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SYMPOSIUM

Beyond Description: The Many Facets of Dental Biomechanics

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Synopsis Teeth lie at the interface between an animal and its environment and, with some exceptions, act as a major component of resource procurement through food acquisition and processing. Therefore, the shape of a tooth is closely tied to the type of food being eaten. This tight relationship is of use to biologists describing the natural history of species and given the high instance of tooth preservation in the fossil record, is especially useful for paleontologists. However, correlating gross tooth morphology to diet is only part of the story, and much more can be learned through the study of dental biomechanics. We can explore the mechanics of how teeth work, how different shapes evolved, and the underlying forces that constrain tooth shape. This review aims to provide an overview of the research on dental biomechanics, in both mammalian and non-mammalian teeth, and to synthesize two main approaches to dental biomechanics to develop an integrative framework for classifying and evaluating dental functional morphology. This framework relates food material properties to the dynamics of food processing, in particular how teeth transfer energy to food items, and how these mechanical considerations may have shaped the evolution of tooth morphology. We also review advances in technology and new techniques that have allowed more in-depth studies of tooth form and function.

Introduction

Lucas (2004, p. ix) begins his book on tooth functional morphology with the following statement: “Teeth cause such dreadful problems in humans that interest in them by non-dentists would seem both unlikely and unhealthy.” Tongue-in-cheek as it is, this potential for problems means that there is a great deal of interest in teeth, much of it focused on human teeth, specifically their evolution (Strait 1997; Daegling and Hylander 2000; Plavcan and Daegling 2006; Berthaume et al. 2010, 2013, 2014), structure (Shellis et al. 1998; Xu et al. 1998; Grine 2002; Constantino et al. 2012), failure (Rasmussen and Patchin 1984; Xu et al. 1998; Lee et al. 2009), and repair (Benalcázar Jalkh et al. 2020; Fontolliet et al. 2020; Yadav and Gangwar 2020). Much of the other work on dental functional morphology focuses on tooth function and failure, usually with the implicit expectation of working in a mammalian system. Many of these studies focus on the functional morphology of the tooth and how overall tooth structure and tooth microstructure affect tooth failure (Lucas et al. 2008, 2016; Chai et al. 2009; Lee et al. 2011; Yilmaz et al. 2015; Constantino et al. 2016; Casteren and Van Crofts 2019), how wear and microwear affect function (Ford et al. 2009; Borrero-Lopez et al. 2015; Casteren and Van Crofts 2019), and how different types of applied loads will affect failure (Lawn and Lee 2009; Chai et al. 2011; Lawn et al. 2013). In addition to working with real teeth, many of these studies incorporate computational models to show the importance of gross tooth morphology. Other studies create physical models, brittle glass “shells” over ductile cores, to describe modes of failure with different cusp morphologies (Qasim et al. 2005; Lawn et al. 2007), different “prey” material properties (Qasim et al. 2007), and with different degrees of wear (Keown et al. 2012).

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This mammalian taxonomic bias to the dental biomechanics literature is problematic, as the structure and materials from which mammalian teeth are made differ from those of other vertebrates (Poole 1956). There have been some studies focused on the materials properties of non-mammalian teeth, such as crocodilians (Enax et al. 2013), elasmobranchs (Whitenack et al. 2010; Enax et al. 2012), and non-avian dinosaurs (Erickson et al. 2012, 2015, 2020). The inherent differences between mammalian and non-mammalian dental material properties detailed in these studies highlight the need for more non-mammalian study to properly understand not only material properties, but overall function, of teeth across vertebrates.

Another push for understanding the structure and function of mammalian teeth comes from work on the mammalian fossil record, which is composed almost exclusively of teeth and tooth-bearing elements for much of mammalian evolutionary history (Kielan-Jaworowska et al. 2005). The largely inorganic composition, density, and structure of enamel make enamel-covered structures like teeth excellent candidates for fossilization. Because paleoecology studies require creative use of limited fossil resources, a wide variety of metrics have been developed to interpret organismal ecology based on tooth shape, and, by extension, dietary ecology in fossil assemblages. Many paleontologists have utilized two-dimensional (2-D) analyses of dental features to interpret function in fossil teeth, and these methods have been validated by numerous studies demonstrating the utility of particular measurements in modern clades. Common approaches have included qualitative and quantitative assessment of wear facets, mesowear, and related chewing behavior (Crompton 1971; Butler 1972; Kay and Hiiemae 1974; Hunter and Fortelius 1994; Dewar 2003; Fortelius and Solounias 2000; Damuth and Janis 2011; Kaiser et al. 2013); linear and geometric morphometrics of whole teeth, tooth rows, and specific dental features (Wesley-Hunt 2005; Friscia et al. 2007; Palmqvist et al. 2007; Gómez Cano et al. 2013; Wilson 2013) and quantification of sharpness via radius of curvature (Popowics and Fortelius 1997; Evans et al. 2005; Hartstone-Rose and Wahl 2008).

