DENTAL FUNCTIONAL MORPHOLOGY

How Teeth Work

Dental Functional Morphology offers an innovative alternative to the received wisdom that teeth merely crush, cut, shear or grind food, and shows how teeth adapt to diet. Providing an analysis of tooth action based on an understanding of how food particles break, it shows how tooth form from the earliest mammals to modern-day humans can be understood using very basic considerations about fracture. It outlines the theoretical basis step by step, explaining the factors governing tooth shape and size, and provides an allometric analysis that will revolutionize attitudes to the evolution of the human face and the impact of cooked foods on our dentition. In addition, the basis of the mechanics behind the fracture of different types of food, and methods of measurement are given in an easy-to-use appendix. It will be an important sourcebook for physical anthropologists, dental and food scientists, palaeontologists, and those interested in feeding ecology.

Peter W. Lucas is a professor of anatomy at the University of Hong Kong. He is particularly interested in the function and evolution of mammalian teeth, but he also studies the factors involved in food choice, particularly in primates.

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PETER W. LUCAS
University of Hong Kong

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To my wife Mariati and my daughters, Katherine and Diana,
with my everlasting love

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Preface

Teeth cause such dreadful problems in humans that interest in them by non-dentists would seem both unlikely and unhealthy. Who could get excited about tooth decay and gum disease? The physical reality of such apparently moribund structures is paralleled in our cultural perception of them. Diseased or not, the whole mouth is viewed as an unclean region of the body in most parts of the world, especially when it is crammed full of food. Parents, particularly in Western countries, often train children to keep their lips sealed when they are eating even though this is difficult to follow exactly and, indeed, little food seems to re-emerge if the instruction is disobeyed. It is debatable if this training is necessary. While it is possible to sit next to someone at a banquet and get sprayed with seafood, for example, from his or her mouth, the nutritive loss to the diner, represented by the sum of those fine particles, seems negligible compared to what is obviously going down their throat. This is a clear sign of the efficiency of the chewing process. The main reason, in fact, that food particles are expelled is that the person is talking while chewing. Talking involves the expiration of air and that is what pushes food particles forwards. This may seem a strange example but it makes a strong point: the thought of even catching sight of food that was, a moment previously, decorating a plate evokes visceral feelings (of a somewhat inside-out kind) rather than artistic ones. The plate, too, seems to lose its appeal after most food has disappeared and may be quickly consigned to the wash. In short, we appear often to be embarrassed, if not disgusted, by the major biological function of feeding and the need that underlies it, although we don't go as far in hiding it from social view as we do activities at the other end of the gut. Presumably, an intuitive understanding of hygiene explains that disparity, but restrictive practices about eating pervade most human societies and, according to an intriguing account by Visser (1991), have many cross-cultural features that are not easily explained on grounds of hygiene (the latter, of course, preoccupies developed societies: Lacey, 1994).

So why write a book on how teeth work? I answer this, not by seeing any disguised elegance in the appearance of a good feed, or in the avocation of new table manners, but by admitting and attempting to transmit through this book a personal fascination with the fundamental role that teeth have had in our evolution and my dissatisfaction with current explanations on both how they work and why they evolved.

How do teeth work? One relatively uniform answer to this is already provided in numerous accounts in top journals, encyclopaedias and even school texts. It is that teeth variously crush, cut, shear or grind food. And with slight complications, that is more or less the prevailing wisdom in dentistry, zoology, palaeontology, anthropology and many other biological fields (with the eminent exception of food science). Despite apparent unanimity, these accounts are completely wrong. A genuine analysis of tooth action, one that could possess explanatory power rather than glib description, starts in the still somewhat obscure world of fracture mechanics – in the understanding of how food particles break. Such an analysis is not likely to be as edible as slogans like shearing or grinding: inevitably, analytical depth requires more than the coining of facile words and phrases.

