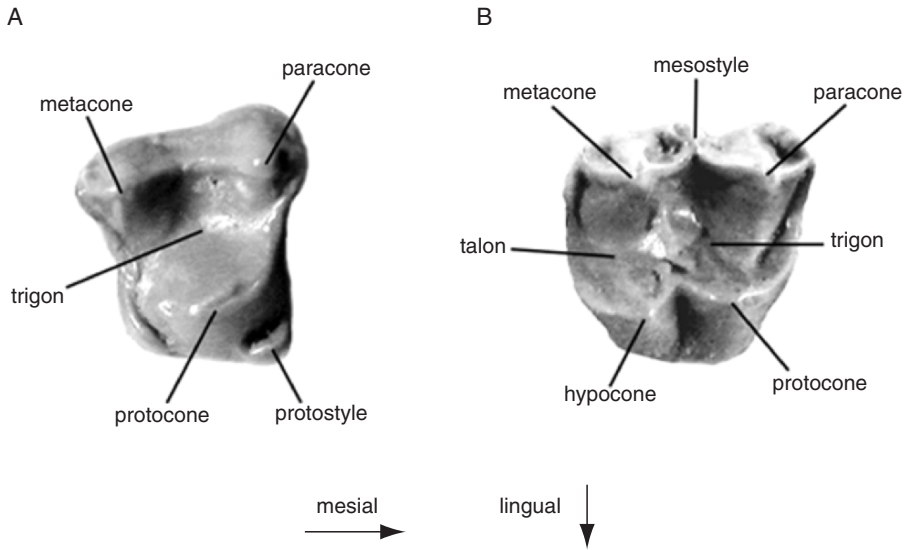
A

B

Figure 6. Occlusal features from casts of upper second molars of (A) *Eulemur rubriventer* (RMNH d) and (B) *Propithecus diadema edwardsi* (RMNH b). Not to scale (photos by Ny Yamashita).

(Tattersall, 1982). The indriids developed a characteristic quadritubercular maxillary molar that extends to their subfossil members (Martin, 1990). A mesostyle is present on the first two molars. A fourth cusp, the hypocone, and its crests surround a second basin, the talon. The hypocone occludes with the trigonid basin (Figure 6). Other families either completely lack the hypocone or it is variably developed, as in the cheirogaleids (Martin, 1990) and *Hapalemur* (Tan, 2000). In *Daubentonia*, the molars are square in outline, though the cusps are not well-defined (Tattersall, 1982).

Generally, lemurids have a more varied molar morphology than indriids (Yamashita, 1998b). In the lower molars, the lemurids have lost the paraconid and lack a hypoconulid. The anterior basin, the trigonid, is tilted mesially and at an angle to the cervical plane of the talonid (Figure 7). The trigonid does not have an occluding cusp. *L. catta* has a lingual notch and a distinct entoconid on the M_2 that are lacking in the other lemurids (except for *Hapalemur*) that interrupts the continuous crest on the postero-lingual aspect of the tooth. *Hapalemur simus* has crenulated enamel on both upper and lower molars (Schwartz and Tattersall, 1985).

Lepilemur also possesses a distinct entoconid and pronounced crests radiating obliquely anteriorly and posteriorly from the hypoconid (Schwartz and Tattersall, 1985). In the cheirogaleids, the molars are variable, with all except
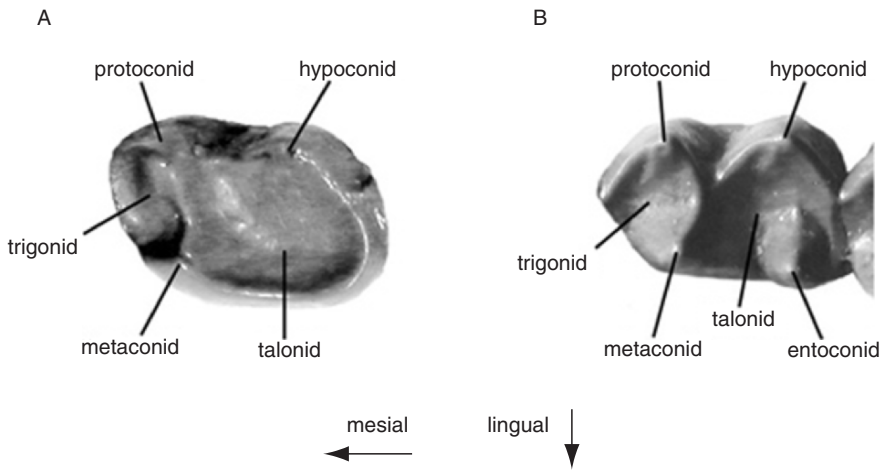
Figure 7. Occlusal features from casts of lower second molars of (A) *Eulemur rubriventer* (RMNH m) and (B) *Propithecus diadema edwardsi* (RMNH b). Not to scale. Note: no distinct entoconid on *E. rubriventer* specimen (photos by Ny Yamashita).

