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Properties of tooth enamel in great apes

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Properties of tooth enamel in great apes

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A comparative study has been made of human and great ape molar tooth enamel. Nanoindentation techniques are used to map profiles of elastic modulus and hardness across sections from the enamel–dentin junction to the outer tooth surface. The measured data profiles overlap between species, suggesting a degree of commonality in material properties. Using established deformation and fracture relations, critical loads to produce function-threatening damage in the enamel of each species are calculated for characteristic tooth sizes and enamel thicknesses. The results suggest that differences in load-bearing capacity of molar teeth in primates are less a function of underlying material properties than of morphology.

1. Introduction

The teeth of mammals have evolved in response to diet [1–4], exhibiting a wide range of configurations. Some herbivorous mammals deliberately expose the dentin to produce sharp enamel ridges breaking down soft but tough sheet foods. On the other hand, the teeth of great apes, including humans, have a blunt cusped form, termed bunodonty, in which a variably thick hard enamel outer layer shields the interior dentin from contact with hard foods. Tooth form is an important factor in determining resilience against damage accumulation. At the macroscopic level the most important dimensions are tooth size and enamel thickness [4,5]. It would seem intuitive that larger values of these dimensions equate to a greater capacity in sustaining biting forces. Values of tooth size and enamel thickness for great apes (and other primates) have been reported by several authors [5–12]. Interestingly, for any given molar these two dimensions do not necessarily scale proportionally between species [5,11,13]. Whereas some work has been reported on the role of elastic modulus (resistance to elastic deformation) on the load-bearing capacity of enamel [14,15], little is known as to how other characteristic material properties of tooth enamel and dentin – hardness (resistance to plastic deformation) and toughness (resistance to crack growth) – might influence the load-bearing capacity of the dentition in different primates. The relative importance of morphological versus material properties also remains somewhat obscure, especially in the context of evolutionary pathways.

The load-bearing capacity of teeth is limited by the susceptibility of the enamel to fracture. Materials engineers investigate this issue by representing the essential tooth structure as a homogenous, isotropic brittle dome encasing a compliant interior, ignoring local cuspal variations in the first approximation [16]. Much can be learned about how cracks initiate and propagate in such structures from simulated occlusal loading tests on model epoxy-filled glass shells with a hard or soft indenter [17,18]. Correlation of the fracture and deformation modes observed in situ in such models with those observed in actual teeth confers a degree of validity on such experiments [19,20]. Model systems of this kind are conveniently amenable to the analysis of fracture and deformation modes in terms of shell (enamel) thickness and dome radius (tooth size), tooth material properties, food size and texture [21]. Explicit equations enable one to predict critical loads for the activation of each such mode for any specified set of tooth dimensions and properties, and to relate these loads to diet [4].

However, tooth enamel is far from homogeneous and isotropic. It has a highly mineralized microstructure consisting of oriented hydroxyapatite (HAP) crystallites bound together in elongate prisms in a dilute organic matrix. The prisms are oriented outwards from the enamel–dentin junction (EDJ) towards the occlusal surface. They tend to cross each other in bundles, as in a basket weave (decussation) [3,22]. The degree of both mineralization and decussation varies between teeth and from species to species. Material properties can also show substantial gradients across a tooth section. Such gradients have been most graphically
were given a light polish with 0.5 in resin mounts with the section surfaces exposed. These surfaces and had relatively unworn occlusal surfaces. They were received on loan from the Natural History Museum, **Pan troglodytes** (studied: human (**Homo sapiens**)), lower second molar; orangutan (**Pongo pygmaeus**), lower second molar; gorilla (**Gorilla gorilla**), upper first molar. These were obtained from the Natural History Museum, London [5]. All were preserved molars sectioned parallel to the long axis through prominent cusps in the buccal–lingual plane and had relatively unworn occlusal surfaces. They were received in resin mounts with the section surfaces exposed. These surfaces were given a light polish with 0.5 μm diamond slurry to remove any residual surface roughness and washed thoroughly for 10 min in running water to remove any accumulated contamination. The resulting sections were examined in a high power reflection optical microscope to confirm that the surfaces were smooth. All teeth were tested in the dry state. Modulus and hardness measurements were made across the sections for each primate. Instrumented nanoindentation tests with 50 nN noise resolution and 1 nm displacement noise floor (Nanoindenter XP, MTS Nano Instruments, Oak Ridge, TN) were carried out on the tooth sections with a Berkovich probe [23,24,29–33]. A fixed penetration of 400 nm was used, sufficiently shallow as to avoid cracking and other serious damage to valuable specimens. Indents were placed along five linear traces on each section from the enamel surface to the EDJ through the tallest cusp, at intervals of 20 μm, producing an average of 250 indents per specimen. Values of enamel plane strain modulus \( E \) (Young’s modulus divided by \( 1 - \nu^2 \), where \( \nu \) is Poisson’s ratio) and hardness \( H \) were deconvoluted from the digital data using the widely adopted quasi-static method of Oliver and Pharr [34]. Inferential probe shape calibrations were made on amorphous silica after each linear trace.

