

# Food Mechanical Properties and Dietary Ecology

Michael A. Berthaume\*

*Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany*

**KEY WORDS** Diet mechanical properties; toughness; Young's modulus; displacement limited index; stress limited index

## Abstract

Interdisciplinary research has benefitted the fields of anthropology and engineering for decades: a classic example being the application of material science to the field of feeding biomechanics. However, after decades of research, discordances have developed in how mechanical properties are defined, measured, calculated, and used due to disharmonies between and within fields. This is highlighted by “toughness,” or energy release rate, the comparison of incomparable tests (i.e., the scissors and wedge tests), and the comparison of incomparable metrics (i.e., the stress and displacement-limited indices). Furthermore, while material scientists report on a myriad of mechanical properties, it is common for feeding biomechanics studies to report on just one (energy release rate) or two (energy release rate and Young's modulus), which may or may not be the most appropriate for understanding feeding mechanics. Here, I review portions of materials science important to feeding biomechanists, discussing some of the basic assumptions, tests, and measurements. Next, I provide an overview of what is mechanically important during feeding, and discuss the application of mechanical property tests to feeding biomechanics. I also explain how 1) toughness measures gathered with the scissors, wedge, razor, and/or punch and die tests on non-linearly elastic brittle materials are not mechanical properties, 2) scissors and wedge tests are not comparable and 3) the stress and displacement-limited indices are not comparable. Finally, I discuss what data gathered thus far can be best used for, and discuss the future of the field, urging researchers to challenge underlying assumptions in currently used methods to gain a better understanding between primate masticatory morphology and diet. *Am J Phys Anthropol* 159:S79–S104, 2016. © 2016 Wiley Periodicals, Inc.

“If I have seen further it is by standing on ye shoulders of Giants.” *Sir Isaac Newton*

Materials science is a branch of engineering that “involves investigating the relationships that exist between the structures and properties of materials (pg. 3, Callister (2004)),” where structures are defined by the arrangement and internal components of a material (e.g., atomic structure). Over the past several decades, anthropologists and biologists have been measuring/calculating mechanical properties of dietary items to investigate differences in feeding strategies, feeding adaptations, and plant defenses (Choong et al., 1992; Hill and Lucas, 1996; Wright and Vincent, 1996; Darvell et al., 1996; Agrawal et al., 1997; Strait and Vincent, 1998; Yamashita, 1998, 2002, 2003, 2008; Lucas et al., 2000, 2001, 2009, 2011; Agrawal and Lucas, 2003; Balsamo et al., 2003; Lucas, 2004; Elgart-Berry, 2004; Williams et al., 2005; Teaford et al., 2006; Quyet et al., 2007; Freeman and Lemen, 2007b; Wright et al., 2008; Dominy et al., 2008; Norconk et al., 2009b; Vogel et al., 2009, 2014; Wiecekowski, 2009; Yamashita et al., 2009; Norconk and Veres, 2011; Onoda et al., 2011; Daegling et al., 2011; Thompson et al., 2014; Venkataraman et al., 2014; Taniguchi, 2015; Hartstone-Rose et al., 2015). While these studies sometimes yield results consistent with their hypotheses, this is not always the case. Incongruence could be due to the hypotheses being false, complications occurring during data collection, and/or investigating the wrong mechanical properties. Minimizing the impact of these latter two factors is fundamental to improving our understanding of primate feeding mechanics.

Over the past several decades, a disconnect has developed between materials science and the biological sciences: this is partially due to disagreements within the field of materials science itself. For example, within materials science, toughness can have units of Joules per meter squared ( $J/m^2$ ) or cubed ( $J/m^3$ ) depending on the source (Atkins and Mai, 1985; Callister, 2004; Courtney, 2005). The field of fracture mechanics frequently assigns toughness units of  $J/m^2$ , and is short hand for more complex concepts (i.e., energy release rate, strain energy release rate, critical energy release rate, or critical strain energy release rate). These complex concepts are measures of the amount of energy needed to propagate a crack. Only some of these toughness values are material properties while others are not, as they are a product of the material and the system (Wang, 1996; Roylance, 2001a; Courtney, 2005).

Additional Supporting Information may be found in the online version of this article.

\*Correspondence to: Michael A. Berthaume, Deutscher Platz 6, Leipzig 04103, Germany. E-mail: michael\_berthaume@eva.mpg.de

Received 18 May 2015; revised 28 August 2015; accepted 21 October 2015

DOI: 10.1002/ajpa.22903  
Published online in Wiley Online Library (wileyonlinelibrary.com).

For example, more energy is needed to produce a crack in a given material with a dull compared to a sharp pair of scissors: this will cause a relatively higher energy release rate, and means that energy release rate is not a mechanical property (See *Material vs. Mechanical Property* and *Fracture Mechanics* sections for definitions of mechanical properties and the energy release rate.) When toughness has units of  $J/m^3$ , it is a mechanical property, and is defined as the amount of energy a material can absorb per unit volume prior to failure (Callister, 2004). In addition, fracture toughness can be given units of  $Pa\sqrt{m}$  or  $J/m^2$  both within materials science (Sun and Jin, 2012) and the biological sciences (Lucas and Pereira, 1990; Lucas et al., 1991, 2013; Choong et al., 1992; Ziscovici et al., 2014). These disagreements within materials science have translated into disagreements between materials science and the biological sciences, where disparate concepts have gained equivalent names, and equivalent concepts given different names. This in turn has led to some confusion, particularly with respect to “toughness” which has been used to describe multiple, distinct properties (Lucas and Pereira, 1990; Lucas et al., 1993; Zioupos, 2001; Lucas, 2004; Ziscovici et al., 2014).

There are a significant number of assumptions involved in the tests and calculations developed by materials scientists, and when these assumptions are violated, the results may be invalid. For example, nearly all the equations and tests employed in dietary studies assume the material being tested is linearly elastic and will undergo elastic fracture (Lucas, 2004). While some biological materials follow these assumptions, many do not. And when they do not, mechanical properties are no longer being measured. In addition, energy release rates obtained from different modes of fracture (e.g., wedge test [mode I] vs. scissors test [mode III]) are not comparable to one another (Hussain et al., 1974; Shi et al., 1994; Amstutz et al., 1995; Dunn et al., 1997). Thus, violating the assumptions of these equations and tests can lead to inaccurate experimental results. In order to improve dietary studies, we must minimize these problems, either by improving testing methods or using more appropriate equations.

In addition, dietary studies can be improved by incorporating mechanical properties that have largely been ignored. Most studies of primate diets focus on two measurements: 1) energy release rate ( $G$ ), commonly referred to as toughness ( $R$ ), a material’s resistance to crack propagation, and Young’s modulus ( $E$ ), a material’s resistance to elastic deformation under tensile or compressive forces. Other metrics, such as the shear modulus (also  $G$ ), a material’s resistance to elastic deformation when shear forces are applied, and toughness, with units of  $J/m^3$ , may be just as, if not more, important. Adding additional mechanical properties to our toolkit can help us expand our understanding of feeding strategies and adaptations in primates.

Finally, researchers commonly use average Young’s moduli and energy release rates to empirically determine whether or not an animal’s diet is tough or hard through the stress- and displacement-limited indices (Williams et al., 2005; Vogel et al., 2008, 2014). Not only are these two metrics not comparable to one another, but they also cannot be used for ductile food items, and

cannot be used to determine whether an animal’s diet is tough or hard (see *Application of Mechanical Property Tests to Feeding Biomechanics* section).

Because of these challenges, it is helpful to revisit the application of mechanical properties to dietary ecology, reevaluate what has been done, and discuss the future of the field. As such, the purpose of this paper is fourfold. First, to briefly review many of the basic mechanical properties used by materials science, going over basic measurements, calculations, and testing methods. This will provide the necessary background for evaluating food mechanical property research in anthropology. Second, to review the measurements, tests, and assumptions most commonly employed in studies concerning dietary mechanical properties in primates. Third, to evaluate the applications and limitations of the data gathered thus far. And finally, to consider the future of the field, and propose ideas to help the field move forward.

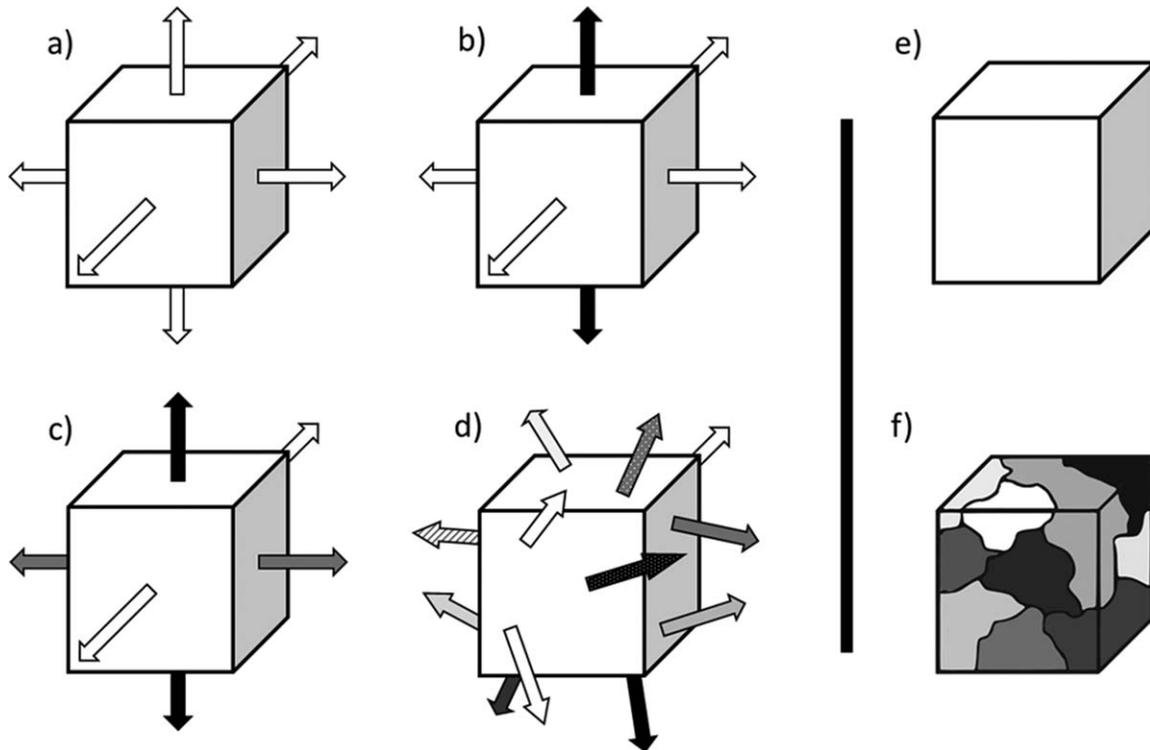
## MATERIAL AND MECHANICAL PROPERTIES

### Material vs. mechanical properties

Material properties are the intensive (size independent) properties of a (quasi-)solid that describe how the substance behaves. There are many types of material properties, such as electrical (e.g., conductivity, permeability), optical (e.g., luminosity, reflectivity), thermal (e.g., boiling point, flammability) and mechanical (e.g., Young’s modulus, toughness). Mechanical properties describe how a material behaves under a given load, are frequently measured using a universal testing machine, and are the subset of dietary material properties most frequently reported on in anthropological studies (Darvell et al., 1996; Lucas, 2004). Most anthropological studies that investigate mechanical properties focus on two variables, toughness and Young’s modulus, as it is assumed these two variables are the most critical to understanding the masticatory apparatus (Agrawal et al., 1997; Agrawal and Lucas, 2003; Lucas, 2004). However, there are a myriad of unexplored mechanical properties that may prove to be just as important in primate biology (see Thompson et al., 2014).

### Directional and locational variation

Mechanical properties can be independent or dependent of direction and location within the material (Fig. 1). Mechanical properties that are directionally independent are isotropic, while ones that are directionally dependent can be transversely isotropic, orthotropic, or anisotropic. In addition, these properties can either be homogeneous (locationally independent) or heterogeneous (locationally dependent) within the material. Most biological tissues are anisotropic and heterogeneous, but some can be treated as orthotropic, transversely isotropic, isotropic and/or homogeneous (Currey and Butler, 1975; Ashman, 1988; Rho et al., 1993, 1995; Peterson and Dechow, 2002, 2003; Dumont et al., 2005, 2012; Peterson et al., 2006; Wang et al., 2006; Currey, 2006; Dechow et al., 2010; Chung and Dechow, 2011; Davis et al., 2011). Assuming a material is isotropic and homogeneous is convenient, as many of the equations from materials science (and, in



**Fig. 1.** Four blocks showing directional (left, a-d) and two showing spatial (right, e-f) variability in mechanical properties. (a-d) Arrows are pointing in the direction in which the mechanical properties are acting: different colors and patterns represent mechanical properties with different magnitudes. (e-g) Different colors represent different sets of mechanical properties. (a) isotropic (b) transversely isotropic (c) orthotropic (d) anisotropic (e) homogeneous (f) heterogeneous.

particular, fracture mechanics) are based on these assumptions (Wang, 1996; Roylance, 2001a,b; Callister, 2004). But doing so is not always appropriate, given the complexity of biological materials (Turner and Burr, 1993; Martin et al., 1998; Peterson and Dechow, 2003; Strait et al., 2005; Currey, 2006; Wang et al., 2006; Berthaume et al., 2012).

In terms of diet, researchers have hypothesized that anisotropy is important in preventing crack propagation in brittle, biological materials (Mai and Atkins, 1989). In brittle isotropic materials, it is easy to concentrate the energy necessary to propagate a crack at the crack tip, making it easier for the crack to propagate. This is why biological materials that are meant to fail, such as amniotic membranes and egg shells tend to have isotropic mechanical properties. However, anisotropy creates a lack of shear stiffness, making it “difficult to concentrate energy into the path of a putative crack (pg. 48, (Mai and Atkins, 1989)).” This could be why brittle leaves which are heavily preyed on have developed anisotropic mechanical properties (Mai and Atkins, 1989; Yamashita, 2003; Yamashita et al., 2009; Onoda et al., 2011).

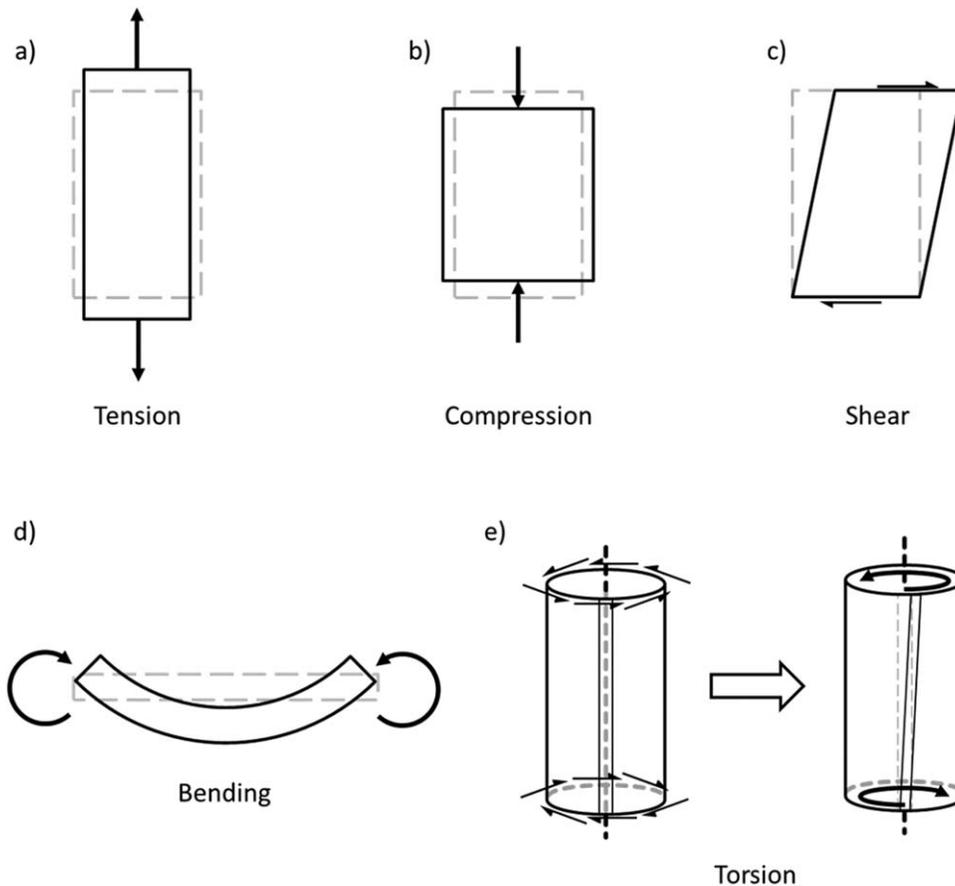
When preying on anisotropic materials, the most efficient way for a predator to circumvent this defense is by evolving sharper teeth, as sharp teeth can concentrate forces/energies and promote crack propagation in the food item more efficiently than dull teeth (Mai and Atkins, 1989). Therefore, sharp teeth may reflect an adaptation to a diet full of anisotropic foods. Conversely, it is not important to concentrate forces/energies in iso-

tropic materials, materials that do not need to be fractured, or when releasing extracellular liquids (e.g., juicy fruits, nectars, and/or highly fibrous foods that are “wadged<sup>1</sup>) (Lucas and Luke, 1984; Wrangham et al., 1991; Vogel et al., 2008; Marlowe, 2010). To process these foods, force, energy and/or stress needs to be spread over a larger portion of the food item, creating an isostress condition, as this allows more cells to burst open per chew than if the force, energy, or stress was concentrated. This isostress condition is most efficiently accomplished through blunter/duller teeth (Evans and Sanson, 1998; Freeman and Lemen, 2007a; Berthaume et al., 2010, 2013, 2014; Berthaume, 2013).

### Measuring mechanical properties

**Loadings.** Forces can be applied through tensile, compressive, and/or shear loads (Fig. 2). When applied in combination with one another, new types of loading, such as bending (tension + compression) can be formed. In addition, many loads can be applied by themselves and in a specific manner to cause new loading scenarios. For example, when a series of shear loads are applied tangentially along the outer surface of one end of a

<sup>1</sup>Wadging is the process by which foods are subjected to molar occlusion or pressed between the lips and anterior dentition (in the case of figs), softened with saliva, and repeatedly compressed between the lips and the anterior dentition. The nutrients are then extracted, followed by expulsion of the pulp/seeds (Lambert, 1999; Vogel et al., 2008; Head et al., 2011). This action has been reported in Pan, Pongo, and Homo, but not Gorilla (Taylor et al., 2008).



