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The Role of Tooth Enamel Mechanical Properties in Primate Dietary Adaptation

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ABSTRACT  Primate teeth adapt to the physical properties of foods in a variety of ways including changes in occlusal morphology, enamel thickness, and overall size. We conducted a comparative study of extant primates to examine whether their teeth also adapt to foods through variation in the mechanical properties of the enamel. Nanoindentation techniques were used to map profiles of elastic modulus and hardness across tooth sections from the enamel-dentin junction to the outer enamel surface in a broad sample of primates including apes, Old World monkeys, New World monkeys, and lemurs. The measured data profiles feature considerable overlap among species, indicating a high degree of commonality in mechanical properties. These results suggest that differences in the load-bearing capacity of primate molar teeth are more a function of morphology—particularly tooth size and enamel thickness—than of underlying mechanical properties. Am J Phys Anthropol 148:171–177, 2012. ©2012 Wiley Periodicals, Inc.

KEY WORDS  dental ecology; elastic modulus; hardness; nanoindentation; diet

The ability of a primate to ingest and process its diet rests not only on the capacity to consume particular food items, but to do so without damaging its own teeth in the process. While much study has gone into how teeth break down food (Lucas, 1979; Lucas and Luke, 1984; Evans and Sanson, 1998; Evans and Sanson, 2003; Lucas, 2004; Freeman and Lemen, 2007), considerably less has been devoted to understanding the protective mechanisms by which teeth survive thousands of functional contacts each day, even though such an avenue of inquiry may provide valuable information on ways in which teeth can or should evolve to withstand the demands of repetitive biting and chewing.

Recent studies have shown how the load-bearing capacity of teeth is limited by the susceptibility of enamel to fracture and deformation (Lucas et al., 2008; Lawn et al., 2009; Lee et al., in press). The testing protocol involves loading extracted teeth, principally molars and premolars, with hard or soft indenting plates at the occlusal cusp, and observing ensuing fracture patterns with a video camera (Chai et al., 2009a). Enamel is only partially translucent, so such in situ observations of damage evolution are effectively limited to the tooth outer surface. Further insight into damage modes has been provided from tests on synthetic models mimicking the basic bunodont form of molar teeth, fabricated as hemispherical glass domes filled with dental epoxy. Loading these model structures at the top surface replicates the damage patterns observed in real teeth, except now the damage is revealed unequivocally to be contained entirely within the (transparent) glass shell (Rhee et al., 2001; Qasim et al., 2005; Rudas et al., 2005; Qasim et al., 2006; Lawn et al., 2007; Qasim et al., 2007). The damage patterns include well-defined longitudinal fractures down the enamel wall, surface plastic deformation and crumbling, and chipping. Mechanics analyses of these fracture and deformation modes have provided equations predicting critical biting forces for any specified set of tooth dimensions, specifically tooth size and enamel thickness. This has led to considerable focus on the role of tooth morphology in the determination of load sustainability (Lucas et al., 2008; Lawn and Lee, 2009; Lawn et al., 2009), with implications as to how teeth respond to various food and nonfood items in relation to dietary adaptation (Lucas et al., 2008).

However, the damage equations are also dependent on characteristic mechanical properties, such as Young’s modulus $E$ (resistance to reversible, elastic deformation), hardness $H$ (resistance to irreversible, plastic deformation), and toughness $T$ (resistance to crack propagation). Modulus and hardness are relevant to wear modes, and toughness to fracture modes (Lucas et al., 2008). In the model studies referred to above it has been implicitly assumed that these properties are invariant within and between species, at least relative to much greater variations in morphological variables. This assumption has


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TABLE 1. Elastic modulus and hardness (mid-point values) with standard deviations for selected primates

