Chapter 4
Inferring Mammal Dietary Ecology from Dental Morphology

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Abstract The teeth of mammals are the key interface between food and animal – where the rubber meets the road. Mammals generally use their teeth for mechanical processing, thereby facilitating and increasing rates of ingestion, digestion and fermentation. The various foods eaten by mammals respond to bite forces in different ways: some foods fracture easily, while others resist cracks propagating through them. In addition, some foods must be broken down to small pieces for effective energy and nutrient extraction; others merely need to be small enough to swallow. The most effective tooth morphology therefore varies with the mechanical properties of the food. Tooth shape can help to determine the typical food sources consumed by mammals at a given fossil locality, which in turn informs the broad environmental conditions and community structure once present at the site. In this chapter, we examine the ways in which mammalian tooth morphology can serve as an indicator of diet and thus past environments by examining the materials science of foods and the functional morphology of mammal teeth.

Keywords Biomechanics • Dental topography • Diet • Dietary mechanical properties • Functional morphology • Performance testing • Teeth

Introduction

Teeth break food. This fundamental ability provides access to a veritable smorgasbord of foods by aiding in the acquisition and mechanical processing of foods that would otherwise be too difficult to digest. Food processing helps to fuel the high metabolic rates of mammals and, in some instances, the eventual loss of effective teeth may even put a limit on lifespan or reproductive ability (Laws 1968; Logan and Sanson 2002; King et al. 2005). Mammal teeth come in a variety of distinctive shapes, both along the tooth row and among the great diversity of mammal species, past and present. They can provide unique information about animals such as their behavior, environment, feeding preferences and even important life events. Teeth are the hardest material in the body and tend to fossilize well, making them especially valuable to paleontologists attempting to reconstruct the diet of fossil mammals.

Mammals can only consume what is available to them, and many foods are restricted to certain types of environment. Simplistically, then:

$$\text{Diet} \subset \text{Environment}$$

such that diet is always contained within (or is a subset of) an animal's environment. Determining the diet of a fossil mammal can thus help to identify the type of ecosystems it was once part of and aid in reconstructing past environments.

In the vast majority of mammals, teeth are the main mechanical interface between food and the body, with their shape typically reflecting foods and associated structures to be acquired and processed. Therefore, it is critical to know both how the shape of the tooth influences the application of force onto food and how food items respond to these bite forces through deformation and/or fracture.

Mammals have four classes of teeth: incisors, canines, premolars and molars (Fig. 4.1A). Incisors are generally peg-like or spade-shaped teeth but occasionally have more

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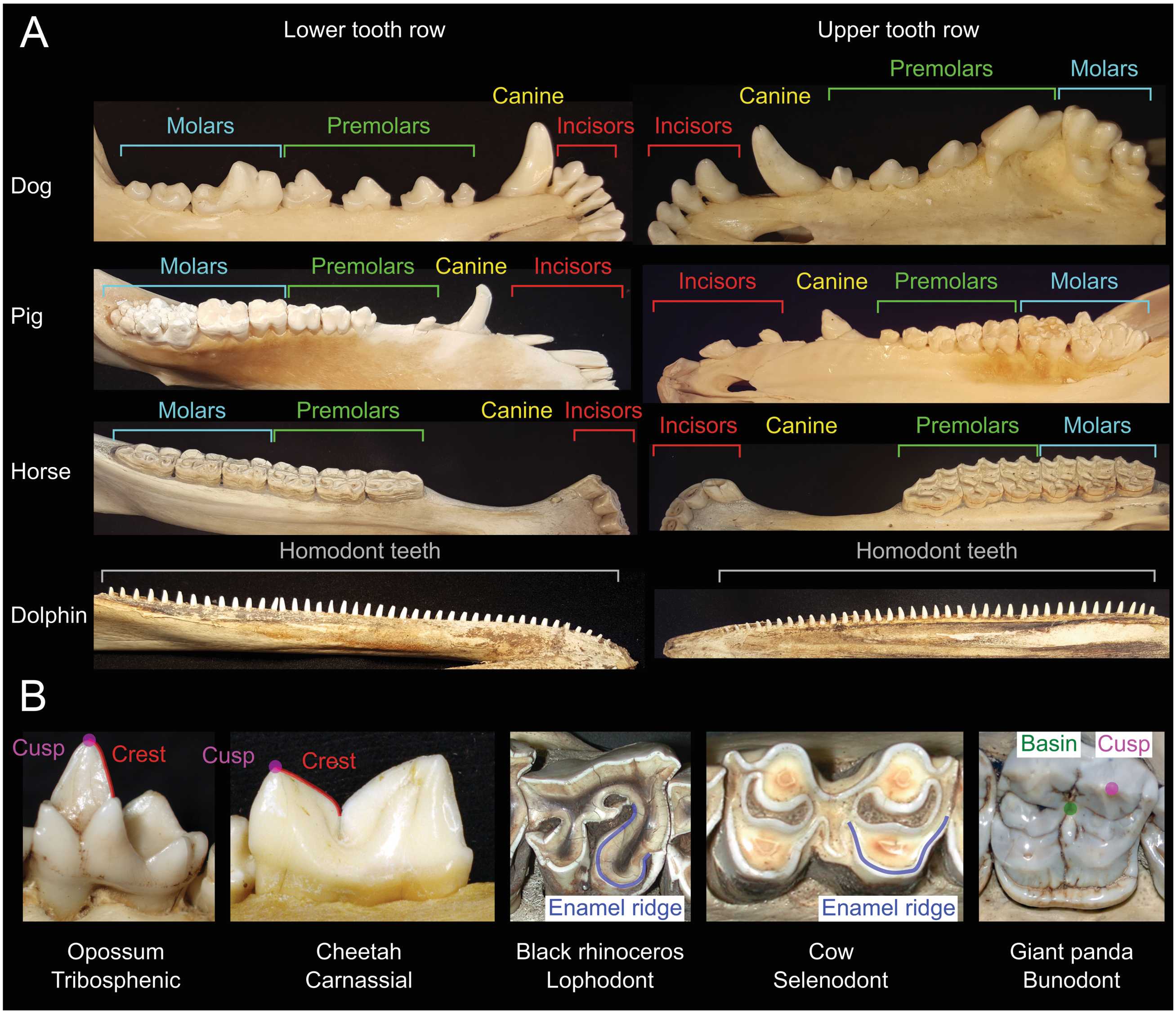

Fig. 4.1 A small sampling of the diversity of tooth morphology in mammals. A, Tooth classes (incisors, canines, premolars and molars, as well as undifferentiated homodont teeth) of lower and upper tooth rows in dog (*Canis lupus familiaris*, MZRC Dog53), wild boar (*Sus scrofa*, MZRC 3304), horse (*Equus ferus*, MZRC 617), and dolphin (*Delphinus* sp., MZRC unregistered). B, Typical features of molars, including crests, enamel ridges, cusps and basins in lower tribosphenic molar of opossum (*Didelphis virginiana*, MZH 1802), lower carnassial molar of cheetah (*Acinonyx jubatus*, MHZ U31), upper lophodont molar of white rhinoceros (*Ceratotherium simum*, ZMB 54402), lower selenodont molar of cow (*Bos taurus*, MZRC 4080), and upper bunodont molar of giant panda (*Ailuropoda melanoleuca*, ZMB 37028). Museum abbreviations: MZH, Helsinki Zoological Museum; MZRC, Monash University Zoology Research Collections; ZMB, Zoological Museum Berlin

complex shapes such as combs. Canines are almost always tall, single-cusped teeth but may have small accessory cusps. These two tooth classes are generally used for capturing, holding, deforming and breaking off fragments small enough to be processed in the mouth. Premolars may also be involved in holding or fragmenting foods. The molars of most mammals are involved in cyclic chewing to fragment foods to small enough particles for fermentation or digestion; when it includes tooth-tooth contact, this is called mastication.