2. Methods and materials

2.1. Morphology and property measurements

Single tooth specimens from the mid twentieth century were studied: human (**Homo sapiens**), lower third molar; chimpanzee (**Pan troglodytes**), lower second molar; orangutan (**Pongo pygmaeus**), lower second molar; gorilla (**Gorilla gorilla**), upper first molar. These were obtained from the Natural History Museum, London [5]. All were preserved molars sectioned parallel to the long axis through prominent cusps in the buccal–lingual plane and had relatively unworn occlusal surfaces. They were received in resin mounts with the section surfaces exposed. These surfaces were given a light polish with 0.5 μm diamond slurry to remove any residual surface roughness and washed thoroughly for 10 min in running water to remove any accumulated contamination. The resulting sections were examined in a high power reflection optical microscope to confirm that the surfaces were smooth. All teeth were tested in the dry state. Modulus and hardness measurements were made across the sections for each primate. Instrumented nanoindentation tests with 50 nN noise resolution and 1 nm displacement noise floor (Nanoindenter XP, MTS Nano Instruments, Oak Ridge, TN) were carried out on the tooth sections with a Berkovich probe [23,24,29–33]. A fixed penetration of 400 nm was used, sufficiently shallow as to avoid cracking and other serious damage to valuable specimens. Indents were placed along five linear traces on each section from the enamel surface to the EDJ through the tallest cusp, at intervals of 20 μm, producing an average of 250 indents per specimen. Values of enamel plane strain modulus \( E \) (Young’s modulus divided by \( 1 - \nu^2 \), where \( \nu \) is Poisson’s ratio) and hardness \( H \) were deconvoluted from the digital data using the widely adopted quasi-static method of Oliver and Pharr [34]. Inferential probe shape calibrations were made on amorphous silica after each linear trace.

2.2. Fracture and deformation relations

Various fracture and deformation modes in enamel, depending on the tooth morphology and manner of loading, have been documented [35–38]. The most relevant of these for our purposes are depicted schematically in Fig. 1 for a dome-shaped shell (enamel) of characteristic base radius \( R \) and thickness \( d \) with a compliant interior (dentin). Given basic material properties and tooth geometry it is possible in principle to predict the loads required to produce critical damage for any tooth using explicit (if approximate) relations derived from contact mechanics [21].

First consider plastic deformation in the near contact region. The stress field in this region is determined by an “effective radius” and “effective plane strain modulus”:

\[
\frac{1}{r_{\text{eff}}} = \frac{1}{R} + \frac{1}{r}
\]

\[
\frac{1}{E_{\text{eff}}} = \frac{1}{E} + \frac{1}{E_t}
\]

where \( r \) is the radius of an indenting (food particle or opposing tooth) and \( E_t \) is the modulus of the indenting material [35]. The critical load for the onset of contact deformation is:

\[
P_c = D H (E_t/E)^{1/2} r_{\text{eff}}^2
\]

with \( D = 1 \) [21]. This mode leads to distributed microcracking within the plastic zone and constitutes a principal source of crumbling and wear.