Phaner possessing a hypoconulid on M_3 and exceptionally low, rounded cusps in *Cheirogaleus* (Tattersall, 1982). Cuozzo (2000) has reported a great deal of morphological variation in the dentition of a large sample (n=126) of mouse lemurs (*Microcebus* c.f. *murinus*) housed at the American Museum of Natural History (Buettner-Janusch and Tattersall, 1985). For example, approximately 7% of the individuals in this sample exhibit a distinct, variably developed lingual cusp, originating from the cingulum disto-lingual to the hypocone on the first maxillary molar (Cuozzo, 2000). In addition, at least one individual in the sample displays this trait on M^2 (Cuozzo, 2000). Even the presence of an M_3 hypoconulid, a trait viewed as diagnostic of the cheirogaleids (e.g., Tattersall, 1982), varies in this sample (Cuozzo, 2000). Indriids have retained the paraconid and have a hypoconulid on the third molar only. The indriid trigonid is on the same occlusal plane as the talonid (Schwartz and Tattersall, 1985). Strong transverse crests connect the anterior and posterior cusps to approach a bilophodont condition that is fully realized in *Indri*.

 For many years the focus of morphological study of lemur teeth has emphasized interspecific differences and lemur taxonomy (e.g., Schwartz and Tattersall, 1985; Swindler, 2002; Tattersall, 1982). More recently, work on a limited number of large samples of extant lemurs has allowed for a better understanding of dental variation, which has implications for addressing a variety of questions in primate paleontology and lemur taxonomy (e.g., Cuozzo, 2000; Cuozzo et al., 2004; Sauther et al., 2001). In the set of 23 dental traits used by Tattersall and Schwartz (1991) and Tattersall (1993) in their analyses of extant lemur taxonomy (critiqued

by Groves and Trueman, 1995), 9 show a distinction between *L. catta* and the other lemurids (e.g., *Eulemur*, *Varecia*). In a pair of studies examining dental variation in the ring-tailed lemurs at Beza Mahafaly (Cuozzo et al., 2004; Sauther et al., 2001), two of these traits do not show a distinction. This includes the presence of several individuals that display distinct protostyles on the lingual cingula of the maxillary molars (Cuozzo et al., 2004), and roughly half of the population exhibiting distinct metaconids on P_4 (Cuozzo et al., 2004; Sauther et al., 2001). The maxillary molar protostyles seen in some individuals at Beza Mahafaly (compare Figures 8 and 9) are exactly what one would expect in other lemurids, such as *Eulemur fulvus* (e.g., Swindler, 2002; Tattersall, 1982, 1993).

