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Evolutionary biology

On the vital role of enamel prism interfaces and graded properties in human tooth survival

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Teeth of omnivores face a formidable evolutionary challenge: how to protect against fracture and abrasive wear caused by the wide variety of foods they process. It is hypothesized that this challenge is met in part by adaptations in enamel microstructure. The low-crowned teeth of humans and some other omnivorous mammals exhibit multiple fissures running longitudinally along the outer enamel walls, yet remain intact. It is proposed that inter-prism weakness and enamel property gradation act together to avert entry of these fissures into vulnerable inner tooth regions and, at the same time, confer wear resistance at the occlusal surface. A simple indentation experiment is employed to quantify crack paths and energetics in human enamel, and an extended-finite-element model to evaluate longitudinal crack growth histories. Consideration is given as to how tooth microstructure may have played a vital role in human evolution, and, by extension, to other omnivorous mammals.

1. Introduction

Teeth are critical to the survival and development of most mammals. It is through the mouth that organisms gain sustenance, and teeth are the primary agents that process food intake. Teeth have to be resilient enough to break food down before they themselves fracture [1]. In humans, they have to endure over a million occlusal bite forces up to 1 kN over a lifetime [2,3]. How then do teeth survive?

It is well recognized that the fundamental structure of the enamel/dentin complex is a major contributing factor in tooth resilience [3,4]. But human tooth enamel is heavily mineralized and inherently fragile: it contains weak interfaces between hydroxyapatite prisms or rods. Inter-prism slippage allows for deformation under concentrated occlusal contacts [5–7]. ‘Tufts’, wavy outward-extending proteinaceous microfissures [8,9] adjacent to the dentino-enamel junction (DEJ), act as sources of crack initiation [10]. Longitudinal fissures in the outer enamel are commonplace in primates and other mammals with low-crowned (bunodont) dentition [11].

But it remains unclear as to how weak inter-prism interfaces offer easy fracture paths yet enable teeth to remain intact [12,13]. We hypothesize that such interfaces are a vital component of tooth survival in humans. The notion of built-in weakness to gain toughness is not new in biomaterials: layered nacre and fibrous bone microstructures, whereby cracks are deflected away from a forward path or are inhibited by other energy dissipation mechanisms, are prime examples [14,15]. How do cracks, once initiated, grow so easily in the

Figure 1. (a) Longitudinal radial (R) and margin (M) cracks in extracted human molar tooth, loaded *ex situ* at its prominent upper cusp at load $P = 390$ N with a flat metal plate [10]. (b) Multiple longitudinal cracks in museum gorilla tooth [11]. (c) Crack paths at indentation on polished enamel plate from human tooth molar with conical indenter of tip radius $r = 200$ μm at load $P = 20$ N, at low magnification. (d) Upper segment of same ring crack at high magnification. (e) Relative crack driving force G (mechanical energy release rate) as function of angle θ for crack deflected around prism. From fig. 2.19 in [16]. (f) Number of cracks passing around (blue) and through prisms (red) as function of θ .

enamel surface without adversely affecting function? What are the energetics of the weak interfaces? What is the role of any property gradients through the enamel thickness? This study describes simple experimental and analytical tests to answer such questions in the context of enamel microstructure, occlusal bite forces and evolutionary pressures.

2. Materials and methods

Photographs from earlier studies of an extracted human molar loaded at its apex in figure 1a [10] and a museum gorilla tooth

specimen in figure 1b [11] illustrate longitudinal cracks in primate enamel, some extending downward from the cusp (radial cracks, R) and others upward from the base (margin cracks, M). Such features have been posited as ‘fingerprints’ of dietary history [11,17].

To identify crack modes and paths, horizontal slices were cut from five extracted human molar teeth immediately below a prominent cusp, top surface diamond ground and fine polished to 0.5 μm smoothness to reveal the prism structure. The slices were loaded with a cone indenter of spherical tip radius 200 μm (Revetest RST3, Anton Paar, Graz, Austria). Ensuing crack patterns were examined in an environmental scanning electron microscope (Quanta 3D, FEI, The Netherlands), at low magnification in figure 1c and higher magnification in figure 1d.

Figure 2. (a) Graded (blue) and uniform (red) toughness T and elastic modulus E properties from outer surface to inner (DEJ) interface of human enamel. (b) XFEM-computed R-crack profiles in dome model of human tooth of height 7.5 mm : red coloration for enamel with uniform properties; blue for enamel with graded properties; grey for uncracked enamel. Starter crack location S–S. (c) Plots of outer and inner enamel crack depth below cusp as function of applied force. From [18,19].