Now consider fracture. Here we are concerned with the critical loads to drive longitudinal cracks within the enamel entirely around the walls of the tooth. Such cracks originate within the near contact region and run toward the margin (radial–median cracks) or from the tooth base and run toward the occlusal (margin cracks), depending on the relative properties of the tooth and contacting object. 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 [20]. The critical load for completion of the first longitudinal fractures can then be represented by a simple relation for margin cracks [38]:

\[
P_{M_t} = C T R d^{1/2}
\]

where \( T \) is toughness and \( C \approx 6.0 \). Strictly, Eq. (3) applies to hard contacts \( (E_t > E) \): a sufficiently compliant indenting material \( (E_t < E) \) 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 occlusal surface and even suppressing formation of radial–median cracks altogether [18,21].

There are other modes of cracking that can occur in contact loading of teeth, including edge chipping. While these alternative modes can provide useful information on the dietary history of any given species [39], they are less likely to act as precursors of total tooth failure and are not considered here.

3. Results

3.1. Enamel properties

Sections of the molar teeth for humans (Homo), chimpanzees (Pan), orangutans (Pongo) and gorillas (Gorilla) are shown at a common scale in Fig. 2. Differences in tooth size $R$ and enamel thickness $d$ are apparent. Some differences in occlusal form are also apparent.

Cross-sectional profiles of modulus $E$ and hardness $H$ from the nanoindentation tests are shown in Fig. 3a and 3b for primate molar enamel. The horizontal spatial coordinate in this figure is normalized to the distance from the EDJ to the outer surface, to enable comparisons between species. There is a consistent upward rise in the data with distance from the EDJ, broadly consistent with the trends reported elsewhere [23,24]. By averaging the $E$ and $H$ datasets between 0.4 and 0.6 normalized distance for each of the individual species in Fig. 3 we obtain the mid-range (0.5 normalized distance) mean values and standard deviations listed in Table 1.

3.2. Prediction of tooth damage and failure

Susceptibility of primate molar enamel to longitudinal fracture can be predicted from Eq. (3) using material properties $E$ and $H$ from Table 1 and a representative toughness $T = 0.7$ MPa m$^{1/2}$ [21,40], along with the values of tooth dimensions $R$ and $d$ listed in Table 2. Tooth radius $R$ was obtained from Demes and Creel as $R = 0.5$ (total molar crown area)$^{1/3}$, where the total molar crown area is summed over all three molars for each primate [7]. Enamel thickness $d$ was computed from the data of Kono as the average enamel cap volume divided by the EDJ area [10]. Mean values of calculated critical loads $P_M$ for fracture are plotted in Fig. 4 for each primate. The values for humans lie at the high end of the range observed experimentally [20], providing some justification for the material parameters used in the calculations. For the great apes the critical loads increase sequentially from chimpanzees through orangutans to gorillas.

The susceptibility of primate teeth to wear relative to fracture may be assessed from the critical load $P_Y$ to induce yield in Eqs. (1) and (2). Accordingly, values of $P_Y$ and $P_M$ are plotted in Fig. 5 as a function of food size $r$ for chimpanzees, assuming extreme food moduli $E_i = 1$ GPa (hard food) and 1 MPa (soft food). This diagram suggests a tendency to tooth wear ($P_Y \ll P_M$) for small hard food particulates (grits and phytoliths) and, conversely, a tendency to tooth fracture ($P_Y \gg P_M$) for large hard particulates (nuts and seeds). Chimpanzees were selected for this illustration simply because they appear to be the most vulnerable to tooth damage. More generally, noting the large variation in critical loads in Fig. 5 (covering almost 10 orders of magnitude), species to species variations in material properties (Table 1) or tooth dimensions (Table 2) will shift the $P_Y$ and $P_M$ curves by much less than one order of magnitude, in which case the inferred behavior can be considered quite general for all the primates studied here.

