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Food mechanical properties, feeding ecology, and the mandibular morphology of wild orangutans

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ABSTRACT

Bornean orangutan mandibular morphology has been functionally linked to the exploitation of hard and tough foods, based on evidence that *Pongo pygmaeus wurmbii* spends a greater percentage of time feeding on bark, seeds and vegetation compared with *Pongo abelii* (Sumatran orangutans) and the assumption that these tissues are more challenging to process than fruit pulp. We measured and compared toughness (*R*) and Young's modulus (*E*) of ripe and unripe foods exploited by *P. abelii* and *P. p. wurmbii*. Additionally, we recorded and compared the percentage of time these orangutans fed on plants/plant parts of varying degrees of *R* and *E*. Compared with *P. abelii*, *P. p. wurmbii* consumed significantly tougher and more displacement limited $(R/E)^{0.5}$ fruit parts, leaves and inner bark, and spent a significantly greater percentage of time feeding on immature leaves, unripe fruit and other vegetation. Modulus did not vary as expected between species, likely because we failed to capture the high-end range of modulus values for tissues consumed by *P. p. wurmbii*. Notably, *P. p. wurmbii* spent ~40% of its feeding time on the toughest foods consumed (between 1000 and 4000 J m^{-2}). Thus, the hypothesis that mandibular robusticity in *P. p. wurmbii* is functionally linked to feeding on tough foods is supported and is likely related to countering relatively larger external forces and/or repetitive loads required to process the toughest tissues. The importance of elastic modulus on morphological divergence awaits future studies capturing the full range of this material property for *P. p. wurmbii*. Finally, phenophase and fruit availability influence orangutan species differences in food material properties and percentage of time spent feeding on various foods, emphasizing the importance of incorporating these variables in future studies of feeding ecology and craniodental morphology in extant taxa.

Introduction

The relationships among primate feeding behavior, diet, and mandibular morphology are of central importance to anthropologists seeking to link behavioral ecology with functional and evolutionary morphology (e.g., Hylander, 1979a; Bouvier, 1986; Ravosa, 1991, 1996a; Daegling, 1992; Taylor, 2002, 2006; Wright, 2005; Daegling and McGraw, 2007; Taylor et al., 2008; Hogg et al., 2011; Ross et al., 2012). When primates chew or bite, their jaw muscles apply loads to the mandible. These loads, in turn, cause internal stresses and strains in the mandible. Food material properties (FMPs) modulate both the magnitude and duration of jaw-muscle activity (Ahlgren, 1966; Luschei and Goodwin, 1974; Hiiemae, 1978; Hylander, 1979b; Thexton et al., 1980; Oron and Crompton, 1985; Chew et al., 1988; Hylander and Johnson, 1994; Agrawal et al., 1998; Ross et al., 2007) such that food elastic modulus and toughness are associated with the complexity of jaw movements, recruitment levels of jaw-muscle force, and/or jaw loads. It is this empirically demonstrated relationship between FMPs, jaw-muscle activity patterns, and mandibular loads that has

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led many investigators to draw functional and adaptive conclusions about feeding behavior and diet from jaw form in both living and fossil primates (Jolly, 1970; Hylander, 1979a, 1988; Smith, 1983; Daegling, 1989, 1992; Cole, 1992; Spencer and Demes, 1993; Antón, 1996; Ravosa, 1996a, 2000; Taylor, 2002, 2006; Wright, 2005; Vinyard and Ryan, 2006; Strait et al., 2009; Dumont et al., 2011). Identifying morphological responses to mandibular loads in extant taxa is key to testing diet-based ecological models of species diversification, and to extending these models to fossil taxa. However, the functional relationships among jaw form, feeding behavior, and diet are complex and expected morphological differences have not been consistently observed (Daegling and Hylander, 2000; Daegling and McGraw, 2001, 2007; Taylor et al., 2008; Ross et al., 2009, 2012).

One reason for the variance between theoretical expectations and empirical findings may relate to the historic reliance on qualitative descriptions of coarse-grained diet classifications (e.g., folivore, frugivore) and food classes (e.g., fruit, terrestrial herbaceous vegetation) as meaningful proxies for FMPs (Hylander, 1979a; Daegling, 1992; Anapol and Lee, 1994; Ravosa, 1996b; Taylor, 2006). Numerous comparative studies of primate mandibular morphology have been based on the classically held assumption that leaves are tough, seeds are hard, and fruits are soft, and thus it has been assumed that food mechanical properties map neatly onto dietary categories (Hylander, 1975; Rosenberger and Kinzey, 1976; Beecher, 1979; Smith, 1983, 1984; Peters, 1987, 1993; Rosenberger, 1992; Anapol and Lee, 1994; Daegling and McGraw, 2001; Taylor, 2006). Not surprisingly, for some of these studies, predicted morphological relationships based on these broad dietary classes have not been systematically borne out by the data (Bouvier, 1986; Ravosa, 1991; Daegling and McGraw, 2001, 2007; Taylor, 2002; Taylor et al., 2008; Wright et al., 2009; Ross et al., 2012). It seems plausible that the reliance on qualitative descriptors in lieu of quantitative data on FMPs clouds these relationships.

Relatively few studies linking jaw morphology to FMPs in wild primates have incorporated quantitative FMPs data such as toughness (R) or Young's modulus (E) (Kinzey, 1978; Peters, 1987; Kinzey and Norconk, 1990, 1993; Dumont, 1995; Yamashita, 1998, 2003; Lucas, 2000; Lambert et al., 2004; Wright, 2005; Teaford et al., 2006; Dominy et al., 2008; Vogel et al., 2008, 2009; Norconk et al., 2009; Vinyard et al., 2009; Daegling et al., 2011). This is primarily because the technology to reliably and accurately measure FMPs in the field was only made available for widespread use around a decade ago (Lucas et al., 2001). The extent to which qualitative dietary descriptions accurately track FMPs remains an open question, but the fact that foods of disparate dietary categories display overlapping material properties (Williams et al., 2005; Vogel et al., 2008) suggests that such qualitative descriptions may not always provide accurate substitutes for FMPs. Thus, for all but a handful of primate species, hominoids included, the expectation of a functional and adaptive relationship between mandibular morphology and food mechanical properties remains largely speculative.

Orangutans as a natural experiment

Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus wurmbii*) orangutans are closely-related species whose dietary differences are well documented (Knott, 1998, 2001; Delgado and van Schaik, 2000; Wich et al., 2006; Morrogh-Bernard et al., 2009). On average, Sumatran and Bornean orangutans incorporate similar average percentages of fruit in their diet, but the minimum percentage of fruits is much higher for Sumatran orangutans (Wich et al., 2006). While Sumatran orangutans spend more time feeding on ripe fruit pulp, Bornean orangutans spend more time feeding on items that have been identified as fallback foods, including inner bark, leaves, and other vegetation. Fallback foods (sensu Marshall and Wrangham, 2007) are low-quality, abundant items that are eaten when preferred foods are scarce. The majority of Bornean orangutan fallback foods is significantly tougher and more resistant to deformation than their preferred fruits (Vogel et al., 2008) and feeding on mechanically challenging fallback foods has been argued to play an important evolutionary role in shaping primate craniodental morphology (Rodman, 1977; Kay, 1981; Lambert et al., 2004; Ungar, 2004; Laden and Wrangham, 2005; Wright, 2005; Taylor, 2006; Marshall and Wrangham, 2007; Taylor et al., 2008; Ungar et al., 2008; Vogel et al., 2008, 2009; Constantino et al., 2009; Marshall et al., 2009; Wright et al., 2009; Daegling et al., 2011; McGraw and Daegling, 2012).

In a previous study, Taylor (2006) compared mandibular morphology among Bornean and Sumatran orangutan populations. At the time the study was conducted, feeding behavior and diet were based on documented differences in habitat productivity, qualitative estimates of FMPS inferred from food type (i.e., bark and some vegetation were presumed to be mechanically more difficult to process than fruit pulp), and field observations of percentage of time spent feeding on these different foods (MacKinnon, 1974; Rodman, 1977, 1988; Rijksen, 1978; Leighton, 1993; van Schaik, 1999; Delgado and van Schaik, 2000; van Schaik and Knott, 2001). Dietary profiles based on these data led Taylor to hypothesize that *P. p. wurmbii* load their jaws more frequently, and possibly with relatively greater forces, compared with *P. abelii*. Thus, Taylor predicted that *P. p. wurmbii* would exhibit mandibular features that reflect the demands of a more mechanically challenging diet. Taylor's predictions were generally supported by the data, which demonstrated that compared with *P. abelii*, *P. p. wurmbii* have relatively deeper mandibular corpora, wider mandibular symphyses and larger condylar areas. Taylor functionally linked these mandibular features in *P. p. wurmbii* to their need to generate and resist relatively larger and/or more frequent occlusal loads associated with processing more mechanically challenging foods. However, in the absence of quantitative data on FMPs, Taylor's conclusions remain largely untested.

Given their close phylogenetic relationship and divergent feeding behaviors and diets, orangutans provide a natural experiment to empirically test the functional relationships among feeding behavior, FMPs, and jaw form. To this end, we quantified the mechanical properties of foods consumed by *P. abelii* (Ketambe, Sumatra) and compare these data with previously reported estimates (Vogel et al., 2008) of FMPs for *P. pygmaeus wurmbii* (Tuanan, Borneo). Given that *P. p. wurmbii* relies more heavily on leaves, seeds, and inner bark (Morrogh-Bernard et al., 2009) and exhibit a relatively more robust mandible, we predict that *P. p. wurmbii* consumes foods that are tougher and have a higher elastic modulus compared with those of *P. abelii*. We also recorded fruit abundance (i.e., high versus low) and compared the percentage of time *P. abelii* and *P. p. wurmbii* spent feeding on various foods. We use these data to test whether differences in feeding behavior and FMPs support previous functional interpretations of variation in mandibular morphology between *P. abelii* and *P. p. wurmbii* (Taylor, 2006) and provide the first test of the functional link between FMPs and jaw form between two closely related hominoid species of the same genus.

