

Marshall University
Marshall Digital Scholar

Biological Sciences Faculty Research

Biological Sciences

4-20-2011

Fracture in teeth—a diagnostic for inferring bite force and tooth function

Paul J. Constantino

Biological Sciences, paulconstantino@gmail.com

Brian R. Lawn

James J.-W. Lee

Peter W. Lucas

Follow this and additional works at: http://mds.marshall.edu/bio_sciences_faculty

 Part of the [Animal Structures Commons](#), [Biological and Physical Anthropology Commons](#), [Biology Commons](#), and the [Dentistry Commons](#)

Recommended Citation

Lee JJ-W, Constantino PJ, Lucas PW, Lawn BR. Fracture in teeth – a diagnostic for inferring tooth function and diet. *Biological Reviews* 86: 959-974.

This Article is brought to you for free and open access by the Biological Sciences at Marshall Digital Scholar. It has been accepted for inclusion in Biological Sciences Faculty Research by an authorized administrator of Marshall Digital Scholar. For more information, please contact zhangj@marshall.edu.

Fracture in teeth—a diagnostic for inferring bite force and tooth function

James J.-W. Lee^{1*}, Paul J. Constantino^{2,3}, Peter W. Lucas², and Brian R. Lawn^{1,2}

¹ *Ceramics Division, National Institute of Standards and Technology, Gaithersburg, MD 20899, USA*

² *Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC 20052, USA*

³ *Department of Biology, Marshall University, Huntington, WV 25755, USA*

ABSTRACT

Teeth are brittle and highly susceptible to cracking. We propose that observations of such cracking can be used as a diagnostic tool for predicting bite force and inferring tooth function in living and fossil mammals. Laboratory tests on model tooth structures and extracted human teeth in simulated biting identify the principal fracture modes in enamel. Examination of museum specimens reveals the presence of similar fractures in a wide range of vertebrates, suggesting that cracks extended during ingestion or mastication. The use of ‘fracture mechanics’ from materials engineering provides elegant relations for quantifying critical bite forces in terms of characteristic tooth size and enamel thickness. The role of enamel microstructure in determining how cracks initiate and propagate within the enamel (and beyond) is discussed. The picture emerges of teeth as damage-tolerant structures, full of internal weaknesses and defects and yet able to contain the expansion of seemingly precarious cracks and fissures within the enamel shell. How the findings impact on dietary pressures forms an undercurrent of the study.

Key words: bite force, cracks, hominins, primates, teeth.

CONTENTS

I. Introduction	960
II. Observations of crack patterns in teeth	961
(1) Cracks in teeth from simulated bite tests	961
(2) Natural cracks in teeth	963
III. Fracture mechanics and bite forces	965
(1) Basic fracture mechanics	965
(2) Tooth models and fracture relations	966
(3) Predictions of critical fracture loads for different species	967
IV. Role of enamel microstructure	968
(1) Sources of crack initiation	968
(2) Inhibition of crack propagation	969
V. Discussion of fracture observations	969
VI. Implications in ecology and evolution	970
VII. Conclusions	972
VIII. Acknowledgements	972
IX. References	972

* Address for correspondence (E-mail: james.lee@nist.gov).

I. INTRODUCTION

Teeth are crucial to the survival of most mammals (DeGusta, Everett & Milton, 2003; King *et al.*, 2005). They can make many thousands of contacts each day, placing tooth surfaces under stringent, continual pressure. They have to be able to withstand contact forces ranging from milli-Newtons (10^{-3} N) to kilo-Newtons (10^3 N) (Lawn & Lee, 2009; Lee *et al.*, 2010; Wroe *et al.*, 2010; Constantino *et al.*, in press) and yet generate sufficient load to break down food objects—some quite hard and tough—without themselves suffering from excessive damage accumulation (Lucas, 2004; Berthaume *et al.*, 2010). Tooth morphology can tell us a great deal about the forces generated during eating (Lucas *et al.*, 2008) and, by extension, the types of foods that individuals eat (Kay, 1981; Janis & Fortelius, 1988; Maas & Dumont, 1999; Lucas, 2004; Lucas *et al.*, 2008). Bite forces inevitably depend on such characteristic morphological dimensions as tooth size and enamel thickness (Molnar & Gantt, 1977; Martin, 1985; Demes & Creel, 1988; Shellis *et al.*, 1998; Schwartz, 2000; Kono, Suwa & Tanijiri, 2002; Smith *et al.*, 2005; Olejniczak *et al.*, 2008). Recent studies on the postcanine teeth of primates (Lee *et al.*, 2010) and sea otters (*Enhydra lutris*) (Constantino *et al.*, in press) are helping to quantify these dependencies. Bite forces are also an important quantitative end product of jaw mechanics, taking into account the musculature and bony support of the skull. Such forces have been evaluated from skull structures of a broad range of living and fossil species (Crompton & Parkyn, 1963; Greaves, 1978; Kiltie, 1982; Demes & Creel, 1988; Thomason, 1991; Spencer, 1998; Rayfield *et al.*, 2001; Wroe *et al.*, 2010). However, estimates from jaw mechanics are limited—they pay little attention to actual tooth properties and require access to well-preserved crania. Teeth are the hardest of all animal tissues and consequently the most enduring in the fossil record. But despite their durability, they are susceptible to damage accumulation through a lifetime of mechanical function. Consequently, much attention has been given to signature damage patterns on teeth in the fossil record, specifically in relation to dietary history. A better understanding of tooth mechanics could reveal valuable clues to our evolutionary past.

Of the various kinds of damage that teeth can sustain, perhaps none has received more attention than that of wear (Grine, 1981; Janis & Fortelius, 1988; Teaford, 1988; Ungar, 1990; Fortelius & Solounias, 2000; Teaford & Ungar, 2000). Microwear results from repeated scratching with small, μm -scale (10^{-6} m) hard silicate crystallites in plant matter (Piperno, 2006) or in the soil (Ungar *et al.*, 1995). These ‘microindenters’ slide across the occlusal surface to produce multiple ‘microplasticity’ ploughing events (Bowden & Tabor, 1986; Guidoni, Swain & Jager, 2009), resulting in cumulative material removal over a lifetime of regular chewing. Prolonged wear can lead to sufficient removal of enamel as to expose the dentine interior (Janis & Fortelius, 1988; Dean, Jones & Pilley, 1992; Logan & Sanson, 2002; King *et al.*, 2005; Sauther & Cuzzo, 2009; Elgart, 2010).

In extreme cases wear can progress down to the gum level, so jeopardising survival. Microwear patterns on intact teeth have long been used to infer dietary habits in animals and fossils. However, while microwear remains a powerful component in the armoury of diagnostic tools available to the biological ‘detective’, the loads required to produce individual microwear traces are in the order of mN, and therefore cannot offer much information on macroevents needed to break down large food objects. Also, because wear features are continually replaced, they do not reveal much about feeding habits in the early stages of life.

Another kind of damage that teeth can sustain is fracture. Tooth enamel is inherently brittle, with a fracture resistance barely higher than those of silicate glasses or dental porcelains (Lawn & Lee, 2010). In humans, dentists have long observed the presence of ‘lamellae’ or vertical crack-like defects running between the crown surfaces and cervical margins, especially in older patients (Bodecker, 1906, 1953; Sognaes, 1950; Osborn, 1981; Koenigswald, Rensberger & Pretzschner, 1987). However, these defects have generally been regarded as little more than clinical curiosities. Recent studies are now proposing that fracture patterns in recovered teeth can in fact provide unique insights into tooth function (Lucas, 2004; Lucas *et al.*, 2008; Lawn *et al.*, 2009; Lawn & Lee, 2010). Fractures are distinctive events, associated with occasional overloads, although they can multiply and evolve over time (fatigue). The forces involved in great apes and other mammals with similar tooth morphology to humans are at the high end of the load scale, in the order of 1 kN (Lee *et al.*, 2010; Constantino *et al.*, in press). The cracks tend to remain contained within the enamel shell, although in extreme cases they can delaminate the enamel from the dentine, or even enter the dentine to cause splitting. Evidence is surfacing that such cracks are indeed quite prevalent in the enamel of extinct and extant species (Constantino *et al.*, 2010). The high fracture loads appear to suggest a diet of large, mm-scale hard food objects, such as nuts and seeds and bone (Lucas, Peters & Arrandale, 1994; Lucas *et al.*, 2008). From a biological perspective, the susceptibility of enamel to fractures constitutes a selective pressure on the morphology and material properties of teeth. This susceptibility achieves formal expression in the engineering materials discipline of ‘fracture mechanics’—the study of how various crack types initiate and grow within a brittle (enamel) shell, along with the forces that drive them.

The notion of teeth as brittle protective shells with soft supporting interiors is a simple but useful descriptor for evaluating usage. Tooth enamel and dentine have complex, hierarchical microstructures that can significantly influence mechanical properties (Osborn, 1981). Enamel is a highly mineralized material with groups of cylindrical rods of nanoscale hydroxyapatite prism-like crystals weakly bound by fluidized protein sheaths. The weak protein interlayers provide easy paths for tension-driven crack growth (Osborn, 1981) and shear-driven plastic deformation (‘yield’) (He & Swain, 2007a). The rods tend to radiate outward from the dentine–enamel junction (DEJ) toward the outer enamel

surface (OES) and upward towards the tooth crown. Rod bundles change orientation relative to their neighbours, forming a ‘decussation’ (crossing) pattern (Boyde & Martin, 1982; Rensberger, 2000). The degree of decussation tends to be most intense in the vicinity of the DEJ, but this varies from species to species, and in some cases is absent altogether. It has been suggested that a decussated microstructure provides some intrinsic impedance to crack growth and deformation (Koenigswald *et al.*, 1987; Bajaj & Arola, 2009*a, b*). Further impedance to damage can arise from continual self-healing of newly formed cracks by infusion of protein-rich fluids (Myoung *et al.*, 2009) and from recovery of newly formed deformation by rejoining of stretched peptide chains within sheared rods (He & Swain, 2007*a*).

Because of their durability, teeth might be envisioned as the consummate damage-resistant biocomposite. However, somewhat paradoxically, tooth enamel also contains internal weaknesses—defects or flaws. Principal among these are ‘tufts’, hypocalcified, wavy interfaces emanating from the DEJ into the enamel (Sognaes, 1949; Osborn, 1969; ten Cate, 1989; Amizuka *et al.*, 1992, 2005; Lucas, 2004). Tufts are considered to form during development. They tend to follow inter-rod paths and have the form of ‘closed cracks’ filled with protein matter (Palamara *et al.*, 1989). Contrary to a long-held view by the dental community that tufts and other such defects are benign (ten Cate, 1989), it has recently been demonstrated that they can act as sources of fractures in teeth (Chai *et al.*, 2009*a*). In this picture, tooth enamel does not so much avoid fractures as contain them, the hallmark of a damage-tolerant structure.

In this article we advance the hypotheses that antemortem tooth fractures are commonplace in mammals and that such events can provide quantitative information relating to bite force and diet. We examine tooth morphologies in a variety of living and extinct mammalian species to support these hypotheses. Fracture mechanics models are presented as the basis of both qualitative and quantitative analysis—experimental and theoretical—for identifying principal fracture modes and predicting attendant bite forces. Explicit relations enable such forces to be determined from characteristic tooth dimensions. We ask what these relations might ultimately tell us about the foods that any given species must have consumed. Our focus will be on animals with low, rounded (bunodont) molar cusps, for which tooth size and enamel thickness are controlling dimensions.

