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Biomechanics

Sea otter dental enamel is highly resistant to chipping due to its microstructure

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Dental enamel is prone to damage by chipping with large hard objects at forces that depend on chip size and enamel toughness. Experiments on modern human teeth have suggested that some ante-mortem chips on fossil hominin enamel were produced by bite forces near physiological maxima. Here, we show that equivalent chips in sea otter enamel require even higher forces than human enamel. Increased fracture resistance correlates with more intense enamel prism decussation, often seen also in some fossil hominins. It is possible therefore that enamel chips in such hominins may have formed at even greater forces than currently envisaged.

1. Introduction

Effective pre-gastric processing of food is essential to the fitness of nearly all mammals, the front line in this survival struggle being the tooth–food mechanical interface [1]. Contacts between teeth and food are made mostly with enamel, a hyper-mineralized tissue with puzzling mechanical behaviour, variously described as 'glassy' [2] or 'metallic' [3]. Despite labels from two ends of the material property spectrum, building blocks of enamel are common to most mammals: elongate crystals of hydroxyapatite, 25–70 nm in cross-section occupying more than 90% of tissue volume, are clumped into long multi-crystalline prisms, 3–5 μm wide, embedded in a protein gel. A tiny 1–10 nm gap separates crystals with approximately 100 nm wide crystal-free spaces at prism borders [4]. Most fractures in human enamel run along these borders, essentially cleaving the gel [5]. Yet, the prism structural arrangements vary greatly in mammals [6–9], offering potential insights into enamel mechanical behaviour via the opportunity to examine different designs. In some mammals, prisms run straight from enamel–dentine junction to tooth surface ('radial' paths), but curved paths with varying phase angles ('decussation') are often seen [5,10], particularly in inner enamel as in humans, impeding cracks better [11]. Measuring the Hunter–Schreger band (HSB) width indicates the intensity of decussation (figure 1a) [5,12].

Toughness is the property resisting crack growth [8]. Enamel must be tough in order to prevent wholesale failure such as crown splitting. This is especially important to mammals eating hard food objects like seeds, bone or shells. In response to these dietary niches, dental adaptations such as bunodonty (teeth with large low rounded cusps) and high levels of decussation have evolved (figure 1a) [7,8,13]. Is such enamel tougher?
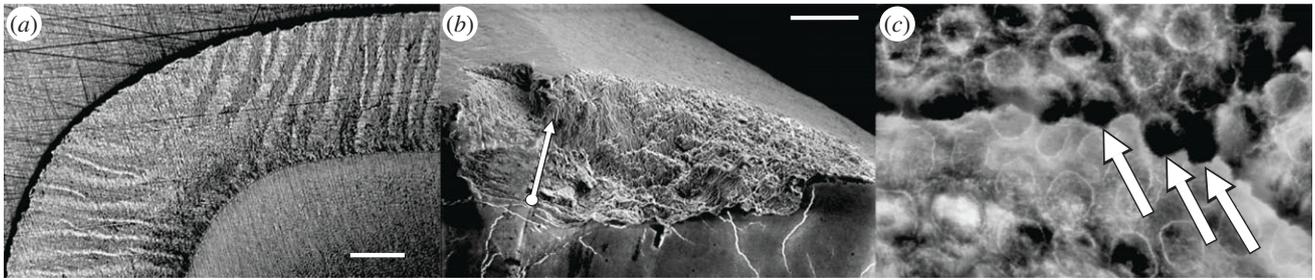
Figure 1. (*a*) Light microscopy (LM) image shows high degree of decussation in sea otter enamel. HSB extend to the tooth surface. Scale bar, 0.2 mm. (*b*) Enamel chip; arrow indicates measurement of *h* (VPSEM in SE mode: accelerating voltage 20 kV; current 300 pA; pressure 75 Pa). Scale bar, 0.5 mm. (*c*) LM at higher magnification showing the circular outlines of prisms in cross-section (each approx. 4 μm in diameter). Arrows indicate where cracks have entered prism edges (variable pressure scanning electron microscopy (VPSEM) in backscattered electron mode: 20 kV; 1 nA; 625 Pa). FW = 32 μm.
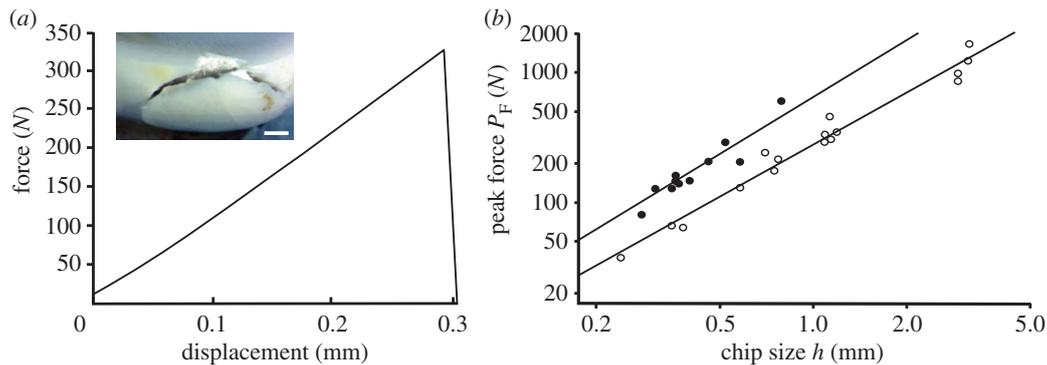
Figure 2. (*a*) Force – displacement graph to produce a chip. Scale bar 1 mm. (*b*) Peak force P_F against chip size *h* for sea otter enamel (filled circles), plotted on logged scales ($r^2 = 0.91$; $p < 0.001$), compared to humans (open circles), produced under identical conditions [11]. For any given chip size, P_F for sea otter enamel is much higher, with average toughness of 2.8 MPa m$^{-0.5}$ comparing to 1.0 MPa m$^{-0.5}$ for humans. (Online version in colour.)

