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Adaptation to hard-object feeding in sea otters and hominins

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ABSTRACT

The large, bunodont postcanine teeth in living sea otters (Enhydra lutris) have been likened to those of certain fossil hominins, particularly the ‘robust’ australopiths (genus Paranthropus). We examine this evolutionary convergence by conducting fracture experiments on extracted molar teeth of sea otters and modern humans (Homo sapiens) to determine how load-bearing capacity relates to tooth morphology and enamel material properties. In situ optical microscopy and x-ray imaging during simulated occlusal loading reveal the nature of the fracture patterns. Explicit fracture relations are used to analyze the data and to extrapolate the results from humans to earlier hominins. It is shown that the molar teeth of sea otters have considerably thinner enamel than those of humans, making sea otter molars more susceptible to certain kinds of fractures. At the same time, the base diameter of sea otter first molars is larger, diminishing the fracture susceptibility in a compensatory manner. We also conduct nanoindentation tests to map out elastic modulus and hardness of sea otter and human molars through a section thickness, and microindentation tests to measure toughness. We find that while sea otter enamel is just as stiff elastically as human enamel, it is a little softer and tougher. The role of these material factors in the capacity of dentition to resist fracture and deformation is considered. From such comparisons, we argue that early hominin species like Paranthropus most likely consumed hard food objects with substantially higher biting forces than those exerted by modern humans.

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Introduction

Early hominins of the genus Paranthropus had what has been termed a ‘robust’ masticatory apparatus that included large jaws and anteriorly positioned musculature, along with very large postcanine teeth with low and rounded (bunodont) cusps (Rak, 1983). Similar tooth morphology has been noted in extant sea otters (Fisher, 1941) (Fig. 1). This has led to the proposition that sea otter dentition may serve as a useful model for inferring the eating habits of Paranthropus (Walker, 1981). However, no detailed comparison appears to have been made on the teeth of these distantly related mammals to assess the degree of morphological, and, presumably functional, convergence.

Sea otters (Enhydra lutris) consume a variety of hard foods including clams, mussels, abalone, snails, crabs, and sea urchins (Murie, 1940; Kenyon, 1969; Van devere, 1969; Ostfeld, 1982; Kvitek et al., 1988; Riedman and Estes, 1990; Watt et al., 2000). In some populations, individuals target particular prey (Estes et al., 2003; Tinker et al., 2008; Newsome et al., 2009). However, even in areas with a high degree of inter-individual dietary variation, all otters appear to have a “hard food component” to their diet (Estes et al., 2003; Tinker et al., 2008). Although the contents of some mollusks are accessed with the aid of stones (Hall and Schaller, 1964), most shelled prey are placed directly in the mouth and chewed whole (Kenyon, 1969; Van devere, 1969; Calkins, 1978). Indeed, the scat of sea otters often contains the remains of mollusk shells and sea urchin plates and spines (Murie, 1940). During consumption of the sea urchin masticatory apparatus, Enhydra actually chews one of the hardest biogenic composites in nature, Aristotle’s lantern (Wang et al., 1997). Several lines of evidence...
suggest that early hominins such as Paranthropus were eating comparably hard foods (Grine, 1981; Rak, 1983; Demes and Creel, 1988; Hylander, 1988; Constantino, 2007; Constantino et al., 2009, 2010). The extent to which the tooth structure of Enhydra and Paranthropus reflects a shared capacity to break down such hard food objects forms a central theme of the present study. Accordingly, here we conduct controlled failure tests on extracted molars of sea otters to quantify sustainable biting forces for these animals. Analogous tests on modern human molars provide a useful basis for comparison, not only in determining relative biting forces but also in illustrating how fracture modes may depend on differences in tooth morphology. Appropriate fracture equations serve to account for the observed fracture modes in terms of characteristic dimensions, namely tooth size (transverse width or radius) and enamel thickness. Indentation tests on tooth sections are also conducted to compare key enamel material properties—modulus, hardness, and toughness. Finally, using the fracture equations as a predictive tool, we draw inferences about the diet of Paranthropus boisei, the most derived of the “robust” australopiths (Constantino and Wood, 2007; Wood and Constantino, 2007).