Materials and methods

Study sites and subjects

The Ketambe research station (3° 41′ N, 97° 39′ E) is located in the Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. The research area is mostly covered by pristine rainforest from the alluvial lowlands at ca. 350 m to higher altitudes around 1000 m above sea level (Rijksen, 1978; van Schaik and Mirmanto, 1985). However, nearly one-fifth of the research area (450 ha) has been subjected to intense selective logging (Hardus et al., 2012). The Tuanan research station (2° 09′ S; 114° 26′ E) is located in the Mawas Reserve in Central Kalimantan, Borneo, Indonesia. This site consists of peat swamp on shallow peat (<3 m); it is disturbed, having been subject to selective commercial logging in the early 1990s followed by almost a decade of informal logging. Since the end of 2002, there has been no logging in the area. Research on orangutans has been continuous at Ketambe since 1971, except for a brief interruption from 2001 to 2003. During the time of this study there were ca. 20 habituated, regularly-followed individuals in the research area. At Tuanan, focal behavioral data on ca. 19 individuals have been collected regularly since 2003 using the same standardized protocols employed at Ketambe (see below).

Behavioral methods

We conducted full-day focal follows on all study animals using standardized methodology at both sites (van Schaik, 1999; Morrogh-Bernard et al., 2002) and only included nest-to-nest data in our analyses. During focal follows, we recorded the activity of the focal animal every two minutes. If the study subject was feeding, we recorded the plant species, the item consumed, and the stage of maturation of the food item (i.e., immature/mature). Feeding data from Ketambe are based on 4992 feeding hours collected from February 2001 until June 2009 while data from Tuanan are based on 7273 feeding hours collected from July 2003–June 2007. Dietary data used to examine the percentage of time spent feeding on different food items were collected on adult females from Ketambe ($n = 8$) and Tuanan ($n = 9$) that were fully habituated at the time of the studies. We restricted these dietary comparisons to females as sex (Harrison et al., 2009; Morrogh-Bernard et al., 2009) and age (Jaeggi et al., 2008, 2010; van Schaik et al., 2009) differences in diet selection have been documented within populations.

Mechanical measurements of foods

Food mechanical properties (FMP) data were collected at Ketambe from August 2007–July 2008 and May 2010–August 2010 and at Tuanan from July 2005–June 2006. Foods eaten by *P. abelii* and *P. p. wurmbii* were collected during standard focal data collection using the same methodology and equipment (Vogel et al., 2008). We sampled the stages of maturity and vegetative tissues of 125 plant species at Ketambe, all of which were included in the orangutan diet during the eight consecutive years of long-term focal observations used for this study (Appendix 1). Fresh fruit, bark, leaves, and other vegetative (e.g., stems, peat, orchids, and non-woody pith) samples were collected during focal feeding bouts. Feeding bouts began at the time the focal individual initiated feeding in a tree and terminated when the individual stopped feeding. Food items for analysis were obtained in situ by ascending trees or by collecting items that had fallen from the tree during a feeding bout (Vogel et al., 2008). At least two specimens were collected from a given food patch whenever possible. Fresh samples were placed in sealed plastic bags with moist paper towels, transported to the field station, photographed, and processed the same day they were collected. We categorized stage of maturation on the basis of external cues that signify the development of a particular species (e.g., color, size, and texture of unripe or ripe fruit and associated seeds).

We measured FMPs with a portable universal tester (Darvell et al., 1996; Lucas et al., 2001). We quantified two FMPs: toughness (R) and Young's (elastic) modulus (E; resistance to deformation). We define toughness (J m-2) as the amount of energy required to initiate and extend a crack of a given area (Ashby, 1992; Vincent, 1992; Lucas, 2004; Lucas et al., 2012a). We define Young's modulus (MPa) as the ratio of stress to corresponding strain along the linear portion of the stress–strain curve (Ashby, 1992; Lucas, 2004; Williams et al., 2005).

Toughness was measured for fruit exocarp, mesocarp and endosperm, leaves, inner bark (i.e., cambium/phloem), and other vegetation. Toughness of fruit parts was measured using the wedge test (Lucas et al., 2001, 2012a; Lucas, 2004). To account for anisotropic variation within a fruit, at least two mechanical measurements were taken from both hemispheres and averaged. Toughness was calculated by dividing the area beneath the force–deformation curve by the product of crack depth (i.e., wedge displacement) and initial specimen width (Lucas et al., 2001). For leaves, inner bark, and other vegetation (e.g., orchids, pith), samples were fractured using cobalt scissors (Dovo, Germany) mounted on the tester (Darvell et al., 1996; Dominy et al., 2003; Dominy and Lucas, 2004; Lucas, 2004). When consuming bark, orangutans typically strip the outer bark from the tree and scrape the cambium/phloem tissues from the tree or outer bark with their incisors.[1] Once scraped from the outer bark, it is then chewed and swallowed or wadged and expelled (spat) from the mouth. Subsequent examination of this quid or wad can provide clear evidence of molar-induced fracture of individual plant fibers. Thus for bark feeding, we use the term phloem/cambium or inner bark as this is the tissue orangutans masticate with their molars. We measured Young's modulus of fruit exocarp (husk), mesocarp (pulp), and endosperm (seed) with cylinder compression tests (Lucas et al., 2001) following Vogel et al. (2008).[2]

In addition to toughness and Young's modulus, we calculated displacement-limited $(R/E)^{0.5}$ and stress-limited $(ER)^{0.5}$ fragmentation indices separately for each fruit part (e.g., exocarp, mesocarp, and endocarp) using the mean of Young's modulus and toughness (Agrawal et al., 1997; Lucas et al., 2002; Lucas, 2004; Williams et al., 2005). To calculate fragmentation indices, we only include food items for which we measured both Young's modulus and toughness (Williams et al., 2005).[3] Displacement-limited foods allow cracks to initiate easily, but resist propagation of the crack through the plant tissues. Foods that are stress-limited generally prevent cracks from initiating easily, but have little structure available to prevent cracks from propagating through the tissue once a crack has been generated (Lucas, 2004; Williams et al., 2005).

Statistical analyses

We calculated average toughness (R) and Young's modulus (E) for food samples collected during a single feeding bout (Vogel et al., 2008, 2009). We used the two-tailed, nonparametric

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[1] While using the anterior teeth to strip bark is an ingestive behavior, we do not consider the forces on the jaw during procurement of this tissue nor how the anterior dentition may intervene to impact these loads (Vinyard et al., 2011). Variation in incisor (Taylor, Unpublished data) and premolar (Uchida, 1998) morphology could impact dental efficiency during bark stripping but would not impact loads associated with the mastication of bark.

[2] We limited our measurements of Young's modulus to fruit tissues due to limitations of our equipment at the time of this study.

[3] While excluding tissues that did not have measurements for both Young's modulus and toughness reduced the number of food items included in these fragmentation indices, results did not differ when we averaged E and R for our complete sample of plant tissues.

Kruskal–Wallis to test for statistical differences in *E* and *R* among food items consumed by *P. abelii* at Ketambe. For post-hoc multiple comparisons, we used Tukey's HSD (Zar, 1999). To test for differences in *E* and *R* between immature and mature tissues of the same plant part we used the Wilcoxon sign-test.

To address the hypothesis that *P. p. wurmbii* ingests and masticates foods that are significantly tougher and more resistant to elastic deformation compared with *P. abelii*, we compared previously published values from Tuanan (Vogel et al., 2008) with the mechanical properties of food items consumed at Ketambe (Appendix 1). We used one-tailed Wilcoxon rank-sum tests (or the parametric equivalent, Welch's ANOVA for unequal variances, if appropriate) to evaluate differences in toughness and modulus of plant tissues (immature and mature parts combined) and differences by stage of maturity. We used the Bonferroni-Holm correction to minimize Type I error for all comparisons (Rice, 1989).

We summarized data on percentage of feeding time spent on food items from Ketambe and Tuanan by taking monthly averages across adult females following Harrison et al. (2009) to avoid issues related to autocorrelation of data among sampling days within the data sets. We used two-tailed tests to evaluate species differences in the percentage of feeding time spent on food items. Additionally, we used the nonparametric Spearman rank correlation to examine associations between percentage of feeding time and FMPs (e.g., *E* and *R*), separately by species.

We set the significance level for all tests at $\alpha < 0.05$ and noted trends toward significance ($0.05 < p < 0.10$). All statistical procedures were carried out using JMP-SAS 8.0.2 (SAS Institute, Cary, NC, USA) and R (The R Foundation for Statistical Computing: http://www.R-project.org).

Results

Mechanical properties of foods at Ketambe

The toughness of foods ingested and masticated by *P. abelii* ranged from 18.7 J m^{-2} for mature fruit pulp of *Palaquium* sp. to 4058.7 J m^{-2} for mature seeds of *Diospyros sumatrana* (Table 1). Similar to findings for *P. p. wurmbii* (Vogel et al., 2008), average *R* of plant tissues masticated by *P. abelii* differed significantly from one another (Table 1 and Fig. 1A), with inner bark the toughest tissue and significantly tougher than fruit mesocarp, fruit exocarp, and leaves. Inner bark was not significantly tougher than fruit endosperm and other vegetation (e.g., pith and orchids). When we evaluated differences in FMPs by phenophase we observed that average immature fruit exocarp and mesocarp tended to be tougher than ripe tissues, although these differences did not reach statistical significance ($0.05 < p < 1.0$) (Table 1). By contrast, maximum *R* of immature fruit mesocarp was 1.5 times that of mature mesocarp (Table 1). Likewise, we found no average difference in *R* between ripe and unripe endosperm (Table 1), but maximum *R* of mature endosperm was higher (Table 1), consistent with previous findings from Tuanan (Vogel et al., 2008). Our sample size for mature leaves consumed by *P. abelii* was too small to test for phenophase differences.

