Hypsodonty in Mammals

Evolution, Geomorphology, and the Role of Earth Surface Processes

The evolution of high-crowned teeth, hypsodonty, is a defining characteristic of many terrestrial herbivores. To date, the most prominent focus in the study of the teeth of grazing herbivores has been co-evolution with grasses and grasslands. This book develops the idea further and looks at the myriad ways that soil can enter the diet. Madden then expands this analysis to examine the earth surface processes that mobilize sediment in the environment.

The text delivers a global perspective on tooth wear and soil erosion, with examples from the islands of New Zealand to the South American Andes, highlighting how similar geologic processes worldwide result in convergent evolution. The final chapter includes a review of elodonty in the fossil record and its environmental consequences. Offering new insights into geomorphology and adaptive and evolutionary morphology, this text will be of value to any researcher interested in the evolution of tooth size and shape.

Richard H. Madden is a research professional in the Department of Organismal Biology and Anatomy at the University of Chicago. In over 30 years of studying mammalian ecology, he has spent extensive periods conducting paleontological surveys throughout South America. His current research focuses on geographic variation in tooth wear rates in herbivores and the impact of environmental and geologic processes.

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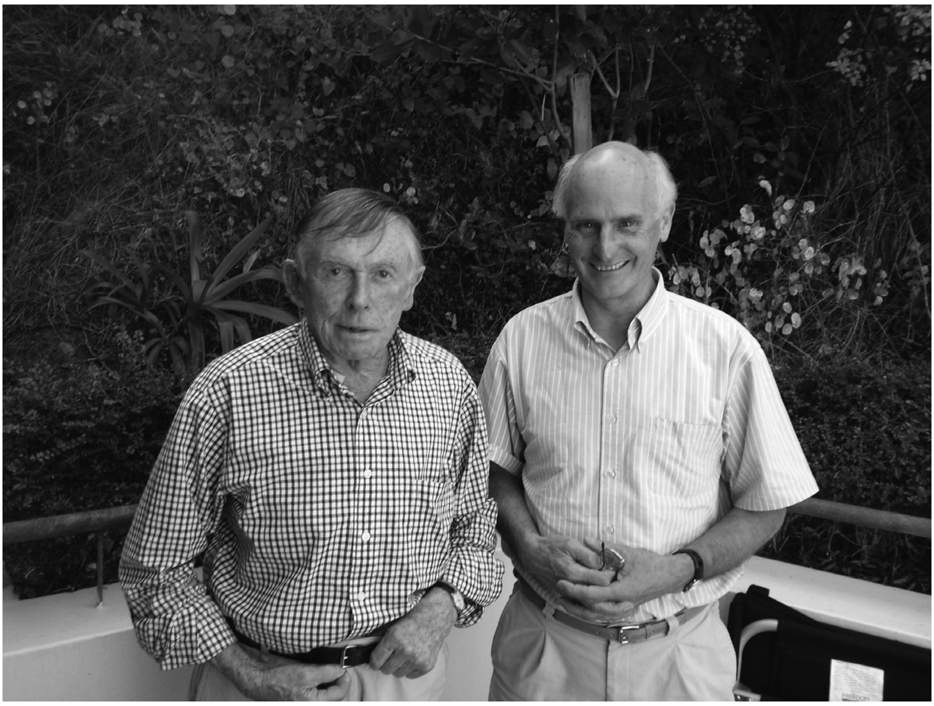

Bernard Healy and Mike Rudge, pioneers in the study of soil ingestion and island comparisons of tooth wear.

For Callum, Fredy, and Guiomar, and the love of Annie, Clay, Kendy, and Regan

Contents

Preface

This work will summarize many years of active research and thinking about an explanation for the evolution of high tooth crowns in South American mammals, and the global path that curiosity has taken me in the search for the causes and broader implications. The subject of the book is nearly iconic in paleontology and is active in the minds of many in evolutionary morphology. The approach used in this book is different. It takes inspiration from diverse disciplines: from the earth sciences (and specifically geomorphology and the study of earth surface processes) to island biogeography, and to the mammalogy, geology, and paleontology of the southern continents in the quest for a universal explanation for both prevalent and unique patterns of tooth shape evolution.