**Fig. 2.** Three basic types of loads, (a) tension, (b) compression, and (c) shear, that can be combined to form other types of loads [e.g., (d) bending] or can be applied in a specific way in order to produce new loads [e.g., (e) shear forces applied to tangentially to the edge of a cylinder produce torsional forces]. Arrows represent the way in which the loads are applied. Hashed, gray lines represent the undeformed shapes and the solid, black lines represent the deformed shapes.

cylinder (see Fig. 2), a torsional load forms about a neutral axis that runs through the center of the cylinder. The torsional load causes shear forces to form along the length of the cylinder, as if a cylinder composed of a series of disks that were trying to rotate.

Loads can be applied statically, dynamically, or cyclically. Static loads are applied extremely slowly or over an “infinite” amount of time, making them time independent (e.g., the load of a leaf on its stem or a person’s weight against their feet as they are standing still). Dynamic loads are applied more quickly, making them time dependent (e.g., teeth against a branch as leaves are being stripped, or incisors biting into a ripe piece of fruit). Finally, cyclic loads are applied repeatedly [e.g., over 1,000s of cycles, see fatigue and S-N curves (Ugural and Fenster, 2003; Callister, 2004)], and are dependent on the amplitude of the loads and the number of cycles applied. Examples of cyclic loads include those applied to the body during mastication and locomotion.

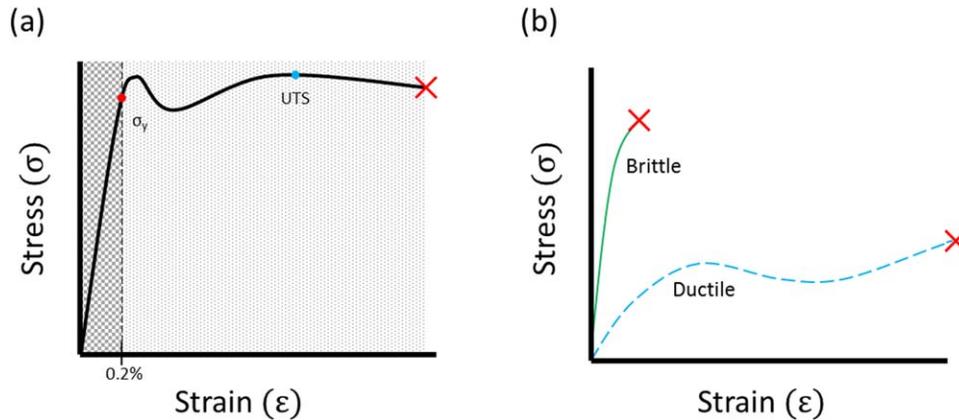
In feeding studies, considering the types and manners in which loads are applied is important, as these factors can affect a material’s strength. For example, beams fail under different loads when bending and tensile forces are being applied. All loads are important during mastication, although some likely play a more important role (i.e., tensile, compressive, and shear) than others (i.e., cyclic and bending) during food breakdown.

**Static vs. dynamic analyses.** There are two common types of structural analyses: static and dynamic. Static analyses are independent of time—these types of analyses are common in feeding biomechanics [e.g., lever mechanics of the mandible, finite element analysis of the crania or mandible, and calculating mechanical advantage of the chewing muscles (Herring and Herring, 1974; Grosse et al., 2007; Davis et al., 2010)]. These analyses involve three equations in 2D and six equations in 3D, which state the sum of forces in a all directions and the sum of moments about all axes are equal to zero. If the sums of forces or moments are not equal to zero, the system is not in equilibrium and would be *moving*. Movement only occurs in dynamic analyses, where the sum of the forces are equal to mass times acceleration, and the sum of the moments are equal to the moment of inertia times the angular acceleration (Beer et al., 2006).

**Impact force.** One force that frequently ignored during masticatory biomechanics is the impact force. Impact force is calculated with the following formula

$$\text{Impact Force} = \frac{\Delta \text{momentum}}{\Delta \text{time}} \quad (1)$$

where change in momentum is equal to the mass of the object times the change in velocity (Beer et al., 2006).



**Fig. 3.** Theoretical stress-strain curves of a ductile material from a tensile test, where fracture, or failure, is depicted by the red X. On the left (a), the yield stress is depicted by the red dot towards the beginning of the curve ( $\sigma_y$ ) and the ultimate tensile strength is depicted by the blue dot at the top of the curve (UTS). The elastic region is the grey, checkered region to the left of the yield stress and the plastic region is the grey, dotted region to the right. On the right (b) are two theoretical curves for a brittle material (green, solid) and a ductile material (blue, dashed).

During chewing, the change in velocity is equal to mandibular speed. (Note: change in velocity is not acceleration. Acceleration is the rate of change of velocity, i.e., change in velocity divided by change in time). The inverse correlation between impact force and time means that, for a given jaw mass and velocity, animals that close their mouths quicker will have larger impact forces than those that close their mouths slower.<sup>2</sup> While this may mean little in terms of breaking down food items, it suggests that an animal with a weak static (isometric) bite force can break open mechanically challenging food items by chewing quicker and increasing the impact force between the tooth and the food item.

All else being equal, impact forces likely play a larger role in small compared to large food item consumption, as there is more clearance between the food item and the maxillary teeth prior to the power stroke, giving the mandible more time to build up speed before tooth-food-tooth contact occurs. Smaller food items may also interact with the teeth for a shorter period of time, which would decrease the change in time, further increasing the impact force.

**Force-displacement and stress-strain curves.** Force-displacement and stress-strain curves are used to measure and calculate many mechanical properties. All loading conditions can be used to measure and calculate these curves: however, the most common loads utilized are tension, compression, and shear. For a comprehensive explanation of how to obtain force-displacement and stress-strain curves, please see the Supporting Information section.

Briefly, stress-strain curves are broken into elastic and plastic regions. The elastic region is the beginning of the curve and, if a sample is loaded only within this region, no permanent deformation will occur—this means the specimen will retain its original shape when unloaded. If the specimen is loaded past the elastic region, it enters the plastic region and experiences per-

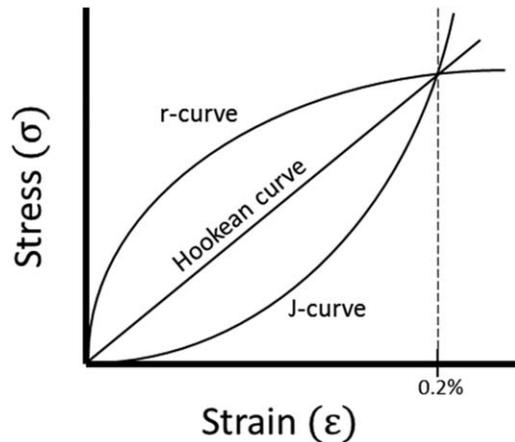
manent deformation (Fig. 3). This transition point is the yield stress—if a material is loaded past the yield stress and then unloaded, this causes a localized increase in the yield stress. During mastication, solid food items must be loaded past the elastic region. If they are not, the food item would rebound to its original shape after a chewing cycle, and the food item would not breakdown.

It is important to keep this in mind when determining what biomechanical “problems” food items might cause the masticatory apparatus during feeding, as some mechanical properties change once the food item has begun to plastically deform. For example, during mastication of a homogeneous, isotropic, ductile food item, new surfaces are formed as the food is fractured. Some of these new surfaces will have some plastic deformation, which will cause a localized increase in the yield stress of the food item: therefore, larger stresses must be achieved in order to cause further plastic deformation at these regions. At the same time, the maximum reaction force produced by the food item will be decreasing, as the food item particles will be decreasing in size and require a smaller amount of force to reach their yield stress.

As food items can have a myriad of mechanical properties that can be homogeneous, heterogeneous, isotropic or anisotropic, it is not possible to come up with a single rule to govern the biomechanical “problems” posed by food items on the masticatory apparatus. Instead, what will be important will be situation dependent.

**Mechanical properties and stress-strain curves.** Mechanical properties can be determined from both the elastic and plastic regions of stress-strain curves. For example, Young’s modulus ( $E$ ), also known as the elastic modulus or the modulus of elasticity, is the slope of the elastic portion of a tension/compression stress-strain curve and the shear modulus ( $G$ ) is the slope of the elastic portion of a shear stress-strain curve. In addition, the stress at which a material transitions from the elastic to the plastic region is the yield stress, and the maximum stress experienced by the material prior to fracture is the ultimate tensile (UTS), compressive (UCS), or shear strength (USS) of the material

<sup>2</sup>Change in time is the time over which impact occurs, which is likely correlated to kinematic aspects of chewing, such as power stroke duration and/or chewing speed.



**Fig. 4.** Within the elastic region, curves can either be linear (Hookean) or non-linear. Non-linear curves can either be shaped like a lower case “r,” indicating that stress initially increases at a faster rate than strain, or like an upper case “J,” indicating that strain initially increases at a faster rate than stress.

(Callister, 2004). In order for food item breakdown to occur, the yield stress, and the ultimate strength, must be surpassed.

Although the relationship between stress and strain in the elastic zone is generally linear (Hookean), it can be non-linear concave (r-shaped curves) or convex (J-shaped curves) (Fig. 4). Brittle biological materials that are designed to fail, such as egg shells and amniotic membranes, tend to have a linear elastic region, meaning that stresses increase proportionally to strains as energy is added to the system (Mai and Atkins, 1989). Brittle biological materials that are designed to resist crack formation, such as leaves, tend to have J-shaped elastic regions, meaning that stresses increase at a faster rate than strains as energy is added to the system—this allows the system to withstand higher levels of stress before reaching the yield stress (Kendall and Fuller, 1987; Mai and Atkins, 1989). Finally, both brittle and ductile materials that are meant to store energy and avoid failure, such as tendons and muscles, tend to have r-shaped elastic regions, meaning that stresses increase at a slower rate than strains as energy is added to the system (Benedict et al., 1968; Zink et al., 2014). This allows the system to store a larger amount of energy while decreasing the risk of failure.

The shape of the linear elastic region can be determined mathematically. During a tension test, the relationship between stress and strain can be represented through the following formula

$$\sigma = E^n \epsilon^2 \quad (2)$$

where  $n$  determines the shape of the curve. If  $n$  is equal to one, the curve is linear, if  $n$  is greater than one, the curve is J-shaped, and if  $n$  is less than one, the curve is r-shaped (Kendall and Fuller, 1987).

After the yield stress but before the ultimate strength is reached, strain hardening can occur (Callister, 2004). During this stage, microscopic changes are occurring in the material as it plastically deforms, increasing its strength. If stresses are held constant during this time, the material will not fail. In order for the material to fail, stresses must increase until the ultimate strength is

surpassed. After the ultimate strength is reached, the material begins to visibly deform: during tensile tests, this phenomenon is called necking. Necking continues to occur until fracture.

The integral of the elastic region of the stress–strain curve is the modulus of resilience ( $U_r$ ), and is a measure of the strain energy, per unit volume, needed to stress a material up until the point of yielding. The integral of the entire stress–strain curve is the energy per unit volume, or toughness, of the material. Toughness has units of  $J/m^3$ , and is different in both calculation and units from the toughness used in fracture mechanics ( $J/m^2$ ) (Ashby, 1992; Callister, 2004; Lucas, 2004; Courtney, 2005). Both the modulus of resilience and toughness are mechanical properties, as they are size independent. For details on how to extract mechanical properties from shear tests, please see Harrison (2006).

If a material fractures soon after the yield stress is reached, it is brittle, and if it has a large plastic region, it is ductile (Fig. 3). A common misconception is that the opposite of brittle is tough, and vice versa (Wright and Vincent, 1996; Currey, 2008; Wood and Schroer, 2012), however the opposite of brittle is ductile, and it is possible for brittle materials to be tough. The distinction of brittle vs. ductile is useful as it informs on how the material will fail: brittle materials fail because of high stresses, while ductile materials fail because of high strains or because they have absorbed a large amount of energy (Callister, 2004).

In materials science, materials are classified into three categories: metals, ceramics, and polymers (Callister, 2004). In general, many metals (e.g., steel) and polymers are ductile, while some metals (e.g., cast iron) and ceramics are brittle. It is difficult to determine the yield stress in some ductile materials, as they do not always appear to have an elastic region. This is particularly common in polymers and biological materials. In these cases, the elastic region is traditionally defined from 0–0.2% strain, and the yield stress occurs at 0.2% strain (Callister, 2004).

#### **Limitations of force-displacement and stress-strain curves.**

These tests assume the material being tested is homogeneous, and if the material is only tested in one direction, isotropic. This means mechanical properties are constant throughout the material and properties are not directionally dependent. Many metals and ceramics conform to these assumptions, but many biological materials do not. For example, cranial bone is heterogeneous and anisotropic, meaning mechanical properties are locationally and directionally dependent (Currey, 2006; Wang et al., 2006; Dechow et al., 2010). Similar to bone, most naturally occurring foods (e.g., leaves, grasses) exhibit heterogeneous and anisotropic properties (Lucas et al., 1997; Teaford et al., 2006). To complicate things further, many of these materials are composites, being comprised of many distinct materials [e.g., insects (Strait and Vincent, 1998)].

While it may be useful to measure the mechanical properties of each component of a composite material individually, the approximate mechanical properties for the system as a whole might be more appropriate. For example, *Cebus libidinosus* uses stones tools and anvils to fracture palm nuts, so if the relationship between humeral morphology and tool use is being investigated, the mechanical properties of the nut as a whole and not

its individual components are pertinent, as all portions of the nut are providing structural integrity (Visalberghi et al., 2008; Wright et al., 2009). However, if the link between diet and tooth morphology is being investigated, the mechanical properties of just the portion of the nut that is being consumed should be considered. Simply put, mechanical properties gathered should be hypothesis and question driven. When choosing which mechanical properties to gather, researchers should not just gather data on the most commonly reported mechanical properties in the literature, but rather choose mechanical properties and testing modes that reflect the way in which the animal is processing the food items.

Mechanical properties are also speed dependent, and the tests previously discussed are run extremely slowly to nullify dynamic effects. As speed increases, materials can experience changes in mechanical properties, and go from being ductile to brittle. For example, when a slow force is applied to silly putty, a soft, clay like substance, it stretches, deforms, and exhibits a high level of ductility. If a fast force is applied, it quickly fractures in a brittle manner. Therefore, it is important to report on the speed at which experiments are being done, and to only compare results to experiments done at similar speeds (Lucas et al., 1997; Strait and Vincent, 1998; Williams et al., 2005; Chanthasopephan et al., 2006; Serrat et al., 2007; Lusk et al., 2010; Thompson et al., 2011). Furthermore, the wedge test (described below) has been shown to be extremely sensitive to speed (Lucas et al., 1993).

During mastication, many primates chew at a rate that is too fast to ignore dynamic effects (Ross et al., 2009; Thompson et al., 2011). However, the tests and mechanical properties discussed in this paper ignore dynamic effects, and assume the system is static. If dynamic effects are of interest (e.g., if differences in chewing rates are being correlated to diet) different mechanical properties, such as the storage and loss moduli (modified versions of Young's modulus)<sup>3</sup> and viscoelastic properties should be considered (Kunzek et al., 1999). Using only static mechanical properties to characterize a dynamic process like chewing, particularly of viscoelastic foods, would lead to inaccurate and/or incomplete results. For example, measures of Young's and shear moduli could be inaccurate, and estimates for the amount of force or energy needed to masticate food items would be inaccurate by ignoring impact forces and work lost due to dampening effects (Zink et al., 2014).

Finally, when running a test and there is slack in the system, it is necessary to "zero out" the force-displacement curve. For example, when running a compression test to assess the efficiency of tooth morphology (Abler, 1992; Anderson and LaBarbera, 2008; Anderson, 2009; Berthaume et al., 2010; Crofts and Summers, 2014), the tooth could start off 1 mm or 10 mm above the specimen, creating different force-displacement curves. This problem can be avoided by assuming a reaction force between 1-5% of the maximum reaction force represents zero displacement, effectively zeroing out the graph. A similar procedure is employed by the HKU and

FLS-1 portable testers commonly used in primatology (Darvell et al., 1996; Lucas et al., 2001).

**Composites.** Many naturally occurring biological materials are composites, constructed of many, distinct structures. The Young's modulus of a composite can be approximated using the volume fractions and the Young's moduli of the individual components that are used to create the composite. The upper limit is estimated using the following equation

$$E_c = E_1 * V_1 + E_2 * V_2 + \dots + E_n * V_n \quad (3)$$

and the lower limit is estimated using the following equation

$$\frac{1}{E_c} = \frac{V_1}{E_1} + \frac{V_2}{E_2} + \dots + \frac{V_n}{E_n} \quad (4)$$

where  $E_1$  and  $E_2$  are the Young's moduli of the two materials,  $V_1$  and  $V_2$  are the volume fractions of the two materials, and  $n$  is the number of materials in the composite.

**Hardness.** Hardness is a measure of a material's ability to resist localized plastic deformation, and is measured using an indentation test. There are many hardness tests available (e.g., Knoop, Rockwell, Vickers, and Martens), most of which have different units and can be done on the macro, micro, or nano scale (Callister, 2004). During a hardness test, an indenter is pressed into the surface of a material, creating localized stress concentrations and plastic deformation. It is important that, during testing, the material is thick enough that the stresses do not permeate the thickness of the material, as this would mean both the specimen and the base of the test rig are supplying a reaction force to the indenter. Hardness is determined by the magnitude of the reaction force or by the depth of indentation, and can be correlated to other mechanical properties, such as ultimate strength and Young's modulus (Callister, 2004).

Because the indenter only encounters the surface of the material, hardness is a superficial measurement that reflects the mechanical properties of the surface of the material. If the material is homogeneous and isotropic, these are also the mechanical properties of the entire material. In terms of feeding, most biological materials do not fit into this category, as they are heterogeneous and anisotropic. This makes hardness a product of the local testing environment, and not a mechanical property of the entire food.

### Fracture mechanics

Fracture mechanics is based on the idea that every object, man-made or organic, has inherent microcracks which compromise their strength. Once a microcrack absorbs enough energy through an applied force, it will propagate through the material and cause fracture (Wang, 1996). At an atomic level, fracture is the separation of atoms through severing of atomic bonds, which can occur by shearing two atoms past each other, changing the angle of the bonds, or by pulling two atoms apart, lengthening the bonds. It is impossible to break bonds by pushing two atoms closer together. Here, I will

<sup>3</sup>Dynamic moduli have real and imaginary components. The storage modulus is the ratio of the real components of stress to strain, and the loss modulus is the ratio of the imaginary components of stress to strain.