Methods and results

Preparation of tooth specimens

Human molar teeth were provided by the Pfaffenberger Laboratories at the National Institute of Standards and Technology (NIST). The teeth were extracted from anonymous male and female patients ranging in age from 18 to 25 years. Approval to test these specimens was granted by the NIST Internal Review Board. Sea otter teeth were obtained “from the United States Geological Survey and Marine Wildlife Veterinary Care and Research Center of the California Department of Fish and Game (CDFG).” These specimens were extracted from the skulls of deceased animals. Permission to transport and test the teeth was granted by the CDFG. All remains of these animals are ultimately to be lodged at the California Academy of Sciences.

Both lower and upper human molars from each position in the tooth row (e.g., M1, M2, etc.) were included in the study. For sea otters, we focused mainly on the lower first molars because of their prominent role in mastication and their relatively large size (Fig. 1).

However, in some tests (e.g., synchrotron imaging) it was necessary to use premolars and canines because of size and orientation constraints imposed by the instrumentation. The human molar specimens were cleaned and stored in distilled water immediately after extraction. The sea otter teeth were received frozen but were stored in aqueous solution for several days before testing. Specimens with noticeable preexisting cracks or other damage incurred during extraction or storage were eliminated from the sample population. Individual teeth for fracture testing were mounted with their roots embedded in epoxy blocks, cusps uppermost. Thereafter and throughout the subsequent testing procedure, these teeth were kept moist by continually squirting drops from a water bottle.

A few human and sea otter molars were sectioned buccolingually along a vertical plane through the most prominent mesial cusps (protoconid and metaconid in lower teeth and protocone and paracone in upper teeth). The sectioning was accomplished by traditional cutting and polishing methods. Examples are shown in Fig. 2 for (A) sea otters and (B) modern humans. These sections demonstrate a common bunodont morphology, i.e., rounded and blunt occlusal surfaces. They also illustrate some important differences, notably a greater tooth base size and thinner enamel coat for the sea otter. The means and standard deviations of these dimensions measured for the two species, along with some values from the literature for humans (Kono, 2004) and P. boisei (Beynon and Wood, 1986; Demes and Creel, 1988), are included in Table 1. Faintly visible within the enamel in the section views is the appearance of ‘Hunter–Schreger bands’ (HS), indicating a crossing (decussation) of mineralized prisms within the enamel structure, previously proposed as a source of impedance of cracks that seek
Failure experiments—fracture modes

Fracture experiments aimed at simulating biting were conducted on sea otter lower first molars (four tests) and modern human upper and lower molars (M1, M2, and M3; 20 tests) by loading the uppermost cusps with a metal disk (prototypical 'hard' contact) in a mechanical testing machine (Lawn et al., 2009; Lee et al., 2009). Each tooth tested was from a different individual and was subjected to a single loading cycle. The load was delivered vertically downward on the most prominent cusp, generating weak but significant 'hoop' tensile stresses in the enamel coat (Chai et al., 2009b). A common loading protocol was used in all tests, and the displacement rate held fixed such that failure occurred over a period of several minutes. Crack progress during the loading sequence was continually recorded by a high resolution camera system in all tests.

Additional fracture tests were run on individual sea otter \((n = 30)\) and human \((n = 10)\) teeth at the 32-ID x-ray imaging beamline at the Advanced Photon Source in Argonne National Laboratory in Illinois. In these experiments, a custom testing stage was rigged onto the beamline stage and the tooth disk-loaded along its axis as before. The tooth was scanned during testing to produce a real-time image of the internal tooth structure under compressive loading.