<table>
<thead>
<tr>
<th>Species</th>
<th>Group</th>
<th>Sex</th>
<th>Tooth</th>
<th>Modulus, $E$ (GPa)</th>
<th>Hardness, $H$ (GPa)</th>
<th>Tooth Radius, $R$ (mm)</th>
<th>Enamel Thickness, $d$ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Homo sapiens</em></td>
<td>Hominoid</td>
<td>M</td>
<td>$M_2$</td>
<td>90.6 ± 4.6</td>
<td>4.01 ± 0.37</td>
<td>4.89 ± 0.07</td>
<td>1.33 ± 0.13</td>
</tr>
<tr>
<td><em>Pan troglodytes</em></td>
<td>Hominoid</td>
<td>F</td>
<td>$M_2$</td>
<td>104.0 ± 2.8</td>
<td>4.80 ± 0.20</td>
<td>5.43 ± 0.19</td>
<td>0.81 ± 0.09</td>
</tr>
<tr>
<td><em>Gorilla gorilla</em></td>
<td>Hominoid</td>
<td>M</td>
<td>$M_2$</td>
<td>93.0 ± 3.2</td>
<td>4.40 ± 0.20</td>
<td>7.30 ± 0.44</td>
<td>0.98 ± 0.10</td>
</tr>
<tr>
<td><em>Pongo pygmaeus</em></td>
<td>Hominoid</td>
<td>F</td>
<td>$M_2$</td>
<td>100.3 ± 2.9</td>
<td>4.83 ± 0.23</td>
<td>6.55 ± 0.44</td>
<td>1.01 ± 0.12</td>
</tr>
<tr>
<td><em>Hyllobates megulii</em></td>
<td>Hominoid</td>
<td>M</td>
<td>$M_2$</td>
<td>106.3 ± 4.1</td>
<td>5.09 ± 0.30</td>
<td>3.11</td>
<td>0.71</td>
</tr>
<tr>
<td><em>Papio ursinus</em></td>
<td>Cercopithecoid</td>
<td>F</td>
<td>$M_2$</td>
<td>97.2 ± 4.4</td>
<td>4.59 ± 0.28</td>
<td>5.55</td>
<td>0.85</td>
</tr>
<tr>
<td><em>Macaca fascicularis</em></td>
<td>Cercopithecoid</td>
<td>F</td>
<td>$M_1$</td>
<td>99.4 ± 3.2</td>
<td>4.93 ± 0.29</td>
<td>3.24</td>
<td>0.73</td>
</tr>
<tr>
<td><em>Chlorocebus aethiops</em></td>
<td>Cercopithecoid</td>
<td>F</td>
<td>$M_1$</td>
<td>100.9 ± 4.9</td>
<td>5.16 ± 0.37</td>
<td>2.39</td>
<td>0.40</td>
</tr>
<tr>
<td><em>Brachyteles arachnoides</em></td>
<td>Platyrhine</td>
<td>M</td>
<td>$M_1$</td>
<td>99.4 ± 3.9</td>
<td>4.69 ± 0.23</td>
<td>4.26</td>
<td>0.59</td>
</tr>
<tr>
<td><em>Cebus apella</em></td>
<td>Platyrhine</td>
<td>M</td>
<td>$M_1$</td>
<td>94.5 ± 3.4</td>
<td>4.44 ± 0.36</td>
<td>2.55</td>
<td>0.58</td>
</tr>
<tr>
<td><em>Eulemur fulvus</em></td>
<td>Strepsirrhine</td>
<td>M</td>
<td>$M_1$</td>
<td>91.0 ± 2.9</td>
<td>4.67 ± 0.12</td>
<td>2.86</td>
<td>0.23</td>
</tr>
<tr>
<td><em>Hapalemur griseus</em></td>
<td>Strepsirrhine</td>
<td>F</td>
<td>$M_1$</td>
<td>104.3 ± 6.3</td>
<td>5.65 ± 0.26</td>
<td>2.46</td>
<td>0.67</td>
</tr>
</tbody>
</table>

Great ape data from Lee et al. (2010).

not been widely quantified by experiment in the literature. There have been studies of mechanical properties in human enamel, mainly using nanoindentation as a probe for documenting variations in modulus and hardness (Xu et al., 1998; Cuy et al., 2002). One study in particular (Cuy et al., 2002) found that property values varied by as much as a factor of 2 between the outer and inner surfaces of the enamel. Those variations correlated with compositional changes in calcium and phosphate content across enamel sections (Cuy et al., 2002). It is possible that such property gradients may help to shield the weak enamel-dentin junction from high external stresses (Huang et al., 2007). Analogous studies in toughness variations have also been reported (Bajaj and Arola, 2009) with larger values closer to the enamel-dentin junction, although fracture testing is more complex and consequently less well documented.