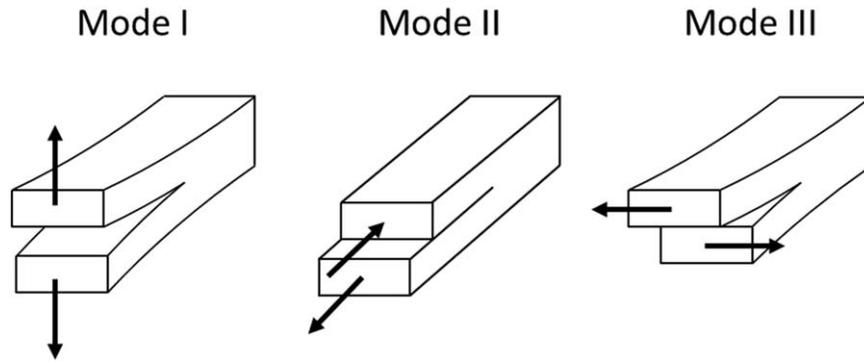


Fig. 5. Modes I, II, and III of fracture. Arrows indicate the direction of the applied load.

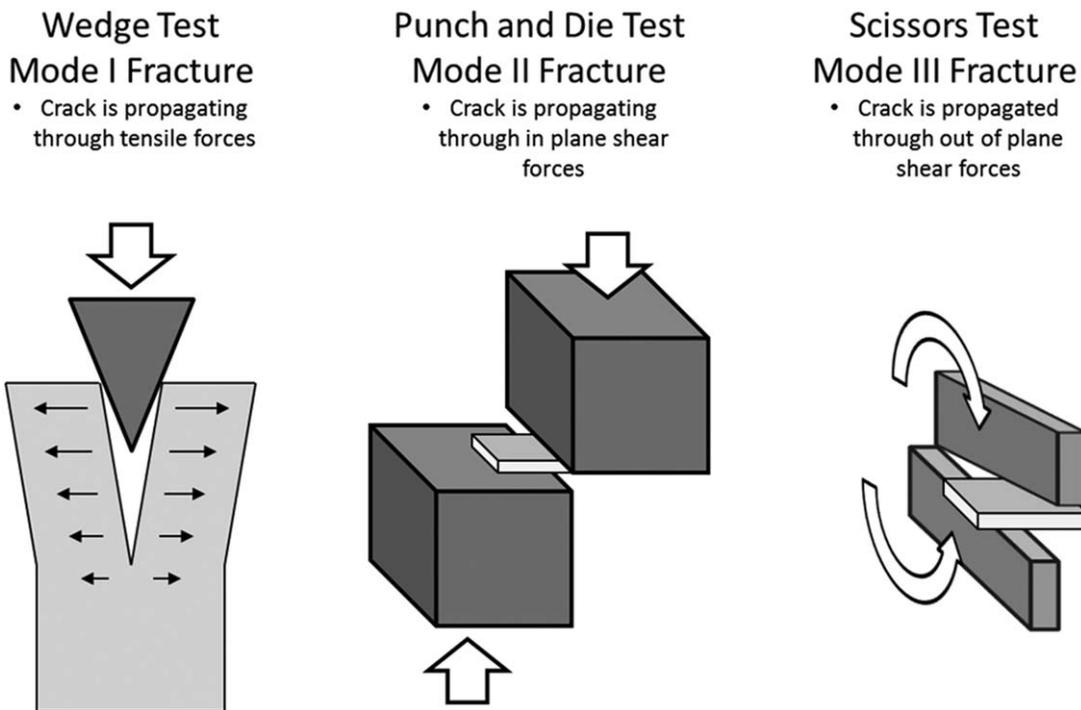


Fig. 6. Primary modes of fracture for commonly used toughness tests. Arrows indicate the direction of the applied load.

be providing a brief overview of fracture mechanics. For a more detailed overview, please see Wang (1996).

**Modes of fracture.** There are three types, or modes, of fracture (Fig. 5). Mode I involves applying tensile loads which open and widen the crack, while both Modes II and III involve applying shear loads that occur in and out of plane, respectively (Figs. 5 and 6). When measuring food item mechanical properties, Mode I fracture can be measured with the wedge test, Mode II can be measured with a punch test, and Mode III can be measured with a scissors test (Fig. 6), although the scissors test could represent mixed mode fracture (Lucas and Teaford, 1994; Darvell et al., 1996). It is of note that these tests are only appropriate for brittle materials, of which many food items are not.

Because some materials differ in their ability to resist tensile and shear loads, results from Mode I, II, and III fracture tests are not comparable. In addition, as the

ratio of a materials ability to resist Mode I and II or III fracture is not constant, no correction factor can be used to compare results across fracture modes (Hussain et al., 1974; Shi et al., 1994; Amstutz et al., 1995; Darvell et al., 1996; Dunn et al., 1997; Sui et al., 2006; Lucas et al., 2011). Direct comparison among modes of fracture is done in feeding biomechanics studies, where results from scissors, wedge, and punch tests are directly compared (Agrawal et al., 1997, 2000; Sanson et al., 2001; Agarwal and Lucas, 2002; Agrawal and Lucas, 2003; Sui et al., 2006; Vogel et al., 2008; Ang et al., 2008; Dominy et al., 2008; Wich, 2009; Kitajima and Poorter, 2010; Lucas et al., 2011; Venkataraman et al., 2014). All three modes likely occur during feeding, but the frequency with which each occurs will depend on jaw kinematics and tooth shape. For example, Mode II and Mode III fracture likely occur more frequently during mastication in primates with low molar relief, while Mode I likely occurs during intraoral ingestion and mastication in primates with high molar relief (Agrawal et al., 1997;

Agrawal and Lucas, 2003; Ang et al., 2006; Sui et al., 2006; Boyer, 2008).

**Crack propagation.** In order to cause a crack to propagate, energy must be concentrated around its tip. The amount of energy needed to cause crack propagation is dependent on the way the material is loaded, the yield stress of the material, and the geometry of the crack itself [i.e., shape and length (Roylance, 2001a; Sun and Jin, 2012)]. Together, these factors are used to calculate the stress intensity factor,  $K$ , which has units of Pascals $\cdot\sqrt{\text{meters}}$  (Atkins and Mai, 1985). This is related to the energy release rate,  $G$ , units Joules/meters<sup>2</sup>, and is the amount of energy required to propagate a crack normalized by crack area (Atkins and Mai, 1985; Wang, 1996). During linear elastic fracture, all the energy concentrated at the crack tip is strain energy, so  $G$  is called the strain energy release rate (Atkins and Mai, 1985; Wang, 1996; Callister, 2004; Courtney, 2005).

Two types of fracture can occur: elastic and elastic-plastic. During elastic fracture, all the energy absorbed by the material is stretching the atomic bonds, and no plastic deformation is occurring. During elastic-plastic (hereafter, plastic) fracture, energy goes into both stretching atomic bonds and rearranging atoms, plastically deforming the material. An easy way to determine whether elastic or plastic fracture has occurred by trying to fit the pieces back together after fracture has occurred. If the pieces can be fit perfectly back together to form the original shape of the specimen, elastic fracture has occurred. If they cannot fit back together because the pieces have distorted, plastic fracture has occurred. Perfectly brittle materials undergo elastic fracture, while ductile materials undergo plastic fracture.

In linearly elastic materials, the energy release rate and stress intensity factor are related to one another through Young's modulus with the following equation

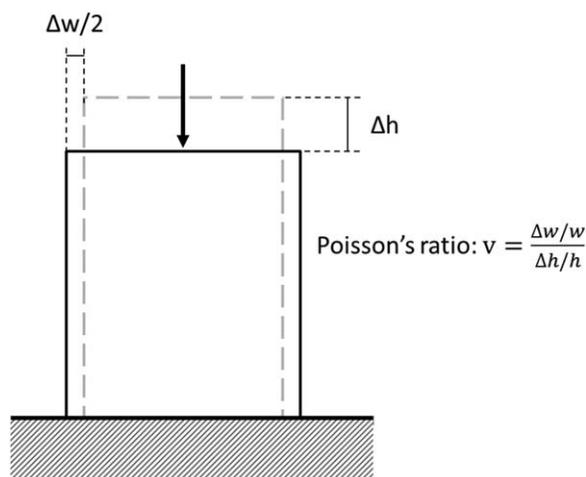
$$G = \frac{K^2}{E} \tag{5}$$

when the specimen is in plane stress, and

$$G = \frac{(1-\nu^2)K^2}{E} \tag{6}$$

when the specimen is in plane strain (Wang, 1996; Roylance, 2001a; Sun and Jin, 2012). Plane stress implies that the specimen is a nearly two dimensional, thin sheet, like a piece of paper, and all the forces, and therefore stresses, are occurring in plane. Both principal and shear stresses acting out of the plane are zero. Plane strain implies that the specimen is 3D, and loads are being applied in a way that all strains are either occurring along one of two perpendicular axes or within the plane that is formed by those axes. All other principal and shear strains are zero. During plane stress, Poisson's ratio ( $\nu$ ), the ratio of lateral to axial strains (see Fig. 7), can be ignored, but during plane strain, it cannot [Eqs. (5) and (6)].

With the exception of a few polymers, Poisson's ratio is always less than or equal to 0.5. A Poisson's ratio of 0.5 indicates that the material is incompressible, meaning that for every millimeter a specimen is compressed, it will expand a millimeter laterally (one half millimeter in each direction). This means the volume is conserved



**Fig. 7.** Poisson's ratio is the ratio of lateral to axial strains. Arrows indicate the direction of the applied load, and  $h$  and  $w$  are the undeformed height and width of the block. Dashed grey lines represent the undeformed shape, solid black lines represent the deformed shape. Hashed rectangle on the bottom represents an impenetrable surface.

as a load is applied. A Poisson's ratio less than 0.5 indicates that for every millimeter the specimen is compressed, it will expand less than one millimeter laterally, and volume will decrease. A Poisson's ratio greater than 0.5 indicates that for every millimeter the specimen is compressed, it will expand more than one millimeter laterally, and volume will increase, violating the theory of elasticity.<sup>4</sup>

The energy release rate ( $G$ ) and stress intensity factor ( $K$ ) represent the driving force for crack growth, but are not the materials resistance to crack growth. They are therefore not mechanical properties, as they are dependent on factors independent of the material (Wang, 1996; Sun and Jin, 2012). A material's internal resistance to crack growth,  $R$ , is a mechanical property (Wang, 1996; Roylance, 2001a; Sun and Jin, 2012). It is equal to the energy release rate only when it has exceeded a critical level. This is known as the critical energy release rate,  $G_C$ , or during elastic fracture, the critical strain energy release rate (Wang, 1996; Roylance, 2001a). Although equivalent in magnitude,  $R$  represents the materials internal resistance to crack extension, which is dependent on temperature, environment and loading rate, while  $G_C$  represents the driving force for crack extension, which is dependent on specimen and microcrack geometry as well as orientation, and loading conditions (Wang, 1996). This makes  $R$  a property of the material, but  $G_C$  a function of the system (Fig. 8).

During linear elastic fracture,  $R$  is constant, but during plastic fracture,  $R$  is a function of crack length (Wang, 1996; Sun and Jin, 2012) (Fig. 8). This is because, during plastic fracture, small amounts of plastic deformation are occurring at the crack tip, causing the crack tip to dull. Longer cracks can cause more dulling to occur, and therefore, require more energy to

<sup>4</sup>While most biological materials have Poisson's ratio that fall at or below 0.5, some values for skin have been reported as high as 1.6–2.5 (Lees et al., 1991; Frolich et al., 1994; Lucas, 2004). If these values are correct, it means skin cannot be modeled as a linearly elastic material.

propagate. Because there is no plastic deformation during elastic fracture, cracks grow and propagate unstably once  $G_C$  is reached. During plastic fracture, stable crack growth will occur once  $G_C$  is reached; if  $G_C$  is exceeded, unstable crack growth will occur.

The critical stress intensity factor,  $K_C$ , is a mechanical property known as fracture toughness, and measures a material's ability to resist fracture when a crack is present (Roylance, 2001a; Sun and Jin, 2012).

$$K_C = \sigma_C Y \sqrt{\pi a_C} \tag{7}$$

$K_C$  is dependent on many properties of the system, including the critical stress ( $\sigma_C$ ), critical crack length ( $a_C$ ), and a geometrical factor ( $Y$ ). The geometrical factor,  $Y$ , is a function of the system: for example, in a beam undergoing bending (Fig. 9a),  $Y$  is a function of beam height and crack length. The equation can be rewritten in terms of critical crack length, which is useful in predicting how long a crack would have to be in order to propagate under a given set of loading conditions.

In terms of masticatory biomechanics, this equation is particularly useful in determining how far a single cusp/

blade (e.g., from a tooth) must indent into a food item in order to cause fracture. For example, it can predict how far the incisor must move into a fruit to cause catastrophic failure during incisal biting.  $G_C$  and  $K_C$  are also dependent on the mode of fracture the specimen is undergoing, and are therefore reported as  $G_{IC}$ ,  $K_{IC}$ ,  $G_{IIC}$ ,  $K_{IIC}$ ,  $G_{IIIc}$ , and  $K_{IIIc}$ , where the subscripts I, II, and III representing Modes I, II and III fracture, respectively.

## FEEDING BIOMECHANICS

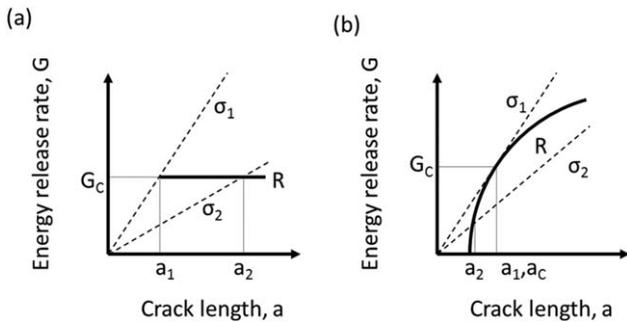
### Process of feeding

In Hiiemae (1967), a model was proposed to explain the process of feeding in rats. As more data has been gathered, this model has been modified and now includes the process by which liquid, semi-solid, and solid foods move from the external environment into the gut in mammals [Fig. 13.3, (Hiiemae, 2000)]. Five main steps occur when feeding on solid foods: ingestion, stage I transport, processing, stage II transport, and swallowing. During ingestion, the food is moved into the mouth. Next, stage I transport occurs, where food is transported posteriorly within the oral cavity. After stage I transport and before stage II transport, food is processed into a bolus by rhythmic chewing at the postcanine dentition and/or by tongue-palate compression. In primates, this type of chewing is mastication and is characterized by a number of features, including precise occlusion of the postcanine dentition. During stage II transport, a food bolus passes through the fauces. Finally, the food bolus is swallowed and passes into the gut (Hiiemae, 1967, 2000).

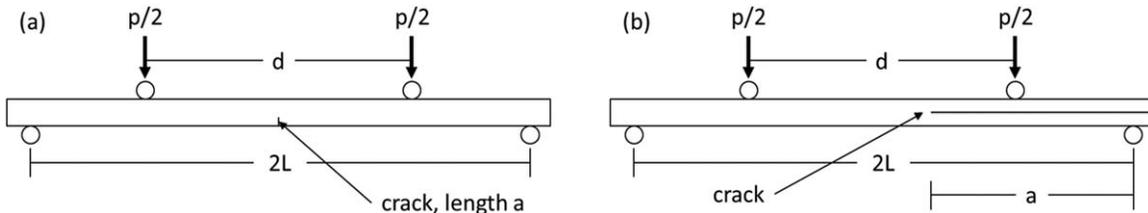
Mechanical properties of foods are important during all four steps of the feeding cycle. For example, compliant, semi-solid foods are ingested and transported differently than rigid, solid foods. However, for the purposes of this paper, stage II transport and swallowing will be ignored, as food item mechanical properties likely play a larger role in ingestion and mastication than in bolus formation or swallowing.

### Ingestion, mastication, and biting

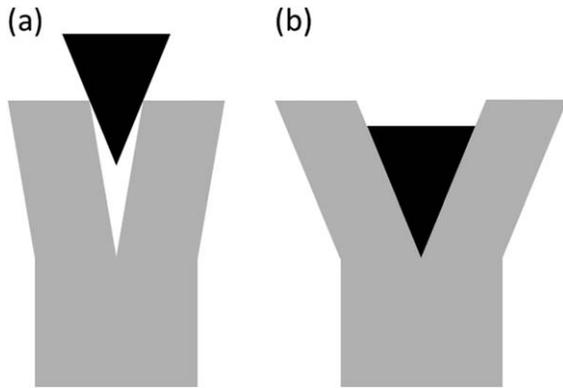
Dietary mechanical properties are correlated with ingestion, mastication, and biting (defined below). During feeding, ingestion can occur through extraoral or intraoral processing. Examples of extraoral processing are tool use to break down foods into manageable pieces (Visalberghi et al., 2008; Wright et al., 2009; Koops et al., 2010, 2014). Examples of intraoral processing include tree gouging in New World monkeys and slow lorises (Thompson et al., 2014; Burrows et al., 2015), orangutans using incisors to break leaves into smaller



**Fig. 8.** Crack resistance curves (R-curves) for fracture of (a) brittle and (b) ductile materials, where there are two loading scenarios causing two different stress states,  $\sigma_1$  and  $\sigma_2$ . In graph (a), the resistance to crack propagation,  $R$ , is constant, meaning the crack will not propagate until the critical energy release rate ( $G_C$ ) is reached. In scenario 1, a shorter crack is needed to propagate the crack ( $a_1$ ) than in scenario 2 ( $a_2$ ). Once the crack begins to propagate, it will propagate unstably through the material. In graph (b), the resistance to crack propagation is a function of crack length, meaning that a higher energy release rate is needed to propagate longer cracks. As long as the energy release rate is lower than the critical energy release rate and the crack is shorter than the critical crack length ( $a_C$ ), the crack will propagate stably through the material. Once the critical energy release rate and the critical crack length are reached, the crack will propagate through the material.



**Fig. 9.** (a) Notched four point bending test (Mode I fracture) and (b) four point bend end-notched flexure test (Mode II fracture). As no objects are being driven into the beams, the cracks are allowed to freely propagate throughout the material, and no energy is being used to plastically deform the material. Symbols:  $p$  = load,  $d$  = distance between the inner points of contact,  $L$  = one half the distance between the outer points of contact,  $a$  = crack length.



