Introduction to the Symposium Issue

Primate Dental Ecology: How Teeth Respond to the Environment

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ABSTRACT Teeth are central for the study of ecology, as teeth are at the direct interface between an organism and its environment. Recent years have witnessed a rapid growth in the use of teeth to understand a broad range of topics in living and fossil primate biology. This in part reflects new techniques for assessing ways in which teeth respond to, and interact with, an organism's environment. Long-term studies of wild primate populations that integrate dental analyses have also provided a new context for understanding primate interactions with their environments. These new techniques and long-term field studies have allowed the development of a new perspective—dental ecology. We define dental ecology as the broad study of how teeth respond to, or interact with, the environment. This includes identifying patterns of dental pathology and tooth use–wear, as they reflect feeding ecology, behavior, and habitat variation, including areas impacted by anthropogenic disturbance, and how dental development can reflect environmental change and/or stress. The dental ecology approach, built on collaboration between dental experts and ecologists, holds the potential to provide an important theoretical and practical framework for inferring ecology and behavior of fossil forms, for assessing environmental change in living populations, and for understanding ways in which habitat impacts primate growth and development. This symposium issue brings together experts on dental morphology, growth and development, tooth wear and health, primate ecology, and paleontology, to explore the broad application of dental ecology to questions of how living and fossil primates interact with their environments. Am J Phys Anthropol 148:159–162, 2012.

Teeth have long been a central focus of study, and are an important source of information on the ecology, behavior, and evolution of humans, nonhuman primates, and other mammals (Hillson, 1986, 2005; Ungar, 2010). Teeth are a unique biological unit in that they preserve a record of an organism's life story, from the time they begin to develop, through their lifetime of use. Teeth are frequently preserved in both the archaeological and fossil records (e.g., Shipman, 1981; Hillson, 2005; Bailey and Hublin, 2007), and often provide the only source of information on the lives of recent and especially long-dead organisms. They have been an especially important component of evolutionary research for more than a century (see Ungar, 2010). As summarized by Cuozzo and Sauther (this volume), the study of how teeth reflect an organism's ecology, most notably diet, dates even further, to at least the time of Aristotle. However, the study of teeth over the past few decades has developed far beyond baseline studies of the link between general dental morphology and diet. The ability to unlock records of growth and development through analyses of dental microstructure (e.g., Schwartz and Dean, 2000; Guatelli-Steinberg, 2001), the understanding of how teeth maintain their function over time (e.g., Ungar and Williamson, 2000), and the use of stable isotope signatures in dental enamel to assess the environment and/or habitat that an individual used while its teeth were developing (e.g., Cerling et al., 2011), all provide examples of how new approaches to dental analyses facilitate a more complete understanding of an organism's ecology. With these advances in technology, new methods of dental analysis, and numerous, now decades-old primate field projects, a more thorough understanding of how teeth reflect an organism's ecology, how they interact with their environment, and how this can inform questions of primate paleobiology, can now be attained. The papers in this volume do just that—present research that builds on that of numerous earlier workers, combined with new data on living primates and new technologies, to answer a range of questions on living and extinct primates: hence the term *dental ecology* as defined and outlined by Cuozzo and Sauther (this volume). In sum, we define dental ecology as the broad study of how teeth respond to or interact with the environment. Specifically, we use the

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term to describe how the environment shapes teeth, whether in evolutionary time, such as links between tooth size and/or dental morphology related to diet, or how the environment shapes an organism's teeth during its life, through patterns of wear, pathology, and/or development. As Cuozzo and Sauther note, the ability to understand such patterns is only possible when dental study is combined with comprehensive ecological data from living primates (and potentially other vertebrates), which is the central principle of our dental ecology concept.