Foods typically undergo both mechanical and chemical breakdown to enable extraction of sufficient nutrients from them. Those foods that are easily broken down and digested in the gut may require very little mechanical processing; mechanical processing merely makes them small enough to swallow. Easily digested foods include many soft animal tissues (muscle and internal organs) and some plant products (pollen, nectar, and sap). Many plant structures represent the greatest processing challenges for mammals feeding on them. The cells of plant structural tissue, including stems, roots, and leaves, contain nutrient-rich cytosol which is encased in relatively indigestible cell walls (Sanson 2006). Herbivores may focus on breaking open the cells to release the contents for digestion or fragmenting the cell walls to increase surface area to ferment the cellulose in them. Mastication is key for both of these steps, with the shape of teeth and precision of occlusion greatly increasing the effectiveness of breaking down plant materials. Teeth may also function in cracking open shells or bones, even when these are not the components to be digested.

Mechanical processing using teeth is either not required or not carried out by some mammals, such as the filter-feeding crab-eater seal *Lobodon carcinophaga* and ant-eating echidna *Tachyglossus aculeatus*. In these animals, the teeth do not reflect the mechanical properties of the diet – making inference of diet from dental morphology unsuccessful – or teeth cannot be studied because they are absent altogether.

Teeth perform many functions in mammals other than capture and processing of food, including grooming, sexual signaling, digging, gouging and gnawing. In general, these additional roles are carried out by the anterior teeth (incisors and canines). Molar teeth are essentially only related to food processing and so generally give stronger dietary signals.

There are many other aspects of teeth that inform about diet and ecology. High tooth height (hypsodonty) can reveal a lot about the diet and environment of a mammal, as discussed by Barr (2018). Processing of food and associated materials usually leaves small physical marks on teeth termed microwear, the patterns of which can vary with diet and environment, as discussed by Green and Croft (2018). Mesowear is another method for interpreting diet from wear-induced shape change and is reviewed in the same chapter.

In this chapter, we review how mammal teeth process particular foods and how this process influences dental morphology. We outline some basic principles of materials science as they relate to food and how it is broken down. Then we discuss how the shape and size of teeth and their component parts are expected to influence their performance and how assessment of performance can be made through computer simulation or physical testing. Through this knowledge, we can make approximations of the diets of fossil mammals based on their gross dental morphology or quantitative assessment of tooth shape. Finally, we explore some recent examples and demonstrate the fundamentals of some of the modern 3D morphology approaches.

Historical Background

General associations among tooth shape, function and diet stretch back to the beginning of the natural sciences, with Aristotle (Physica; Hardie and Gaye 1930) commenting on the differences between cutting incisors and grinding molars. In modern Western science, these themes have been further explored and expanded, such as by Hunter (1771–1803 [1865 post.]), who observed that teeth are used to catch, collect and prepare food for digestion, and that the physical properties of food affect how they are acquired and prepared. Gregory (1922) suggested that tooth shape evolved in order to improve mechanical efficiency for certain foods, and Simpson (1933a) correlated the direction of jaw motion with specific food specializations. Kay (1975) summarized these and other intellectual advances of our knowledge of the functions of teeth through the 18th to 20th centuries.

Consideration of overall tooth shape was a frequently-used approach in early modern paleontology to interpret the likely diet of fossil mammals, and this method was vastly improved by quantification of form. One of the earliest such quantitative studies of dental morphology was that of Crusafont-Pairó and Truyols-Santonja (1956). These authors estimated the degree of carnivory in fossil carnivorans based on angular measurements of the carnassial tooth that quantified the elongation of the carnassial blade and reduction of the talonid basin. The work of Rensberger (1973) deserves highlighting as a landmark in quantitative functional dental morphology, in which he carried out computer simulations of 3D model tooth shapes to examine the effects of enamel band orientation, dentine basin depth and tooth wear on pressure and effectiveness of herbivore dentitions.

From the 1970s onwards, more detailed studies and refined approaches made significant advances in revealing relationships between teeth and diet. First, new methods to quantify tooth shape enabled more precise comparisons among species and correlations with diet (e.g., Kay 1975). Second, several authors undertook more theoretical considerations of how the shape of a tooth affects its ability to fracture food items and what shapes would be expected to most effectively fracture certain foods (e.g., Osborn and Lumsden 1978; Lucas 1982; Lucas and Luke 1984). Third, the crucial role that the mechanical properties of different foodstuffs play in this process began to come to the fore (Kay and Hiiemae 1974; Kay 1975; Rosenberger and Kinzey 1976), along with the necessity to accurately quantify the mechanical properties of the foods (Lucas 1979). These studies began to lay the foundation of a clearer conception of how foods break and the role that tooth shape plays in facilitating breakage.

Approach

We can consider there to be two main approaches for inferring the diet of a mammal from the shape of its teeth: analogy and biomechanics. These approaches have different logical bases and thus vary in the scope and precision of the predictions they are able to make. The choice of methodology often largely depends on the generality of the question and the nature of the available material.

Prediction by Analogy

A straightforward way of inferring what an extinct mammal may have fed on is to compare its dentition to that of extant species with known diets. This is the foundation of much of comparative anatomy and has a long and distinguished history. In its application to the teeth-diet relationship, if the teeth of the extinct and extant species resemble each other, then analogy suggests that both species specialized on similar foodstuffs.

Using analogy for dietary inference from teeth has often been based on tooth type, i.e., the general shape of the teeth (Fig. 4.1A). For instance, tribosphenic tooth shapes are usually interpreted as indicating an insectivorous diet, bunodont a hard food diet, lophodont a plant-based diet, and homodont a piscivorous diet. In a more general sense, a fossil tooth bearing a series of occlusal ridges would resemble the teeth of many extant herbivores and thus may well have belonged to a herbivore. Gregory (1920: 141) used analogy to speculate that the molars of early notharctine primates were adapted to an insectivorous diet, while those of later members of the group were for “vegetable food, especially leaves and fruits”.

