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Cutting food in terrestrial carnivores and herbivores

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Insects and mammals cut their food up into small pieces to facilitate ingestion and chemical digestion. Teeth and jaws act as cutting tools, but, unlike engineering tools designed for a specific purpose, must generally cope with substantial variation in food properties and work at many scales. Knowing how teeth and jaws work effectively requires an understanding of the cutting on the edges and the mechanisms that remove cut material. Variability and heterogeneity of diet properties are not well known, and, for example, may be higher and overlap more in the browsing and grazing categories of plant diets. A reinterpretation of tooth function in large mammal browsers and grazers is proposed.

1. Introduction

Arguably the most widespread naturally occurring cutting events involve the millions of animals cutting up their food with their teeth or jaws. However, we know very little about the biomechanical processes involved even in well-studied herbivorous mammals [1]. The lack of knowledge about biomechanical processing of food is apparent when compared with the published information on feeding behaviour, the chemical constituents of the food and the chemical processes involved in digestion, collectively referred to as the functional response [2].

It is important to distinguish between cutting in order to acquire and ingest food, which has been described as cropping, biting and even feeding, and the cutting actions involved in processing a mouthful of food into smaller fragments as an aid to digestion. This paper addresses cutting associated with food processing rather than with food acquisition. Chewing processes food by increasing the surface area to volume ratio and liberating digestible materials sequestered by indigestible matter, and is a critical factor in digestion [1]. Chewing is a repetitive action by the molar teeth, but the term is sometimes conflated with eating or feeding. In insects, the distinction is less clear, because insects synchronize cutting a small piece of food from a larger body, while acquiring a food item, with cutting that processes or damages the piece in the same action. The 'incisor' and 'molar' regions of the mandibles occlude during the same stroke. In mammals, acquiring and processing food is asynchronous and separated, but acquisition and processing affect each other through handling time. Handling time is usually related to the abundance, structure and spatial distribution of preferred food items [2], but handling time of chewing and swallowing a mouthful before another acquiring bite can be taken [3,4] is rarely considered. Clarity and consistency in terminology would be valuable.

Animals invest substantial amounts of time processing their food. For example, cows may spend over 11 h a day chewing [5] and chew differently on different lengths of silage [5,6]. Chewing behaviour links to physiology: cows lactating with their first calf chew their feed more thoroughly and more slowly than older cows that have had more calves [7]. Grinding the food for ruminants, which use bacteria to digest the plant cell wall, can reduce digestibility as the nutrients pass through the gut too quickly [8], while grinding the food for a non-ruminant mammal increases digestibility [9]. Tooth efficiency affects physiology and changes with dental wear, which can reduce digestibility [10]. In koalas, animals with worn teeth produce fewer small particles [11] and increase the chews per leaf by 25%, with a 116% increase in the number of

chews per day (from 16 000 to over 38 000) [12]. The increased time spent feeding has negative effects on social status [13]. The relationship between mechanical and chemical digestion in mammals is complicated by body size, energy requirements, the kind of digestive system [14] and the teeth [15]. Mechanical preparation of food is an integral and essential part of feeding and digestion. Therefore, it is surprising that so little attention is given to the processes and investment animals make in physically processing their food before the chemical digestive processes start to operate [1,15].

The complex factors regulating nutrient intake in insects are readily understood in experiments that use artificial food. However, Clissold [16] argued that in 'the "real-world" nutrient assimilation is rarely indicated by plant chemistry'—rather that leaf anatomical structure is an important factor in controlling not only the rate but also the ratio of protein and carbohydrate assimilation in insects. Furthermore, it is increasingly recognized that leaf structure may have more important effects than leaf chemistry on deterring herbivory [16–18], and the leaf mechanical traits contributing most to defence is being explored [19].

The way foods are constructed and fracture affect the ways animals need to physically process them. This important functional relationship between foods and teeth as tools was revealed by Lucas [20], and rests on the engineering science of fracture of composite materials elucidated most clearly by Atkins & Mai [21,22]. Biologists have been reluctant to incorporate physical properties of diets into their studies of feeding and digestion and, when they do, use terms loosely and ambiguously that have specific meanings in engineering. Arguably, researchers who are comfortable with a sound cross-disciplinary understanding of material properties and fracture mechanics have failed to expound this understanding with sufficient clarity. Biologists are accustomed to higher levels of uncertainty than engineers perhaps are comfortable with or experience. This uncertainty is partly driven by the extraordinary variability and heterogeneity of natural materials and environments, and the plasticity (in a biological sense) of ways in which an organism may respond.