Indentation experiments—material properties

Nanoindentation tests were run on modern human \((n = 1)\) and sea otter \((n = 1)\) molar tooth sections to obtain information on two basic material properties, plane strain elastic modulus \(E\) (Young's modulus divided by \(1 - \nu^2\), with \(\nu\) Poisson's ratio) and hardness \(H\). A three-sided Berkovich pyramidal indenter was used at a fixed penetration of \(0.4 \, \text{nm}\) corresponding to loads in the range \(1 \, \text{mN} \text{ to } 2 \, \text{mN}\), sufficient to probe below any surface damage and to encompass enamel prism diameters within the contact zone. For each tooth, three transects running from the EDJ to the outer enamel surface (OES) with indents \(20 \, \text{nm}\) apart, were placed at the two most mesial cusps and the central occlusal basin that connects them. The quantities \(E\) and \(H\) were deconvoluted from the digital load-displacement data using the widely adopted approach of Oliver and Pharr (1992).

Vickers microindentation tests were made in the enamel of molar sections at somewhat higher loads, \(1 \, \text{N} \text{ to } 5 \, \text{N}\), in order to produce contact impressions with well-defined corner cracks. Toughness \((T)\) was then estimated from the lengths of the corner cracks using a well-documented indentation toughness equation (Anstis et al., 1981). Mean and standard deviation values of \(T\) thus obtained (six indents in a single specimen per species) are included in Table 1.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Tooth size (R) (mm)</th>
<th>Enamel thickness (d) (mm)</th>
<th>Modulus (E) (GPa)</th>
<th>Hardness (H) (GPa)</th>
<th>Toughness (T) (MPa m(^{1/2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea otter (Enhydra lutris)</td>
<td>7.0 ± 0.2(^a)</td>
<td>0.65 ± 0.1(^a)</td>
<td>77 ± 4(^a)</td>
<td>3.0 ± 0.3(^a)</td>
<td>0.8 ± 0.2(^a)</td>
</tr>
<tr>
<td>Human (Homo sapiens)</td>
<td>4.9 ± 0.1(^b)</td>
<td>1.3 ± 0.1(^c)</td>
<td>80 ± 4(^c)</td>
<td>4.0 ± 0.4(^*)</td>
<td>0.7 ± 0.1(^*)</td>
</tr>
<tr>
<td>Hominin (Paranthropus boisei)</td>
<td>9.0 ± 0.2(^d)</td>
<td>2.8 ± 0.2(^d)</td>
<td>80 ± 4(^d)</td>
<td>4.0 ± 0.4(^*)</td>
<td>0.7 ± 0.1(^*)</td>
</tr>
</tbody>
</table>

Teeth tested in wet state.

\(^a\) Data from current measurements.
\(^b\) Data from Demes and Creel (1988). Demes and Creel report molar crown areas as the sum of product of buccoclingual and mesiodistal diameters of the 3 M teeth for each species. From their data, we calculate human molar size as \(R = 0.5 \times \text{total molar crown area}^{1/2}\).

\(^c\) Data from Kono (2004), average enamel cap volume divided by EDJ area.

\(^d\) Data from Beynon and Wood (1986), Demes and Creel (1988).

\(^e\) Assumed same as for human.

Figure 3. Radial—median (R) and margin (M) fracture modes in (A) sea otter M\(_1\) and (B) human M\(_3\). Schematic in (C) shows simplified tooth geometry and fracture modes.
in Table 1. The value for sea otters is a little higher than for humans, suggesting that the former may have a slightly greater intrinsic resistance to crack growth. The indentation corner crack patterns were less well formed in the sea otter teeth, so the toughness value for this animal is subject to greater uncertainty.