However, the use of the analogy approach with gross tooth morphology has some major limitations. In particular, there are no clear rules on how similar teeth have to be to justify the assumption of similar diets, which means that assessments of analogy can be highly subjective. Likewise, problems arise when the shape of a fossil tooth does not obviously resemble any living species and therefore cannot be interpreted in a modern context. The phylogenetic history of a species can also substantially influence tooth form. For example, all species of a group may have quite similar dentitions despite varying somewhat in diet (e.g., Chemisquy et al. 2015). This may be because insufficient time has elapsed for sufficient evolutionary adaptation, or the dentition is relatively generalized and can adequately process the range of diets found in the group.

To help address the issue of how to analogize disparate shapes, we can seek ways to quantify shape, allowing more objective assessments of the extent and the manner in which two shapes are similar. Length:width ratios have been the main staple of tooth measurement (e.g., Kieser 1990), but they ignore any detail of tooth morphology beyond the aspect ratio of the whole tooth. Quantification of 2D linear or area measurements of teeth and component parts can give keen insights to some dietary and ecological questions, particularly in taxonomically-limited samples (e.g., Van Valkenburgh 1989).

More sophisticated analyses of 2D shape have sought to hone in on shape characteristics. A pioneer in this field was Schmidt-Kittler (1984), with his work on quantifying 2D parameters of the enamel occlusal surface in herbivores. More recently, Occlusal Enamel Index (OEI) has been developed to quantify the relative length of occlusal enamel bands compared to the tooth area in herbivorous mammals (Famoso et al. 2013; Famoso and Davis 2016). Grazing mammals feeding on more complex and fibrous vegetation typically display higher values of OEI. Fractal Dimensionality, based on fractal theory, computes how the measured length of the enamel ridge changes with measurement resolution (Stone and Telford 2005; Candela et al. 2013). It has been used to study the relationship between morphology and diet and has an advantage over OEI of being more independent of body size (Famoso et al. 2016).

3D linear measurement has been an additional challenge but has been successfully used to differentiate diets based on tooth morphology (e.g., Strait 1993). However, the high degree of variation in mammal tooth shape (Fig. 4.1B) has been a fundamental stumbling block for comparisons across Mammalia.

Detailed shape analysis of the dentition can be captured by geometric morphometric analysis, as detailed by Curran (2018), but the strict requirements of identical number of landmarks means that the use of this technique to compare diverse dental morphologies with differing numbers of cusps or crests is limited.

Prediction Through Biomechanics

Instead of searching for analogues, the biomechanical approach to diet reconstruction borrows concepts from mechanics and materials science to model teeth as tools whose performance under certain conditions can be tested. This functional or performance analysis can consider how teeth fracture food from a bottom-up, theoretical approach by building on materials science concepts, or from a top-down, experimental approach by directly testing real or idealized tooth shapes with food materials. Either way, it is necessary to take into account the properties of both the tool (i.e., the tooth), and the material (i.e., the food) to which it is applied.

Mechanical Properties of Foods

The mechanical properties of a food influence how it can be handled, fractured, and broken into smaller pieces (fragmented) for swallowing and digestion in the gut and are best described using the terms and concepts employed by materials scientists. The concepts are highly detailed and use specific terms, some of which have closely related words in general use with somewhat different meanings, such as ‘plastic’. Below, we provide brief descriptions of the most important terms and give relatable examples of everyday foods or materials. A more detailed review is provided by Berthaume (2016). When a force is applied to a material, it is referred to as ‘loading’ the material, as in a load is being applied.

Materials scientists investigate how a material behaves when it is loaded by mounting it in a force testing machine that pulls (in tension) or pushes (in compression) the material and measures the distance that is applied and the force that results from that movement. When these are plotted against one another, the force-displacement graph (Fig. 4.2 A) can reveal how much force and energy are required to initially deform and then fracture the material. However, it is generally desired that the properties measured be standardized by size. Therefore, we can calculate the relative change in dimensions of the material as the force is applied, called the *strain*, and the standardized force through a cross-section of the material, called the *stress*. The resulting stress-strain graph (Fig. 4.2B) can be used to determine many standard material properties, some of which are described below. Berthaume (2016) explains the details of how to calculate stress and strain.

Strength: The stress that the material can withstand before yielding or fracturing; in practice this means that a stronger material will require a higher force to fracture should all other factors (e.g., shape, size, loading conditions) be held constant. We know that bone is stronger than fingernail or insect exoskeleton, as it takes higher stress to fracture it. For a force-displacement graph, we can measure the breaking strength, or the maximum force that was required to fracture the object (Fig. 4.2A), while the ultimate tensile strength is the maximum engineering stress that a standardized test piece can withstand (Fig. 4.2B).

Elastic modulus (Young’s modulus): How much a material deforms when it is loaded while the deformation is still elastic (i.e., before it is permanently deformed). It can be calculated from the slope of the initial, linear part of a stress-strain graph (Fig. 4.2B). Bone has a high elastic modulus, but that of skin is low. In lay terms, this is often considered to be ‘stiffness’, but materials science often uses ‘stiffness’ to describe the response of a structure rather than a material therefore, it is scale-dependent.

Toughness: How much energy it takes to propagate a crack through the material (called ‘energy release rate’ by Berthaume 2016). This can be determined from the area under a stress-strain graph (Fig. 4.2B). Breaking materials such as glass, nut shells, or eggshells can require very little energy because cracks become self-propagating and do not require additional input of energy; more energy must be used to extend a crack in plasticine or muscle tissue.

Brittle: A material that does not deform prior to fracturing (opposite of ductile). The blue line in Fig. 4.2C shows very little strain (deformation) before fracture at high stress. Glass and eggshells are classic examples of brittle materials, as they do not change shape before they fracture – in fact, you can put the pieces back together again, as they have