In contrast to molecular data, in which *L. catta* is most closely allied with *Hapalemur* (e.g., Karanth et al., 2005; Poux et al., 2005), these dental data suggest that *L. catta* and the other lemurids are more similar dentally than has generally been recognized (Cuozzo et al., 2004). This example, along with our discussion of dental variation in mouse lemurs, emphasizes the need for large samples when considering traits used in systematic and phylogenetic analyses, and indicates that morphological variation, even within single populations, is pronounced in extant lemurs. Understanding the degree of dental variation in extant lemur species therefore has a number of implications for interpreting variation in fossil assemblages and identifying species in the primate fossil record (Cuozzo, 2000, 2002; Cuozzo et al., 2004; Sauther et al., 2001).
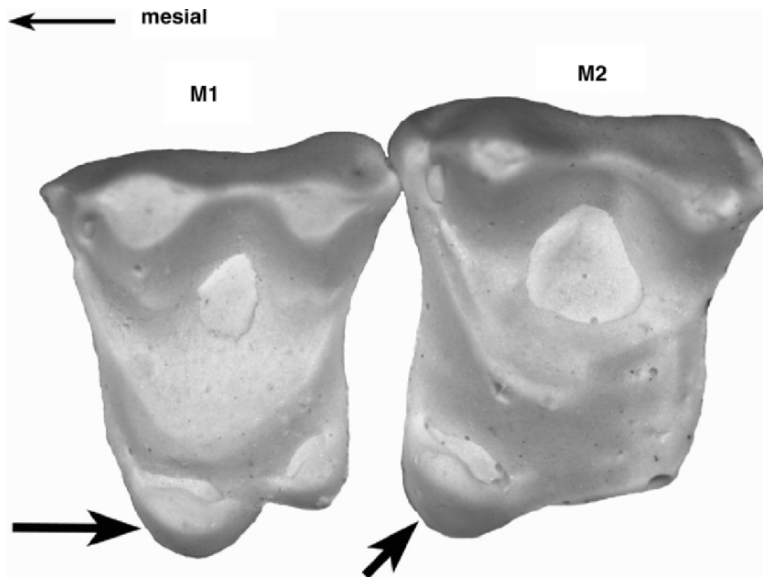

Figure 8. Lingual molar morphology as shown in a cast of an adult ring-tailed lemur from Beza Mahafaly (Hot Pink II 199) with distinct protostyles (black arrows) common to species of *Eulemur* (photo by Frank Cuozzo).
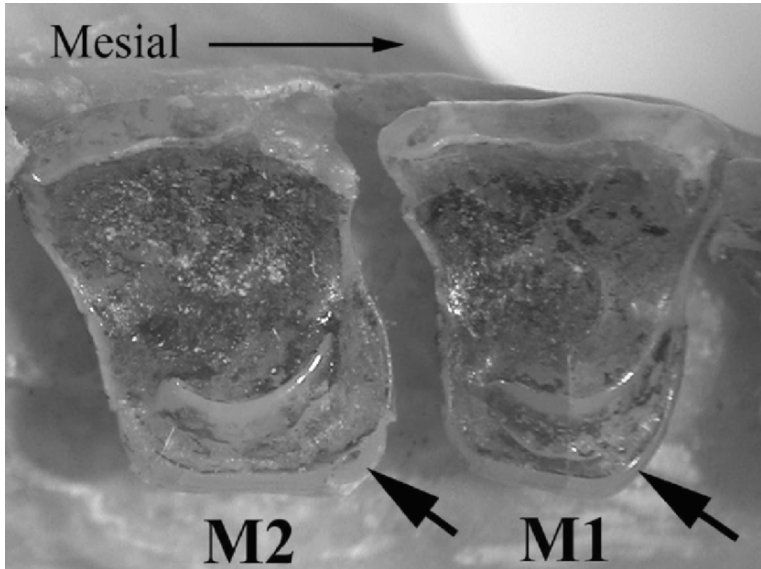
Figure 9. Lingual molar morphology in *Lemur catta* (AMNH 170740), showing the common presence of a thick cingulum (black arrows) without the distinct cusps (protostyles) common to species of *Eulemur* (photo by Frank Cuozzo).

Functional Morphology: Relationships between Tooth Form and Diet

Most Frequently Eaten versus Most Stressful Foods

As discussed above, tooth form is primarily related to the material components of the foods encountered. The heterogeneity found in the cheek teeth among lemur families is directly related to the mechanical variety of the foods they chew. The close relationship between tooth form and food properties increases efficiency, which is here defined as maximizing reduction of food particles with a minimum of time and energy. Molar efficiency has been investigated through analyses of strepsirhine (Kay and Sheine, 1979; Sheine and Kay, 1977) and marsupial (Moore and Sanson, 1995) fecal particles and cercopithecine stomach contents (Walker and Murray, 1975) that related finer size reduction to the presence of specific molar morphologies.