Results

During the loading experiments, cracks formed within the enamel and ran longitudinally around the side wall adjacent to the loaded cusp, as shown in Fig. 3A for sea otters and Fig. 3B for humans. Crack visibility is enhanced by reflection from the interior crack walls in the translucent enamel. The final crack patterns in Fig. 3 are similar in the two species. The longitudinal cracks either started from the cuspal contact region and ran downward toward the base (radial–median cracks, R), or started from the cervical margin and ran upward toward the contact (margin cracks, M). In

![Image of tooth sections](https://example.com/image1)

**Figure 4.** Transverse sections cut through molars: (A) sea otter M₃, loaded to 550 N and sectioned to depth 2.2 mm below the cuspal surface, (B) human M₃, loaded to 450 N and sectioned to depth 4.4 mm. Sections shown at same scale. From Chai et al. (2009).

![Image of tooth sections](https://example.com/image2)

**Figure 5.** Sequence of three longitudinal synchrotron x-ray images of a sea otter canine during loading: (A) zero load, (B) intermediate load, radial crack initiated near the EDJ (arrows), (C) critical load, tooth failure from crack propagation around side walls of enamel. Cracks are visible as light shadow regions within the enamel.
most instances, the two crack types evolved simultaneously, although there was a tendency for M cracks to extend completely around a side wall first (Lee et al., 2009). In both human and sea otter teeth, the critical loads required to attain any such visually observed fracture condition ranged from 400 N up to 700 N. Ultimately, at loads in excess of 1000 N, the enamel began to delaminate from the underlying dentin. Post-test examinations of the cuspal areas of the indented teeth revealed noticeable cuspal flattening from plastic deformation in the contact area, even at loads well below those for crack initiation.

Transverse sections cut through partially fractured sea otter and human teeth at depths sufficient to intersect the dentin are shown in Fig. 4 (Chai et al., 2009a). These images confirm that longitudinal cracks remain contained within the enamel shell in a ribbon configuration, i.e., a channel-like geometry with long edges intersecting the outer and inner enamel surfaces (Fig. 3C). Also observed in Fig. 4 are wavy, microcrack-like defects, termed ‘tufts’ (T), weak hypocalciﬁed interfaces emanating from the enamel–dentin junction (EDJ) into the enamel (Sognnaes, 1949; Osborn, 1969; Palamara et al., 1989). The appearance of these tufts in the two images highlights a certain commonality in the tooth microstructure in mammalian species. Previous studies have shown tufts to be principal sources of longitudinal crack initiation (Chai et al., 2009a; Myoung et al., 2009). Such defects are not ordinarily visible in images of the external enamel surface, such as Fig. 3.

Fig. 5A–C shows a sequence of three longitudinal views generated from the x-ray image data for a single sea otter canine: (A) zero load, no cracks, (B) intermediate load, radial crack initiation at the EDJ, and (C) critical load, crack propagation around the enamel wall. The cracks in Fig. 5C are seen as the light shadow regions. Rotation of the x-ray image conﬁrmed that the cracks circumvent the tooth crown and remain conﬁned within the enamel walls (Lucas et al., 2009). Fig. 6 shows a virtual transverse section generated from the x-ray computed tomography data for a partially fractured human molar. This view is analogous to the optical section view in Fig. 4B, with the advantage that the x-ray technique is completely non-destructive and thus free of potential specimen-preparation artifacts. Again, cracks are seen emanating from tuft-like defects in the enamel adjacent to the EDJ (Chai et al., 2009).

Nanoindentation results are shown in Fig. 7 as a function of normalized distance from the EDJ to the OES, to enable comparisons between species. There is a consistent increase in $E$ and $H$ with distance from the EDJ, broadly consistent with the trends reported for molars of humans and howler monkeys (Cuy et al., 2002; Darnell et al., 2009). Mean and standard deviation mid-range values for $E$ and $H$, evaluated from the data within 0.4–0.6

