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Dental enamel as a dietary indicator in mammals

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Summary

The considerable variation in shape, size, structure and properties of the enamel cap covering mammalian teeth is a topic of great evolutionary interest. No existing theories explain how such variations might be fit for the purpose of breaking food particles down. Borrowing from engineering materials science, we use principles of fracture and deformation of solids to provide a quantitative account of how mammalian enamel may be adapted to diet. Particular attention is paid to mammals that feed on 'hard objects' such as seeds and dry fruits, the outer casings of which appear to have evolved structures with properties similar to those of enamel. These foods are important in the diets of some primates, and have been heavily implicated as a key factor in the evolutionary history of the hominin clade. As a tissue with intrinsic weakness yet exceptional durability, enamel could be especially useful as a dietary indicator for extinct taxa.

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Introduction

Mammalian enamel is a heavily mineralized tissue, formed by a slow, two-stage, secretion–maturation process. The final product, shown schematically in Fig. 1, provides a hard, durable veneer on the surface of a tooth that overlies a much larger volume of less mineralized dentine.(1) A third mineralized tissue, cement (or cementum), covers the root—the part of the tooth lacking enamel—and anchors the tooth in its socket by providing a bed for the collagen fibres within the periodontal ligament connecting the tooth to the walls of the bone alveolus. Once formed, mammalian enamel tissue cannot be substantially modified except by ion exchange within the mouth.(2) Only small amounts are formed in a lifetime: a modern human probably secretes less than 4 cubic cm of enamel over some 12 years of cellular activity. Yet enamel is highly variable in shape, size, structure and properties, both within and between mammalian species.(3) In a given modern human, its distribution may vary considerably between adjacent teeth or even within a single tooth crown (Fig. 1A).(4,5) There are also considerable variations in the thickness of molar enamel between primates; relative to modern humans, the enamel is considerably thinner in our closest living relatives, the African great apes, while in orangutans it is only slightly thinner.(6–9) Detailed functional explanations for these differences are lacking, with most current research directed instead towards understanding the development of both enamel cap and tooth crown as an integral structure.(10)

It is of course possible that enamel, the product of a rich interplay among at least 200 genes,(11) is phylogenetically conservative and relatively unresponsive to selective pressures. However, most mammalian fossils are teeth (and, very often, little else), providing us with some of our strongest clues to the evolutionary history of taxa, including dietary adaptation. A working hypothesis might thus take the following form: *protective enamel coats appear so definite in form—shape, thickness and microstructure—that they carry an unambiguous adaptive signal*. We will show how microstructural differences might be most readily manifested in the fracture and deformation properties of enamel, noting that structural complexity often dictates crack patterns in biological tissues. As to enamel thickness, two notions have been considered in attempts at explaining why it might be greater in some mammals than in others. First, thick enamel may prolong tooth lifetime where chewing causes progressive surface loss.(12,13) Second, it may enhance resistance to fracture from biting on hard objects.(14) We will argue that the second of these notions, considered together with microstructural variations, is of special relevance to hominin enamel adaptation.

We begin by discussing the structure of enamel and the ways selective pressures can influence the external form and internal structure of enamel. We use concepts on 'fracture and deformation' mechanics from the materials science literature to describe the way that enamel coating layers may undergo irreversible damage under loading. Such a description allows for estimates of the forces required to break down seeds and other hard food objects. This approach provides a rigorous, quantitative basis for testing our adaptation hypothesis. We will not discuss theories of adaptation of tooth shape, e.g. the form of cusps and linking crests, leaving those for other

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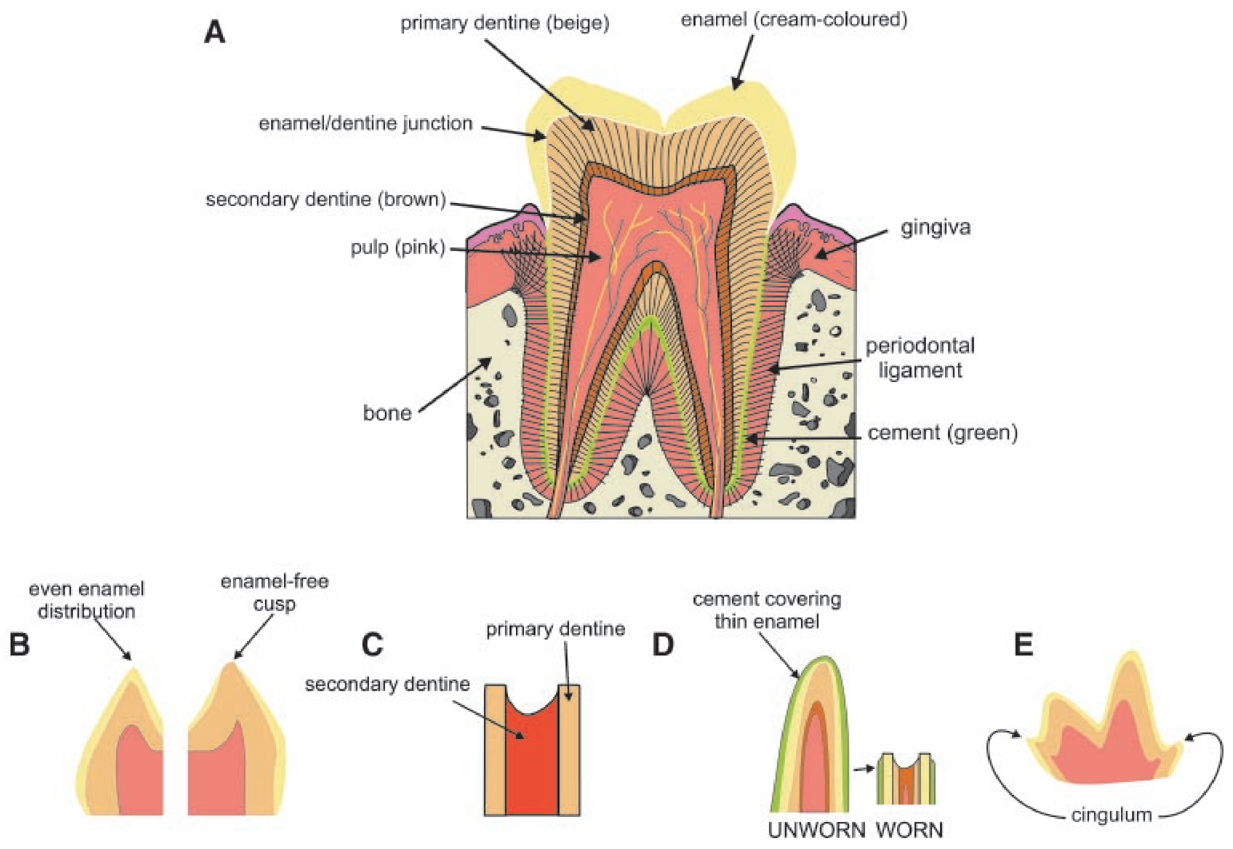