II. OBSERVATIONS OF CRACK PATTERNS IN TEETH

(1) Cracks in teeth from simulated bite tests

Fracture modes in tooth-like structures have been investigated by conducting loading tests with indenters to simulate biting contacts, either from opposing teeth or from hard or soft food objects. Exploratory tests conducted on ‘model’ dome specimens consisting of glass shells

(‘enamel’) filled with polymer composite (‘dentine’) have been instrumental in identifying and documenting basic fracture modes (Qasim *et al.*, 2005; 2006, 2007; Rudas *et al.*, 2005; Kim *et al.*, 2007; Lawn *et al.*, 2007; Berthaume *et al.*, 2010; Lawn & Lee, 2010). Video cameras enable crack evolution to be followed *in situ*, from initiation to failure, during actual loading. While the model structures are simplistic idealizations of real teeth, the transparency of the glass reveals how cracks initiate and propagate within the brittle shell, remaining confined within the shell up to the point of catastrophic, splitting failure. Analogous experiments on teeth extracted from human subjects and recovered from deceased mammals reveal the same kinds of fractures, albeit with much reduced subsurface visibility (Lawn *et al.*, 2009; Lee *et al.*, 2009; Constantino *et al.*, 2010; Lawn & Lee, 2010). Principal fracture types are depicted schematically in Fig. 1 for (A) longitudinal fracture (Lawn & Lee, 2009; Lee *et al.*, 2009) and (B) edge chipping (Constantino *et al.*, 2010; Chai, Lee & Lawn, 2011). Longitudinal fractures can extend either from the contact zone towards the margin (radial–median cracks) or from the margin towards the contact (margin cracks). Chipping occurs when the loads

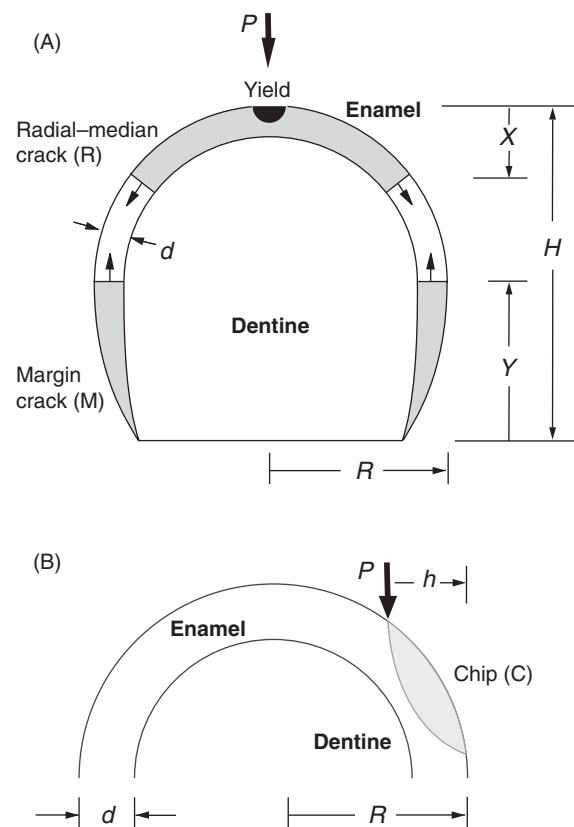


Fig. 1. Schematic showing fracture modes in enamel ‘dome’ structure of characteristic tooth radius R , tooth height H and enamel thickness d , loaded axially with force P . (A) Radial–median ‘R’ and margin ‘M’ cracks with characteristic dimensions X and Y . Hard, sharp contacts produce yield deformation in contact zone. (B) Chipping ‘C’ cracks, developed at load-point distance h from tooth side wall.

are concentrated and applied close to a side wall. Both crack types are driven by weak tensile stresses normal to the principal compressive stresses. Experiments of this kind have facilitated the derivation of simple equations for the loads required to generate each mode, providing a quantitative basis for predicting critical bite forces (see Section III).

Images of extracted human molar teeth after testing are shown in Figs 2 and 3. The selected specimens were stored and tested in a moist environment. Fig. 2A illustrates longitudinal radial–median (R) and margin (M) fractures produced by a hard indenter loaded onto a prominent molar cusp (Chai *et al.*, 2009a). R cracks generally appeared first immediately beneath the contact but ultimately tended to be overtaken by M cracks extending from the tooth base.

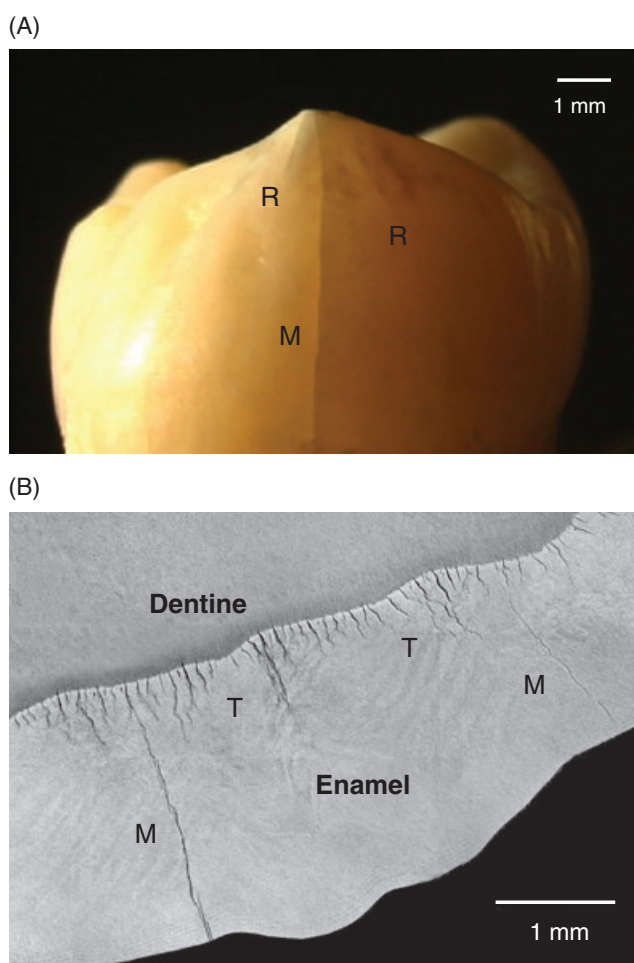


Fig. 2. (A) Human molar indented with a flat metal plate, showing longitudinal radial–median R and margin M cracks. R cracks propagate from the contact around the tooth side wall, M cracks upward from the cervical base. Minor cuspal flattening is apparent at the contact site. (B) Segment of a transverse section at depth 4.4 mm below the cuspal surface of a human molar after contact loading to fracture. Tufts ‘T’ are observed at the dentine–enamel junction (DEJ). Traces of M cracks demonstrate localization of longitudinal fractures within the enamel. Reproduced from Chai *et al.* (2009a).

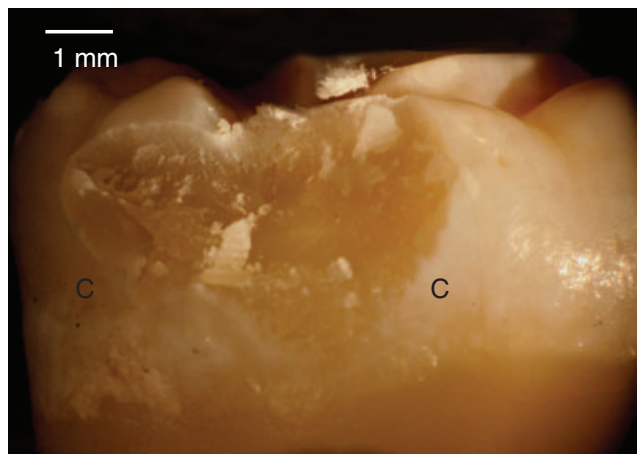


Fig. 3. Chipping C fracture on rounded cuspal surface of extracted human molar after loading with sharp (Vickers) indenter near side wall. Image courtesy of H. Chai.

Many M cracks appeared to extend along the enamel wall from incipient lamellae (see Section III). Both these crack types grew stably and smoothly around the enamel side walls, indicating easy fracture paths. Fig. 2B is a transverse section cut through a tooth to intersect M cracks. The image confirms that these cracks remain confined in a ribbon-like configuration within the outer and inner surfaces of the enamel, at least up to the point of overload where they link with neighbours to cause spallation of the enamel (Popowics, Rensberger & Herring, 2001; Qasim *et al.*, 2005). In cases where the cusp was closer to the tooth centre, or when a small ball was loaded between cusps, M or R cracks were able to enter the dentine and cause splitting, albeit at much higher loads (Chai *et al.*, 2009a).

Fig. 3 illustrates a typical chipping (C) fracture produced by a hard, sharp (Vickers) indenter near a side wall (Constantino *et al.*, 2010; Chai, Lee & Lawn, 2011). In this mode there is no externally visible indication of crack activity within the enamel up to abrupt chip formation. However, an earlier study of chip formation in glass specimens clearly demonstrates that spallation is preceded by a substantial precursor stage of slow crack penetration to a critical depth within the enamel interior (Chai & Lawn, 2007). The ensuing scallop-shaped fracture exhibits a typical surface roughness, with clear evidence that the fracture must cross and break prism bundles during part of its evolution, especially in the final stages (Chai, Lee & Lawn, 2011). Chipping can be more pronounced in teeth with worn surfaces and sharp edges.

Fig. 4 plots characteristic crack dimensions in human molars as a function of bite force. For R and M crack data (Fig. 4A,B) (Lee *et al.*, 2009; Chai, Lee & Lawn, 2011) the dimensions X and Y are measured as projections onto an axial plane (see Fig. 1A). Each data point represents an individual crack measurement, and each line connecting the points represents a crack on a different tooth. These tests were conducted with hard, metal (filled symbols) or soft, polymer (unfilled symbols) indenting plates, representing extremes of contact conditions during normal dental function. R cracks

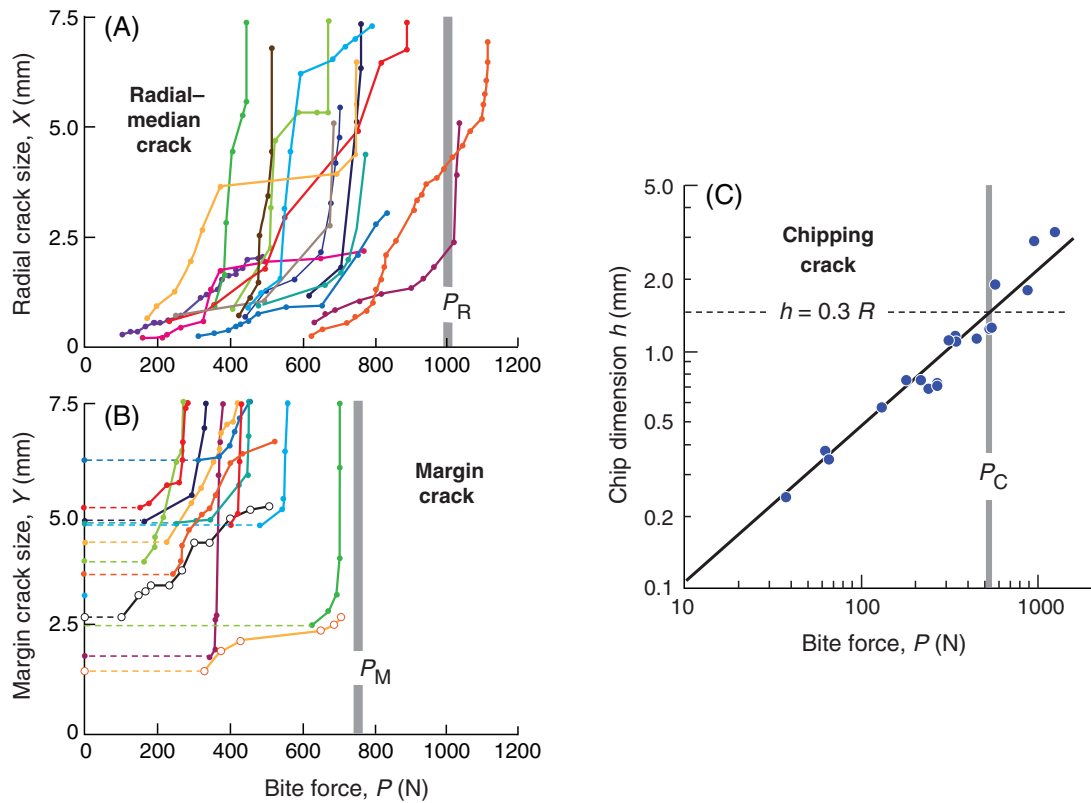


Fig. 4. Data showing crack dimensions in human molars as function of applied force P . Longitudinal fractures, plots of dimensions X and Y for (A) radial–median and (B) margin cracks for flat indenters at crown cusps (see Fig. 1A). Filled symbols indicate hard (metal) indenter, unfilled symbols indicate soft (polymer) indenter. Horizontal dashed lines in B indicate pre-existing margin cracks (lamellae). (C) Distance h of sharp (Vickers) indenter from tooth side wall, as function of load P to produce chip fracture (see Fig. 1B). Horizontal dashed line indicates upper limit to crack size. Solid vertical lines are predicted forces for R, M and C fracture modes.

formed under hard indenters soon after initial contact, and continued growing slowly at loads up to ~ 1000 N, with considerable tooth-to-tooth variability. No such cracks formed under soft indenters. M cracks tended to initiate from pre-existing lamellae (horizontal dashed lines) soon after appearance of the R cracks, but grew more rapidly up to ~ 600 N, again with considerable variability. These cracks formed regardless of the indenter type, but in the case of soft indenters extended only partially around the side walls from the margin. Both R and M cracks occasionally showed unstable increments in growth, particularly at higher loads. Theoretical upper bounds to the forces P_R and P_M at which each of these crack types fully traversed one side of the tooth wall (nominal height ~ 7.5 mm) are indicated as the solid vertical lines (see Section III).

