Functional Dental Morphology of Insectivorous Microchiropterans: Spatial Modelling and Functional Analysis of Tooth Form and the Influence of Tooth Wear and Dietary Properties

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Frontispiece: Reconstruction of the upper second molar of Gould's Wattled Bat *Chalinolobus gouldii*.

Table of Contents

LIST OF TABLES 7

LIST OF FIGURES 9

LIST OF PLATES 11

ABSTRACT 13

GENERAL DECLARATION 15

ACKNOWLEDGEMENTS 17

CHAPTER 1. INTRODUCTION 19

- 1.1. Functional Morphology 19
- 1.2. Recent Approaches in Functional Dental Morphology 20
- 1.3. Engineering and Tooth Function 21
- 1.4. Dilambdodont and Tribosphenic Tooth Function 24
- 1.5. Tooth Wear 25
- 1.6. Insectivore Dietary Properties 26
- 1.7. Microchiropterans 26
- 1.8. Three-dimensional Tooth Modelling 27
- 1.9. Structure of Thesis 27

CHAPTER 2. THE TOOTH OF PERFECTION: FUNCTIONAL AND SPATIAL CONSTRAINTS ON MAMMALIAN TOOTH SHAPE 33

- 2.1. Introduction 33
- 2.2. Materials and Methods 34
  - 2.2.1. Definitions 34
  - 2.2.2. Modelling tooth shapes 37
- 2.3. Results 39
  - 2.3.1. Functional parameters 39
  - 2.3.2. ‘Anatomical’ constraints 41
- 2.4. Discussion 42
  - 2.4.1. Functional merits of model tools 42
  - 2.4.2. Relationships between model shapes and real tooth shapes 43
  - 2.4.3. Dietary properties 45
  - 2.4.4. Interactions of constraints 46
  - 2.4.5. Tooth modelling 47
- 2.5. Conclusions 47

Chapter 3. Spatial and Functional Modelling of Carnivore and Insectivore Molariform Teeth 53
3.1. Introduction 53
3.1.1. Occlusal geometry 55
3.2. Methods 55
3.2.1. Models 57
3.3. Results 58
3.4. Discussion 69
3.4.1. Influence of protocone on tooth shape 69
3.4.2. Comparisons of models and real teeth 70
3.4.3. Autocclusion 72
3.4.4. Therian molar modelling 74
3.4.5. Tooth modelling 75
3.5. Conclusions 76
Chapter 4. Confocal Imaging, Visualisation and 3-D Surface Measurement of Small Mammalian Teeth 79
4.1. Introduction 79
4.2. Materials and Methods 80
4.2.1. Moulding 80
4.2.2. Casting 81
4.2.3. Imaging 81
4.2.4. Visual representation 84
4.2.5. Measurement 84
4.3. Results 86
4.3.1. Imaging 86
4.3.2. Visual representation 86
4.3.3. Measurements 86
4.4. Discussion 86
Chapter 5. Connecting Morphology, Function and Tooth Wear in Microchiropterans 91
5.1. Introduction 91
5.2. Functional Parameters 93
5.3. Materials and Methods 94
5.3.1. Tooth wear 94
5.3.2. Functional parameters 95

5.3.3. Statistical methods 98
5.4. Results 99
5.4.1. Functional parameters 99
5.4.2. PCA and NMDS 102
5.5. Discussion 113
5.5.1. Functional parameters 113
5.5.2. Crest size 115
5.5.3. Shape and function maintenance during wear 116
5.5.4. Functional relationships of attrition and abrasion of crests 117
5.6. Conclusions 119
CHAPTER 6. THE MATERIAL PROPERTIES OF INSECTS IN RELATION TO INSECTIVORY: CUTICLE THICKNESS AS AN INDICATOR OF INSECT 'HARDNESS' AND 'INTRACTABILITY' ... 121
6.1. Introduction 121
6.1.1. 'Hardness' 122
6.1.2. Materials and structures 124
6.1.3. Cuticle structural properties 127
6.2. Methods 129
6.2.1. Biomechanical properties of cuticle 129
6.2.2. Cuticle thickness in bat faeces 130
6.3. Results 131
6.4. Discussion 138
6.4.1. Cuticle thickness as a measure of biomechanical properties 138
6.4.2. Biomechanical properties of beetles and moths 141
6.4.3. Insect biomechanical properties 142
6.5. Conclusions 145
CHAPTER 7. DENTAL SPECIALISATION IN INSECTIVOROUS MICROCHIROPTERANS CONSUMING 'INTRACTABLE' AND 'TRACTABLE' INVERTEBRATES 147
7.1. Introduction 147
7.2. Methods 149
7.2.1. Study species 149
7.2.2. Functional parameters 150
7.2.3. Statistical methods and size correction 150
7.3. Results 151
7.4. Discussion 163
7.4.1. Three hypotheses 163