This paper focuses on some aspects of cutting in the dominant terrestrial organisms: plants, insects and mammals. Vascular plants, which dominate terrestrial ecosystems [23], are consumed by insects, the dominant terrestrial herbivores, and in turn insects eat each other. Mammals are successful consumers of plants, insects and other mammals. This paper addresses only the stems and leaves of angiosperms, the flowering plants; it does not cover storage organs, seeds, fruits or roots. Nor does it attempt to comprehensively review what is known about the biomechanical properties of plants, insects and mammals as food, and the instruments that animals have evolved to cut up such foods. Rather it explores basic patterns that are sometimes overlooked and questions some common assumptions by providing, as an example, an alternative explanation of tooth form and function in the particular case of large browsing and grazing mammalian herbivores. This explanation is based on a preliminary analysis of new data that can only be briefly reported here.

1.1. Patterns in biomechanical properties of terrestrial plants, insects and mammals as food

Plant biomechanical properties relative to form and function have been well studied [24], but as food less so, even though their physical properties affect the way food fractures [20]. Cells in developing leaves are surrounded by a primary cell wall largely composed of hemicellulose, which is digestible to many animals. Leaves grow by cell expansion and at the final size extra layers of cell wall, largely composed of cellulose that is indigestible to virtually every animal, are laid down around each cell [25]. During the growth phase, leaves take less work to fracture [26,27], though monocots can be tough through the expansion phase [28] and are relatively nutritious because cell wall forms a smaller proportion of leaf mass. Consequently, young leaves are often chemically defended to deter predation [17], but are ephemeral, making it difficult for animals to specialize on them as a resource.

Mature leaves have more cell wall diluting and shielding the digestible cell contents. Bacteria are capable of digesting plant cell wall, but that takes time, which might explain why it is not a strategy adopted in insects with short gut passage rates [16]. High energy demands and gut size also inhibit small mammals from using plant cell wall [29], and like insects they must fracture the cell walls to access the digestible cell contents.

The arrangement and structure of plant cells provide a hierarchy of toughening mechanisms that include interfaces between cells, between the cell wall layers and even between the components of the layers; all of which contribute at various scales to the energy required for fracture [30]. Plant leaves vary considerably in their biomechanical properties for other reasons [17], including age [27], light [28] climate [31], local soil fertility [32] and global factors [33,34], and in their nutritional value at hierarchical levels from individual leaves to patches [4]. Collectively, these factors make plants very variable in their properties.

The flowering plants comprise two main groups (morphologically, if not in their systematic relationships). The dicots generally have a major vein, the midrib, which conducts photosynthetic products and water from and to lower-order secondary and tertiary veins, collectively stiffening the leaf [35]. The secondary veins in dicots tend to converge on the midrib in a wide variety of orientations, whereas the smaller tertiary veins are often divaricating and connect with surrounding secondary veins. In contrast monocots, which include the grasses, sedges and palms, are less variable in organization, are not woody and typically have parallel, relatively closely spaced, veins. The relatively high packing density of monocot veins compared with dicot veins inevitably means that monocots tend to have higher concentrations of cell wall and this is related in general to higher toughness [28]. A high vein density and cell wall density do not necessarily make monocots less digestible [36]. 'Browse', the leaves of dicots, is consumed by browsing herbivores, whereas grass is consumed by grazing herbivores, an enduring terminology reflecting differences between the two plant groups as food resources for mammals [37] and insects [16], but perhaps in different ways.

Compared with plants where each cell is surrounded by strong tough materials, insects have a stiff framework of jointed plates on the outside of the whole body that provides protection and a skeleton for muscles to work against. Stiff plates, which can be hardened by tanning, are connected by tough flexible regions allowing movement but increasing biomechanical heterogeneity [38]. While different insect groups vary in their overall hardness, e.g. moths are soft-bodied and beetles often hard-bodied [39], and larvae are

usually softer than adults, variation of the biomechanical properties across insect groups is poorly known [40].

Unlike mammals, insects have an open blood supply; once the external skeleton is breached, the blood is readily accessible and is a rich and balanced source of nutrition, particularly for small insectivorous mammals with high metabolic demands. Muscles are a major source of protein but are protected from chemical digestion by internal projections of the skeleton. To facilitate rapid digestion, the predator must shear the skeleton and associated tissues finely. Successive sectioning of insect larvae followed by *in vitro* protein digestion has shown that the more the larvae were comminuted the more protein was digested [41]. However, small insectivorous mammals seem to process insects more finely than is necessary to digest the protected protein [41], and it is not clear why this occurs. Small particles pass through the gut more quickly than large particles in herbivores [29] and this perhaps allows rapid clearance of indigestible insect skeleton. Very little is known about the mechanics of insects cutting up other insects.