**Fig. 10.** Wedge tests with two different materials. The material on the left (a) is perfectly brittle, and the tip of the wedge (black arrow) is never interacting with the tip of the crack. All the energy being transferred from the wedge to the specimen is causing elastic deformation. Once enough elastic energy has been absorbed, the crack propagates. The material on the right (b) is ductile, and the wedge is interacting with the tip of the crack. The energy being transferred from the wedge to the specimen is causing both elastic and plastic deformation. Therefore, not all the energy being absorbed by the material is being used to propagate the crack.

pieces (Ungar, 1994, 1996), and lemurs using premolars to crack open the pod of the kily fruit (Yamashita, 2008; Yamashita et al., 2009). As stated before, mastication is a purely intraoral process, taking place on the postcanine teeth.

Biting is difficult to define in comparison to ingestion and mastication because it can occur during ingestion (intraoral processing), and/or mastication (the first step in mastication) and can therefore be considered a sub-category of these behaviors. It can also stand alone as a non-feeding behavior, relating to social and/or defensive actions, but as dietary mechanical properties do not relate to these latter categories, they are ignored for the purposes of this paper. Biting may often be distinctive in applying the largest load to the masticatory complex. Larger food items require higher forces and require more energy to break down than smaller food items with the same shape, composition, and mechanical properties (Lucas, 2004; Crofts and Summers, 2014). Therefore, forces transmitted from the food item to the masticatory process will decrease as the food item breaks down.

Mechanical properties that are important during ingestion, biting, and mastication may differ, as the goals of these actions are different and distinct. The main goal of ingestion is to break food items into smaller pieces, making mechanical properties related to fracture important. Alternatively, one of the main goals of mastication is to increase a food's surface area to volume ratio, increasing mean particle size and giving digestive enzymes a larger surface area to work on, thereby releasing more energy and nutrients from the food items (Clauss et al., 2002, 2015; Fritz et al., 2009; Venkataraman et al., 2014). This is done by fracturing or by permanently deforming the food item, making mechanical properties related to fracture, elastically deforming, and plastically deforming the food items important. Finally, as biting can be an ingestive or masticatory behavior, several mechanical properties related to ingestion or mastication will also relate to biting.

### Elastic vs. plastic deformation

As the point of mastication is to fracture or cause plastic deformation, it is critical for food items to leave the elastic range during mastication, making properties that describe how the object elastically deforms, such as Young's modulus, important aspects of feeding. Other aspects related to elastic deformation (e.g., viscoelasticity, non-linearity etc.) are also likely important and should be considered in the future.

During elastic deformation, atomic bonds are shortened or lengthened through the application of a load, causing the volume of the object to change. This means that while the load is being applied, volume is not conserved. During plastic deformation, bonds are broken and (sometimes) reformed, but bond lengths do not change: this means volume is conserved (Courtney, 2005). The only way to mechanically increase the surface area to volume ratio during elastic deformation is by keeping a constant, high force on the object. This is unlikely to occur during digestion in a biologically meaningful manner.

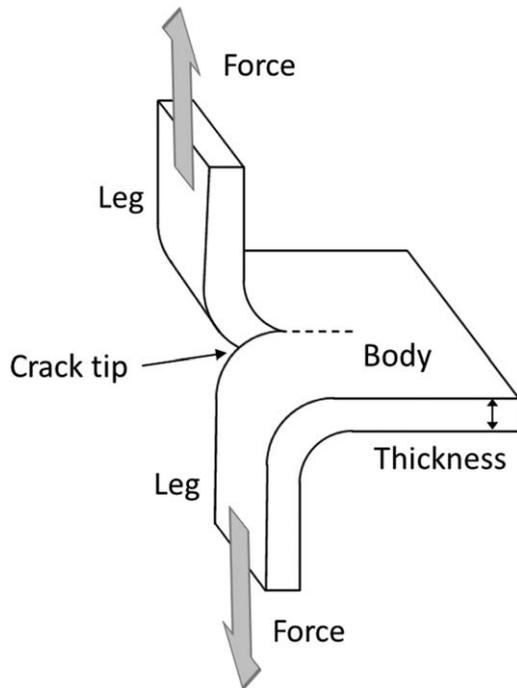
However, the surface area to volume ratio can be increased in a meaningful way through plastic deformation. For example, take a spherical ball of putty with a radius of 1 cm. As a sphere, it has a volume of  $4.19 \text{ cm}^3$ , surface area of  $12.57 \text{ cm}^2$ , and a surface area to volume ratio of  $3 \text{ cm}^{-1}$ . If flattened down to a 1 mm high cylinder, giving it a radius of 3.65 cm, its surface area and surface area to volume ratio would increase to  $86.07 \text{ cm}^2$  and  $20.55 \text{ cm}^{-1}$ , respectively. This would result in a 685% increase in the surface area to volume ratio without fracture. Therefore, increases in surface area to volume ratio due to plastic deformation may be important during mastication.

### APPLICATION OF MECHANICAL PROPERTY TESTS TO FEEDING BIOMECHANICS

#### Toughness

In anthropology, toughness, sometimes referred to as fracture toughness (Atkins and Vincent, 1984; Lucas and Pereira, 1990) is denoted by  $R$ , defined as resistance to crack propagation, and given units of Joules/meters<sup>2</sup>. This is the same as energy release rate,  $G$ , from fracture mechanics (Wang, 1996; Roylance, 2001a; Sun and Jin, 2012). It was argued that  $R$  should be used because  $G$  is generally restricted to elastic fracture and "the term  $R$  is more loosely defined as the energy involved in crack resistance (266; Lucas, 2004)." While true, this is because  $R$  is a mechanical property that can be measured during both elastic and plastic fracture (see *Crack Propagation* section), while  $G$ , which is not a mechanical property, is only equal to  $G_C$  and subsequently  $R$  during elastic fracture. Because, as will be shown in the following paragraphs, the data being gathered on diet are not, in fact, mechanical properties, and are instead energy release rates, I suggest energy release rate and  $G$  be used instead of toughness and  $R$ .

The "toughness" data gathered on diet are not mechanical properties for two main reasons. First, the tests used to calculate energy release rate assume all the energy is going into crack propagation, and none is plastically deforming the material. For this to be true in the case of the wedge or scissors tests, the tip of the crack would always be slightly ahead of, and never touching, the tip of the wedge or scissor's blades (see

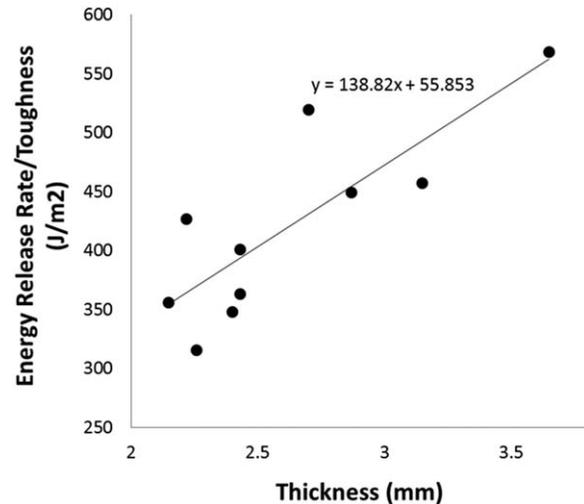


**Fig. 11.** Trouser tear test, which can be used to measure the critical energy release rate during Mode III fracture. The critical energy release rate is equal to the non-elastic energy of the system, approximating the force applied times the displacement of the legs ( $Energy = Force * displacement$ ). This is the critical energy release rate, and not just the energy release rate, as the crack is being allowed to self-propagate and is not having a wedge driven into it.

Fig. 10) (Atkins and Mai, 1979; Atkins and Vincent, 1984; Lucas and Pereira, 1990; Vincent et al., 1991; Khan and Vincent, 1993; Lucas et al., 1993; Ang et al., 2008).<sup>5</sup> This is not true for most biological materials, a point proven by the fact that changes in scissor sharpness cause changes in energy release rate (Darvell et al., 1996). If the tip of the scissor's blades were not touching the tip of the crack, all the energy absorbed by the material would be strain energy, and the material would absorb the same amount of energy per unit area during fracture, regardless of blade sharpness. If plastic deformation were occurring, the energy absorbed by the material would be increasing as the blades got duller, as more plastic deformation would be occurring with the duller scissors. When the portable tester was first constructed, the effect of blade sharpness on energy release rate when cutting Whatman 542 filter printing paper was tested. It was found that blade sharpness had a significant effect on energy release rate (Darvell et al., 1996), thus demonstrating that the scissors test is not measuring mechanical properties.

The same scenario is true for the other toughness tests, where an object is being driven into the material (e.g., punch and die, razor, or wedge test) and the crack is not allowed to run freely [e.g., a notched four point bending test (Mode I), four point bend end-notched flex-

<sup>5</sup>The one notable exception is the wire test, which takes the energy used to cause plastic deformation into account (Kamyab et al., 1998; Goh et al., 2005).

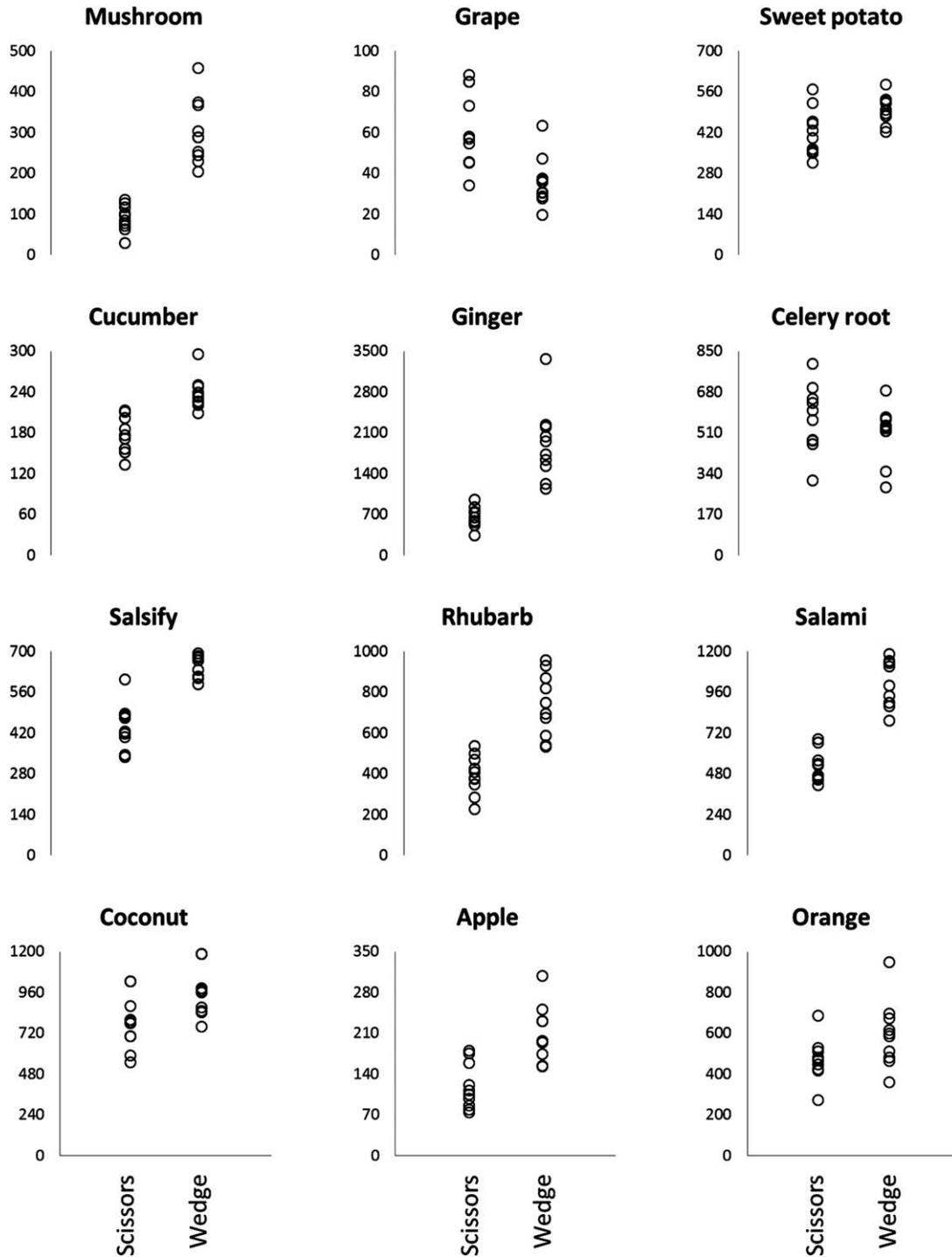


**Fig. 12.** Plot of energy release rate (toughness) vs. thickness for ten samples of sweet potato run through the scissors test. Samples were cut with the scissors running along the long axis. Thickness is significantly correlated to energy release rate (Spearman rank correlation:  $\rho = 0.778$ ,  $P = 0.008$ , Pearson correlation:  $r = 0.8234$ ,  $P = 0.003418$ ). The proposed cut off, above which thickness should not be correlated to energy release rate, is 2 mm (Lucas et al., 2000, 2011).

ure test (Mode II) or a trouser tear (Mode III), Figs. 9 and 11]. However, no experiments have quantified how much plastic deformation is occurring in any other test, or with any other material. Therefore, the energy release rates gathered with the wedge, scissors, razor, and punch and dies are not critical energy release rates, and are not mechanical properties.

Second, mechanical properties are, by definition, intrinsic, meaning they are independent of size. It has been shown that, during the scissors test, the energy release rate is sensitive to specimen thickness, which is why it is recommended that the specimen be at least 1–2 mm thick (Darvell et al., 1996; Lucas et al., 2000, 2011; Lucas, 2004). Up until 1–2 mm thickness, there is a strong linear correlation between thickness and toughness. Past 1–2 mm thickness, this correlation disappears in most foods (c.f. sweet potato, Fig. 12). If the scissors test must be used, thickness should be held constant, and if this is not possible, multiple thicknesses should be tested per specimen in order to understand the relationship between thickness and size, and then the toughness for a given thickness should be estimated. The fact that the energy release rate is highly dependent on specimen thickness, even if only for a small range, is further evidence that this is not a mechanical property.

A second issue with energy release rate, mentioned previously, results from different tests (e.g., scissors and wedge test) being directly compared to one another (Agrawal et al., 1997, 2000; Sanson et al., 2001; Agarwal and Lucas, 2002; Agrawal and Lucas, 2003; Sui et al., 2006; Vogel et al., 2008; Ang et al., 2008; Dominy et al., 2008; Wich, 2009; Kitajima and Poorter, 2010; Lucas et al., 2011; Venkataraman et al., 2014). As scissors, wedge, punch, razor, and wire cutting tests represent different modes of fracture, and materials exhibit different levels of resistance to Mode I, II, and III fracture, the results are not directly comparable [see Fig. 13, Table 1 (Sui et al., 2006; Freeman and Lemen, 2007b;



**Fig. 13.** Scissors test vs. wedge test for twelve domestic food items, ten tests per food item, performed on the FLS-1 Tester, using protocols described in Lucas (2004). Mini salami was Dulano brand. Mushrooms, grapes, sweet potato, cucumber, celery root, salsify, mini salami, and apple were tested with the crack being driven along the long axis, and ginger and rhubarb were tested orthogonal to the fibers. Coconut and orange peel were tested orthogonal to the outer surface. All fruits and vegetables were purchased at Hit in Leipzig, Germany in May, 2015, stored appropriately, and tested within four days of acquisition. The salami was purchased at the same time at Aldi in Leipzig, Germany. With the exception of the celery root and orange peel, there were statistically significant differences between the scissors and the wedge tests ( $P < 0.05$ , see Table 1).

Lucas et al., 2011)]. Furthermore, the ratio of results between modes of fracture (e.g., Mode I/Mode II) are not comparable, as materials differ in their ability to resist tensile and shear stresses (Shi et al., 1994; Dunn et al.,

1997). For example (assuming the same amount of plastic deformation is occurring in the scissors and the wedge test, which may or may not be true), it appears that fibrous foods are more efficient at resisting fracture

TABLE 1. Energy release rate ( $G$ , toughness) averages and standard deviations for twelve domestic food items using both the scissors test ( $n = 10$ ) and wedge test ( $n = 10$ )

	Scissors ( $\text{J}/\text{mm}^2$ )			Wedge ( $\text{J}/\text{mm}^2$ )			$R_{\text{scissors}}/R_{\text{wedge}}$	Mann-Whitney U test	
	$n$	Avg	Stdev	$n$	Avg	Stdev		U	$P$ -value
Chestnut mushroom	10	90.1	32.15	10	300.33	77.96	0.30	0	0.00001083
Red grape	10	62.51	19.16	10	35.7	12.18	1.75	88	0.002825
Sweet potato	10	420.4	90.3	10	495.51	47.68	0.85	20	0.02323
Cucumber	10	175.76	26.91	10	238.13	23.81	0.74	2	0.0000433
Ginger	10	666.87	173.44	10	1907.63	635.03	0.35	0	0.00001083
Celery root	10	568.09	139.67	10	510.27	114.21	1.11	61	0.4359
Salsify	10	444.6	77.27	10	644.44	37.94	0.69	1	0.00002165
Rhubarb	10	393.36	94.24	10	733.32	156.32	0.54	1	0.00002165
Mini Salami	10	519.91	93.01	10	1028.26	148.39	0.51	0	0.00001083
Coconut	10	783.59	160.85	10	958.91	140.47	0.82	23	0.04326
Apple	10	119.06	39.25	10	209.04	47.82	0.57	8	0.0007253
Orange peel	10	471	103.12	10	593.61	160.85	0.79	26	0.07526

Tests were performed on the FLS-1 Tester using protocols described in Lucas (2004). Friction during the wedge and scissors test was accounted for using the protocol set forth in Lucas (2004). Orientation of the specimens is described in the caption of Figure 14. Mann-Whitney U-test revealed statistically significant differences between the scissors and the wedge test for all food items except celery root and orange peel.

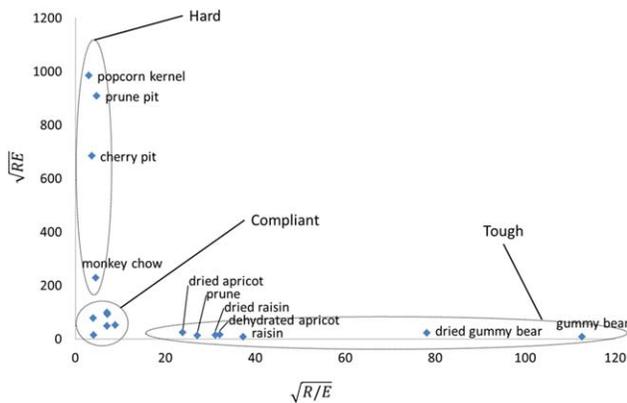


Fig. 14. Plot of displacement-limited index vs. stress-limited index for food items used in experimental studies of primate masticatory function, data taken from (Williams et al., 2005). Foods in the compliant oval include almond, apple pulp, apple skin, carrot, pear skin, and sweetgum leaf.

through tensile forces than shear ones (see ginger and rhubarb in Fig. 13, Table 1, which were tested perpendicular to their fibers).