On April 14, 2010, 39 researchers (presenters and coauthors) convened a symposium on primate dental ecology at the 79th Annual Meeting of the American Association of Physical Anthropologists in Albuquerque, New Mexico. These included scholars from numerous countries and continents coming together to present a range of work on the many ways in which teeth inform the ecology of living and extinct primates, humans, and other mammals. Of the 13 presentations at this symposium, 10 are included here as part of this special issue. In addition, two other invited papers are included herein despite not having been presented as part of the symposium in Albuquerque. The papers included come from a wide range of scholars, and span the primate order, from living and subfossil Malagasy lemurs, to New and Old World Monkeys, extant hominoids, and fossil humans. These papers represent a collection of methodologies addressing ways in which teeth can be analyzed and inform ecology and behavior, and a series of case studies from living and fossil forms that utilize new techniques and data from living primates to provide new insights into primate ecology.

This special edition of the *American Journal of Physical Anthropology* (AJPA) maintains the organizational structure of the symposium in presenting the resulting papers from the 2010 symposium, beginning with introductory, conceptual, and methodological papers, followed by papers focused on one or several taxa, and applying various methods to understand and assess dental ecology of a range of primates. As with regular submissions to AJPA, all papers appearing here were peer-reviewed and followed standard submission protocols of AJPA.

SUMMARY OF PAPERS: DENTAL ECOLOGY METHODS AND TECHNIQUES

The first conceptual paper by Cuozzo and Sauther presents a definition of dental ecology and how this builds on, yet differs from, many earlier analytical approaches to using teeth as indicators of an organism's ecology and behavior. Specifically, we (FPC and MLS) argue that a dental ecology approach combines the long foundation of dental studies, with sometimes new and novel techniques of analysis (e.g., stable isotopes from dental enamel), and long-term behavioral and ecological data from living primate populations, which began in earnest in the 1970s and 80s, and now provide a broad framework for "whole organism" ecology in a dental context.

Following this introduction, a set of papers explore new and/or updated approaches, building upon new data, to understand teeth in an ecological context. This includes papers by Constantino et al. and Campbell et al., both of which apply nanoindentation techniques to understand the mechanical properties of dental enamel and thus how dental morphology may reflect an organism's ecology. Nanoindentation studies of modern human enamel date to the later 1990s (e.g., Cuy et al., 2002), but only in recent years has this type of work been conducted on nonhuman primates. Both of these papers find a similarity in enamel mechanical properties (e.g., elastic modulus, hardness) across the taxa studied. The data presented by Constantino et al. indicate that across the anthropoid primates, there is a high degree of overlap in these mechanical properties, suggesting that differences in the load-bearing ability of primate molar teeth is primarily a function of the tooth's structure and morphology (e.g., size and enamel thickness) rather than enamel's mechanical properties *per se*. Consistent with this result, Campbell et al. studied the enamel properties of three sympatric lemurs from southern Madagascar, and concluded that the mechanical properties of enamel are similar among these three species. As two of three species (*Propithecus verreauxi* and *Lepilemur leucopus*) are dedicated folivores, and the third (*Lemur catta*) is an opportunistic omnivore at this location (the Beza Mahafaly Special Reserve), the similarity of enamel properties provides a backdrop for understanding the ecology of these species, specifically the pattern of frequent, severe wear in ring-tailed lemurs. Given that there are no differences in enamel properties, the use of a mechanically challenging fallback food by ring-tailed lemurs appears to be a "mismatch" with their dental structure, as has been previously suggested (Cuozzo and Sauther, 2006).