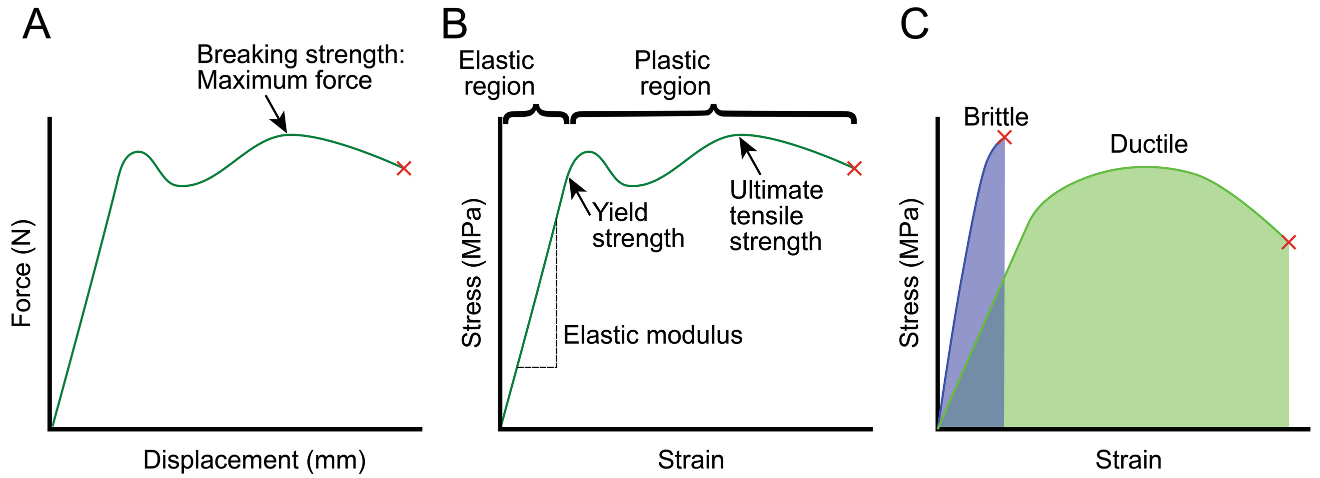

Fig. 4.2 Materials testing graphs illustrating key concepts in materials testing. A, Force (in Newtons, N) exerted by the test piece when the opposing end of the piece is pulled in tension (displacement, in mm). Fracture of the test piece is shown by a red x. B, When force is standardized by cross-sectional area of the test piece, it shows the engineering stress (in megapascals, MPa) in the test piece; engineering strain is the proportional change in the length of the test piece (unitless, or in percentage). The elastic region at the initial part of loading shows a linear change in stress, and the slope of this region is the elastic modulus. The yield stress is the stress at which elastic behaviour ceases and permanent deformation has occurred. The ultimate tensile strength is the highest stress that the material withstands before failure. C, Schematic plots of tensile stress-strain for brittle and ductile metals. Shaded areas under the graphs show that toughness is generally higher for ductile materials than brittle ones. Adapted from Berthaume (2016) and Callister and Rethwisch (2014)

retained their shape; this can also be called elastic fracture.

Ductile (also plastic): A material that deforms permanently before fracturing (opposite of brittle). The green line in Fig. 4.2C shows that substantially more strain (deformation) has occurred before fracture. Plasticine and ripe banana flesh behave in a ductile manner and so are permanently deformed when a force is applied to them.

Elastic: The deformation is not permanent, so the material will spring back to the original shape when the force is removed. Many materials behave in an elastic manner, with a linear stress-strain curve over very small strains (the 'elastic region' in Fig. 4.2B). Truly elastic materials, where the stress-strain curve is linear during moderate strain, are very rare. The clothing material we generally call 'elastic' has the property that, after moderate stretching, allows it to bounce back to its original length when no longer being stretched. However, 'elastic' and rubber behave in a more complex fashion termed hyperelastic. Vertebrate skin and muscle behave in a generally elastic manner.

Viscosity: The behavior of the material varies with time or speed of loading. While this may make you think about liquids with very different viscosities like water and honey, solids can also behave differently when loaded quickly or slowly. Most biological materials combine aspects of elasticity and viscosity and so are *viscoelastic*; the way they respond to loads changes with time (such as speed of loading). 'Silly Putty' is an extreme example of this, as it can bounce or brittle fracture when loaded quickly but flow when the load is applied slowly.

Fracture Mechanics

The surface area of food can be increased by plastic deformation and/or by dividing it into multiple fragments. Very few foods undergo extensive plastic deformation without fracture, perhaps including some soft fruits. To fragment a food, first a crack must be initiated in the material. This crack may then be propagated through the material. Fracture occurs when atomic bonds are broken in the material, usually by pulling atoms apart or sliding them past one another. Real materials generally have tiny cracks throughout, and when loaded, these cracks may elongate or propagate, eventually causing the material to fail. When a tooth first penetrates a food, a crack is initiated. A crack will only propagate when sufficient energy is concentrated at the crack tip, increasing stress and causing more bonds to fail. This is much easier to do when the crack tip is sharp and the material has a higher elastic modulus; both result in a larger percentage of energy being transferred to the crack tip rather than absorbed by the material through plastic deformation.

Cracks are easier to propagate through materials like eggshell that have a low toughness (critical energy release rate) than through materials like plasticine with high toughness. They also propagate much more easily if they are running through a homogeneous material. When a crack hits an interface between different materials, it is usually diverted, which blunts the crack, and energy is wasted in the crack running in alternative directions. Second, the surface energy at the interface between the materials may be higher than the energy needed to continue to propagate the crack through the first material, so the crack cannot initiate and propagate into the second material. Third, large numbers of microcracks in the material cause the energy to be dispersed among them, resulting in a much higher level of energy needed to propagate any single crack. Such crack-stopping mechanisms in structures with plywood-like layering make it less likely that the structure is easily fractured, and increase its toughness.

Tool Shape

Because different foods vary in how they break when force is applied, tooth shape can be optimized to achieve more efficient processing. One way to investigate this optimization process is to test how specific changes in tooth shape alter effectiveness. In such tests, the force and energy required to fracture and fragment a particular type of food are useful indicators of performance (Evans and Sanson 1998). Thus, for a particular tooth shape to be effective, the required force must not exceed the maximum bite force that can be generated by the muscles and lever mechanics of the jaws. Also, the average energy required to process it must be below the amount of energy that can be extracted from the food, such that there is a net gain of energy from all food consumed. A particular food may still be worth consuming even if it requires more energy to process it than is gained if it fulfills other requirements such as providing essential minerals or vitamins.

Teeth come in a great variety of shapes (Fig. 4.1), each of which differs from the next in the number, size, and shape of cusps, crests (including tall blades and low enamel ridges), basins, and valleys that make up the tooth crown. Which of these tools predominate largely depends on the type of food being processed. Lucas and Luke (1984) hypothesized that crack propagation in tough or ductile foods like grass or muscle tends to require an elongate blade, whereas brittle foods like nuts are more efficiently processed by a mortar-and-pestle arrangement. The critical material property requiring blades may actually be fibers that need to be cut rather than high toughness per se (Wright 2005).

Cusps: A cusp is a local topological maximum of the tooth surface, analogous to a hill. Some teeth, such as human canines, have only one cusp, while premolars and molars generally each have two or more cusps, such as the bunodont molars of the giant panda (Fig. 4.1B). The distribution and shape of cusps can vary both within a tooth and across the dentition. Cusps frequently initiate cracks in a food item, sometimes alone and sometimes by occluding into the space between other two cusps or crests. For simple cone- or mound-shaped cusps, there are two main aspects of shape that influence the force and energy required to penetrate and drive through food.

First, the radius of curvature at the tip of the cusp (*tip sharpness*) determines the area of contact between the cusp and food and thus also the pressure (Fig. 4.3A). A smaller radius of curvature (higher tip sharpness) will increase stress in the food for a given bite force (Lucas 1982). Once the tip of the cusp has penetrated the food, the shape of the shaft will determine the force and energy required for the cusp to drive though. This is *cusp sharpness*, which can be quantified as the volume of the cusp at a given distance from the tip (Evans and Sanson 1998). A smaller volume (higher cusp sharpness) will take less force and energy to penetrate most foods.

Most mammal teeth have multiple cusps, and the relative sizes, shapes, and arrangement of all cusps may affect how they interact with foods. Some of these factors have been considered by Berthaume (2014) and are discussed below. When tall cusps have ridges running down their sides, such as many bat canines (Freeman 1988), they may be considered to be crests, and so some of the crest shape characteristics discussed below will also be relevant (Freeman and Lemen 2006).