Notably, while there were significant differences in FMPs among food categories (e.g., fruit, leaves, inner bark), we observed considerable overlap between traditional plant part categories in both toughness and Young's modulus (Table 1 and Appendix 1). Equally important, plant phenophase and plant part (e.g., endosperm, mesocarp, exocarp) influence variation in the mechanical properties of foods consumed by these orangutan populations. Collectively, these findings underscore the inadvisability of inferring FMPs for a specific food item or food part from qualitative descriptions of whole foods or food classes.

Young's modulus (*E*) of foods consumed by *P. abelii* ranged from less than 1.0 MPa for mature fruit pulp of *Palaquium* sp. to 8.5 MPa for immature husk of *Ficus* sp. (Table 1). Tissues masticated by *P. abelii* differed in average *E*, with fruit endosperm and exocarp significantly more resistant to deformation compared with mesocarp (Table 1). Tests of fruit (all parts combined) by phenophase further showed that unripe fruit was significantly more resistant to deformation compared with ripe fruit (Table 1). In particular, *E* of unripe (immature) fruit exocarp and mesocarp was significantly higher compared with ripe (mature) tissues (Table 1; Fig 1B). However, at Ketambe, there were no differences in Young's modulus of mature and unripe endosperm (Table 1; Fig. 1B), whereas at Tuanan, mature seeds were significantly more resistant to deformation (Vogel et al., 2008). We note, however, that our sample size for seeds of unripe fruit consumed at Ketambe was low ($n = 4$), resulting in low statistical power for this analysis (power = 0.27).

Food mechanics compared between P. abelii and P. p. wurmbii

Toughness (*R*) *P. pygmaeus wurmbii* consumed significantly tougher ripe and unripe fruits (all parts combined) compared with *P. abelii* (Fig. 2A). Upon further examination of differences by fruit part and phenophase, we observed that compared to *P. abelii*, *P. p. wurmbii* consumed significantly tougher ripe fruit exocarp and endosperm, and significantly tougher unripe exocarp and mesocarp (Table 2 and Fig. 2B–D). With respect to non-fruit tissues, *P. p. wurmbii* masticated significantly tougher inner bark and leaves compared with *P. abelii* (Table 2 and Fig. 3).

Young's modulus (*E*) *Pongo p. wurmbii* consumed ripe fruit with significantly higher modulus (all parts combined) compared with *P. abelii* but there were no species differences in modulus of unripe fruits (Fig. 4A). Breaking down fruit into its constituent tissues by phenophase, *P. p. wurmbii* masticated mature fruit mesocarp with a significantly higher modulus compared with *Pongo abelii* (Table 2 and Fig. 4B). *Pongo pygmaeus wurmbii* also consumed mature fruit endosperm with an average modulus (*E*) 1.5 times greater than that of *P. abelii*, but this difference was not statistically significant. However, contrary to our predictions, *P. abelii* masticated immature fruit exocarp with a significantly higher modulus compared with *P. p. wurmbii* (Table 2).

Fragmentation indices Fruits (all parts combined) consumed by *P. p. wurmbii* were significantly more displacement-limited ($\chi^2 = 3.8$, df = 1, $p = 0.03$) and stress-limited ($\chi^2 = 3.1$, df = 1, $p = 0.04$) compared with *P. abelii*. The higher displacement-limited index for *P. p. wurmbii* is accounted for largely by higher $(R/E)^{0.5}$ for both immature and mature exocarp and immature endosperm (Table 3). All ripe and unripe fruit parts have higher stress-limited indices for *P. p. wurmbii* with the exception of immature exocarp, with the greatest differences for mature mesocarp and endosperm (Table 3).

Food selection compared between P.p. wurmbii and P. abelii

Compared with female *P. abelii*, female *P. p. wurmbii* spent a significantly greater percentage of feeding time on immature leaves, unripe fruit, flowers, and other vegetative parts (Table 4). These differences were apparent during periods of both high and low fruit abundance for unripe fruit and other vegetative parts, but the percentage of time spent feeding on immature leaves and flowers was greater only during periods of low fruiting (Table 4). *Pongo abelii* spent more feeding time on ripe fruit during both high and low fruit abundance and, unexpectedly, on inner bark and mature leaves during high fruiting periods (Table 4).

Table 1

Means ± standard errors, sample sizes (in parentheses), minimum–maximum values [in brackets], and results of statistical tests for differences in toughness and Young's modulus among food items, and between immature and mature stages of foods, consumed by *Pongo abelii* (Ketambe, Sumatra). Data for *Pongo pygmaeus wurmbii* are provided for comparison (updated from Vogel et al. (2008) with additional data).[a–d]

Food items	*Pongo abelii*				*Pongo pygmaeus wurmbii*	
	Toughness (R; J m^{-2})	Immature versus mature	Young's modulus (E; MPa)	Immature versus mature	Toughness (R; J m^{-2})	Young's modulus s (E; MPa)
Fruit exocarp	703.7 ± 118.9 (26)		4.5 ± 0.7 (19)		1361.2 ± 151.2 (60)	2.8 ± 0.3 (29)
Immature	895.8 ± 183.0 (10) [240.6–2211.3]	$p = 0.09$	6.4 ± 0.4 (8) [4.9–8.5]	$\boldsymbol{p = 0.03}$	1436.3 ± 186.1 (38) [5.3–6977.7]	3.2 ± 0.4 (22) [0.4–7.0]
Mature	583.5 ± 152.5 (16) [48.9–2053.3]		3.1 ± 0.9 (11) [0.1–8.5]		1231.4 ± 261.9 (22) [182.5–8164.1]	1.8 ± 0.4 (7) [0.4–3.1]
Fruit mesocarp	424.5 ± 66.9 (51)		1.5 ± 0.4 (25)		686.3 ± 85.3 (67)	2.7 ± 0.2 (60)
Immature	504.1 ± 98.2 (20) [50.0–1517.4]	$p = 0.07$	2.6 ± 0.8 (10) [0.5–7.2]	$\boldsymbol{p = 0.01}$	868.3 ± 121.0 (40) [10.2–5440.6]	3.1 ± 0.3 (37) [0.61–8.2]
Mature	373.2 ± 90.1 (31) [18.7–2235.9]		0.8 ± 0.2 (15) [0.01–2.5]		416.7 ± 92.9 (27) [10.6–2084.0]	2.1 ± 0.4 (23) [0.2–6.5]
Fruit endosperm	949.9 ± 202.3 (32)		4.1 ± 0.6 (14)		1784.5 ± 208.3 (57)	4.2 ± 0.5 (28)
Immature	954.5 ± 542.7 (8) [224.8–3016.2]	$p = 0.66$	5.4 ± 1.3 (4) [3.1–7.9]	$p = 0.15$	1807.8 ± 274.2 (35) [59.3–5952.8]	3.7 ± 0.5 (19) [0.34–8.7]
Mature	948.3 ± 246.3 (24) [51.7–4058.7]		3.6 ± 0.6 (10) [0.5–6.5]		1747.3 ± 325.7 (22) [72.3–7344.0]	5.3 ± 1.2 (9) [0.2–12.0]
Leaf	526.9 ± 162.9 (22)		–	–	697.1 ± 66.9 (42)	–
Immature	519.2 ± 86.2 (20) [108.3–1742.7]		–	–	606.1 ± 65.3 (29) [115.5–1414.5]	–
Mature	603.6 ± 75.4 (2) [528.1–679.0]	–	–	–	900.2 ± 149.4 (13) [219.8–2426.0]	–
Inner bark (mature)	1364.1 ± 156.1 (32) [152.9–3178.1]	–	–	–	2341.2 ± 268.0 (7) [1129.6–3650.0]	–
Flower (mature)	729.9 ± 262.5 (9) [99.6–1548.5]	–	–	–	–	–
Other vegetation (mature)	1198.7 ± 654.3 (6) [126.6–3734.7]	–	–	–	355.9 ± 168.5 (3) [116.7–681.1]	–

[a] Whole model tests for variation in mechanical properties of foods consumed by *P. abelii* include all seven food items but do not include stage of maturity: toughness: Kruskal–Wallis test: $\chi^2 = 33.0$, df = 6, $p < 0.0001$; Young's modulus: Kruskal–Wallis test $\chi^2 = 19.35$, df = 2, $p < 0.0001$.

[b] Multiple post-hoc pairwise comparisons for differences in toughness among food items using Tukey–Kramer HSD: inner bark is significantly tougher than fruit exocarp ($p = 0.04$), leaves ($p = 0.04$), and fruit mesocarp ($p < 0.0001$) and approaching significance for fruit endosperm ($p = 0.06$); fruit endosperm is significantly tougher than fruit mesocarp ($p = 0.03$). All other pairwise comparisons for toughness were not significantly different ($p > 0.05$).

[c] Multiple post-hoc pairwise comparisons for differences in Young's modulus among food items were calculated using Tukey–Kramer HSD: compared with fruit mesocarp, E was significantly higher for endosperm ($p = 0.001$) and exocarp ($p < 0.0001$). Overall, unripe fruit was also more resistant to deformation compared with ripe fruit (Wilcoxon rank-sum test $\chi^2 = 10.32$, df = 1, $p = 0.0014$). All other comparisons for Young's modulus were not significantly different ($p > 0.05$).

[d] We used Wilcoxon rank-sum test to examine differences in food items by stage of maturity. The sample size for toughness of mature leaves was too small to use a pairwise test.