Diets, however, are usually mechanically quite variable, though they may be dominated by foods of a single property. Whether the properties of the most frequently eaten or the most mechanically stressful foods have the highest correlations with molar morphology is a matter of some debate (Kay, 1975; Kinzey, 1978; Rosenberger and Kinzey, 1976). The question has been framed to take into

account seasonal differences in diets and food availability. Either the foods that are eaten during peak abundance are most related to the morphology, or those eaten during periods of scarcity, when animals are supposedly eating less preferred and more mechanically challenging foods ("fallback foods"), are more significant. An estimated 45% has been suggested as the minimum amount that an animal must eat of a food category in order for its mechanical properties to have an impact on tooth form (Kay, 1975). Rosenberger and Kinzey (1976) and Kinzey (1978) emphasize the importance of "critical" secondary dietary items that are eaten at times of resource scarcity. Tooth features that enable an animal to process foods during marginal periods are presumably under strong selection (Lambert et al., 2004). Yamashita (1998a) found that the most stressful foods were more highly correlated with molar features than the most frequently eaten foods, though the result was not applicable to all tooth features (e.g., crest lengths).

Correlates between Tooth Morphology and Physical Properties

An increasing number of studies are investigating food properties in the field (e.g., Happel, 1988; Kinzey and Norconk, 1990, 1993; Kitko et al., 1996; Lucas et al., 1991, 1995; Strait and Overdorff, 1996; Wright, 2004; Yamashita, 1996, 2002), though for the most part primate diets have not been characterized mechanically. Among the Malagasy lemurs, few studies on physical food properties have been conducted to date.

Yamashita (2002) carried out extensive work on mechanical dietary properties of two sympatric lemurs. The diets of sympatric groups of *L. catta* and *P. v. verreauxi* were tested throughout the year at Beza Mahafaly, a deciduous dry forest in southwestern Madagascar. Though the pooled species dietary toughness values were not significantly different, individual sifaka groups often had tougher diets than those of ring-tailed lemurs, while the converse never occurred. The two species overlapped significantly in the hardness of foods consumed (Yamashita, 2000). However, sifakas had a higher hardness threshold. Sifaka groups were uniform in toughness values regardless of location within the microhabitat gradient of this particular site, whereas toughness of ring-tailed lemur diets differed by group. This is consistent with, on a lower taxonomic level, the larger pattern of greater overall similarity in indriid teeth compared to those of lemurid taxa.

Crests. Long molar crests are frequently associated with a folivorous or insectivorous diet (Kay, 1975, 1978; Kay and Hylander, 1978; Kay et al., 1978; Kinzey, 1978; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Seligsohn and Szalay, 1978). Although dietary categories themselves are usually not sufficient to classify foods mechanically ("frugivory" for example encompasses an array of foods with a variety of physical properties ranging from seeds to fleshy mesocarp), these particular foods are similar in either shape or consistency.

Leaves have a uniform geometry and composition that contribute to toughness when mature. Though the lamina comprises most of the volume of leaf tissue,

toughness is conferred by sclerenchyma fibers that sheathe the midrib and veins (Lucas et al., 1991; Vincent, 1982). Leaves are notch insensitive (Vincent, 1983), that is, local cracks do not weaken the leaf. The veins blunt cracks or divert crack energy without fragmenting the leaf tissue. As a result, strain energy must be continuously fed into a crack to propagate it. A tooth design that encourages and directs continued crack propagation would be the most efficient for producing leaf failure.

Folivorous primates have reciprocal crests on occluding molars that slide past one another along their lengths. These well-developed crests appear to be functionally analogous to the elaborate lophed patterns found in herbivorous browsers and grazers for dividing tough, fibrous foods (Hiiemae and Crompton, 1985; Janis and Fortelius, 1988; Lumsden and Osborn, 1977). Insectivore molars also emphasize the development of crests. However, as Strait (1997) has demonstrated, there is a distinction between fragmenting hard-bodied as opposed to soft-bodied insects. The former are strong, brittle, and stiff (stress-limited), requiring a shorter crest that concentrates stresses along its length, and the latter are soft and tough (displacement-limited) and are best fractured with a crest with a longer contact area.