Crests: A crest is an elongated, blade-like feature with higher curvature in one direction. The newly-erupted tooth crown is referred to as the primary occlusal morphology, and is covered with enamel in most teeth. Prominent enamel-covered crests are found on carnassial and tribosphenic teeth (Fig. 4.1B). Following wear, the underlying dentine becomes exposed and enamel ridges are formed as part of the secondary occlusal morphology (Fortelius 1985). Enamel ridges are found on lophodont and selenodont teeth (Fig. 4.1B).

In a manner similar to cusps, the radius of curvature along the crest edge (*edge sharpness*) will influence how the blade initiates a crack in food (Fig. 4.3B). Occluding blades have one leading or rake surface, and the angle between the rake surface and a line perpendicular to the direction of movement is the *rake angle*. A higher rake angle decreases the contact area between the blade and the food and therefore displaces less material as the blade is driven through the food. Overall, a blade with a high rake angle thus tends to fracture food using less force (Evans and Sanson 2003).

The angle between the long axis of the blade and a line perpendicular to the direction of movement is the *approach angle* (Fig. 4.3C). An approach angle of zero is equivalent to pushing a horizontal knife blade directly down onto food. Increasing the approach angle increases the mechanical advantage of the blade by reducing the amount of material cut per unit distance moved. A higher approach angle therefore tends to reduce force requirements when propagating a crack through food (Evans and Sanson 2003).

Manufactured blades, such as scissors, typically have a small space (called *clearance* or *relief*) behind the edge of the blade (Fig. 4.3B). This reduces friction between blades and also reduces the tendency for material to force occluding blades apart.

Basins and opposing cusps: A basin is a depression in the tooth surface, in some ways the inverse of a cusp (Fig. 4.1B). Some basins, like the talonid basin of a tribosphenic lower molar, accommodate the occlusion of an opposing cusp. Shape characteristics that affect the function of basins are less clear than for the other tool types discussed here. It is possible that simply the area of the basin indicates how much food can be crushed between it and its occluding

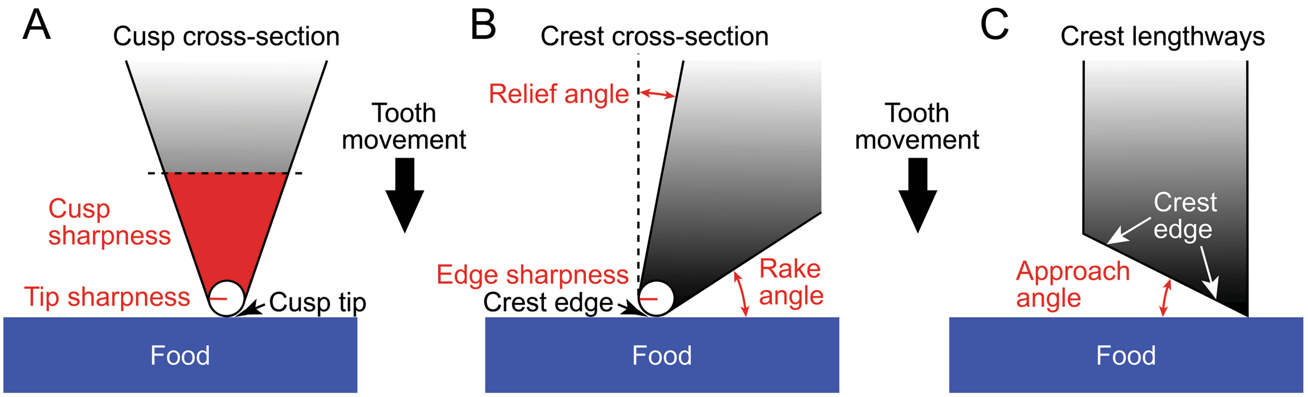

Fig. 4.3 Diagrammatic illustrations of functional parameters for: A, a cusp; B-C, a crest. In all three diagrams, the tooth is moving down from the top of the page to fracture food (blue). The long axis of the crest is perpendicular to the page in B and parallel to it in C. Partly adapted from Evans and Sanson (2003) and Evans (2005)

cusp. Lucas and Luke (1984) predict that some difference in the curvature of the basin and occluding cusp would improve performance. Yamashita (1998) tested this relationship in Malagasy lemurs by hypothesizing that the radius of curvature of the basin should increase relative to the radius of the opposing cusp with increasing food hardness, aiding food fracture by allowing for lateral excursions of the cusp within the basin. However, hard foods were actually correlated with a cusp radius more similar to the corresponding basin radius, creating a tight fit. This may indicate that these hard foods require precise occlusion of the crests surrounding the basin to improve fracture of foods. Basin volume has been measured in chimpanzees through the wear sequence by Klukkert et al. (2012) and in other hominids by Zuccotti et al. (1998) but without specific functional hypotheses.

Quantifying Tooth Shape

One of the significant challenges of investigating the relationships of potential shape parameters with performance and diet is the difficulty of measuring them from real teeth. Parameters such as rake angle are essentially cross-sectional shape measurements. Traditional methods for measuring these characteristics would involve physically sectioning the tooth or a replica, followed by optical projection or imaging for measurement. For example, Freeman (1992) investigated the cross-sectional shape of bat canines using sectioned replicas. Other metrics such as 3D surface area, volume, or surface curvature are even more difficult to assess using physical methods. The challenge is exacerbated by the particularly small teeth of some mammals. Along with the initial application of 3D shape capture methods to teeth (Reed 1997; Zuccotti et al. 1998; Jernvall and Selänne 1999; Evans et al. 2001) came the ability to measure these functional parameters and associate them with performance, diet and tooth wear (Evans 2005; Evans and Sanson 2005; Evans et al. 2006).

Tool Number

Each tooth is comprised of one or more component tools that may vary in type, shape and size. The overall performance of a tooth will depend on the action of all of these tools as they process food. While the precise performance of each component will vary with its shape and mode of occlusion, the number and type of these features will give an indication of how many opportunities there are for food fracture. For instance, when two teeth bearing a single blade occlude, there is one opportunity for the blades to trap a food item between them. However, if each of these teeth had two blades, each of which occluded against the two blades of the opposing tooth, there would be four opportunities for food fracture. Extending this analogy to more complex teeth, one can assume that the total number of food fracture opportunities is likely greater than proportional to the number of component tools.

This approach assumes that all tools act equally in fracturing food, which is unlikely to be the case in most instances. Small features may not interact or have sufficient space to successfully fracture food, while sharper enamel ridges may be more effective than blunter ones. However, for broad comparisons among tooth types and diets, counting the number of available tools may still be informative.