Sea otters (*Enhydra lutris*), the largest living mustelids, inhabit the North Pacific coast [14,15], eating invertebrates and fish [14]. They are renowned for predating hard-shelled marine invertebrates such as abalone, sea urchins, clams, mussels and crabs [13–15]. Most shells are fractured with the teeth [13], with frequent contacts between tooth cusps and heavily mineralized exoskeletons. The postcanine teeth of a sea otter are bunodont, very different from other Carnivora and remarkably similar to hominin teeth [16]. Previous studies have used sea otter teeth as a model for exploring hard object feeding by hominins, particularly *Paranthropus boisei* [13], making their dental architecture of general interest.

Here, we use a chipping technique increasingly used in brittle materials to indicate fracture resistance [11,17–19]. For a Vickers indentation near a right-angled edge on a fine-grained ceramic, the peak force is

$$P_F = \beta T h^{1.5}, \tag{1.1}$$

where *h* is chip size, measured from indentation point to tooth edge (figure 1*b*), *T* is fracture toughness (in MPa m$^{-0.5}$), sometimes called the 'critical stress intensity factor', and β is a coefficient [17]. We hypothesized that sea otter enamel will have high toughness to accommodate blunt trauma encountered during feeding (figure 1*c*). We discuss our findings relative to the adaptive capabilities of dental structures and to assumptions about early hominin bite forces.