Most recently, impetus has arisen from the fruits of a research project that Cambridge University Press published in 2010 (*The Paleontology of Gran Barranca)*. In many ways, this book is an extension of that work and might be considered a companion volume to that title. . .in effect, this is all the stuff left out of that book for lack of space.

Further impetus has come through the generosity of the National Evolutionary Synthesis Center (NESCent) in Durham, North Carolina, which supported a catalysis meeting in April 2011 on the subject of *Earth Surface Processes in the Evolution of Mammalian Tooth Shape*, to which many attending listened patiently.

The range of life and earth science disciplines incorporated into the whole is diverse, and it has required much effort on my part, as a nonspecialist paleontologist, to approach reasonable familiarity with disciplines this diverse. Moreover, the geographic coverage is vast, and obtaining familiarity with every geography used in the argument has been demanding.

Were the contents published piecemeal in the standard journal format and following the narrow disciplinary strictures of that format, each individual component would become subject to easy criticism, and the case made in each chapter might be dismissed as circumstantial. The deficiencies in each component are not hard to find, and some (in fact, many) are obvious to me. Serious criticism of each component, while perhaps meritorious in the narrow application of each, would probably prove devastating.

Taken together, however, the case for the environmental causation I invoke seems to explain a lot of mammalian tooth evolution, and in its entirety, is far stronger as an integrated theory than its parts taken separately. In other words, the central idea of this book is stronger than the sum of its individual parts.

Adequate explanation requires that we consider two different timescales, ecological and evolutionary. An ecological timescale is a mere day in the life compared with the evolutionary timescale. Excess tooth wear is the pathology that drives the evolution of hypsodonty and elodonty. Etiology, the study of causes in veterinary or animal pathology, is the science that deals with the causes of excess tooth wear. Epidemiology, the study of temporal and geographic patterns of animal health and pathology and their associated factors at the population level, is the cornerstone of this treatise. While it deals with the study of causes, distribution, and control of pathology in animal populations, epidemiological associations or correlations never prove causation; that is, they cannot prove that a specific agent actually causes excess tooth wear.

Causality is the relationship between an event (the cause) and a second event (the effect), where the second event is a consequence of the first. Aristotle distinguished four causes: material, formal, efficient, and final. Although cause and effect typically are related to events, characterizing the causal relationship can be the subject of much debate.

In a causal pathway, there is a natural flow to events and cause precedes effect. Factual causation is established by answering the question: did the agent act in the loss of tooth mineral substance? This is equivalent to finding a phytolith embedded in tooth enamel at the end of a long scratch. On the basis of its morphology, a phytolith could be attributed to a grass plant, but the phytolith may have been ingested along with other soil minerals directly off the soil surface. In this case, the physical cause of this wear event was the phytolith, but the temporal cause of excess tooth wear would be the ingestion of soil minerals.

Concurrent causes where separate acts combine to produce the effect and sufficient combined causes where either would have been sufficient to produce the effect complicate the picture further. As I will argue, there may be concurrent causes, but only one is sufficient to produce the effect. If this one sufficient cause results in extraordinary results in one place at one time, is it fair to hold the actor responsible for all resultant consequences everywhere?

When we ask whether the agents of abrasion are either phytoliths or soil mineral particles, and attempt to distinguish them and weigh their relative roles by proposing to search for distinctive features in the wear striations they produce on the tooth surface, we are demarcating a disciplinary boundary between the life and earth sciences. Either we are trying to establish a claim for the role of botany by restricting the view to substances within the organic foods animals consume, or alternatively, we may be trying to establish a claim for the role of geomorphology by placing emphasis on mineral particles external to the foods animals eat.

To say it is either phytoliths or soil mineral particles is to assert the boundary. Adversarial "either/or" approaches that would look for a smoking gun (or abrasive) embedded in the tooth enamel at the end of a scratch, to prove that one or the other has a dominant role in the evolution of tooth shape, is, in my judgment, a misguided search for legalistic proof and would be fruitless in the face of the complexity of the real world. Why would we expend any energy or resources in an effort to simplify what are naturally complex processes, especially when we have tools at our disposal for managing complexity? To assert that one or the other dominates tooth wear (and thereby partake in a dialog in paleontology that perpetuates a false dichotomy but a convenient straw man), denies the ability of science to manage complexity and diminishes appreciation for the complexity of the thinking of scientists.