Interestingly, very little is known as to how any of these mechanical properties vary among different species, even though such variations could potentially contribute to differences in the capacities to eat particular food items. A study on the enamel of howler monkeys (Alouatta palliata) revealed less variation in modulus and hardness than in human enamel (Darnell et al., 2010) while nanoindentation data on the enamel of great apes (Lee et al., 2010) using averaged data from Demes and Creel (1988) and Kono (2004); for monkeys and lemurs, from

**MATERIALS AND METHODS**

Single molar specimens were obtained for each species: specimens of great apes (*Homo sapiens, Pan troglodytes, Pongo pygmaeus*, and *Gorilla gorilla*) from the Natural History Museum, London (Martin, 1985); apes (*Hyllobates megulii*), Old World monkeys (*Macaca fascicularis, Papio ursinus* and *Chlorocebus aethiops*), New World monkeys (*Brachyteles arachnoides and Cebus apella*), and lemurs (*Eulemur fulvus* and *Hapalemur griseus*) from private collections of the authors. These species, along with representative mechanical properties, are listed in Table 1.

All tooth specimens were sectioned and polished on a buccolingual plane through the mesial cusps. They were then set in resin mounts with the section surfaces exposed. These surfaces were given a final light polish to 0.5 μm using a diamond slurry to smooth out any residual surface roughness, and then rinsed for 10 min in running water to remove any accumulated contamination. The prepared sections were examined in a high-power reflection optical microscope to confirm that the surfaces were smooth and free from debris, and then allowed to dry for a minimum of 24 h prior to indenting. Slight cuspal wear was evident on some specimens, but we believe this to be of minor consequence since the primary goal of this research is to compare average through-section property values among species. Representative tooth sizes $R$ and enamel thicknesses $d$, depicted schematically in Figure 1, were obtained as follows: for the great apes, from a previous study (Lee et al., 2010) using averaged data from Demes and Creel (1988) and Kono (2004); for monkeys and lemurs, from...
direct measurements on our single specimens as a plumb line from the top of the prominent mesial cusp to the enamel-dentin junction. These dimensions are included in Table 1.

Additional comparative tests were made on two extracted molar teeth from modern human patients, using specimens from an earlier study (Chai et al., 2009b). These were sectioned as above, but were kept in a wet state throughout preparation and testing.

Measurements of elastic modulus $E$ and hardness $H$ were made across each of the enamel sections using instrumented nanoindentation (Nanoindenter XP system, MTS Nano Instruments, Oak Ridge, TN) with a Berkovich probe (Lee et al., 2010). Tests were made at a fixed penetration of 400 nm, sufficiently shallow as to avoid visible surface damage. Indents were placed along five linear traces per specimen at intervals of 20 μm from the enamel outer surface to the enamel-dentin junction through the tallest cusp on each section (see Fig. 2). Values of $E$ and $H$ were extracted from the digital data using the widely adopted approach of Oliver and Pharr, assuming a Poisson’s ratio 0.23 (Oliver and Pharr, 1999; Oliver and Pharr, 2004). All teeth were tested in a common dry state. Since we are primarily concerned with interspecific differences in $E$ and $H$, and all our teeth were tested in a dry state, the effect of moisture content on the tooth properties was not considered.

**RESULTS**

Cross sectional profiles of modulus $E$ and hardness $H$ from the nanoindentation tests on molar enamel are shown in Figures 3 and 4 as a function of normalized distance between the inner and outer surface: for apes (see Fig. 3), and for monkeys and lemurs (see Fig. 4). The data for any given species show broad scatter over the coordinate range, with considerable overlap among profiles of different species. Mid-range ($0.5 \times$ normalized distance) mean and standard deviation values were computed by averaging over each $E$ and $H$ dataset between 0.4× and 0.6× normalized distance. These mid-range values are listed in Table 1. The wide scatter in data in Figures 2 and 3, upward of 15% in $E$ and 20% in $H$ in maximum and minimum values, are large compared to variations of less than 2% in $E$ and $H$ for homogeneous fused silica surfaces used in nanoindenter calibrations, suggesting considerable point-to-point variations in local enamel microstructure. For humans, the mean and standard deviation values of $E = 91$ GPa ± 5 GPa and $H = 4.0$ GPa ± 0.4 GPa lie within the range of values reported in other studies (Spears, 1997; Cuy et al., 2002; He et al., 2006).