The final two methods papers by Guatelli-Steinberg et al. and Yamashita et al. provide additional insight into primate ecology, through analyses of patterns of dental growth and development (linear enamel hypoplasias [LEH]) in great apes and the mechanical properties of foods eaten by wild lemurs. Guatelli-Steinberg et al. show that the duration of enamel development varies between sexes in great apes, and that mountain gorillas evince a lower frequency of LEH than the other apes. Although disruptions in enamel formation, seen for example in LEH presence, reflect periods of physiological stress, Guatelli-Steinberg et al. further invoke the link between ecology and LEH expression, noting that dietary variation, such as the gradient of fruit availability across *Gorilla*, may account for the gradient in LEH expression across this genus. Thus, it is clear from this work that dental developmental anomalies can be a direct reflection of an organism's ecology. The work by Yamashita et al. follows the earlier paper by Campbell et al. which also focused on *Lemur catta*. Here, data on the mechanical properties of various ring-tailed lemur foods are presented from multiple field seasons at a single locality, and illustrate that the primary fallback food used in these habitats is the most physically (largest) and mechanically (hardest and toughest) challenging food eaten. Linking back to the enamel data presented by Campbell et al., Yamashita et al. suggest that the challenging properties of ring-tailed lemurs' fallback food in riverine gallery forests result in the molar microcracking seen by Campbell et al., a result of repeated processing of this food and the cause of the frequent pattern of severe wear and tooth loss in this population. Thus, when combined with Campbell et al., Yamashita et al. illustrate the potential of an approach that combines extant primate feeding behavior data with dental analyses to inform primate ecology.

Summary of papers: Dental ecology case studies

The case studies presented here include nonhuman primates from a variety of places and time intervals, with three papers focused on living and/or subfossil lemurs, as well as discussions of New World monkeys, Asian colobines, and extant hominoids. Godfrey et al. and King et al. follow an additional theme of this special issue in applying dental topographic techniques to questions of primate ecology. Godfrey et al., using a variant of dental topographic analysis (i.e., orientation patch counts or "OPC") and an example of the comparative method, assess the relationship between dental morphology and diet in living lemurs to provide an interpretative framework for understanding the ecology of the recently extinct "giant" subfossil lemurs. They conclude that there has been a reduction in the dietary diversity of Malagasy lemurs with the extinction of the subfossil lemurs. Thus, Godfrey et al. use a dental ecology approach to assess ecological change over time. King et al. take a similar approach in assessing habitat quality at Ranomafana National Park Madagascar. King et al. consider tooth wear rates in two lemur species (*Propithecus edwardsi* and *Microcebus rufus*) living in habitats with varying levels of anthropogenic disturbance. Contrary to their predictions, neither species has higher rates of dental wear in disturbed habitats. They conclude that these data support their earlier work on Edwards' sifaka, which suggested an effect of dental senescence on female reproductive success, and that this pattern at Ranomafana is not a product of a disequilibrium model, as has been hypothesized for ring-tailed lemurs living in the gallery forests of southwestern Madagascar (Cuozzo and Sauther, 2006; Sauther and Cuozzo, 2009).

Another case study in this special issue looks at lemur dental ecology from the perspective of the impact of dental impairment on the ability to process food. Millette et al. provide data on fecal food particle size, and illustrate that ring-tailed lemurs with notable dental impairment (severe wear and/or tooth loss) do indeed produce larger food particles in their feces, as has been described for other mammals (e.g., Lanyon and Sanson, 1986). The implications of this work are far-reaching and have the potential to inform questions about how dental impairment affects an organism's ability to survive, and even to reproduce effectively, as seen in the important, previous work on Edward's sifaka (King et al., 2005). The next step to follow in this line of research is to actually assess the ability of dentally impaired primates to adequately absorb nutrients from the food they process, which will shed further light on the interesting hypotheses presented by King et al. (2005; this volume) and Millette et al.