When it is observed that suspended sediment yield cannot possibly have anything to do with soil ingestion or tooth wear, and that most tooth wear occurs when the animal grazes not when soil mineral particles are being swept downstream, the same disciplinary boundary between life and earth sciences is being demarcated to establish a claim against the role of geomorphology in evolution.

For zoology, what I propose does not deny the role of animals in both creating and modifying the interaction between their oral environment and the external environment. Animals are active agents that live on the surface of the Earth and interact with it. To claim that food texture and food physical properties drive the evolution of tooth shape arises from the obvious fact that what is important about diet is the energy and nutrients animals derive from the food they eat. This is certainly true and it is only rational that the shape of teeth is related to the requirements of reducing the foods animals eat.

What I am definitely not saying, however, is that zoology, botany, and geomorphology have nothing to do with mineral particle ingestion or tooth wear. There is a role for earth surface processes in the delivery and movement of mineral abrasives through the animal's environment, but ultimately, animals must be the active agents that bring these soil mineral particles into their mouths.

Much of the lack of a history of the idea could be described as a consequence of the tension at the boundary between these traditional disciplines. We have ignored the role of earth surface processes in tooth evolution, much like we have ignored the role of the earth system on human economic activity. Changing the way we think about tooth evolution is like changing the way we think about climate change; we confront the entrenched interests that benefit from ignorance. Disciplinary boundaries in the funding of life and earth science still exist.

However, pervasive evidence for the evolution of many conspicuous features of tooth shape makes it equally certain that much of tooth shape evolution has been driven by abrasive wear. It may be that tooth mineral substance itself evolved in response to the confrontation inherent in the interaction between life and the Earth's surface.

We do not live outdoors, and we have little to no idea what the experience of living outdoors entails. If you have ever been a Scoutmaster trying to teach urban children (and their parents) how to experience life outdoors, you will know what I mean. There is a huge disconnect between the urban and natural worlds, and many are afraid of the outdoors.

If we are lucky, we occasionally do fieldwork. True lovers of fieldwork who spend long intervals outdoors over many years are few and far between and seem to be getting fewer all the time. Fewer still travel outdoors extensively, so even fewer have had the experience of living outdoors in diverse environments. Most highly paid experimentalists and most theoreticians in our discipline do not do so, and the museum collection or herbarium is as close to the outdoors as they get. While it is my belief and my hope that fieldworkers have a better appreciation of the things I am talking about, I am not sanguine about the prospect that others have.

I have done a lot of paleontology fieldwork, over 54 times in South America, almost all of it in the Andes. I do not know how many days and nights I have spent outdoors in the Andes, but conservatively, I would guess about 2000. I have worked in Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, and Argentina, and during that work, have traveled and walked over much of the cordillera. What I have seen, and my cumulative experiences have shaped my understanding of the natural world.

Soil ingestion is acknowledged to contribute to tooth wear, but is rarely an area of active study. Why? In domestic animal husbandry, effective management solutions for excess tooth wear are known and used every day. Stocking rates are adjusted and the animals are provisioned during harsh seasons. Consequently, excess tooth wear is not a problem of active interest because it is a problem that can be solved. Excess tooth wear in Patagonia is solved by sending older animals out of the "roaring 40s" in the Southern Volcanic Zone to lower latitudes for final fattening. Excess tooth wear is solved in New Zealand by carefully controlling the season of exposure. Excess tooth wear is solved in Australia by careful attention to stocking rates in winter.

Our own experience is also wrapped tightly by food preparation. This is big industry. Washing harvests and preparing and packaging foods prevent soil contamination and shield us from experiences that might wear out our teeth and open our eyes.

All the diverse ethnic cuisines that thrill the palate and all of ethnography's description of human diet variation document an impressive array of cultural diversity in food handling. However, ethnographers rarely if ever describe the mineral grit in the human diet and it is not evident by their accounts. Archaeologists also spend considerable effort in understanding the long history of changing human diets and cultural activities associated with food procurement, gathering, preparation, and consumption. One thing we can conclude from all this is that humans put a lot of effort into avoiding dirt.