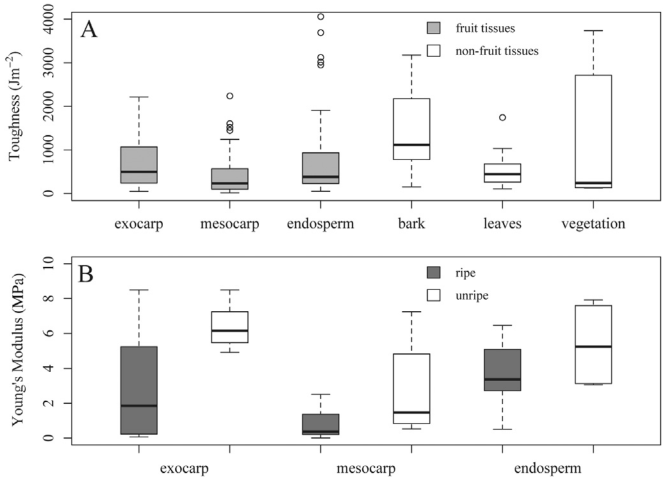

Figure 1. Box plots demonstrating significant variation in (A) Toughness (J m^{-2}) of plant tissues consumed by *Pongo abelii* at Ketambe Research Station, Sumatra (Kruskal Wallis test $\chi^2 = 33.0$, df = 6, $p < 0.0001$) and (B) Young's modulus (MPa) among ripe and unripe fruit tissues consumed by *Pongo abelii* (Wilcoxon rank-sum test $\chi^2 = 10.3$, df = 1, $p = 0.0014$); see also Table 1. For all box plots, the bottom and top of the box represent the first and third quartiles, the solid line in the box represents the median, the whiskers represent the maximum and minimum values, and the circles represent outliers.

For *P. abelii*, we observed a low but significant inverse correlation between percentage of time spent feeding and R ($\rho = -0.262$, $p = 0.004$) and a slightly higher inverse correlation between percentage of time spent feeding and E ($\rho = -0.319$, $p = 0.062$). These correlations were non-significant for *P. p. wurmbii* (R, $\rho = 0.022$, $p = 0.756$; E, $\rho = 0.092$, $p = 0.400$).

Discussion and conclusions

Food mechanical properties and feeding behavior at Ketambe and Tuanan

We predicted that compared with *P. abelii*, *P. p. wurmbii* ingest and masticate significantly tougher foods. This prediction is affirmed by our findings that *P. p. wurmbii* consumed significantly tougher fruit parts, leaves and inner bark, and foods with a significantly higher displacement-limited index. *Pongo abelii* selected for less tough fruit parts (both ripe and immature) compared with *P. p. wurmbii* (Table 1) and spent a greater percentage of feeding time on foods that were less tough and less resistant to deformation, supporting previous reports that *P. abelii* prefer ripe fruit (e.g., Wich et al., 2006). Preliminary data from Ketambe also suggest that ripe fruit is higher in total kilojoules of energy per item compared with unripe fruits (Zulfa, 2011). Thus, orangutans likely select fruits based on a combination of factors, including lower food mechanical properties and greater caloric gain, potentially along with additional features such as food size and shape (e.g., Norconk et al., 2009).

By contrast, our data do not consistently support the prediction that *P. p. wurmbii* ingest and masticate tissues with a significantly higher modulus (but see further discussion below). While *P. p. wurmbii* consumed mature fruit mesocarp that was more resistant to deformation, *P. abelii* consumed immature exocarps with higher modulus and we observed no species differences in modulus of endosperm (Table 2). *Pongo p. wurmbii* did consume fruits with a significantly higher stress-limited index compared with *P. abelii* (Table 3). However, our highest modulus values for *P. abelii* and *P. p. wurmbii* were 8.5 MPa (for immature husk of *Ficus*) and 12.0 MPa (for ripe fruit endosperm of *Elaeocarpus mastersii*), respectively, placing these tissues somewhere between carrot and apple-skin

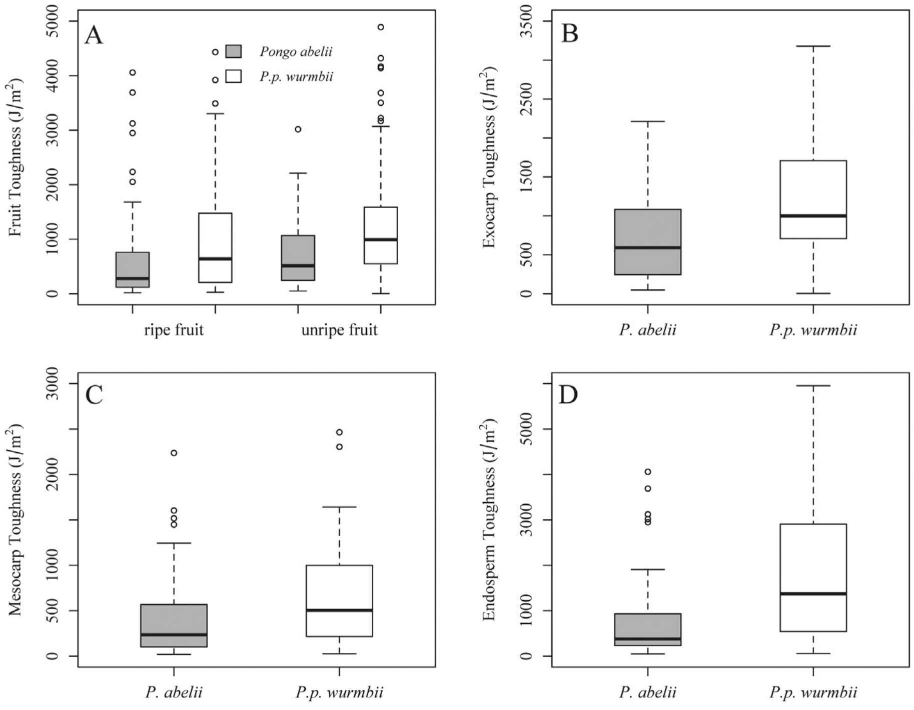

Figure 2. Box plots of toughness (J m^{-2}) of fruits and fruit parts masticated by *Pongo abelii* (Sumatra) and *P. p. wurmbii* (Borneo). (A) Both ripe and unripe fruits consumed by *P. p. wurmbii* are significantly tougher compared with those consumed by *P. abelii* (Ripe fruits: Wilcoxon sign test $\chi^2 = 8.77$, df = 1, $p = 0.0015$; Unripe fruits: Wilcoxon sign test $\chi^2 = 13.7$, df = 1, $p = 0.0001$). Compared with *P. abelii*, *P. p. wurmbii* consumed significantly tougher (B) fruit exocarp (Wilcoxon sign test: $\chi^2 = 9.51$, df = 1, $p = 0.001$), (C) fruit mesocarp (Wilcoxon sign test: $\chi^2 = 6.42$, df = 1, $p = 0.005$), and (D) fruit endosperm (Wilcoxon sign test: $\chi^2 = 8.30$, df = 1, $p = 0.002$).

Table 2
Results of pairwise species comparisons for differences in toughness and Young's modulus of plant tissues consumed by *Pongo abelii* and *Pongo pygmaeus wurmbii*.[a–b]

Plant tissue	Stage of maturity	*p*-values of differences in toughness (R; J m^{-2})	Direction of difference	*p*-values of differences in Young's modulus (E; MPa)	Direction of difference
Fruit exocarp	Overall	***0.0010***/–	*P.p.w* > *P.a*	NS/NS	NS/NS
	Immature	0.0521/–	*P.p.w* > *P.a*	NS/**0.0004**	NS/*P.a* > *P.p.w*
	Mature	***0.0114***/–	*P.p.w* > *P.a*	NS/NS	NS/NS
Fruit mesocarp	Overall	***0.0057***/–	*P.p.w* > *P.a*	***0.0003***/–	*P.p.w* > *P.a*
	Immature	***0.0098***/–	*P.p.w* > *P.a*	NS/NS	NS/NS
	Mature	NS/NS	NS/NS	***0.0035***/–	*P.p.w* > *P.a*
Fruit endosperm	Overall	***0.0020***/–	*P.p.w* > *P.a*	NS/NS	NS/NS
	Immature	0.0756/–	*P.p.w* > *P.a*	NS/NS	NS/NS
	Mature	***0.0194***/–	*P.p.w* > *P.a*	NS/NS	NS/NS
Leaf lamina	Immature & mature combined	***0.0311***/–	*P.p.w* > *P.a*	–	–
Inner bark	Mature	***0.0079***/–	*P.p.w* > *P.a*	–	–

[a] *P.p.w*, *Pongo p. wurmbii*; *P.a*, *Pongo abelii*.
[b] We used one-tailed Wilcoxon rank-sum tests for all pairwise comparisons and report *p*-values as described below. First entry is the *p*-value from a one-tailed test of predicted differences between *P. p. wurmbii* and *P. abelii*. Second entry provides results of a two-tailed test for differences between the two species only when the one-tailed test resulted in no statistical difference in the predicted direction. A significant result for a two-tailed test indicates a difference between the two species opposite the predicted pattern. Bold and italicized *p*-values signify significant species differences ($\alpha = 0.05$) in toughness or modulus after accounting for multiple pairwise comparisons using the Bonferroni-Holm correction (Holm, 1979) per mechanical property per plant tissue. Bold *p*-values signify $p < 0.05$ but not significant following the Bonferroni-Holm correction. *P*-values that are not bold indicate trends toward significance $0.05 < p < 1.0$ in the predicted direction. Statistical tests are not reliable for $n < 5$. Given the limitations of our equipment, we did not test for differences in Young's modulus for leaf lamina or inner bark.

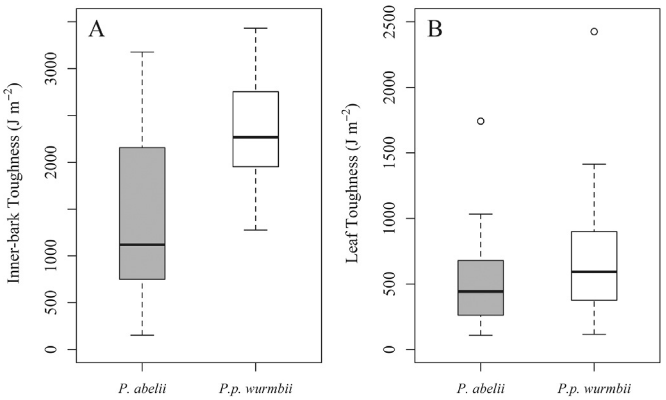

Figure 3. Box plots demonstrating that *P. p. wurmbii* at Tuanan (Borneo) consumes significantly tougher (A) inner-bark (Wilcoxon sign test $\chi^2 = 5.60$, df = 1, $p = 0.02$) and (B) leaves (Wilcoxon sign test $\chi^2 = 6.45$, df = 1, $p = 0.01$) compared with *P. abelii* at Ketambe (Sumatra).