Recently, 3D approaches to quantifying functional tooth morphology have become the norm in mammalian dental paleoecology. Building on the aforementioned 2D techniques, these 3D approaches are a logical next step because teeth function in three dimensions, and μCT scanning has become widespread, logistically reasonable, and affordable. 3D shape analyses stem from the same general principles as 2D analyses, focusing on quantification of shape and relative size of dental features, and aiming to place extinct forms in functional context via comparison with extant forms associated with known dietary ecologies (Evans 2013). 3D modeling has been used not only to understand the genetic and developmental origins of diverse dietary ecomorphology in mammals (Salazar-Ciudad and Jernvall 2010; Jernvall and Thesleff 2012), but also to quantify shearing capability and model tooth interactions during chewing stroke (Strait 1993; Strait 2001; Evans and Sanson 2003; Evans and Sanson 2006; Evans and Fortelius 2008; von Koenigswald et al. 2013). Dental topographic metrics like orientation patch count, relief index, Dirichlet normal energy, and average surface slope (Evans et al. 2007; Boyer 2008; Bunn et al. 2011; Evans and Janis 2014; Winchester et al. 2014; Pampush et al. 2016; Pineda-Munoz et al. 2017; López-Torres et al. 2018) can be applied to individual teeth or full tooth rows, and have the added advantage of being "homology-free," as opposed to geometric morphometric approaches that require homologous landmarks. This flexibility has led to the application of dental topographic analyses outside of Mammalia (e.g., Melstrom 2017), but this application is not yet commonplace, and the utility of these metrics in teeth without precise occlusion has not been fully explored.

Classification schemes

Although many of the existing experimental approaches used to study mammalian teeth can be applied to other tooth morphologies, mammalian teeth differ qualitatively from those of other vertebrates in the high precision of their occlusion, complex morphology, and regional specialization. Therefore, in order to systematically discuss dental biomechanics in a broader set of tooth forms, we need to look beyond mammals. A comparative approach, first proposed for marine reptiles, correlates tooth morphology with diet (Fig. 1; simplified from Massare 1987). Based on these correlations, teeth can be classified into overlapping "feeding guilds" that exist along continua between three morphological and dietary extremes: robust, molariform teeth are for crushing shelled prey items, moderately robust but pointed teeth with cutting edges are for seizing and processing fleshy prey like large fish and tetrapods, and long pointed teeth are for piercing soft prey like squid or small fish (Massare 1987). While the correlation between tooth morphology and prey

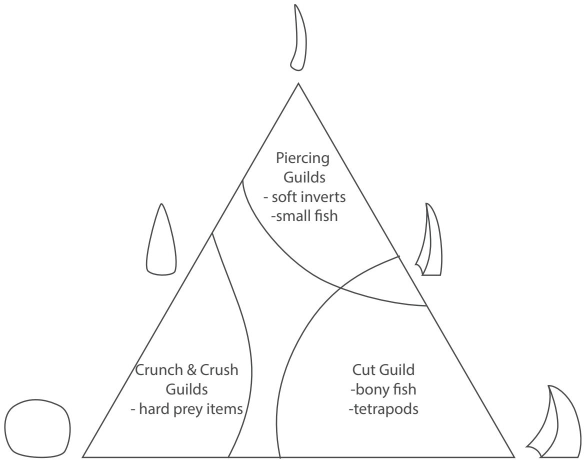


Fig. 1 Simplified diagram showing stylized tooth types and associated feeding guilds. Tooth morphologies exist along gradients between vertices, and there is overlap between guilds/morphologies. Some guilds have been combined, and others omitted for clarity. Modified from Massare (1987).

type implies an underlying correlation between food material properties and tooth function, this relationship is not explicitly tested. Especially in the case where guilds overlap or exist in a continuum along one axis of morphological variation (e.g., Fig. 1, simplified from Massare 1987), the observed correlation of tooth morphology and prey preference does not explain the functional underpinnings of the observed morphology.

While these descriptions, “crushing,” “cutting,” and “piercing,” are intuitive and frequently used, they have little to do with the underlying fracture mechanics at play. Instead of focusing on the correlation between prey type and tooth shape, we should examine the material properties of the food items teeth must process. Specifically we should consider the stiffness and toughness of the food, as well as how it behaves when subjected to loads and in failure (see Box 1).