Figure 1. Schematic views of variation in dental enamel in mammals. **A:** The structure of a modern human tooth early in function. The enamel (cream-coloured) is unevenly distributed over the tooth crown. Primary dentine (beige) is the compliant base on which enamel rests and is permeated by tubules in most mammals. Secondary dentine (brown) forms after tooth eruption, continuing throughout the life of the tooth, with thickness, structure (and thus properties) that depend on loading and wear. Adapted from earlier work.(15) **B:** Many mammals have an even enamel coat on the crown, but some rodents have enamel-free cusp tips indicating that local control of tissue deposition is possible. **C:** Sloths lack enamel, but still produce complex surfaces by way of typical mammalian tubular dentine that surrounds a softer dentine (riddled with vascular channels). **D:** Cement (green) covers the crown in some high-crowned (hypsodont) herbivores like horses where it assists the dentine in supporting enamel ridges. Exposure of dentine produces a complex surface and, in some species, additional surface roughness is provided by Hunter-Schreger bands. **E:** The cingulum, a low shelf on the crowns of many mammalian teeth, not in food contact.

accounts.(15) We will focus rather on hard-object feeding in primates, as well as in pigs and peccaries(16) and sea otters,(17) because consumption of such foods is widely perceived to relate to enamel thickness(18) and because analytical solutions for critical conditions are possible. Comments on adaptation to other food types will be offered purely for comparative purposes.

Enamel variation

The basic structural unit of mammalian enamel is the rod or prism, an elongate multi-crystalline structure that is at least partially bound by an organic sheath (Fig. 2A,B).(19,20) Rods begin close to the enamel–dentine junction, often extending almost to the outer surface of the tissue. Sometimes the rods are straight,(21) but often they display a 'planar crimp'—a wave restricted to one plane—rather like the fibres of wool (Fig. 2A).(3) Adjacent bundles of rods often wave slightly out of phase, with a progressive change across a region referred to as 'decussation' (crossing). Such patterns are readily detected under a polarizing light microscope as an optical illusion whereby the enamel appears to be striped. Alternating light and dark stripes are called Hunter-Schreger bands, the width and spacing of which reflects the characteristics of the wave—in primates, the more curved these bands, the more decussated the enamel (Fig. 2B).(3) Decussation is a feature of the enamel of many mammals, and a variety of patterns has been documented:(22) (i) radial enamel in which rods pass towards the surface without deviating (e.g. early mammals),(21) (ii) enamel where decussation is restricted to the region close to the dentine (e.g. modern humans, Fig. 2A),(3)

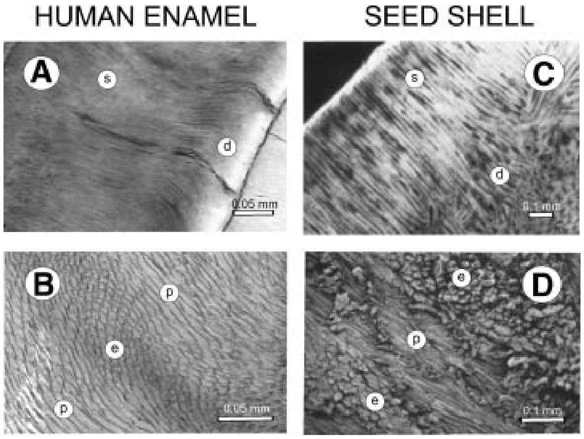

Figure 2. Convergence of microstructures in human enamel (**left, A,B**) and seed shell (*Mezzettia parviflora*, Annonaceae) (**right, C,D**). **A:** Smooth changes in enamel fibre/rod morphologies from decussation (d) to straight (s) as they pass towards the shell/tooth surface upwards and to the left. **B:** Fibres/rods viewed end-on (e) and near-parallel to the field of view (p), so forming Hunter-Schreger bands. A tuft is seen as a dark wavy line extending upwards and to the left into the enamel. **C:** Decussating (d) fibres in the *Mezzettia* shell, becoming straight near surface at upper left. D: Decussation of fibre bundles in seed shell, resembling Hunter-Schreger bands in enamel.

and (iii) enamel where decussation occurs through the thickness of the enamel, with Hunter-Schreger bands extending close to the tooth surface (molars of rhinoceroses,(23,24) many extinct mammals(25) and New World pitheciin monkeys(26)). Additional features in enamel such as 'lamellae' and 'tufts' have been described. Lamellae are closed cracks extending through the enamel thickness, while tufts are wavy hypocalcified strands extending from the enamel–dentine junction hundreds of micrometers into the enamel (Fig. 2A).(27,28) Lamellae are only present in erupted (functional) teeth.(28,29) Tufts *sensu stricto* probably develop before eruption.(27)

