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The Influence of Fallback Foods on Great Ape Tooth Enamel

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KEY WORDS fracture mechanics; diet; evolution

ABSTRACT Lucas and colleagues recently proposed a model based on fracture and deformation concepts to describe how mammalian tooth enamel may be adapted to the mechanical demands of diet (Lucas et al.: *Bioessays* 30[2008] 374–385). Here we review the applicability of that model by examining existing data on the food mechanical properties and enamel morphology of great apes

(*Pan*, *Pongo*, and *Gorilla*). Particular attention is paid to whether the consumption of fallback foods is likely to play a key role in influencing great ape enamel morphology. Our results suggest that this is indeed the case. We also consider the implications of this conclusion on the evolution of the dentition of extinct hominins. *Am J Phys Anthropol* 140:653–660, 2009. © 2009 Wiley-Liss, Inc.

During certain times of the year, many primates resort to less preferred foods when preferred foods are scarce. The importance of these “fallback foods” has been the subject of much debate (Constantino and Wright, in press). Nevertheless, the study of such foods is proving to be valuable to our understanding of primate ecology and evolution, particularly regarding selective pressures leading to morphological change (Lambert, 2007; Marshall and Wrangham, 2007). Fallback foods have been invoked as the reason for the thick tooth enamel in grey-cheeked mangabeys (Lambert et al., 2004), and as a likely influence on the masticatory morphology and behavioral ecology of great apes and early hominins (Laden and Wrangham, 2005; Grine et al., 2006; Lambert, 2007; Ungar, 2007; Ungar et al., 2008; Vogel et al., 2008).

In this article, we examine whether fallback foods have influenced great ape enamel morphology. Our approach is in two main parts. First, we review mechanical property data indicating that fallback foods of great apes tend to be tougher or harder than their preferred foods. We then present a model explaining how tooth enamel responds to loading (Lucas et al., 2008; Lawn et al., 2009) and argue that several aspects of the dental morphology of these apes may be explained in terms of adaptation to the consumption of fallback foods. We focus principally on enamel thickness and tooth size, with some discussion on the potential role of prism decussation. Finally, we consider the relevance of these conclusions to the dentition of extinct hominins.

GREAT APE DIET

Understanding the complex relationship between tooth and food requires an examination of underlying mechanical properties. Figure 1 lists values of two such mechanical properties, “elastic modulus” (resistance to reversible deformation) and “toughness” (resistance to fracture), for a representative selection of primate foods and dental tissues. (The elastic modulus is often referred to as “hardness,” and we shall follow this usage here, although strictly hardness applies to permanent, plastic deformation.) Note the very large range of values cov-

ered in Figure 1, highlighted by the use of logarithmic coordinates. Note also the considerable variability in the data, indicated by the horizontal bars. Even allowing for these factors, the opposite trends in the modulus and toughness data are clear; softer and more compliant materials tend to be tougher. In particular, tooth enamel is hard but not very tough, meaning that while it is well suited to breaking down food, it is also relatively brittle.

Notwithstanding the difficulty of determining dietary preference in wild populations, the preferred food of common chimpanzees (*Pan troglodytes*), Bornean orangutans (*Pongo pygmaeus*), and lowland gorillas (*Gorilla gorilla gorilla* and *Gorilla beringei graueri*) appears to be soft, ripe fruit. Each species supplements its diet with other items, but studies correlating fruit availability with time spent feeding indicate that if ripe fruit is present, all of these apes prefer it and select it (Leighton, 1993; Nishihara, 1995; Remis, 1997; Doran and McNeilage, 1998; Knott, 1998; Delgado and Van Schaik, 2000; Conklin-Brittain et al., 2001; Remis et al., 2001; Doran et al., 2002; Rogers et al., 2004; Vogel et al., 2008). When ripe fruit is scarce or unavailable, each group has a somewhat different behavioral response. Chimpanzees tend to continue searching out ripe fruit, especially figs, and they do so by fissioning into smaller parties and sometimes increasing their range (Tutin et al., 1991; Furuichi et al., 2001; Yamagiwa and Basabose, in press). Some chimpanzee populations also expand the breadth of their

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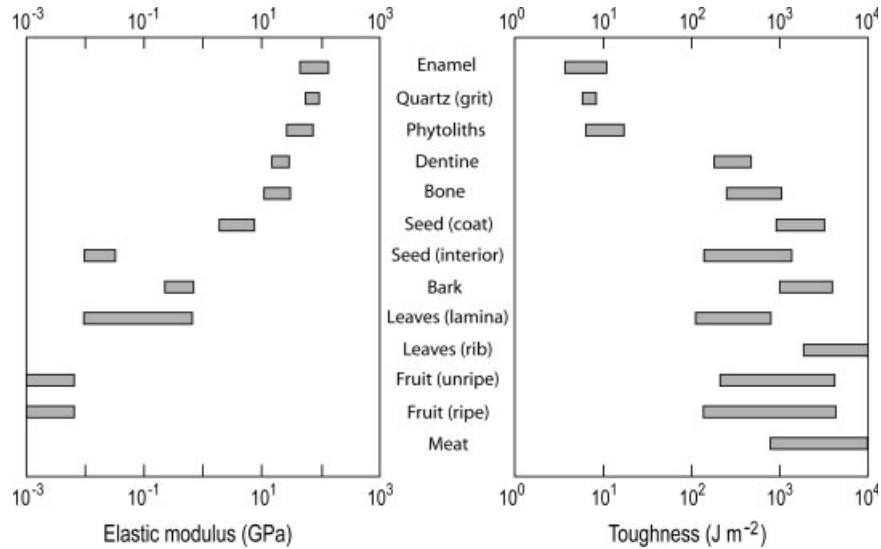


Fig. 1. Elastic modulus and fracture toughness of primate dental tissues and selected food items that may contact them. Note that the horizontal axes are in logarithmic scale. Note also the opposite data trends for modulus versus toughness (From Hepburn and Chandler, 1976; Baker et al., 1959; Hillerton et al., 1982; Lucas et al., 1991; Lawn, 1993; Spatz et al., 1996; Strait and Vincent, 1998; Niklas, 1999; Cuy et al., 2002; Schofield et al., 2002; Lucas et al., 2004; Vogel et al., 2008).

diet, either by increasing their consumption of low-quality, terrestrial herbaceous vegetation (THV) and herbaceous pith (Wrangham et al., 1991, 1996, 1998; Malenky and Wrangham, 1994; White, 1996; Furuichi et al., 2001), or through the addition of more animal products (Yamagiwa et al., 1996; Yamagiwa and Basabose, in press).