(Williams et al., 2005). In addition, stress-limited indices for both orangutan species are low compared with domesticated foods fed to primates in a laboratory (cf. Williams et al., 2005)[4] and compared with *Sacoglottis gabonensis* seeds commonly masticated by sooty mangabeys (Daegling et al., 2011). Given the similarities in modulus values of foods masticated by the two orangutan species, differences in $(ER)^{0.5}$ (Lucas et al., 2012b) are largely accounted for by differences in toughness.

Importantly, at Tuanan, *P. p. wurmbii* demonstrated a preference for several foods of high elastic modulus that were not quantified due to the measurement limitations of the load cell and our inability to reduce the size of the seeds for testing (see Lucas et al., 2009). These include the mature seeds of *Mezzetia parvifolia*, which are regularly comminuted when available and have previously been estimated at a Young's modulus of 9.4 GPa (Lucas et al., 2012b), and *Mezzetia umbellate* and *Xylopia fusca*. Bornean orangutans have been observed to feed on *M. parvifolia* seeds by placing the seed between the molars with the germinating band running both vertically and horizontally and cracking open the seed (Lucas et al., 2012b; Vogel, Personal observation). When available, *Mezzetia parvifolia* seeds comprise ~11% of total monthly feeding time and are high in lipids (Vogel, Unpublished data), suggesting that they are an important source of lipids for the Tuanan orangutans. The Tuanan FMP data (Vogel et al., 2008) thus likely underestimate maximum elastic modulus of tissues ingested and masticated by *P. p. wurmbii* by several orders of magnitude. By contrast, while no tissues ingested and masticated by *P. abelii* were excluded from analysis due to load cell limitations, many fruits sampled at

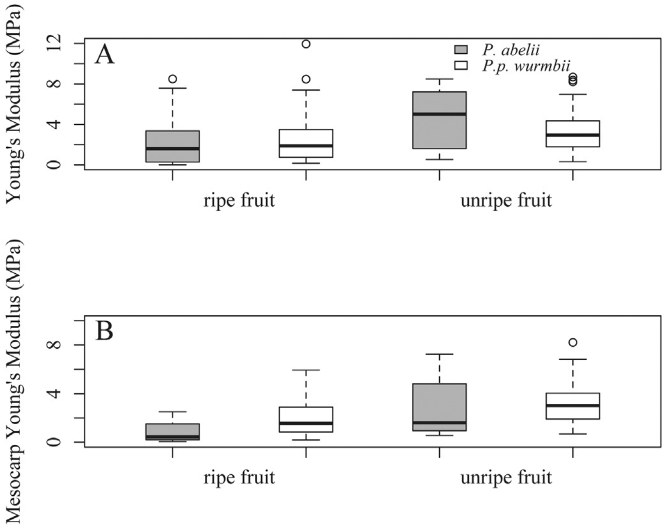

Figure 4. Box plots demonstrating Young's modulus (MPa) of ripe and unripe fruits masticated by *P. abelii* (Sumatra) and *P. p. wurmbii* (Borneo). (A) There was no difference in Young's modulus between the two species for unripe fruits (Welch test for unequal variance $F_{1,28} = 1.22$, $p = 0.13$), but *P. p. wurmbii* masticated ripe fruit with higher Young's modulus (Welch test for unequal variance $F_{1,58} = 3.39$, $p = 0.035$). (B) On average, *P. p. wurmbii* consumed ripe fruit mesocarp with significantly higher Young's modulus (MPa) (Wilcoxon sign test $\chi^2 = 7.30$, df = 1, $p = 0.0035$) compared with *P. abelii* but there were no differences in Young's modulus (MPa) for unripe fruit (Wilcoxon sign test $\chi^2 = 1.49$, df = 1, $p = 0.22$).

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[4] Williams et al. (2005) tested the food material properties on a range of foods fed to nonhuman primate species in experimental studies of the masticatory apparatus. Though these foods do not represent foods primates eat in the wild, the range of mechanical properties overlaps with mechanical properties of foods consumed by primates in their natural setting.

Table 3

Comparisons of the displacement-limited $(R/E)^{0.5}$ and stress-limited $(ER)^{0.5}$ indices of fruits parts consumed by *Pongo abelii* and *P. p. wumbii* (sample sizes in parentheses).[a–b]

Part	Stage	*P. abelii*	*P. p. wurmbii*	(*P.p.w*–*P.a*/*P.a*)	*P. abelii*	*P. p. wurmbii*	(*P.p.w*–*P.a*/*P.a*)
			$(R/E)^{0.5}$			$(ER)^{0.5}$	
Exocarp	Immature	12.29 (5)	17.95 (10)	0.46	80.69	68.44	−0.15
	Mature	11.12 (5)	24.32 (7)	1.19	43.58	51.41	0.18
Mesocarp	Immature	24.66 (5)	18.03 (18)	−0.27	31.65	47.99	0.52
	Mature	29.49 (10)	22.30 (13)	−0.24	17.90	29.83	0.67
Endosperm	Immature	15.47 (4)	24.45 (11)	0.58	74.73	82.21	0.10
	Mature	14.36 (9)	17.85 (7)	0.24	48.32	91.37	0.89

[a] *P.p.w*, *P. p. wurmbii*; *P.a*, *Pongo abelii*.

[b] Only plant tissues for which both *R* and *E* were measured are included in this analysis.

Ketambe had thin exocarps, which could not be processed for measuring Young's modulus. Thus, we speculate that the average modulus of fruit exocarps consumed by *P. abelii* may decrease with a better sample of the low-end range. Given these limitations, we consider our modulus data for Ketambe and Tuanan as preliminary.

Consistent with previous studies of orangutan feeding behavior (Morrogh-Bernard et al., 2009), Sumatran orangutans spent more feeding time on ripe fruit during both high and low fruiting periods while Bornean orangutans spent a greater percentage of feeding time on immature leaves, particularly during low fruiting periods, along with unripe fruits, flowers, pith, and other structural vegetation. These differences in fruit consumption reflect, to some extent, the higher fruit productivity on Sumatra compared with Borneo (Wich et al., 2011). At the same time, orangutans feed on fallback foods such as leaves even when fruit is available likely to maximize protein intake. Recent studies have found that Bornean orangutans tend to experience protein deficits during both low and high fruit periods (Vogel et al., 2012, 2014). When fruit is scarce, orangutans rely on these lower energy foods to maintain a positive or neutral energy balance state (Emery Thompson and Knott, 2008; Vogel et al., 2014).

Notably, however, we observed no species differences in time spent feeding on inner bark during low fruiting periods and during high fruiting periods, *P. abelii* actually spent significantly more time feeding on inner bark compared with *P. p. wurmbii*. Our results thus not only conflict with previous reports that Sumatran orangutans spend a lower percentage of time feeding on inner bark compared with Bornean orangutans (Delgado and van Schaik, 2000; Wich et al., 2006; Morrogh-Bernard et al., 2009), but indicate that during this study Sumatran orangutans fed more regularly on inner bark compared with Bornean orangutans. Our preliminary nutritional data from Tuanan and Ketambe suggest that inner bark is relatively low in protein but similar to fruit in total non-structural carbohydrates (Vogel, Unpublished data), and thus likely serves as an important source of energy for both orangutan species. Conflicting findings in bark consumption between the current and previous studies may reflect variation in feeding behavior across sampling periods and sites, particularly given sizeable temporal and regional fluctuations in fruit availability (Wich et al., 2011). Rothman et al. (2006) found that decaying bark provides sodium to mountain gorillas, and thus it is possible that bark consumption may also be linked to the acquisition of limiting nutrients.

Table 4

Means ± standard errors, ranges (in parentheses) and results of statistical tests for differences in the percentage of time spent feeding on food items between *Pongo abelii* (Ketambe, Sumatra) and *P. p. wurmbii* (Tuanan, Central Kalimantan, Borneo).[a–b]

Plant Part	Fruit Abundance[c]	Species (mean ± SE [min–max])		*p*-value
		Pongo abelii	*P. p. wurmbii*	
Inner bark/cambium	*Combined*	6.9 ± 1.1 (0.0–41.0)	5.6 ± 1.1 (0.0–37.0)	0.3914
	High	**8.6 ± 1.4 (1.6-35.0)**	2.0 ± 0.9 (0.0–12.0)	**<0.0001**
	Low	13.2 ± 3.3 (3.4–41.0)	10.4 ± 2.3 (0.0–37.0)	0.1109
Mature leaves	*Combined*	**8.2 ± 0.7 (0.0-28.0)**	2.9 ± 0.7 (0.0–28.0)	**<0.0001**
	High	**5.9 ± 1.0 (2.7-12.0)**	2.9 ± 0.70 (0.0–16.0)	**0.0049**
	Low	5.4 ± 3.3 (0.6–12.0)	3.0 ± 5.9 (0.0–28.0)	0.0018
Immature leaves	*Combined*	6.4 ± 1.0 (0.0–20.0)	**14.7 ± 0.1 (2.0-40.0)**	**<0.0001**
	High	9.4 ± 2.3 (1.4–19.0)	12.1 ± 1.5 (1.6–39.0)	0.5801
	Low	8.9 ± 2.5 (3.4–20.3)	**18.2 ± 1.7 (3.3-39.8)**	**0.0073**
Unripe fruit	*Combined*	11.6 ± 2.2 (0.0–29.0)	**30.3 ± 2.2 (0.0-68.0)**	**<0.0001**
	High	3.9 ± 4.5 (0.0–20.0)	**32.9 ± 2.8 (0.0-68.0)**	**<0.0001**
	Low	26.9 ± 2.9 (0.0–29.0)	**7.1 ± 4.0 (3.0-59.0)**	**0.0002**
Ripe fruit	*Combined*	**50.5 ± 2.9 (4.0-94.0)**	30.6 ± 2.9 (0.0–87.0)	**<0.0001**
	High	**59.2 ± 5.6 (25.0-75.0)**	37.7 ± 3.6 (0.0–87.0)	**0.0002**
	Low	**50.8 ± 4.9 (30.0-75.0)**	21.0 ± 3.4 (0.8–76.0)	**<0.0001**
Flowers	*Combined*	2.1 ± 1.3 (0.0–25.0)	**7.8 ± 1.4 (0.0-66.0)**	**0.0044**
	High	0.71 ± 2.3 (0.0–5.0)	4.7 ± 1.5 (0.0–49.0)	0.0382
	Low	3.2 ± 4.2 (0.0–18.0)	11.9 ± 3.0 (0.0–66.0)	0.1796
Other vegetation	*Combined*	0.17 ± 0.30 (0.0–5.0)	**2.9 ± 0.3 (0.0-15.0)**	**<0.0001**
	High	0.7 ± 2.3 (0.0–0.0)	**4.7 ± 1.5 (0.0-6.0)**	**<0.0001**
	Low	0.0 ± 1.1 (0.0–0.0)	**4.4 ± 0.7 (0.0-15.0)**	**<0.0001**

[a] For each plant part, data were analyzed collectively (combined), and separately for high and low fruiting periods.

