

Enamel Thickness in Bornean and Sumatran Orangutan Dentitions

Tanya M. Smith,^{1,2*} Kornelius Kupczik,^{2,3} Zarin Machanda,¹ Matthew M. Skinner,² and John P. Zermeno¹

¹Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138

²Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig D-04103, Germany

³Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Jena D-07743, Germany

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ABSTRACT Dental enamel thickness has received considerable attention in ecological models of the adaptive significance of primate morphology. Several authors have theorized that the degree of enamel thickness may reflect selective pressures related to the consumption of fallback foods (dietary items that may require complex processing and/or have low nutritional value) during times of preferred food scarcity. Others have speculated that enamel thickness reflects selection during mastication of foods with particular material properties (i.e., toughness and hardness). Orangutans prefer ripe fruit when available, but show interspecific and sex differences in the consumption of fallback foods (bark, leaves, and figs) and other preferred foods (certain seeds). Bornean orangutans (*Pongo pygmaeus*) have also been reported to masticate more mechanically demanding foods than Sumatran orangutans (*Pongo abelii*). To test these ecological models, we assessed two-dimensional

enamel thickness in orangutan full dentitions using established histological and virtual quantification methods. No significant differences in average enamel thickness (AET) were found between species. We found significant differences in the components of enamel thickness indices between sexes, with males showing greater enamel-dentine junction lengths and dentine core areas, and thus relatively thinner enamel than females. Comparisons of individuals of known sex and species revealed a dentition-wide trend for Bornean females to show greater AET than Sumatran females. Differences between small samples of males were less evident. These data provide only limited support for ecological explanations of enamel thickness patterns within great ape genera. Future studies of dietary ecology and enamel thickness should consider sex differences more systematically. *Am J Phys Anthropol* 147:417–426, 2012. © 2012 Wiley Periodicals, Inc.

Studies of dental morphology are informative for understanding human and primate evolution, particularly given the relative abundance of fossilized teeth and the interrelationships among mastication, energy acquisition, and survival. Enamel thickness has featured prominently in reconstructions of the taxonomy and dietary specializations of fossil apes and humans for nearly a century (Miller, 1918; Jolly, 1970; Simons and Pilbeam, 1972; Gantt, 1977; Kay, 1981; Beynon and Wood, 1986; Grine and Martin, 1988; Andrews and Martin, 1991; Smith et al., 2003; Olejniczak et al., 2008b,c; Smith et al., 2009). Moreover, broad comparative studies of enamel thickness have provided important insight into primate systematics, functional morphology, and dietary ecology (Gantt, 1977; Kay, 1981, 1985; Martin, 1985; Dumont, 1995; Shellis et al., 1998; Shimuzu, 2002; Martin et al., 2003; Kono, 2004; Tafforeau, 2004; Grine et al., 2005; Smith et al., 2005; Kono and Suwa, 2008; Olejniczak et al., 2008a).

Initial considerations of the relationship between primate enamel thickness and diet often delineated broad dietary categories (e.g., frugivore, folivore, omnivore, hard-object feeder, and soft-object feeder) (Gantt, 1977; Kay, 1981, 1985; Andrews and Martin, 1991; Dumont, 1995). Dumont (1995) contrasted relative enamel thickness (RET) between congeneric primate and chiropteran pairs, demonstrating that hard-object feeders showed thicker enamel than soft-object feeders. Contemporary views of primate ecology acknowledge that most prima-

tes prefer ripe fruit when available, but they demonstrate remarkably diverse diets over annual periods, and incorporate fallback foods when their preferred foods are scarce (Wrangham, 1980; Chapman and Chapman, 1990; Strier, 1994; Marshall and Wrangham, 2007). Fallback foods are often of low nutritional quality, low abundance, and/or are particularly hard to process (Marshall and Wrangham, 2007). Lambert et al. (2004) advocated for a more nuanced consideration of enamel thickness in light of the material properties of preferred versus fallback food items. They found that two sympatric cercopithecines, which showed highly overlapping frugivorous diets during certain periods, differed in the composition and material properties of seasonal fallback foods. Mangabeys (*Lophocebus albigena*) consumed harder seeds and

Additional Supporting Information may be found in the online version of this article.