Among the lemurs, crest length and degrees of folivory have been linked in *Lepilemur mustelinus* (Seligsohn and Szalay, 1978), the indriids (Seligsohn, 1977; Yamashita, 1998b), and *L. catta* (Seligsohn, 1977; Yamashita, 1998b). Seligsohn (1977) also associated insectivory with crest development. The inclusion of *L. catta* in this list may be surprising; however, Kay et al. (1978) earlier grouped it with folivorous taxa based on crest length. Although often viewed as a mixed-fruit eater (e.g., Godfrey et al., 2004b), *L. catta* is best viewed as an opportunistic omnivore (e.g., Sauther et al., 1999). In southwestern Madagascar, *L. catta* spent equal amounts of time on fruits and leaves (Yamashita, in preparation) and were more folivorous than rainforest confamilials (Yamashita, 1996). Furthermore, the toughness of their diets was not significantly different from that of sympatric groups of the indriid *Propithecus v. verreauxi* (Yamashita, 2002). *L. catta* and *Indri* had relatively the longest crests within their respective families (Yamashita, 1998a).

Indriids possess molars dominated by crests (Seligsohn, 1977; Yamashita, 1998b). Though the degree of folivory in indriids differs by population, season, and location, all indriids are folivorous to some extent (Powzyk and Mowry, 2003; Richard, 1978; Yamashita, 1996, 1998b), and they possess additional specializations of the gastrointestinal tract to facilitate leaf eating (Campbell et al., 2000, 2004).

Yamashita (1998b), however, did not find a relationship between crest length and food shear strength in comparisons of five lemurid and indriid species, though there was a positive correlation between total crest length and percent folivory. Crest sharpness, and not just crest length, may be an important and heretofore largely unquantified feature that is relevant for understanding tooth–food interactions (Lucas, 2004). For example, a recent study of longitudinal tooth wear on *Propithecus diadema edwardsi* at Ranomafana (King et al., 2005) suggested that

with continued wear, second molar crests continually "readjust" themselves, remaining secondarily sharp, in order to maintain functional occlusion. Only with excessive age and wear do these teeth experience declining function, which corresponds to a decline in reproductive success among females in this population (King et al., 2005).

Bilophodonty in Indriids. The bilophodont (or cross-lophed) crests of *Indri* have been compared to those of cercopithecids (the crests of other indriids approach the bilophodont condition). A puzzling aspect of the diets of the indriids is the occurrence of seed predation in addition to folivory (Hemingway, 1996; Powzyk and Mowry, 2003; Yamashita, 1998b). These two food types would seem to require different morphologies. However, Lucas and Teaford (1994) describe how bilophodont colobine crests combine wedges with blades. The blunter wedges split apart tough seeds and the sharp crests fracture leaf material. In cercopithecines, the central basin of the lower molars, formed by the anterior and posterior bilophs, presumably holds seeds in place while the occluding molar shatters them (Happel, 1988). Bilophodonty in indriids converges on a similar morphology to that described for Old World monkeys, which combines two different crest types for fracturing leaf material and seeds.

Cusps and Basins. Blunt cusps have been linked to frugivorous diets that include seeds, nuts, and insects in *Cebus* and soft fruits in *Pithecia* (Kinzey, 1978; Rosenberger and Kinzey, 1976). Hard/brittle foods, such as seeds, are stiff (high E) and require high stresses to initiate crack formation since stress increases with stiffness. Blunt cusps should be better able to tolerate high stresses than acute cusps, and their greater surface area would more efficiently fracture brittle foods that readily propagate cracks once they start. Furthermore, though a tight fit of a cusp to its occluding basin can produce high forces, reducing hard foods to fine particles can be achieved by unrestricted movement of the cusp in the basin to find weak points in the foods as they are being fragmented.