Lucas (2004) takes this approach to understand the relationship between tooth morphology and function: considering how tooth morphology serves to reduce the energy required to break down food items, and how food material properties affect tooth morphology. By plotting potential food items by their toughness (Jm^{-2}) and Young’s modulus (GPa), Lucas (2004) maps out broad tooth types required to process different sorts of food (Fig. 2). Toughness describes a material’s ability to absorb energy through deformation prior to failure. Young’s modulus is a description of the stiffness of a material, particularly in the early stages of loading. Blades and wedges are required for breaking down tough foods with low and high Young’s moduli, respectively. In this scheme, cusped teeth are required to break down most food items that fall below the given toughness threshold, save those that have both low toughness and low Young’s moduli, which require no teeth to process.

Lucas’ (2004) book represents the most recent comprehensive effort to take a thorough look at tooth biomechanics, but is not without its limitations. The focus of the book is almost exclusively on mammals and the evolution of the mammalian dentition. Coupled with this is the stated assumption that tooth morphology is tied to the ability to create the amount of fracture in food items required for efficient digestion. This means a different amount of processing for different food items: cutting off chunks of meat for carnivores, breaking seeds into multiple fragments, or increasing surface area by reducing particle size in frugivores. However, Lucas’ (2004) study is a very mammal-centric interpretation of tooth function. Lucas (2004) partially addresses this problem by considering how different teeth are used for “ingestion,” or obtaining food, versus “mastication,” processing the food for further digestion, but does not address the fact that specialized teeth are many and varied outside of the mammalian radiation.

A more general view

When discussing dental biomechanics, thinking of teeth as energy transfer tools is important (Lucas 2004). However, it is also key to understand how that energy is used. On the one hand, many mammals, and indeed non-mammals, use their teeth to procure and/or reduce food items to facilitate digestion. On the other hand, there are many examples of teeth, mammalian, and otherwise, that have other end goals and even secondary uses, like display. For the purposes of this review, we will focus on the broad functional goals associated with obtaining and processing food. While some teeth are used to break food particles down into smaller pieces, thereby increasing surface area, other teeth may instead be used to create and propagate holes or fractures through food items, allowing for the capture of evasive prey or injecting toxins. What still unites these disparate strategies is the connection between tooth morphology and the material properties of the food items being captured, processed, or manipulated (Lucas 2004). However, this is complicated as food item material properties, like toughness, are context dependent, and difficult to measure and compare (Lucas 2004; Berthaume 2016). Another aspect of tooth function that should be

Box 1. A brief primer on fracture mechanics.

A Brief Primer on Fracture Mechanics

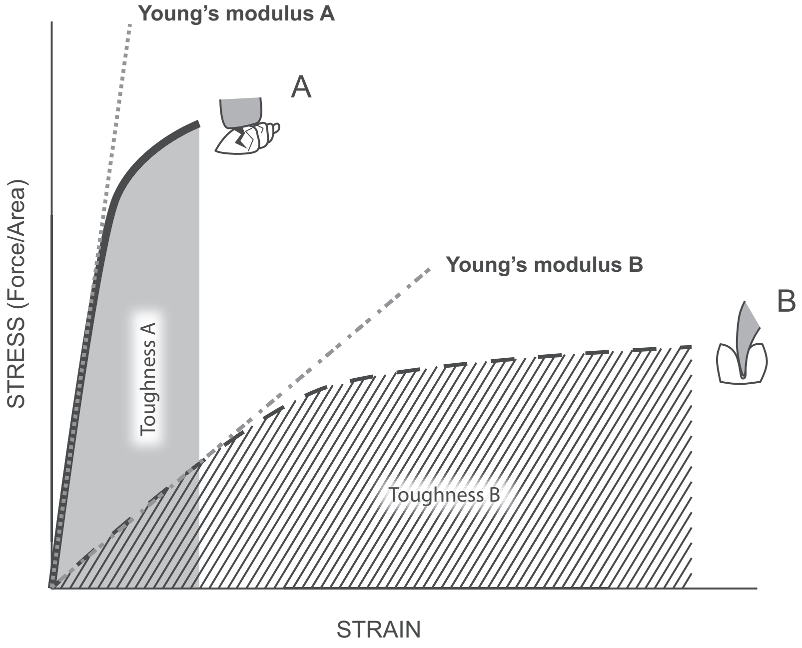
The following terms describe basic material properties, particularly those that relate to energy, and modes of failure discussed in the text. Material property values are based on stress/strain curves, which show the amount of deformation (strain) seen in a material for a given applied force (stress).

Stiffness/Young's modulus: How much a material resists deformation, measured as the initial slope of a stress-strain curve (thin grey dotted and dot-dash lines below).

Toughness: How much energy can be absorbed before a material fails, measured as the area under a stress strain curve (shaded and line filled areas below). By deforming under loads, tough materials increase the energy required for failure.

Brittle materials, like the shell drawn below (A), have a higher stiffness and store energy instead of deforming. Stored energy builds up in brittle materials until they shatter.