7.4.2. Biomechanical properties and tooth form in previous studies 168
7.4.3. Additional differences in tooth form 171
7.5. Conclusions 172
CHAPTER 8. THE SCALING OF TOOTH SHARPNESS 175
8.1. Introduction 175
8.2. Functional Scaling of Tooth Sharpness 175
8.3. Processes that Influence Tooth Sharpness 177
8.4. Empirical Data on Tooth Sharpness 180
CHAPTER 9. DISCUSSION 187
9.1. Comparative Function of Protoconoid Tooth Forms 187
9.2. Comparative Function in Protoconoid and Carnassial Tooth Forms 190
9.3. Effect of Size and Diet on Gross Morphology 193
9.4. Thesis Conclusions 196
9.5. References 198
PLATES 215
APPENDICES 221

List of Tables

Table 2.1. Shape and functional parameters for points and blades 37

Table 2.2. The important functional advantages of the protoconoid 43

Table 4.1. Measurements from scans of upper second molar of three specimens of *Chalinolobus gouldii* 86

Table 4.2. Relationship between resolution, number of scans accumulated at each z height and the time taken to scan 88

Table 5.1. Functional parameters relating to cusps for paracone and metacone for three wear states in *C. gouldii* 103

Table 5.2. Functional parameters relating to upper molar ectoloph crests for three wear states in *C. gouldii* 104

Table 5.3. Cusp occlusion relief and fragment clearance for paracone and metacone basins and trigon groove for three wear states in *C. gouldii* 105

Table 6.1. Results of regression analyses for logged values of cuticle thickness vs punch strength, specific punch strength, work to punch and specific work to punch according to insect and sclerotisation...132

Table 6.2. Species means of median and maximum thickness of cuticle fragments in the faeces of microbats, and number of fragments/mg...133

Table 6.3. Published reports of diets for species in Table 6.2 that were investigated using the cuticle thickness measurement technique 134

Table 7.1. Diets of the intractable (I) and tractable (T) feeding species examined in this study 153

Table 7.2. Functional parameters relating to cusps for paracone and metacone for six species of intractable and tractable feeding bats 155

Table 7.3. Functional parameters relating to upper molar ectoloph crests for six species of intractable and tractable feeding bats...156

Table 7.4. Cusp occlusion relief and fragment clearance for paracone and metacone basins and trigon groove for six intractable or tractable feeding species...................157

Table 7.5. Results of statistical comparisons of functional parameters within three microchiropteran families...158

Table 8.1. Two isometric animals, A and B, of length *l* and 2*l*, respectively, and their proportions for features that relate to tooth function...176

Table 9.1. Comparison of functional features in upper protoconoid-based tooth forms ...190

Table 9.2. Comparison of features that function in carnassial and protoconoid-based tooth forms 193

List of Figures

Fig. 1.1. a) Dimensions of a single-point cutting tool; b) one type of chip breaker on a cutting tool designed to help clearance of fragments 29

Fig. 2.1. Tool design features. 36

Fig. 2.2. Single-bladed tool shapes and shape and functional parameters 38

Fig. 2.3. Double-bladed tool shapes and shape and functional parameters. 40

Fig. 2.4. Anatomical criteria for tool design 42

Fig. 2.5. Comparisons between the models and real mammalian tooth forms 44

Fig. 2.6. Putative relationships between tooth functional characteristics 46

Fig. 3.1. a) The ‘reversed triangles’ model of molar occlusion. b) The Crompton and Sita-Lumsden (1970) model of therian molar function 60

Fig. 3.2. Simple single-bladed models used as starting points for modelling mammalian teeth 61

Fig. 3.3. Simple double-bladed models used as starting points for modelling mammalian teeth 62

Fig. 3.4. Crest shapes that are possible for occluding upper and lower teeth with blades when the lower moves along a linear occlusal vector 63

Fig. 3.5. Modified models of mammalian tooth forms 64

Fig. 3.6. The effect of wear and crest shape on the alignment of occluding notches 65

Fig. 3.7. Improved model of dilambdodont molars 66

Fig. 3.8. Three-dimensional reconstruction of model shown in Crompton and Sita-Lumsden (1970) 68

Fig. 4.1. Two views of the standard glass specimen for moulding, casting and imaging.... 81

Fig. 4.2. Surface scans of standard glass specimen 82

Fig. 4.3. Relationship between number of scans and surface noise in scan for two different surface noise-reduction methods 82

Fig. 4.4. Surface data representations of upper second molar of *Chalinolobus gouldii* 83

Fig. 4.5. Virtual reality modelling language reconstructions of upper second molar of *Chalinolobus gouldii* 84

Fig. 4.6. Virtual reality modelling language reconstructions of occlusion of upper and lower molar rows in *Chalinolobus gouldii* 85

Fig. 5.1. Rake angle, relief angle, wear land and edge sharpness of a crest viewed end-on 106