The thickness of the enamel cap on mammalian teeth is under strong genetic control(30) and can range from 0.05 to 5.0 mm, depending on tooth type, species and location on the crown. (In baboons, $h^2 = 0.32–0.44$, equal to or exceeding the heritability of other skeletal measurements.) While some species have a relatively even distribution of enamel over the dental cap (e.g. insectivorous mammals(21) and the spider monkey, Fig. 1B(26)), others develop much thicker enamel over the cusps, especially over the cusp tips (e.g. modern humans, Fig. 1A(8)). In contrast, in other mammals, the enamel is thinner over the cusps than elsewhere (e.g. hippopotamus(31)). In extreme cases, the tooth may be entirely free of enamel over the cusps (e.g. mouse, Fig. 1B);(32) or indeed over the entire tooth, as in the sloth where differential wear is caused by differences in dentinal structure (Fig. 1C).(33) In some mammals with tall crowns, the enamel is coated by cement, a tissue usually found only in the tooth socket (Fig. 1D).(34) Early insectivorous mammals tended to have thin enamel, with a pronounced 'shelf' near the cervical region called the cingulum (Fig. 1E). The cingulum may bear cusps, but this feature is often completely away from contact with food. (Note, however, that in early molar evolution the cingulum did not bear such cusps).(35–37) The cingulum is currently viewed as a protection for the gums and periodontal ligament,(38) but we suggest an alternative role in this paper. Clearly, the form of the enamel cap—and indeed of the whole tooth structure—varies greatly among mammals.

Selective pressures on enamel form

Several lines of evidence indicate that enamel structure and integrity are vital for tooth function. Modern humans with amelogenesis imperfecta suffer easy fracture of the enamel.(39,40) This disease is also known in domesticated animals—cattle with it cannot feed on a normal diet because their cheek teeth do not develop the enamel ridges needed for breaking down grass blades.(41) The fitness of such animals is inevitably affected, as has been shown in a lemur species when molar ridges are lost (due to senescence, not disease).(42) In the enamel of modern humans, post-eruption cracks (lamellae) provide pathways for carious infections.(43)

The microstructure of enamel has an effect on tooth function because enamel deforms and cracks preferentially between rods rather than across them.(44–47) Enamel decussation plays an important role in resisting crack propagation—it makes the tooth tougher.(48,49) As indicated, the degree of rod decussation varies across the tooth crown. There is also evidence in modern human enamel of a gradient in hardness and modulus through the thickness of enamel,(50) confirming an inhomogeneity in properties, but such gradients are not seen in all primates (e.g. howler monkeys).(51) Generally though, gradients in enamel have been less well studied than any corresponding gradients in dentine, possibly because the latter comes in larger volumes.(52–54)

There has never been any integrated analysis of the roles of enamel thickness (long recognised as an important taxonomic characteristic),(6) microstructure and properties in sustaining the integrity of a tooth. Modern humans have 1 to 2 mm thick molar enamel that has to withstand forces that can exceed 700 N.(55) We suggest that the key to matching form to function is to ensure that the geometrical characteristics of the dentition match the properties of food objects without incurring tooth fracture. Hard foods in particular make small areas of contact with the enamel cap, thereby producing high stress concentrations and enhancing any tendency to fracture.(14,56) What, then, are the physical requirements for successful function in enamel forms?

Conventional stress analysis and materials evaluation

Two different approaches to investigating mechanical explanations of tooth function and longevity have received a great deal of attention: finite element analysis (FEA) and indentation. FEA models tooth function on a computer by dividing a virtual volume mathematically into a large number of interconnected cells and then applying virtual forces at the outer surface. Distributions of ensuing stress (transmitted force at any point within the volume divided by the area over which it acts, units $N/m^2 = Pa$) are then tracked by numerical iteration. An early two-dimensional study on a modern human molar model suggested that tensile stresses can spread round the enamel cap to the cervical margin (the neck of the tooth where the crown meets the root).(57) A later three-dimensional study suggested that stresses remain confined to the region below the loaded area if the Young's modulus of enamel were to be direction-dependent, i.e. anisotropic.(58,59) Yet another study predicted that stresses decrease slightly as enamel is thickened, but can sometimes be high near the enamel–dentine junction.(12,59) Analyses in the materials literature on tooth-like dome structures came to similar conclusions.(60–62) Clearly, a wide range of stress distributions is feasible, depending on the geometries and properties used to construct the tooth model. The closest association of FEA with material properties comes from identifying the maximum tensile stress with strength S (resistance to abrupt fracture), and the maximum shear stress with yield stress Y (resistance to onset of plasticity). However, such identifications provide little insight into the way damage initiates and evolves within any given structure.

Indentation is a mechanical probe used to measure elastic (Young's) modulus E (resistance to elastic deformation) and hardness H (resistance to irreversible deformation, or plasticity). It usually involves contact between a surface and a hard, sharp-point diamond pyramidal or conical indenter. Both E and H have units of stress (Pa), and can be deconvoluted from impression sizes or load–displacement measurements at the contact site. Automated nanoindentation has been employed to map out E and H variations within tooth sections.(50,63,64) Hardness is related to yield stress by the so-called 'constraint' relation $H = 3Y$.(65) Microindentation has been used to measure toughness T (resistance to crack propagation) from the size of any cracks emanating from the impression corners.(64,66) Toughness involves units of stress and crack size ($MPa\ m^{1/2}$). Toughness is related to strength by the widely used Griffith relation,(67) $S = T/(\pi c_f)^{1/2}$, where c_f is a characteristic flaw size ("weak link" concept). In enamel, flaws are most likely associated with lamellae in the rod-like microstructure, in the range ~100 μm, relatively large in the context of ordinary brittle solids.(67) Typical, averaged values of E, H, S and T are given in Table 1 for materials of interest in this paper.

Both FEA and instrumented indentation approaches have shortcomings. Finite element analysis computes stress distributions but, as indicated above, provides little insight into the role of material properties. Indentation, in its simplest form, provides information on material properties but little on the role of tooth geometry and stress distribution. Neither approach provides much predictive insight into how differences in geometric or material variables affect tooth function. Any hypothesis that seeks to relate enamel form to dental function must tie together essential stress characteristics in the tooth cap with mechanical properties of enamel. It is our contention that the keys to such an understanding are most likely to be found in the discipline of fracture and deformation mechanics. This discipline seeks to determine interrelationships between applied loads for initiation and propagation of irreversible damage in terms of structural geometry and materials properties. General descriptions are available in standard texts.(15,67–69) We simply summarise below some relevant results in the context of 'contact mechanics', the area of mechanics that deals with the mechanical responses of bodies in mutual contact.