4. Discussion

We have measured basic material properties, modulus $E$ and hardness $H$, across sections of molar tooth enamel for humans and other great apes using nanoindentation. All teeth were tested in a common as-received state, similar in age and from the same museum source, so that species to species comparisons may be considered valid. The data in Fig. 3 for all tooth enamel specimens tested show lower values of $E$ and $H$ near the EDJ relative to the outer surface. These gradients are smaller than the previously reported factor of 2 from digitized $E$ and $H$ maps across entire cross-sectional areas of dental enamel [23,24], although our data represent just one specimen per species. A correlation between such gradients and mineral composition over the sections has previously been demonstrated [23], but decussation and the presence

Fig. 2. Longitudinal sections through molar teeth of primates: human (Homo), lower third; chimpanzee (Pan), lower second; orangutan (Pongo), lower second; gorilla (Gorilla), upper first. Ape specimens in this figure were all females; the sex of human specimen is unknown. Note commonality in bunodont shape between species, but differences in enamel thickness and tooth size.
of microstructural defects (tufts) in the vicinity of the EDJ could also be factors [27].

Recall that the tooth specimens represented in this study were received and tested in a dried-out state. Teeth are highly sensitive to environmental history, with a measurable tendency for $E$ and $H$ to decrease with intake of moisture, by as much as 23% for $E$ and 35% for $H$ [32]. Toughness $T$ of brittle materials also tends to diminish with increasing moisture content [41,42]. Accordingly, the critical load values reported here may be considered to overestimate those that prevail in the functional wet state. However, since we are mainly concerned with comparisons between species, and all specimens had similar provenances, the precise moisture state of the enamel was not a major concern here.

It is interesting to note that the representative values of $E$, $H$ and $T$ quoted in Section 3 are comparable with those for glass or porcelain [27]. The comparability in toughness $T$ in particular warrants special comment, for it highlights the extreme brittleness of enamel. In making this comparison we acknowledge that enamel has a

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**Table 1**

Elastic modulus and hardness of primate molar enamel.

<table>
<thead>
<tr>
<th></th>
<th>Elastic modulus, $E$ (GPa)</th>
<th>Hardness, $H$ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gorilla gorilla</td>
<td>93.0 ± 3.2</td>
<td>4.40 ± 0.20</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>100.3 ± 2.9</td>
<td>4.83 ± 0.23</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>104.0 ± 2.8</td>
<td>4.80 ± 0.20</td>
</tr>
<tr>
<td>Homo sapiens</td>
<td>90.6 ± 4.6</td>
<td>4.01 ± 0.37</td>
</tr>
</tbody>
</table>

Values are means ± standard deviations for data between 0.4 and 0.6 normalized distance in Fig. 3.

**Table 2**

Tooth dimensions for primate molar crowns.

<table>
<thead>
<tr>
<th></th>
<th>Tooth radius, $R$ (mm)$^a$</th>
<th>Enamel thickness, $d$ (mm)$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gorilla gorilla</td>
<td>7.30 ± 0.44</td>
<td>0.98 ± 0.10</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>6.65 ± 0.44</td>
<td>1.01 ± 0.12</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>5.43 ± 0.19</td>
<td>0.81 ± 0.09</td>
</tr>
<tr>
<td>Homo sapiens</td>
<td>4.89 ± 0.07</td>
<td>1.33 ± 0.13</td>
</tr>
</tbody>
</table>

$^a$ Data from Demes and Creel [7]. Demes and Creel reported molar crown areas as the sum of the product of the buccolingual and mesiodistal diameters of the three molar teeth for each species. From their data we calculated $R = 0.5(\text{total molar crown area})^{1/2}$ for males of each species. Values quoted are means ± standard deviations.

$^b$ Data from Kono et al. [10], average enamel cap volume divided by EDJ area. Values quoted are means ± standard deviations.
The most striking feature of the results lies not so much in the absolute values for any one species but in the similarity of values from species to species. The greatest difference between the smallest and largest values for any pair of species in Table 1 is 15% for $E$ and 20% for $H$. On the other hand, the corresponding ranges in $R$ and $d$ values in Table 2 are 59% and 64%. This is our basis for arguing that differences in the load-bearing capacity of the teeth of the different apes are more a function of morphology than of underlying material properties [49]. Although the cuspal geometry of any animal species is generally complex, the notion that its essence may be represented by two characteristic (averaged) scaling dimensions, tooth size $R$ and enamel thickness $d$ (Fig. 1), presents itself as an attractive concept. Then one may make use of the explicit relations in Eqs. (1)–(3) to provide estimates of maximum sustainable biting forces. Ignoring details of cusp form is less likely to be of concern if we again concern ourselves primarily with relative rather than absolute values of these biting forces.