Frugivorous and gummivorous strepsirhines had low, blunt cusps, short crests, and shallow basins (Seligsohn, 1977). However, as noted earlier, fruits are a mechanically diverse dietary category. Presumably the mechanical properties of these foods were responsible for the association. The Malagasy taxa identified with this morphology were *Microcebus, Phaner*, and *Cheirogaleus. Microcebus rufus* has a diet that consists primarily of small fruits and insects (Atsalis, 1999). The hardness values of the ripe and unripe fruits eaten are comparable to the average hardness values found for three sympatric lemur species (Yamashita, 1996). *Cheirogaleus medius* and *C. major* appear to have a similar diet, consisting primarily of small fruits and berries (Fietz, 2003; Hladik et al., 1980). The exceptionally rounded molar cusps of *Cheirogaleus* suggest a hard fruit diet. The majority of the *Phaner* diet consists of plant exudates with secondary contributions from insects and flowers (Schülke, 2003). Its molar morphology may be more indicative of secondary dietary items, though the molars are bunodont.

The expected positive association between blunt cusps and food hardness was not clear-cut in Yamashita (1998b) since the relationship was positive for upper molars

only. However, the harder diet of *Eulemur rubriventer* was reflected in blunter cusps and deeper basins than the sympatric *E. fulvus rufus*. Seligsohn (1977) found that crest length was negatively correlated with cusp acuity. *E. rubriventer* shared this pattern, while the features had mixed positive and negative correlations in *L. catta* and *E. fulvus rufus*.

The featureless molars of *Daubentonia* are probably related to its diet of insect larvae and seeds, which would not require much more than crushing platforms since the anterior dentition perform the hard work of extraction. Hard food items were correlated with short cusps, a tight occlusal fit of the protocone to the talonid, small trigon and large talonid areas, and deep, acute basins in a study of five lemur species (Yamashita, 1998a,b). Unrestricted basins were correlated with shear strength (mostly of leaf material) and not with food hardness. The larger basin area increased the excursion of the crest, a finding also noted by Kay (1975).

Indicators of Dental Health

The postcanine dentition is central for food processing, therefore, the patterns of dental pathology in premolars and molars are most often related to diet and the breakdown of food. This contrasts with patterns seen in the anterior teeth across primates, in which dental damage (often leading to disease) results from social behaviors, for example interindividual aggression (Lovell, 1990; Smith et al., 1977) or, in the case of ring-tailed lemurs at Beza Mahafaly, the possible impact of human activity and introduced foods (Sauther et al., 2006). As noted earlier, to date there is a paucity of information on lemur dental pathology, including patterns of wear (see Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Cuozzo et al., 2004; King et al., 2005; Sauther et al., 2002). Classic studies, such as the seminal work of Schultz (1935), and Miles and Grigson's (1990) revision of Colyer's work, present few if any examples of lemur dental health.

The lemur community at Beza Mahafaly, because of its long-term study (including the collection of skeletal remains from the reserve (Cuozzo and Sauther, 2004a, 2006, in press), allows for an initial understanding of dental health in wild lemurs, and provides important data for recognizing the role of ecology and the environment in dental pathology and tooth wear. Both ring-tailed lemurs and Verreaux's sifakas have been the focus of long-term dental study at Beza Mahafaly (e.g., Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Cuozzo et al., 2004; Lawler et al., 2005; Sauther et al., 2001, 2002, 2006; Yamashita, 1996, 1998a,b, 2000, 2002, 2003). Despite their sympatry, these taxa display quite different patterns of dental health and tooth wear. For example, while *L. catta* at Beza Mahafaly exhibits a high frequency of severe postcanine wear and antemortem tooth loss (Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Sauther et al., 2002), *P. v. verreauxi* does not (Cuozzo and Sauther, in press). In fact, in comparison to ring-tailed lemurs, in which 27% of the living individuals studied displayed antemortem tooth

loss, most of which have been lost due to excessive wear (Cuozzo and Sauther, 2004a, 2006, in press), only 6% of the sifaka skeletal specimens at the reserve exhibit tooth loss (Cuozzo and Sauther, in press; Cuozzo, unpublished data). Among sifaka, most tooth loss results from dental pathology, not excessive wear (Cuozzo and Sauther, in press; Cuozzo, in preparation). In addition, the degree of tooth wear in the sifaka sample, while sometimes pronounced in older individuals relative to others in the sample (including the anterior dentition [Cuozzo and Sauther, in press; Cuozzo, unpublished data]), is far exceeded by ring-tailed lemurs, in which many teeth are worn down to the roots, and often completely lost, a condition seen in both living individuals and skeletal specimens (e.g., Cuozzo and Sauther, 2004a, 2005, 2006, in press; Sauther et al., 2002). A recent study of tooth wear in *Propithecus edwardsi* at Ranomafana National Park (King et al., 2005) illustrates that, although sifaka experience noticeable wear, even at advanced ages the degree of tooth wear is far less than that displayed by ring-tailed lemurs at Beza Mahafaly (Cuozzo and Sauther, in press).