**Hardness.** When used, hardness has been discussed in three ways. First, it is discussed using some of the previously described mechanical property tests (Lucas et al., 2009, 2014; Thompson et al., 2014). Second, a force gauge has been used to measure puncture resistance (Kinzey and Norconk, 1990, 1993; Lambert et al., 2004; Norconk and Veres, 2011; Alvarez and Heymann, 2012). While useful, puncture resistance is not a mechanical property, as it will change depending on the shape of the object being driven into the material (Abler, 1992; Evans and Sanson, 1998; Freeman and Lemen, 2007a; Anderson and LaBarbera, 2008; Anderson, 2009; Berthaume et al., 2010; Barnett et al., 2015). Third, it is used as a synonym for brittleness, or to mean the opposite of toughness (Agrawal et al., 1997; Lucas et al., 2000; Yamashita, 2003, 2008; Dominy et al., 2008; Norconk

et al., 2009a; Yamashita et al., 2009). This should be avoided, as hard materials can either be brittle (e.g., cast iron) or ductile (e.g., steel), and soft items can either be brittle (e.g., crackers) or ductile (e.g., silly putty/plasticine).

### Young's modulus/elastic modulus/modulus of elasticity

The methods used to measure Young's modulus are largely the same between anthropology and materials science (i.e., tension, compression, bending, and indentation tests) (Agrawal et al., 1997; Agrawal and Lucas, 2003; Lucas, 2004; Vogel et al., 2008, 2009; Lee et al., 2010; Thompson et al., 2014). It should be remembered that, during compression tests, the specimen must have a constant cross-sectional area and be loaded along its long axis. In addition, during bending tests, the specimen should be at least 10 times as long as it is high, otherwise the specimen is no longer in pure bending and the shear stresses running along the long axis of the specimen can no longer be ignored (Beer et al., 2006).

### Stress and displacement limited

The classification of stress and displacement limited is used to describe how tough or hard food items are, respectively (Agrawal et al., 1997; Agrawal and Lucas, 2003; Yamashita, 2003; Lucas, 2004; Williams et al., 2005; Strait et al., 2009; Wright et al., 2009; Dumont et al., 2011), where stress limited is defined as  $\sqrt{ER}$  and displacement limited is defined as  $\sqrt{R/E}$  ( $E$  is Young's modulus and  $R$  is energy release rate). There are critical problems with the comparison of these indices to classify food items as tough or hard, which could make their broad application in feeding biomechanics studies inappropriate.

In order to determine whether food items are tough or hard, stress and displacement-limited values are compared within categories, between food items (e.g.,  $\sqrt{ER}_{\text{prune}}$  vs  $\sqrt{ER}_{\text{almond}}$ ) and between categories, within food items (e.g.,  $\sqrt{ER}_{\text{prune}}$  vs  $\sqrt{R/E}_{\text{prune}}$ ). The first comparison puts food items in three categories: hard (high  $\sqrt{ER}$ , low  $\sqrt{R/E}$ ), tough (low  $\sqrt{ER}$ , high  $\sqrt{R/E}$ ), or compliant (low  $\sqrt{ER}$ , low  $\sqrt{R/E}$ ). This gives poor results, as

some foods classically classified as relatively hard or tough (e.g., almonds, carrots, fruit skins) can be categorized as relatively compliant (Fig. 14).

For the second comparison, the displacement and stress-limited indices cannot be compared to each other to determine if a food item is hard or tough (Yamashita, 2003; Strait et al., 2009; Daegling et al., 2011; Pontzer et al., 2011; Ungar, 2011), as this contrast will only reflect Young's modulus: if Young's modulus is greater than one, the food item will be hard, if Young's modulus is less than one, the food item will be tough. If the displacement and stress limited indices are related to each other by a factor of  $C$ , the following equation can be written

$$C * \sqrt{\frac{R}{E}} = \sqrt{RE} \tag{8}$$

Simplifying Eq. (8), we get

$$\begin{aligned} C * \frac{\sqrt{R}}{\sqrt{E}} &= \sqrt{R} * \sqrt{E} \\ C * \frac{1}{\sqrt{E}} &= \sqrt{E} \\ C &= \sqrt{E} * \sqrt{E} \\ C &= E \end{aligned}$$

Therefore, the magnitude of the difference between the indices is Young's modulus (Fig. 15). Furthermore, the difference between the stress and displacement-limited indices is sensitive to the units used to measure Young's modulus: if megapascals are used, the results will be 1,000 times different than if gigapascals are used. This makes the selection of units, which should not matter, matter greatly. For these reasons, the indices cannot be directly compared.

The way in which the indices were derived also makes their use problematic in feeding biomechanics studies. The stress-limited index was proposed in Agrawal and Lucas (2003), where humans were asked to bite into food items with linear elastic properties with their incisors. Then, using the following equations from linear elastic fracture mechanics, Agrawal and Lucas (2003) derived a correlation between fracture stress, crack length, Young's modulus, and energy release rate

$$K_I^2 = C_1 E G_I = ER \tag{5 altered eqn}$$

$$K_I = C_2 \sqrt{ER}$$

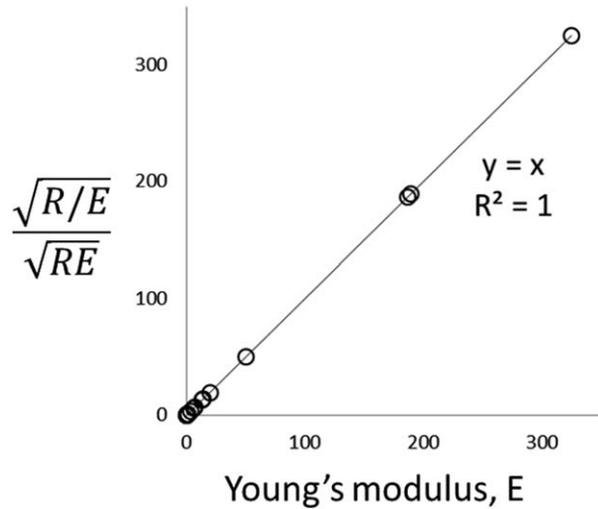
$$K_I = C_3 \sigma_f \sqrt{a} \tag{7 altered eqn}$$

$$C_2 \sqrt{ER} = C_3 \sigma_f \sqrt{a} \tag{combining previous eqns}$$

$$C_4 \sqrt{ER} = \sigma_f \sqrt{a} \tag{9}$$

where  $\sigma_f$  is fracture stress,  $a$  is crack length and  $C_1$ ,  $C_2$ ,  $C_3$ , and  $C_4$  are arbitrary constants. By showing there was a strong correlation between  $\sqrt{ER}$  and  $\sigma_f \sqrt{a}$ , the stress limited index was created. This makes the general use of the stress limited index problematic for five reasons, all of which may cause the correlation between  $\sqrt{ER}$  and  $\sigma_f \sqrt{a}$  to fall apart.

First, the equations used to derive this metric assume linear elastic fracture and plane stress, and are therefore only applicable to perfectly brittle, flat specimens that are being loaded in plane. As previously mentioned,



**Fig. 15.** Plot of ratio of displacement-limited index to stress-limited index vs. Young's modulus using data from Thompson et al. (2014).

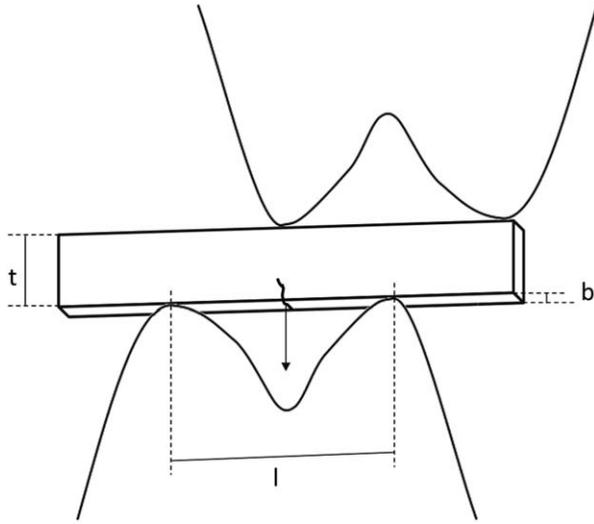
many naturally occurring biological materials violate linear elastic fracture assumptions, and plane stress assumptions are rarely met during feeding (particularly with leaves, which are frequently loaded out of plane). Second, experimental results were based on a single, ingestive, incisal bite, and therefore these results are not applicable to mastication or ingestion where other teeth are used, as incisors function differently than canines, premolars, and molars. Third, this relationship was only tested during Mode I fracture, and may not hold true in Mode II or III fracture, which occur during feeding. Fourth, the linear relationship between  $\sqrt{ER}$  and  $\sigma_f \sqrt{a}$  was calculated ignoring the variation, and therefore error, in the  $\sqrt{ER}$  term. Finally, the slope of the linear relationship ( $C_4$ ) varied greatly between the 10 human participants (from 7.12 to 25.24): if  $\delta_f/a$  were as dependent on  $\sqrt{ER}$  as has been proposed, there should not be a statistically significant difference in the slopes between individuals.

In addition,  $\sqrt{ER}$  was never correlated to food toughness, as tough foods were never shown to have higher  $\sqrt{ER}$  values, making it an inadvisable metric for food toughness.

The displacement-limited index was first proposed in Agrawal et al. (1997), where humans were asked to bite into food items that were mostly linearly elastic with their postcanine teeth. Then, using a series of equations derived from beam theory and elastic fracture mechanics,  $\sqrt{R/E}$  was correlated to a fragmentation index. To do so, Agrawal et al. (1997) assumed that only three cusps were interacting with a food item at a time, and therefore the maximum displacement of the food item,  $\delta$ , could be defined using equations from beam theory

$$\delta = \frac{3Fl^3}{4Ebt^3} \tag{10}$$

Where  $l$  was the distance between the cusps,  $b$  is the thickness of the food item, and  $t$  is the height of the food item (Fig. 16). If only three cusps are interacting with the food item and the food item is acting like a beam, and the maximum stresses ( $\sigma_f$ ) incurred by the food item are



**Fig. 16.** Modified figure from Agrawal et al. (1997), showing how three cusps could cause a flat food item to bend like a beam, where  $l$  is the distance between the lower cusps,  $t$  is the thickness of the food item, and  $b$  is the depth of the food item. Note that, in order for beam theory to apply, no more than three cusps can be touching the food item and  $l$  must be at least 10 times greater than  $t$ .

$$\sigma_f = \frac{3Fl}{2bt^2} \quad (11)$$

Combining Eqs. (10) and (11) gives

$$\frac{\sigma_f}{E} = \frac{2\delta t}{l^2} \quad (12)$$

Assuming the material undergoes elastic failure and is in plane stress, Eq. (8) can be modified to produce

$$K_I = c\sigma_f\sqrt{\pi a} \quad (13)$$

Assuming  $c$ , a constant, is equal to 1, the following equation can be produced by dividing by Young's modulus

$$\frac{K_I}{E} = \frac{\sigma_f}{E}\sqrt{\pi a} \quad (14)$$

Then substituting in KI from Eq. (5) yields

$$\begin{aligned} \frac{\sqrt{ER}}{E} &= \frac{\sigma_f}{E}\sqrt{\pi a} \\ \frac{\sqrt{ER}}{\sqrt{E^2}} &= \frac{\sigma_f}{E}\sqrt{\pi a} \\ \sqrt{\frac{R}{E}} &= \frac{\sigma_f}{E}\sqrt{\pi a} \end{aligned} \quad (15)$$

Finally, substituting in the equation for failure stress from Eq. (11) yields

$$\sqrt{\frac{R}{E}} = \frac{2\delta t}{l^2}\sqrt{\pi a} \quad (16)$$

Therefore, during plane stress and three point bending, linearly elastic materials with a higher  $\sqrt{R/E}$  require a larger displacement ( $\delta$ ) to fracture. Given this

derivation, the displacement-limited index is inappropriate to use in feeding biomechanics for five reasons.

First, it assumes the material being tested fractures elastically and that plane stress conditions are met: as explained before, this is not true. Second, Eqs. (10) and (11) assume that a) only three cusps are touching the food item and b) the food item is acting like a beam. During biting, it is rare that only three cusps of two postcanine teeth contacting a food item and that a food item is acting like a beam (as this would imply the food item is thinner than one-tenth the distance between the lower cusps). Third, these equations assume Mode I, and ignore Mode II and III fracture. Fourth, during experimentation,  $\sqrt{R/E}$  was never correlated to a displacement or stress at fracture. Instead, it was correlated to a fragmentation index, which is independent of displacement or stress at fracture.

Finally,  $\sqrt{R/E}$  was never shown to be correlated to food toughness or hardness, meaning it has never been demonstrated as an appropriate metric to determine if a food item is tough or hard. Further testing is warranted before this metric can be used for this purpose.

Finally, assuming the aforementioned problems did not exist these two indices were derived using two completely different methods: one relating biting to fracture stress and one relating chewing to a fragmentation index. These two indices cannot, therefore, be used to break food items into an "either/or" classification system (i.e., hard vs. tough) (Strait et al., 2009; Dumont et al., 2011; Ungar, 2011), as it is possible for both metrics to be high or low.

### How do mechanical properties relate to feeding

Given the wealth of literature, it has been concluded that dietary mechanical properties have many effects on the masticatory apparatus: exactly what these effects are and their role in feeding remains up for debate. For example, chewing foods with higher energy release rates leads a relative increase in balancing side masseter activity, implying greater work done on the occlusal surface of the tooth is necessary to break down foods with higher energy release rates, such as gummy bears (Vinyard et al., 2006). In addition, energy release rate is negatively correlated to the total number of chews per sequence in Cebus (Reed and Ross, 2010). Dietary mechanical properties have also been found to play a role in food selection patterns (Hill and Lucas, 1996; Teaford et al., 2006; Taniguchi, 2015) and foraging behaviors (Vogel et al., 2009) in primates. In terms of functional morphology, evidence has been gathered supporting the idea that more mechanically challenging diets (higher energy release rate, stress-limited index, or displacement-limited index) lead to thicker enameled molars (Lambert et al., 2004; Vogel et al., 2008; Wiczowski, 2009) and a more robust craniomandibular complexes (Dominy et al., 2008; Daegling et al., 2011; Thompson et al., 2014).

Despite all these correlations, the role of mechanical properties in feeding is still up for debate. One of the big reasons goes back to the problems with a) measuring toughness, and b) calculating the stress-limited and displacement-limited indices. While it is safe to say a gummy bear will always have a higher energy release rate than a raisin, the exact correlation between variables like jaw muscle forces and energy release rate cannot be empirically determined if the mechanical

properties are being measured/calculated inaccurately. In terms of functional morphology, researchers are realizing that we know less concerning the relationship between morphology and diet than we thought we did (e.g., the relationship between skull morphology and diet in *Paranthropus boisei* and *Hadropithecus stenognathus* (Godfrey et al., 2015; Constantino and Wood, 2007; Cerling et al., 2011; Dumont et al., 2011; Dzialo et al., 2013; Smith et al., 2015).

A second reason is the lack of an ability to characterize the mechanical properties of diet completely. While energy release rate may turn out to be the property that affects feeding the most, it is impossible for researchers to know this now as no animal has had the mechanical properties of its diet completely characterized. Finally, an investigation of a complete profile of mechanical properties may lead to correlations between mechanical properties, environment, and/or geographic location (Strait, 1997) that would have gone under the radar before, giving us a new way to reconstruct the mechanical properties of the diets of extinct animals.

## FUTURE OF THE FIELD

### A need for standardization

Inconsistencies in terminology have led to both miscommunications between fields and issues within the field of dietary biomechanics [e.g., the comparison of results of the wedge, scissors, and/or punch and die tests, Fig. 13, (Agrawal et al., 1997; Agrawal and Lucas, 2003; Dominy et al., 2008; Vogel et al., 2008, 2009, 2014; Lucas et al., 2011; Venkataraman et al., 2014; Zink et al., 2014)]. While it is unlikely one set of terms will develop that encompass all possible mechanical properties, it is possible to formulate general rules to minimize miscommunications within and between fields and improve future work. Below are a few suggestions that, if followed, should help minimize confusion and error within and between fields.

#### ***1. Use quantitative and not descriptive terms for quantitative properties.***

Stiffness has been used quantitatively in biomechanics to describe a material's resistance to deformation, but it is a descriptive term that describes the slope of a bivariate plot: a material with a higher slope is stiffer, whether that is the slope of a force-displacement or a stress-strain plot (Williams et al., 2005; Anderson, 2009; Zack et al., 2009; Claverie et al., 2011; Gutiérrez-Rodríguez et al., 2013; Perry et al., 2015). As stiffness can take on multiple meanings, caution should be taken when comparing stiffness values across studies.

#### ***2. Use one term to describe each quantitative property.***

*2a. If multiple terms have been applied to a single property, use the term that is unique to that property.*

Toughness and energy release rate are both used to describe energy required to propagate a crack, but toughness is also used to describe the amount of energy a material can absorb per unit volume prior to fracture (Callister, 2004). Therefore, energy release rate, and not toughness, should be used to describe energy required to propagate a crack.

*2b. If a single term has been applied to multiple properties and is unique to only one of those properties, use it only with that property.*

This is the case for toughness, which has been used with multiple properties, but it is only unique to one, when it is the amount of energy a material can absorb per unit volume prior to failure and has units ( $J/m^3$ ).

*2c. If multiple, unique terms have been applied to a single property, list all terms when the measurement is first discussed, and then use only one for the rest of the analysis.*

Young's modulus, elastic modulus, and modulus of elasticity are three terms used to describe the same property, and no other properties. All are acceptable to use, but researchers should be consistent to avoid possible confusion.

It is critical that testing methods between the two fields are as consistent as possible. Tests used to quantify mechanical properties are derived and based on concepts from materials science. Therefore, it is important to minimize the violation of assumptions behind the tests put forth by materials science.