Accordingly, some general conclusions may be drawn from the computed critical loads in this study. The values of $P_{\text{M}}$ for longitudinal cracking in Fig. 4 may be considered as limits above which the prospect of irreversible tooth damage becomes likely. Recall that whereas longitudinal cracks may develop from either radial–median or margin cracks (Fig. 1), it is implicit in Eq. (3) that it is margin cracks that proceed to failure first. This is borne out in compression loading tests on extracted human molars, in which each fracture mode can evolve simultaneously but margin cracks dominate in the final stages [20]. Fig. 6 compares $P_{\text{M}}$ for each species with estimates of maximum biting force $P_{\text{jaw}}$ from analysis of jaw mechanics [7]. The height of each box indicates the spread from upper and lower bound values in Tables 1 and 2; the width indicates the spread between male (high values) and female (low values) data from Demes and Creel [7]. The straight line represents the condition $P_{\text{M}} = P_{\text{jaw}}$. Allowing for uncertainties in both fracture mechanics [21] and jaw mechanics [50,51], a broad correlation is observed, particularly among the great apes, suggesting that Eq. (3) can indeed be a useful indicator of trends in biting force capacity.

The results of this study raise important anthropological questions concerning the relationship between hominoid tooth form and diet [52]. The suggestion is that the critical loads are associated with the mastication of hard foods. Soft foods are less likely to produce such extensive deformation and fracture damage; recall the dramatic upward shift in the $P_Y$ curve in Fig. 5 and our reference to complete and partial suppression of radial–median and margin cracks, respectively, in Section 2.2. There is developing evidence

Fig. 4. Critical loads to drive longitudinal cracks around enamel wall in humans and great apes. Curves are predictions from Eq. (3). Error bars reflect the data spread in Table 1.

Fig. 5. Critical loads for fracture $P_{\text{M}}$ and yield deformation $P_Y$ for chimpanzees as a function of food object size $r$. Yield loads calculated for soft and hard foods. Predictions from Eqs. (1)–(3).

significantly different microstructure to that of glass; enamel is highly anisotropic and inhomogeneous, with weak inter-prism interfaces providing preferred pathways for slippage and fracture [29–33]. In our calculations in Fig. 4 we have taken $T = 0.7$ MPa m$^{1/2}$ to be a single value constant. This value is toward the lower end of microindentation measurements, i.e., in the so-called “short crack” region [43,44]. Recent measurements of toughness using “long crack” specimens indicated that toughness may increase with progressive crack extension, up to some three or four times higher than our representative value [45,46]. Such increases may be attributable to crack impediment in regions of high decussation [47] or, over time, to self-repair of crack interfaces [48]. Nevertheless, the ease with which longitudinal cracks extend around enamel side walls suggests that the fracture follows inter-prism paths of low resistance, i.e., in the short crack domain. Despite these differences, enamel remains a highly brittle, glass-like material, reliant on a propitious morphology to mitigate catastrophic failure of the composite tooth structure.
from field studies that great apes may indeed consume hard foods, with orangutans consuming the hardest [53]. This raises the question: are the predicted loads from our analysis sufficient to account for the forces needed to break down really hard foods? Bornean orangutans have been observed to break open the cases of Mezzettia parviflora seeds with their teeth. Mezzetta is an exceptionally hard food, which in independent failure tests required critical loads in excess of 1 kN to crack the seed case [54]. This force level is in the vicinity of the tooth load-bearing capacity for orangutans estimated in Fig. 6. Even allowing for scatter in the data, uncertainties in material properties (including tooth to tooth variations and potential effects of moisture) and approximations in the theoretical derivations, the critical force estimates are commensurate with observed eating function for orangutans. Analogous correlations between diet and tooth fracture loads have yet to be established for chimpanzees and gorillas. We will pursue such biological aspects of tooth performance in primates in more detail elsewhere.

Acknowledgements

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References