Contact fracture and deformation of hard materials

Consider a hard, brittle monolithic solid with properties representative of tooth enamel (Fig. 3A). A concentrated load P is applied by a rigid spherical indenter at the top surface. The effective indenter radius r is given by $1/r = 1/r_i + 1/r_s$, where subscripts i and s refer to indenter and specimen, respectively.(70) Note that r is to be distinguished from the contact radius, which will generally be considerably smaller. The stresses are concentrated at or near the top surface, so fracture or deformation will be generated there. Fracture

Table 1. Representative properties of materials

Material	Modulus E (GPa)	Hardness H (GPa)	Strength S (MPa)	Toughness T ($MPa\ m^{1.2}$)
Human enamel	90	3.5	30	0.9
Human dentine	20	0.6	—	3.1
Macadamia shell	5.3	0.18	58	1.5
Macadamia kernel	0.03	—	—	0.04

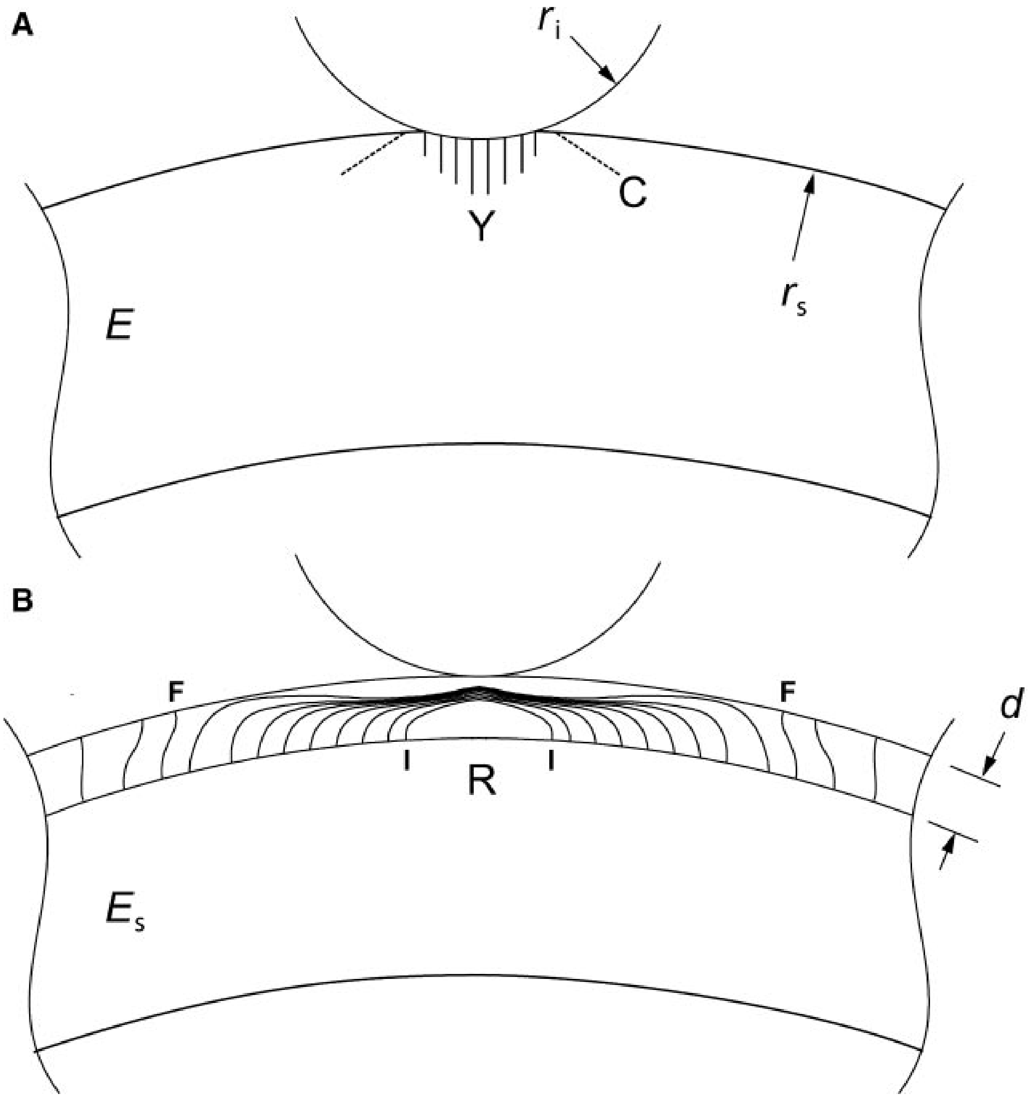

Figure 3. Schematic depicting surface and subsurface damage modes in curved surface of radius r_s from contact with a curved surface of radius r_i: **A:** monolithic brittle structures, cone cracks (C) and yield deformation (Y); **B:** bilayers, radial cracks (R), indicating evolution from initiation (I) to through-thickness failure (F) and beyond.

occurs by formation of a so-called Hertzian 'ring' or 'cone' crack C in the tensile region immediately outside an elastic contact. Deformation occurs by yield Y in the shear region immediately below the contact. In homogeneous, isotropic materials the distribution of damage is guided strictly by the stress distributions whereas, in enamel, we can expect both cracking and slip to occur preferentially along lamellae planes of microstructural weakness in the microstructure.(45)

Fracture and deformation testing is not easily carried out on actual teeth, for a variety of obvious reasons. Materials scientists attempt to simulate the essence of enamel/dentine tooth structure by constructing glass domes back-filled with polymer resin.(60,71,72) These materials are conveniently transparent, enabling direct observation of damage evolution during contact loading with hard spheres. Glass may be considered representative of enamel (although it is a little more brittle), polymer resin representative of dentine (although a little softer). In thick glass coatings, cone fractures form at the top surface, and overloading produces extensive chipping (Fig. 4A). In thinner coatings, radial cracks form at the coat undersurface, and overloading drives them to the dome margins (Fig. 4B). In the special case where an ultra-soft indenter is used (simulating a bolus of soft food), damage in the near-contact region can be suppressed within a contact compression zone, redistributing the stress concentrations outward and initiating margin fractures that lead to