In an ideal world, no assumptions would be violated, as doing so violates the principles governing the equations behind the tests and potentially invalidates the metrics. However, reality dictates some of these assumptions must be violated, particularly in the field, where it is impossible for all tests to be precisely controlled. It is therefore important to understand the effect of violating these assumptions in order to provide a set of "error bars" for the results. Furthermore, guidelines should be constructed that dictate at which point the results have become invalid, as assumptions are violated (Darvell et al., 1996; Lucas et al., 2000, 2011; Lucas, 2004).

### Data gathered thus far

A myriad of studies have been conducted over the past several decades investigating dietary mechanical properties. From a material's science perspective, data gathered on Young's modulus will remain valid and useful, as will data on hardness, where mechanical property tests were employed (Lucas et al., 2009, 2014; Thompson et al., 2014). However, data gathered on energy release rate will have limited uses, and the stress and displacement-limited indices should no longer be used for reasons listed above. Furthermore, there are some problems with how the tests are conducted in general, that must be also addressed.

To date, few studies in primate feeding report on crosshead speed with which data was gathered. Of the studies that do report on speed, some are running tests much faster than advisable [up to 60 mm/min (Strait and Vincent, 1998)], at which point there may be dynamic effects, making the mechanical properties inaccurate. The only published study the author is aware of that investigates the effects of speed on results was conducted on mung bean gels, and speed was found to have a significant effect on the results (Lucas et al., 1993). It is imperative that more mechanical property data be

gathered, particularly on natural occurring biological materials, in order to quantify the effects of speed on mechanical properties within different materials. This will help determine whether results from dietary mechanical property studies are comparable to one another, as the mung bean data suggests that not all data are, in fact, comparable. The portable universal tester first published by Darvell et al. (1996) is a hand-cranked machine, as it is nearly impossible to power a universal tester in the field. This makes it difficult to control for speed and to ensure speed does not vary within a trial.

While researchers attempt to keep crosshead speed constant within a single test and between tests, this is not always possible. Therefore, studies also need to be conducted investigating how mechanical properties are affected by intra-test variations in speed. A protocol for such a study could be as follows

1. Obtain a perfectly brittle material with homogeneous, isotropic mechanical properties (e.g., ceramics or plastics situated on the brittle side of the glass transition zone).
2. Run 10 mechanical property tests at a constant speed.
3. Run 10 more tests where speed is varied, but the average speed is the same as from step 2 and there is a standard deviation of at least 20%.
4. Repeat step 3 twice with increased standard deviations.
5. Repeat steps 2–4 for at least three more speeds.
6. Repeat this process for ductile, heterogeneous, and anisotropic materials.
7. Repeat for all mechanical properties of interest.

The error in mechanical property measurements associated with changes in speed both within and between trials can be calculated for a variety of materials and tests, and be used to create error bars for data gathered in the field.

Another possible problem may lie with the equipment used to gather mechanical property data. The portable tester is, by necessity, a light and compliant machine compared to non-portable, full-scale universal testers. Non-portable universal testers are large and heavy to prevent them from elastically deforming during mechanical property testing. If the testers cannot resist deformation, the crosshead displacements are wrong, and the compliance of the machine needs to be taken into account by subtracting out the predicted displacements due to the machines compliance at each load step. While the compliance of the portable testers has been investigated and an upper limit for acceptable reaction forces has been determined for some tester versions (Vinyard, personal communication), the compliance of the machine is frequently not reported when presenting dietary mechanical property data. As the compliance of the non-portable testers is taken into account when gathering mechanical property data (e.g., ASTM E4-14), it should also be taken into account with the portable tester during dietary mechanical property testing. If the compliance cannot be taken into account, the specimen needs to be cut as small as possible in order to minimize compliance within the machine due to high reaction forces. The smaller specimen size will not affect the results when testing mechanical properties, as mechanical properties are size independent.

Energy release rate is one of the most commonly reported mechanical properties in the dietary mechanical property literature for primates. As previously discussed, the data gathered have largely not been mechanical properties, but are rather system specific: by changing a part of the system (e.g., angle of the wedge, sharpness of the scissors), the results will change (see *Toughness* section in *Application of Mechanical Property Tests to Feeding Biomechanics*). Therefore, results from these tests cannot be used in conjunction with mechanical property equations, as they are not, themselves, mechanical properties.

The data on energy release rate (aka toughness) has limits on its use. Energy release rate is system dependent, therefore changing the system (e.g., by altering tooth morphology) will change the energy release rate. This means it might require the same amount of energy to propagate a crack for an animal with sharp teeth and a “tough” diet as an animal with dull teeth and a “compliant” diet. This would greatly affect the results of a study that is comparing the mandibular shape of these two species, as the biomechanical effect on the mandible would be identical for both species even though their diets are mechanically distinct. Similarly, if an animal primarily shears its foods and another primarily splits its foods (i.e., Mode II/III vs. Mode I fracture), use of just the wedge or scissors test would be inappropriate as results from the two tests cannot be directly compared. However, if interspecies variation in diet or if two animals with nearly identical masticatory apparatuses are being compared, these tests can be used for comparative purposes. Because of this, it is inadvisable to compare dietary energy release rates, particularly through the wedge or scissors tests, of any two or more animals with disparate tooth morphologies or masticatory apparatuses (Dominy et al., 2008; Taylor et al., 2008; Vogel et al., 2009).

Finally, results of the toughness tests can be used to address questions that are non-system specific where the principles from mechanical properties are not needed. For example, several studies have investigated the mechanical properties of plants and leaves, where questions about the plants, and not animals, are being asked [e.g., correlation between fiber content and resistance to crack propagation (Lucas et al., 2000; Westbrook et al., 2011)]. In addition, questions can be asked about ontogenetic changes in leaves and fruits (Yamashita, 2008). As long as tests are being held consistent and principles from materials science are not being employed, it is very useful to use the data for these purposes (Onoda et al., 2011).

### Are we looking in the right places?

**Challenging underlying assumptions of the field.** During the birth of a field, assumptions are made out of necessity—it is impossible to take into account every detail, and to understand how small variations from these assumptions will affect the results. One of the biggest assumptions held in the field of dietary mechanical properties is that primate diets consist of linearly elastic foods—this is an assumption that can be easily tested. When gathering data, simple tension tests can be run on the food items to construct stress–strain curves. If the stress–strain curves are linear and exhibit little to no plastic deformation, this assumption is valid. If the stress–strain curves are non-linear and/or exhibit plastic

deformation, it is important to quantify what percentage of the animal's diet consists of non-linearly elastic foods. These curves can be further used to investigate any plastic deformation that may be occurring and investigate the effects of violating the assumption of linear elasticity on the results.

Another assumption is that mechanical properties can be measured using solely static, and not dynamic, equations. As mentioned previously, during mastication, many primates chew at a rate that is too fast to ignore dynamic effects, so it would be useful to understand how much our results change when we consider dynamic effects.

A third assumption is that foods can be treated as being elastic rather than viscoelastic. The effects of viscoelasticity, particularly when saliva, water, and/or urine are applied to the food item (e.g., marmoset urinate on wood when they are gouging) should be quantified to better understand the validity of the results.

***Understanding the relationship between masticatory biomechanics and diet.*** Currently, our understanding between craniomandibular and dental morphology and diet is imperfect, and the more we learn about morphology and diet, the more imperfect this relationship can become. For example, there are some extant [e.g., *Lemur catta* and *Macaca* (Boyer, 2008; Cuozzo and Sauter, 2012; Kato et al., 2014)] and extinct primates [e.g., *Hadropithecus stenognathus* and *Paranthropus boisei* (Godfrey et al., 2015; Ungar et al., 2008; Cerling et al., 2011; Dumont et al., 2011; Smith et al., 2015)] in which contradicting morphological signatures exist, or in which morphological signatures do not match the other dietary signatures (e.g., isotope and microwear).

The first step in moving the field of dietary mechanical properties forward is to gain a better understanding of how food items break down during mastication, and how this relates to dental morphology. For example, researchers know that primates with second molars that are sharper, have relatively longer shearing crests, and higher relief, tend to be more folivorous or insectivorous. Conversely, primates with second molars that are duller, have relatively shorter shearing crests, and lower relief, tend to be more omnivorous or frugivorous (Kay, 1981; Boyer, 2008; Bunn et al., 2011; Winchester et al., 2014). While hypotheses have been generated to explain, biomechanically, why this relationship exists, they have never been rigorously tested. This is largely because we do not have a firm understanding of how food items interact with teeth, and how tooth shape affects food item breakdown.

Once we gain a better understanding of how food items both interact with teeth and breakdown during mastication, which can be done in an experimental or theoretical approach [e.g., (Brainerd et al., 2010; Berthaume et al., 2013, 2014; Müller et al., 2014, 2015)], we can better conclude what mechanical property data should be gathered in the first place. Building on these empirical findings, we can make better links between diet and both craniomandibular and dental morphology.

***Moving forward.*** In moving the field forward, we need to begin to more carefully link the questions we are asking to the dietary properties (both mechanical and non-mechanical) that will inform us the most about primate morphology and behavior. In a foundational paper,

Thompson et al. (2014) examined the process of marmoset tree gouging step by step, and based on their analysis, predicted which mechanical properties would most affect the masticatory apparatus. Briefly, marmosets first anchor their maxillary incisors in the bark, during which time bark hardness, friction between the tree and incisors, and indentation force were predicted to be important. Next, they use their mandibular incisors to initiate a crack in the bark, where fracture toughness, Young's modulus, and the critical strain energy were predicted to be important. Finally, the mandibular incisors propagate a crack through the tree, where work to peel was predicted to be important. While not all mechanical properties were significantly correlated to feeding, possibly because marmosets utilize both adaptive behaviors and morphologies to during tree gouging, this study showed a useful conceptual process that can be used to link mechanical properties to feeding before collecting mechanical properties.

Here, I propose a list of mechanical and non-mechanical properties that likely impact ingestion, biting, and/or mastication (Table 2). That is not to say these are the only properties that are linked to feeding biomechanics, but it is an idea of some of the properties that are likely to be important. In order to understand the role of food properties on the feeding complex, new properties, in addition to the ones that have been used in the past, should be investigated.

Both mechanical and non-mechanical properties are listed because during feeding *size matters*. There are size dependent, and therefore non-mechanical, properties of diet, that are important in feeding biomechanics. For example, the force needed to access a food item has been hypothesized to be linked to bite force, enamel thickness, and stresses and strain experienced by the craniofacial complex during mastication, and relative food item size has been related to gape angle, food item placement, stretch of the masticatory muscles, and possibly tooth morphology (Dumont and Herrel, 2003; Martin, 2003; Herrel et al., 2005; Taylor and Vinyard, 2009; Dumont et al., 2009, 2011; Eng et al., 2009; Lawn et al., 2009; Santana et al., 2012; Daegling et al., 2013; Strait et al., 2013; Berthaume et al., 2014; Smith et al., 2015). But as non-mechanical properties are system dependent [e.g., puncture resistance (Norconk and Conklin-Brittain, 2015)], how should they be measured?

In the past two decades, researchers have been attempting to do this by using models of teeth in universal testers to break down food items, recording the force or energy necessary to break down the foods (Abler, 1992; Evans and Sanson, 1998; Anderson, 2009; Berthaume et al., 2010). These models have provided us with an unparalleled understanding about how teeth break down food items, about how mechanical properties affect optimal tooth morphologies, and ask interesting questions concerning tooth morphology (Anderson, 2009). For example, how much are incisors acting like a "tool" and driving crack propagation when biting into a block of cheese (Agrawal and Lucas, 2003; Ang et al., 2006)? If performed in the field with teeth (or models of teeth) of the animals being studied, these types of tests could aid researchers in understanding what type of forces the masticatory apparatus is experiencing, and how much force or energy is necessary to fracture the food found in the animal's natural diet (Barnett et al., 2015). For example, marmoset teeth coated in human saliva were used to measure friction between incisors

TABLE 2. Properties of diet likely linked to feeding biomechanics

Action	Food item categorization	Mechanical properties	Non-mechanical properties
Ingestion	Brittle	Young's modulus Yield stress Energy release rate Critical energy release rate Ultimate strength Hardness	Friction between teeth and food item Energy to initiate crack propagation Energy release rate as the teeth penetrate the food item Reaction force from food item onto tooth Forces exerted by muscles Energy exerted by muscles Stresses in the enamel Stresses in the food item
	Ductile	Young's modulus Yield stress Toughness (energy per unit volume) Hardness	Friction between teeth and food item Energy to initiate crack propagation Energy release rate as the teeth penetrate the food item Energy to fracture food item Forces exerted by muscles
Biting	Brittle	Young's modulus Yield stress Energy release rate Critical energy release rate Ultimate strength Hardness	Energy to initiate crack propagation Energy release rate as the teeth penetrate the food item Reaction force from food item onto tooth Forces exerted by muscles Stresses in the enamel Stresses in the food item
	Ductile	Yield stress Toughness (energy per unit volume) Hardness	Energy to initiate crack propagation Energy release rate as the teeth penetrate the food item Energy to fracture food item Stresses in the enamel
Mastication	Brittle	Young's modulus Yield stress Critical energy release rate Ultimate strength Viscoelasticity	Total energy absorbed during breakdown Energy release rate as the teeth break down the food item Energy exerted by muscles Stresses in the enamel Stresses in the food item
	Ductile	Yield stress Toughness (energy per unit volume) Critical energy release rate Viscoelasticity	Total energy absorbed during breakdown Energy release rate as the teeth break down the food item Energy exerted by muscles Residual stresses in the craniofacial complex

and bark/wood in Thompson et al. (2014). Furthermore, these tests could be used to address interesting questions, such as how food item breakdown efficiency is affected by changes in dentition (i.e., deciduous vs. permanent) and tooth wear. A word of caution, however, is that placing teeth in a universal tester only models biting, can only currently model vertical tooth movements, does not include saliva, and does not model soft tissue. New methods need to be developed to model mastication through physical experimentation (e.g. chewing machines/simulator).

### Ingestion

During intraoral ingestion, food items are parsed into smaller pieces with the incisors, canines, and/or premolars (Hylander, 1975; Ungar, 1994; Yamashita, 2008). Therefore, properties related to fracture and crack initiation as well as propagation are likely to be important. In particular, the energy release rate as a tooth is driven into the food item is likely to be the most important factor, as teeth likely do not fracture food items in a purely elastic manner. Reaction forces and stresses may also be important.

### Mastication

In order to increase the surface area to volume ratio of a food item, foods need to be either fractured or plasti-

cally deformed, making properties related to plastic deformation and fracture important. Relatively speaking, properties related to how the material elastically deforms prior to fracture are not likely to be as important. Total energy to masticate the food item, energy exerted by the muscles, and residual stresses (internal stresses "trapped" inside a material)<sup>6</sup> in the craniofacial complex will be important. While energy exerted by the muscles and residual stresses are not directly a property of the food items, the properties of the food items will certainly affect energy exerted and the presence/absence of residual stresses. One could investigate residual stresses by performing a tension test on a food item before it has been chewed, and comparing it to a tension test from a sample taken near the fracture site after it has been chewed, as residual stresses will be present near the fracture site. An increase in Young's modulus, brittleness, or the yield stress, or a decrease in the energy absorbed by the food item would indicate a presence of residual stresses.

<sup>6</sup>Residual stresses are those that remain in a material when it is no longer being subjected to any external loading. These stresses could greatly affect the masticatory complex, causing microcracks in the enamel and bone, triggering bone remodelling, and/or desensitizing bone to external stimuli.

## Biting

All mechanical properties that are important during ingestion and some mechanical properties that are important during mastication will be important during biting, as biting can be ingestive, masticatory, or related to a non-feeding behavior. Some properties that are important during mastication will not be important during biting (i.e., those related to cyclic loading), as biting is not a cyclic process.

### An alternative classification system

Instead of using the tough/hard or stress/displacement-limited classification systems when describing mechanically challenging food items, it may be more sensible to use the brittle/ductile classification system. As mentioned before, materials can be both tough and hard, and the only difference between stress and displacement-limited food items is Young's modulus. It is impossible for a material to be both brittle and ductile. Furthermore, brittle and ductile inform us about how the food items will break down. Brittle food items will not plastically deform so they must be fractured, while ductile food items can plastically deform or fracture.

Brittle materials follow the rules of elasticity up until fracture and can be divided into two subcategories: linear and non-linear (Mai and Atkins, 1989). Once the material has been classified as brittle linear or brittle non-linear, appropriate elastic fracture mechanics equations can be applied to understand how the material fails. Furthermore, as brittle materials experience little to no yielding, the yield stress is correlated to fracture (Fig. 3), making it an invaluable mechanical property.

Ductile materials experience high levels of plastic deformation, and therefore do not follow the rules of elasticity up until fracture. Properties that govern how a material plastically deforms (e.g., fracture strain, displacement to fracture, total energy to failure) will be important during ductile fracture (as opposed to fracture of brittle materials). Therefore, selection may have acted on the masticatory complex of an animal that consumes mostly ductile food items to minimize energy expended during mastication, but this might not be true for an animal that consumes brittle food items. Other fracture mechanics equations (e.g., Elastic-Plastic Fracture Mechanics, EPFM, equations) govern fracture in ductile materials.

### The next steps

**Quantification of ingestion, biting, and mastication.** As it stands today, researchers have the infrastructure and analytical tools to get very precise information about dietary mechanical properties, but one of the biggest things lacking is information concerning the physiology of feeding, and how it varies as the extrinsic and intrinsic food properties vary. In order to address this, behavioral data needs to be gathered on ingestion, biting, and mastication in order to more precisely quantify how animals deal with food items of different sizes, shapes, and with different properties (Ungar, 1994, 1996; Yamashita, 2008; Daegling et al., 2011). This can be best done by creating a database of videos of animals consuming different types of foods, complimented by dietary property data (when possible). In addition, by comparing how wild and captive animals deal with different food items (e.g., breakdown of large vs. small food

items), we may find that we can simply carry out focal observations at local zoos and sanctuaries and do not necessarily need to perform field work to gather such data (German et al., 1989; Lucas et al., 1994; Perry and Hartstone-Rose, 2010; Hartstone-Rose et al., 2015; Perry et al., 2015). Finally, this should be accompanied by experimental data, so researchers can better test the hypotheses generated from focal observations and better investigate the relationships between these behaviours and dietary mechanical properties (Ross et al., 2009; Reed and Ross, 2010).