Ductile materials, like the meat drawn below (B), have a lower stiffness and readily deform under applied loads. Deformation requires energy that then cannot be used to cause fracture. When a fracture does form in a ductile material, there is no stored energy to propagate the crack, so additional energy must be applied by the tooth.



Example Stress-Strain Curves

considered is the speed at which teeth are used: tooth action can fall anywhere along a spectrum between low, quasi-static speeds ($\ll 1$ m/s) and high, dynamic speeds (>1 m/s). Strain rate, the speed with which a load is applied to a material, affects the material's response to mechanical loads (McElhaney 1966; Shergold et al. 2006; Van Sligtenhorst et al. 2006; Song et al. 2007; Karunaratne 2016; Karunaratne et al. 2018; Zhu et al. 2018). Therefore, the speed at which a food item is loaded will impact (or not, apologies for the pun) the relative amount energy that goes into fracture formation or is lost to deformation and momentum transfer (Anderson et al. 2019).

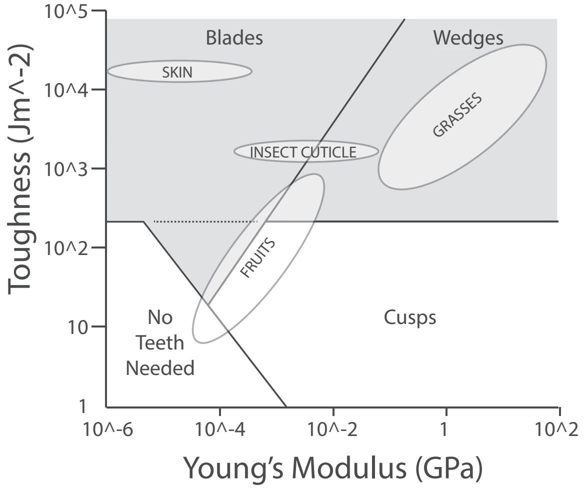


Fig. 2 Diagram plotting tooth type by food material properties, with some example food item ranges. Foods above a set toughness (Jm^{-2}) threshold, like skin, insect cuticle, or grass blades, require a bladed tooth morphology (gray region), either simple blades or wedges. Food below this threshold, like some fruits, with a high Young's modulus (GPa) require teeth with cusps. Foods, particularly some fruits, with low toughness and low Young's modulus do not require teeth. Modified from Lucas (2004, Fig. 7.1).

While both Massare (1987) and Lucas (2004) capture key aspects of dental functional morphology, neither presents a complete picture of energy transfer and how it is affected by (1) food-item material properties, (2) mode of food-item failure, or (3) the speed at which energy transfer occurs. Incorporating aspects of each approach, we propose a modified scheme for relating tooth form to diet and ecology (Fig. 3). This will allow us to compare teeth across a range of taxa, and develop testable hypotheses about tooth functional morphology. Furthermore, if we consider the three morphological extremes to be tool archetypes rather than teeth, this scheme can be used to explore the diversity of function in multi-cusped teeth as well as "simpler" single-cusped teeth. What follows is a brief, and by no means exhaustive, summary of the work done on the biomechanics of archetypal "crushing," "cutting," and "piercing" dental tools, considering these questions of energy transfer, and mode of failure.

Crushing

"Crushing" dental tools are blunt, typically low-crowned, and are used to induce widespread fracture and fragmentation in brittle food items, typically hard protective shells. When thinking about Lucas' toughness-Young's modulus scheme, "crushing" dental tools fall into the "cusped" tooth morphology region (Lucas 2004). Because they are working on

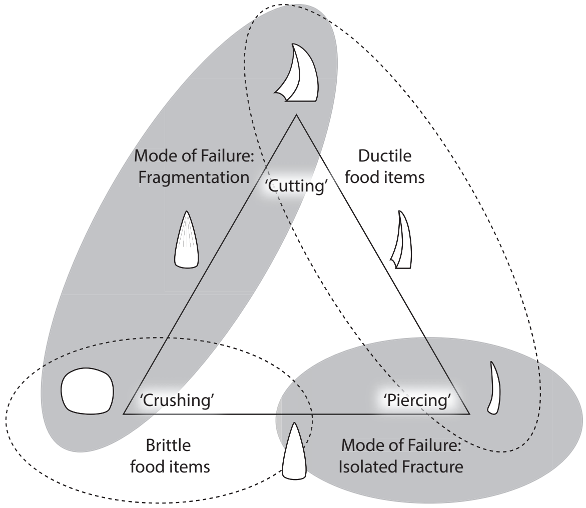


Fig. 3 Proposed scheme for future work in dental biomechanics, based on the work of Massare (1987) and Lucas (2004). Dental tools are differentiated by their mode of failure (dark gray ovals), and the material properties of the food item being processed (white ovals with dotted lines). Both metrics exist along a gradient, and dental tool archetypes are associated with combinations of these factors: "Crushing" dental tools are used at semi-static speed to elicit fragmentation of brittle food items. "Cutting" dental tools are used at a range of speeds to fragment ductile food items. "Piercing" dental tools are used to create isolated holes in ductile food items, typically under dynamic loads but not always.

brittle food items, the energy being fed into the system is not dissipated via deformation. Instead energy is stored in the food item until it is catastrophically released, causing fragmentation.