For C crack data (Fig. 4C) (Constantino *et al.*, 2010), the measurable variables are the distance h from the side wall and the critical bite force P to cause chip spallation (see Fig. 1B). In this case tests were conducted with a sharp, hard (Vickers) indenter. Each symbol represents a different tooth, and the solid inclined line is a theoretical best fit to the data (see Section III). The chip size covers a broad range, but is limited within $0 < h < 0.6 R$, with $R = 4.9$ mm a mean radius for human molars (Osborn, 1981; Constantino *et al.*,

2010); at $h > 0.6 R$, the tooth tends to split. The vertical solid line is a theoretical representative value P_C , evaluated for chips formed at a mid-point contact location $h = 0.3 R$ (see Section III).

(2) Natural cracks in teeth

A key question is whether fracture modes generated in laboratory experiments are representative of damage produced during day-to-day mastication. In humans there can be little doubt. We have already mentioned the ubiquitous presence of lamellae in tooth enamel—closed crack-like defects filled with proteinaceous matter—observed by dentists, particularly in older patients. An example of lamellae cracks in the dentition of a live human is shown in Fig. 5. As indicated above, such defects appear to be common precursors of longitudinal cracks, especially M cracks. Fully developed margin cracks [sometimes termed ‘abfractions’ (Grippio, Simring & Schreiner, 2004)], and even tooth splitting, are observed in teeth with a history of excessive loading. Natural staining by accumulation of calculus and polyphenolics (tannins) from food products in patients with lower dental hygiene tend to enhance the visibility of such cracks (Bacon & Rhodes, 2000; Prinz & Lucas, 2000). Veterinarians observe similar staining products in the dentition of live animals. Chipping

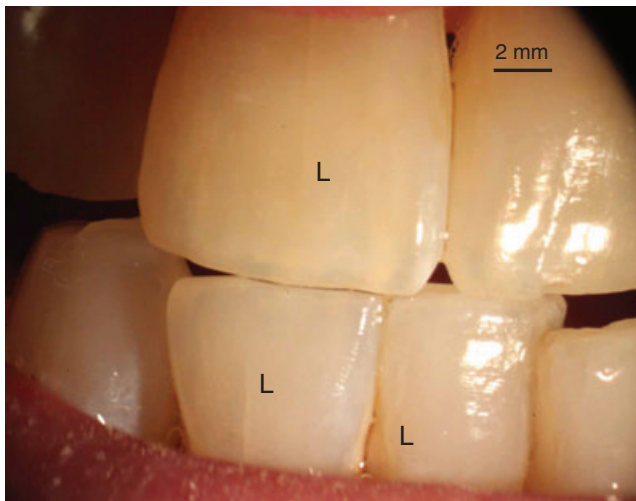


Fig. 5. Photograph of teeth in a live male human, showing lamellae cracks (L) extending vertically within the enamel from the margins.

fractures have also been commonly observed in the crown regions of teeth in extant mammals (Constantino *et al.*, 2010) and fossil hominins (Robinson, 1954; Tobias, 1967; Wallace, 1973). The simulation tests described in Section II.1 would

therefore appear to replicate essential features of clinically observed tooth damage. Severe forms of trauma, e.g. axial splitting of teeth, transverse fractures and gum line wear, have also been observed.

Much less has been reported for other animal species beyond anecdote. However, examination of the dentition of museum specimens of extant species suggests that such features are not uncommon. Fig. 6 shows side-view images of such dentitions from select deceased mammals with bunodont teeth. There is clear evidence of copious margin and other longitudinal cracking in these examples (*cf.* Fig. 2A). In some cases, especially the gorilla (*Gorilla beringei*) and baboon (*Papio ursinus*), the patterns appear to be dominated by margin cracks that do not extend all the way to the crown, consistent with soft contacts. In orangutans (*Pongo pygmaeus*) and peccaries (*Tayassu pecari*) the cracks are more complete and frequent, suggesting harder contacts. The longitudinal cracks in Fig. 6 are highlighted by the same kind of staining observed by dentists in the teeth of living humans, especially in patients with poor dental hygiene. In museum specimens the dentine can shrink away from the enamel, resulting in cracks without stains. Faintly visible horizontal cracks in some of the teeth in Fig. 6 may fall into this latter category. It is arguable that staining could occur postmortem, for instance from the soil or from specimen preservation treatments, but the fracture patterns in Fig. 6 nevertheless

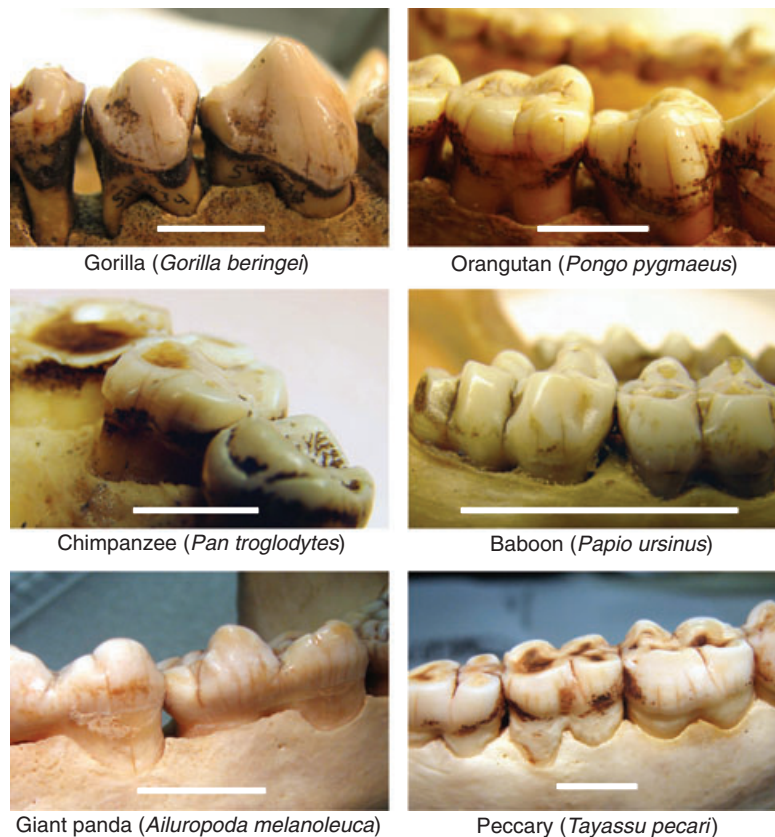


Fig. 6. Photographs of longitudinal fractures from natural biting in tooth enamel of select extant mammals. All images are of specimens from the Museum of Natural History at the Smithsonian Institution in Washington, DC. Scale markers 10 mm.

show all the defining characteristics of longitudinal cracks formed in near-axial compressive loading.

Fig. 7 shows views of chipped animal teeth, as well as from hominin fossils (*Paranthropus robustus* and *Australopithecus anamensis*). In these cases chip fractures extending down the side walls are apparent at the crown edges (cf. Fig. 3). Chip frequency data for selected mammals are shown in Table 1 (Constantino *et al.*, 2010). An interesting comparison is the high frequency of chipping in orangutans and peccaries relative to chimpanzees (*Pan troglodytes*) and gorillas, indicative of a greater reliance on hard foods in the first two species (Kiltie, 1982; Vogel *et al.*, 2008). The higher incidence of chipping in Sumatran orangutans (*Pongo abelii*) relative to Bornean orangutans (*Pongo pygmaeus*) may be reflective of a less productive habitat and an increased consumption of hard fallback foods (Vogel *et al.*, 2008; Constantino *et al.*, 2009; Marshall *et al.*, 2009).

Fig. 8 is an image of a tooth remnant in a peccary. In this case a crack generated by centric loading has completely split the tooth.

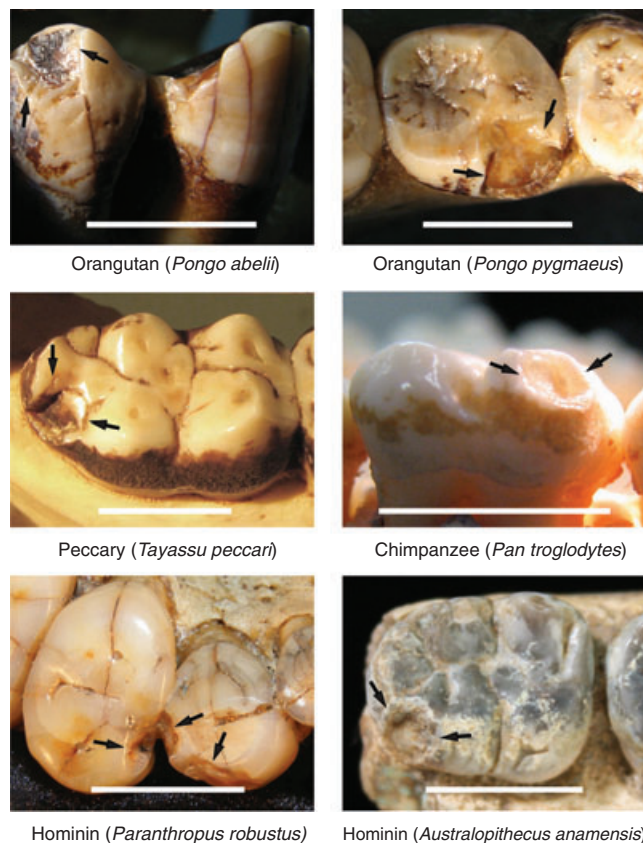


Fig. 7. Photographs of chipping fractures (arrows) in tooth enamel of extant mammals and fossils from natural biting. Images are from specimen collection at the Museum of Natural History at the Smithsonian Institution in Washington, DC. Hominin images courtesy of Bernard Zipfel (*Paranthropus robustus*) and Ashley Hammond (*Australopithecus anamensis*). Scale markers 10 mm.

Table 1. Frequency of tooth chipping in selected mammalian species

Species	Chip frequency (%)
Orangutan (<i>Pongo abelii</i>)	16.0
Peccary (<i>Tayassu pecari</i>)	10.8
Orangutan (<i>Pongo pygmaeus</i>)	7.1
Gorilla (<i>Gorilla gorilla</i>)	3.9
Chimpanzee (<i>Pan troglodytes</i>)	2.2

Data from Constantino *et al.* (2010).



Fig. 8. Tooth splitting in a peccary (*Tayassu pecari*). Image is from specimen collection at the Museum of Natural History at the Smithsonian Institution in Washington, DC. Scale marker 10 mm.