Fig. 5.2. 3-D reconstruction of *Chalinolobus gouldii* upper second molar 107
Fig. 5.3. Occlusal and anterior views of the right upper second molar of *Chalinolobus gouldii* showing three wear states 108
Fig. 5.4. Cusp sharpness for the first 400 μm from the tip of the paracone and metacone of upper molars for three wear states in *Chalinolobus gouldii*.................. 109
Fig. 5.5. Changes in cusp occlusion relief behind the mesostyle for three wear states in *Chalinolobus gouldii*... 110
Fig. 5.6. a) PCA (Factor 1 vs Factor 2) and b) 2-D NMDS plots for all functional parameters for three wear states in 20 individuals of *Chalinolobus gouldii*.............. 111
Fig. 5.7. a) The effect on the relief behind a crest of relative wear on the rake and relief surfaces. b) Relief angle is maintained after wear on rake surface for a linear relief surface but increases if relief surface is convexly curved... 112
Fig. 6.1. Cuticle thickness (μm) vs punch strength (a), specific punch strength (b), work to punch (c) and specific work to punch (d) from punch tests of fresh cuticle according to insect type and level of sclerotisation. 135
Fig. 6.2. Cuticle thickness (μm) vs punch strength (a), specific punch strength (b), work to punch (c) and specific work to punch (d) from punch tests of fresh cuticle according to the region of the body from which the sample was taken..................... 136
Fig. 6.3. Insect body mass (mg) vs minimum, median and maximum thickness (μm) of cuticle fragments used in punch testing. 137
Fig. 7.1. Shaded relief reconstructions of upper second molars of six microchiropteran species 160
Fig. 7.2. PCA (Factor 1 vs Factor 2) plot for all functional parameters for three intractable and three tractable feeding species of microchiropterans. 161
Fig. 7.3. Eight functional parameters are depicted schematically for a cusp/crest structure, such as the paracone with pre- and postparacristae, and comparison of the expected tooth shapes for the three hypotheses in the text 162
Fig. 8.1. Possible scaling regimes for tooth sharpness vs body mass............................... 184
Fig. 8.2. Wear and enamel distribution in protoconoid, carnassial and lophodont forms. 185
Fig. 8.3. Edge sharpnesses of a wide range of body masses and dietary types 186

List of Plates

Plate 1. (Top) Three-dimensional reconstruction of the protoconoid, a fundamental double-bladed tool. (Bottom) Comparisons between the models and real mammalian tooth forms. 216
Plate 2. Three-dimensional reconstruction of the improved dilambdodont model......218
Plate 3. Front cover of *Journal of Microscopy*, November 2001......220

Abstract

The relationship between tooth form and function is a long-standing issue in the realm of functional morphology. However, in contrast to many other aspects of functional morphology, where many concepts and methods from engineering have been embraced, functional dental morphology has in many ways lagged behind in the application of these principles. The complexity and poor understanding of engineering applications such as tool function and fracture mechanics, which can be seen as analogous to the function of teeth and the fracture of food, have meant that techniques that allow the prediction of dental function from morphology have been lacking. This thesis seeks to address this deficit by the comprehensive application of several aspects of engineering to the issue of how teeth work, specifically, how the shape of an insectivore's teeth can be related to function.

The first major step in understanding dental function was to use engineering principles of machine tools to directly relate shape characteristics of teeth to how they will function. The result is a set of shape parameters, any alteration in which can be used to predict the relative change in the amount of force or energy that would be required for a tooth to function. These functional parameters are: tip sharpness and edge sharpness for cusps; rake, relief and approach angles, food capture and fragment clearance for crests.

Using these shape parameters as the dimensions of a multidimensional morphospace that includes all possible tooth shapes, only a very limited number will allow proper occlusion of the cusps and crests and have advantageous characteristics for all of the functional parameters listed above. From a search of this morphospace, the very few tooth shapes that do meet these criteria are remarkably similar to several tooth forms or structures that occur in extinct and extant mammals. These shapes can be considered 'ideal' in that they are very close to the morphology predicted to be the best functional shape. It appears, then, that these tooth forms are ideal functional shapes and are relatively unconstrained by the development and evolutionary history of mammals.

These ideal forms were then used to construct virtual three-dimensional model teeth that very closely emulate the shape and function of real tooth forms such as zalambdodont, insectivore premolars, dilambdodont and tribosphenic.

New fluorescent confocal imaging techniques for three-dimensional reconstruction of small teeth were developed and used to measure the important functional characteristics of microbat teeth. The use of Virtual Reality Modelling Language (VRML) allows the three-dimensional reconstruction of tooth occlusion of mammalian teeth for the first time,

representing a significant improvement on the use of occlusal diagrams to understand tooth occlusion. Measurements of the functional parameters from the digital tooth reconstructions demonstrate significant quantitative differences in morphological characters that predict a change in tooth function with wear, which has not been achieved with alternative approaches.

The concept of 'hardness' has long been used to describe the biomechanical properties of many groups of animals. However, due to the lack of a consistent definition, and the multitude of uses to which the term has been put, the use of the term 'intractability' has been advocated in this thesis to represent the extent to which the structural strength, stiffness and toughness are increased in a foodstuff. The thickness of the cuticle of an insect was found to be a good measure of the intractability of cuticle. The tremendous advantage of the use of cuticle thickness as a measure of the biomechanical properties of invertebrates means that the properties of a living insectivore can be directly quantified according to the thickness of the cuticle in its faeces. The quantitative measurement of intractability obtained through this technique can be used in correlations with adaptations of the masticatory apparatus, including tooth and skull morphology. This is a major advance on previous measures of the biomechanical properties of insectivore diets, and may represent the best technique of any dietary group in assessing the properties of its diet.