**Integration.** Two forms of integration need to occur to improve our understanding of feeding biomechanics. The first is to use more properties, both mechanical and non-mechanical, in conjunction with animal behavior and morphology to describe what is occurring during feeding. The second is to have a larger level of integration between food and material scientists, engineers, and anthropologists, so that people with skills from the different fields can work together to generate new ideas, questions, and hypotheses. For example, tests such as the notched four point bending test, four-point bend end-notched flexure test, and trouser tear can be added to calculate critical energy release rate, so energy release rates that are mechanical properties can also be gathered.

**Standardized data sharing.** As many researchers will be interested in the properties gained from these studies, for both comparative and meta-studies (Dominy et al., 2008; Onoda et al., 2011), the construction of a database for sharing raw data will become increasingly important. The biological community has become characterized by the sharing of large amounts of data in recent years, particularly through the use of ontologies (Grosse et al., 2005; Rockwell et al., 2008; McPherson et al., 2013; McPherson, 2014), two of the most famous being the Gene Ontology and Open Biomedical Ontologies consortiums (Ashburner et al., 2000; Smith et al., 2007).

In order for meta-analyses to produce valid results, data must be gathered in similar fashions. In terms of dietary properties, several variables describing environmental conditions that are not always reported should be included, such as temperature, rainfall, season, environment, plant part, and location (altitude, latitude, and longitude). Temperature can affect mechanical properties: materials can act more brittle in colder temperatures and more ductile in warmer temperatures [see *The Glass Transition*, in Callister (2004)]. Rainfall, season, environment, and part of the plant being tested have been shown to affect mechanical properties (Yamashita, 2003; Teaford et al., 2006; Vogel et al., 2008, 2009, 2014). Finally, latitude and longitude should be reported to consider potential regional changes in properties (Onoda et al., 2011; Kato et al., 2014).

## CONCLUSION

Scientists today are operating on a platform past researchers could only have dreamed of, and it is our responsibility to continue raising this platform for future generations. The field of dietary mechanical properties has made many great strides in the past few decades, but in order to raise that platform for future generations, we must continue to embrace new concepts and

ideas, as others have done before us. One way of doing this is by going back to materials science, critically rethinking what type of data needs to be gathered, and incorporating previously unused metrics, equations, and classification systems.

This paper has discussed some of the basic, underlying concepts of materials science and given some ideas of how they can be applied to dietary mechanical and non-mechanical properties. By incorporating these concepts into the existing toolkit, we will be able to understand more about the selective forces underlying feeding biomechanics, and may be able to answer larger questions concerning the evolution of the masticatory apparatus.

### ACKNOWLEDGMENTS

The authors thank Chris Vinyard, Erin Vogel, Ian Grosse, Robert Hyers, Elizabeth Dumont, Laurie Godfrey, David Strait, Kes Schroer, Paul Constantino, Steve King, Adam van Casteren, and Kornelius Kupczik for helpful conversations about dietary mechanical properties over the years, Kornelius Kupczik for the use of the FLS-1 Tester, Adam van Casteren for training on the FLS-1 Tester, Chris Vinyard, Kes Schroer, Ellen Schulz-Kornas, and Viviana Toro-Ibacache for their insightful comments on the manuscript, and Chris Vinyard and Trudy Turner for their help in publishing this manuscript.

### LITERATURE CITED

- Abler W. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology* 18:161–183.
- Agarwal K, Lucas P. 2002. A review: neural control of mastication in humans as influenced by food texture. *Ind J Dent Res* 13:125–134.
- Agrawal K, Lucas P, Bruce I. 2000. The effects of food fragmentation index on mandibular closing angle in human mastication. *Arch Oral Biol* 45:577–584.
- Agrawal KR, Lucas PW, Prinz JF, Bruce IC. 1997. Mechanical properties of foods responsible for resisting food breakdown in the human mouth. *Arch Oral Biol* 42:1–9.
- Agrawal KR, Lucas PW. 2003. The mechanics of the first bite. *Proc Biol Sci* 270:1277–1282.
- Alvarez SJ, Heymann EW. 2012. Brief communication: a preliminary study on the influence of physical fruit traits on fruit handling and seed fate by white-handed Titi monkeys (*Calli- cebus lugens*). *Am J Phys Anthropol* 147:482–488.
- Amstutz BE, Sutton MA, Dawicke DS, Newman JC. 1995. An experimental study of CTOD for Mode I/ModeII stable crack growth in thin 2024-T3 aluminum specimens. In: Reuter WG, Underwood JH, Newman JC, editors. *Fracture Mechanics*, Volume 26. Philadelphia: ASTM International. p 834.
- Anderson PSL, LaBarbera M. 2008. Functional consequences of tooth design: effects of blade shape on energetics of cutting. *J Exp Biol* 211:3619–3626.
- Anderson PSL. 2009. The effects of trapping and blade angle of notched dentitions on fracture of biological tissues. *J Exp Biol* 212:3627–3632.
- Ang KY, Lucas PW, Tan HTW. 2006. Incisal orientation and biting efficiency. *J Hum Evol* 50:663–672.
- Ang KY, Lucas PW, Tan HTW. 2008. Novel way of measuring the fracture toughness of leaves and other thin films using a single inclined razor blade. *New Phytol* 177:830–837.
- Ashburner M, Ball CA, Blake JA, Botstein D, Butler H, Cherry JM, Davis AP, Dolinski K, Dwight SS, Eppig JT, Harris MA, Hill DP, Issel-Tarver L, Kasarskis A, Lewis S, Matese JC, Richardson JE, Ringwald M, Rubin GM, Sherlock G. 2000. Gene ontology: tool for the unification of biology. The Gene Ontology Consortium. *Nat Genet* 25:25–29.
- Ashby M. 1992. *Materials selection in mechanical design*. Oxford: Pergamon Press.
- Ashman RB. 1988. Elastic modulus of trabecular bone material. *J Biomech* 21:177–181.
- Atkins AG, Mai YW. 1979. On the guillotining of materials. *J Mater Sci* 14:2747–2754.
- Atkins AG, Mai YW. 1985. *Elastic and plastic fracture: metals, polymers, ceramics, composites, biological materials*. West Sussex, England, England: Ellis Horwood; Halsted Press.
- Atkins AG, Vincent JFV. 1984. An instrumented microtome for improved histological sections and the measurement of fracture toughness. *J Mater Sci Lett* 3:310–312.
- Balsamo RA, Bauer AM, Davis SD, Rice BM. 2003. Leaf biomechanics, morphology, and anatomy of the deciduous mesophyte *Prunus serrulata* (Rosaceae) and the evergreen sclerophyllous shrub *Heteromeles arbutifolia* (Rosaceae). *Am J Bot* 90:72–77.
- Barnett AA, Santons PJP, Boyle SA, Bezerra BM. 2015. An improved technique using dental prostheses for field quantification of the force required by primates for the dental penetration of fruit. *Folia Primatol* 86:398–410.
- Beer FP, Johnston ER, DeWolf JT. 2006. *Mechanics of materials*, 4th ed. New York, NY: McGraw-Hill.
- Benedict JV, Walker LB, Harris EH. 1968. Stress-strain characteristics and tensile strength of unembalmed human tendon. *J Biomech* 1:53–63.
- Berthaume M, Grosse IR, Patel ND, Strait DS, Wood S, Richmond BG. 2010. The effect of early hominin occlusal morphology on the fracturing of hard food items. *Anat Rec* 293: 594–606.
- Berthaume MA, Dechow PC, Iriarte-Diaz J, Ross CF, Strait DS, Wang Q, Grosse IR. 2012. Probabilistic finite element analysis of a craniofacial finite element model. *J Theor Biol* 300:242–253.
- Berthaume MA, Dumont ER, Godfrey LR, Grosse IR. 2013. How does tooth cusp radius of curvature affect brittle food item processing? *J R Soc Interface* 10:20130240.
- Berthaume MA, Dumont ER, Godfrey LR, Grosse IR. 2014. The effects of relative food item size on optimal tooth cusps sharpness during brittle food item processing. *J R Soc Interface* 11: 20140965.
- Berthaume MA. 2013. Tooth cusp radius of curvature as a dietary correlate in primates. Dr Diss Available from Proquest 1–184.
- Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other eurchontan mammals. *J Hum Evol* 55:1118–1137.
- Brainerd EL, Baier DB, Gatesy SM, Hedrick TL, Metzger KA, Gilbert SL, Crisco JJ. 2010. X-ray reconstruction of moving morphology (XROMM): precision, accuracy and applications in comparative biomechanics research. *J Exp Zool A Ecol Genet Physiol* 313:262–279.
- Bunn JM, Boyer DM, Lipman Y, St Clair EM, Jernvall J, Daubechies I. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. *Am J Phys Anthropol* 145:247–261.
- Burrows AM, Hartstone-Rose A, Nash LT. 2015. Exudativory in the Asian loris, *Nycticebus*: evolutionary divergence in the toothcomb and M3. 158:663–672.
- Callister WD. 2004. *Fundamentals of Materials Science and Engineering: An integrated approach*. Second. New York: John Wiley & Sons.
- Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci U S A* 108:9337–41.
- Chanthasopeephan T, Desai JP, Lau ACW. 2006. Determining Fracture Characteristics in Scalpel Cutting of Soft Tissue. In: *The First IEEE/RAS-EMBS International Conference on Biomedical Robotics and Biomechatronics*, 2006. *BioRob* 2006. IEEE. p 899–904.

- Choong M, Lucas P, Ong J, Pereira B, Tan H, Turner I. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytol* 121:597–610.
- Chung DH, Dechow PC. 2011. Elastic anisotropy and off-axis ultrasonic velocity distribution in human cortical bone. *J Anat* 218:26–39.
- Clauss M, Lechner-Doll M, Streich J. 2002. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. *Oecologia* 131:343–349.
- Clauss M, Steuer P, Erlinghagen-Lückerath K, Kaandorp J, Fritz J, Südekum K-H, Hummel J. 2015. Faecal particle size: digestive physiology meets herbivore diversity. *Comp Biochem Physiol A Mol Integr Physiol* 179:182–191.
- Claverie T, Chan E, Patek SN. 2011. Modularity and scaling in fast movements: power amplification in mantis shrimp. *Evolution* 65:443–461.
- Constantino P, Wood B. 2007. The Evolution of *Zinjanthropus boisei*. *Evol Anthropol Issues, News, Rev* 16:49–62.
- Courtney TH. 2005. *Mechanical behavior of materials*, 2nd ed. Long Grove, IL: Waveland Press, Inc.
- Crofts SB, Summers AP. 2014. How to best smash a snail: the effect of tooth shape on crushing load. *J R Soc Interface* 11:20131053.
- Cuozzo FP, Sauter ML. 2012. What is dental ecology? *Am J Phys Anthropol* 148:163–170.
- Currey JD, Butler G. 1975. The mechanical properties of bone tissue in children. *J Bone Joint Surg Am* 57:810–814.
- Currey JD. 2006. *Bones: structure and mechanics*. Princeton, N.J.: Princeton University Press. p 436.
- Currey JD. 2008. Bioceramics and their clinical applications. In: Kokubo T, editor. Boca Raton, FL: CRC Press LLC. p 760.
- Daegling DJ, Judex S, Ozcivici E, Ravosa MJ, Taylor AB, Grine FE, Teaford MF, Ungar PS. 2013. Viewpoints: feeding mechanics, diet, and dietary adaptations in early hominins. *Am J Phys Anthropol* 151:356–371.
- Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PLoS One* 6:e23095.
- Darvell BW, Lee PKD, Yuen TDB, Lucas PW. 1996. A portable fracture toughness tester for biological materials. *Meas Sci Technol* 7:954–962.
- Davis JL, Dumont ER, Strait DS, Grosse IR. 2011. An efficient method of modeling material properties using a thermal diffusion analogy: an example based on craniofacial bone. *PLoS One* 6:e17004.
- Davis JL, Santana SE, Dumont ER, Grosse IR. 2010. Predicting bite force in mammals: two-dimensional versus three-dimensional lever models. *J Exp Biol* 213:1844–1851.
- Dechow PC, Wang Q, Peterson J. 2010. Edentulation alters material properties of cortical bone in the human craniofacial skeleton: functional implications for craniofacial structure in primate evolution. *Anat Rec* 293:618–629.
- Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol Biol* 35:159–175.
- Dumont ER, Dávalos LM, Goldberg A, Santana SE, Rex K, Voigt CC. 2012. Morphological innovation, diversification and invasion of a new adaptive zone. *Proc Biol Sci* 279:1797–1805.
- Dumont ER, Grosse IR, Slater GJ. 2009. Requirements for comparing the performance of finite element models of biological structures. *J Theor Biol* 256:96–103.
- Dumont ER, Herrel A. 2003. The effects of gape angle and bite point on bite force in bats. *J Exp Biol* 206:2117–2123.
- Dumont ER, Piccirillo J, Grosse IR. 2005. Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats. *Anat Rec a Discov Mol Cell Evol Biol* 283:319–330.
- Dumont ER, Ryan TM, Godfrey LR. 2011. The Hadropithecus conundrum reconsidered, with implications for interpreting diet in fossil hominins. *Proc Biol Sci* 278:3654–3661.
- Dunn ML, Suwito W, Cunningham S, May CW. 1997. Fracture initiation at sharp notches under mode I, mode II, and mixed mode loading. *Int J Fract* 84:367–381.
- Dzialo C, Wood SA, Berthaume M, Smith A, Dumont ER, Benazzi S, Weber GW, Strait DS, Grosse IR. 2013. Functional implications of squamosal suture size in *paranthropus boisei*. *Am J Phys Anthropol* 298:145–167.
- Elgart-Berry A. 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. *Am J Primatol* 62:275–285.
- Eng CM, Ward SR, Vinyard CJ, Taylor AB. 2009. The morphology of the masticatory apparatus facilitates muscle force production at wide jaw gapes in tree-gouging common marmosets (*Callithrix jacchus*). *J Exp Biol* 212:4040–4055.
- Evans AR, Sanson GD. 1998. The effect of tooth shape on the breakdown of insects. *J Zool* 246:391–400.
- Freeman PW, Lemen Ca. 2007a. The trade-off between tooth strength and tooth penetration: predicting optimal shape of canine teeth. *J Zool* 273:273–280.
- Freeman PW, Lemen CA. 2007b. Using scissors to quantify hardness of insects: do bats select for size or hardness? *J Zool* 271:469–476.
- Fritz J, Kienzle E, Hummel J, Arnold C, Nunn C, Clauss M. 2009. Comparative chewing efficiency in mammalian herbivores. *Oikos* 118:1623–1632.
- Frolich LM, LaBarbera M, Stevens WP. 1994. Poisson's ratio of a crossed fibre sheath: the skin of aquatic salamanders. *J Zool* 232:231–252.
- German RZ, Saxe SA, Crompton AW, Hiiemae KM. 1989. Food transport through the anterior oral cavity in macaques. *Am J Phys Anthropol* 80:369–377.
- Godfrey LR, Crowley BE, Muldoon KM, Kelley EA, King SJ, Berthaume MA. 2015. What did Hadropithecus eat, and why should paleoanthropologists care? *Am J Primatol*.
- Goh SM, Charalambides MN, Williams JG. 2005. On the mechanics of wire cutting of cheese. *Eng Fract Mech* 72:931–946.
- Grosse IR, Dumont ER, Coletta C, Tolleson A. 2007. Techniques for modeling muscle-induced forces in finite element models of skeletal structures. *Anat Rec (Hoboken)* 290:1069–1088.
- Grosse IR, Milton-Benoit JM, Wileden JC. 2005. Ontologies for supporting engineering analysis models. *AI EDAM* 19:1–18.
- Gutiérrez-Rodríguez E, Lieth HJ, Jernstedt JA, Labavitch JM, Suslov TV, Cantwell MI. 2013. Texture, composition and anatomy of spinach leaves in relation to nitrogen fertilization. *J Sci Food Agric* 93:227–237.
- Harrison SK. 2006. Comparison of shear modulus test methods (Masters thesis).
- Hartstone-Rose A, Parkinson JA, Criste T, Perry JMG. 2015. Brief communication: Comparing apples and oranges—the influence of food mechanical properties on ingestive bite sizes in lemurs. *Am J Phys Anthropol*.
- Head JS, Boesch C, Makaga L, Robbins MM. 2011. Sympatric Chimpanzees (Pan troglodytes troglodytes) and Gorillas (Gorilla gorilla gorilla) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. *Int J Primatol* 32:755–775.
- Herrel A, Podos J, Huber SK, Hendry AP. 2005. Evolution of bite force in Darwin's finches: a key role for head width. *J Evol Biol* 18:669–675.
- Herring S, Herring S. 1974. The superficial masseter and gape in mammals. *Am Nat* 57:1–576.
- Hiiemae KM. 1967. Masticatory function in mammals. *J Dent Res* 46:883–893.
- Hiiemae KM. 2000. Feeding in mammals. In: Schwenk K, editor. *Feeding: Form, function and evolution in tetrapod vertebrates*. San Diego: Academic Press. p 411–448.
- Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) in Yakushima. *Am J Primatol* 38:221–231.
- Hussain MA, Pu SL, Underwood J. 1974. Strain energy release rate for a crack under combined Mode I and Mode II. In: *Materials AS for T and, editor. Fracture Analysis, ASTM STP* 560. p 2–28.