Mammals are very different from plants and insects in that their bone skeleton is an internal scaffold that can be avoided by 'shearing the meat off the bone'. Mammalian soft tissues, such as cartilage, tendon and muscle, vary in their biomechanical properties but require little physical processing apart from cutting off pieces small enough to swallow [20]. Mammals are relatively similar in their structure compared with insects, yet neither compare with the more heterogeneous and variable plants.

1.2. Scale

All leaves are susceptible to herbivory at the scale of small insects to large mammals [15]. It is not clear how much of the shape and structure of leaves is directly influenced by predation or at which scale. However, insects dominate in terms of biomass because of their prodigious numbers [42] and therefore might exert stronger selective pressure than larger animals on the evolution of plant chemistry and mechanical structure, and this might be most manifest at the scale at which insects operate. Phytophagous insects range in size from leaf miners, with a mass of the order of micrograms, to large chewers such as the grasshoppers, which may exceed 30 g but this is uncommon. The smallest miners are so small they can complete their larval life cycle within the tissues of a single leaf and their jaws operate close to the scale of individual plant cells. The largest insects are small enough to be able to target and bite off parts of leaves, enabling them to specialize on different leaf tissues and avoid tougher and less nutritious parts. The change in size from the early larval stage to the adult may be substantial, but the feeding consequences are poorly understood [16], though there is an effect [43].

The smallest mammals are predominantly insectivorous, probably because of the scaling of their energy requirements, whereas the largest mammalian carnivores consume other vertebrates. Insect and mammal body size overlaps in the region of 5–35 g. The smallest mammalian herbivores, like the largest insects, are of a size that allows them to target different parts of leaves. However, the largest herbivores are orders of magnitude larger than the leaves they consume, which they process in bulk, many at a time, with little opportunity to avoid tougher or more indigestible parts. Herbivory is about scale, the smallest adapted to cells, the mid-sized to

leaf tissue and the largest to many whole leaves that may include stems [15]. In insects, the mandible patterns differ among browsing or grazing grasshoppers [44]. Patterns exist between leaf biomechanical properties and leaf feeding sites [45] and the densities of insect feeding guilds [18]. There are equivalent patterns in mammals [4] but what these patterns mean and how they function is not clear. Scale is important, as Atkins [22] noted in regard to fragment formation during cutting. Factors such as tool rake angle, speed of cut and depth of cut affect how materials behave when cut. These variables influence the friction, elastic moduli, yield stresses and toughness. How such factors operate at the scale of small or large animals is unknown.

1.3. Patterns in the mechanical processing of terrestrial plants, insects and mammals

Chewing effectiveness (CE), how effectively and efficiently teeth work as tools, is difficult to measure, and there is no clear consensus on what should be measured [1]. Trying to estimate CE is valuable in helping to understand the processes of chewing, but that may not be just about optimizing outputs compared with inputs. In engineering, tools can be designed from scratch for a specific purpose where the quality control of the variation in the properties of the material to be cut may be very high. Careful artisans grind different chisels to different angles to work different kinds of woods. Animals do not have this luxury and must use one tool for many foods. Animal tools are not necessarily optimized for some, unless the animal is extremely specialized, but compromised for many foods. In biology, tools are invariably limited in their function and should be less than ideal because of the constraints of phylogeny and the often critical requirement of animals to be able to manage different types of food in lean times. Animals live in variable environments and work with what their ancestors gave them. Therefore, good design of biological tools may require selection for compromises where CE is traded for a capacity to cope with variability in diet properties [46]. Despite these expectations, some teeth approach ideal functional forms, raising the important issue of how space, or size, constrains shape and function [47].

Effective cutting is not just about maximizing the effectiveness of food fracture on the cutting edges [47]. A complete understanding of tooth form and function must take into account all the competing and constraining factors and should include material removal from the cutting site so as not to clog the cutting edge. Good cutting tool design is as much about material clearance as cutting. The orientation and angle of cutting edges to each other affects mechanical advantage and material capture for effective shear, but the food fragments must be able to escape somewhere and providing adequate escape channels may limit the amount of cutting edge that can be packed into a tooth, a factor that is worth further study.

Cuticle, which makes insects difficult to fracture, provides stiff, strong and hard mandibles that enable insects to process other organisms [38]. Insects moult many times as they grow, each moult providing new mandibles [15,16]. There are few studies on mandible wear in insects [48] and very few have related feeding behaviour and comminution performance to energy expended, mandible wear, diet biomechanical properties and particle size [49].