[b] We used two-tailed Welch ANOVAs for unequal variances if $n > 20$ for each site or Wilcoxon rank-sum tests if $n < 20$ for either site. Bold *p*-values signify significant differences in the % of time spent feeding on a given plant part after accounting for multiple comparisons using the Bonferroni-Holm correction across all possible comparisons.

[c] For Ketambe, there are 36 months during which fruit abundance data were not available. Those data are included in the 'Combined' category and not in the 'High' or 'Low' categories.

Table 5
Comparative data on primate food mechanical properties.[a]

	Toughness (J m^{-2})		Young's modulus (MPa)	
	Average	Maximum	Average	Maximum
Alouatta palliata	479.5	868.0	–	–
Cebus apella	668.6	10908.8	–	–
Cebus olivaceus	390.0	2728.8	–	–
Cebus libidinosus	–	10350.0	–	–
Cercocebus atys	2000.0–7000.0			>200.00
Papio (spp.)	833.0	1243.0	6.50	9.40
Pongo abelii	767.7	4058.7	3.11	8.49
Pongo p. wurmbii	1152.9	6977.7	3.08	12.00–9400

[a] Data are averaged across multiple food items and plant species unless otherwise noted and taken from the following sources: *A. palliata* (data are for most common leaves eaten and are averaged here between wet and dry seasons; Teaford et al., 2006); *Cebus apella* and *C. olivaceus* (Wright, 2005); *C. libidinosus* (average fracture toughness not published but noted as comparable to *C. apella*; Wright et al., 2009); *Cercocebus atys* (these values are for *Sacoglottis gabonensis* and *Coula edulis* nuts, reportedly the hardest items processed by sooty mangabeys; McGraw et al., 2011); *Papio* spp. (these values are for corms of *Cyperus cristatus* and tubers of *Nymphaea* and data are combined for *P. ursinus* and *P. anubis*; Dominy et al., 2008); *Pongo abelii* (this study); *Pongo p. wurmbii* (toughness data are from Vogel et al. (2008) and modulus data are from this study and Lucas et al. (2012b)).

Additional long-term studies and systematic sampling at multiple sites are needed to better understand the role of inner bark in the orangutan diet.

Linking feeding behavior, food material properties and mandibular morphology in orangutans

Compared with *P. abelii*, *P. p. wurmbii* ingested and masticated significantly tougher foods and foods characterized by a significantly higher displacement-limited index. In comparison to other large-bodied hominoids, our data show that *P. p. wurmbii* feed on some of the toughest tissues, and previously published data indicate that they feed on tissues with exceptionally high elastic modulus (Table 4; Lucas et al., 1994; Elgart-Berry, 2004; Taylor et al., 2008; Vogel et al., 2008; Lucas et al., 2012b). We note, however, that some smaller-bodied platyrrhines (e.g., *Cebus apella* and *Cebus libidinosus*) and catarrhines (e.g., *Cercocebus atys*) feed on exceptionally tough foods equivalent to those ingested and masticated by *P. p. wurmbii* (Table 5).

At Tuanan, the greatest percentage of time spent feeding on any single item was 9.5% during the study period (Vogel, Unpublished data), and we found no relationship between percentage of time spent feeding and FMPs. While the greatest percentage of time spent feeding by *P. abelii* on any single item was also fairly low (6.5%), percentage of time spent feeding was significantly inversely correlated with food toughness (and trended towards a significant inverse correlation with modulus). Collectively, these findings support the hypothesis (Taylor, 2006) that the relatively robust mandible of *P. p. wurmbii* is functionally linked to generating and dissipating loads associated with feeding on significantly tougher foods.

What of the role of fallback foods in driving species differences in mandibular morphology? Our data on percentage of time spent feeding in relation to fruit abundance permit us to comment on inner bark and its potential influence as a fallback food in exerting selection pressures on orangutan mandibular morphology (e.g., Lambert et al., 2004; Wright et al., 2009). Marshall and Wrangham (2007) define fallback foods as foods of low preference but high seasonal importance and exploited during periods when preferred foods are unavailable. Consumption of inner bark is negatively correlated with the availability of preferred foods in *P. p. wurmbii* (Vogel et al., 2008) while *P. abelii* fed on bark during both high and low fruiting periods (Table 4). Thus, following Marshall and Wrangham (2007), inner bark would seem to qualify as a fallback food for *P. p. wurmbii* but whether it meets the definition of a fallback food for *P. abelii* is less clear. Even if inner bark is a fallback food for both species, it is difficult to marshal a case in favor of inner bark as a fallback food influencing mandibular robusticity in *P. p. wurmbii* given that we find that both species exploit inner bark when preferred foods are unavailable. As noted previously, *P. p. wurmbii* fed on significantly tougher inner bark compared with *P. abelii* (Table 2). Therefore, it seems likely that inner bark toughness (i.e., its mechanical property) plays more of a role in shaping the relatively robust mandible of *P. p. wurmbii* than its classification as a fallback food, and if fallback foods exert selection pressures for mandibular adaptations in orangutans, additional foods (i.e., leaves) are involved.

We speculate that strain magnitudes associated with the habitual mastication of foods by *P. p. wurmbii* are relatively low. Several factors suggest this is a reasonable speculation. First, *P. p. wurmbii* spent approximately 60% of their feeding time on foods with toughness values of ~1000 J m^{-2} or less (Vogel, Unpublished data). Data for macaques (Hylander et al., 1998) indicate average working- and balancing-size corpus shear strains of 724 με and 501 με, respectively, for foods ranging in toughness between ~663 and 1000 J m^{-2} (Williams et al., 2005). Average principal strains experienced by macaques are somewhat lower for these same foods (Hylander, 1979b). These strain magnitudes are relatively low in comparison to empirically observed habitual strain magnitudes as high as 1000–3000 με experienced by a range of vertebrates (Vinyard et al., 2007). Of the remaining 40% of feeding time on items greater than 1000 J m^{-2} at Tuanan, 15% of feeding time was spent on tissues ranging in toughness between 1000 and 2000 J m^{-2}, 10% on tissues between 2000 and 3000 J m^{-2} and 15% on tissues greater than 3000 J m$^{-2.}$

Thus, if, as argued by Ross et al. (2012), the number of chews generated in a primate's lifetime at strain magnitudes of between 2000 and 3000 με is unlikely to be sufficient to result in fatigue failure, the relatively robust mandible of *P. p. wurmbii* may be functionally related to countering larger external forces required to process the toughest tissues. Toughness has been linked to mandibular robusticity in other extant primates (e.g., Wright, 2005; Norconk et al., 2009) and fossil hominins (Daegling et al., 2011). Importantly, loads are cumulative and reflect both frequency and magnitude; repetitive cycling at 2000–3000 με coupled with countering relatively large loads could result in fatigue failure. We further hypothesize that additional modulus data for the high-end range of tissues ingested and masticated by *P. p. wurmbii*, as documented by Lucas et al. (1994, 2012b), are likely to support a functional relationship between the relatively robust mandible of *P. p. wurmbii* and their feeding on stress-limited foods, as the influence of these two material properties on mandibular morphology need not be mutually exclusive.

We acknowledge that bone modeling and remodeling in response to applied loads are dynamic, micro-level processes that occur throughout an animal's lifetime, while our morphological comparisons of orangutan mandibles are drawn on static snapshots of adult phenotypes. We do not know how these micro-level processes mitigate the risks of yield strain or fatigue failure and these risks increase with age-related declines in bone strength (Biewener, 1993). Nor, for that matter, is it well understood how these processes relate to peak loads for the mandible (Rubin and Lanyon, 1984, 1985; Frost, 1987, 2003; Rubin et al., 1991; Daegling, 2010; Ravosa et al., 2010; Daegling et al., 2013). Thus, we acknowledge that our FMPs data are several steps removed from data necessary to directly link the observed variation in feeding behavior and FMPs with mandibular robusticity.

Mandibular versus dental correlates of orangutan feeding behavior and diet: mixed signals?

In a recent study, Smith et al. (2012a) found no significant variation in average tooth enamel thickness between Bornean and Sumatran orangutans, observing only a trend toward relatively thicker enamel in Bornean compared with Sumatran females. Smith et al. (2012a) conclude that their results offer only limited support for ecological explanations of enamel thickness variation in great apes. These findings are somewhat unexpected given that enamel thickness has been functionally and evolutionarily linked to the mastication of mechanically challenging foods (Molnar and Gantt, 1977; Kay, 1981; Teaford and Ungar, 2000; Grine, 2005; Teaford, 2007; Lucas et al., 2008a,b; Constantino et al., 2009; Lee et al., 2010).