The functional morphology work on "crushing" dental tools broadly overlaps with work done on bunodont and hominid dentitions, hypothesized to have evolved to break brittle shells of nuts and seeds (Berthaume et al. 2010). While some of these studies focus on multi-cusped dentitions (e.g., Berthaume et al. 2013, 2014), many studies that look at the function of single cusps can also be applied to "crushing" dental tools. It is important to remember that energy transfer is not a one-way street, and that teeth are also under high loads during these interactions and may be subject to failure. A number of these studies create physical models, modeling cusps as brittle glass layers (a stand-in for enamel) over more ductile cores (a stand-in for dentine). The purpose of these physical models is to document the location and progression of cracks in the brittle outer coat under a number of different experimental conditions: with convex versus concave surfaces (Qasim et al. 2005), surfaces with varying convexity (Lawn et al. 2007), and with worn occlusal surfaces (Keown et al. 2012). These brittle shell models were also used to investigate how loading the model with "food items" of different material properties, particularly those that can dissipate energy, will affect crack formation and crown failure (Qasim et al. 2007). Other work has focused on simple computational models to describe where and how cusps will fail, considering how factors like food modulus, particle size, or type of load affect failure (Lawn and Lee 2009; Lawn et al. 2013).

Other work, less focused on hominid teeth, has tested for functional trade-offs in a range of possible "crushing" shapes, comparing the tool's ability to induce fracture with the likelihood of failure of a tooth with the same shape. Some of these studies focus on the amount of force required to fracture prey items. Experimental work on physical models of teeth inferred to be for processing hard prey has shown that they are capable of crushing brittle shells, but incapable of cutting tough prey materials (Schulp 2005). Meanwhile, simplified model teeth with more pronounced tips or cusps required less force and energy to induce fracture (Crofts and Summers 2014). Contrasting the ability of these simplified models to induce fracture with the distributions of stresses and strains under simulated loads shows a trade-off where a weakly rounded, but not flat, tooth shape is best able to crush brittle prey while resisting failure (Crofts 2015). In many hard-prey specialists, especially fish, "crushing" teeth are arrayed in a broad plate. Similar mechanical methods have been used to test how variation in the curvature of upper and lower tooth plates affects fracture in a range of shelled food items (Kolmann et al. 2015). There are also well studied examples of crushing teeth in mammals, such as otters (Chai et al. 2009) and the convergent evolution of bone-crushing in extinct borophagine canids and hyenas (Tseng and Wang 2011). Most of this work, however, has focused on describing how these hard-prey specialists apply high forces to their prey, describing various musculo-skeletal adaptations in a range of taxa, as opposed to investigating tooth shape directly (Summers 2000; Huber et al. 2008; Gidmark et al. 2014; Kolmann et al. 2016; Campbell and Santana 2017; Laurence-Chasen et al. 2019; Rutledge et al. 2019).

There is little work on the mechanics of crushing food with teeth at high speeds. Generally speaking, crushing teeth apply relatively high loads, but do so slowly and typically cyclically (Summers 2000; Schaerlaeken et al. 2012; Kolmann et al. 2016). One documented group that uses high-speed crushing to obtain food is the mantis shrimp. These crustaceans smash open snails and other hard-shelled prey at speeds in excess of 30 m/s, often creating cavitation bubbles in the water (Patek et al. 2004; Patek and Caldwell 2005). While a definite example of high-speed, dynamic crushing, the mantis shrimp's tools are appendages, not teeth. Crushing shells with teeth at similar speeds would be tricky, considering that mantis shrimp use cavitation bubbles to break the brittle shells of their prey (Patek et al. 2004), and generating cavitation bubbles in one's mouth is generally inadvisable.

Cutting

Like "crushing" dental tools, the main purpose of "cutting" tools is to reduce food items into multiple smaller pieces. However, in the case of "cutting" tools, food items are tough and deformable. The high toughness of these food items places "cutting" dental tools in the blades and wedges portion of the Lucas (2004) scheme, and means that food items fail very differently than those processed by "crushing" tools. High-toughness materials require a great deal of energy to not only create fractures, but also to extend them, as opposed to the catastrophic failure via self-propagating cracks seen in more brittle materials (Lucas 2004). High-toughness (ductile) food items also tend to be highly deformable (like raw meat), which can act as an energy sink, preventing some of the applied energy from contributing to fracture growth. A key feature to "cutting" dental tools is the presence of one or more bladed edges, which concentrate applied loads. As with "crushing" tools, the action of "cutting" dental tools is cyclical; however, cutting teeth are used over a range of speeds, from quasi-static to dynamic, across groups.