Comparisons between microbats that specialise on intractable or tractable insects illustrate some functional differences between tooth shape that arguably relate more to the risk of tooth fracture and increased wear rather than differences in the biomechanical properties of the diet. This conclusion challenges current views of insectivore tooth form and function.

Data gathered on the sharpness of microbat teeth was used to reassess the theoretical and empirical aspects of the scaling of tooth sharpness with body size. For large animals, it appears that the effect of tooth wear has the greatest influence on tooth sharpness, but the influence of development may be more important in smaller mammals.

Finally, aspects of general tooth morphology are addressed. Mammals of all sizes that consume tough foods will require crests for the forced crack propagation (cutting) of dietary items. It is suggested that cusps represent an adaptation to the concentration of forces, and therefore would be more prevalent in tooth forms of smaller animals with a smaller absolute bite force. This would predict that cusps are not required in larger animals, with larger bite forces, and their tooth forms should be dominated by crests. This is generally borne out in many groups of mammals.

General Declaration

In accordance with Monash University Doctorate Regulation 17/Doctor of Philosophy the following declarations are made:

I hereby declare that this thesis contains no material that has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes two original papers published in peer-reviewed journals. The core theme of the thesis is the functional dental morphology of microchiropteran insectivores. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, Alistair R. Evans, working within the School of Biological Sciences under the supervision of Professor Gordon Sanson.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of Chapters 2 and 4 my contribution to the work involved the following:

Thesis chapter	**Publication title**	**Publication status**	**Nature and extent of candidate's contribution**
2	The tooth of perfection: functional and spatial constraints on mammalian tooth shape	Published	Conception and execution Contribution: 90%
4	Confocal imaging, visualization and 3-D surface measurement of small mammalian teeth.	Published	Partial conception and full execution Contribution: 80%

Signed: .... Date: ....

Alistair R. Evans

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Chapter 1. Introduction

1.1. Functional Morphology

The awareness of the influence of morphology on function has progressed substantially over the last few decades such that the mechanics of many biological systems are fairly well understood. Many systems, including terrestrial locomotion, flight, swimming, acoustics and certain aspects of feeding, have been successfully analysed using conventional mechanics and engineering concepts of force vectors, mechanical advantage, energetics and fluid dynamics (e.g. Alexander 1983, 1992; Bels *et al.* 1994). These techniques have allowed rigorous functional analyses and the construction of useful hypotheses from sound theoretical foundations. The use of these methods has profoundly increased the level of understanding of the factors involved in function in these systems. Questions of interest, such as the comparison of locomotion in bipeds and quadrupeds (McGeer 1992) and the flight mechanics of birds and bats (Norberg 1990), have been successfully addressed.

Like many aspects of morphology, the study of relationships between form and function of the dentition has a long history, extending back to Empedokles and Aristotle (Russell 1916; Kay 1975). It was recognised that the tooth forms of particular animals such as lions and horses appeared to match their diet extremely well. Despite what in many respects appears to be an obvious correlation, the exact reasons and the extent to which diet and dentition are matched are still issues of great significance and in many cases are unresolved.

Advances in understanding the function of the dentition has not been as rapid or successful as other morphological systems. Studies of the dentition have rarely examined function from a mechanical point of view, which is one aspect in which functional dental morphology falls behind most of functional morphology. In many respects, questions relating to systems like terrestrial locomotion and flight deal with structures and processes that more closely resemble engineering problems that are more amenable to analysis compared to investigating dental function. This thesis will examine the question of tooth form and function in insectivorous microchiropterans by the extensive application of engineering concepts.

1.2. Recent Approaches in Functional Dental Morphology

There was a great resurgence of interest in tooth function starting from the late 1960s. This was encouraged by new fossil finds and interpretations (Crompton 1971; Crompton and Sita-Lumsden 1970) along with technical and methodological innovations such as cinefluorography to examine mastication and oral transport in mammals (Crompton and Hiiemae 1970; Kallen and Gans 1972) and scanning electron microscopy for analysis of dental microwear (Gordon 1982; Rensberger 1978; Ryan 1979; Teaford 1988; Walker *et al.* 1978). Conceptual advances have been just as important, including the use of wear facets in reconstructing occlusal dynamics of teeth (Butler 1952; Mills 1966). This new work was built on the foundations of earlier important work in dental function and evolution (Butler 1941; Gregory 1920; Osborn 1888; Patterson 1956).

An important step in understanding the relations between tooth shape and function was made with Osborn and Lumsden's (1978) work. This paper identified some specific aspects of tooth shape that affected function. One aspect that was not explicit in that work, however, was expounded by Rosenberger and Kinzey (1976) and Lucas (1979), who argued that the biomechanical properties of foods are the primary determinants of the functional shape. This reasoning was expanded by Lucas and Luke (1984) who considered the major tooth forms that would function best for a variety of food types, characterised by their biomechanical properties. Blades are best for tough foods (where cracks must be continually driven through the food), and a mortar and pestle for brittle (with self-sustaining crack propagation) and most probably juicy foods. However, one of the most important aspects of Osborn and Lumsden's (1978) analysis, the identification of specific tooth shape characteristics that could be used to assess tooth function, was lacking in the later papers. In addition, the group of specific interest in this thesis, insectivores, was largely ignored in this body of work.