Bornean orangutans fall back through much of the year on unripe fruits and hard seeds. Soft, ripe fruit is relatively scarce in most orangutan habitats except during a mast, and so hard fallback foods make up a significant portion of the diet. Moreover, the seeds of fallback unripe fruits eaten by orangutans appear to be the hardest foods in their diet. For example, the hardest foods eaten by orangutans at the site of Gunung Palung are probably the seeds of *Lithocarpus* (Fagaceae) (A. Marshall, personal communication). Orangutans seek out these and other immature seeds when available (Leighton, 1993), probably because they are softer than ripe seeds (Vogel et al., 2008). However, the fact that such seeds are eaten during times of low overall fruit availability highlights their potential role as fallback foods. It has been reported that orangutans at Tuanan and other sites eat the seeds of *Mezzettia parviflora* (Galdikas, 1982; Vogel et al., 2008). These seeds have a modulus greater than 7 GPa (Lucas et al., 1991) while the vast majority of orangutan foods at Tuanan have maximum elastic modulus values under 9 MPa (Vogel et al., 2008). Therefore, *Mezzettia* seeds represent a potential 1,000-fold increase in elastic modulus over more typical food items. In laboratory tests, Lucas determined that mature *Mezzettia* seeds require a load over 2000 N to cause fracture (Lucas et al., 1994). (Vogel and colleagues were unable to obtain property data for these seeds at Tuanan because the values exceeded the capacity of their equipment.) When unripe fruits and seeds are unavailable, orangutans also fall back on bark and leaves (Rodman, 1977; Knott, 1998; Delgado and Van

Schaik, 2000; Vogel et al., 2008), and these appear to be the toughest foods eaten at Tuanan (Vogel et al., 2008).

Lowland gorillas fall back largely on low-quality THV, as well as bark, woody pith, and fibrous fruits (Rogers et al., 1988, 1994, 2004; Yamagiwa et al., 1996; Tutin et al., 1997; Doran and McNeilage, 1998; Conklin-Brittain et al., 2001; Doran et al., 2002; Yamagiwa and Basabose, in press). While there are few mechanical property data available on lowland gorilla fallback foods, several indirect lines of data exist to support the idea that the fallback foods of these animals are tougher than their preferred foods. First, "low-quality" THV is higher in fiber than preferred THV, and increasing the amount of fiber increases fracture toughness (Hill and Lucas, 1996; Lucas et al., 2000). Second, lowland gorillas eat bark as a fallback food (Rogers et al., 1994), and mechanical property data on barks eaten by mountain gorillas show that these foods can be exceptionally tough (Elgart-Berry, 2004). In fact, barks are reportedly the toughest foods that mountain gorillas eat, considerably tougher than any bark consumed by orangutans and at least four times tougher than any reported chimpanzee food (Dominy, 2001). Lowland gorillas also consume woody pith as a fallback food. As opposed to nonwoody pith, woody pith is lignified meaning that the compound lignin has filled in spaces in the plant's cell walls. This process increases the structural complexity and anisotropy of the cell walls (Esau, 1977), thereby increasing the toughness of the tissue (Lucas et al., 2000).

THE RESPONSE OF TOOTH ENAMEL TO BITING AND CHEWING FORCES

In recent studies, our enamel adaptation hypothesis has been presented in terms of fracture and deformation mechanics of teeth (Lucas et al., 2008; Lawn et al., 2009). Those studies identify enamel thickness and tooth size as key variables that determine the level of biting

force any given dentition may sustain without catastrophic fracture. Of course, there are other factors that can play a role in tooth mechanics, notably those relating to fine details in the shape (e.g., molar flare, hypsodonty), but we consider these to be secondary in the broader context of tooth failure. The tooth structure is modeled as a bilayer consisting of a hard hemispherical shell of uniform thickness d and cuspal radius r_e encasing a compliant, soft interior. Load is applied at the top surface by an “indenter” (i.e., opposing dentition or food particle) of characteristic radius r_i . We focus only on essential results here, without exploring the underlying mathematical relations.

It might at first seem logical that damage to teeth during mastication would initiate at or near the point of contact (i.e., on the external surface of the tooth). If this were to be the case, the damage would be determinable exclusively by the local Hertzian contact stresses (Lawn, 1998). The governing geometric dimension is then the “composite radius” $1/r = 1/r_i + 1/r_e$, where r_i is the radius of curvature of the indenter and r_e is the radius of curvature of the tooth cusp. In this event, the thickness of the enamel is not at all relevant. It turns out that enamel, although brittle, is more susceptible to “yield” from small local contacts, with resulting plastic deformation, than it is to fracture. The plasticity is accommodated principally by sliding within the weak protein sheaths that bind the mineralized prisms (He and Swain, 2007). Such sliding is a general feature of fibrous biological composites (Keckes et al., 2003; Fratzl et al., 2004), and can occur even if the fibers (prisms) are interwoven (Yang et al., 2005; Cox and Yang, 2006) or are loaded off-axis (Fratzl et al., 2004). The critical load to induce this yield mode is termed P_Y , whose value is determined (primarily) by the enamel modulus and hardness. The plastic deformation disrupts the local microstructure, ultimately crumbling the material within the deformation zone, and is the main contributor to wear of the dentition.