The action of the teeth cannot be separated from that of the mouth, so an attempt is made consistently to understand oral processing as whole. However, this is the oral processing of solids, not liquids. The ingestion of liquids like nectar and honey is all tongue and no teeth, and drinking is actually not that common an activity in mammals – certainly not in primates – once they grow up. The process of growing up, of development, is not discussed, so those interested in suckling and weaning and how the young cope will not find anything on it. The largest body of information to be excluded here though is neurobiology: there is no space to include much of it here and some of its alleys seem currently to be very dark.

I am sensitive to the knowledge that the further the book sinks into a world requiring the learning of new terms, the more potential readers will be lost. Accordingly, I have tried to present my viewpoint in as simple a way as possible, deliberately seeking light generalization rather than long and dark specifics. One of the worst aspects of biology is the plethora of terms that it employs. If I added a full suite of terms from mechanics, then the book would be a slow read. Sensitive to this, I have made a deliberate effort to reduce the number of terms to a minimum. The overall intention is to provide a fundamental analysis of the feeding apparatus of mammals, based on the interface between outside and inside, i.e. the contact between foods and teeth. If this interface is properly understood, then I contend that the optimal design of the working surface of teeth, the organization of the structural support for this surface and the production of bite forces by muscles that move it – all should follow in a predictable way. If this analysis succeeds, then it should open the way to a fundamental understanding of the evolution of feeding adaptations in mammals. On the plus side, I hope that this book will be of value to anyone in bioscience with an interest in feeding. On the debit side, I will undoubtedly have made some dreadful mistakes and may sometimes appear uncharitable to those with other views. However, the book is meant to be constructive and, in this sense, research life has some resemblance to a game of chess: no one ever excels by just making moves that have been seen before. Unless I am mistaken, a lot of the 'moves' recorded here are new.

I hope that this book offers a cohesive framework on the function of teeth. For dentists and those basic scientists whose work might be covered by the term 'oral biology', this is an account of how teeth break foods down, untainted by the modern reverse trend. For food scientists and those concerned with food texture, it is about oral physics, on which psychophysical investigations of food texture can be superimposed (see Chapter 7). Common to both dentistry and food science has been a strong interest in 'applied science'. Whereas dentists look at patients, food scientists look at consumers. However, dental surgery exists as a discipline entirely separated from medicine because the dentition is the one area of the body requiring regular surgery. It can be argued then that in many parts of the world, 'the patient' is also 'the consumer'. Both dentists and food scientists might benefit from basic models of oral processing in order, on the one hand, to predict the outcome of surgery or, on the other, to provide a foundation for psychophysical investigations of food texture. Until recently, there was very little cross-talk between these disciplines in most countries (I exclude Japan from this), something possibly caused by lack of a sufficiently overarching viewpoint. For ecologists, I describe the actual mechanical properties of foods that could influence dietary niches and feeding rates. For materials scientists, it may provide some information on a restricted group of biomaterials – foods. For palaeontologists and those concerned with the evolution of the feeding apparatus in a wide group of organisms, the hope must be that enough is explained here to help in the generation of general theories for evolutionary change.

It seems a book tradition to tell people where they can find articles on its subject matter. Each of the above fields has scientific journals responsible for the vast literature on the structure and function of mammalian teeth, but if the definition of this book's scope is taken to encompass feeding, then the answer to this is really just about anywhere, even in physical sciences. Well-cited journals here include the *American Journal of Physical Anthropology*, *Archives of Oral Biology*, *Journal of Dental Research*, *Journal of Human Evolution* and *Journal of Texture Studies*. Some, such as the *Journal of Prosthetic Dentistry*, are underrepresented because of their clinical slant. Unfortunately, in recent years, there is another candidate for this roll of honour, one that likes to bestow its own credits. The *Annals of Improbable Research* has devoted much of its space to feeding research and several papers have won IgNobel awards. Sometimes, this recognition is truly deserved, but the frequency with which food research gets treated this way in the journal seems to suggest that its contributors are actually obsessed with the field too, although clearly from a different perspective.