Figure 5 shows combined results for all species from Figures 3 and 4. The curves in this plot are obtained by spline fits to all datasets between 0.05 and 0.95 normalized distance—the truncation in data is to eliminate edge effects in the nanoindentation tests. The inclusion of all taxa in these plots allows one to compare property values between species without complication. In most cases, there appear to be some gradients in the $E$ and $H$ curves, but the trends are somewhat dwarfed by the scatter. Two-way ANOVA tests on the data within the 0.4× to 0.6× normalized distance range revealed no significant property differences between any of the primate species in Table 1 ($P < 0.05$).

The data in Figures 3 and 4 relate to specimens tested in the dry state. Analogous nanoindentation mid-range modulus evaluations for two wet modern human teeth indicate lower values of $E = 80 \pm 4.1$ GPa relative to 90.6 ± 4.6 GPa for the aged Homo specimen in Table 1.

**DISCUSSION**

Data trends

The potential role of enamel mechanical properties in contributing to primate dietary adaptation has not previously been examined. This study presents evaluations of basic mechanical properties—modulus $E$ and hardness $H$—from nanoindentation measurements across sections of molar tooth enamel for a taxonomically broad selection of primates. The most compelling feature of the results lies not in the absolute values of $E$ and $H$ for any one primate, nor even in the gradients between the outer and inner surfaces of the enamel, but in the overall similarity of $E$ and $H$ values among the different species in Figures 3–5. The greatest difference between smallest and largest values for any pair of species in Table 1 is 17% for $E$ and 40% for $H$, whereas the corresponding ranges in $R$ and $d$ values are over 300% and 500%. Accordingly, it may be asserted that tooth morphology is likely to be more important than mechanical properties in accounting for any dietary trends (Zaslansky et al., 2006; Lee et al., 2010).

Notwithstanding this similarity in data trends between species, some minor shifts may perhaps be discerned in the $E$ and $H$ data of Figures 3–5 and Table 1. For instance, the values for Pan, Pongo, and Hylabates in Figure 3 appear to lie some 10% above those for Homo and Gorilla. In Figure 4b, values for Hapalemur appear to be about 5% higher than the average for the group, and Cebus about 5% lower. It might be concluded that any such shifts reflect dietary adaptation. However, it needs to be reiterated that our data came from just one specimen per species and differences in provenance could account for any slight variations. This means that due caution should be exercised in attributing absolute values of $E$ and $H$ to any one of the species examined here. Nevertheless, given the high degree of overlap among property sets for each species, the fact remains that mechanical property values appear to be highly conserved among primates.

Similar comments may be made about the gradients in properties observed in Figures 3–5. Mention was made...
in the introductory comments of gradients as high as a factor of 2 in digital maps of $E$ and $H$ across tooth sections in human enamel, with lower values at the inner surface and higher values toward the outer (Cuy et al., 2002). Darnell et al. (2010) and Lee et al. (2010) reported analogous gradients in the nonhuman primates, albeit considerably lower in magnitude. A correlation between such gradients and mineral composition has previously been argued for humans (Cuy et al., 2002), but decussation and the presence of microstructural defects (tufts) in the vicinity of the enamel-dentin junction could be additional factors (Chai et al., 2009a). However, the broader taxonomic sample in the present study suggests that such gradients may not be universal for all primates. In some species the gradients in Figure 4 are slight to nonexistent (Hylabates, Papio, Cebus) or even reversed (Macaca and Chlorocebus). In several species, the point of maximum modulus or hardness appears not at either the inner or outer surface but somewhere in between. Once more, limitations in the specimen pool render specific conclusions uncertain.