Insectivore tooth form and function, in comparison with insect mandibles, is well described and emerging three-dimensional digitizing techniques are changing our understanding of function [46,47,50,51], and challenge existing interpretations [52]. A major challenge will be to incorporate food items into three-dimensional occlusal models particularly to examine food clearance. There is a wide diversity of insectivore tooth form and function, suggesting high diversity of prey. In bats, teeth that are specialized for soft-bodied insects differ in size from those that specialize on hard-bodied prey [39]. However, the detailed form and function, analysed in engineering terms, show no consistent differences [46]. There is some suggestion that the effectiveness of teeth of feeders of 'intractable' foods tends to be lower, possibly providing protection against fracture and wear [46], and the latter causing an overall deterioration of function [50]. This is an example of compromise and constraint affecting tooth effectiveness.

The teeth of mammals that consume other mammals have lost the puncture and crushing components of their processing teeth, correlating with the prey not having an exoskeleton. Shear dominates and is usually concentrated on a single tooth, the carnassial [20], that is notched, thereby trapping food for effective cutting [53]. Speed of cutting and swallowing a captured prey item before it can be stolen by competitors may be important, especially as it is not necessary to process such food finely for digestion [20]. New methods of analysing shape in carnivore dentitions are revealing functional constraints of geometry and relative motion of the mandible on teeth during occlusion [54].

Mammalian herbivores have very different occlusal mechanics from carnivores with well-developed cutting ridges on many teeth coupled with horizontal translation of the jaw and associated craniomandibular differences that have been well described. The relative development of cutting crest lengths has long been related to the degree and type of herbivory [55–57] and quantifying the degree of folding or 'enamel complexity' in relation to diet is an important step forward [51]. Because of teeth durability and their common occurrence as fossils, there is an enormous literature on form, but function in relation to the biomechanical properties of the diet is poorly understood.

Herbivory (excluding the consumption of fruits, seeds and roots) encompasses the browsing to grazing continuum. Grasses are considered to have higher cell wall fractions (usually measured as neutral detergent fibre, NDF) in the range of 50–70%, with browse ranging from 30% to 50% [58,59]. However, it is misleading to categorize browse as a high-quality food because it often has lower digestibility, for many reasons, than grass [58]. Neatly separating fibre levels into apparently non-overlapping categories is not the whole picture. Young grass leaves start with very low NDF levels and only after maturation do they reach the high values quoted above. One possible benefit of grazers aggregating in herds is the maintenance of grass shoots at an early maturation stage [4]. Browse, as consumed by many browsers, is not always limited to leaves of low NDF levels. Many animals during winter or summer deciduous periods include twigs in the diet [60] and as the twigs become thicker cropping switches from incisors to molars as more force is required [61] and eventually stems become too thick to crop [4]. Stems of the shrub *Vaccinium alaskensis*, a common and palatable plant food for deer, can be as high as 67% NDF

[2] at the top end of the grass scale. Browse is not always an easy diet to process.

Very high fibre levels reduce digestibility and limit intake affecting bite size and chew rate, all important factors in the complex functional response of animals to variable diets [4]. Therefore, it is not surprising that many animals prefer low-fibre diets when they are available, and finding plants of different qualities allows animals to manage their fibre intake [4]. The substantial domestic ruminant literature suggests that, for optimum performance, cattle, normally considered grazers, consume diets of 22–46% NDF [62], raising the interesting concept of 'effective fibre' [5]. Such studies have to be carefully interpreted as the diets are usually formulated, but the relevance for wildlife is that animals will probably always do better on low-fibre diets, even grazers, and will search them out when they can, but must be able to cope with much higher fibre diets, including woody stems and twigs, when necessary. Under these circumstances, browsing is about consuming a very heterogeneous diet, and some elements of browse will have as high if not higher NDF levels as any grass.

Toughness correlates with fibre level, but it is not a simple relationship as it depends on how the toughness is measured and the orientation of tissues within the leaf [26,30]. Unfortunately, there are no empirical studies on the structure and fracture patterns of grass and dicots [36], and no large datasets comparing the toughness of the two groups measured the same way. The observation that dicots fracture into more polygonal particles while grass particles tend to be elongate [2] may not be a surprise; grasses are already long and narrow, and so it may simply reflect the original leaf shape.

While the fracture properties of leaves in different modes correlate in grasses [26] and for different fracture tests [63], the degree of correlation varies. There is no single study comparing the three modes of fracture across a range of dicots and grasses measured consistently. It is generally assumed that mode III out-of-plane shear is the most common fracture mode in chewing and readily equates to our limited understanding of herbivore tooth and jaw function. However, examination of particles from the stomach of sheep [26] indicates mode II and even mode I fracture occurs at some time, though it is not clear whether mode I fracture, revealed by fibre pullout, occurs during cropping or chewing. More studies are needed to resolve this. While the differences in the magnitude of the three fracture modes in grasses can be explained [26], it may be more complicated in dicots where vein density and orientation varies from parallel to reticulate.