The quantification of tool type and number was pioneered by Jernvall (1995; Jernvall et al. 1996), who classified tooth crowns based on their number of large cusps (buccal and lingual) and crests (longitudinal and transverse). More recent methods have instead used 3D tooth surface data in combination with Geographic Information Systems (GIS) algorithms (Evans et al. 2007). Specifically, the orientation at each point on a digitized 3D surface of a tooth can be expressed in terms of one of eight cardinal compass directions, such as north or south-east (Fig. 4.4D). Adjacent points on the tooth surface with the same direction can be grouped together as a ‘patch’ or ‘clump’, with the number of these orientation patches giving a measure of the total number of topographic features and therefore the ‘complexity’ of the tooth surface. This measure is termed ‘orientation patch count’ or ‘OPC’.

The patches isolated by the OPC method do not uniquely count features such as cusps, crests, or wear facets. Any one feature may vary in how many patches it represents according to its shape and size – a large, conical cusp will have eight patches, while a small one may have only four patches (because of the finite size of the elements representing the surface), and a horizontal blade sometimes only two. Because of the great diversity of component shapes, the OPC method gives an overall estimate of tooth components that have the potential to apply force to food and is expected to be highly correlated with the number of potential breakage sites on the tooth.

The OPC method was first used to compare the cheek tooth row complexity of carnivorans (species in the order Carnivora) and rodents (species in the order Rodentia), two highly divergent groups among mammals that nonetheless have overlapping dietary specializations in their component species (Evans et al. 2007). In that study, tooth row complexity clearly distinguished broad diet types (including hypercarnivory, animal-dominated omnivory, and herbivory), but there was significant overlap between carnivorans and rodents in the same diet class. This indicates some degree of scale- and phylogenetic independence, meaning that dental complexity gives a good indication of general

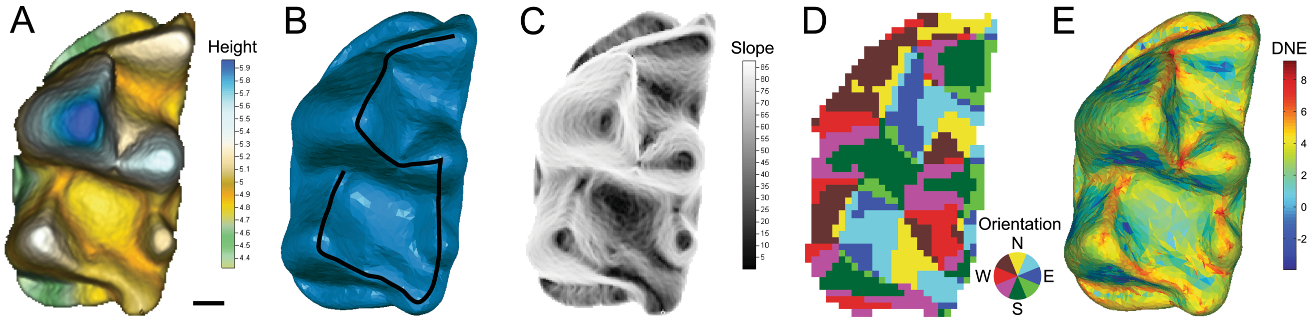

Fig. 4.4 Dental topography and complexity measures in occlusal view, demonstrated using the left lower second molar of the dasyurid marsupial *Antechinus agilis* NMV C12676 (Museums Victoria): A, Height-encoded map (height in mm); B, Shearing edges measured for calculation of shear ratio; C, Slope (in degrees); D, Orientation map for OPC calculation (colour wheel shows orientation and compass directions: north, south, east and west); E. Dirichlet normal energy (DNE). Scale bar = 0.2 mm. Adapted from Evans (2013)

diet regardless of the size or taxonomic affinities of a species. Some difference in the OPC-diet relationship was found between platyrrhines and prosimians by Winchester et al. (2014), but the general patterns of OPC with diet for these groups were similar.

Tooth Topography

Like the number and shape of its component tools, topographic measures of the entire tooth surface can also reveal diet. GIS or topographic algorithms can calculate the slope at each point of the tooth surface (grid point of a GIS map or vertex of a polygonal surface; Fig. 4.4C) with respect to the horizontal occlusal plane (Ungar and Williamson 2000). The mean slope of all points is the *average slope*.

Variation in height over the tooth surface can be quantified using the *relief index*. The relief index is based on the 3D true surface area of the crown (SA) and the 2D projected area of the tooth in occlusal view (PA), either as SA/PA (Ungar and Williamson 2000) or $\ln(\sqrt{\mathrm{SA}}/\sqrt{\mathrm{PA}})$ (Boyer 2008).

Sharper cusps and crests are likely to improve performance of teeth when fracturing ductile foods. Rather than measuring the sharpness of separate cusps, the average curvature or sharpness of the entire tooth surface can be quantified using Dirichlet normal energy (DNE; Fig. 4.4E; Bunn et al. 2011). DNE measures the degree of bending of the surface (bending energy), in essence giving the average curvature of the tooth surface.

Tool and Tooth Size

The absolute size of a tool or tooth affects its overall performance. Two cusps of the same shape that differ in size will vary in their performance in penetrating food because their interaction with the food occurs at the true size of the tool, not as size-removed shape (Evans and Sanson 1998). The function of a tooth therefore cannot be divorced from its size. In general, a larger tool can process more food with each bite, either through a larger area of contact or because it forms a longer blade. A blade cannot cut food any longer than itself, and a blade of twice the length can, in principle, divide a food item twice as long.

For great apes, Berthaume (2014) showed that cusp radius of curvature is significantly correlated to cusp size, but only weakly. Cusp radius of curvature and the arrangement of multiple cusps interact to influence the optimal tooth shape for a given food size (Berthaume et al. 2014).

Some of the most common dental metrics, such as measures of relative crest length (Kay 1975, 1978), are related to size. In particular, the objective of *shear quotient* and *shear ratio* is to standardize the length of crests relative to the size of the tooth (Fig. 4.4B). Higher shear quotients are associated with foods that require more processing, such as leaves and insects, compared to foods such as fruits (see Bunn et al. 2011 for review). This could be because longer crests are likely to be associated with taller, sharper cusps (Evans and Sanson 1998) or to ensure more food is processed per chew (such as undulating crests in ungulates).

Increasing tool size, and thus the amount of food processed, generally comes at the cost of increased force and energy for a given occlusal stroke, but the overall processing time (such as number of bites or chews) may be reduced. Depending on how much mechanical processing is required, there is likely to be a trade-off between the size and the number of tools present on a given tooth. While "bigger must be better" is often the mantra regarding teeth, as it implies more processing per bite (such as with more potential food fracture events), it also requires a higher bite force. Larger teeth may also increase the chance of missing small foods due to larger gaps between tooth features. Selection may be for minimum number of chews (maximum amount processed per bite), or minimum bite force. If selecting for the former, then current bite force must be adequate or there will be selection pressure for increased bite force.

The total size of a tooth crown has implications for the number of tools (e.g., cusps, crests, basins, etc.) and their relative sizes that can be accommodated. For a fixed tooth size, average tool size must decrease if the number of tools increases, and vice versa. Alternatively, increasing tooth size will increase the number of tools of a given size that can fit on the tooth surface. The overall processing ability (typically of chewing) can be assessed by looking at all occluding teeth, usually the molars and sometimes the premolars. The scaling relationships of tooth to body size in fossil taxa can also be investigated when combined with body size estimation (Hopkins 2018).