The problem with being sure about scientific novelty is the need to wade through the mounds of information that modern biology accumulates so rapidly. Really, there is too little time to sit down with the enormous body of relevant literature to see if a theory fits well with the evidence or, alternatively, casts it into serious doubt. The purpose of this book is overtly to try to bring together some of these piles according to the overarching theoretical model that dominates the book. Anyone who reads it will probably know some of the areas that I have explored here, and in particular areas of expertise, may well know more than I do, but what I am banking on is that few will be acquainted with the full scope of this book.

One of the great benefits of writing this, afforded for the only time in my career, is the space that it provides in the preface to thank those who have been seminal influences. I am very grateful to some of the great men of materials science and biomechanics who sat down and just had a word (or several) with me. To give their names would be to suggest that they might support some of what is written here or even know about it at all. They don't necessarily know in either sense, so the temptation to thank them by name is resisted. Early influences are always the strongest. Of these, Bob Martin was extremely important in directing my thoughts as an undergraduate at University College London. As a postgraduate, the seminal influence was Jeffrey W. Osborn. Although we overlapped at Guy's Hospital for only 18 months, his influence was so powerful that it pervades the book. He was, and still is, the greatest of teachers and the most powerful thinker that I have ever met: I am grateful for the chance to thank him here. I should have learnt from Jeff just how hard it is to write a coherent book in uniform style, but I didn't. Although his research papers and a (now out of print) co-authored book called *Advanced Dental Histology* (many editions, published by Wright, Bristol) have probably been most influential, a much underrated (also out of print) book for dental undergraduates that he edited, entitled

Dental Anatomy and Embryology (Volume 2 of *A Companion to Dental Studies*, edited by A. H. R. Rowe & R. B. Johns, Blackwell, Oxford, 1981) has provided a magnificent general guide while writing this book. I would also like to thank Karen Hiiemae for getting me started in research, for persevering with me and for offering general advice on research directions. The subtitle of the book is adapted from an article by A. W. Crompton and K. Hiiemae, entitled 'How mammalian molar teeth work', published in *Discovery* (Yale University) **5**: 23–34 (1969). Douglas Luke helped me survive and turned me from a neophyte into, well . . . into something else. He also kept me in the business by pushing me to apply for a postdoctoral fellowship, which led to several years of joint publication.

Despite all this, if I had to pinpoint any particular period when I began to feel comfortable and capable in research, then it would have to be nine years spent in the Department of Anatomy at the National University of Singapore. I am eternally grateful to all the members of that department and to Professor Wong Wai Chow, its then head, for supporting me while I grew up. I miss that department and its staff very much and would like to take this opportunity to offer my greetings to them. In particular, I recall with gratitude, the advice offered in many conversations by Samuel Tay, Gurmit Singh and K. Rajendran (acknowledged for Fig. 2.17). To the current head, Professor E. A. Ling, I wish you all the best in your energetic leadership of the department. Mark Teaford was for a long time a co-author of this book. His sense of perspective and great friendship has helped sustain me through many crises of confidence. Mark very kindly read through much of the text and helped correct and clarify it in many areas. Through both Singapore and Hong Kong, I have collaborated at length with Richard Corlett, who taught me ecology. Brian Weatherhead brought me to the University of Hong Kong: thanks a million to you, Brian, and to the Anatomy staff here. I have had a warm working relationship with Brian Darvell in Dental Materials Science for most of my 10 years here, and also with his technicians, Paul Lee and Tony Yuen. Together, they designed the HKU Darvell field tester, described in Appendix A. A long-term collaboration with Iain Bruce in Physiology has also been very stimulating and fruitful. In recent years at the University of Hong Kong, I have been lucky enough to associate with several PhD students (Choong Mei Fun, Nicola Parillon, Jon Prinz, Kalpana Agrawal and Nathaniel Dominy) and postdoctoral fellows (David Hill and Nayuta Yamashita), all of whom have had great influence on me. Of these, Jon and Nate have been towering influences. P. Y. Cheng has worked with me for 11 years: I am deeply grateful for all his help. Recently, a medical student with strong palaeontological leanings,