Grasses may not be tougher than the toughest dicot leaves. Shear toughness data for whole leaves are presented for 78 species (13 families) of dicot [32,63] and 20 species of grasses (G Sanson and J Read 2015, unpublished data) from the south of Kruger National Park, South Africa, in the wet season (10 sites each, on basalt and granite soils). Exactly the same machine and protocols were used as for the dicot studies. Grass leaf and stem were measured and include all the grass species analysed by Codron *et al.* [59] for NDF. Grass toughness was also measured in the dry season, but values were on average lower, and are not included.

The distribution of shear toughness data is presented as absolute work to shear (mJ; figure 1) and as specific work to shear (kJ m^{-2}; figure 2), where the absolute work to shear is adjusted for the cross-sectional area of the leaf at the point of fracture. These preliminary findings challenge
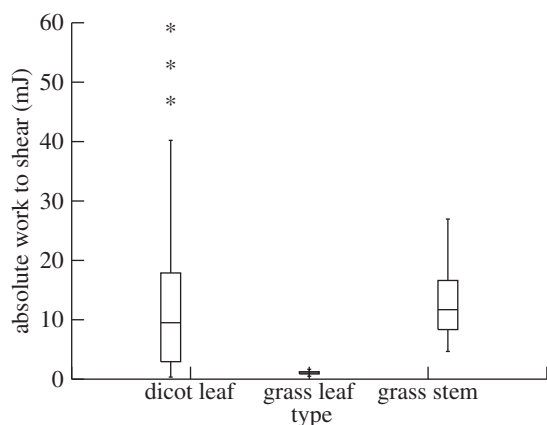
Figure 1. Comparison of absolute work to shear among different dietary groups. Boxplots show variation across the entire leaf for 78 species of dicot [32,63] and 20 species of grass (G Sanson and J Read 2015, unpublished data).

Figure 2. Comparison of specific work to shear among different dietary groups. Boxplots show variation of specific work to shear (absolute work to shear adjusted for the cross-sectional area of the leaf at the point of fracture) across the entire leaf for 78 species of dicot [32,63] and 20 species of grass (G Sanson and J Read 2015, unpublished data).

Figure 3. Traces of the occlusal cutting edges of the second upper molar and the posterior half of the first upper molar (thin lines) and the second lower molar (thick lines) of a kudu (browser) and a buffalo (grazer) illustrating the higher enamel complexity of the grazer. The lower molar is aligned at the beginning of the occlusal stroke. Scale bars, 10 mm.

the assumption that grass leaves are always tougher than dicot leaves. Grasses may commonly be tougher than many dicots, but not all. Browsers may be forced to consume much tougher tissues than any grass at certain times that might include petiole and stem. An important question is how much tough browse material has to be consumed to affect the evolution of the complex cutting edges observed in the teeth of grazing animals. Continuing to categorize diets as 'browse' and 'grass' but only measuring the leaf component of soft low-fibre browse, and confounding 'fibrousness' and toughness, may be hindering progress in understanding the effect of plant biomechanical properties on the evolution and function of the teeth and jaws of herbivores.

Perhaps more important is that there are animals that consume relatively tough dicot materials, such as twigs, stems or tough leaves, at certain times of the year and do not have the complex enamel cutting edge patterns characteristic of grazers. Consequently, we must question whether grazing dental and mandible adaptations are primarily owing to toughness and fibre.

1.4. Functional occlusal mechanics in large browsers and grazers

The literature and evolutionary history of browsing and grazing have been extensively examined and reviewed [64,65], and the number of papers devoted to this subject indicate how significant the paradigm is of browsing lineages being replaced by ones adapted for more 'fibrous diets', i.e. grazing, with rare reversals [65]. Browsing and grazing are associated with different plant cell wall (fibre) proportions, venation pattern, toughness and fractured particle shapes, and have recognizable dental adaptations that include differences in the complexity of the enamel occlusal pattern [51,56,65,66]. However, it is argued above that fibre and toughness, while showing some correlation, may not be a sufficient explanation for the observed complexity of the cutting-edge development. This requires a reassessment of occlusal function and the drivers of the evolution of complex cutting edges in grazers.