Measurement of crack deflection angles θ around individual prisms, along with an energy balance analysis in figure 1*e,f*, was used to evaluate the energetics of the prism interface relative to that of bulk hydroxyapatite.

An extended-finite-element model (XFEM) was employed to determine the mechanics of longitudinal crack growth in enamel [18]. Human molar teeth were modelled as a dome-like shell of height 7.5 mm and enamel thickness 1.5 mm with in-filled interior (dentin). A starter crack was placed either at the cusp to simulate R cracks or at the base to simulate M cracks. The starter cracks are proxies for pre-existing defects (such as tufts) in the enamel and enable one to focus on the ensuing propagation rather than initiation phase of fracture. Input material properties for the model were elastic modulus E and toughness T , both graded and uniform through the enamel wall thickness as in figure 2*a* [19]. The dome structure was loaded at its cusp incrementally, enabling stable crack growth to be followed stepwise to completion around the enamel walls, as depicted in figure 2*b,c*.

Details of the methods are outlined in the electronic supplementary material.

3. Micromechanics of tooth survival

The sphere indentation in figure 1*c,d* reveals critical information about crack paths in rod-like structures with weak interfaces. Whereas some cracks deflect around the prisms, others pass through them. Of particular interest is the ring crack around the indent circumference in figure 1*c*. Any local deflections are not enough to prevent the crack following the circular path governed by the principal stress

trajectories around the contact: the crack has directional stability [20]. This is different from the case of nacre, where deflections along ultra-weak lamella interfaces deviate cracks completely away from their forward propagation direction and arrest them. In the case of enamel, the prism diameters are small relative to the scale of typical contact diameters, so individual deflections amount to little more than a blip in crack paths. It is apparent in the full-tooth examples of figure 1*a,b* that longitudinal crack propagation is relatively unimpeded by any such local deflections, directed predominantly by hoop tensile strains in the compressively loaded shell structure, almost as if the outer enamel behaves as an isotropic, homogeneous glass.

The fact that the crack paths sometimes deflect around prisms and sometimes through them enables us to estimate the interface cohesive energy. Close inspection of 60 crack-prism impingement sites in several images of the kind in figure 1*d* reveals that deflection occurs when $\theta \sim 62.5^\circ$ or less in figure 1*f*. The requirement for crack equilibrium is that the rate of mechanical energy released G should just balance the corresponding surface energy W required to separate the material at each extension increment. Now G declines with θ [16], so the condition for the crack to deflect is that $G(\theta)/G(0) > W_I/W_B$, where I and B denote interface and bulk (hydroxyapatite), respectively. The deflection condition $\theta \sim 62.5^\circ$ corresponds to $W_I \sim 0.5W_B$ in figure 1*e* (dashed straight lines). That is, the interface energy is about one half that of bulk hydroxyapatite, high enough to bond the structure but low enough to ensure significant local crack deflections.

The effect of graded elastic modulus E and toughness T through the enamel in figure 2a on longitudinal crack evolution is demonstrated in the XFEM analysis. Figure 2b shows half-cross sections of R-crack profiles: red coloration for cracks in uniform enamel (no gradation, load $P = 840$ N); blue for cracks in enamel with graded properties (load $P = 420$ N); grey for uncracked enamel. The entire development of crack growth around the tooth walls from starter crack (S–S) to completion is plotted in figure 2c. Note that this growth is stable with respect to applied axial load across its entire development, i.e. extends stepwise with each increment in load. (Similar stable growth histories are obtained for M cracks.) The effect of gradation is to promote crack extension in the outer regions and similarly to inhibit it in the inner regions. For the graded structure, it would take an inordinately high occlusal load approaching 2 kN, i.e. much higher than normal bite forces, to drive the crack to the DEJ. If the enamel were to have a uniform property gradient, the cracks would advance more or less on a straight front, penetrating to the DEJ all along the way, as visually demonstrated in simulated molar tooth models of epoxy-filled transparent glass shells [21].