Simulation and Performance Testing

Computer simulations can be used to model and test the performance of different tool and tooth shapes under particular circumstances. Finite element analysis (FEA) is based on computer models of the object of interest (e.g., a tooth), with each model comprising many simple triangular or polygonal elements (Rayfield 2007). Simulated loads are applied to the computer model and then used to calculate the distribution of stress and strain. The majority of dental FEA studies so far have focused on the risk of tooth fracture rather than the question of how effectively a given tooth will fracture a given food. For instance, Macho and Spears (1999) used 2D FEA models to relate the differences in occlusal topography in great apes to the stresses in the tooth when exposed to loads required to fracture food items. Recent work by Berthaume et al. (2010) on fossil hominins has greatly extended those early efforts to assess the influence of tooth size and shape along with food size on stress in loaded foods. More precise information on loading, based on simulated tooth contacts using the Occlusal Fingerprint Analyzer, and of the ligamentous and bony support of the tooth leads to greater confidence in interpretation of likely stresses during chewing (Benazzi et al. 2011, 2012, 2014).

Though promising, FEA studies at present are generally limited in that the material properties of foods (e.g., anisotropy and viscoelasticity) are greatly simplified or even ignored (see Skamniotis et al. 2016 for an exception). Likewise, they cannot simulate fracture mechanics, including crack propagation, in a broad array of foods (fibrous foods, leaves, grasses, nuts, seeds, meat, and bone). In addition, crack propagation in enamel and dentine requires further research. As a result, physical testing currently remains the best way to examine such questions further. Abler (1992) was a pioneer in his investigation of the functional consequences of blade shape and serrations in tyrannosaurids and other animals. Anderson and LaBarbera (2008) tested a number of the hypotheses put forward by Abler (1992) and Evans and Sanson (1998), examining the effect of approach angle when fracturing asparagus and shrimp. Berthaume et al. (2010) used steel casts of hominin teeth to load synthetic domes. Other notable examples include Whitenack and Motta (2010) testing performance in shark teeth, and Crofts and Summers (2014) using model morphologies of fish teeth for crushing shells.

Strengths of Approach

Tooth morphology represents the evolved response to many factors, including the mechanical processing of foods and the need to resist fracture and wear. It is obvious that the teeth of any given species of mammal are sufficient for processing relevant foods (where necessary), with the shape of teeth having evolved in response to the mechanical properties of the diet.

Computer simulation and physical testing provide independent sources of information about expected tooth shapes for given foods, as well as the likely performance of both modern and fossil teeth. Control of shape variables of the teeth and mechanical properties of test foods in carefully designed experiments are extremely important in being able to tease apart the influences of these components.

Biases and Shortcomings

The fundamental assumption underlying the use of fossils to reconstruct biology is that there is a tight match between form and function (Bock and Wahlert 1965), although there may be many forms that can produce the same function. Here, we are specifically interested in whether tooth shape truly reflects diet. Given a large enough bite force with a strong, flat tooth surface, probably any food could be consumed, including bone. However, such a system would be over-engineered, more expensive than necessary, and therefore evolutionarily unstable. Nevertheless, current techniques and interpretations of dental morphology cannot reveal all of the foods consumed by an animal.

Limits of Prediction

Foods that require no mechanical processing do not exert a selection pressure for tooth shape, and thus cannot be inferred from tooth morphology. It may be that tooth shape is correlated with the most mechanically challenging foods in a diet. Such foods may be "fallback foods": foods that are only occasionally consumed (e.g., depending on the season or life stage) and that require more or alternative processing effort than the typical diet of the species but that are crucial to the survival of the individual (i.e., under strong natural selection).

While some mammals have evolved an essentially ideal tooth shape for their diet, such as many carnivores and insectivores (Evans and Sanson 2003), dental morphology often represents a trade-off between performance and various constraints, including mechanical (e.g., risk of tooth fracture), developmental, spatial, and phylogenetic. For example, overall tooth shape and number in each class (incisors, canine, premolars and molars) is often conserved across higher taxonomic groups to the point that most postcanine teeth can relatively easily be identified to family level. Similarly, tooth shape may not always entirely reflect the diet of the species in question but rather preserve a 'memory' of the foods consumed by its ancestors. The polar bear *Ursus maritimus* is a dedicated carnivore but retains a relatively complex tooth shape similar to its close relative the brown bear *Ursus arctos*, which is much more omnivorous (Evans et al. 2007). The short divergence time between these two species may have been inadequate to drastically change polar bear molar shape, even though it is visibly less complex. As lineages evolve, there may be a substantial delay between changes in food preferences and subsequent dental morphological adaptations (Davis and Pineda Munoz 2016); however, the rate at which tooth morphology can change has yet to be quantified.

Limitations of Techniques

While the new morphological approaches described above have greatly improved analyses of dental morphology, there are still challenges to establishing consistent, objective and informative techniques. For example, 3D data may be captured via many different scanning systems, such as X-ray computed tomography (CT and microCT), surface scanning (structured light, laser) and photogrammetry. Each imaging method has its limits and biases that must be taken into account. CT enables detailed structural information to be obtained, including from the interior of the object, but requires expensive equipment ($100K–$2M), often based in medical or engineering facilities, and significant data storage (often >2 GB raw data per scan). Surface scanning typically has the advantages of faster data capture and smaller data storage requirements (2–200 MB per scan) but will only scan external, easily visible surfaces. Some laser and structured light scanners can be relatively expensive ($20K–$200K), while size- and resolution-limited machines now exist for less than $5K. Photogrammetry has markedly improved over the last few years, including using mobile phone apps like 123D Catch (Autodesk), but high quality surfaces require sufficient texture on the surface and dozens to hundreds of photographs from many angles followed by hours to days of computer processing.

3D scanning of teeth can be particularly difficult with light-based scanners due to the opalescence and reflectivity of enamel and can require powder-coating to achieve high quality surface reconstructions (e.g., Smith and Strait 2008). Small teeth (less than approximately 4 mm in length) are challenging to scan. Very few surface scanners can successfully scan small, high relief tribosphenic molars, particularly when they are embedded in the jawbone (though Laser Design and Breuckmann can do isolated teeth of this type). MicroCT is the preferred method for these small teeth, as it easily deals with undercuts and closely approximated teeth and bone and can achieve sufficiently high resolution (<10 micron voxel sizes).

Processing of 3D data also includes many complex steps, such as image segmentation, alignment of multiple scan passes, smoothing, downsampling and file format conversion. There remains a need to establish reliable protocols providing consistent results, although a reasonable amount of testing has established boundary conditions for good practice.

Examples of Applications

This chapter reviews a diverse range of approaches and methods to reveal the diets of extinct mammals. Below we provide some examples of how these methods can be applied to specific research questions.