Butler pioneered the use of occlusal diagrams to explain occlusal function, superimposing traces of the upper and lower cutting edges on each other in different phases of occlusion [67], but these are difficult to quantify. Rensberger [68]
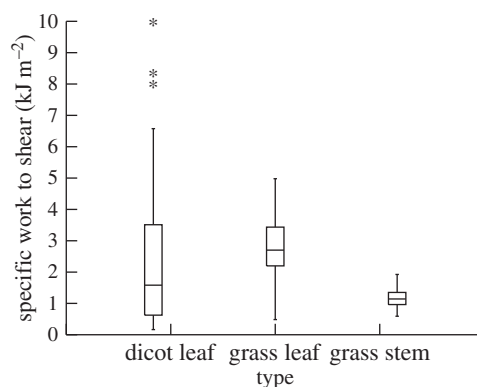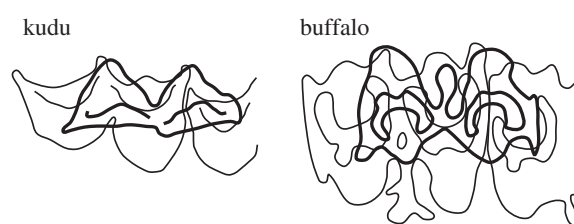
developed digital models to analyse occlusal interactions, which are still exemplary. However, these models do not take into account the biomechanical properties of the diet and the potential influence on tooth form and function. A software application is being developed to examine occlusal interactions between opposing cutting edges in large ruminant molars during an occlusal event [69] to explore wider implications.

2. A new model of occlusal function

2.1. Methods

Scale traces of enamel cutting edges (the upper second molar and the posterior half of the lower first molar and the occluding lower second molar) of some large browsers and grazers (figure 3) were digitized at the same resolution and the coordinates imported into the application. The cutting-edge coordinates are two-dimensional and do not reflect the three-dimensional surface of an unworn molar. However, wear reduces the crown surface to a relatively flat plane where two-dimensional coordinates suffice. Three-dimensional occlusion is being developed.

As the lower edges are moved over the upper edges, each upper coordinate is taken in turn and the x,y distance to every lower coordinate is calculated. If the distance is less than a user-defined distance, normally the average incremental distance between coordinates, then a contact is recorded. For this analysis, contacts from adjacent coordinates are excluded, and only the first coordinate encountered in an adjacent series is counted as a contact.
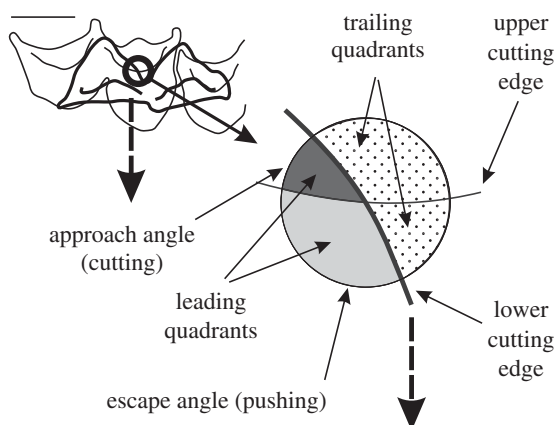
Figure 4. A representative occlusal contact, indicated by the circle drawn on an occlusal diagram of upper and lower molars (top left) of a kudu. The single contact is magnified on the bottom right. In both diagrams, the upper cutting edges are indicated by thin lines and the lower cutting edges by thick lines. The upper edges are stationary, and the lower edges are moving across the upper in the direction of the dotted arrows. Leading quadrants are shaded, trailing quadrants are stippled. The acute (cutting) approach angle is indicated by dark shading; the obtuse (pushing) escape angle is indicated by light shading. Scale bar, 10 mm.

The coordinates on either side of a contact coordinate are then used to reconstruct a line tangential to the contact coordinate, for both the upper and lower cutting edges. The intersection of the upper and lower tangents, unless the two tangents are exactly parallel, produces four quadrants, two on the leading edge of the lower tangent and two on the trailing edge. As the lower tooth is moved incrementally across the upper tooth from the buccal (cheek) side to the lingual (tongue) side, replicating an occlusal stroke, every contact is counted and the associated leading quadrant angles are calculated (figure 4). Together, the two leading quadrant angles add up to 180°, unless opposing cutting edges are parallel. One leading quadrant angle is always acute and the other is obtuse, unless the edges are at right angles. Quadrant approach angles (AAs) less than 90° show positive rake and have the potential to pinch, hold and shear unconstrained material caught between the cutting edges as they converge. Quadrant angles greater than 90° have negative rake. Unless material is held very firmly, food will be pushed ahead of the moving (lower) edge, because there is no cutting convergence with the upper edge. Quadrant included angles that are acute are termed AAs and quadrant angles that are obtuse and push are termed escape angles (EAs). Trailing quadrant angles are irrelevant as the cutting edges neither push nor cut (figure 4).