III. FRACTURE MECHANICS AND BITE FORCES

(1) Basic fracture mechanics

We find that fracture patterns in teeth are most amenable to analysis by the discipline of ‘fracture mechanics’—the study of how cracks initiate and propagate within structures (Lawn, 1993). In brittle materials cracks tend to start from microcrack-like ‘flaws’ (Griffith, 1920)—pre-existing, stress-concentrating defects in the microstructure. Once initiated, cracks are driven by tensile stresses perpendicular to the crack plane (‘mode I’ fracture), occasionally augmented by shear stresses (‘mode II’ or ‘mode III’ fracture). In compressive loading, cracks tend to extend closely parallel to the axis of greatest compression, in order to maximize mode I. Fracture is not always abrupt, but can be preceded by an extended stage of stable growth (e.g. Fig. 4). It is not determined by a critical tensile stress at any specific location, but rather by the intensity of the stress field at a crack tip—the so-called ‘stress intensity factor’ K . Cracks extend when this quantity reaches a critical value $K_C = T$, termed the ‘toughness’ (resistance to crack propagation). Toughness has unusual units, incorporating both stress (Pa) and dimension (m), i.e. $\text{Pa m}^{1/2} = \text{N m}^{-3/2}$. It is widely considered to be a material

property, particularly in homogeneous materials like glasses and fine-grain ceramics. However, in more heterogeneous structures toughness can become a function of crack history. For instance, in polymeric composites reinforced by stiff fibres (or layers—e.g. nacre) cracks usually find it easiest to travel along weak fibre–matrix interfaces. Accordingly, toughness for fracture across fibres can be much higher than between them (anisotropy). Cracks that are forced off an easy path may face increasing resistance as they progress, due to bridging of the crack walls by fibres pulling out behind the advancing tip ('R-curve' behaviour) (Marshall, Cox & Evans, 1985). Materials can therefore contain inherent weakness but nevertheless possess respectable toughness ('damage tolerance'). Other factors can act to diminish toughness: chemical intrusion of water, by lowering the fracture surface energy; and cyclic fatigue, by mechanically eroding the weak fibre interfaces. We shall consider some of these factors in the context of enamel microstructure in Section IV.

(2) Tooth models and fracture relations

A basic dome model enables determination of working fracture relations for common fracture modes in bunodont teeth (Lawn & Lee, 2009). The tooth is idealised as a hard, brittle shell (enamel) on a soft, tough interior (dentine). For simplicity, both enamel and dentine are taken as homogeneous, isotropic materials with fixed toughness T . Important dimensions are lateral tooth radius R , tooth height H and enamel thickness d (Fig. 1). Loading is assumed to be applied axially by either a hard or soft indenter. Notwithstanding the simplicity of the representation, the model embodies the main features of interest here. Importantly, the model is amenable to formal fracture mechanics analysis, *via* determination of stress intensity factors for the individual cracking modes in Fig. 1.

Despite the complex evolution of the different fracture modes, basic relations for the critical loads to drive cracks in their final, 'far-field' stages have been developed and refined for bunodont configurations. Various incarnations of these relations have been proposed for radial–median (R) cracks (Rudas *et al.*, 2005; Lee *et al.*, 2010; Barani *et al.*, 2011) and margin (M) cracks (Chai *et al.*, 2009b; Barani *et al.*, 2011) over the past few years. While margin cracks appear to go to completion somewhat more easily, the end result is the same, i.e. a longitudinal ribbon or channel crack fully contained within the enamel and extending completely around one side wall (Lee *et al.*, 2009). The critical load for completion of longitudinal fractures P_L can then be represented by a single power-law relation (Chai *et al.*, 2009b):

$$P_L = CTRd^{1/2} \quad (1)$$

where C is a dimensionless coefficient. For teeth of fixed tooth height $H = 1.5R$, we obtain $C \approx 8.0$ for R cracks and $C \approx 6.0$ for M cracks (Barani *et al.*, 2011). Thus the form of the equation is the same for R cracks ($P_L = P_R$) and

M cracks ($P_L = P_M$), but with slightly different coefficients. An analogous form is obtained for chipping (C) fractures (Constantino *et al.*, 2010; Chai, Lee & Lawn, 2011):

$$P_C = ATR^{3/2} \quad (2)$$

where A is another numerical coefficient. The coefficient depends on the point of contact relative to the tooth axis at the top surface: for a mid-point location $h/R = 0.3$ (Fig. 1B, Fig. 4B) we obtain $A \approx 2.2$, independent of H and d . (In reality, the coefficients C and A depend slightly on the elastic modulus ratio between enamel and dentine, but that dependence may be considered negligibly small between most mammalian species). Note the explicit dependence of P_L and P_C on the key dimensions R and d (for fixed H). The principal material property is the enamel toughness T , with linear dependence. Whereas the initiation of the cracks inevitably depends on the size of the starting flaws from which the cracks originate within the enamel (Lucas *et al.*, 2008; Lawn *et al.*, 2009), as well as on the indenter type at the contact, no such dependencies are evident in Equations 1 and 2, consistent with the existence of a stage of stable precursor crack growth into the contact far field (e.g. Fig. 4).

Values of P_R , P_M and P_C are included for each fracture mode in the data plots of Fig. 4 as the vertical solid lines, using $R = 4.9$ mm and $d = 1.3$ mm in Equations 1 and 2 for human molars (Osborn, 1981). The tendency for the predictions to lie at the higher ends of the data ranges is not altogether surprising given the simplicity of the axially symmetric dome model. Cuspal radii are considerably smaller than the side-wall tooth radii (Berthoume *et al.*, 2010), and the enamel thickness tapers off toward the margins, so the mean values of R and d used in the calculations may be inappropriately high (Kono *et al.*, 2002). Similarly, reductions in tooth height H may lower the critical loads, by diminishing the length of the crack path. Off-axis contact and sliding motion can further reduce the actual critical loads, by enhancing tensile hoop stresses (Qasim *et al.*, 2006). Additional reductions in critical loads may be caused by chemical effects of moisture, manifested as a reduction in toughness. Moreover, variations in material properties such as elastic modulus and hardness within the enamel (Cuy *et al.*, 2002) may be expected to influence the fracture evolution. Strictly, Equations 1 and 2 apply to hard contacts—a sufficiently compliant food material may engulf the entire crown of the tooth in a state of triaxial compression, preventing margin cracks from extending fully around the side wall to the crown surface and even suppressing formation of radial–median cracks altogether (Qasim *et al.*, 2007; Lawn & Lee, 2009). We alluded to this last issue in our description of the data trends in Fig. 4. Notwithstanding all these factors, estimates of critical loads from Equations 1 and 2 appear to provide useful bounding estimates, above which the tooth is at risk of catastrophic failure.

(3) Predictions of critical fracture loads for different species

The explicit nature of the relations in Equations 1 and 2 renders them especially suitable for predicting maximum bite forces for bunodont teeth in different vertebrates. All that is required are representative values of the dimensions R and d , along with a value for the toughness T . We proceed here on the assumption that variations in morphological dimensions from species to species far outweigh those in material properties (Lee *et al.*, 2010), so that $T = 0.7 \text{ MPa m}^{1/2}$ can be regarded as a representative, invariant quantity. Average values of R and d for molar teeth for selected animals and hominins are listed in Table 2, with data taken from various literature sources (Beynon & Wood, 1986; Demes & Creel, 1988; Ward, Leakey & Walker, 2001; Kono, 2004; Grine *et al.*, 2005; Olejniczak *et al.*, 2008) or measured directly in our laboratories from photographs. In our measurements, we found considerable variability in the dimensions for any species, consistent with the data scatter in Fig. 4. The table includes sea otters and peccaries, animals known to eat hard foods with a similar bunodont tooth morphology to humans and robust hominins (Walker, 1981; Constantino *et al.*, in press).

Fig. 9 presents fracture forces $P_L = P_M$ (using $C = 6$ for margin cracks) and P_C for the species listed in Table 2, along with comparative estimates of bite forces from jaw mechanics (where available) (Demes & Creel, 1988). The different force estimates for any given species agree to better than 40%, which is perhaps surprising given all the assumptions underlying the calculations. Absolute values lie in the range 500 N to 2000 N, sufficient to break open many hard food objects (Lucas *et al.*, 1994; Lucas, 2004). Relative values

among species may be regarded with greater confidence. Thus, the great apes show sequentially increasing bite forces from chimpanzees to orangutans to gorillas. Of the hominins, *Paranthropus boisei* ('nutcracker man') appears to have been

Table 2. Data for molar teeth of various mammalian species. Values are means \pm standard deviations

Species	Tooth size R (mm)	Enamel thickness d (mm)
Human (<i>Homo sapiens</i>)	4.9 ± 0.1^a	1.3 ± 0.1^b
Chimpanzee (<i>Pan troglodytes</i>)	5.4 ± 0.1^a	0.81 ± 0.1^b
Orangutan (<i>Pongo pygmaeus</i>)	6.6 ± 0.4^a	1.0 ± 0.1^b
Gorilla (<i>Gorilla gorilla</i>)	7.3 ± 0.4^a	1.0 ± 0.1^b
Baboon (<i>Papio ursinus</i>)	6.2^c	0.85^c
Sea otter (<i>Enhydra lutris</i>)	7.0 ± 0.2^d	0.65 ± 0.1^d
Peccary (<i>Tayassu pecari</i>)	7.5^d	1.0^d
Giant panda (<i>Ailuropoda melanoleuca</i>)	11^d	1.3^d
Australopith (<i>Australopithecus anamensis</i>)	6.7^e	1.9^e
Paranthrop (<i>Paranthropus boisei</i>)	9.0 ± 0.2^f	2.8 ± 0.2^f

^aData for male animals from Demes & Creel (1988), $R = 1/2$ (total molar crown area/3)^{1/2}, with molar crown areas as the sum of the product of buccolingual and mesiodistal diameters of the three molar teeth for each species.

^bData from Kono (2004), average enamel cap volume divided by DEJ area.

^cData from Grine *et al.* (2005) and Olejniczak *et al.* (2008).

^dData from new measurements, calculated as in Demes & Creel (1988).

^eData from Ward *et al.* (2001).

^fData from Beynon & Wood (1986) and Demes & Creel (1988).

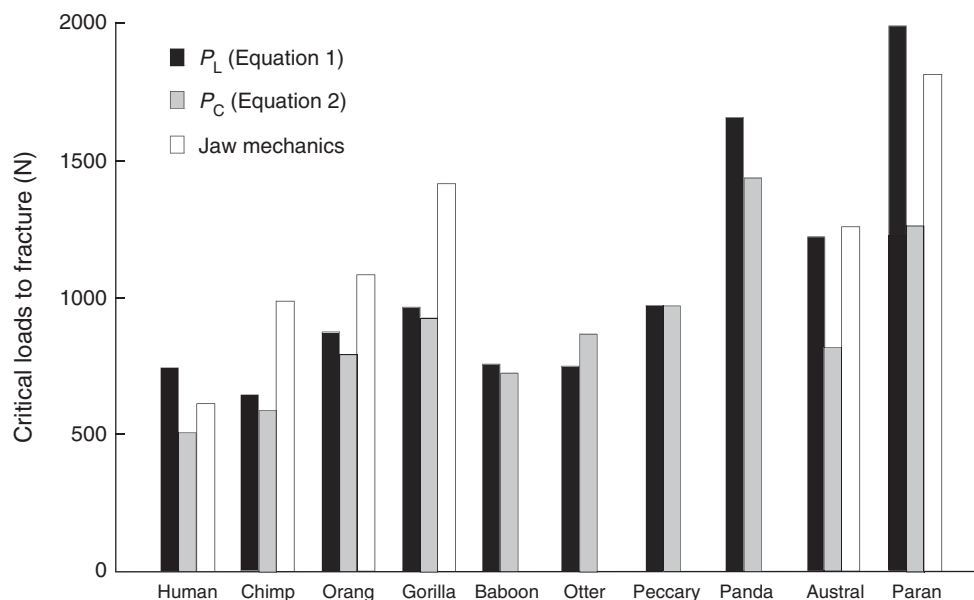


Fig. 9. Predicted critical forces for longitudinal fracture (P_L) (using a dimensionless coefficient $C = 6$ for margin cracks) and chipping (P_C) for selected extant mammal and hominin species, calculated from Equations 1 and 2 in conjunction with data from Table 2. Also included for comparison are jaw mechanics estimates of bite force from Demes & Creel (1988).

capable of exceptionally high bite forces (Wroe, McHenry & Thomason, 2005; Wroe *et al.*, 2010; Constantino *et al.*, in press).

IV. ROLE OF ENAMEL MICROSTRUCTURE

(1) Sources of crack initiation

The analysis in Section III is predicated on the existence of well-developed cracks in enamel. We have demonstrated that any such cracks in axially loaded dome structures will grow stably prior to 'failure'. The notion of tooth enamel as an homogeneous continuum is perfectly adequate to account for this propagation phase of the fracture evolution. But how and where do such cracks start in the first place? Allusions have already been made to the role of 'Griffith flaws' in facilitating the initiation of cracks in brittle materials. In the context of tooth failure, such flaws have their origins in the unique structural architecture that makes up the enamel coat.