The main line of inquiry that has attempted to relate specific aspects of tooth shape to function and diet is due to Richard Kay and his co-workers and followers (Kay 1975, 1978, 1984; Kay and Covert 1984; Kay and Hylander 1978; Kay *et al.* 1978; Anthony and Kay 1993; Benefit and McCrossin 1990; Covert 1986; Dumont *et al.* 2000; Kirk and Simons 2001; Meldrum and Kay 1997; Strait 1991, 1993a, 2001; Ungar and Kay 1995; Williams and Covert 1994) examining primates. These studies have used 'shear quotient' or 'shear ratio', a measure of relative crest length (by a criterion of subtraction or standardised to tooth length or area or body mass), as a functional measure of tooth shape. The length of individual crests (such as the cristid obliqua) or the sum of several crests (crests 1-6 of Kay and Hiiemae 1974) have been used.

Shear ratio-type measures are not used in this thesis because they do not take into account the effect of cusp and crest shape on function. They are more indicative of the size of the crests rather than the comparative function, which will be as greatly affected by the non-occluding tooth surfaces as the occluding cusps and crest edges.

Strait (1991, 1993c) employed shear ratio to examine tooth form in insectivorous mammals, where it was found that hard feeders had lower shear ratios than soft feeders. This finding was predicted by Strait (1991, 1993c), but the reasoning behind this expectation has been challenged (Evans and Sanson 1998).

There have been many other studies that have incorporated useful functional analyses of teeth, or identified, expanded and/or measured some of the shape characteristics that will influence tooth function (Abler 1992; Bryant and Russell 1995; Evans and Sanson 1998; Frazzetta 1988; Freeman and Weins 1997; Lucas 1982; Mellett 1981, 1985; Popowics and Fortelius 1997; Rensberger 1973, 1975, 1986, 2000; Sanson 1980; Seligsohn 1977). Some of these in particular (e.g. Rensberger 1973; Seligsohn 1977) have made very substantial contributions to the understanding of dental form, but in large part their methods and approaches have not been followed or applied any further. Other important developments have been made, particularly in associating enamel microstructure with evolution and diet (Koenigswald and Clemens 1992; Koenigswald *et al.* 1987; Rensberger and Koenigswald 1980; Rensberger and Pfretzschner 1992), but these are not specifically addressed in this thesis.

Despite the significant conceptual and informational advances, few studies have attempted a complete analysis of tooth shape to compile a comprehensive list of shape variables that will affect function, and even fewer have measured these variables in teeth. These steps are necessary to achieve a holistic understanding of tooth function, not just in the theoretical sense but also in terms of the practical applications that exist in organisms.

1.3. Engineering and Tooth Function

The approach adopted in this thesis is that the form of the tooth largely dictates the function and occlusion of the tooth (for a food of given biomechanical properties). An understanding of how the shape and arrangement of cusps and the edges and associated surfaces of crests affect function is critical to the reconstruction of function for a given tooth form. The biomechanical properties of the diet will have a functional, and therefore selective, influence on the tooth form. In view of a considerable overlap in many of the questions that engineers and biologists tackle, the search for correlations between shape, function and biomechanical properties of teeth and food should start with investigating the ways in which engineering analysis will improve understanding of tooth form and function.

Many of the issues explored in this thesis have been addressed by mechanical and materials engineers to some extent (Gordon 1976, 1978). The advantages of engineering are manifold: engineers deal with a designed structure of greater simplicity in terms of materials and structure compared to biological systems; there is a greater understanding of the basis of the materials and structures; and they are more able to perform tightly controlled experiments. The phenomenal success of engineering is apparent in every aspect of modern life. These do not guarantee a perfect answer in engineering, but the major advances in materials engineering in the last few decades are indicative of the advantages of the current approaches.

From a mechanical perspective, there are two factors that have the most influence on the success with which a tooth will fracture food and reduce it to small fragments if necessary. First, the shape of a tooth will largely dictate how the stresses and strains are applied to the food. This requires the identification of specific aspects of tooth shape that influence function. Second, how the food responds to the applied stress and strain depends on its material and structural properties. This is the recognition of the influence of biomechanical properties of the diet on the function of teeth. In engineering, the first has been considered to some extent in the design and use of machine tools, e.g. lathe tools, that are designed to fracture materials. The second is the realm of materials engineering and fracture mechanics.

In mechanical engineering, the function and design of machining tools have many parallels to the bladed structures of teeth (Oberg *et al.* 2000; Ostwald and Muñoz 1997; Nee 1998; Pollack 1976). A single-point machining tool has cutting edges with its faces set at particular angles to the direction of movement and the workpiece (e.g. rake and relief angles; Fig. 1.1). Also, it may have features to clear material away from the edge of the tool to prevent clogging, such as a chip breaker, which is a notch or groove in the tip of the tool (Fig. 1.1).