4. Discussion

(a) Structural considerations

The presence of longitudinal R and M cracks in tooth walls (figure 1a) under normal bite forces attests to the inbuilt weakness of enamel in humans and potentially in other omnivorous mammals. The stability of these cracks on loading indicates that their presence does not constitute failure, even when they propagate fully around the side wall. The tooth can sustain a multiplicity of such longitudinal cracks (figure 1b). Allowing teeth to dry *ex vivo* widens the outer fissures (figure 1b) [11]. Ordinarily, these cracks do not penetrate to the vulnerable interior. Other, more deleterious fracture modes—chipping [22], splitting [23], transverse fracture [24] and spallation [21]—can indeed cause some form of tooth failure, but only from inordinately high bite forces [17].

So what are the vital roles of inter-prism weakness and property gradation in maintaining tooth integrity? It is well documented that decussation is responsible for enhanced toughness in the human enamel interior depicted in figure 2a [25]. Relative misorientation of prism bundles adjacent to the DEJ cause ingrowing cracks to bifurcate, resulting in a slowed down, bridged fracture path. For this to occur, the prism interfaces have to be weak enough to deflect the cracks between the bundles. The specific nature of the interface is not an issue here [4]: it needs only to be of sufficiently low energy W_i relative to bulk hydroxyapatite W_B . As seen in figure 1c,d, not all crack increments pass around the prisms; it is necessary only for a substantive fraction of these to do so, in order that the main crack front suffers some degree of bifurcation. If the prism interfaces were to be strong, an incoming crack would undergo no such bifurcation. Augmenting this inner crack toughness enhancement is the corresponding fall-off in modulus (figure 2a), redirecting the bulk of stresses in occlusal loading toward the outer tooth walls.

(b) Biological implications

While the data presented here relate specifically to human teeth, the results may have a broader reach. Teeth in a

wide range of mammals show the kind of surface fissures evident in figure 1a,b, yet remain intact [11]. Most mammals are diphyodont—they produce just two sets of teeth during their lifetime. Maintaining dental integrity is therefore paramount, especially in omnivores that need to protect against both fracture and wear from food sources encompassing a range of material properties. Species with bunodont teeth, including some other primates but also ursids (bears) and suids (pigs), may have achieved this in the same manner as humans, with graded microstructures of weakly bonded prisms decussated adjacent to the DEJ [3,26–28]. Primates in particular show common cross-section tooth geometries and enamel property gradients [29,30]. Any variants in inter-prism energetics or decussation patterns may provide different degrees of protection, but not alter the underlying fracture-suppression mechanism. At the same time, prisms in human teeth intersect the outer surface nearly radially, conferring abrasive wear resistance and restricting chipping [4,31,32]. Thick enamel further protects against fracture and wear at high or prolonged bite forces [4,33–35]. Most of the chewing load in omnivores is supported by the molars, which in humans can sustain uncommonly high bite forces approaching 1 kN [36], i.e. within the range displayed in figure 2c.

These elements of dental resiliency may not emerge as so critical in other tooth forms, for instance in carnivores and herbivores with more elongate teeth, if only because it requires much higher forces to drive longitudinal cracks further distances to completion [37]. The elongate canines of carnivores and aprismatic conical teeth of reptiles have relatively thin enamel and are more likely to fail by transverse fracture from isolated extreme bite events [17]. Non-mammals such as sharks and crocodilians are polyphyodont and produce several sets of teeth during their lifetime, thus mitigating against the need for ultra-resilient enamel microstructures in those species.

A shift to omnivory affords compelling evolutionary benefits, including adaptability to novel habitats, changing environmental conditions and broader geographic ranges [38–40]. Humans have proved most adaptable, surely due in large part to their cultural advantages, but also to their distinctive enamel structure.

Ethics. Approval to conduct this research on human tissue was obtained from the Bioethics Committee of the University of Extremadura (permit number 213//2019).

Data accessibility. Data novel to this manuscript can be found in the electronic supplementary material.

Authors' contributions. O.B.L. conducted the indentation experiments. M.B.B. performed the XFEM analysis. P.C. and B.L. performed some of the initial fracture studies seen in figure 1a,b. B.L. analysed fracture mechanics. B.L. and P.C. wrote the manuscript, with input from O.B.L. and M.B.B. All authors agree to be held accountable for the content therein and approve the final version of the manuscript. Extracted human molars were provided by Dr Florencio Monje Gil (CICOM clinic, Badajoz, Spain). Fernando Rodríguez-Rojas assisted in the preparation of enamel test specimens for the indentation tests. Amir Barani contributed to the XFEM computations.

Competing interests. We declare we have no competing interests.

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