Two main sources of cracks within the enamel microstructure have been identified. The first of these sources are tufts, hypocalcified, protein-dense fissures originating at the DEJ. These are present in the enamel of several mammals including primates (Chai *et al.*, 2009a) and sea otters (Constantino *et al.*, in press), but have not been documented comprehensively in vertebrates. As mentioned earlier, these defects are weak interfaces within the organic sheaths that bind the mineralized enamel rods, and thereby have the characteristics of filled microcracks. They tend to align along axial planes and extend longitudinally around the enamel walls. Consequently, they are most apparent in transverse sections, such as that in Fig. 2B. Their wavy, disjointed traces in such sections are attributed to decussation of the rod bundles. Despite their disjointed appearance on the section surfaces, individual tuft segments tend to reconnect onto contiguous pathways within the enamel interior (Amizuka *et al.*, 2005; Chai, Lee & Lawn, 2010).

That tufts can act as sources of fracture is readily demonstrated by sectioning enamel slices from extracted teeth and subjecting the slices to loading configurations that simulate the 'hoop' tensile stresses experienced in biting function (Chai *et al.*, 2009a, 2010). The advantage of such tests is that the evolution of any cracks that ordinarily initiate from within the enamel interior can be followed *in situ* with a video camera. An example of one such test on a portion of a transverse slice from a human molar is shown in Fig. 10 (Chai *et al.*, 2010). Values of the tensile stresses acting normally to the tufts are indicated for each frame of the sequence. Tufts are visible in the enamel as the array of microcrack-like defects immediately adjacent to the DEJ. Also visible are cracks extending from the DEJ to the OES. Some of these cracks were present prior to tensile loading, indicating past damage history for this particular tooth. As the load increases, the pre-existing cracks become more visible as they open up. But importantly, new cracks (arrows) emerge from the tuft array and propagate steadily, if sometimes

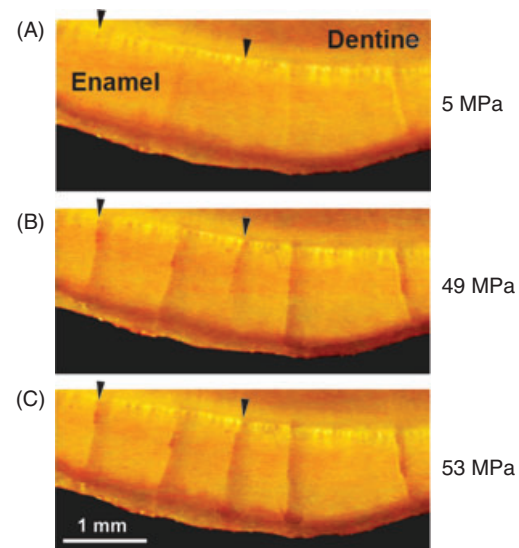


Fig. 10. Transverse slice of enamel tested in tension. Only part of the enamel periphery is shown. Continual loading from A to C causes cracks to generate at tufts (arrows) and propagate progressively from the dentine–enamel junction (DEJ) to the outer enamel surface (OES). Tensile stresses normal to tufts are shown on the right. Reproduced from Chai *et al.* (2010).

discontinuously, across the section. The spacings between the cracks have a certain regularity, consistent with a form of interaction between neighbours known as 'stress shielding' (Chai *et al.*, 2010). This shielding effectively relaxes the stress intensity acting on any individual tuft, with a consequent stabilizing influence on the ensuing crack evolution. It may be emphasized that tests on several specimens showed that crack initiation always occurred at the DEJ and never at the OES, contrary to conventional wisdom within the dental community.

The second main source of crack initiation in enamel is yield deformation from hard, concentrated contacts. Weak interfaces within the microstructure render enamel highly susceptible to shear-activated slippage along inter-prism boundaries. Shear stresses can be a significant component of contact fields, typically three or more times greater in magnitude than tensile stresses (Tabor, 1951). In a recent series of publications using the nanoindentation methodology, L.H. He and M.V. Swain and co-workers have documented extensively how such slippage accounts for contact yield in enamel (He, Fujisawa & Swain, 2006; He & Swain, 2007a, b, c, 2008; Xie, Swain & Hoffmann, 2009a; Xie *et al.*, 2009b). We see the same kind of yield deformation in our experiments on extracted teeth in loading with hard indenters, manifested as a cuspal flattening (Lawn *et al.*, 2009). Deformation of this kind intensifies local stress concentrations at the ends of 'slip faults' in the enamel subsurface, and this intensification increases with applied loading until the faults open up into internal fissures (Lawn & Evans, 1977). At much lower loads, well below the crack initiation threshold, repeated reverse slipping from multiple microcontacts can cause frictional attrition of the slippage

interfaces, leading to material removal and exacerbated wear (Lawn *et al.*, 1994).

(2) Inhibition of crack propagation

Upon initiation, longitudinal cracks can propagate through the enamel as depicted in Fig. 1A. Radial–median cracks can either originate from tufts at the DEJ (radial) or from shear faults within the near-surface yield zone (median) (Lucas *et al.*, 2008): radial cracks are more likely in thinner enamel, because of high flexural tensile stresses at the enamel undersurface; conversely, median cracks are more likely in thicker enamel, because tensile stresses then concentrate immediately beneath the contact. Once cracks penetrate through the enamel thickness, any distinction between radial and median becomes blurred, and the fracture front is free to propagate around the enamel wall as R cracks. Margin or M cracks are believed to originate at tufts, or from lamellae that subsequently develop from these tufts. Chipping or C cracks begin within the enamel interior from the yield zone beneath a concentrated load as indicated in Fig. 1B.

The influence of microstructure is not limited to the initiation stage of fracture. Repeated reference has been made to the role of weak inter-rod interfaces in providing preferred crack paths. However, periodic reorientation of the fibre bundles in regions of high decussation tends to disrupt such easy paths, by causing cracks to deflect and bifurcate (Koenigswald *et al.*, 1987). To continue propagating, the cracks have to break up and re-form continually along their front—and, in the process, pull out any unruptured prisms that bridge the crack walls behind the advancing front. Crack-interface bridging is a common occurrence in fibre-reinforced composites, and is capable of dissipating considerable energy, with consequent progressive increase in toughness (Marshall *et al.*, 1985). It is a bit like trying to split a log of wavy grained wood. Decussation in human teeth is highest adjacent to the DEJ, so toughness may be expected to be enhanced in this region. Experiments in which controlled cracks are driven through sectioned and sliced enamel specimens suggest that toughness near the DEJ may be up to four times higher than at the OES (Bajaj & Arola, 2009*a, b*). Thus, because they initiate near the DEJ, radial and margin cracks may be initially impeded, but once they penetrate to the OES they become free to extend longitudinally around the outer enamel surface regions with relatively small inhibition. This would explain why the traces of well-developed longitudinal cracks in transverse sections (e.g. Fig. 2B) often appear wider at the OES than at the DEJ. Thus, as demonstrated in Fig. 10, the conclusion that the cracks must have started from the OES cannot be justified from such *post-mortem* examinations of fracture alone.

Other microstructure-related factors can have a stabilizing influence on the fracture of enamel. Elastic modulus, as well as toughness, can exhibit significant gradients across the enamel thickness. Digital mapping of modulus from nanoindentation data indicates values up to twice as high at the OES than at the DEJ (Cuy *et al.*, 2002; Darnell *et al.*,

2010; Lee *et al.*, 2010). Such gradients may be attributable to point-to-point variation in mineral content within the microstructure. It is arguable that a lower modulus may relax the build-up of tensile stresses near the DEJ. In addition, newly extended cracks can self-heal, by infusion of protein-rich fluids from the saliva or from the tooth itself, in much the same way as the tufts from which they originate. Such healing has been demonstrated by emplacing Vickers microindentations immediately adjacent to traces of aged margin cracks on transverse sections (Myoung *et al.*, 2009). Penetration of indentation corner cracks across the larger margin crack interface signifies the presence of solidified adhesive matter. Healing of this kind can inhibit otherwise unrestricted extension of the cracks over time (Roach, Lathabai & Lawn, 1988).

V. DISCUSSION OF FRACTURE OBSERVATIONS

We argue that the presence of cracks in teeth can reveal unique information about the history of different vertebrates—what forces they used to consume their food and ideally even the nature of the food itself. Our argument, foreshadowed in earlier articles (Lucas *et al.*, 2008; Constantino *et al.*, 2010) and here refined and expanded into a broader perspective, emerges from the confluence of two seemingly disparate areas: biological function and fracture mechanics (Lucas, 2004). The basis of the fracture mechanics is a test protocol that simulates biting, in which dome tooth models or actual extracted molar teeth are subjected to axial loading with hard or soft indenters. *In situ* observations with video recorders demonstrate the distinctive nature of the cracking process. Different fracture modes are identified, primarily longitudinal (radial–median R and margin M) cracks and chipping (C) cracks, both usually contained fully within the enamel. It takes extreme overloading to drive these cracks into the dentine to split the tooth. Once initiated, cracks can grow incrementally, heal, grow again, over the loading history; their development tends to be highly stabilised. The tooth shell structure distributes essentially compressive contact stresses around the enamel walls, rather like the dome of a cathedral. The stiff enamel shell shields the soft dentine from the external forces, offering mechanical protection. However, secondary, tensile stresses within the enamel are by no means insignificant, and occur at sufficient levels to drive fracture. Enamel microstructures contain weak inter-rod interfaces and defects such as tufts, affording easy fracture and slippage paths. Crack containment comes from stress relaxation interactions between defect arrays, rod decussation, and self-healing by intrusion of proteinaceous fluids. This last may explain how human teeth can contain a plethora of fissures without accelerated carious infection. The picture emerges of teeth as ideally adapted to sustain damage, structured to live with cracks rather than to avoid them—they are ‘built to last’ (Maas & Dumont, 1999).

The strength of the fracture mechanics approach embodied in Equations 1 and 2 is the capacity to quantify bite

forces for animals with bunodont teeth from straightforward measurements of tooth dimensions R and d , along with a representative value for toughness T . Our fracture mechanics estimates in Fig. 9 provide upper bounds for bite forces in the largest teeth in selected species, exceeding 1 kN in some cases. Such estimates enable a useful ‘ranking’ of bite-force capacity for different species. They fall in the same range as those from biomechanical analysis of skull musculature (see Fig. 9) (Demes & Creel, 1988; Thomason, 1991; Spencer, 1998; Rayfield *et al.*, 2001; Wroe *et al.*, 2010), as well as from fracture tests on hard food objects themselves (Kiltie, 1982; Lucas *et al.*, 1994; Berthaume *et al.*, 2010) and from bite-force gauge measurements on extant species (Braun *et al.*, 1995). Our fracture mechanics relations come from analyses of stress intensity factors K for cracks in dome structures, resulting in equations that express morphological and material factors in elegantly simple forms. We have acknowledged several sources of uncertainty in these relations (see Section III.2), commensurate with the wide scatter that typifies tooth-to-tooth variations, even within a single species (e.g. Fig. 4). It needs also to be emphasized that Equations 1 and 2 pertain to fully formed cracks—initiation of each type generally occurs at much lower loads. Thus the enamel may contain only partially developed cracks (e.g. lamellae), and some cracks that initiate first may ultimately be overtaken by a competing mode. Notwithstanding all these considerations, Equations 1 and 2 help formalise what might seem intuitively obvious—that animals with large tooth radius and enamel thickness are best equipped to exert high bite forces.

The identification of stress intensity factor K as the principal driving force for fracture warrants further comment in the light of common misconceptions concerning the condition for structural failure. In their paper on bite forces, (Demes & Creel, 1988, p. 666) state that . . . ‘force per unit area exerted on the molar crown (occlusal pressure) must be much the same in all species, regardless of tooth size’. The compression stress $P_M/\pi R^2$ across the base area of the tooth at the critical load P_M to cause full margin cracking has a mean and standard deviation of $6.9 \pm 1.7 \text{ N mm}^{-2}$ (MPa) averaged over all species in Fig. 9. The relatively small variation of <25% over the species range might thus appear to support the thesis of Demes & Creel (1988). However, in larger teeth and thicker enamel cracks have further to travel through and around the side walls and thus require higher bite forces to propagate them to failure. This is because the stress intensity factor K is not sufficiently specified by a stress, but depends also on some characteristic tooth dimension. It follows that conventional finite element modelling (FEM) widely used in mapping out stress states in geometrically complex tooth and skull morphologies (Wroe *et al.*, 2005, 2010; Strait *et al.*, 2009) is inadequate for predicting critical fracture loads. However, the newest, ‘extended’ incarnations of finite element analysis (XFEM) do in fact contain provision for incorporation of stepwise crack growth through complex structures, with capacity to compute K functions through an entire stable crack evolution, from initiation to failure. In

the context of tooth structures, the use of XFEM has proved to be a useful adjunct for validating the fracture mechanics relations in Equations 1 and 2 (Barani *et al.*, 2011).