A factor that may contribute to the differences between our findings for mandibular morphology and those of Smith et al. (2012a) for enamel thickness pertains to our different sampling strategies. As in the current study, Taylor (2006) tested functional predictions about mandibular morphology between *P. abelii* and select geographic populations of Bornean orangutans, specifically focusing on *P. p. wurmbii* and *P. p. morio* of known locality, and whose feeding behavior and diet were well documented. By contrast, Smith et al. (2012a) pooled dental samples from Bornean orangutans (*P. pygmaeus* spp.) of unspecified locality for comparison with Sumatran (*P. abelii*) orangutans. Given the well documented craniomandibular (Courtenay et al., 1988; Groves et al., 1992; Taylor, 2006), dental (Uchida, 1998), and ecological (Delgado and van Schaik, 2000; Morrogh-Bernard et al., 2009) variation amongst Bornean orangutan populations, averaging enamel thickness across Bornean specimens has the potential to obscure ecologically meaningful patterns of variation both among Bornean orangutan populations and between *P. abelii* and Bornean subspecies. Future studies of the functional significance of tooth enamel thickness in orangutans and other primates would benefit from meticulous geographic analyses amongst species or populations of known locality and whose feeding ecology is well documented, including data on abrasives in the diet in addition to FMPs (Rabenold and Pearson, 2011; Pampush et al., 2013).

Implications for ecological models of craniodental morphology in fossils

The comparative anatomy of primate jaws and teeth continues to play a central role in ecological models linking primate morphology with feeding behavior and performance in living (Vinyard et al., 2003; Wright, 2005; Norconk et al., 2009; Wright et al., 2009; Yamashita et al., 2009; Daegling et al., 2011; McGraw et al., 2012; Smith et al., 2012a; Terhune, 2013) and fossil taxa (Lucas et al., 2008c; Smith et al., 2012b; Eng et al., 2013; Strait et al., 2013). This approach is useful for revealing a species' full range of functional capabilities. However, ecological context is what allows us to narrow this range to capture how species utilize their masticatory anatomy in their biological role (sensu Bock and von Wahlert, 1965), and to hypothesize adaptations to variation in feeding behavior and diet.

As seen in the present study, even with data on feeding behavior integrated with higher resolution FMP data, our interpretations remain limited. Does the morphological profile we observe for *P. p. wurmbii* reflect the ingestion or biting of items with exceptionally high modulus involving peak bite forces, similar to what has been reported for *C. atys* (McGraw et al., 2011)? Does it reflect the ingestion or chewing of fibrous foods of low or moderate toughness, potentially involving an increased number of masticatory cycles (i.e., repetitive loading of the mandible), but not necessarily high muscle and bite forces, as may be the case for some baboons (Dominy et al., 2008)? Does it reflect the exploitation of hard or exceptionally tough fallback foods, when preferred foods are unavailable (Lambert et al., 2004; Wright, 2005; Wright et al., 2009)? Or does it reflect some combination of these behaviors? We cannot pinpoint the precise mechanism(s) underlying the increased jaw robusticity in *P. p. wurmbii*, particularly as we lack a full appreciation of the additive and synergistic effects of strain frequency and magnitude on mandibular form. That said, our findings that *P. p. wurmbii* ingest and masticate significantly tougher foods compared with *P. abelii* while *P. abelii* select for less tough foods, and the likelihood that additional studies will find that *P. p. wurmbii* feed on tissues of exceptionally high modulus, all point to a mechanical link between peak loads and mandibular robusticity in orangutans.

The challenges we face in interpreting the functional and adaptive significance of mandibular morphology in extant orangutans are only compounded in paleontological investigations. Indeed, given the absence of quantitative empirical data on feeding behavior in the fossil record and the uncertainties surrounding the specific loading conditions responsible for alterations in mandibular bone morphology, it is not surprising that there are various interpretations of the adaptive significance of the robust australopith skull (Daegling et al., 2013; Strait et al., 2013). These limits to current fossil analyses underscore the importance of further refining our modern comparative ecomorphological studies and incorporating multiple lines of evidence to improve our understanding of the relationship between feeding behavior and morphology in extant taxa. Studies that enable us to narrow the gap between what is functionally possible based on a particular morphological profile, and how animals actually utilize their morphology in their biological role, have the greatest potential to refine our interpretations and transform current perspectives on primate/hominin paleobiology.

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Appendix 1. Mean toughness (J m^{-2}) and Mean Young's Modulus (MPa) of species and items masticated by *Pongo abelii* at the Ketambe Research Station in Sumatra, Indonesia. Averages for each species/item are taken across all individual feeding bouts.

Local Name	Family	Latin Name	Part	Stage	Mean Toughness (J m^{-2})	Mean Young's Modulus (MPa)
Latong gajah	Urticaceae	*Laportea sinuata*	veg	mature	3734.70	
Jelmaan tikus			seed	mature	3690.70	
Gala-gala rau			bark	mature	3178.08	
Lengen	Annonaceae	*Cananga odorata*	seed	mature	3123.10	
Rampah	Leguminosae	*Parkia intermedia*	seed	immature	3016.17	3.20
Kayu kemong	Myrsinaceae	*Ardisia* sp.	seed	mature	2947.85	2.87
Rambung keraping	Moraceae	*Ficus benjamina*	bark	mature	2843.65	
Kayu karet	Euphorbiaceae	*Pimelodendron amboinensis*	bark	mature	2720.28	
Medang licin	Lauraceae	*Litsea* sp.	veg	mature	2712.33	
Ipoh	Moraceae	*Antiaris toxicara*	bark	mature	2610.45	
Rambung tampuk pinang kecil	Moraceae	*Ficus* sp.	bark	mature	2461.35	
Kayu arang	Ebenaceae	*Diospyros* sp.	seed	mature	2392.46	
Kayu kerupuk	Sterculiaceae	*Pterocymbium javanicum*	bark	mature	2384.74	
Rambung konyel anggur	Moraceae	*Ficus* sp.	pulp	mature	2235.85	1.60
Rambung konyel anggur	Moraceae	*Ficus* sp.	husk	immature	2211.25	8.49
Rambung tampuk pinang besar	Moraceae	*Ficus altissima*	bark	mature	2174.05	
Rambung kusim	Moraceae	*Ficus* sp.	bark	mature	2088.00	
Durian hutan	Bombacaceae	*Durio graveolens*	husk	mature	2053.30	
Rambung kekerawilan	Moraceae	*Ficus* sp.	bark	mature	2022.40	
Geseng tanduk	Fagaceae	*Lithocarpus* sp.	seed	immature	1908.28	7.92
Cemimis			leaf	immature	1742.73	
Sentalun rawan			pulp	mature	1603.18	
Entap	Dipterocarpaceae	*Parashorea lucida*	bark	mature	1563.68	
Dukut dasih	Lecythidaceae	*Planchonia vallida*	flower	mature	1548.50	
Jambu hutan	Myrtaceae	*Eugenia grandis*	pulp	immature	1517.40	
Kukuran jantan	Rhizophoraceae	*Carallia brachiata*	whole	immature	1447.55	2.75
Gala-gala biasa	Moraceae	*Ficus Racemosa*	bark	mature	1395.75	
Jambu air	Myrtaceae	*Eugenia densiflora*	husk	mature	1390.98	5.98
Rambung beringin	Moraceae	*Ficus sumatrana*	bark	mature	1342.38	
Pohon hijau-putih			seed	mature	1318.58	5.75
Latong gajah	Urticaceae	*Laportea sinuata*	flower	mature	1270.15	
Medang pisang	Lauraceae	*Litsea robusta*	pulp	mature	1243.50	2.51
Rambung rembebel	Moraceae	*Ficus virens glabella*	bark	mature	1196.78	
Rambung kuda	Moraceae	*Ficus drupacea*	pulp	immature	1139.73	0.56
Lengen bunga selanga	Anacardiaceae	*Mangifera* sp.	whole	immature	1119.38	6.41
Rampah	Leguminosae	*Parkia intermedia*	bark	mature	1095.33	
Gala-gala rau			husk	immature	1069.70	5.83
Bungur	Lythraceae	*Lagerstroemia* sp.	husk	mature	1069.40	
Terap	Moraceae	*Artocarpus elasticus*	leaf	immature	1034.00	
Rambung ipoh	Moraceae	*Ficus annullata*	husk	immature	1026.95	
Rambung uah uah	Moraceae	*Ficus* sp.	whole	mature	1001.55	
Banitan tai ayam	Annonaceae	*Mitrephora* sp.	seed	mature	993.60	
Kayu melinjo			pulp	immature	973.33	
Gala-gala rube	Moraceae	*Ficus schwarzii*	husk	immature	960.20	5.10
Akar belimbing anggur			whole	mature	956.40	
Rumpi rawan	Euphorbiaceae	*Mallotus sphaerocarpus*	bark	mature	948.85	
Rambung kuda	Moraceae	*Ficus drupacea*	bark	mature	884.33	
Kerakah	Sapindaceae	*Paranephelium nitidum*	seed	mature	874.45	3.06
Akar bayam	Myrsinaceae	*Maesa* sp.	leaf	immature	853.03	
Akar tanduk besar			seed	immature	851.10	
Medang lede	Tiliaceae	*Elaeocarpus glaber*	husk	mature	850.98	
Rambung ipoh	Moraceae	*Ficus annullata*	bark	mature	846.00	
Bungur	Lythraceae	*Lagerstroemia* sp.	bark	mature	841.35	
Kapuk rimba	Bombacaceae	*Bombax valetonii*	seed	mature	834.93	2.72
Sentalun	Combretaceae	*Terminalia bellirica*	pulp	immature	834.18	4.82
Lelemas			leaf	immature	832.00	
Jerik			seed	mature	831.03	
Rambung rembebel	Moraceae	*Ficus virens glabella*	pulp	immature	806.28	1.61
Akar kusim besar	Icacinaceae	*Ioides ovalis*	bark	mature	797.23	
Terap	Moraceae	*Artocarpus elasticus*	pulp	mature	792.40	
Bayur	Sterculiaceae	*Pterospermum javanicum*	bark	mature	792.20	
Bau langit	Annonaceae	*Cyathocalyx sumatranus*	seed	immature	786.55	
Pala hutan	Myristicaceae	*Myristica* sp.	pulp	immature	784.25	