Much of the recent work on "cutting" dental tools has focused on discerning the key aspects that allow for efficient cutting. Ductile materials pose a problem for "cutting" dental tools that "crushing" tools generally do not have to contend with: energy lost to deformation of the food item. Adding blades to a tool significantly reduces the force required to create fracture in tough materials with relatively low Young's moduli, like skin or muscle (Freeman and Lemen 2006). It is, therefore, unsurprising that meat-specialized animals have sharper cutting edges, measured as the radius of curvature of the transverse section through the blade, than non-meat-specialists (Popowics and Fortelius 1997). In addition to simply adding blades, the structure and orientation of the blades can make a difference. Adding serrations to bladed edges allows tools to "grip-and-rip" as they cut, rather than simply depending on concentrated applied force (Abler 1992). Multiple blades can also be oriented at angles to each other to create a V-shaped blades, which limits the amount of deformation tough food items undergo. For instance, experimental work has shown that V-shaped blades, like the carnassials of mammalian carnivores or the effective cutting unit formed by a row of single-cusped bladed teeth as in sharks, increase cutting efficiency by limiting deformation and increasing localized stress and strain in the food item (Anderson and LaBarbera 2008; Anderson 2009; Anderson and Rayfield 2012).

Changing the way energy is introduced to the system, such as changing the action of the blade, can also affect how efficiently deformable food items are processed. In some cases, as modeled by Anderson's double-guillotine experiments (Anderson and LaBarbera 2008; Anderson 2009), cutting occurs via uni-directional motion of the tool, where concentrated forces drive the "cutting" tool into the food item. Taking place in a single plane of movement, this action is similar to that of some carnivorous mammals and most reptiles, where there is little lateral movement of the jaw (Schwenk 2000; Evans and Fortelius 2008). Other cutting systems incorporate a lateral draw component that follows the initial tool puncture. Experimental results show that both tooth morphology and food item material properties affect puncture and draw performance in a diversity of different shark tooth morphologies (Whitenack and Motta 2010). Other work has used finite-element analysis (FEA) to determine how different "cutting" tool morphologies will respond to the different loads associated with the initial puncture and following lateral draw motions (Whitenack et al. 2011; Jones et al. 2012).

Finally, the work discussed so far has focused on quasi-static cutting, loads applied at low speeds, but cutting can occur at a wide range of speeds. The high speed application of force, as discussed previously, can effectively stiffen food materials and make them less able to dissipate energy through deformation (McElhaney 1966; Shergold et al. 2006; Song et al. 2007; Van Sligtenhorst et al. 2006; Karunaratne 2016; Karunaratne et al. 2018; Zhu et al. 2018). Little work has focused on the biomechanics of dynamic cutting, save for a recent study on shark tooth function. This study quantified cutting ability by attaching morphologically diverse assemblies of teeth to a reciprocating saw to apply high speed, repeated cuts to food items, mimicking head shaking behaviors seen in shark. Not only were there significant performance differences between tooth morphologies, but the study also demonstrated the effects of wear on "cutting" tool performance at high speeds (Corn et al. 2016).

Piercing

Unlike "crushing" and "cutting" dental tools, the end goal for "piercing" tools is not the break-down of a food item into smaller pieces. Instead, "piercing" tools, which are often relatively long and tapered with a sharp tip, are used to create localized fractures that will allow for the insertion of the tool, and occurs in two steps, both of which require energy. The initial step creates a fracture, and the second propagates the fracture and drives the body of the tool into the food item. These tools most often interact with ductile materials, with interactions generally taking place at high speeds. The high speed of these interactions serves to stiffen the material and limit the energy lost to deformation. However, these are not hard and fast rules. There is at least one instance, in a small fish, of "piercing" teeth being used to punch holes in brittle snail shells (Norton 1988). Another example of quasi-static piercing would be exudativory in some mammals, where individuals use their teeth to gouge plant surfaces to extract sap or gum (Starr and Nekaris 2013).