We mentioned at the beginning of this review the use of wear patterns in anthropological studies of dentition. On a macroscopic scale, wear can be an important factor in determining tooth lifetime, by removing the protective enamel coat in the occlusion region and exposing the soft dentine interior. [In some animals, such as horses, such wear is an important element of tooth function, by creating ridges for processing vegetable matter (Rensberger, Forsten & Fortelius, 1984; Lucas, 2004)]. Interestingly, preliminary calculations for dome structures with their tops completely polished off suggest that even severely worn teeth may still be able to support high bite forces, by redistributing the loads onto the enamel rim (Ford, Bush & Lawn, 2009). The interactive role between progressive wear and fracture is an issue that remains relatively unexplored. On a microscopic scale, wear from multiple contacts with μm -scale particulates—grits and phytoliths—leaves telltale striae, scratches and pits that can be interpreted in terms of dietary history and subjected to in-depth statistical analysis (Teaford, 1988; Teaford & Ungar, 2000; Grine *et al.*, 2010). Microwear analysis is indeed a useful diagnostic tool for inferring tooth dietary history. We would contend that fracture mechanics, by providing quantitative information on actual bite forces that any species must have used to consume its food, offers a powerful alternative methodology. Fracture can tell us much more about how teeth work at the upper extremes of function, commensurate with the high forces exerted by jaw musculatures and those needed to break down large food objects. Accordingly, fracture and wear offer information at opposite ends of the force spectrum, and should be viewed as complementary rather than mutually exclusive.

Finally, a few brief words on directions in which future dental fracture mechanics might head. There is room for further work on fracture patterns in the teeth of different animal species. We have been studying such fractures in sea otters, animals with an anatomically similar dentition to that of humans but with different molar radius (larger) and enamel thickness (smaller), with a view to examining the competition between radial–median and margin cracks (Constantino *et al.*, in press). Extension of our model to animals with non-bunodont teeth and to enamel with graded mechanical properties, in both worn and unworn tooth morphologies, is also under consideration. In those cases, a combined fracture-mechanics/XFEM approach may be required to handle the geometrical complexities.

VI. IMPLICATIONS IN ECOLOGY AND EVOLUTION

The evidence reviewed here implies that mammals have evolved specific mechanisms to control crack propagation in enamel, rather than to prevent cracks from forming in the

first place. This is a common pattern of structural protection in biological organisms (Lucas *et al.*, 2004). It is proposed here that mammalian teeth have evolved to resist fractures on two levels:

(1) *Tooth geometry*. One evolutionary defence involves the enlargement of tooth dimensions. Equations 1 and 2 predict that both longitudinal fractures and chipping fractures can be constrained in their development *via* an increase in tooth radius R . The critical force to failure also depends on enamel thickness d , notably in longitudinal fissures, although the dependence is not as strong. [Thicker enamel might serve other purposes, e.g. to suppress initiation of radial cracks in the first place and to provide protection against wear (Lucas *et al.*, 2008)]. These predictions are in line with intuitive reasoning—as discussed in the preceding section, larger dimensions increase the load-bearing capacity by redistributing the stresses over a greater base area. Such scaling dimensions in the critical force equations are important because of the enormous interest in dental allometry (Corruccini & Henderson, 1978; Wood & Stack, 1980; Perzigian, 1981; Gingerich, Smith & Rosenberg, 1982; Fortelius, 1985; Kay & Grine, 1988; Ungar, 1998; Lucas, 2004).

(2) *Enamel microstructure*. The second type of defence against enamel fracture comes from the microstructure. Non-mammalian vertebrates tend to have structureless enamel with all mineralized crystals separated by approximately 3 nm gaps containing remnant peptide fragments after maturation (Robinson *et al.*, 1997). The peptides bind the tissue into a resilient biocomposite (Sander, 2000). In mammalian enamel, the gaps are much larger, on the order of 100 nm. In this case the gaps or rod sheaths separate groups or bundles of crystals. The relatively large sheaths allow for flow of proteins within a fluid-rich suspension (Shellis & Didbin, 2000). Excessive shear displacements can cause stress concentrations leading to median crack initiation, but the deformable sheaths diminish the ‘brittleness’ of the enamel. It is the capacity of such large gaps to self-heal by continual replenishment of protein-rich fluids, coupled with stress shielding between tufts and decussation of rod bundles, that gives mammalian enamel its long-term damage control. It is not known how prevalent tuft structures may be in other animal species or fossils, although enamel voids in some larger dinosaur species may represent their equivalent (Hwang, *in press*). The prevalence of lamellae structures in other species has also not been widely reported, other than in rats (*Rattus norvegicus*, strain unknown) (Will, River & Rosen, 1971). Further studies are needed to elaborate on the form of enamel microstructure in the context of biological evolution.

We have asserted that clues to biological function may be found in the examinations of cracked dentitions from living and extinct animals. The fracture patterns in Figs 6 and 7 have the same characteristics as those produced in the *ex vivo* laboratory compressive loading tests on human molars, implying that they formed during function. Chipping cracks, by virtue of their rough, scallop-shaped spall, leave

the clearest fingerprint. Longitudinal cracks may require judicious illumination to reveal them, in the same way that dentists light up lamellae in human teeth (Fig. 5). The question then arises: did these cracks occur antemortem or postmortem? Shrinkage stresses associated with long-term dehydration or inadvertent stresses arising during specimen preparation may generate additional tension in enamel, inducing existing cracks to open up or new ones to form. In the case of chipping, an oft-cited argument as evidence for life events is the presence of use-wear rounding at the chip edges (Wallace, 1973; Ward *et al.*, 2001). As to longitudinal cracks, providential deep brown staining by tannins (Prinz & Lucas, 2000) can expose any larger in-life fissures. Stains from consumption of immature leaves (Coley, 1983) and fruits (McArthur, Sanson & Beal, 1995) are often used as proof of tooth eruption in herbivorous mammals (Kelley & Schwartz, 2010). We suggest that this, together with the strong similarity between fracture patterns in museum tooth specimens and laboratory-tested human molars, constitutes compelling evidence for crack formation from near-axial loading during function. However, even if the cracks observed in Figs 6 and 7 did not occur during lifetime activity, Equations 1 and 2 remain a powerful means of estimating bite forces, bearing in mind our verification of the essential fracture mechanics by failure tests on human tooth specimens.

This brings us to the issue of diet. Repeated allusion has been made to hard *versus* soft food eating among different mammalian species, particularly as to how such foods influence the evolution of skull and tooth morphology. Enamel fracture patterns such as those in Figs 6 and 7 can shed some light on this issue, although care needs to be exercised in drawing broad conclusions. While the fracture mechanics is quantitatively explicit in its predictions of bite forces, inferences in relation to diet are more subjective. As pointed out, soft contacts tend to prevent margin cracks from extending to the crown surface, and to suppress radial–median cracking altogether. Accordingly, the appearance of partial margin cracks in the gorilla and baboon teeth in Fig. 6 is consistent with a soft food diet. The presence of incomplete radial cracks localized about the cuspal regions would indicate hard food contacts, although clear examples are not evident in Fig. 6. It is possible that any such top-surface damage might be worn away over a lifetime of eating. In many of the cases shown in Fig. 6 the longitudinal cracks extend completely around the tooth side wall, suggesting that at least part of the diet was hard foods. A more definitive indicator of hard food contacts is the presence of chips, for these can only initiate beneath highly concentrated forces at the crown surface (Constantino *et al.*, 2010). For example, relative to chimpanzees, orangutans include nuts and seeds on their menu (Vogel *et al.*, 2008), and show a correspondingly higher incidence of chipping fractures (Table 1) (Constantino *et al.*, 2010). This implied greater capacity for orangutans to consume hard foods is consistent with the calculated critical loads in Fig. 9, some 50% greater than for chimpanzees. Gorillas, on the other

hand, chew tougher materials over more extended periods, necessitating larger teeth to deal with a higher work rate. We suggest that fracture resistance of mammalian dentition is subject to strong selective pressures, with tooth dimensions optimised to enable maximum efficiency in food processing (Lucas, 2004).

Consideration in the present work has focused on teeth with low, rounded, bulbous, bunodont cusps. The same types of cracks also pose a threat to other forms of dentition, including the hypsodont (high-crowned) form in herbivores such as artiodactyls or perissodactyls where teeth more resemble tall columns (Lucas 2004). The dependence of critical load on tooth height H alluded to briefly in Section III.2 is potentially of importance in understanding the evolution of hypsodonty. The teeth of herbivores continually wear down during chewing, exposing enamel ridges separated by dentine. In addition, the enamel of many herbivores is covered by a thin layer of cementum, a bone-like tissue usually only found on the tooth root in other vertebrates. Most non-mammalian vertebrates do not face long-term damage because they produce many generations of teeth (polyphyodonty), replacing individual teeth rapidly. Non-mammalian vertebrates do not need long-term damage control, and thus lack a prism sheath, with all crystallites tightly bound (Sander, 2000) to resist surface wear. It is diphodont mammals that have the issues, particularly with their permanent dentition that must survive through adulthood. Investigation into some of these different morphological configurations is underway.

VII. CONCLUSIONS

(1) Enamel is susceptible to antemortem cracking which can be used to infer tooth function and, by extension, dietary history.

(2) Two principal fracture modes in enamel are identified: side-wall ribbon (or channel) cracks running longitudinally either from the cuspal surface toward the margin (radial–median cracks) or from the margin toward the cuspal surface (margin cracks); chipping cracks, running laterally from a concentrated contact at the occlusal surface to cause a side-wall spall.

(3) Analysis of the fracture patterns in tooth enamel provides explicit critical load relations for each mode in terms of material properties and characteristic tooth dimensions.

(4) The critical load relations provide a simple means for predicting bite forces in living and extinct mammals with bunodont teeth. Tooth morphology is shown to be the dominant variable controlling these forces.

(5) The unique microstructure of tooth enamel confers teeth with an innate resilience against continual stress over a lifetime of function. Despite inherent microstructural weaknesses, enamel is well configured to stabilise and contain fractures within the overall tooth structure.

VIII. ACKNOWLEDGEMENTS

Human teeth were supplied by Gary Schumacher and Anthony Giuseppetti (Paffenbarger Research Center at the National Institute of Standards and Technology). Bernard Wood (George Washington University, Washington, DC, USA) and Fred Grine (Stony Brook University, Stony Brook, NY, USA) granted access to their hominin cast collections; Linda Gordon (Museum of Natural History at the Smithsonian Institution in Washington, DC, USA) and Stephany Potze (Transvaal Museum, Pretoria, RSA) granted access to animal specimens; and Bernhard Zipfel (University of the Witwatersrand, Johannesburg, RSA), Ashley Hammond and Carol Ward (University of Missouri, Columbia, MO, USA) provided photographs of fossil teeth. Informative discussions with many colleagues on observations of fracture in human teeth are gratefully acknowledged: Herzl Chai (Tel Aviv University, Tel Aviv, Israel); Susanne Scherrer (University of Geneva, Geneva, Switzerland); Mark Bush, Amanda Keown and Amir Barani (University of Western Australia, Nedlands, Australia); Stephen Wroe (University of New South Wales, Kensington, Australia). Funding for this work was provided by the National Science Foundation (grant 0851351, P.W.L., P.J.C., J.J.-W.L., and B.R.L.; grant 0725122, P.W.L.), the George Washington University Research Enhancement Fund (P.J.C.), and an NRC fellowship (J.J.-W.L.).