The other side of the equation is represented by materials engineering, which examines the causes and consequences of stresses on materials and the mechanisms of failure and fracture (Atkins and Mai 1985; Ashby and Jones 1996; Askeland and Phulé 2003). Materials engineering uses concepts such as stress, strain, strength, stiffness, ductility and toughness to describe and quantify these effects. The objective of the dentition is to fracture food while not being fractured itself, so the material properties of both tooth and food are relevant.

However, the application of engineering principles to biological questions is complicated for many reasons. The principal reason is the great differences between the disciplines of engineering and biology in the aims of study and the methods that must be used. Engineers want to design structures that work; biologists want to understand working structures that they had no input in designing. One of the keys to successful engineering is a comprehensive understanding of all interactions of components within a structure before assembly, which is normally achieved by extensive testing of the components, including materials and component structures. Not only are biologists not privy to the results of pre-testing, but this is not how biological structures were designed and built. Biological structures were not planned and constructed from the ground up – in large part they are haphazard adaptations of pre-existing structures to new uses, the products of the blind watchmaker (Dawkins 1986). Despite the lack of foresight, organismic design has the advantages of structural control at the atomic level and immense periods of time for extensive testing of designs. The history of biological study is replete with examples of how the resulting highly complex structures are extremely well adapted to their function (Alexander 1983; Vincent 1990; Wainwright *et al.* 1976).

Functional morphology is essentially the reverse engineering of biological structures, with all the mystery of why the structures exist, what their habitual function is, and how their function can be predicted from the morphology. The contrast between engineering and biology shows the greater requirement for prediction of function from form in biology compared to engineering.

This difference is apparent in the limits to which current engineering cannot confidently address biological questions. For instance, machine tool engineering practice is largely dependent on experimental results rather than a general theory of the function of the shape of machining tools. There has been surprisingly little analysis on the quantification of knife shape and function for cutting ductile materials (Frazzetta 1988; Abler 1992).

Likewise in materials engineering, there is inadequate knowledge of the processes of fracture, particularly the fracture of biological materials, for the prediction of how different structures will fail (Atkins and Mai 1985). This is largely due to the composite and intricate nature of the materials and structures of organisms, so that their mode of failure and fracture are highly complex. Engineers are mostly only interested in initial failure or fracture of a structure, and so the majority of the work reflects this. However, when considering the fracture of food by teeth, progressive and sustained fracture of structures and substructures is required. Some subdisciplines of materials engineering have sought to deal with this issue (e.g. Lowrison 1974), and have been applied in the biological realm (Lucas and Luke 1983a, b), but they frequently deal with relatively homogeneous structures with properties incongruent with biological structures.

Some aspects of traditional engineering theory have been successfully applied to teeth, such as beam theory (Van Valkenburgh and Ruff 1987; Farlow *et al.* 1991), but these have limited use in their ability to model and predict the function of more complex teeth. One very promising technique for understanding the influence of tooth shape and biomechanical properties on function is the use of finite element stress analysis (FESA). It is only now emerging from its embryonic stage of development, and results have begun to reveal much about stress distribution in teeth and foods (Crompton *et al.* 1998; Macho and Spears 1999; Rensberger 1995; Spears 1997; Spears and Crompton 1996; Spears and Macho 1998; Spears *et al.* 1993; Yettram *et al.* 1976).

The arguably lack of success of functional dental morphology compared to other areas of functional morphology can be seen to be due to the difficulty of both the examination of the complex structures and the application of the principles established in engineering to the biological sphere. Also, though with less relevance today, there is the reluctance of the biologist to cross the language barrier and employ the knowledge of the engineer.

The conceptual and operational tools developed in engineering can give great insight into aspects that should be considered when examining biological function. But we should be cautious of the degree to which engineering principles can be usefully transferred to biology. Ironically, engineering concepts may be more applicable to biomaterials than engineering materials in some cases, as the properties of the latter may be considered to be affected by the distribution of flaws, whereas the former may be perfect materials to which the theory is more suited (Atkins and Mai 1985).

This thesis aims to establish the relevance and usefulness of engineering principles to functional dental morphology, particularly in terms of insectivorous dentitions, and set out aspects of tooth shape that can be used in the prediction of tooth function.

1.4. Dilambdodont and Tribosphenic Tooth Function

Functional analysis of dilambdodont and tribosphenic molars, found in microbats, shrews, moles and tree shrews, has largely lagged behind that of primates, with a more derived tribosphenic or quadritubercular form, and herbivores. The first two tooth forms are often considered primitive in the sense of being not as well adapted as the more recently-evolved forms. This perhaps has influenced interpretation of these forms, where insectivore teeth are most often considered as inferior to the herbivore dentition for herbivory, and carnivore dentition for carnivory rather than focussing on the special adaptations required for insectivory. An important aim of this thesis is to reveal the superb adaptations of the insectivore tooth form to an invertebrate diet. The great similarities in the molar structure of dilambdodont when compared to zalambdodont (the molar form of solenodons, tenrecs and golden moles) and tribosphenic (primitive mammals and some marsupials) tooth forms mean that a firm functional foundation of the dilambdodont form will have application in these other forms.