Multituberculates

The typical conception of mammalian evolution has been that mammals did not diversify until after the extinction of the non-avian dinosaurs at the end-Cretaceous mass extinction 66 million years ago. The multituberculates were the most abundant mammals during the Mesozoic and the longest-lived group of mammals, surviving from around 180–35 million years ago. Dental diversity within multituberculates was relatively high, ranging from taxa with a large blade-like lower molars to those with highly complex low-crowned teeth. However, because there are no close extant relatives of multituberculates, their diets have been hotly debated. Wilson et al. (2012) used OPC to study the dental morphology of multituberculate mammals across the Cretaceous-Paleogene boundary. Their findings reveal a major morphological radiation before the mass extinction event, which suggests that mammal diversification had commenced well before the disappearance of non-avian dinosaurs. Many of these new multituberculates appear to have been herbivorous, perhaps feeding on the newly dominant angiosperms. Therefore, mammals may have played a broader ecological role in Mesozoic ecosystems than previously thought.

Marsupials and Placentals

Marsupials and placentals, the two main groups of extant mammals, diverged around the Early Cretaceous and independently radiated on multiple continents throughout the Mesozoic and Cenozoic. Despite multiple reports of morphological convergence in features such as skull shape, body form, and locomotion, it has so far remained unclear whether dental morphology changed with diet in a similar way in both groups. To address this, Pineda-Munoz et al. (2017) developed a new methodology called Multi-Proxy Dental Morphology Analysis (MPDMA), which combines detailed information on diet with multiple quantitative measures of tooth shape described in this review, including OPC, average slope, and relief index. MPDMA was tested for four mammal orders (Carnivora, Diprotodontia, Primates and Rodentia) across eight dietary specializations (herbivory, carnivory, frugivory, granivory, insectivory, fungivory, gumivory, and generalized) and thus offered the possibility to draw more accurate dietary inferences that better represent the multidimensional nature of dental morphology and dietary specializations across all mammals (Davis and Pineda Munoz 2016). The results show that, like carnivorans and rodents (Evans et al. 2007), marsupials and placentals with the same dietary specializations have evolved morphologically similar dentitions, highlighting the tight connection between high-level morphology and diet in tooth evolution.

Large Herbivores and Lophs

Reconstruction of past environments across the globe has been a major challenge for paleoecologists. Important requirements for such a task include taxa that are widespread with fossilized characteristics that reliably indicate ecological variables such as net primary productivity. Liu et al. (2012) correlated dental characteristics of large herbivores (orders Perissodactyla, Artiodactyla, Primates, and Proboscidea) with climate data across the globe to test whether net primary productivity could be estimated from fossil teeth. In large herbivores, the processing capability of a tooth can be estimated by counting the number of longitudinal lophs (LOP) or enamel ridges, with higher LOP values correlating with an increased ability to process plant matter. Likewise, hypsodonty is the relative height of the tooth and is an adaptation to high rates of wear, particularly in arid environments with higher loads of exogenous grit (see Barr 2018). Both correlate with drier environments, where vegetation exercises a higher abrasive effect on tooth surfaces. Liu et al. (2012) observed that the average LOP/hypsodonty ratio of the members of a community is correlated with climate in modern ecosystems and applied this metric to the western Eurasian Sansanian and Pikermian chronofaunas (both Miocene) to interpret their paleoclimates.

Plagiaulacoid Teeth

Bladed teeth with serrations, termed ‘plagiaulacoid’ by Simpson (1933b), have independently evolved in several groups of mammals: marsupials (several times independently within this group), carpolestid primates, and multituberculates. The importance and likely diet of fossil species with plagiaulacoid teeth has been debated since Simpson’s (1933b) first description (Krause 1982; Biknevicius 1986; Dumont et al. 2000). To investigate the functional capabilities of these teeth, Pollock (2016) measured crest shape parameters in marsupials and multituberculates and used the range of values to create 3D printed models of simplified bladed teeth with or without serrations. Each of the models was used in physical force testing with two foods that emulate plant (asparagus) and animal (gelatine) materials. Higher rake angle improved performance for gelatine but not asparagus, while higher approach angle and added serrations did so for asparagus but not gelatine. These observations suggest that a plagiaulacoid tooth shape is likely to be more advantageous for plant feeders and that most extinct plagiaulacoid taxa were probably herbivorous.

Hard Food Feeding in Hominins

During the evolution of the human lineage, several hominin species are thought to have consumed hard foods, including the robust australopith ‘Nutcracker Man’ *Paranthropus boisei* (Leakey 1959). Molar shape varies among fossil hominins, including the degree of occlusal relief. How could one determine the likely diet of the various hominins based on dental morphology? Berthaume et al. (2010) examined how molar shape affected the fracture of hard foods using both physical testing and finite element analysis. Metal replicas of teeth were used in force tester experiments to fracture acrylic hemispheres (emulating nut shells), where the force and displacement to fracture were measured. Each physical test was directly compared with an equivalent finite element simulation, and these showed reasonable correspondence. While the study did not unambiguously identify dental features that optimize hard food fracture, the approach paved the way for tightly-controlled experiments along with high resolution quantification of dental morphology to resolve these questions.

Methods Demonstration

Below we give a basic outline of the steps required to scan, process, and import a 3D model for calculation of OPC and other dental topographic metrics. Given the variety of available scanning devices and software packages, it is not possible for us to be comprehensive, but this outline will serve as a list and recommendations for requisite operations.

1. Obtain surface or volume scans of tooth surface. Surface scans from laser scanners (NextEngine, Laser Design) or light scanners (Artec, Breuckmann, ATOS); sometimes manual alignment of partial surface models are required (e.g., software Geomagic, SolidWorks). Volume scans from X-ray computed tomography (SkyScan, Xradia) to give image stacks of cross-sections through the specimen; surfaces can be extracted using thresholding or segmentation (software Avizo, Mimics).
2. Process surface model. Remove extraneous surface, undertake smoothing and minor editing.
3. Align surface model to given axis system. For instance, occlusal direction pointing along positive Z axis, anterior/mesial along positive Y axis.
4. Convert to required file format. Software packages for creation and calculations use many different 3D surface file formats including .ply, .obj., .dxf and .stl – some in either binary or ASCII encoding. You will need to ascertain what file formats are imported by your calculation software.
5. Import into calculation software and run analyses. Software packages include Surfer Manipulator (Evans et al. 2007), Teether (Bunn et al. 2011), MorphoTester (Winchester 2016), and molaR in R (Pampush et al. 2016).
6. Interpretations of diet will generally be based on a modern comparative database of species with known diets. Conventional statistical tests can be used to determine whether the fossil population/species differs from extant species (t-test, ANOVA) and discriminant function analysis/canonical variates analysis (DFA/CVA) of extant species can be used to interpret values from focal taxa.

Future Prospects

With the advent of further methods and approaches to quantify tooth shape, we will be entering a new golden age of dental morphology. High-throughput 3D imaging and processing will be key in compiling large datasets of modern and fossil morphologies. In addition, we must continue to strive for a better fundamental understanding of the mechanical properties of foods and their interaction with morphology. We look forward to the application of these advances to better interpret the paleoecology of mammals throughout the world.

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