- Hylander W. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science* (80-) 189:1095–1098.
- Kamyab I, Chakrabarti S, Williams JG. 1998. Cutting cheese with wire. *J Mater Sci* 33:2763–2770.
- Kato A, Tang N, Borries C, Papakyrikos AM, Hinde K, Miller E, Kunimatsu Y, Hirasaki E, Shimizu D, Smith TM. 2014. Intra- and interspecific variation in macaque molar enamel thickness. *Am J Phys Anthropol*.
- Kay RF. 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55:141–151.
- Kendall K, Fuller KNG. 1987. J-shaped stress/strain curves and crack resistance of biological materials. *J Phys D Appl Phys* 20:1596–1600.
- Khan AA, Vincent JFV. 1993. Anisotropy in the fracture properties of apple flesh as investigated by crack-opening tests. *J Mater Sci* 28:45–51.
- Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am J Phys Anthropol* 81:5–15.
- Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by Pithecia and Chiropotes in Surinam and Venezuela. *Int J Primatol* 14:207–227.
- Kitajima K, Poorter L. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytol* 186:708–721.
- Koops K, McGrew WC, Matsuzawa T. 2010. Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treculia africana* fruits? Preliminary data on a new form of percussive technology. *Primates* 51:175–178.
- Koops K, Visalberghi E, van Schaik CP. 2014. The ecology of primate material culture. *Biol Lett* 10:20140508.
- Kunzek H, Kabbert R, Gloyna D. 1999. Aspects of material science in food processing: changes in plant cell walls of fruits and vegetables. *Zeitschrift Für Leb und -Forsch a* 208:233–250.
- Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am J Phys Anthropol* 125:363–368.
- Lambert JE. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *Am J Phys Anthropol* 109:365–386.
- Lawn BR, Lee JJ-W, Constantino PJ, Lucas PW. 2009. Predicting failure in mammalian enamel. *J Mech Behav Biomed Mater* 2:33–42.
- Lee JJ-W, Morris D, Constantino PJ, Lucas PW, Smith TM, Lawn BR, Lee JJ-W, Lucas PW, Morris D, Smith TM. 2010. Properties of tooth enamel in great apes. *Acta Biomater* 6: 4560–4565.
- Lees C, Vincent JF, Hillerton JE. 1991. Poisson's ratio in skin. *Biomed Mater Eng* 1:19–23.
- Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee PK, Osorio D, Ramsden L, Yamashita N, Yuen TD. 2001. Field kit to characterize physical, chemical and spatial aspects of potential primate foods. *Folia Primatol (Basel)* 72: 11–25.
- Lucas PW, Casteren A, van Al-Fadhlah K, Almusallam AS, Henry AG, Michael S, Watzke J, Reed DA, Diekwisch TGH, Strait DS, Atkins AG. 2014. The role of dust, grit and phytoliths in tooth wear. *Ann Zool Fennici* 51:143–152.
- Lucas PW, Choong MF, Tan HTW, Turner IM, Berrick AJ. 1991. The fracture toughness of the leaf of the dicotyledon *calophyllum inophyllum* L. (Guttiferae). *Philos Trans R Soc B Biol Sci* 334:95–106.
- Lucas PW, Constantino PJ, Chalk J, Ziscovici C, Wright BW, Fragaszy DM, Hill DA, Lee JJ-W, Chai H, Darvell BW, Lee PKD, Yuen TDB. 2009. Indentation as a technique to assess the mechanical properties of fallback foods. *Am J Phys Anthropol* 140:643–652.
- Lucas PW, Copes L, Constantino PJ, Vogel ER, Chalk J, Talebi M, Landis M, Wagner M. 2011. Measuring the toughness of primate foods and its ecological value. *Int J Primatol* 33:598–610.
- Lucas PW, Luke DA. 1984. Chewing it over: basic principles of food breakdown. Eds. Chivers DA, Wood BA, Bilsborough A. New York, NY: Plenum Press. p. 283–301.
- Lucas PW, Oates CG, Lee WP. 1993. Fracture toughness of mung bean gels. *J Mater Sci* 28:1137–1142.
- Lucas PW, Omar R, Al-Fadhlah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Strait DS, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J R Soc Interface* 10:20120923.
- Lucas PW, Pereira B. 1990. Estimation of the fracture toughness of leaves. *Funct Ecol* 4:819.
- Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orang-utans with their teeth in captivity and a new technique for estimating forces produced in the wild. *Am J Phys Anthropol* 94:365–378.
- Lucas PW, Tan HTW, Cheng PY. 1997. The toughness of secondary cell wall and woody tissue. *Philos Trans R Soc B Biol Sci* 352:341–352.
- Lucas PW, Teaford MF. 1994. Colobine monkeys: their ecology, behaviour and evolution. In: Davies G, Oates J, editors. Colobine monkeys: their ecology, behaviour, and evolution, Vol. 24. Cambridge: Cambridge University Press. p 173–203.
- Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000. Mechanical Defences to Herbivory. *Ann Bot* 86:913–920.
- Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press.
- Lusk CH, Onoda Y, Kooymann R, Gutiérrez-Girón A. 2010. Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *New Phytol* 186:429–438.
- Mai Y-W, Atkins AG. 1989. Further comments on J-shaped stress-strain curves and the crack resistance of biological materials. *J Phys D Appl Phys* 22:48–54.
- Marlowe F. 2010. The Hadza: Hunter-gatherers of Tanzania. Berkeley and Los Angeles, CA: University of California Press.
- Martin L. 2003. Enamel thickness and microstructure in pitheciid primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. *J Hum Evol* 45: 351–367.
- Martin RB, Burr DB, Sharkey NA. 1998. Skeletal tissue mechanics. New York, NY: Springer New York.
- McPherson J. 2014. Towards Accessible, Usable Knowledge Frameworks in Engineering. Masters Theses 1896 - Febr 2014.
- McPherson JD, Grosse IR, Krishnamurty S, Wileden JC, Dumont ER, Berthaume MA. 2013. Integrating Biological and Engineering Ontologies. In: Volume 2B: 33rd Computers and Information in Engineering Conference. ASME. p V02BT02A022.
- Müller J, Clauss M, Codron D, Schulz E, Hummel J, Fortelius M, Kircher P, Hatt J-M. 2014. Growth and wear of incisor and cheek teeth in domestic rabbits (*Oryctolagus cuniculus*) fed diets of different abrasiveness. *J Exp Zool A Ecol Genet Physiol* 321:283–298.
- Müller J, Clauss M, Codron D, Schulz E, Hummel J, Kircher P, Hatt J-M. 2015. Tooth length and incisal wear and growth in guinea pigs (*Cavia porcellus*) fed diets of different abrasiveness. *J Anim Physiol Anim Nutr (Berl)* 99:591–604.
- Norconk MA, Conklin-Brittain NL. 2015. Bearded saki feeding strategies on an island in Lago Guri, Venezuela. *Am J Primatol*.
- Norconk MA, Veres M. 2011. Physical properties of fruit and seeds ingested by primate seed predators with emphasis on sakis and bearded sakis. *Anat Rec (Hoboken)* 294:2092–2111.
- Norconk MA, Wright BW, Conklin-Brittain N Lou, Vinyard CJ. 2009a. Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: South American primates developments in primatology: progress and prospects. New York: Springer. p 279–319.

- Norconk MA, Wright BW, Conklin-Brittain NL, Vinyard CJ. 2009b. South American primates. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. South American primates. New York, NY: Springer New York. p 279–319.
- Onoda Y, Westoby M, Adler PB, Choong AMF, Clissold FJ, Cornelissen JHC, Díaz S, Dominy NJ, Elgart A, Enrico L, Fine PVA, Howard JJ, Jalili A, Kitajima K, Kurokawa H, McArthur C, Lucas PW, Markesteijn L, Pérez-Harguindeguy N, Poorter L, Richards L, Santiago LS, Sosinski EE, Van Bael SA, Warton DI, Wright IJ, Wright SJ, Yamashita N. 2011. Global patterns of leaf mechanical properties. *Ecol Lett* 14: 301–312.
- Perry JMG, Bastian ML, St Clair E, Hartstone-Rose A. 2015. Maximum ingested food size in captive anthropoids. *Am J Phys Anthropol* 158:92–104.
- Perry JMG, Hartstone-Rose A. 2010. Maximum ingested food size in captive strepsirrhine primates: scaling and the effects of diet. *Am J Phys Anthropol* 142:625–635.
- Peterson J, Dechow PC. 2002. Material properties of the inner and outer cortical tables of the human parietal bone. *Anat Rec* 268:7–15.
- Peterson J, Dechow PC. 2003. Material properties of the human cranial vault and zygoma. *Anat Rec A Discov Mol Cell Evol Biol* 274:785–797.
- Peterson J, Wang Q, Dechow PC. 2006. Material properties of the dentate maxilla. *Anat Rec A Discov Mol Cell Evol Biol* 288:962–972.
- Pontzer H, Scott JR, Lordkipanidze D, Ungar PS. 2011. Dental microwear texture analysis and diet in the *Dmanisi hominins*. *J Hum Evol* 61:683–687.
- Quyet LK, Duc NA, Tai VA, Wright BW, Covert HH. 2007. Diet of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in the Khau Ca area, Ha Giang Province, Northeastern Vietnam. *Vietnamese J Primatol* 1:75–83.
- Reed DA, Ross CF. 2010. The influence of food material properties on jaw kinematics in the primate, *Cebus*. *Arch Oral Biol* 55:946–962.
- Rho JY, Ashman RB, Turner CH. 1993. Young's modulus of trabecular and cortical bone material: ultrasonic and microtensile measurements. *J Biomech* 26:111–119.
- Rho JY, Hobatho MC, Ashman RB. 1995. Relations of mechanical properties to density and CT numbers in human bone. *Med Eng Phys* 17:347–355.
- Rockwell JA, Witherell P, Fernandes R, Grosse I, Krishnamurty S, Wileden J. 2008. A Web-Based Environment for Documentation and Sharing of Engineering Design Knowledge. In: Volume 3: 28th Computers and Information in Engineering Conference, Parts A and B. ASME. p 671–683.
- Ross CF, Washington RL, Eckhardt A, Reed DA, Vogel ER, Dominy NJ, Machanda ZP. 2009. Ecological consequences of scaling of chew cycle duration and daily feeding time in primates. *J Hum Evol* 56:570–585.
- Roylance D. 2001a. Introduction to Fracture Mechanics. In: Press M, editor. Cambridge, MA, MA.
- Roylance D. 2001b. Stress-strain curves. In: Press M, editor. Cambridge, MA, MA.
- Sanson G, Read J, Aranwela N, Clissold F, Peeters P. 2001. Measurement of leaf biomechanical properties in studies of herbivory: opportunities, problems and procedures. *Austral Ecol* 26:535–546.
- Santana SE, Grosse IR, Dumont ER. 2012. Dietary hardness, loading behavior, and the evolution of skull form in bats. *Evolution* 66:2587–2598.
- Serrat MA, Vinyard CJ, King D. 2007. Alterations in the mechanical properties and composition of skin in human growth hormone transgenic mice. *Connect Tissue Res* 48:19–26.
- Shi YW, Zhou NN, Zhang JX. 1994. Comparison of mode I and mode II elastic-plastic fracture toughness for two low alloyed high strength steels. *Int J Fract* 68:89–97.
- Smith AL, Benazzi S, Ledogar JA, Tamvada K, Smith LCP, Weber GW, Spencer MA, Lucas PW, Michael S, Shekeban A, Al-Fadhalah K, Almusallam AS, Dechow PC, Grosse IR, Ross CF, Madden RH, Richmond BG, Wright BW, Wang Q, Byron C, Slice DE, Wood SA, Dzialo C, Berthaume MA, van Casteren A, Strait DS. 2015. The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *Anat Rec* 298:145–167.
- Smith B, Ashburner M, Rosse C, Bard J, Bug W, Ceusters W, Goldberg LJ, Eilbeck K, Ireland A, Mungall CJ, Leontis N, Rocca-Serra P, Ruttenberg A, Sansone S-A, Scheuermann RH, Shah N, Whetzel PL, Lewis S. 2007. The OBO Foundry: coordinated evolution of ontologies to support biomedical data integration. *Nat Biotechnol* 25:1251–1255.
- Strait DS, Constantino P, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA, Weber GW, Wang Q, Byron C, Slice DE, Chalk J, Smith AL, Smith LC, Wood S, Berthaume M, Benazzi S, Dzialo C, Tamvada K, Ledogar JA. 2013. Viewpoints: diet and dietary adaptations in early hominins: the hard food perspective. *Am J Phys Anthropol* 151:339–355.
- Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA. 2005. Modeling elastic properties in finite-element analysis: how much precision is needed to produce an accurate model? *Anat Rec A Discov Mol Cell Evol Biol* 283:275–287.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, Grosse IR, Wright BW, Constantino P, Wood BA, Lawn B, Hylander WL, Wang Q, Byron C, Slice DE, Smith AL. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci U S A* 106:2124–2129.
- Strait SG, Vincent JFV. 1998. Primate faunivores: physical properties of prey items. *Int J Primatol* 19:867–878.
- Strait SG. 1997. Tooth use and the physical properties of food. *Evol Anthropol Issues, News, Rev* 5:199–211.
- Sui Z, Agrawal KR, Corke H, Lucas PW. 2006. Biting efficiency in relation to incisal angulation. *Arch Oral Biol* 51:491–497.
- Sun CT, Jin Z-H. 2012. Fracture mechanics, 1st ed. Oxford: Elsevier.
- Taniguchi H. 2015. How the physical properties of food influence its selection by infant Japanese macaques inhabiting a snow-covered area. *Am J Primatol* 77:285–295.
- Taylor AB, Vinyard CJ. 2009. Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. *J Hum Evol* 57:710–720.
- Taylor AB, Vogel ER, Dominy NJ. 2008. Food material properties and mandibular load resistance abilities in large-bodied hominoids. *J Hum Evol* 55:604–616.
- Teaford MFF, Lucas PWW, Ungar PSS, Glander KEE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). *Am J Phys Anthropol* 129:99–104.
- Thompson CL, Donley EM, Stimpson CD, Horne WI, Vinyard CJ. 2011. The influence of experimental manipulations on chewing speed during in vivo laboratory research in tufted capuchins (*Cebus apella*). *Am J Phys Anthropol* 145:402–414.
- Thompson CL, Valença-Montenegro MM, Melo LCoD, Valle YBM, Oliveira MABd, Lucas PW, Vinyard CJ. 2014. Accessing foods can exert multiple distinct, and potentially competing, selective pressures on feeding in common marmoset monkeys. *J Zool* 294:161–169.
- Turner CH, Burr DB. 1993. Basic biomechanical measurements of bone: a tutorial. *Bone* 14:595–608.
- Ugural AC, Fenster SK. 2003. Advanced strength and applied elasticity, 4th ed. Upper Saddle River, New Jersey: Prentice Hall PTR.
- Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS One* 3:e2044-
- Ungar PS. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. *Am J Phys Anthropol* 95:197–219.
- Ungar PS. 1996. Relationship of incisor size to diet and anterior tooth use in sympatric sumatran anthropoids. *Am J Primatol* 38:145–156.

- Ungar PS. 2011. Dental evidence for the diets of Pliocene hominins. *Am J Phys Anthropol* 146 (Suppl 53): 47–62.
- Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). *Am J Phys Anthropol* 155:17–32.
- Vincent JFV, Jeronimidis G, Khan AA, Luyten H. 1991. The wedge fracture test a new method of for measurement of food texture. *J Texture Stud* 22:45–57.
- Vinyard CJ, Wall CE, Williams SH, Johnson KR, Hylander WL. 2006. Masseter electromyography during chewing in ring-tailed lemurs (*Lemur catta*). *Am J Phys Anthropol* 130:85–95.
- Visalberghi E, Sabbatini G, Spagnoletti N, Andrade FRD, Ottoni E, Izar P, Fragaszy D. 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *Am J Primatol* 70:884–891.
- Vogel ER, Haag L, Mitra-Setia T, van Schaik CP, Dominy NJ. 2009. Foraging and ranging behavior during a fallback episode: *hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *Am J Phys Anthropol* 140:716–726.
- Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: pan troglodytes *schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol* 55:60–74.
- Vogel ER, Zulfa A, Hardus M, Wich SA, Dominy NJ, Taylor AB. 2014. Food mechanical properties, feeding ecology, and the mandibular morphology of wild orangutans. *J Hum Evol* 75: 110–124.
- Wang CHH. 1996. Introduction to fracture mechanics. Melbourne: DSTO Aeronautical and Maritime Research Laboratory.
- Wang Q, Strait DS, Dechow PC. 2006. A comparison of cortical elastic properties in the craniofacial skeletons of three primate species and its relevance to the study of human evolution. *J Hum Evol* 51:375–382.
- Westbrook JW, Kitajima K, Burleigh JG, Kress WJ, Erickson DL, Wright SJ. 2011. What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant woody species in a neotropical forest. *Am Nat* 177:800–811.
- Wich SA. 2009. Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press.
- Wieczkowski J. 2009. Brief communication: puncture and crushing resistance scores of Tana river mangabey (*Cercocebus galeritus*) diet items. *Am J Phys Anthropol* 140:572–577.
- Williams SH, Wright BW, Truong V, den, Daubert CR Vinyard CJ. 2005. Mechanical properties of foods used in experimental studies of primate masticatory function. *Am J Primatol* 67: 329–346.
- Winchester JM, Boyer DM, St Clair EM, Gosselin-Ildari AD, Cooke SB, Ledogar JA. 2014. Dental topography of platyrrhines and prosimians: convergence and contrasts. *Am J Phys Anthropol* 153:29–44.
- Wood B, Schroer K. 2012. Reconstructing the diet of an extinct hominin taxon: the role of extant primate models. *Int J Primatol* 33:716–742.
- Wrangham RW, Conklin NL, Chapman CA, Hunt KD, Milton K, Rogers E, Whiten A, Barton RA. 1991. The significance of fibrous foods for kibale forest chimpanzees. *Philos Trans R Soc B Biol Sci* 334:171–178; discussion 178.
- Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodhan R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. *Int J Primatol* 29:1455–1466.
- Wright BW, Wright KA, Chalk J, Verderane MP, Fragaszy D, Visalberghi E, Izar P, Ottoni EB, Constantino P, Vinyard C. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. *Am J Phys Anthropol* 140:687–699.
- Wright W, Vincent JFV. 1996. Herbivory and the mechanics of fracture in plants. *Biol Rev* 71:401–413.
- Yamashita N, Vinyard CJ, Tan CL. 2009. Food mechanical properties in three sympatric species of Hapalemur in Ranomafana National Park, Madagascar. *Am J Phys Anthropol* 139: 368–381.
- Yamashita N. 1998. Functional dental correlates of food properties in five Malagasy lemur species. *Am J Phys Anthropol* 106:169–188.
- Yamashita N. 2002. Diets of two lemur species in different microhabitats in beza mahafaly special reserve, Madagascar. *Int J Primatol* 23:1025–1051.
- Yamashita N. 2003. Food procurement and tooth use in two sympatric lemur species. *Am J Phys Anthropol* 121:125–133.
- Yamashita N. 2008. Food physical properties and their relationship to morphology: the curious case of kily. In: Vinyard C, Ravosa MJ, Wall C, editors. Primate craniofacial function and biology. New York, NY: Kluwer Academic Press. p 387–446.
- Zack TI, Claverie T, Patek SN. 2009. Elastic energy storage in the mantis shrimp's fast predatory strike. *J Exp Biol* 212: 4002–4009.
- Zink KD, Lieberman DE, Lucas PW. 2014. Food material properties and early hominin processing techniques. *J Hum Evol* 77:155–166.
- Ziopoulos P. 2001. Ageing human bone: factors affecting its biomechanical properties and the role of collagen. *J Biomater Appl* 15:187–229.
- Ziscovici C, Lucas PW, Constantino PJ, Bromage TG, van Casteren A. 2014. Sea otter dental enamel is highly resistant to chipping due to its microstructure. *Biol Lett* 10:20140484.