So does evolution. A lot of physiological and structural adaptation involves the avoidance of mineral grit and windborne particulates. Eyelids, the nictitating membrane, lacrimal apparatus, guard hairs around the nostrils, vermillion lips, orbicularis oculi and oris, histamine reactions to dust, the sneeze reflex, coughing, and outsized salivary glands with ducts that deliver saliva at the point of contact between tooth surfaces are all adaptations to an environment rich in mineral particles.

This whole idea that earth surface processes may have a role in the evolution of tooth shape has been building for thirty years. As the idea for this book began to take shape and throughout its gestation, I have been plagued with doubts about it. I do not see this idea as displacing any pre-existing ideas about tooth shape evolution. Too much good work has been done and too many interesting and plausible ideas have been voiced. All these ideas seem worthy and all of them probably true for some times and some places. The only new insight really is that the sedimentary rocks in which we find fossils may preserve something besides the fossils, something so obvious that we have overlooked it: the mineral particles that shape teeth.

The relationship between mineral particles and tooth shape (or at least many features of tooth shape) seems to be direct, was "discovered" in many different ways and in many different places, and can be expressed in many different graphical forms over many different timescales. If the idea of this relationship is original, then the question becomes: why have we missed it? There are many possible reasons and a host of suspicions fill my mind.

As will become evident, the edifice is built upon vulnerable foundations. The weakest and most vulnerable parts of the foundation are my own limitations. This is a very deeply seated doubt that keeps me humble, and until now has kept me silent. While there are benefits to silence (peace of mind, room for contemplation and better concentration, more maturity, and time to complete laborious tasks and make more ambitious collections), there are also costs.

In many ways, none of the ideas in this presentation are my own. I borrow shamelessly, and maybe sometimes without attribution, and I apologize for this. The fact that the pace of accumulating ideas, images, and experiences seems to be accelerating, is no excuse.

Finally, as I grow older, I appreciate that the idea is more important than the purveyor. If the idea is to have any future at all, it must be aired and preferably to an audience in the best position to judge. This audience, hopefully, will include specialists from the disciplines I borrow from so shamelessly, as well as young people with critical minds and fresh energy.

There are only two directions to take the idea now, and these are plausibility and universality. Plausibility is to be judged by the reader; universality is to be tested in the field. Readers taking their own path through the thicket of the text must examine the relationship in terms of a complex exercise in mass balance between sediment source and its ultimate sink on the sea-floor. In the balance hangs the mineral particle flux that passes through the mouths of herbivores. For universality, we must take the best tools possible to diverse islands where we will find the empirical truth and the limitations of its expression. We must measure soil loss, soil ingestion, and tooth wear rates, on each and every one of these islands, and we must compare among the islands to learn where the evolutionarily significant differences reside. It is growing late. Goats and rabbits are being eradicated from islands, and many, too many islands have been and are being liberated from their burden.

Note: The editors requested that the term “hypsodonty” be used in the title of this book because of the popularity of the term. To a paleontologist, hypsodonty conveys more precise meaning. I try to explain my use of the term hypsodonty and related terms like elodonty for expressing tooth shape evolution where appropriate in the text. Once defined, I also try to be consistent throughout.

How to read this book

Chapter 1 is important, as it defines the problem and sets the stage for the remainder of the book.

Chapter 2 provides a lot of background to the South American fossil record. However, the chapter also has many details about the Patagonian fossil record of the “precocious” evolution of tooth crown height and these details can be tedious, and can be skipped by readers not familiar with the South American fossil mammal record.

Chapter 3 explores the broad patterns of association between the prevalence of high-crowned teeth in South American mammals, and a host of environmental variables. Some of these associations suggest a role for earth surface processes. Additionally, broader global patterns are examined, and these serve to confirm this suspicion.

Chapter 4 begins with a history of the study of excess tooth wear in New Zealand. Then, it presents the evidence for temporal and geographic variation in tooth wear and soil ingestion on the North Island. This is followed by a discussion of El Niño–Southern Oscillation (ENSO) interannual climate cycles and erosion. Suspended sediment yield, the fine-grained sediment transported in suspension by rivers that varies with erodibility is highly correlated with annual tooth wear. The lake sediment record of rainstorm deposits varies with decadal timescale phases in the intensity of ENSO and suggests how longer-term variation in erosion has its expression in soil ingestion and tooth wear.