AAs up to 90° are not equally effective at cutting, even though they are acute, as the tendency to push the material ahead of the cutting contact increases as the AA approaches 90°. Cutting a small stem or matchstick with a pair of scissors illustrates the issue, because the stem is pushed ahead of the converging blades, unless it is held very firmly. As the scissors continue to close, the stem eventually stops sliding down the blades at the point where the friction between the blades and the stem neutralizes the vectors generating a tendency to push the stem and escape cutting. The escape function will be affected by the coefficient of friction and the surface area contact between the scissor blades and the stem. Blunt blades and more plastic food items will meet

over a larger contact area, increasing friction and reducing the escape function. Large diameter food items, such as stems or midribs of leaves, trapped between shearing blades require a higher AA, increasing the tendency to escape. Thin materials such as grass leaves can be cut at lower AAs where the escape tendency is low. Thin materials can fit between blades of low AA, but thick materials cannot. Consequently, the effectiveness of cutting and escape varies with the dimensions, sharpness and properties of the shearing blades and the food item and the AA of the cutting edges.

In the occlusal analysis, the lower tooth is aligned and positioned where occlusal contact between the upper and lower molars normally starts and is then moved through a set of incremental steps in the buccal direction to a position where occlusal contact ceases as the jaw starts to open at the end of the occlusal stroke. Narrower molars move a smaller number of increments. A specimen from two large browsers and three large grazing bovids [56] has been analysed (table 1).

3. Results and discussion

The number of contacts at each increment for the five specimens is presented (figure 5). The frequency of the accumulated AAs and EAs for each specimen during an occlusal stroke is plotted (figure 6). The symmetry of the distribution of angles is evident, with a very similar pattern of angle distributions across the specimens, but the frequencies differ. The frequency of angles rises more sharply above 45° for the grazers, particularly for the long grass feeding roan and buffalo, where more significant escape effects will occur. With the caution that this is a very preliminary analysis, the pattern indicates that more of the contacts push than effectively cut in the grazers. In an attempt to model the effect of pushing and generating food flow away from contacts, an escape vector is calculated for each contact at an angle that bisects each lead quadrant. The magnitude of the vector (i.e. the length of the drawn arrow) is directly proportional to the included angle (figure 7). Not surprisingly, there is a simpler pattern in the browsers

Deep wide valleys between cutting edges restrict the length and degree of folding of the cutting edges that can be developed for a given tooth size. Conversely, complex folding, with an associated increase in cutting edge length, restricts valley development to being narrow and shallow. The former is characteristic of browsers that have a heterogeneous diet in terms of tissue dimensions and toughness. Clearing such foods during occlusion is important and deep wide valleys may be necessary. Grass diets of relatively thin, narrow but potentially long leaf and stem blades are associated with narrow shallow valleys. The conventional paradigm is that consuming a tough fibrous diet is challenging compared with, by implication, relatively easy to chew (ancestral) browse diets, but this may not be the case. It may be advantageous, if not necessary, to have simple cutting-edge patterns with deep wide valleys for particularly heterogeneous diets. Consuming grasses that are relatively homogeneous in size, shape and toughness may allow, rather than require, complex folded edges with shallow narrow valleys. If diet toughness is a limiting factor, then having more contacts at any one point in the occlusal cycle is counter-effective, there should be fewer contacts, which is not the case. Therefore, toughness, while a factor, does not appear to be a primary driver for the evolution of complex enamel patterns in large grazers; but then what is? Visual inspection of the escape vectors (figure 7)

Table 1. Specimens used in the occlusal analysis.

| species	common name	diet	specimen
Connochaetes taurinus	blue wildebeest	grazer	American Museum of Natural History no. AMNH81789
Hippotragus equinus	roan antelope	grazer	Natural History Museum of Zimbabwe no. 61017
Syncerus caffer	African buffalo	grazer	American Museum of Natural History no. AMNH179170
Taurotragus oryx	eland	browser [56]	American Museum of Natural History no. AMNH53531
Tragelaphus strepsiceros	kudu	browser	American Museum of Natural History no. AMNH81162
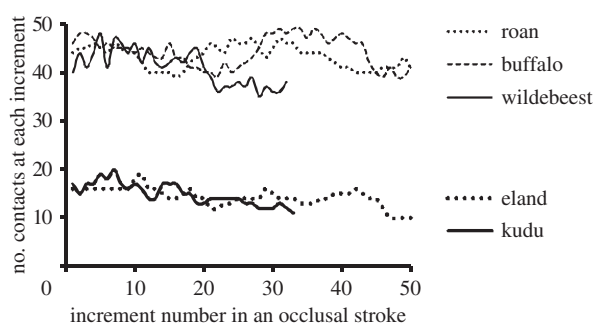
Figure 5. Number of contacts plotted against each increment of the occlusal stroke of a lower second molar crossing the occluding upper molars for each of the five specimens. Narrower tooth rows have fewer increments in an occlusal stroke. The grazers have over twice the number of simultaneous contacts as the browsers.
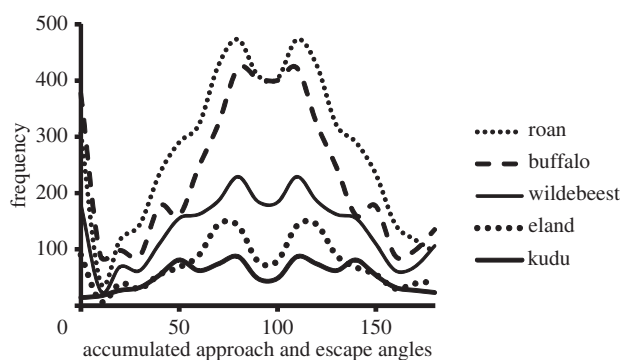