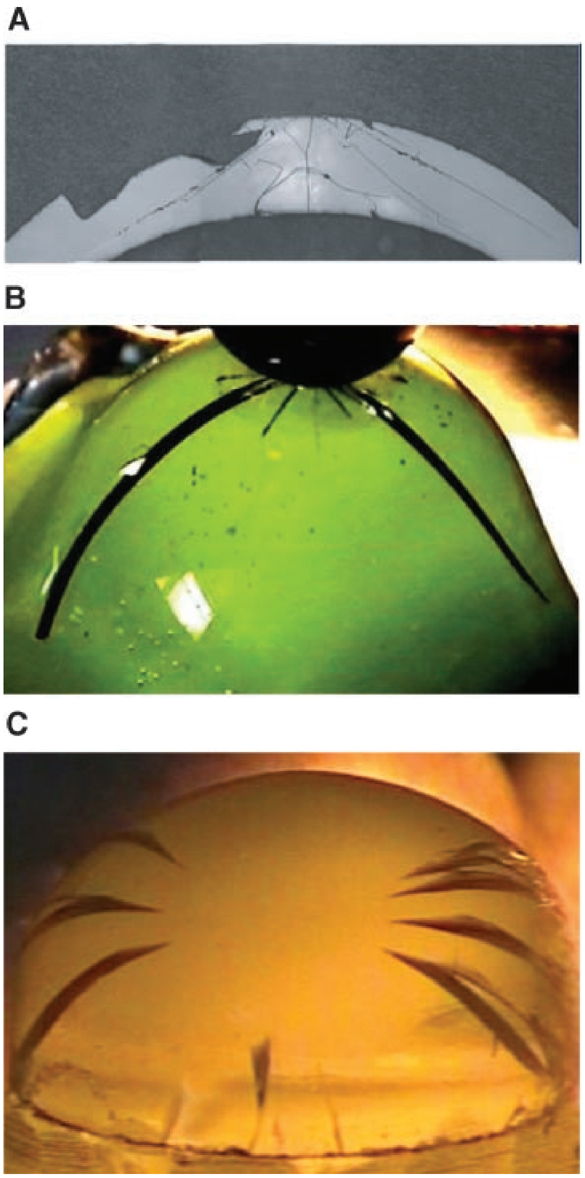

Figure 4. Damage in simulated tooth structure made from glass domes with polymer resin back-fill. **A:** Surface damage localised below contact, showing chipping fractures initiating from a dome top surface.(71) **B:** Subsurface radial cracking from contact site to margin. Once they propagate a certain distance from the contact, the cracks become unstable and propagate quickly to the dome base.(60) **C:** Margin fracture from soft contacts, leading ultimately to 'semi-lunar' or 'abfraction cracks'.(72)

'abfractions' (Fig. 4C).(73) Explicit relations relating critical loads for each of the fracture and deformation modes to material and geometrical variables,(74) derived from basic indentation fracture and deformation theory, are described in Box 1. All these modes are exacerbated by cyclic loading and by the presence of moisture.

Box 1. Mechanics of contact deformation and fracture

The critical loads for onset of cone cracks (C) and yield (Y) in a thick brittle layer from contact with a rigid indenter of effective radius r at load P (Fig. 3A) are well documented in the materials literature.(70) They have the explicit form

$$P_c = A(T^2/E)r \tag{1a}$$

$$P_y = DH(H/E)^2r^2 \tag{1b}$$

where E is modulus, T is toughness and H is hardness of the brittle material, and $A = 8.5 \times 10^3$ and $D = 0.85$ are approximate numerical coefficients. An interesting feature of the fracture/deformation competition implicit in equation 1 is an intrinsic 'size dependence'. Such dependence arises because of a difference in scaling: fracture relates to surface area, plasticity to volume.(75,76) The resulting different dependency on r in equation 1 leads to a so-called brittle–plastic transition as the size of the contact is scaled down. Consequently, there exists a threshold indenter dimension, determined by writing $r = r_{th}$ at $P_c = P_y$ in equation 1(70)

$$r_{th} = (A/D)(E/H)(T/H)^2 \tag{2}$$

For $r > r_{th}$ fracture dominates, and for $r < r_{th}$ plasticity dominates. Brittle fracture and plastic deformation are therefore in competition, and which dominates depends primarily on the ratio T/H and secondarily on E/H ('brittleness indices').

On increasing the load beyond initiation, the damage zones C and Y in Fig. 3A intensify and expand downward and outward in a continuous and stable manner, leading ultimately to material removal, e.g. by a complex mechanism of plastic surface attrition and subsurface microcrack coalescence ("pitting"). This removal is exacerbated in cyclic loading, by the presence of water, and by sliding forces at the contact.(77)

Now suppose that the monolithic structure is replaced by a bilayer (Fig. 3B) consisting of a hard and brittle outerlayer of thickness d (enamel) on a more compliant inner layer (dentine).(74,77) If the coat remains sufficiently thick, stresses will remain concentrated in the surface region and damage will again initiate there. Under these conditions, equations 1 and 2 remain reasonably valid. However, if the coat is sufficiently thin it can flex and thereby place the lower half in a state of high tension.(56) Cracks can then form at the junction (enamel/dentine) and propagate upwards and sideways into a 'radial' configuration R. The critical loads for initiation (I) and through-thickness failure (F) for a coat of strength S have the form

$$P_{\mathrm{I}} = B_{\mathrm{I}} S d^2 / \log(E/E_{\mathrm{d}}) \tag{3a}$$

$$P_{\mathrm{F}} = B_{\mathrm{F}} T d^{3/2} / \log(E/E_{\mathrm{d}}) \tag{3b}$$

where subscript d in E_{d} refers to dentine, with approximate coefficients $B_{\mathrm{I}} = 2$(56) and $B_{\mathrm{F}} = 22$ (for specimens with curved surfaces, $r_{\mathrm{s}} < 5$ mm) or $B_{\mathrm{F}} = 60$ (for specimens with flatter surfaces, $r_{\mathrm{s}} > 20$ mm).(62) Arrested radial cracks can be made to grow further around the coat by increasing the load, until they penetrate to the top surface, as depicted in Fig. 3B. At this point they tend to become unstable, defining the 'failure' condition. This cracking mode is most destructive because it can extend to the coat margins, ultimately splitting the structure into two or more parts. Failure of this kind is accentuated when a tooth surface has high curvature.(60,62)