2. Material and methods

Canine and first molar teeth were excised from frozen sea otter jaws and their roots embedded in epoxy resin. Longitudinal sections were cut to expose HSBs, which were then counted, normalized to the length of the enamel junction (electronic supplementary material, figure S1) [12]. For chipping, crowns were cut transversely to obtain a flat surface, then polished to a 1 μm finish. Prior to chipping, teeth were kept hydrated in water, then placed onto a mechanical testing stage. A tungsten carbide Vickers macro-indenter was pushed vertically down onto enamel at a distance *h* from an enamel edge with increasing load until, at a peak force P_F, a scallop-shaped chip broke away (figure 2*a*). The critical chip dimension *h*, measured to ±0.01 mm, was varied to determine its effect on P_F. Enamel decussation was viewed by light microscopy (LM). Post-test specimens were imaged uncoated by variable pressure scanning electron microscopy (VPSEM; Zeiss EVO 50). Sea otter data were compared to that existing for humans [11], testing differences between slopes and intercepts (figure 2*b*) using analysis of covariance. When slopes were similar, the interaction term was removed and a new model run to test difference between intercepts.

3. Results

Twelve experimental chips, varying *h* between 0.16 and 0.79 mm (upper limit dictated by enamel thickness), required a peak force P_F of between 53 and 605 N to fracture. P_F was proportional to *h* raised to the power 1.45 (s.e. 0.14; 95% CI 1.13–1.77), according to equation (1.1). Plotting log P_F against log *h* (figure 2*b*), then from equation (1.1), assuming $\beta = 9.3$ for this geometry [12], the toughness of sea otter enamel is calculated as 2.8 (s.e. 0.3) MPa m$^{-0.5}$. Comparing to humans (figure 2*b*), analysis of covariance showed slopes of the regressions did not differ significantly ($F_{2,24} = 0.625$, $p = 0.437$), but intercepts did: otter enamel is 2.5 times tougher than

that of humans ($F_{1,25} = 67.9$, $p < 0.001$). Sea otter enamel had a mean of 19.4 (s.d. 2.5) HSB mm^{-1} (figure 1a). Enamel chips passed through these bands (figure 1b). Higher magnification (figure 1c) indicates cracks may avoid prism cores, but 'nick' their borders.

4. Discussion

Sea otter enamel is much tougher than that of humans (figure 2b). Estimates for human enamel range from 1.0 to 2.4 MPa m$^{-0.5}$ [17–20], depending on test method [10,11,17–22]. Chipping has the lowest estimate. Toughness often increases with crack length in the human [20], but the important structural variable is decussation in the fracture path. An upper bound toughness of 2.4 MPa m$^{-0.5}$ in humans [10] lies below the chipping estimate for sea otters. The principal toughening mechanism is 'bridging' where secondary cracks initiate beyond interfaces [10,20,21]. This only happens in decussating enamel, particularly near HSB boundaries [21]. Its effectiveness depends on raising the force initiating these secondary cracks compared with that which initiated the preceding crack [22]. So the more interfaces in the crack path, the higher the toughness. A maximum of 14 HSB mm^{-1} in human enamel lateral to a cusp [12] compares to a mean of 19 in sea otter enamel (figure 1a): in itself, this explains the latter's elevated toughness. Additionally, the outermost 20%–30% of human enamel is radial [10], while in sea otters, HSBs run almost to the surface. So only large chips in humans involve decussation, explaining why chipping resistance in modern human teeth is uniformly low [11,23], while all chips in sea otters encounter it.

Prism shapes may factor into this. Circular prisms in sea otters (figure 1c) are not seen in human enamel, but the functional importance of shape differences is unknown. Decussation seems the major factor. Importantly, some sectional images of fossil hominin teeth show greater decussation than in modern humans [24–29]. Estimates of 16 bands mm^{-1} in East African early Homo sapiens and 19 bands mm^{-1} in P. boisei [28] fossils are strikingly similar to sea otter data. The explanation may be dietary—to avoid teeth being chipped during hard object feeding involving high bite forces [13,16]. Using toughness estimates for modern human enamel [22], the sizes of some ante-mortem chips in fossil hominin enamel suggest kilonewton forces [13]. If the toughness of sea otter enamel were assumed for robust hominins like P. boisei, then this would predict exceptionally high critical tooth fracture loads. This indicates a strong reason to quantify decussation better. Understanding more about extreme adaptations and variability in the enamel of extant animals will aid in deciphering dietary habits of our own lineage and close relatives [30].

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