Chapter 5 examines the only available long-term study of tooth wear in dry climates, in southeastern Australia. This evidence is equivocal. There are suitable routing systems and a sediment cascade is evident, but there is little concrete evidence for its action on tooth wear. While much that was ingested was ignored during this classic study (and one wonders why), there is room for a contribution from earth surface processes. Australia is a unique continent, and today has only a very thin mantle of surface sediment available for these processes. During deglaciation phases of the Quaternary, however, this system did operate and may have contributed to slow tooth size evolution in modern humans.

Chapter 6 describes the evidence for independent evolution of tooth crown height in insular mammals on islands in the Mediterranean. The fossil record of mammal evolution on these islands is remarkable, although probably deficient for any serious study of surface processes in the past. Islands are not usually hospitable for the preservation of fossil records, but the energy and persistence of paleontologists is legendary and the allure of islands too great to convey through mere words. This chapter also makes a comparison of tooth wear in feral goat and sheep populations from three small islands in the South Pacific with contrasting vegetation and soil erosion regimes. These examples suggest a way forward.

Chapter 7 turns from the ecological to the evolutionary timescale and examines the fossil record of tooth shape evolution in the Plio-Pleistocene of East Africa. This may be the best fossil record of tooth shape evolution on Earth. Tooth shape evolution in many lineages of mammals can be followed here, unlike almost everywhere else on Earth. This record is made even more compelling because of the close coupling between this terrestrial fossil record and the downwind terrestrial sediment record on the sea-floor of the Gulf of Aden and North Arabian Sea. Here it is possible to track the intensity of surface processes as they deflated, entrained, transported, and then deposited surface mineral particles onto the sea surface and eventually the sea-floor. This remarkable record of the source-to-sink sediment cascade allows the capture of detailed records of volcanic eruption frequency, the intensity of erosion and surface winds, the flux of mineral particles through the atmosphere, and their consequences for the evolution of tooth structures that serve to prolong the functional utility of the dentition.

Chapter 8 provides some arguments for asserting that records of tooth wear and tooth evolution on islands provide meaningful inspiration and new tools for reconstructing and understanding broadly similar mechanisms as preserved in less continuous records elsewhere, particularly in Patagonia and the Southern Ocean. This chapter presents an example of the application of these principles to the fossil record in deep time, in particular, the middle Cenozoic record of tooth shape evolution in Patagonia. This is one of the few records that captures tooth evolution in clades of mammals in deep time, and in the context of a rich geology and paleooceanography.

Chapter 9 explores elodonty, and is more speculative. It presents some thoughts about the evolution of ever-growing teeth and their possible significance to earth surface processes. Of the 26 clades of mammals that evolved high-crowned teeth in South America, half of them went on to evolve ever-growing teeth. The significance of the evolution and appearance of completely elodont dentitions in so many mammals is explored. Eventually this exploration turns the relationship around, and points out how elodont herbivores may have left an important and unique signal in the history of surface erosion.

The final chapter attempts to summarize what I think I have learned.

Acknowledgments

Where to begin?

It all began with Richard Frederick Kay, my professor, mentor, colleague, and friend. Nobody could ever have inspired work on the relationship between tooth shape and the environment in a more disinterested and informed way. The subject of tooth shape evolution has been Rich's life, and I am a mere usurper into his domain. He has graciously made space for me by providing intellectual life and liberty. Others at Duke tolerated my presence, and I will be forever grateful to Matt Cartmill, Elwyn Simons, Paul Baker, Dan Livingstone, John Lundberg, Joseph Bailey, Steve Churchill, and Naomi Quinn for their many courtesies and inspiration.

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It is so obvious, but it needs to be said, that nothing gets done in science without the work of librarians. Their work has changed mightily over time, but the whole edifice of knowledge is organized and maintained by their devotion. Only through their work and the custodial function of university libraries, is it possible to check bibliographic citations 30 years after having read something interesting.

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To think I might actually have provided meaningful service to these institutions is almost beyond belief, and that this service could be performed in the noblest setting humanity has imagined, surrounded by the best students in the world is beyond words. Assaults on intellectual freedom be damned, here I will stand at the barricades.

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