A comment about the state of the tooth specimens tested in this study is in order. All specimens were received and evaluated in a dry state, after years of storage out of an aqueous environment. Water in the enamel can have substantial effects on mechanical properties, with both $E$ and $H$ decreasing substantially with greater moisture content (He and Swain, 2008). Recall the comparatively low value of $E = 80 \pm 4.1$ GPa for two wet modern human teeth cited above relative to the value $E = 90.6 \pm 4.6$ GPa for the aged Homo specimen in Table 1. Accordingly, the values reported here may be considered to overestimate those pertinent to the functional wet state. Nevertheless, since we are primarily concerned with relative trends between species, the comparative data trends reported here may be expected to remain valid. And, interestingly, the variations in standard deviation values for each of these human specimen types is comparable, i.e., on order 5%, indicating some commonality in tooth-to-tooth variation.

One mechanical property not explored systematically in this study is toughness $T$—the resistance of a material to crack extension. Enamel toughness can be estimated through the use of Vickers diamond pyramid microindenters (Anstis et al., 1981). However, we did not estimate toughness in this study because the loads and indentation sizes necessary to produce measurable cracks at the indentation corners are much higher than can be achieved by nanoindentation. Some of our specimens were too rare and valuable for such semidestructive testing. However, given that there is little variation...
in $E$ and $H$ among the species examined, we may expect that $T$ is also relatively stable. This is supported to a degree by property values from a variety of biological materials that show covariation between $T$ and $E$, albeit in opposing directions (Constantino et al., 2009). As with $E$ and $H$, toughness $T$ is also likely to be susceptible to moisture content.

Finally, a word about nonprimate species: given well documented differences in enamel microstructures for such species, it would clearly be unwise to extrapolate our present conclusions beyond the Order Primates. A case in point is the sea otter ($Enhydra lutis$), an animal proposed as a potentially useful comparative model in the study of hominin eating habits (Walker, 1981; Constantino et al., 2011). An earlier comparative nanoindentation study of human and sea otter teeth (under common moist testing conditions) actually found similar values of $E$ in the otter enamel, but lower $H$ and higher $T$. It might be argued that the differences in mechanical properties between otters and primates are a result of phylogeny rather than function. It is not to say that the higher hardness and lower toughness of primate enamel cannot convey a certain adaptive advantage under particular feeding parameters, but it seems likely that any such advantages or disadvantages are largely a byproduct of evolutionary history and not a product of targeted selection at the species level.

Implications concerning tooth survivability

Once the mechanical properties and relevant tooth dimensions have been characterized for any given species, predictive estimates can be made of the critical loads required to cause damage that threatens tooth survivability. Simple equations expressing the loads $P_Y$ to initiate irreversible yield or crumbling (surface wear) and $P_F$ to cause side-wall longitudinal cracking of the enamel in tooth-on-tooth contact have been developed progressively in several studies (Rhee et al., 2001; Lucas et al., 2008; Chai et al., 2009b; Lawn and Lee, 2009; Lee et al., in press):

$$P_Y = DH(H/E)^{4}R^2$$

(1a)

$$P_F = CTRd^{1/2}$$

(1b)

where $D \sim 1$ and $C \sim 6$ are dimensionless constants. Given our conclusions in the preceding subsection, it is the tooth dimensions rather than mechanical properties that are likely to wield the greater influence in determining biting forces among species.

Figure 6 is a bar graph of $P_Y$ and $P_F$ for each of the species studied here, using Eqs. (1a) and (1b) in conjunction with the mechanical properties $E$ and $H$ and tooth dimensions $R$ and $d$ in Table 1, along with a representative value of toughness $T = 0.7$ MPa m$^{1/2}$ (Xu et al., 1998; Lawn and Lee, 2009). Any biting forces exceeding these values puts the dentition at risk. Note that the loads to produce the onset of yield are somewhat lower than those to cause large-scale fracture, consistent with actual observations of loading with a hard object on molar tooth cusps (Lawn et al., 2009). Given the approximations and uncertainties alluded to above in the values of the inserted variables, the force estimates are probably not much more accurate than a factor of 2 in absolute terms. However, relative estimates may be considered more reliable, perhaps to within 15–20%, judging from the scatter ranges for $E$ and $H$ in Figures 3 and 4.
Estimates from Eq. (1b) have in fact been demonstrated to be consistent with evaluations from jaw mechanics (Lee et al., in press).