The superb work of Percy Butler has shown insight into many aspects of insectivore dentition (Butler 1937, 1939, 1941, 1961, 1972, 1982, 1990, 1995, 2001). It established many important features of the relations between premolars and molars in development and evolution, and determined or confirmed cusp homologies along the tooth row and among mammal groups. Other important work on the dentition and occlusion in insectivorous mammals includes that undertaken by Mills (1966), as well as the work on the tribosphenic form of *Didelphis* (Crompton and Hiiemae 1970; Crompton and Sita-Lumsden 1970; Crompton *et al.* 1994; Stern *et al.* 1989). Comparisons of the molar effectiveness of different insectivore forms was compared by Sheine and Kay (1977) and (Moore and Sanson 1995).

1.5. Tooth Wear

Recognition of the value of tooth wear for the reconstruction of tooth use is now well established through the application of techniques such as wear facet analysis and microwear. However, on the whole, the effect of wear on the function of the tooth has still been neglected. Studies of herbivores have revealed the influence of wear on tooth function (Lanyon and Sanson 1986; Logan and Sanson 2002; McArthur and Sanson 1988; Skogland 1988), which are based on qualitative wear states of the molars. It would be greatly preferable to use tooth features for which *a priori* predictions can be made regarding how changes in shape with wear will affect function. For many tooth forms, particularly those of insectivores, it has been assumed that increased wear will impede function (e.g. Verts *et al.* 1999a), but no quantitative predictions or measurements have been made of worn insectivore teeth to examine this presumption. Canine height is most frequently used as a measure of tooth wear; this may correlate with postcanine wear but does not make any specific prediction about the function of canine or postcanine teeth. Any measures of tooth function, including those used in this thesis, are only valuable if they have predictive value for worn teeth as well as unworn teeth.

1.6. Insectivore Dietary Properties

Explicit in Lucas's (1979) view of tooth function is the necessity for information on the biomechanical properties and the modes of fracture of foods. However, very little work has been done in describing the properties of the insectivore diet. Descriptions of the invertebrates, particularly insects, as food only extended as far as concluding that some may be hard and brittle, and some soft and ductile (Lucas 1979; Lucas and Luke 1984).

The extent of knowledge of the biomechanical properties of insects and their constituent components has gradually increased (Hepburn and Chandler 1976; Hepburn and Joffe 1976; Hillerton 1984; Strait and Vincent 1998; Vincent 1992a), but is still fairly limited considering the immense range of material and structural adaptations that exist in such a large and important group of animals.

Classifications of insects as dietary items have used 'hardness', either according to a qualitative scale (Freeman 1981a) or by generalisations of hard insects as strong, tough, stiff and brittle compared to soft insects (weak, fragile, pliant and ductile; Strait 1993c). However, these characterisations are limited in their usefulness or have not been quantitatively tested. This thesis aims to establish sounder principles and methods of characterising the biomechanical properties of insects with the purpose of understanding the influence of insectivore dietary properties on tooth form.

1.7. Microchiropterans

Despite comprising approximately one fifth of mammalian species, investigations into most aspects of bats, including nutritional ecology, were scarce until the last few decades. This can be explained by the difficulty in gathering data on their foraging habits due to their crepuscular flight and aerial feeding. A significant amount of work on the comparative and functional morphology of this group is due to Patricia Freeman's series of studies on Chiroptera (Freeman 1979, 1981a, b, 1984, 1988, 1992, 1995, 1998, 2000; Freeman and Weins 1997). This work, along with comparable investigations in other groups, stimulated a great deal of other studies relating morphology of chiropteran skull and teeth to diet (Barlow *et al.* 1997; Czarnecki and Kallen 1980; Dumont 1995, 1997, 1999; Fenton *et al.* 1998c; Jacobs 1996; Reduker 1983; Rodríguez-Durán *et al.* 1993).

Examination of the diet of microchiropterans has revealed that some species appear to specialise on certain insect groups, such as beetles or moths (Black 1974; Ross 1967; Vaughan 1977; Warner 1985; Whitaker and Black 1976). Freeman (1979, 1981a) found that feeding on 'hard' invertebrates such as beetles correlated with robustness of jaws, areas for jaw muscle attachments, and the size of molars. Other patterns have since been found that relate to the biomechanical properties of the insectivore's diet (Dumont 1995; Strait 1993b, c). However, differentiation between specialist insectivores with regard to the fine morphology of the molars has not been demonstrated.

1.8. Three-dimensional Tooth Modelling

A significant challenge in the comprehension of tooth form and function is the three-dimensional shape and occlusion through time of the complex morphologies of teeth. In the past this has not been possible, and reconstructions (at least published ones) are generally through line drawings, which cannot hope to sufficiently indicate the relations between teeth. Representation of the tooth in three dimensions is preferable, and various forms of imaging or scanning technology have made this possible (Boyde and Fortelius 1991; Reed 1997; Ungar and Williamson 2000; Zuccotti *et al.* 1998).