IX. REFERENCES

- AMIZUKA, N., UCHIDA, T., FUKAE, M., YAMADA, M. & OZAWA, H. (1992). Ultrastructural and immunocytochemical studies of enamel tufts in human permanent teeth. *Archives of Histology and Cytology* **55**, 179–90.
- AMIZUKA, N., UCHIDA, T., NOZAWA-INOUE, K., KAWANO, Y., SUZUKI, A., LI, M., NASU, M., KOJIMA, T., SAKAGAMI, N., OZAWA, H. & MAEDA, T. (2005). Ultrastructural images of enamel tufts in human permanent teeth. *Journal of Oral Bioscience* **47**, 33–41.
- BACON, J. R. & RHODES, M. J. C. (2000). Binding affinity of hydrolyzable tannins to parotid saliva and to proline-rich proteins derived from it. *Journal of Agricultural and Food Chemistry* **48**, 838–43.
- BAJAJ, D. & AROLA, D. D. (2009a). On the R-curve behavior of human tooth enamel. *Biomaterials* **30**, 4037–46.
- BAJAJ, D. & AROLA, D. D. (2009b). Role of prism decussation on fatigue crack growth and fracture of human enamel. *Biomaterials* **30**, 4037–46.
- BARANI, A., KEOWN, A. J., BUSH, M. B., LEE, J. J.-W., CHAI, H. & LAWN, B. R. (2011). Mechanics of longitudinal cracks in tooth enamel. *Acta Biomaterialia* **7**, 2285–2292.
- BERTHAUME, M., GROSSE, I. R., PATEL, N. D., STRAIT, D. S., WOOD, S. & RICHMOND, B. G. (2010). The effect of early hominin occlusal morphology on the fracturing of hard food items. *The Anatomical Record* **293**, 594–606.
- BEYNON, A. D. & WOOD, B. A. (1986). Variations in enamel thickness and structure in East-African hominids. *American Journal of Physical Anthropology* **70**, 177–93.
- BODECKER, C. F. (1906). Enamel of the teeth decalcified by the celloidin method and examined with ultra-violet light. *Dental Reviews* **20**, 317–37.
- BODECKER, C. F. (1953). Enamel lamellae and their origin. *Journal of Dental Research* **32**, 239–45.
- BOWDEN, F. P. & TABOR, D. (1986). *The Friction and Lubrication of Solids*, Second edition. Clarendon Press, Oxford.
- BOYDE, A. & MARTIN, L. (1982). Enamel microstructure determination in hominoid and cercopithecoïd primates. *Anatomy and Embryology* **165**, 193–212.
- BRAUN, S., BANTLEON, H. P., HNAT, W. P., FREUDENTHALER, J. W., MARCOTTE, M. R. & JOHNSON, B. E. (1995). A study of bite force. I. Relationship to various physical characteristics. *Angle Orthodontist* **65**, 367–72.

- CHAI, H. & LAWN, B. R. (2007). A universal relation for edge chipping from sharp contacts in brittle materials: A simple means of toughness evaluation. *Acta Materialia* **55**, 2555–61.
- CHAI, H., LEE, J. J.-W., CONSTANTINO, P. J., LUCAS, P. W. & LAWN, B. R. (2009a). Remarkable resilience of teeth. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 7289–93.
- CHAI, H., LEE, J. J.-W., KWON, J.-Y., LUCAS, P. & LAWN, B. R. (2009b). A simple model for enamel fracture from margin cracks. *Acta Biomaterialia* **5**, 1663–67.
- CHAI, H., LEE, J. J.-W. & LAWN, B. R. (2010). Fracture of tooth enamel from incipient microstructural defects. *Journal of Mechanical Behavior of Biomedical Materials* **3**, 116–20.
- CHAI, H., LEE, J. J.-W. & LAWN, B. R. (2011). On the chipping and splitting of teeth. *Journal of Mechanical Behavior of Biomedical Materials* **4**, 315–21.
- COLEY, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**, 209–33.
- CONSTANTINO, P. J., LEE, J. J.-W., CHAI, H., ZIPFEL, B., ZISCOVICI, C., LAWN, B. R. & LUCAS, P. W. (2010). Tooth chipping can reveal the diet and bite forces of fossil hominins. *Biology Letters* **6**, 826–29.
- CONSTANTINO, P. J., LEE, J. J.-W., MORRIS, D., LUCAS, P. W., HARSTONE-ROSE, A., LEE, W.-K., DOMINY, N. J., CUNNINGHAM, A., WAGNER, M. & LAWN, B. R. (in press). Adaptation to hard-object feeding in sea otters and hominins. *Journal of Human Evolution*.
- CONSTANTINO, P. J., LUCAS, P. W., LEE, J. J.-W. & LAWN, B. R. (2009). The influence of fallback foods on great ape tooth enamel. *Amer. J. Phys. Anthropol.* **140**, 653–60.
- CORRUCCINI, R. S. & HENDERSON, A. M. (1978). Multivariate dental allometry in primates. *American Journal of Physical Anthropology* **48**, 203–08.
- CROMPTON, A. W. & PARKYN, D. G. (1963). On the lower jaw of *Diarthrogathus* and the origin of the mammalian lower jaw. *Proceedings of the Zoological Society of London* **140**, 697–749.
- CUY, J. L., MANN, A. B., LIVI, K. J., TEAFORD, M. F. & WEIHS, T. P. (2002). Nanoindentation mapping of the mechanical properties of human molar tooth enamel. *Archives of Oral Biology* **7**, 281–91.
- DARNELL, L. A., TEAFORD, M. F., LIVI, K. J. & WEIHS, T. P. (2010). Variations in the mechanical properties of *Alouatta palliata* molar enamel. *American Journal of Physical Anthropology* **141**, 7–15.
- DEAN, M. C., JONES, M. E. & PILLEY, J. R. (1992). The natural history of tooth wear, continuous eruption and periodontal disease in wild shot great apes. *Journal of Human Evolution* **22**, 23–39.
- DEGUSTA, D., EVERETT, M. A. & MILTON, K. (2003). Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). *Proceedings of the Royal Society of London Series B* **270**, S15–17.
- DEMES, B. & CREEL, N. (1988). Bite force, diet and cranial morphology of fossil hominids. *Journal of Human Evolution* **17**, 657–70.
- ELGART, A. A. (2010). Dental wear, wear rate, and dental disease in the African apes. *American Journal of Primatology* **72**, 481–91.
- FORD, C., BUSH, M. B. & LAWN, B. R. (2009). Effect of wear on stresses and potential failure modes in teeth. *Journal of Materials Science: Materials Medicine* **20**, 2243–47.
- FORTELIUS, M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica* **180**, 1–76.
- FORTELIUS, M. & SOLOUNIAS, N. (2000). Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* **3301**, 1–36.
- GINGERICH, P. D., SMITH, B. H. & ROSENBERG, K. R. (1982). Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology* **58**, 81–100.
- GREAVES, W. S. (1978). Jaw lever system in ungulates—a new model. *Journal of Zoology* **184**, 271–85.
- GRIFFITH, A. A. (1920). The phenomena of rupture and flow in solids. *Philosophical Transactions of the Royal Society of London* **A221**, 163–98.
- GRINE, F. E. (1981). Trophic differences between ‘gracile’ and ‘robust’ australopithecines: a scanning electron microscope analysis of occlusal events. *South African Journal of Science* **7**, 203–30.
- GRINE, F. E., JUDEX, S., DAEGLING, D. J., OZCIVICI, E., UNGAR, P. S., TEAFORD, M. F., SPONHEIMER, M., SCOTT, J., SCOTT, R. S. & WALKER, A. (2010). Craniofacial biomechanics and functional and dietary inferences in hominin paleontology. *Journal of Human Evolution* **58**, 293–308.
- GRINE, F. E., SPENCER, M. A., DEMES, B., SMITH, H. F., STRAIT, D. S. & CONSTANT, D. A. (2005). Molar enamel thickness in the chacma baboon, *Papio ursinus* (Kerr 1792). *American Journal of Physical Anthropology* **128**, 812–22.
- GRIPPO, J. O., SIMRING, M. & SCHREINER, S. (2004). Attrition, abrasion, corrosion and abfraction revisited. *Journal of the American Dental Association* **135**, 1109–18.
- GUIDONI, G. M., SWAIN, M. V. & JAGER, I. (2009). Wear behaviour of dental enamel at the nanoscale with a sharp and blunt indenter tip. *Wear* **266**, 60–68.
- HE, L. H., FUJISAWA, N. & SWAIN, M. V. (2006). Elastic modulus and stress–strain response of human enamel by nano-indentation. *Biomaterials* **27**, 4388–98.
- HE, L. H. & SWAIN, M. V. (2007a). Contact induced deformation of enamel. *Applied Physics Letters* **90**, 171916, 1–3.
- HE, L. H. & SWAIN, M. V. (2007b). A ‘metallic-like’ deformable biocomposite. *Journal of Dentistry* **35**, 431–37.
- HE, L. H. & SWAIN, M. V. (2007c). Influence of environment on the mechanical behavior of mature human enamel. *Biomaterials* **28**, 4512–20.
- HE, L. H. & SWAIN, M. V. (2008). Understanding the mechanical behavior of human enamel from its structural and compositional characteristics. *Journal of the Mechanical Behavior of Biomedical Materials* **1**, 18–29.
- HWANG, S. H. (in press). The evolution of dinosaur tooth enamel microstructure. *Biological Reviews of the Cambridge Philosophical Society*, doi: 10.1111/j.1469-185X.2010.00142.x.
- JANIS, C. M. & FORTELIUS, M. (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews of the Cambridge Philosophical Society* **63**, 197–230.
- KAY, R. F. (1981). The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *American Journal of Physical Anthropology* **55**, 141–51.
- KAY, R. F. & GRINE, F. E. (1988). Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from Southern Africa. In *Evolutionary History of the “Robust” Australopithecines* (ed. F. E. GRINE), pp. 427–47. Aldine de Gruyter, New York.
- KELLEY, J. & SCHWARTZ, G. T. (2010). Dental development and life history in living African and Asian apes. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 1035–40.
- KILTIE, R. A. (1982). Bite force as a basis for niche differentiation between rain-forest peccaries (*Tayassu tajacu* and *T. pecari*). *Biotropica* **14**, 188–95.
- KIM, J.-W., BHOWMICK, S., CHAI, H. & LAWN, B. R. (2007). Role of substrate material in failure of crown-like layer structures. *Journal of Biomedical Materials Research* **81B**, 305–11.
- KING, S. J., ARRIGO-NELSON, S. J., POCHRON, S. T., SEMPREBON, G. M., GODFREY, L. R., WRIGHT, P. C. & JERNVALL, J. (2005). Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 16579–83.
- KOENIGSWALD, W. V., RENSBERGER, J. M. & PRETZSCHNER, H. U. (1987). Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* **328**, 159–62.
- KONO, R. T. (2004). Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Anthropological Science* **112**, 121–46.
- KONO, R. T., SUWA, G. & TANIJIRI, T. (2002). A three-dimensional analysis of enamel distribution patterns in human permanent first molars. *Archives of Oral Biology* **47**, 867–75.
- LAWN, B. R. (1993). *Fracture of Brittle Solids*, Second edition. Cambridge University Press, Cambridge.
- LAWN, B. R., BHOWMICK, S., BUSH, M. B., QASIM, T., REKOW, E. D. & ZHANG, Y. (2007). Failure modes in ceramic-based layer structures: a basis for materials design of dental crowns. *Journal of the American Ceramic Society* **90**, 1671–83.
- LAWN, B. R. & EVANS, A. G. (1977). A model for crack initiation in elastic/plastic indentation fields. *Journal of Materials Science* **12**, 2195–99.
- LAWN, B. R. & LEE, J. J.-W. (2009). Analysis of fracture and deformation in teeth subjected to occlusal loading. *Acta Biomaterialia* **5**, 2213–21.
- LAWN, B. R., LEE, J. J.-W. & CHAI, H. (2010). Teeth: among nature’s most durable biocomposites. *Annual Reviews of Materials Research* **40**, 55–75.
- LAWN, B. R., LEE, J. J.-W., CONSTANTINO, P. J. & LUCAS, P. W. (2009). Predicting failure in mammalian enamel. *Journal of Mechanical Behavior of Biomedical Materials* **2**, 33–42.
- LAWN, B. R., PADTURE, N. P., CAI, H. & GUIBERTEAU, F. (1994). Making ceramics ‘ductile’. *Science* **263**, 1114–16.
- LEE, J. J.-W., KWON, J.-Y., CHAI, H., LUCAS, P. W., THOMPSON, V. P. & LAWN, B. R. (2009). Fracture modes in human teeth. *Journal of Dental Research* **88**, 224–29.
- LEE, J. J.-W., MORRIS, D., CONSTANTINO, P. J., SMITH, T. M. & LAWN, B. R. (2010). Properties of tooth enamel in great apes. *Acta Biomaterialia* **6**, 4560–65.
- LOGAN, M. & SANSON, G. D. (2002). The association of tooth wear with sociality of free-ranging male koalas (*Phascolarctos cinereus* Goldfuss). *Australian Journal of Zoology* **50**, 621–26.
- LUCAS, P. W. (2004). *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge, U.K.
- LUCAS, P. W., CONSTANTINO, P. J., WOOD, B. A. & LAWN, B. R. (2008). Dental enamel as a dietary indicator in mammals. *BioEssays* **30**, 374–85.
- LUCAS, P. W., PETERS, C. R. & ARRANDALE, S. (1994). Seed-breaking forces exerted by orangutans with their teeth in captivity and a new technique for estimating forces produced in the wild. *Amer. J. Phys. Anthropol.* **9**, 365.
- MAAS, M. C. & DUMONT, E. R. (1999). Built to last: the structure, function, and evolution of primate dental enamel. *Evolutionary Anthropology* **8**, 133–52.
- MARSHALL, A. J., ANCRENAZ, M., BREARLEY, F. Q., FREDRIKSSON, G., GAHAFFAR, N., HEYDON, M., HUSSON, S., LEIGHTON, M., MCCONKEY, K. R., MORROGH-BERNARD, H., PROCTOR, J., VANSCHAIK, C. P., YEAGER, C. P. & WICH, S. A. (2009). The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans: Are Sumatran forests better orangutan habitat than Bornean forests? In *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (eds S. A. WICH, S. UTAMI, T. M. SETIA and C. P. VANSCHAIK), pp. 97–117. Oxford University Press, Oxford.