Figure 6. Frequency plot of both the approach and escape angle (i.e. both angles of the leading quadrants of an occlusal contact, figure 4) for every contact accumulated over each increment of occlusal movement during a single occlusal stroke. Each of the five specimens analysed are plotted. The approach and escape angles of a single contact always add up to 180° with the escape angle being larger than the approach angle (AA). Therefore, there will always be symmetry in such a plot. Angles above 90° can only push (generating escape). AAs also contribute to escape and when that angle increases above 45° the tendency for food to escape rather than being cut becomes more important. Therefore, in all species, the tendency for food to escape predominates over the tendency for food to be cut. The plot shows that the browsers tend to have relatively low and even profiles of pushing and cutting, but the grazers, and particularly the tall grass feeders, have a higher proportion of contact angles above 45°, suggesting a greater relative emphasis on pushing food rather than cutting food.
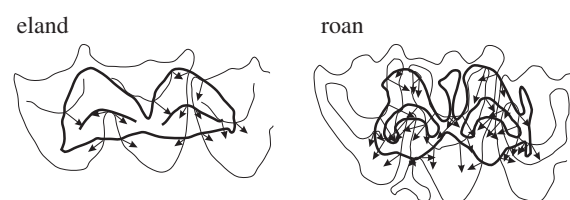
Figure 7. Escape vectors (arrows) for the lower M2 of an eland and a roan antelope occluding with upper molars at the same stage of the occlusal cycle. The length of the vector is proportional to the included angle of each leading quadrant, and the direction bisects the included angle. Upper teeth cutting edges are outlined with a thin line and the lower molar edge with a thick line. Scale bar, 10 mm.

This very preliminary occlusal analysis shows that in grazers, compared with browsers, more of the contact leading edge quadrants are pushing rather than cutting. This suggests that grazers optimize pushing food compared with browsers. Thick materials in the browser diet are more susceptible to pushing than thin grass material. The relatively high numbers of contacts that are parallel in the grazers would require more force than for inclined blades [53], reinforcing the suggestion that grazing tooth adaptations are not primarily about reducing the forces involved when chewing tough materials. Therefore, it must be considered that the evolution of complex cutting patterns is about trading cutting for more pushing. A shift to more pushing in order to reduce the cutting force required as a result of the increased number of contacts seems unlikely.

An additional possibility is that complex folded cutting edges are a response to the problems of chewing leaves that have high aspect ratios, i.e. ones that are long, thin and narrow. Fractured particles from such leaves, pushed into deep wide valleys by relatively few advancing contacts, will flow away from cutting contacts, which may be beneficial for broad and relatively short leaves with heterogeneous tissues. On the other hand, there may be an advantage in disrupting flow when chewing long thin particles as the leaf blades will be stochastically arranged and trapped in different orientations to the cutting edge, promoting mode II and mode III fracture at all orientations to the dominant venation. Fractured particles in insect herbivores do not seem to need a flow requirement, because each cutting stroke affects one piece of tissue, but in large bulk feeders using very different heterogeneities in the food, flow and valley development may be more important.

The physical characteristics of browse and grass have been identified as a major driver of the digestive strategies of browsers and grazers [58] and the differences have been related to the way plant fragments stratify and float in fibrous rafts that have possibly driven the morphological adaptations

indicates that, in the browser, food flows relatively unimpeded into the valleys away from each contact. However, in the grazer, the vectors collide more frequently with neighbouring edges, which will generate disruptive flow of food.

of the rumen [58,70]. Shape and fracture patterns of the diet are clearly important in the digestive system, and it should not be a surprise that tooth function is related to the shape and size of the diet as much as toughness and fibre level.

4. Conclusion

Understanding teeth and jaws as tools has important benefits. However, the range and distribution of diet biomechanical properties and the variability and heterogeneity of diets need more systematic study. Interpretation of cutting processes should take into account the scale of the tool with respect to the scale of the diet. Cutting is not just about

optimizing fracture initiation and propagation at the cutting edge, it is also about controlling food flow onto and off the cutting edges, which requires some part of the tool to drive that flow.

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