However, the enamel is not at all immune to fracture. An illustration is shown in Figure 2 of a human molar subjected to loading with a hard indenter at the top surface (Lawn et al., 2009). One form of fracture comes from the deformation process itself, as the microstructure progressively degrades and develops nuclei for ensuing “median” cracks. These cracks emerge from the plastic zone (seen as the flattened cusp in Fig. 2), and propagate downward toward the enamel-dentine junction (EDJ). Because it requires less energy for cracks to travel along weak material interfaces than across them, these cracks tend to propagate on paths between the enamel prisms (Rasmussen et al., 1976; Xu et al., 1998; He and Swain, 2007). Once they penetrate through the thickness of the enamel, the median cracks spread longitudinally around the side walls, ultimately reaching the cervical margin. Attainment of this stage of fracture is deemed “failure.” The governing mechanical property is now toughness. A second form of near-surface fracture is “cone” cracking, widely reported in isotropic brittle materials but less likely in enamel because of the difficulty of propagating such cracks laterally across the mineralized prism structure (Lawn et al., 2009).

A different form of fracture is “radial” cracking. Radial cracks initiate below the contact, but at the EDJ, from flexure of the enamel on a more compliant dentine underlayer (Lawn et al., 2001, 2004, 2007; Rhee et al., 2001; Qasim et al., 2005, 2006, 2007; Rudas et al., 2005). In this scenario, the thickness d of the enamel is the cru-

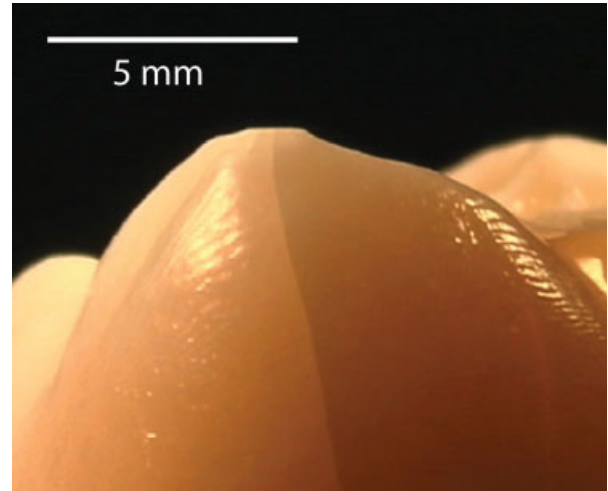


Fig. 2. Example of deformation and fracture of an extracted human molar tooth loaded with a metal disk. Some yield flattening has occurred at the upper cusp, and longitudinal cracks have propagated between the contact zone and the tooth margin. These cracks are confined to the thickness of the enamel coat (Reproduced from Lawn BR et al. Predicting failure in mammalian teeth. *Journal of the Mechanical Behavior of Biomedical Materials* 2:33–42. © 2009 Elsevier).

cial dimension for crack initiation, with the tooth size r_e a secondary factor. The dependence on d is quadratic, meaning that it requires four times the load to initiate cracks in enamel twice as thick. Once initiated, radial cracks spread stably upward toward the occlusal surface and sideways around the enamel walls. This latter, lateral growth stage is stable, at least initially, and once more the cracks extend continuously with increasing load until they run around the entire side wall of the enamel. In this advanced propagation stage the radial crack is indistinguishable from median cracks; hence the common terminology “radial-median.” The radial crack failure load P_{RF} depends to some extent on the cuspal curvature r_e , as well as on d .

Yet another form of fracture is that of “margin” cracking. In this mode, cracks initiate at the cemento-enamel junction (CEJ) and propagate longitudinally upward in a stable manner, increasing in length with the applied loading, somewhat analogous to their radial-median counterparts but with growth in the opposite direction (Ford et al., 2008). As with radial-median cracks, the failure load P_{MF} for margin cracks depends on tooth dimensions, although somewhat less on d and more on r_e . In fact, P_{MF} scales approximately linearly with r_e , whereas P_{RF} is much less dependent on r_e . This change in dependence reflects the fact that margin cracks are driven by tensile stresses near the cervical base of the tooth crown; these stresses are determined more by tooth size than by enamel thickness, within the confines of a hemispherical dome model. As alluded to above, other tooth shape factors, such as the presence of a cingulum and greater tooth height (hypsodonty), may diminish P_{MF} by suppressing initiation of margin cracks (Lucas et al., 2008).

A feature of all the fracture modes is the large increment in applied load required to drive them from first inception to final failure. Teeth are brittle, but extremely damage tolerant (Chai et al., 2009). It is arguable that most teeth contain a high population of damage accumu-

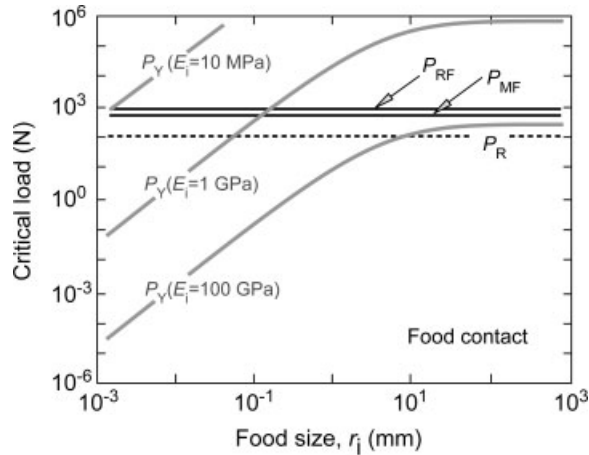


Fig. 3. Plot of critical loads to cause onset of yield at top surface (P_Y), onset of radial cracks at EDJ (P_R), and failure from radial-medial and margin cracks (P_{RF} and P_{MF}), as a function of characteristic food (“indenter”) size r_i . Yield plots shown for three values of food modulus E_i (see Fig. 1). At any given value of r_i , increasing load is equivalent to traversing upward along an appropriate vertical line. Note wide range of critical loads over food size and modulus range.

lation defects, and yet remain entirely functional. Much higher loads still are required to cause adjacent cracks to link up and delaminate the enamel from the dentine, or to drive cracks into the dentine (Popowics et al., 2001).