As with "cutting" dental tools, much of the biomechanics work on "piercing" teeth has focused on identifying and measuring morphologies tied to performance. There are a wide range of morphological sharpness measures in the literature including measures of both tip morphology and overall tooth shape (Frazzetta 1988; Freeman and Weins 1997; Popowics and Fortelius 1997; Evans and Sanson 1998; Evans et al. 2005; Freeman and Lemen 2007; Jones et al. 2012; Schofield et al. 2016). Experimental work has shown that the included angle of the tool tip, and to a lesser extent measurements of radius of curvature, is the best predictors of the applied force required to initiate fracture (Crofts et al. 2019). Other work has shown the importance of overall tool aspect ratio and taper on reducing the force to penetrate tough materials, and that adding bladed edges to "piercing" tools similarly reduces the force and work required to penetrate a range of tough materials (Freeman and Lemen 2006, 2007). Coupled with this is work that has examined the functional trade-offs in "piercing" tools, dental, and otherwise, using beam theory and FEA to predict the likelihood of failure, and contrasting this with puncture performance in mammalian canines (Freeman and Lemen 2007), lionfish spines (Galloway and Porter 2019), and shark teeth (Whitenack and Motta 2010; Whitenack et al. 2011).

Piercing is a more complicated action than it may initially appear, and the diversity of piercing tools in nature has been recently reviewed (Anderson 2018), but for the purposes of this work we will focus only on piercing teeth. The performance of "piercing" tools is highly dependent on the material properties of the object being pierced, with both toughness and Young's modulus influencing how much energy is lost to deformation (Freeman and Lemen 2006). Moreover, most of the work to date on "piercing" dental tools has been undertaken at quasi-static speeds, well below the impact speeds ($\gg 1$ m/s) at which many biological piercing events occur (Grubich et al. 2008; Higham et al. 2017). Stiffening strain rate effects are especially important for "piercing" dental tools, as they may not have other means to prevent materials from dissipating energy via deformation. The kinetic energy involved in "piercing" is the best predictor of success, and understanding how energy transfer varies at different speeds is key to understanding the function of "piercing" dental tools (Anderson et al. 2016, 2019).

Further complicating the story of "piercing" dental tools is the fact that they so often serve specialized functions. The most immediately evident are the fangs of venomous snakes, which have been modified to not only pierce tissue but also convey venom down a groove or tube. There has been a great deal of work on the evolution of this system, considering the developmental processes underlying fang morphology (Kardong 1979; Jackson 2007; Vonk et al. 2008), how fangs are deployed (Cundall 2009), how morphologies associated with different snake lineages resist failure (Broeckhoven and du Plessis 2017; du Plessis et al. 2018), and how fang tip morphology affects puncture performance (Crofts et al. 2019). Other "piercing" teeth that capture the imagination are the sabre-teeth that evolved in a number of disparate lineages. Evidence suggests that sabre-toothed taxa, especially those converging on the sabre-toothed "cat" niche, probably did use their outsized fangs in taking-down prey animals (Biknevicius et al. 1996; Christiansen 2007; Antón et al. 2019). However, in some instances these teeth were not likely used for to catch or process prey, such as those of the planktivorous sabre-toothed salmon (*Oncorhynchus rastrosus*) (Eiting and Smith 2007). Despite their appearance, there are other functions long pointed dental tools may serve, like trapping prey (for a more broad overview of "piercing" tool functions, including but not limited to teeth, see Anderson 2018).

"Complex" teeth

Moving beyond the morphological and functional extremes discussed above, we can begin to think about teeth with greater complexity. To begin, dental complexity is not unique to mammals, despite the prevailing narrative in the dental biomechanics literature. Multi-cusped teeth occur in a range of taxa, spanning cartilaginous fish, bony fish, amphibians, and reptiles, and allow for multiple dental tools to co-occur (Zahradnicek et al. 2014). The formation of cusps is under developmental control, and recent work has begun to describe the pathways involved and how cusp number can increase and decrease (Harjunmaa et al. 2012, 2014; Jernvall and Thesleff 2012). Having multiple cusps increases dental complexity and can allow for more complicated interactions with food items. Herbivorous mammals have specialized teeth with multiple blades, derived from new cusps and/or infolding of tooth materials, that work against each other to break down fibrous plant materials (Popowics and Fortelius 1997; Evans et al. 2007). There is a similar pattern of increasing dental complexity in extant herbivorous reptiles (Melstrom 2017). Some ornithischian dinosaurs achieved functionally similar dental arrays via differential wear of tooth materials in successive rows of teeth in their dental batteries (Erickson et al. 2012, 2015). Similarly, omnivorous or hard-prey specialized diets may call for a "grinding" dentition, where blunt cusps of different size and shape work together to hold food items in place while breaking them (Berthaume et al. 2010, 2013; Constantino et al. 2016; Crofts et al. 2017).