(*continued*)

Local Name	Family	Latin Name	Part	Stage	Mean Toughness (J m^{-2})	Mean Young's Modulus (MPa)
Rambung uah uah	Moraceae	*Ficus* sp.	bark	mature	779.93	
Rambung kusim	Moraceae	*Ficus* sp.	leaf	immature	766.00	
Kayu mayang	Sapotaceae	*Payena lucida*	pulp	mature	725.15	0.37
Tampu biasa	Euphorbiaceae	*Macaranga tanarius*	bark	mature	722.05	
Akar tombang	Araceae	*Photos* sp.	bark	mature	711.00	
Gala Gala rau	Moraceae	*Ficus variegata*	pulp	immature	688.10	
Dedap	Leguminosae	*Erythrina subumbrans*	leaf	mature	679.00	
Rambung kuda	Moraceae	*Ficus drupacea*	husk	immature	671.93	6.53
Tampu biasa	Euphorbiaceae	*Macaranga tanarius*	seed	mature	640.60	5.09
Gala-gala rau			husk	mature	611.23	7.57
Punti	Sapotaceae	*Palaquium* sp.	pulp	immature	587.32	
Setur badak	Meliaceae	*Aglaia speciosa*	pulp	mature	578.83	
Kelempen	Rubiaceae	*Anthocephalus cadamba*	pulp	immature	572.47	
Akar kusim besar	Icacinaceae	*Ioides ovalis*	flower	mature	571.60	
Durian hutan	Bombacaceae	*Durio graveolens*	pulp	immature	531.93	
Akar kusim besar	Icacinaceae	*Ioides ovalis*	leaf	mature	528.12	
Rambung ipoh	Moraceae	*Ficus annullata*	leaf	immature	511.43	
Akar manil	Araliaceae	*Schefflera longifolium*	bark	mature	485.65	
Dedap	Leguminosae	*Erythrina subumbrans*	leaf	immature	477.88	
Asam kanis			leaf	immature	475.00	
Kapuk rimba	Bombacaceae	*Bombax valetonii*	bark	mature	472.50	
Latong gajah	Urticaceae	*Laportea sinuata*	leaf	immature	461.00	
Rutih	Apocynaceae	*Alstonia scholaris*	bark	mature	454.93	
Rambung kekerawilan	Moraceae	*Ficus* sp.	whole	mature	430.94	
Pandan hutan			leaf	immature	424.03	
Ipoh rawan			leaf	immature	420.15	
Mangga hutan	Anacardiaceae	*Mangifera* sp.	pulp	immature	409.80	
Ipoh	Moraceae	*Antiaris toxicara*	husk	immature	405.40	6.47
Gerupel	Moraceae	*Artocarpus gomezianus*	pulp	mature	396.53	0.93
Medang licin	Lauraceae	*Litsea* sp.	flower	mature	396.30	
Terap	Moraceae	*Artocarpus elasticus*	seed	mature	393.40	
Akar rambut galang	Leguminosae	*Acacia pennata*	leaf	immature	384.85	
Jambu hutan	Myrtaceae	*Eugenia grandis*	husk	mature	381.95	4.50
Terap	Moraceae	*Artocarpus elasticus*	bark	mature	380.28	
Akar yo ate	Leguminosae	*Mucuna* sp.	flower	mature	379.06	
Kapuk rimba	Bombacaceae	*Bombax valetonii*	flower	mature	376.64	
Bau langit	Annonaceae	*Cyathocalyx sumatranus*	pulp	mature	375.00	
Asam kanis			pulp	immature	374.45	0.74
Akar ceri			husk	mature	367.03	
Kayu karet	Euphorbiaceae	*Pimelodendron amboinensis*	seed	immature	364.88	7.28
Akar lete	Vitaceae	*Tetrastigma lanceolarium*	whole	mature	361.60	1.87
Asam king	Anacaridaceae	*Dracontomelon dao*	pulp	mature	358.25	0.18
Asam ubi			pulp	immature	340.30	0.84
Rambung uah uah	Moraceae	*Ficus* sp.	whole	immature	339.50	
Kerakah pagar anak	Fagaceae	*Castanopsis* sp.	seed	mature	338.77	3.67
Banitan biasa	Cornaceae	*Mastixia trichotoma*	seed	mature	336.20	
Rambung konyel tingkam	Moraceae	*Ficus aurianteacea*	husk	mature	332.75	
Medang licin	Lauraceae	*Litsea* sp.	leaf	immature	316.70	
Bergang gajah	Euphorbiaceae	*Baccaurea deflexa*	pulp	mature	316.35	
Kayu karet	Euphorbiaceae	*Pimelodendron amboinensis*	husk	immature	308.73	
Anggrek bawang			veg	mature	305.53	
Mancang			pulp	mature	288.28	
Gerupel	Moraceae	*Artocarpus gomezianus*	seed	mature	283.13	
Asam bunter			pulp	mature	277.03	
Urel tenge	Euphorbiaceae	*Cleidion spiciflorum*	seed	mature	276.70	
Rambe kekure	Euphorbiaceae	*Baccaurea racemosa*	whole	mature	264.83	1.22
Akar keketep			leaf	immature	261.20	
Akar manil	Araliaceae	*Schefflera longifolium*	leaf	immature	256.05	
Akar berbaling			seed	immature	251.60	
Tingkam	Staphyleaceae	*Bischofia javanica*	husk	mature	248.68	
Akar jengkol			seed	mature	243.00	6.46
Dongra			seed	immature	232.63	
Cempedak rawan			seed	mature	232.00	
Cempedak rawan			pulp	mature	226.55	
Kayu kerupuk	Sterculiaceae	*Pterocymbium javanicum*	seed	immature	224.80	3.06
Rambung uah uah	Moraceae	*Ficus* sp.	leaf	immature	222.95	
Akar susu	Apocynaceae	*Alyxia stellata*	pulp	mature	220.15	
Rambung tampuk pinang besar	Moraceae	*Ficus altissima*	pulp	mature	219.45	0.06
Akar cengkadok	Piperaceae	*Piper mimlatum*	whole	mature	206.28	
Geseng rawan	Polygalaceae	*Xanthophyllum rufum*	leaf	immature	200.38	
Rambung beringin	Moraceae	*Ficus sumatrana*	whole	mature	198.45	
Akar papan	Vitaceae	*Tetrastigma hookeri*	bark	mature	186.80	
Tampang	Euphorbiaceae	*Blumeodendron tokbrai*	pulp	immature	178.63	

(*continued on next page*)

(*continued*)

Local Name	Family	Latin Name	Part	Stage	Mean Toughness (J m^{-2})	Mean Young's Modulus (MPa)
Akar tombang	Araceae	*Photos* sp.	veg	mature	178.00	
Sepang			seed	mature	177.50	
Rambung tampuk pinang kecil	Moraceae	*Ficus* sp.	husk	mature	169.50	
Akar susu kambing	Menispermaceae	*Tinomiscium phytocrenoides*	pulp	immature	164.95	
Kedondong hutan	Combretaceae	*Terminalia copelandii*	leaf	immature	159.90	
Rambung kuda	Moraceae	*Ficus drupacea*	husk	mature	156.06	0.69
Akar tepus	Moraceae	*Poikilospermum suaveolens*	bark	mature	152.90	
Rambung beringin	Moraceae	*Ficus sumatrana*	whole	immature	139.28	1.34
Rambutan biawak	Sapindaceae	*Nephelium rambutan*	pulp	immature	135.00	
Akar tepus	Moraceae	*Poikilospermum suaveolens*	veg	mature	134.00	
Pakis			veg	mature	126.60	
Durian hutan	Bombacaceae	*Durio graveolens*	pulp	mature	121.97	
Kayu karet	Euphorbiaceae	*Pimelodendron amboinensis*	seed	mature	117.53	0.51
Akar merah-hijau			pulp	immature	115.97	
Akar tombang	Araceae	*Photos* sp.	leaf	immature	108.28	
Latong rusa	Urticaceae	*Dendrocnide stimulans*	flower	mature	99.55	
Asam ubi			pulp	mature	93.60	
Babi kurus	Sapindaceae	*Elatoostachys* sp.	seed	mature	90.13	3.08
Setur gajah	Meliaceae	*Aglaia odoratissima*	pulp	mature	85.65	0.21
Akar lelonka kecil			pulp	immature	85.03	
Langsat hutan	Meliacaea	*Lansium domesticum*	pulp	mature	68.88	
Akar susu kambing	Menispermaceae	*Tinomiscium phytocrenoides*	pulp	mature	64.58	0.35
Kayu gading	Symplocaceae	*Symplocos fasciculata*	husk	mature	62.58	
Setur padi	Meliaceae	*Aglaia korthalsii*	pulp	mature	61.27	
Rambung keraping	Moraceae	*Ficus benjamina*	husk	mature	59.67	
Rumpi rawan	Euphorbiaceae	*Mallotus sphaerocarpus*	pulp	mature	52.98	
Akar susu	Apocynaceae	*Alyxia stellata*	seed	mature	51.73	
Asam peder	Sapotaceae	*Pouteria* sp.	pulp	immature	49.95	
Ipoh	Moraceae	*Antiaris toxicara*	husk	mature	48.93	0.97
Punti	Sapotaceae	*Palaquium* sp.	pulp	mature	48.15	0.13
Aren	Arecaceae	*Arenga pinnata*	pulp	mature	43.53	0.52
Medang licin	Lauraceae	*Litsea* sp.	pulp	mature	24.65	
Akar cengkadok	Piperaceae	*Piper mimlatum*	pulp	mature		1.51
Akar rambut galang	Leguminosae	*Acacia pennata*	leaf	mature		
Rambung kusim	Moraceae	*Ficus* sp.	husk	mature		0.07
Rambung kusim	Moraceae	*Ficus* sp.	husk	immature		7.28
Rambung tampuk pinang besar	Moraceae	*Ficus altissima*	husk	mature		3.05
Rambung tampuk pinang kecil	Moraceae	*Ficus* sp.	pulp	mature		0.20

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