![Figure 6. X-ray tomography transverse section computer-generated from the image data for a human M3 loaded to 200 N, at depth 4.4 mm below the tooth cusp. Note tufts emanating into the enamel from the EDJ (cf. Fig. 4B). Circular fringes are a diffraction artifact.](image-url)
normalized distance in Fig. 7, are included in Table 1. Whereas the data for modulus \( E \) in humans and sea otters tend to overlap within the scatter, the values of \( H \) are systematically lower in sea otters. The latter result indicates notably softer enamel in the sea otter dentition. As for \( P. boisei \), measurements of material properties are unavailable for this species, so for the sake of ensuing calculations we assume them to have the same average values as for modern humans. Justification for this assumption comes from the apparently similar degrees of enamel prism decussation in the two species (Grine and Martin, 1988; Teaford and Ungar, 2000), as well as from the fact that enamel material properties do not appear to show strong variation among the great apes (Maas and Dumont, 1999; Lee et al., 2010).

Fracture analysis

Explicit equations have previously been obtained for the critical contact loads required to drive longitudinal cracks around the side wall of an idealized dome-shaped enamel/dentin structure of enamel thickness \( d \) and base radius \( R \) as shown in Fig. 3C (Lee et al., 2009). The critical load for first (margin) fracture may be represented by a simple relation

\[
P_{M} = CTRd^{1/2}
\]

(1)

where \( T \) = toughness of the enamel coat and \( C \approx 6.0 \) is a dimensionless quantity (Lee et al., 2009). The critical load \( (P_{M}) \) may be considered to represent a ‘failure’ condition, in that longitudinal cracks are the precursor for delamination of the enamel from the dentin underlayer (Popowics et al., 2001). Note that once representative values of tooth dimensions and material parameters are ascertained, equation (1) can be used to make \textit{a priori} predictions of critical fracture conditions.

Values of \( P_{M} \) determined for sea otters, modern humans and \( P. boisei \) using input data from Table 1 are plotted in Fig. 8. First consider sea otters and modern humans. The magnitudes of \( P_{M} \) for these two species are similar, with \( P_{M} \approx 750 \text{ N} \). These loads lie at the upper end of the range of observed critical loads in the experimental fracture tests. The comparability of \( P_{M} \) for the two species is interesting, for sea otters have much thinner enamel, seemingly making the teeth of this animal more vulnerable to fracture in equation (1). However, any such susceptibility is mitigated to some extent by the greater molar base radius, providing greater support for the applied load. The predicted value of \( P_{M} \) for \( P. boisei \) is two to three times as high as for sea otters or modern humans, because of greater tooth size and enamel thickness. This uncommonly high value indicates a considerably greater capacity to resist tooth fracture for this group of fossil hominins, implying a greater capacity to consume hard foods.

Discussion

The results above indicate interesting similarities between sea otter and modern human molar teeth. The most immediate similarity lies in the tooth morphology: rounded with blunt (bunodont) cusps. This suggests an element of commonality in the nature of the diet between the two species. The dome-like morphology of a bunodont tooth is well configured to dissipate tensile stresses arising from high occlusal forces. Quantitative evaluation of the load-bearing capacities of sea otter and human teeth indicates that both species can indeed sustain substantial biting forces. The estimates for humans and hominins in Fig. 8 are commensurate with those from jaw mechanics (Demes and Creel, 1988), and in the case of sea otters are more than adequate to account for the breakdown of shelled and other hard food objects. Other similarities lie in the nature of the microstructure, indicated by the appearance of tufts at the EDJ in Fig. 4, providing sources for crack initiation; and Hunter–Schreger bands, providing intrinsic resistance to the propagation of ensuing cracks. The common presence of tufts highlights an intrinsic weakness of the enamel structure. On the other hand, the

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**Figure 7.** Plane strain elastic modulus \( (E) \) and hardness \( (H) \) across sections of sea otter and modern human molar tooth enamel, plotted as function of normalized distance from EDJ to outer enamel surface. Each data point is an individual nanoindentation.