Dental complexity need not refer specifically to cusp number, but may result from how the tooth is used to transfer energy. Surface ornamentation can have a significant effect on performance, as with the effect of adding serrations to a bladed edge (Abler 1992). As discussed already, serrations change the way cutting occurs: as fibers in the tissue get caught between serrations, the blade "grip-and-rips" through tissue instead of simply propagating fracture (Abler 1992). Another common type of surface feature is apicobasal ridges, which run along the long axis of the tooth and occur in a wide range of taxa. These ridges have been hypothesized to help teeth puncture prey (Zverkov et al. 2018), grip prey (Vaeth et al. 1985; Zverkov et al. 2018), disengage from prey (Vaeth et al. 1985), and strengthen the tooth (Vaeth et al. 1985; Young and Kardong 1996; see McCurry et al. [2019] for a recent review). Finally, otherwise "simple" teeth may lack morphological complexity but can be used in complex ways, such as the teeth of the bamboo shark (*Chiloscyllium plagiosum*) where tooth mobility allows them to serve as "piercing" teeth when interacting with soft prey, and to act as "crushing" teeth by folding over when interacting with hard prey (Ramsay and Wilga 2007).

Biomechanics methods

An understanding of both tooth morphology and action is key to the study of dental biomechanics. Since the publication of Lucas' book in 2004, advances in technology and computing power have greatly expanded the toolkit we use to study dental biomechanics and interrogate the assumptions underlying much of the work to date. As an example, greater availability of CT scanning and µCT scanning facilities allows for the 3D visualization and measurements of a greater diversity of teeth, and the resultant 3D models can be used in a wide array of methodologies. The use of high speed video, a classic technique that has seen technological improvements and increased frame rates, can help us better understand tooth action during use, especially dynamic interactions like snake strikes (some examples include Clark et al. 2012; Kolmann et al. 2016; Higham et al. 2017; Ryerson and Tan 2017).

"New" methods in biomechanics have also been adopted, many co-opted from other fields. One example of this is FEA, an engineering technique increasingly used by biologists to study the distribution of stress and strain in skeletal elements or teeth under load (some toothsome examples include: Anderson et al. 2011; Whitenack et al. 2011; Grubich et al. 2012; Jones et al. 2012), or in the food item under load (Anderson and Rayfield 2012). Another example is the use of geographic information system (GIS) mapping, a tool typically used to map geography, which has been modified to describe dental complexity (Evans et al. 2007; Melstrom 2017). Computer simulations have been used to reconstruct the 3D motion of teeth, based on the wear facets formed when teeth rub against each other (Evans and Fortelius 2008). Similarly, X-ray reconstruction of moving morphology (XROMM) is a relatively recently developed technique that combines 3D models with biplanar, high-speed X-ray videos to reconstruct actual biological movements, and has been used to show food processing action in 3D in a range of taxa (Gidmark et al. 2014; Bhullar et al. 2019; Laurence-Chasen et al. 2019). Finally, particle tracking velocimetry (PTV), more typically used to understand fluid dynamics, can be used to understand what happens to a food item when loaded by a dental tool, by visualizing fracture formation and measuring the energy lost to deformation (Anderson et al. 2019).

Less high-tech methods are still immensely powerful tools to understand tooth function as well. Semi-static testing of physical models, which can be rapid prototyped, machined, or assembled from other man-made tools, can demonstrate if certain tooth morphologies are capable to processing different types of prey or be used to measure the amount of force or work required (Schulp 2005; Anderson 2008; Anderson and LaBarbera 2008; Crofts and Summers 2014; Kolmann et al. 2015; Crofts et al. 2019). Dynamic testing is also possible using a range of set-ups, including crossbows or a simple pendulum (Anderson et al. 2016, 2019).

Summary

The purpose of this review has been to consider the past and present of dental biomechanics, and to propose a conceptual framework for future work encompassing the interplay between gross morphology, food material properties, and the dynamics of tooth action. This framework considers the energy requirements to elicit the desired mode of failure (fragmentation or creating an isolated hole or fracture) in different materials (brittle to ductile) and at different speeds (quasi-static to impact speed). The overlap between the extremes of these parameters represents dental tool archetypes: "crushing," "cutting," and "piercing" dental tools. These tools may represent a single tooth, or may be combined into more complex dental forms. Moreover, there is potential for overlap along these axes, such as similarities between the puncture action of a "cutting" dental tool and the action of a "piercing" tool, or the "piercing sculpin teeth punching holes in snail shells (Norton 1988; Whitenack et al. 2011; Galloway et al. 2016). These sorts of observed patterns of tooth use provide us with *a priori* hypotheses regarding tooth function which can be experimentally tested to find correlations between tooth morphology, speed of tooth action, prey material properties, and mode of failure. Finally, while we have discussed these tools in the context of dental morphology, similar tools exist in invertebrates (pancrustacean claws and mandibles, cephalopod beaks, or cone snail harpoons, for example) as well as man-made tools. Exploring the role of energy transfer in the action of these different tools can illustrate common themes to their functional morphology. Our hope is that researchers interested in dental biomechanics will revisit old assumptions, taking into account the importance of energy transfer, and taking advantage of new technologies to continue to explore the evolution and function of teeth.

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