The responses of dentition to mastication depend not only on the form and mechanical properties of the enamel (e), but on the food “indenter” (i) as well (see Fig. 1). Allowance for the properties of the food material can be made via the Hertzian contact relations by substituting “effective radius” $1/r = 1/r_i + 1/r_e$ and “effective modulus” $1/E = 1/E_i + 1/E_e$ into mathematical formulae for P_Y (onset of yield), P_R (onset of radial cracking), P_{RF} (radial-medial failure) and P_{MF} (margin failure) (Lucas et al., 2008). A plot of these critical loads is given in Figure 3 as a function of food particle radius r_i , for $E_i = 100$ GPa (direct tooth-tooth occlusal contact), 1 GPa (moderately hard food) and 10 MPa (soft food), for human molars ($d = 1.2$ mm, $r_e = 4$ mm). On this Figure 3, increasing load is equivalent to traversing upward along a vertical line, for an appropriate food size. The dominant damage mode corresponds to the curve intersected first along such a line. Note that the failure loads P_{RF} and P_{MF} are of comparable value in this case, and independent of food properties. However, the initiation load P_Y for yield is highly sensitive to both r_i and E_i , as expected for a near-contact process. A salient point of this graph is the very large range of critical loads covered by the logarithmic vertical axis, amounting to several orders of magnitude. In this context, a factor of 2 would barely shift any of the curves on the plot, and so the model is insensitive to minor uncertainties in assumptions.

From Figure 3, we see that small, hard objects (low r_i , high E_i) such as grits and phytoliths favor surface yielding in the enamel. Large, hard objects (high r_i , high E_i) such as seeds and nuts can cause longitudinal cracks to grow to failure before incurring any yield. Soft foods ($E_i \ll 1$ GPa) tend to suppress both surface yield and deep radial cracks by smothering the surface of the tooth and

redistributing stresses to the tooth’s margins (Qasim et al., 2007). Margin fractures can then result, leading to abfraction failures (Grippio, 1991).

ENAMEL THICKNESS AND TOOTH SIZE

The perceived influence of different foods on the fracture pattern of tooth enamel leads to differing predictions regarding how tooth enamel may be adapted to diet. Here we address how fracture is affected by enamel thickness and tooth size. There have been two proposed benefits to thick tooth enamel in mammals. First, it may prolong the life of the tooth simply by increasing the amount of hard material that must be worn through before the softer underlying dentine is exposed (Jolly, 1970; Molnar and Gantt, 1977). Alternatively, thick enamel may provide increased resistance to fracture (Kay, 1981). Our model suggests that both hypotheses may be correct in certain conditions. Small, hard objects should cause surface wear from cumulative near-contact yield, while large, hard objects may initiate and grow radial-medial cracks that serve as the precursor to tooth failure. Thicker enamel would help to alleviate both conditions by increasing the amount of wear necessary to expose the underlying dentine and increasing the force required to fracture the enamel (Lucas et al., 2008). Therefore, thick enamel would appear to confer a selective advantage for any mammal that chews or bites hard foods. In this description, it is absolute enamel thickness that appears in the critical load equations (Lawn et al., 2009; Lawn and Lee, in press), and therefore determines the failure condition. Tooth size also enters the equations for critical loads. Basically, for given enamel thickness d , critical loads P_{RF} and P_{MF} will increase with characteristic cuspal radius r_e . This radius may be expected to scale in some way with animal weight, although not in a linear manner (Teaford and Ungar, 2000). Hence thinner enamel may be compensated to some degree by larger tooth size.

Chimpanzees have thinner occlusal enamel than either gorillas or orangutans, and this has been supported in studies using both 2D (Smith et al., 2005) and 3D (Kono, 2004; Kono and Suwa, 2008; Olejniczak et al., 2008b) methods. In addition, chimpanzees have similar lateral enamel thickness to orangutans and gorillas (Kono and Suwa, 2008), but the smaller size of their postcanine teeth (Pilbeam and Gould, 1974) makes them more susceptible than the other great apes to margin cracks. Thus, chimpanzee enamel morphology agrees well with a fallback strategy of changing group structure to continue searching out ripe fruit. The fact that the lateral enamel thickness of chimpanzees is generally greater than their occlusal enamel thickness (Kono and Suwa, 2008) may be indicative of their occasional need to consume leaves, THV, and herbaceous piths as fallback foods when figs are not available (Wrangham et al., 1991, 1996; Malenky and Wrangham, 1994; White, 1996; Dominy, 2001; Furuichi et al., 2001; Vogel et al., 2008; Yamagiwa and Basabose, in press). However, these chimpanzee fallback foods are not as tough as the fallback foods of gorillas or orangutans (Vogel et al., 2008), allowing chimpanzees to maintain their smaller tooth size (and greater susceptibility to margin fractures).

As discussed above (Great Ape Diet), orangutans are known to process fallback foods of relatively high hardness with their postcanine teeth. Thicker enamel on the occlusal surfaces of orangutan teeth is consistent with

our model. The occlusal surface is specified because this is where the food contacts the enamel and potentially causes tensile stresses at the EDJ, and thicker occlusal enamel inhibits these tensile stresses. Orangutans also occasionally consume tough, pliable foods which tend to smother the surface of the tooth, diminishing the contact stresses there and redistributing tensile stresses to the cervical margins (Qasim et al., 2007). Such stress redistribution inhibits deep cracks but favors margin fractures. Orangutans and chimpanzees have similar lateral enamel thickness (Kono and Suwa, 2008), but the larger size of orangutan postcanine teeth makes them less susceptible to margin fractures than chimpanzees.