**Figure 8.** Values of critical forces \( P_{M} \) for sea otters, modern humans, and \( Paranthropus boisei \), calculated from equation (1) in conjunction with data in Table. Error bars reflect data uncertainties in Table 1.
criss-crossing prism pattern within the decussation zone suggests some inbuilt mechanism of resistance to subsequent crack propagation. In this view, teeth are remarkably damage-tolerant structures (Chai et al., 2009a); enamel is innately configured to contain cracks, not to avoid them.

There are also some distinctive differences in the tooth structures of sea otters and modern humans. Most striking is the considerably thinner enamel in the sea otters, by a factor of about two (Table 1). This makes the tooth more vulnerable to initiation of radial cracks beneath the contact, from enhanced flexure of the enamel coat on the underlying soft dentin substrate (Lucas et al., 2008), e.g., as observed in Fig. 5. On the other hand, the base radius of sea otter molars is considerably greater than that of humans, diminishing the magnitude of the hoop tensile stresses that drive the cracks and hence providing some compensatory resistance to failure (Rudas et al., 2005). There may be subtle differences in the microstructure, too. A preliminary visual inspection appears to indicate that sea otter enamel features a somewhat higher intensity of Hunter–Schreger bands, signifying more pronounced changes of direction from one band of prisms to the next. If confirmed, such an enhancement in the decussation pattern may go a part way to explaining the slightly greater toughness in the sea otter enamel. In this context, the measurements of Bajaj and Arola (2009b), confirming enhanced toughness in the regions of high decussation near the EDJ, could have some bearing on the differences between the two species.

We have focused on the role of thick enamel in inhibiting fracture, but thick enamel is also a factor in combating wear through abrasion and microcracking (crumbling) (Molnar and Gantt, 1977; Osborn, 1981; Macho and Spears, 1999). Severe wear can expose the inner dentin and result in the inability of the animal to break down harder foods (Cuozzo and Sauther, 2006), thereby threatening its longevity (DeGusta et al., 2003; King et al., 2005). Contrary to the observations of Walker (1981), the dentition of some deceased sea otters evinced excessive wear, possibly from the pervasive presence of sand particulates in the diet (Lawn et al., 2009). In this context, recall the softness (diminished H) of sea otter enamel relative to humans in Fig. 7B, making sea otters more susceptible to wear. In such cases, the dentition may continue to function under some duress, albeit with a tendency toward a softer diet. Wear can also enhance the initiation of fracture by further thinning the enamel coat in the occlusal region and thereby increasing flexure, although it is less likely to affect the critical load \( P_M \) in equation (1) needed to drive side-wall fractures to completion in the contact far field (Ford et al., 2009). The interaction between wear and fracture in animals such as sea otters is a subject that bears further exploration.

Conclusions

The capacity of the fracture relations in equation (1) to account broadly for the magnitudes of the forces required to cause tooth failure in our simulated biting tests lends confidence in making predictions about the bite forces exerted by ancestral hominins in dietary function. We have given special mention to \( P. boisei \) because of its extreme postcanine tooth size and enamel thickness, the greatest of any known hominin (Beynon and Wood, 1986; Wood, 1991; Aiello and Dean, 2002). Such extreme dimensions protect the teeth during biting (Fig. 8), particularly in relation to the incidence of radial and margin cracks, and probably also to the incidence of crumbling (Constantino et al., 2010), suggesting an adaptation to very hard and tough foods. The high degree of wear noted on many \( Paranthropus \) teeth also suggests that wear from frequent chewing on foods containing small hard particles may have been as important as fracture in selecting for thick tooth enamel. It is interesting to reflect that severe tooth wear can also occur in modern humans, not only from grinding (bruxism) but also from variations in diet (Molnar, 1972). There, however, conspecific care can extend the life of the afflicted human individual well beyond the loss of normal tooth function. Our ancestors may have engaged in analogous behavior as early as two million years ago (Lordkipanidze et al., 2005), although no evidence has yet been presented to suggest that this is the case with \( Paranthropus \).

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