The final three extant nonhuman primate case studies included in this issue explore a series of questions related to anthropoid primate teeth. Deane considers the anterior teeth, which have been studied less frequently than the postcanine dentition. In this study, incisor curvature and its potential relationship to diet are explored in nine genera of New World monkey to test hypotheses previously developed from work on extant hominoids. As seen in hominoids, incisor curvature increases in frugivorous platyrrhine primates, with the exception of the hard-object feeding pitheciins who frequently use their canines in the initial processing of foods (e.g., Martin et al., 2003). Thus, we see a putative link between feeding ecology and dental morphology in these taxa, which may also have the potential to inform interpretations of fossil primate incisors in the New World and beyond. Next, Wright and Willis assess the connections between incisor and molar morphology and diet among Asian leaf monkeys. They collected primate dental metric and nonmetric data for a large (600+) sample representing 24 species, and combined them with detailed, published feeding behavior data. The major finding of this paper is that dietary predictions based solely on morphology do not match the information from studies of feeding ecology. Wright and Willis suggest that this disassociation between diet and dental morphology reflects such things as the impact of fallback foods on dental morphology, a theme seen in an earlier AJPA special issue focused on fallback foods (Constantino and Wright, 2009), anthropogenic impacts that may alter food availability and use, or the need to emphasize food categorization based on their mechanical properties rather than broad "taxonomic" labels based on food type. Thus, their work illustrates the importance of integrating studies of wild primates with studies of dentition, the analysis of food properties, and documenting fallback food use, whether from living animals or museums samples, to fully understand primate ecology.

Klukkert et al. present a third paper in this special issue that uses dental topographic methods to assess changes and/or variation in wear-related tooth shape. Specifically, they examined three variables (slope, relief, and angularity) in extant chimpanzee subspecies to assess diet-related dental morphology. The primary result of this work is that there are not significant differences between the subspecies in wear-related tooth shape (slope, relief and angularity) at given wear stages. However, though previous work has shown that slope and relief can vary within a species (Dennis et al., 2004; Bunn and Ungar, 2009), these new data on chimpanzees do suggest that angularity (i.e., "jaggedness") may also vary in more worn specimens, in contrast to these earlier studies. This reduction in angularity at the later stages of wear may reflect sampling of teeth that are approaching dental senescence, i.e., the loss of a functioning tooth surface. They also conclude that the lack of significant differences between these topographic variables across the subspecies may support Sussman's (1987) "species-specific dietary hypothesis" which suggests that conspecifics will consume foods with similar properties, thus resulting in similar patterns of wear-related tooth shape across the chimpanzee subspecies.

As a final illustration of the breadth of the dental ecology approach, Grine et al. present a synopsis of early hominin (e.g., "pre-*Homo*") ecology based on analyses of dental microwear and stable isotopes collected from dental enamel. Specifically, this contribution summarizes the most up-to-date information on early hominin diet, utilizing both of these rapidly developing techniques. Notable in this review is the importance of primate field studies for addressing certain questions in hominin paleobiology, specifically related to diet and ecology. In fact, at numerous points in their review, the value of long-term primate field studies is noted explicitly; as we argue above, such studies are central to the dental ecology approach. Among the results presented, a key finding is the discordance of dietary interpretations from biomechanical analyses compared with those from dental microwear and biogeochemistry. This suggests (as do many of the other papers included in this special issue) that the links between ecology, behavior, and dental morphology go far beyond simple relationships. This final contribution further illustrates the role that new techniques play in assessing primate ecology through teeth.

CONCLUSIONS

The papers in this issue provide a broad look at how teeth inform questions of primate ecology and paleoecology. While some may question the need for a new term in the lexicon of dental and biological study, we feel that we are truly entering a new period in the study of animal ecology through teeth. Given the rapid expansion and development of analytical techniques and the number of comprehensive primate field projects that integrate dental study (some of which are entering their third or fourth decade), a more comprehensive and synthetic way of using teeth to study ecology is upon us. One of the key findings of several of the papers is that dietary predictions based solely on morphology often do not match what primates are actually doing in the wild. Thus, while it makes interpretations of fossils more difficult, the dental ecology approach provides a more thorough and accurate portrayal of the relationships between teeth and ecology. We very much hope that this collection of papers on primate teeth from across the order, and their relationship to ecology and behavior among both living and fossil forms, will stimulate future studies that will better elucidate the interactions of primates with their environments.

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