Thick enamel has also been proposed as a tool to protect against surface wear caused by abrasion (contact with abrasive substances), attrition (tooth-to-tooth contact), or erosion (dissolution caused by acidic or corrosive chemicals) (Jolly, 1970; Every, 1972; Seligman et al., 1988; Gandara and Truelove, 1999; Kaidonis, 2008). Our model indicates that large hard objects such as seeds and hard fruits are likely to cause deep fractures (Lucas et al., 2008), while small hard objects cause surface wear. Therefore, the fallback foods of orangutans are more likely to lead to fracture than wear (see Fig. 5 in Lucas et al., 2008). It is possible that tooth wear could result from phytoliths or grits in the plant foods of orangutans, or corrosive acids in the fruits of orangutans, and increased enamel thickness could then be an evolutionary response to this loss of dental tissue. However, orangutans are typically not known to have heavily worn or eroded teeth, and generally exhibit less wear than either gorillas or chimpanzees (Welsch, 1967). It is therefore most likely that the thick occlusal enamel of orangutans is adaptive for protecting against deep fracture.

Gorillas consume tougher fallback foods than the other great apes and rely on these foods for a greater proportion of their fallback diet. Their lateral enamel is similar in thickness to that of the other great apes, but their relatively larger tooth size gives them greater protection from margin fractures. It is noteworthy that the occlusal enamel of gorillas is also close in thickness to that of orangutans. Since gorillas do not eat large, hard seeds, their teeth would not seem to be susceptible to deep fractures in the occlusal area. The question then arises as to why their occlusal enamel is so thick. The answer may lie in the barks eaten by gorillas, some of which have elastic modulus values close to those of seed shells (see Fig. 1). In a study of cercopithecine monkeys, Lambert et al. (2004) found barks eaten by grey-cheeked mangabeys (*Lophocebus albigena*) to be particularly hard and even argued that bark and seeds were the two fallback foods selecting for thick tooth enamel in these monkeys. Also, a preliminary study noted that gorilla teeth feature more wear on their occlusal surfaces than do the teeth of either orangutans or chimpanzees (Welsch, 1967). Therefore, the thick occlusal enamel of gorillas may be a protection against heavy surface wear. This is an issue that remains to be studied further, and additional mechanical property data on gorilla foods would go a long way toward addressing this question.

ENAMEL MICROSTRUCTURE

Enamel is composed of rods or prisms that originate at the EDJ and extend almost to the outer surface of the tissue. The prisms can be straight, but more often than

not exhibit at least a small degree of decussation, or crossing. Decussation is caused by adjacent enamel prisms orienting themselves in waves that are slightly out of phase as they grow from the EDJ toward the enamel surface. Cracks in enamel preferentially travel between prisms rather than across them. Decussation can slow crack growth by either causing the cracks to deviate along reoriented prism directions or (in more severe cases) to cut across prisms in order to maintain a well-defined fracture surface (Koenigswald et al., 1987; Bajaj et al., 2008).

Decussation most often occurs only in the inner part of the enamel (Rensberger, 2000). It has been suggested that this is due to the importance of abrasion resistance conferred by parallel prisms at the occlusal surface (Rensberger and Koenigswald, 1980). However, it could also be that decussation is a mechanism that serves primarily to slow down cracks that initiate at or near the EDJ. Deep radial cracks can begin at the EDJ when a large, hard object contacts the tooth with considerable force (Lucas et al., 2008). Stalling these cracks early could protect the tooth from catastrophic failure. Of the great apes, orangutans should be in the most danger of growing these deep cracks because of the high biting loads needed to break down large hard seeds (Lucas et al., 1994, 2008). This may explain why orangutans have the most pronounced decussation of all great apes (Macho et al., 2003). Chimpanzees and gorillas are unlikely to experience such high tensile stresses at the EDJ. Therefore, the enamel of gorillas (Shellis and Poole, 1977; Boyde and Martin, 1984; Maas and Dumont, 1999) and chimpanzees (Macho et al., 2003) features relatively little decussation.

The bulk of the evidence from enamel thickness, tooth size, and enamel microstructure indicates that fallback foods influence the enamel morphology of great apes. However, there is no reason to believe that fallback foods will always influence primate masticatory morphology. Presumably, fallback foods are less preferred than other foods for a reason, but that reason does not have to be because of increased mechanical demand in processing (i.e., because the food is harder or tougher). The fallback food could be less preferred simply because it is less nutritious, more difficult to find or acquire, or because it has chemical or physical defenses (Lambert, 2007). The food may also have a low intake rate either because it requires preparation prior to ingestion, or because it is small. Such is the case with grass corms (Altmann, 1998). Therefore, one could easily envision scenarios where the primary influence on masticatory morphology is a preferred food and not a fallback food. Such may be the case with the pitheciines who have evolved masticatory adaptations to puncture and process the hard pericarp of unripe fruits in order to get to the seeds as their preferred food items (Kinzey and Norconk, 1990, 1993; Martin et al., 2003). In this case, it seems that the mechanical cost of sclerocarpic harvesting is offset by the significant nutritional quality of the seeds. Nevertheless, it seems clear from this study and several others (Lambert et al., 2004; Lambert, 2007) that fallback foods should not be overlooked in terms of their ability to influence evolution in primates and other animals.