It should be iterated that the formalism above is generally applicable to any bilayer system—not just teeth—consisting of a brittle outer shell on a compliant support. A pertinent example is that of a seed or nut with hard outer casing and soft inner kernel. The most likely mode of failure in such a case is that of circumferential radial fracture. This failure condition may be estimated from equation 3b, here re-symbolized as

$$P_{\mathrm{F}} = B_{\mathrm{F}} T d^{3/2} / \log(E_{\mathrm{shell}}/E_{\mathrm{kernel}}) \tag{4}$$

Fracture of enamel

What are the functional requirements of a well-adapted enamel cap?We consider this question in relation to the blunt-contact fracture modes in Fig. 3, for enamel of thickness d in contact with a rigid, hard-food object of radius r. Define enamel thickness by dropping a line from the point of contact to the enamel–dentine junction in the direction of action of the occlusal force.(78,79) While this 'plumb-line' method has fallen out of favour, mainly because it is subject to error in orienting sections for measurement,(6,8) it is the dimension most relevant to hard-object feeding. The well-documented fracture and deformation relations shown in Box 1 can then be used to make predictions of critical loads for tooth damage in any given enamel/dentine combination as a function of indenter radius r. Fig. 5 shows such predictions for modern humans and some primates (such as orangutans) for a representative enamel thickness $d = 2$ mm, using values of E, H, S and T from Table 1. Inclined blue lines are plots of critical loads P_{C} and P_{Y} for onset of cone cracking and yield at the enamel top surface—the crossover point between P_{C} (equation 1a) and P_{Y} (equation 1b) defines the threshold indenter dimension r_{th} (equation 2). Horizontal red lines are plots of P_{I} (equation 3a) and P_{F} (equation 3b) for initiation of radial cracking at the bottom surface and subsequent through-thickness failure (with $B_{\mathrm{F}} = 22$ corresponding to specimen surfaces with $r_{\mathrm{s}} < 5$ mm).(62) (Again, whereas P_{C} and P_{Y} are dependent on r, P_{I} and P_{F} are not, since the latter relate to far-field flexural rather than near-contact stress fields.) Note the logarithmic scales in Fig. 5, encompassing a wide range of sphere sizes, from macroscopic at right to microscopic at left, and the corresponding wide range of critical contact loads. We would reemphasise that the calculations in this plot are approximations, using 'typical' values for the parameters. Nonetheless, we may expect them to be representative of the physiological condition.

Regions where each damage mode may be expected to dominate are mapped out in Fig. 5. In this plot, increasing the biting force on a hard object of given r is equivalent to proceeding upward along a vertical line. In the context of the present work, such vertical lines may be contained within one or other of the filled bands shown in the figure—that at $r = 5$ to 50 μm representing small hard objects (grits and phytoliths), that at $r = 2$ to 20 mm representing large hard objects (nuts and seeds). The first apparent damage mode is then determined by whichever of P_{C}, P_{Y} and P_{I} is lowest along any such vertical lines. For biting on a large object ($r > 10$ mm, right band), the enamel will first undergo subsurface radial cracking. Higher loads will cause these cracks to propagate until either they penetrate to the top surface or (in extreme cases) secondary surface damage occurs. This defines a 'brittle' region where teeth undergo large-scale fracture. For biting on a small object ($r < 50$ μm, left band), damage will first occur by surface yield. Increased load will simply enlarge the scale of the deformation zone, possibly followed by cone cracking and pitting. This defines a 'plastic' region where ductile scratching dominates, leading to degradation by wear and pitting processes. Such transitions from brittle to plastic behavior are well documented in the literature on friction and wear.(75,76)

The benefits of thick enamel become clear from Fig. 5. Whereas P_{C} and P_{Y} in equation 1 are independent of enamel thickness d, P_{I} in equation 3a depends on d squared. Recall that the red lines in Fig. 5 are plotted for one enamel thickness ($d = 2$ mm). For primates with thinner enamel, these lines will displace downward, reducing the capacity for the tooth to resist radial cracking. This could explain why the diets of chimpanzees contain only small particulates, while orangutans can eat a diet that includes large, hard nuts. It could also explain why small-object feeders—perhaps like some hominins (i.e. members of the human lineage after the split from chimpanzees)—feeding on grasses, leaves and seeds with phytoliths and also ingesting quartz grit, tend to show substantial surface wear.(80) For large-object feeders, damage may accumulate in a different way, by continual