Sham Wing Hang, has done a lot to focus my thoughts clearly. I am deeply grateful. In addition, I have benefited greatly from interaction with Kathryn Stoner and Pablo Riba during the 'Pantropical Primate Project'. For help during production of this book, I thank Eastman Ting, for several pieces of artwork that set the style, and Johnny Leung for photographs. Henrique Bernardo (rickybernardo@hotmail.com) did the cover and offered much helpful advice. Gavin Coates (gavincoa@netvigator.com) created the flick art. In addition, I would like to thank for either direct help or inspiration: Holger Preuschoft, Charles Peters, Roland Ennos, Walter Greaves, Patricia (Trish) Freeman, Mikael Fortelius (for lengthy correspondence as well as his papers, the influence of both of which permeates the book in many places), Josefina Diaz-Tay, Robin Heath, Jukka Jernvall, Michael LaBarbera, Mark Spencer, Peter Ungar and Chris Vinyard. I am also extremely grateful to Dr Rob Hamer (Wageningen Centre of Food Sciences) for inviting me to a food summit in Wageningen in November 1999, without the influence of which this book would not have been finished. I had the great privilege there of meeting many of the greats of food science, such as Drs Alina Scszesniak and Malcolm Bourne.

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Finally, to Tracey Sanderson and Cambridge University Press, thank you very much for sticking with this. To my mother and my extended family back in England, thank you for all your support. Lastly, and most importantly, to members of my immediate family, my wife Mariati and my daughters, Katherine and Diana: you have supported me loyally throughout my career and I simply do not have the words . . . emotions are better and mean much more.

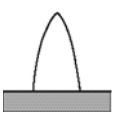
Flickart

A flick-page animation starts here, illustrating the evolution of the human lower molar from the single-cusped tooth of an early synapsid that lived about 300 million years ago. The sequence is designed to 'morph' between existing fossils and may, inadvertently, involve variation off the main lineage. It is hardly possible to know for sure, but only basic features are shown anyway. Some partial restoration of cusp form has been necessary for fossils with worn teeth. The timescale is kept relatively even, so some changes are more rapid than others. Only the evolution of the lower molars is figured because that of the upper molars is more complex. The original names for their cusps, given in the nineteenth century (Osborn, 1888), make no evolutionary sense and tend to confuse.

Each diagram shows the jaw bone in grey with tooth crown evolution displayed above it. The tooth is viewed from the lingual aspect. The mesial side of the tooth is always to the left. Root development is indicated only by the bifurcation into two roots a little further on. Note though that the earliest teeth in the sequence did not have roots.

The trends in the animation can be noted as follows:

(1) A single-cusped reptiliomorph tooth, equivalent to the protoconid cusp of a mammalian molar, is the sole initial cusp. It always forms first, even in living mammals, and is generally very large.
(2) Two separate cusps form on either side of the protoconid. These are the mesial paraconid and the distal metaconid. Early mammaliaforms had this 'three-in-a-line' molar form.
(3) A small shelf develops low down on the crown. This is the cingulum.
(4) The three cusps then triangulate by relative movement of the paraconid and metaconid to form a trigonid. This tooth form is called a 'tritubercular' molar.
(5) The cingulum extends distally to start forming the talonid, a shelf that starts to develop three cusps. The resulting six-cusped tooth is a



'tribosphenic' molar from which those of all living therian mammals have adapted.

(6) On the primate lineage towards humans, the cingulum and paraconid are lost. The talonid evens up in height to match the remnants of the trigonid. Late on, all the cusps become blunter and reduce in height.