RELEVANCE FOR EXTINCT HOMININS

This study has implications for inferring the diets of early hominins. The megadont australopiths belonging

to the genus *Paranthropus*, in particular the East African species *Paranthropus boisei*, are known for having very thick enamel (Grine and Martin, 1988). What may be less well known is that *P. boisei* not only had thick occlusal enamel, but thick lateral enamel as well (Beynon and Wood, 1986). This suggests that *P. boisei* may have had a varied diet of hard and tough foods—the thick occlusal enamel protective of hard object feeding and the thick, lateral enamel and large tooth size protective of margin cracks from softer, tougher foods.

A recent 3D examination of the enamel thickness of *Paranthropus robustus* from South Africa found that this species also had thick occlusal enamel, but the lateral enamel was not much thicker than that of other hominins (Olejniczak et al., 2008a). This indicates a hard, but not tough, diet and supports the finding from studies of dental microwear that small hard objects were contacting the teeth (Grine, 1981, 1987; Scott et al., 2005). However, the large tooth size of *P. robustus* would have still provided some protection against margin fractures. We would also caution that the absence of a surface microwear signal for larger hard objects in both *P. robustus* and *P. boisei* (Ungar et al., 2008) may be misleading. Evidence for feeding on such objects may be indicated instead by the presence of deep cracks stalled near the EDJ (Lucas et al., 2008). We have observed initiation of such deep cracks during in situ loading of teeth from a variety of extant mammals by imaging with a synchrotron x-ray beam. Similar high powered x-ray imaging could be extended to look for deep cracks in the teeth of *Paranthropus*.

Limited evidence from tooth sections shows that the teeth of *Paranthropus*, and especially those of *P. boisei*, can feature substantial prism decussation (Grine and Martin, 1988; Teaford and Ungar, 2000), although apparently not in all directions (Beynon and Wood, 1986). A high degree of prism decussation would further support the idea that both *P. robustus* and *P. boisei* were adapted to eat hard foods. However, this does not preclude the possibility that *Paranthropus* enamel served to combat considerable tooth wear. The combination of extensive prism decussation and a high degree of postcanine tooth wear observed on many *Paranthropus* teeth (Robinson, 1954) suggests that both fracture and wear were major threats to tooth integrity.

Finally, although not a point of focus in this article, the degree of cusp curvature also plays a role in determining the forces required to deform and fracture enamel. Higher forces are generally needed to damage more bunodont teeth, suggesting that the low, rounded cusps of *Paranthropus* postcanines offered protection against fracture, regardless of the thickness of the enamel or the microstructural pattern.

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LITERATURE CITED

- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press. 608 p.
- Bajaj D, Nazari A, Eidelman N, Arola DD. 2008. A comparison of fatigue crack growth in human enamel and hydroxyapatite. *Biomaterials* 29:4847–4854.
- Baker G, Jones LHP, Wardrop ID. 1959. Cause of wear in sheeps' teeth. *Nature* 184:1583–1584.
- Beynon AD, Wood BA. 1986. Variations in enamel thickness and structure in East African hominids. *Am J Phys Anthropol* 70: 177–193.
- Boyde A, Martin L. 1984. The microstructure of primate dental enamel. In: Chivers DJ, Wood BA, Bilsborough A, editors. *Food acquisition and processing in primates*. New York: Plenum. p 341–367.
- Chai H, Lee J-JW, Constantino PJ, Lucas PW, Lawn BR. 2009. Remarkable resilience of teeth. *Proc Nat Acad Sci, USA*. doi: 10.1073/pnas.0902466106.
- Conklin-Brittain N-L, Knott CD, Wrangham RW. 2001. The feeding ecology of apes. In: *The apes: challenges for the 21st Century*. Brookfield Zoo, May 10–13, 2000, Conference Proceedings. Brookfield: Chicago Zoological Society. p 167–174.
- Constantino PJ, Wright BW. The importance of fallback foods in primate ecology and evolution. *Am J Phys Anthropol*, in press.
- Cox B, Yang QD. 2006. In quest of virtual tests for structural composites. *Science* 314:1102–1107.
- Cuy JL, Mann AB, Livi KJ, Teaford MF, Weihs TP. 2002. Nano-indentation mapping of the mechanical properties of human molar tooth enamel. *Arch Oral Biol* 47:281–291.
- Delgado RA, Van Schaik CP. 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evol Anthropol* 9:201–218.
- Dominy NJ. 2001. Trichromacy and the ecology of food selection in four African primates [Ph.D. thesis]. Hong Kong: University of Hong Kong.
- Doran DM, McNeilage A. 1998. Gorilla ecology and behavior. *Evol Anthropol* 6:120–131.
- Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *Am J Primatol* 58:91–116.
- Elgart-Berry A. 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. *Am J Primatol* 62: 275–285.
- Esau K. 1977. *Anatomy of seed plants*. New York: John Wiley & Sons.
- Every RG. 1972. A new terminology for mammalian teeth: founded on the phenomenon of theogesis. Parts 1 & 2. Christchurch, New Zealand: Pegasus.
- Ford C, Qasim T, Bush MB, Hu X, Lawn BR. 2008. Margin failures in crown-like brittle structures: off-axis loading. *J Biomed Mater Res* 85:23–28.
- Fratzl P, Burgert I, Gupta HS. 2004. On the role of interface polymers for the mechanics of natural polymeric composites. *Phys Chem Chem Phys* 6:5575–5579.
- Furuichi T, Hashimoto C, Tashiro Y. 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *Int J Primatol* 22:929–945.
- Galdikas B. 1982. Orang-utans as seed-dispersers at Tanjung Puting, Central Kalimantan: implications for conservation. In: de Boer LEM, editor. *The Orang Utan: its biology and conservation*. The Hague: W. Junk. p 285–298.
- Gandara BK, Truelove EL. 1999. Diagnosis and management of dental erosion. *J Contemp Dent Pract* 1:1–17.
- Grine FE. 1981. Trophic differences between “gracile” and “robust” australopithecines: a scanning electron microscope analysis of occlusal events. *S Afr J Sci* 77:203–230.
- Grine FE. 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. *Scan Microsc* 1:647–656.
- Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. *Evolutionary history of the “robust” Australopithecines*. New York: Aldine de Gruyter. p 3–42.
- Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J Hum Evol* 51:297–319.