- MARSHALL, D. B., COX, B. N. & EVANS, A. G. (1985). The mechanics of matrix cracking in brittle-matrix fibre composites. *Acta Metallurgica* **23**, 2013–21.
- MARTIN, L. (1985). Significance of enamel thickness in hominoid evolution. *Nature* **314**, 260–263.
- MCARTHUR, C., SANSON, G. D. & BEAL, A. M. (1995). Salivary proline-rich proteins in mammals—roles in oral homeostasis and counteracting dietary tannin. *Journal of Chemical Ecology* **21**, 663–91.
- MOLNAR, S. & GANTT, D. G. (1977). Functional implications of primate enamel thickness. *American Journal of Physical Anthropology* **46**, 447–454.
- MYOUNG, S., LEE, J. J.-W., CONSTANTINO, P. J., LUCAS, P. W., CHAI, H. & LAWN, B. R. (2009). Morphology and fracture of enamel. *Journal of Biomechanics* **42**, 1947–51.
- OLEJNICZAK, A. J., TAFFOREAU, P., FEENEY, R. N. M. & MARTIN, L. B. (2008). Three-dimensional primate molar enamel thickness. *Journal of Human Evolution* **54**, 187–95.
- OSBORN, J. W. (1969). The 3-dimensional morphology of the tufts in human enamel. *Acta Anatomica* **73**, 481–95.
- OSBORN, J. W. (1981). Dental tissues. In *Dental Anatomy and Embryology*, vol. 1 (ed. J. W. OSBORN). Blackwell, Oxford.
- PALAMARA, J., PHAKEY, P. P., RACHINGER, W. A. & ORAMS, H. J. (1989). The ultrastructure of spindles and tufts in human dental enamel. *Advanced Dental Research* **3**, 249–57.
- PERZIGIAN, A. J. (1981). Allometric analysis of dental variation in a human population. *American Journal of Physical Anthropology* **54**, 341–45.
- PIPERNO, D. R. (2006). *Phytoliths: A Comprehensive Guide for Archaeologists and Paleocologists*. AltaMira Press, Lanham, MD.
- POPOWICZ, T. E., RENSBERGER, J. M. & HERRING, S. W. (2001). The fracture behavior of human and pig molar cusps. *Archives of Oral Biology* **46**, 1–12.
- PRINZ, J. F. & LUCAS, P. W. (2000). Saliva tannin interactions. *Journal of Oral Rehabilitation* **27**, 991–94.
- QASIM, T., BUSH, M. B., HU, X. & LAWN, B. R. (2005). Contact damage in brittle coating layers: influence of surface curvature. *Journal of Biomedical Materials Research* **73B**, 179–85.
- QASIM, T., FORD, C., BUSH, M. B., HU, X. & LAWN, B. R. (2006). Effect of off-axis concentrated loading on failure of curved brittle layer structures. *Journal of Biomedical Materials Research* **76B**, 334–39.
- QASIM, T., FORD, C., BUSH, M. B., HU, X., MALAMENT, K. A. & LAWN, B. R. (2007). Margin failures in brittle dome structures: relevance to failure of dental crowns. *Journal of Biomedical Materials Research* **80B**, 78–85.
- RAYFIELD, E. J., NORMAN, D. B., HORNER, C. C., HORNER, J. R., SMITH, P. M., THOMASON, J. J. & UPCHURCH, P. (2001). Cranial design and function in a large theropod dinosaur. *Nature* **409**, 1033–37.
- RENSBERGER, J. M. (2000). Pathways to functional differentiation in mammalian enamel. In *Development, Function and Evolution of Teeth* (eds M. F. TEAFORD, M. M. SMITH and M. W. J. FERGUSON), pp. 252–68. Cambridge University Press, Cambridge.
- RENSBERGER, J. M., FORSTEN, A. & FORTELIUS, M. (1984). Functional evolution of the cheek tooth pattern and chewing direction in tertiary horses. *Paleobiology* **10**, 439–52.
- ROACH, D. H., LATHABAI, S. & LAWN, B. R. (1988). Interfacial layers in brittle cracks. *Journal of the American Ceramic Society* **71**, 97–105.
- ROBINSON, C., BROOKS, S. J., BONASS, W. A., SHORE, R. C. & KIRKHAM, J. (1997). Enamel Maturation. In *CIBA Foundation Symposia 205—Dental enamel*, vol. 205, pp. 156–74. John Wiley, Chichester.
- ROBINSON, J. T. (1954). Prehominid dentition and hominid evolution. *Evolution* **8**, 324–34.
- RUDAS, M., QASIM, T., BUSH, M. B. & LAWN, B. R. (2005). Failure of curved brittle layer systems from radial cracking in concentrated loading. *Journal of Materials Research* **20**, 2812–19.
- SANDER, P. M. (2000). Prismless enamel in amniotes: terminology, function, and evolution. In *Development, Function and Evolution of Teeth* (eds M. F. TEAFORD, M. M. SMITH and M. W. J. FERGUSON), pp. 92–106. Cambridge University Press, Cambridge.
- SAUTHER, M. L. & CUOZZO, F. P. (2009). The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology* **140**, 671–86.
- SCHWARTZ, G. T. (2000). Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *American Journal of Physical Anthropology* **111**, 221–244.
- SHELLIS, R. P., BEYNON, A. D., REID, D. J. & HJEMAE, K. M. (1998). Variations in molar enamel thickness among primates. *Journal of Human Evolution* **35**, 507–522.
- SHELLIS, R. P. & DIBBIN, G. H. (2000). Enamel microporosity and its functional implications. In *Development, Function and Evolution of Teeth* (eds M. F. TEAFORD, M. M. SMITH and M. W. J. FERGUSON), pp. 242–51. Cambridge University Press, Cambridge.
- SMITH, T. M., OLEJNICZAK, A. J., MARTIN, L. B. & REID, D. J. (2005). Variation in hominid molar enamel thickness. *Journal of Human Evolution* **48**, 575–92.
- SOGNNAES, R. F. (1949). The organic elements of enamel. II. The organic framework of the internal part of the enamel, with special regard to the organic basis for the so-called tufts and schreger bands. *Journal of Dental Research* **28**, 549–57.
- SOGNNAES, R. F. (1950). The organic elements of enamel. IV. The gross morphology and the histological relationship of the lamellae to the organic framework of the enamel. *Journal of Dental Research* **29**, 260–269.
- SPENCER, M. A. (1998). Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. *Journal of Human Evolution* **34**, 25–54.
- STRAIT, D. S., WEBER, G. W., NEUBAUER, S., CHALK, J., RICHMOND, B. G., LUCAS, P. W., SPENCER, M. A., SCHREIN, C., DECHOW, P. C., ROSS, C. F., GROSSE, I. R., WRIGHT, B. W., CONSTANTINO, P. J., WOOD, B. A., LAWN, B. R., HYLANDER, W. L., WANG, Q., SLICE, D. E., BYRON, C. & SMITH, A. L. (2009). The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 2124–29.
- TABOR, D. (1951). *Hardness of Metals*. Clarendon, Oxford.
- TEAFORD, M. F. (1988). A review of dental microwear and diet in modern mammals. *Scanning Microscopy* **2**, 1149–66.
- TEAFORD, M. F. & UNGAR, P. S. (2000). Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 13506–11.
- TEN CATE, A. R. (1989). *Oral Histology: Development, Structure, and Function*, Third edition. Mosby, St. Louis.
- THOMASON, J. J. (1991). Cranial strength in relation to estimated biting forces in some mammals. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **69**, 2326–33.
- TOBIAS, P. V. (1967). *The Cranium and Maxillary Dentition of Australopithecus (Zinjanthropus) boisei. Olduvai Gorge*. Cambridge University Press, Cambridge, UK.
- UNGAR, P. S. (1990). Incisor microwear and feeding behavior in *Alouatta seniculus* and *Cebus olivaceus*. *American Journal of Primatology* **20**, 43–50.
- UNGAR, P. S. (1998). Dental allometry, morphology, and wear as evidence for diet in fossil primates. *Evolutionary Anthropology* **6**, 205–17.
- UNGAR, P. S., TEAFORD, M. F., GLANDER, K. E. & PASTOR, R. F. (1995). Dust accumulation in the canopy—a potential cause of dental microwear in primates. *American Journal of Physical Anthropology* **97**, 93–99.
- VOGEL, E. R., WOERDEN, J. T. v., LUCAS, P. W., ATMOKO, S. S. U., SCHAIK, C. P. v. & DOMINY, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution* **55**, 60–74.
- WALKER, A. C. (1981). Diet and teeth: dietary hypotheses and human evolution. *Philosophical Transactions of the Royal Society of London* **B292**, 57–64.
- WALLACE, J. A. (1973). Tooth chipping in the australopithecines. *Nature* **244**, 117–18.
- WARD, C. V., LEAKEY, M. G. & WALKER, A. (2001). Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution* **41**, 255–368.
- WILL, P. D., RIVER, J. D. & ROSEN, S. (1971). Frequency of enamel lamellae in molars of rats on coarse and fine particle diets. *Journal of Dental Research* **50**, 902–05.
- WOOD, B. A. & STACK, C. G. (1980). Does allometry explain the differences between 'gracile' and 'robust' australopithecines? *American Journal of Physical Anthropology* **52**, 55–62.
- WROE, S., FERRARA, T. L., MCHENRY, C. R., CURNOE, D. & CHAMOLI, U. (2010). The craniomandibular mechanics of being human. *Proceedings of the Royal Society of London B*.
- WROE, S., MCHENRY, C. R. & THOMASON, J. (2005). Bite club: comparative bite force in big biting mammals and the prediction of predatory behavior in fossil taxa. *Proceedings of the Royal Society of London* **B272**, 619–25.
- XIE, Z.-H., SWAIN, M. V. & HOFFMANN, M. J. (2009a). Structural integrity of enamel: experimental and modeling. *Journal of Dental Research* **88**, 529–33.
- XIE, Z.-H., SWAIN, M. V., SWADENER, G., MUNRO, P. & HOFFMANN, M. (2009b). Effect of microstructure upon elastic behavior of human tooth enamel. *Journal of Biomechanics* **42**, 1075–80.

(Received 29 October 2010; revised 31 March 2011; accepted 1 April 2011; published online 20 April 2011)