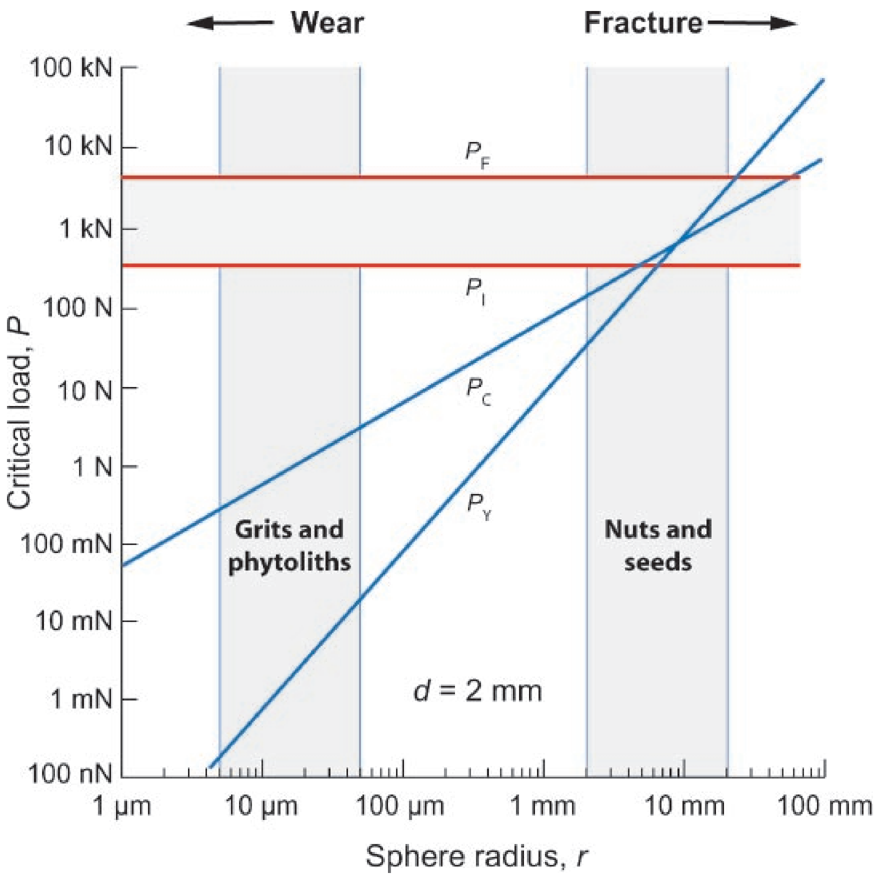

Figure 5. Plot of critical loads as a function of indenter radius r for enamel/dentine bilayer for modern humans and primates with similar tooth thickness $d = 2$ mm: P_C for cone fracture and P_Y for plastic yield at surface (blue lines); and P_I and P_F for radial fracture at subsurface (red lines). Filled vertical bands indicate the approximate size domains of small hard grits and phytoliths (left) and large hard nuts and seeds (right).

incidence of stable deep (radial) cracks. Individual events, one bite out of the thousands made per day, could produce such cracks, providing a permanent record of the functional load.

In summary, thick enamel is likely to benefit mammals that feed on hard objects by extending tooth life. In small-object feeders, a thick cap protects the teeth against wear; in hard-object feeders, it protects against large-scale fracture. Note that there are other situations where thick occlusal enamel may confer no direct benefit, such as in mammals that use more transverse jaw movements to break down thin sheets of vegetation. In these cases, the wearing down of enamel to expose enamel–dentine ridges is actually critical to the animal's feeding performance (Fig. 1D).

Features that protect the enamel

Several features of the dental microstructure may play a large role in determining the fracture behaviour of the enamel cap when it comes in contact with hard foods. We have mentioned how weak planes associated with a rod-like microstructure, including lamellae and tufts, may provide preferred paths and incipient flaw sites for crack growth. At the same time, a decussated microstructure may confer toughness, by stopping cracks from growing too easily at the enamel–dentine junction—a kind of 'fibrous' fracture often observed in woody structures. The equations above, derived on the basis of averaged, isotropic material properties, ignore these factors. It is interesting to note that dentine is more resilient and fracture resistant than enamel (lower H, higher T), so any cracks formed in the enamel are generally likely to be confined there.(54,64) In this context, the enamel–dentine junction shows a steep property gradient, rather than an abrupt step.(81,82) Scalloping of this junction may also help prevent cracks entering the dentine.(83,84) Controlled mechanical tests on enamel to quantify such concepts, and to validate predictions from the equations in Box 1, should be a fruitful area of future research. One predicted outcome is that dimensions of the tooth crown other than enamel thickness will not profoundly affect radial crack resistance.

Adaptations to soft food diets can be expected to produce a very different enamel form to hard food diets, as indicated in the schema of Fig. 6. Enamel in soft-food feeders is likely to be relatively thin, with a simple radial structure and little decussation. Recall that soft foods tend to smother the tooth surface and redistribute tensile stresses to the margins, suppressing radial fractures that otherwise form below the occlusal contact. One feature of the mammalian dentition, that of limited occlusal contact between opposing teeth, is thus explained. However, the same stress redistribution potentially enhances abfraction fractures.(72) An intriguing possibility in such cases is that the feature referred to as the cingulum (Fig. 1E), which is under strong genetic control,(30) may act to prevent any such abfraction failures. This feature is less evident in many higher primates,(85) suggesting that those primates are ill-adapted for the breakdown of low modulus, tough foods.

Seed eating: as the teeth, so the food

The commonest hard objects eaten by mammals small and large are probably mechanically protected seeds or fruits. The shells of seeds are often derived from fruit tissues anyway, so the distinction scarcely matters. Seeds contain baby plants and so there can hardly be any more important interaction between mammals and plants than this. Exceptionally large stresses may be generated during the first bite.(16,88) Like enamel, seeds are designed to resist fracture and are often bilayered with a hard shell encasing a soft kernel. Fig. 2 shows structural similarities between human teeth (Fig. 2A,B) and seed shells (Fig. 2C,D). There is some evidence that seed