- Grippio JO. 1991. Abfraction: a new classification of hard tissue lesions of teeth. *J Esthet Restor Dent* 3:14–18.
- He L, Swain MV. 2007. Contact induced deformation of enamel. *App Phys Lett* 90:171916.
- Hepburn HR, Chandler HD. 1976. Material properties of arthropod cuticles: the arthroal membrane. *J Comp Physiol B* 109:177–198.
- Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) in Yakushima. *Am J Primatol* 38:221–231.
- Hillerton JE, Reynolds SE, Vincent JFV. 1982. On the indentation hardness of insect cuticle. *J Exp Biol* 96:45–52.
- Jolly CJ. 1970. The seed eaters: a new model for hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Kaidonis JA. 2008. Tooth wear: the view of the anthropologist. *Clin Oral Invest* 12(Suppl 1):S21–S26.
- Kay RF. 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55:141–151.
- Keckes J, Burgert I, Fruhmann K, Muller M, Kolln K, Hamilton M, Burghammer M, Roth SV, Stanzl-Tschegg S, Fratzl P. 2003. Cell-wall recovery after irreversible deformation of wood. *Nat Mater* 2:810–814.
- Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am J Phys Anthropol* 81:5–15.
- Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int J Primatol* 14:207–227.
- Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *Int J Primatol* 19:1061–1079.
- Koenigswald Wv, Rensberger JM, Pretzschner HU. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* 328:150–152.
- Kono RT. 2004. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Anthropol Sci* 112:121–146.
- Kono RT, Suwa G. 2008. Enamel distribution patterns of extant human and hominoid molars: occlusal versus lateral enamel thickness. *Bull Natl Mus Nat Sci Ser D* 34:1–9.
- Laden G, Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *J Hum Evol* 49:482–498.
- Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar PS, editor. *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford: Oxford University Press. p 324–343.
- Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain N-L. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am J Phys Anthropol* 125:363–368.
- Lawn BR. 1993. *Fracture of brittle solids*. 2nd ed. Cambridge: Cambridge University Press.
- Lawn BR. 1998. Indentation of ceramics with spheres: a century after Hertz. *J Am Ceram Soc* 81:1977–1994.
- Lawn BR, Bhowmick S, Bush MB, Qasim T, Rekow ED, Zhang Y. 2007. Failure modes in ceramic-based layer structures: a basis for materials design. *J Am Ceram Soc* 90:1671–1683.
- Lawn BR, Deng Y, Thompson VP. 2001. Use of contact testing in the characterization and design of all-ceramic crownlike layer structures. *J Prosthet Dent* 86:495–510.
- Lawn BR, Lee JJ-W. Analysis of fracture and deformation modes in teeth subjected to occlusal loading. *Acta Biomater*, in press.
- Lawn BR, Lee JJ-W, Constantino PJ, Lucas PW. 2009. Predicting failure in mammalian teeth. *J Mech Behav Biomed Mater* 2:33–42.
- Lawn BR, Pajares A, Zhang Y, Deng Y, Polack MA, Lloyd IK, Rekow ED, Thompson VP. 2004. Materials design in the performance of all-ceramic crowns. *Biomaterials* 25:2885–2892.
- Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *Int J Primatol* 14:257–313.
- Lucas P, Constantino P, Wood B, Lawn B. 2008. Dental enamel as a dietary indicator in mammals. *Bioessays* 30:374–385.
- Lucas PW. 2004. *Dental functional morphology: how teeth work*. Cambridge: Cambridge University Press. 355 p.
- Lucas PW, Choong MF, Tan HTW, Turner IM, Berrick AJ. 1991. The fracture toughness of the leaf of the dicotyledon *Calophyllum inophyllum* L. (Guttiferae). *Philos Trans R Soc Lond B* 334:95–106.
- Lucas PW, Lowrey TK, Pereira BP, Sarafis V, Kuhn W. 1991. The ecology of *Mezzetia leptopoda* (Hk. f. et Thoms) Oliv. (Annonaceae) seeds as viewed from a mechanical perspective. *Funct Ecol* 5:545–553.
- Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orangutans with their teeth in captivity and a new technique for estimating forces produced in the wild. *Am J Phys Anthropol* 94:365–378.
- Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000. Mechanical defences to herbivory. *Ann Bot (Lond)* 86:913–920.
- Maas MC, Dumont ER. 1999. Built to last: the structure, function, and evolution of primate dental enamel. *Evol Anthropol* 8:133–152.
- Macho GA, Jiang Y, Spears IR. 2003. Enamel microstructure—a truly three-dimensional structure. *J Hum Evol* 45:81.
- Malenky RK, Wrangham RW. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *Am J Primatol* 32:1–12.
- Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1219–1235.
- Martin LB, Olejniczak AJ, Maas MC. 2003. Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. *J Hum Evol* 45:351–367.
- Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. *Am J Phys Anthropol* 46:447–454.
- Niklas KJ. 1999. The mechanical role of bark. *Am J Bot* 86:465–469.
- Nishihara T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* 36:151–168.
- Olejniczak AJ, Smith TM, Skinner MM, Grine FE, Feeney RNM, Thackeray JF, Hublin JJ. 2008a. Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biol Lett* 4:406–410.
- Olejniczak AJ, Tafforeau P, Feeney RNM, Martin LB. 2008b. Three-dimensional primate molar enamel thickness. *J Hum Evol* 54:187.
- Pilbeam DR, Gould SJ. 1974. Size and scaling in human evolution. *Science* 186:892–901.
- Popowics TE, Rensberger JM, Herring SW. 2001. The fracture behavior of human and pig molar cusps. *Arch Oral Biol* 46:1–12.
- Qasim T, Bush MB, Hu X, Lawn BR. 2005. Contact damage in brittle coating layers: influence of surface curvature. *J Biomed Mater Res B Appl Biomater* 73:179–185.
- Qasim T, Ford C, Bush MB, Hu X, Lawn BR. 2006. Effect of off-axis concentrated loading on failure of curved brittle layer structures. *J Biomed Mater Res B Appl Biomater* 76:334–339.
- Qasim T, Ford C, Bush MB, Hu X, Malament KA, Lawn BR. 2007. Margin failures in brittle dome structures: relevance to failure of dental crowns. *J Biomed Mater Res B Appl Biomater* 80:78–85.
- Rasmussen ST, Patchin RE, Scott DB, Heuer AH. 1976. Fracture properties of human enamel and dentine. *J Dent Res* 55:154–164.
- Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *Am J Primatol* 43:87–109.
- Remis MJ, Dierenfeld ES, Mowry CB, Carroll RW. 2001. Nutritional aspects of western lowland gorilla (*Gorilla gorilla go-*

- rilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *Int J Primatol* 22:807–836.
- Rensberger JM. 2000. Pathways to functional differentiation in mammalian enamel. In: Teaford MF, Smith MM, Ferguson MWJ, editors. *Development, function and evolution of teeth*. Cambridge: Cambridge University Press. p 252–268.
- Rensberger JM, Koenigswald WV. 1980. Functional phylogenetic interpretation of enamel microstructure in rhinoceroses. *Paleobiology* 6:447–495.
- Rhee Y-W, Kim H-W, Deng Y, Lawn BR. 2001. Contact-induced damage in ceramic coatings on compliant substrates. *J Am Ceram Soc* 84:1066–1072.
- Robinson JT. 1954. Prehominid dentition and hominid evolution. *Evolution* 8:324–334.
- Rodman PS. 1977. Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 383–413.
- Rogers E, Tutin C, Parnell R, Voysey B, Fernandez M. 1994. Seasonal feeding on bark by gorillas: an unexpected keystone food? In: Thierry B, Anderson JR, Roeder JJ, Herrenschmidt N, editors. *Current primatology, Vol. 1: Ecology and evolution*. Strasbourg, Universite Louis Pasteur. p 34–43.
- Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CE. 2004. Western gorilla diet: a synthesis from six sites. *Am J Primatol* 64: 173–192.
- Rogers ME, Williamson EA, Tutin CEG, Fernandez M. 1988. Effects of the dry season on gorilla diet in Gabon. *Primate Rep* 22:25–33.
- Rudas M, Qasim T, Bush MB, Lawn BR. 2005. Failure of curved brittle layer systems from radial cracking in concentrated surface loading. *J Mater Res* 20:2812–2819.
- Schofield RMS, Nesson MH, Richardson KA. 2002. Tooth hardness increases with zinc-content in mandibles of young adult leaf-cutter ants. *Naturwissenschaften* 89:579–583.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436:693–695.
- Seligman DA, Pullinger AG, Solberg WK. 1988. The prevalence of dental attrition and its association with factors of age, gender, occlusion, and TMJ symptomatology. *J Dent Res* 67: 1323–1333.
- Shellis RP, Poole DFG. 1977. The calcified dental tissues of primates. In: Lavelle CLB, Shellis RP, Poole DFG, editors. *Evolutionary changes to the primate skull and dentition*. Springfield: Charles C. Thomas. p 197–279.
- Smith TM, Olejniczak AJ, Martin LB, Reid DJ. 2005. Variation in hominoid molar enamel thickness. *J Hum Evol* 48:575–592.
- Spatz H-C, O'Leary EJ, Vincent JFV. 1996. Young's moduli and shear moduli in cortical bone. *Proc R Soc Lond B Biol Sci* 263: 287–294.
- Strait SG, Vincent JFV. 1998. Primate faunivores: physical properties of prey items. *Int J Primatol* 19:867–878.
- Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. *Proc Natl Acad Sci USA* 97: 13506–13511.
- Tutin CE, Fernandez M, Rogers ME, Williamson EA, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Philos Trans R Soc Lond B* 334:179–185; discussion 185–186.
- Tutin CEG, Ham RM, White LJ, Harrison MJS. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *Am J Primatol* 42: 1–24.
- Ungar PS. 2007. Dental topography and human evolution with comments on the diets of *Australopithecus africanus* and *Paranthropus*. In: Bailey SE, Hublin J-J, editors. *Dental perspectives on human evolution: state of the art research in dental paleoanthropology*. New York: Springer Verlag. p 321–343.
- Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3:e2044.
- Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol* 55: 60–74.
- Welsch U. 1967. Tooth wear in living pongids. *J Dent Res* 46(Suppl. 5):989–992.
- White FJ. 1996. Pan paniscus 1973 to 1996: twenty-three years of field research. *Evol Anthropol* 5:11–17.
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant L, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 45–57.
- Wrangham RW, Conklin NL, Chapman CA, Hunt KD, Milton K, Rogers E, Whiten A, Barton RA. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Philos Trans R Soc Lond B* 334:171–178.
- Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int J Primatol* 19: 949–970.
- Xu HH, Smith DT, Jahanmir S, Romberg E, Kelly JR, Thompson VP, Rekow ED. 1998. Indentation damage and mechanical properties of human enamel and dentin. *J Dent Res* 77: 472–480.
- Yamagiwa J, Basabose AK. Fallback foods and dietary partitioning among *Pan* and *Gorilla*. *Am J Phys Anthropol*, in press.
- Yamagiwa J, Maruhashi T, Yumoto T, Mwanza N. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 82–98.
- Yang QD, Rugg KL, Cox BN, Marshall DB. 2005. Evaluation of macroscopic and local strains in a three-dimensional woven C/SiC composite. *J Am Ceram Soc* 88:719–725.