The patterns of wear in this population of ring-tailed lemurs are clearly related to ecology, diet, and tooth use. In *L. catta*, the most frequently worn and missing teeth (P3, P4, and M1) are those used in the initial processing of tamarind fruit (Cuozzo and Sauther, 2004a, 2006, in press). This fruit (*Tamarindus indica*) is both hard and tough when ripe (Yamashita, 2000), and dominates the diet of ring-tailed lemurs living in gallery forest (Sauther, 1998; Simmen et al., in press), despite their opportunistic omnivory (e.g., Sauther et al., 1999). In contrast, *P. v. verreauxi* displays more excessive wear on P3, P4, and M3 (sifakas have only two premolars in each quadrant, see Table 1 [e.g., Swindler, 2002; Tattersall, 1982]), with M1 and M2 often retaining much of the original crown structure (Cuozzo and Sauther, in press; Cuozzo, unpublished data). The more limited wear and lower frequency of tooth loss in *P. v. verreauxi* at Beza Mahafaly when compared to *L. catta* likely reflects differences in diet, as well as tooth form. Although both taxa have relatively thin dental enamel (Table 2) (e.g., Godfrey et al., 2005), sifakas have very large molars relative to skull size (Godfrey et al., 2002), in addition to a specialized folivorous morphology (see comparisons of the molar morphologies of the lemurid *Eulemur* and indriid *Propithecus* in Figures 7 and 8) (Tattersall, 1982; Yamashita, 1998a,b). Sifakas at Beza Mahafaly do consume tamarind fruit, but most often eat the less tough, unripe fruits (e.g., Yamashita, 2002). As such, sifaka teeth are apparently a "better match" for their diet than seen in ring-tailed lemurs, which appear to represent an ecological "mismatch" between tooth structure and diet (Cuozzo and Sauther, 2005, in press). Understanding this relationship between ecology and dental health in living lemurs, in addition to aiding in our knowledge of lemur biology, provides an important context in which to understand lemur paleobiology and evolution (Cuozzo and Sauther, 2004b, in press), as seen in recent work on the subfossil lemurid *Pachylemur*, which displays noticeable tooth wear (Godfrey et al., this volume; Vasey et al., 2005).

CONCLUSIONS

In this chapter, we have presented lemur tooth morphologies as having specific designs related to the material properties of the foods they consume. Of course, this relationship is not perfect, seen for example in the patterns of severe tooth wear in some taxa (e.g., *L. catta*) living in specific habitats and utilizing diets dominated by specific food sources. The simple model for optimal designs used here does not take into account phylogenetic history and physical heterogeneity of food items that appear in individual diets, or in various habitats used by members of the same species. The relative importance of specific food parts to tooth form is still a matter of some debate, and perhaps, can never be completely resolved given variation in diets between seasons and regional differences in food availability, even within a single subspecies or widely dispersed specific populations. What animals ultimately eat involves a dialogue between what they can eat (dictated by their morphology, in a broad sense) and what is available (determined by the environment), a dialogue also influenced by socioecology (e.g., female dominance, social rank).

Further research on food properties is clearly needed in many Malagasy lemur taxa, especially for those with wide geographic ranges (e.g., *L. catta*), and the nocturnal members of the radiation that are barely represented in this review. As seen in our discussion of ecology and dental health (i.e., tooth wear and loss), much of the data for the better-known forms (e.g., *L. catta*, *P. v. verreauxi*) come from long-term studies at a limited number of locations (e.g., Beza Mahafaly). Therefore, comprehensive research on food properties and feeding from a wide range of habitats is imperative. Further quantification of lemur tooth morphology is also required, especially for the smaller-bodied, nocturnal forms.

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