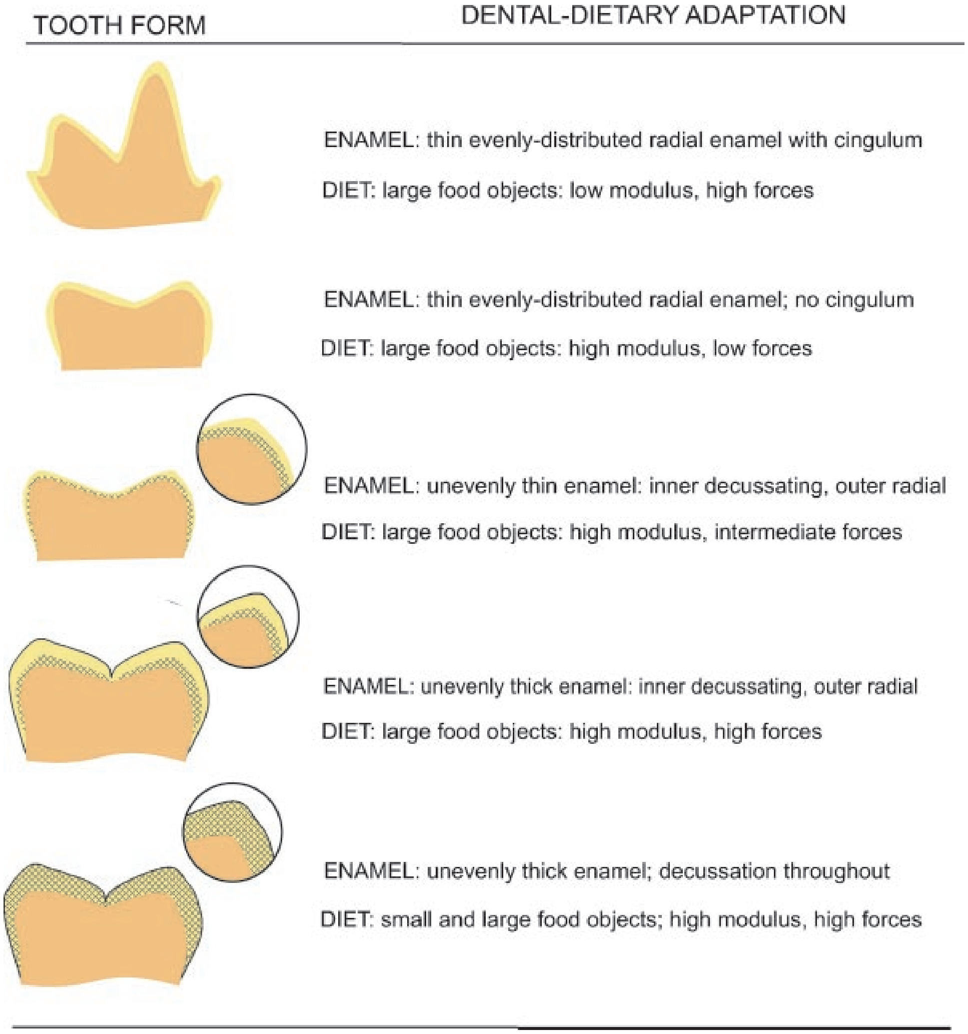

Figure 6. Predicted relationships between mammalian enamel form and diet. Enamel shown yellow, remainder of tooth brown. Decussated region of enamel shown as cross-hatching (greater detail in insets).

shells show adaptations similar to those of enamel. There are shells with radial fibres (e.g. the candlenut, *Aleurites moluccana*, Euphorbiaceae),(87) shells with decussating fibres throughout the thickness (e.g. the mongongo nut, *Schinziophyton rautanenii*, Euphorbiaceae; and macadamia nut, *Macadamia ternifolia*, Proteaceae),(88,89) and shells with decussating fibres restricted to the inner part of the shell, with radially oriented fibres in the outer part (e.g. *Mezzettia parviflora*, Annonaceae).(90)

Clearly, the forces required to break such shells must be lower than those to fracture enamel. Take macadamia nuts as a case study. Orangutans have strong jaws, and can break these nuts (and also the *Mezzettia* nuts that are part of their wild diet(91)) with their teeth. Macadamias are roughly 25 mm in diameter with 2 mm thick shells. Lucas et al.(86) measured the forces required to break such shells using flat metal platens and cobalt-chrome replicas of orangutan teeth at $P_F = 1700 \pm 600$ N (mean and SD, 90 tests). These measured forces are in the same range as reported by others using similar platen tests.(90,92) They may be compared with $P_F = 1910$ N estimated from the radial crack failure relation in equation 4 (Box 1), using appropriate material properties from Table 1 (with $B_F = 60$ for specimen surfaces with $r_s > 20$ mm). Such forces are considerably greater than those achievable by modern humans, but are in the range achievable by orangutans. The critical loads did not appear to depend on the loading configuration,(86) and the cracks ran around the circumference of the shell, indicating internal failure by radial cracking. Observe that the experimental condition for fracture of macadamia nuts ($r = 12.5$ mm at $P_F = 1700 \pm 600$ N) lies within the bounds of P_I and P_F for enamel in Fig. 5 indicating that continual feeding on ultra-hard objects, however enticing, could well produce a proliferation of stable radial cracks within the enamel structure, as foreshadowed earlier. Equation 4, in combination with the plots in Fig. 5, suggests a way to predict a lower bound to the bite forces used by a given animal, once the hard-food source is identified.

Conclusions and implications

The cap of enamel that covers the dentine of primates and other mammalian teeth varies considerably in shape, thickness and microstructure, factors under strong genetic control and apparently adaptive to selective pressure. In this article, we have proposed that these factors in the enamel complexion carry an unambiguous adaptive signal in relation to diet. Invoking fracture and deformation mechanics from materials science, we have argued that life-limiting damage in enamel initiates and propagates not only from the top, near-contact surface, but also from the lower surface at the enamel–dentine junction. Thick enamel is favoured to extend the life of teeth in such mammals that feed on large, hard objects by providing resistance to fracture from the radial cracks that form at the enamel–dentine junction under the contact area. Decussation of the enamel microstructure in the vicinity of this junction most likely provides some internal resistance to this mode by inhibiting crack extension. In mammals that feed on small hard objects, or whose teeth encounter large amounts of grit and/or phytoliths, thick enamel protects the teeth against excessive wear at the cap surface. We also suggest that a function of the cingulum is to protect the neck of the tooth from damage sustained in chewing of soft foods. Finally, the striking structural similarities between the casings of seeds and tooth enamel suggest that both these structures have independently evolved similar strategies for resisting damage.

The implications of this study fit well with existing dietary inferences of early hominins. The megadont australopiths belonging to the genus *Paranthropus*, in particular the East African species *Paranthropus boisei*, are known for their 'hyper-thick' enamel.(93) Studies of dental microwear on South African *P. robustus*(94,95) suggest that hard objects made up a significant component of the diets of these creatures, which is consistent with our predictions for a taxon with such thick enamel. This is not to say that this was all these creatures were eating. However, we suggest that the mastication of hard objects was important enough to select for a thick enamel cap, and that an increased enamel thickness of the postcanine dentition resulted in relatively greater fitness and hence was under positive selection pressure. This study also has potential relevance for paleontological investigations of feeding performance. For example, a measure of 'plumb-line' enamel thickness at the bite location of a presumed hard-object feeder may allow one to obtain an upper bound to the biting force of that creature from the fracture and deformation relations above.

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