It is of interest to note the groupings in Figure 6. Such rankings may be useful in inferring dietary constraints. The teeth of great apes, particularly those of Gorilla gorilla and Pongo pygmaeus, can accommodate higher loads than can those of most other primates, mostly due to their larger size. For Gorilla gorilla, higher values of $P_F$ may protect the animal from fractures that can arise at the cervical margins (Chai et al., 2009b; Lee et al., in press) when high bite forces are applied to soft but tough foods such as bark, woody pith, fibrous fruits, and low-quality terrestrial herbaceous vegetation (Rogers et al., 1988; Yamagiwa et al., 1996; Tutin et al., 1997; Doran and McNeilage, 1998; Conklin-Brittain et al., 2001; Doran et al., 2002; Rogers et al., 2004; Yamagiwa and Basabose, 2009). For Pongo pygmaeus, high $P_F$ may protect against similar fractures when eating bark or leaves (Rodman, 1977; Vogel et al., 2008) or from fractures that start beneath the point of contact (Lucas et al., 2008) when eating large hard foods such as seeds and unripe fruit (Galdikas, 1982; Leighton, 1993; Vogel et al., 2008). High $P_F$ in these larger primates corresponds to a higher resistance to deformation micro-processes that could lead to excessive wear. The lower values of $P_F$ and $P_Y$ for Pan troglodytes are consistent with a heavier reliance on soft foods, even in periods of relative food scarcity (Tutin et al., 1991; Tutin and Fernandez, 1993; Furuichi et al., 2001; Constantino et al., 2009; Yamagiwa and Basabose, 2009).

The patterns evident within the monkey and lemur groups are also consistent with known differences in diet. Papio ursinus has a level of protection against tooth fracture that is comparable to that of Pan troglodytes and greater than that of the other monkeys included in this study. Its broad diet includes such odurante foods as grass corms and other underground storage organs (Whiten et al., 1987; Byrne et al., 1993). Such foods have been shown to require quite high loads to break them down in comparison to other, softer foods (Dominy et al., 2008), and have been tied to high levels of enamel surface wear due to the adherence of exogenous grit on their surfaces (Daebling and Grine, 1999). In this context of wear, it may be pointed out that Eq. (1a) for yield strictly applies to a tooth-on-tooth contact, and that the critical load $P_Y$ is greatly diminished for contacts with smaller particles (Lucas et al., 2008; Lawn et al., 2009). Cebus apella features the next most durable teeth of the monkeys examined. This species has also been shown to eat foods of exceptional toughness (Wright, 2004; Wright, 2005). Finally, as a bamboo consumer, Hapalemur griseus likely has a tougher diet than Eulemur fulvus (Tan, 1999; Yamashita et al., 2009), consistent with a higher value of $P_Y$, although the two species are similar in their values of $P_F$, indicating similar susceptibility to surface wear.

**SUMMARY**

The similarity in modulus $E$ and hardness $H$ among the broad sample of primates in this study implies that these and other mechanical properties (e.g., toughness $T$) may be highly conserved throughout the evolutionary history of the Order Primates. Accordingly, variation in mechanical properties does not appear to be a primary route through which natural selection has acted to optimize primate dietary fitness. Nevertheless, the values of $E$ and $H$ in Figures 3–5 and Table 1 (along with $T$) are critical to the quantitative determination of bite forces via fracture and yield relations such as those in Eq. (1), and thereby form a valuable part of the knowledge base for tooth properties. Differences in bite forces between primates are found to be more closely linked to aspects of tooth geometry such as tooth size, enamel thickness, and cuspal morphology. Reported differences in enamel mechanical properties between primates and sea otters (Constantino et al., 2011) leave open the possibility that such properties may vary more extensively in nonprimate vertebrates. Study of such animals in this context would appear to be warranted.

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PRIMATE ENAMEL MECHANICAL PROPERTIES