Two important aspects of this can be considered. First, three-dimensional analysis is required to understand more completely the fundamental aspects of tooth shape and the principles of morphology for occluding upper and lower teeth. Second, measurement of functional characteristics of teeth in three-dimensional space requires a full representation of teeth. Revolutions in computer and imaging technology have resulted in microscopes and computing software and hardware that can carry out these onerous tasks. Fluorescence laser confocal microscopy is able to build a three-dimensional model of an object, including small mammalian teeth. Any measurement that can be carried out by conventional calipers or protractors can be made on the teeth reconstructions, as well as surface areas, volumes and curvature, which would have been either impossible or laborious with previous methods. Virtual reality modelling language (VRML) allows the construction of three-dimensional computer models of any shape, along with real-time movement of objects. Simplified models of VRML teeth can be used to investigate principles of tooth shape and occlusion, and VRML reconstructions of upper and lower mammalian teeth can be occluded in virtual space to scrutinise the occlusion of mammalian molars in the full three dimensions for the first time.

1.9. Structure of Thesis

The main objective of this thesis is to demonstrate that the types of rigorous functional analyses carried out in other morphological systems are possible in dental systems. To achieve this, it sets out to attain a greater understanding of the influence of insectivore tooth shape on function through use of tool engineering and understanding of occlusal geometry. The result should be a more predictive relationship between the important aspects of wear and the biomechanical properties of foods on the quantitative function of insectivore teeth.

Chapter 2 establishes the functional characteristics of cusps and crests that can be gleaned from engineering principles or previous dental studies. These are used in the exploration of all possible tools (morphospace) to find those tools that best meet functional criteria. The final shapes from this exploration are used in Chapter 3 to construct three-dimensional functional models of carnivore and insectivore molars and premolars. Chapter 4 describes the use of fluorescent confocal microscopy to generate three-dimensional reconstructions of microchiropteran teeth. These models can be used for the measurement of the functional parameters established earlier, and the reconstruction of occlusal dynamics of upper and lower molars. A comprehensive study of the molar form of a single microchiropteran species forms the basis of Chapter 5, which also examines the effect on function due to tooth wear. Chapter 6 explores the ways in which insects have been characterised as a dietary item, and specifically looks at the ‘hardness’ of invertebrates. It sets out to validate the use the of cuticle thickness as a measure of the biomechanical properties of invertebrates. Chapter 7 investigates the tooth form of ‘hard-feeding’ and ‘soft-feeding’ insectivorous microchiropterans in an effort to elucidate the influence of dietary properties on the tooth form of insectivores. A discussion on the scaling of tooth sharpness forms Chapter 8, setting out a theoretical model for the scaling of sharpness and incorporating data gathered in this thesis with published data. The thesis discussion (Chapter 9) looks more broadly at some of the issues raised throughout the thesis, such as the comparative function of tribosphenic-like and carnassial tooth forms and the influence of size and diet in mammals generally.

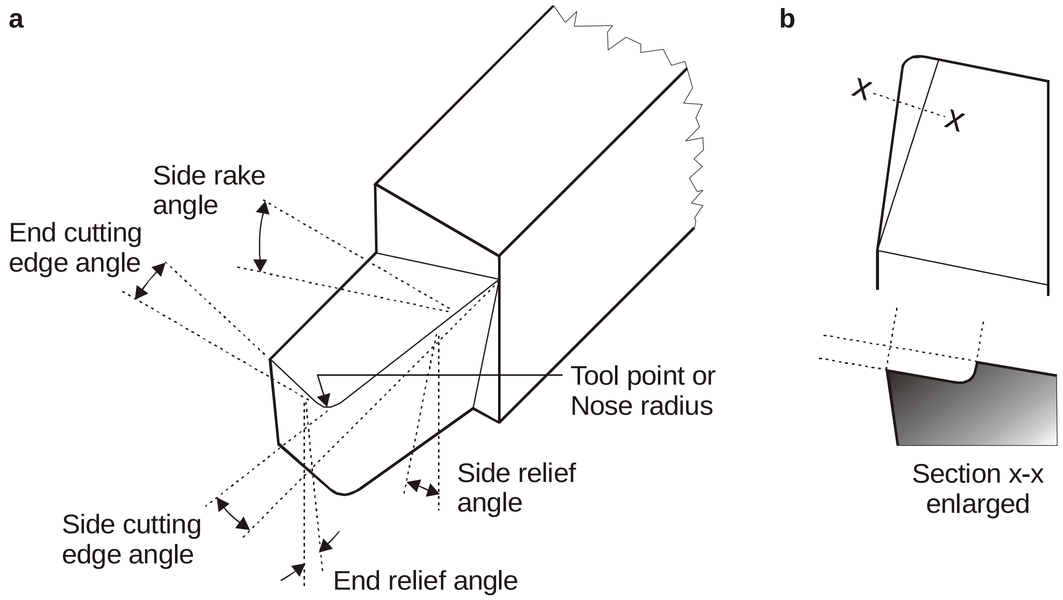

Fig. 1.1. a) Dimensions of a single-point cutting tool; b) one form of chip breaker on a cutting tool designed to help the clearance of fragments. (Redrawn from Oberg *et al.* 2000.)