*Correspondence to: Tanya M. Smith, Department of Human Evolutionary Biology, 11 Divinity Avenue, Harvard University, Cambridge, MA 02138, USA. E-mail: tsmith@fas.harvard.edu

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TABLE 1. Sample of orangutan teeth employed in this study

Species	Row	Sex	I1	I2	C	P3	P4	M1	M2	M3	M4	Total
<i>P. pygmaeus</i>	Max	Female	1	2	0	3	3	7	6	6	0	28
		Male	3	3	0	4	4	3	4	3	0	24
		Unknown	0	2	0	2	2	3	2	2	0	13
<i>P. abelii</i>		Female	1	2	2	2	2	3	3	3	0	18
		Male	1	0	0	2	2	3	2	1	0	11
		Unknown	1	1	0	2	3	3	2	2	0	14
<i>P. sp.</i>		Mixed	1	2	0	2	1	2	0	0	0	8
<i>P. pygmaeus</i>	Mand	Female	2	2	2	3	3	5	7	5	1	30
		Male	2	3	0	2	4	4	5	4	0	24
		Unknown	0	0	0	2	1	5	2	2	0	12
<i>P. abelii</i>		Female	1	2	2	2	2	3	4	3	0	19
		Male	0	0	0	1	1	2	2	1	0	7
		Unknown	1	0	0	1	1	2	3	3	0	11
<i>P. sp.</i>		Mixed	2	2	1	2	0	8	4	0	0	19

Max, maxillary; Mand, mandibular; I1, central incisor; I2, lateral incisor; C, canine; P3, third premolar; P4, fourth premolar; M1, first molar; M2, second molar; M3, third molar; M4, fourth molar.

bark than guenons (*Cercopithecus ascanius*), and also possess thicker enamel, leading the authors to suggest that selection for enamel thickness may be driven by less commonly exploited resources. Vogel et al. (2008) documented the material properties of preferred and fallback dietary items consumed by Bornean orangutans and thinner-enamelled common chimpanzees. They found that both preferred and fallback foods consumed by orangutans were harder and tougher than chimpanzees, which is consistent with predictions from the thicker molar enamel found in orangutans.

Bornean and Sumatran orangutan species (*Pongo pygmaeus* and *Pongo abelii*, respectively), which appear to have diverged between 0.4 and 3.6 million years ago (Xu and Arnason, 1996; Arora et al., 2010; Locke et al., 2011), have highly overlapping frugivorous diets when fruit is available (reviewed in Rodman, 1988; Fox et al., 2004; Taylor, 2006; Morrogh-Bernard et al., 2009; Harrison and Marshall, 2011). Some differences are found in the percentage of time spent feeding on bark, leaves, unripe fruits, and insects, but this varies among sites and across seasons (reviewed in Morrogh-Bernard et al., 2009; Russon et al., 2009). Taylor (2006) argued that the primary difference is in bark consumption during fallback periods; Bornean orangutans from multiple sites consumed several times more bark on average than Sumatran orangutans (also see Rodman, 1988). She also demonstrated specific differences in mandibular morphology, as Bornean orangutans possess more robust mandibles that appear to be more resistant to loading during mastication. Vogel et al. (2011) provided additional support for this by demonstrating that several dietary items consumed more commonly by Bornean orangutans resist fracture or deformation better than items masticated by Sumatran orangutans. Moreover, Bornean orangutans consume certain tough foods more often than Sumatran orangutans, which have ripe fruit available more consistently year-round (reviewed in Vogel et al., 2008; Marshall et al., 2009). Dietary sex differences have also been reported, as Bornean males are able to consume large, high-quality fruit items (such as *Neesia* and *Durio* fruits) that are difficult for females to mechanically process (Knott, 1999; van Schaik et al., 2009). Van Schaik et al. (2009) reported that although (flanged) Bornean males consume harder foods than females, the toughness of dietary items is comparable. Moreover, Bornean and Sumatran females have been observed to consume more bark than males, and

have a more diverse diet overall (Rodman, 1988; Knott, 1999; Wich et al., 2006).

Comparisons of orangutans permit fine-scale tests of the adaptive model for enamel thickness proposed by Lambert et al. (2004). If processing more mechanically demanding fallback foods leads to adaptations in aspects of craniodental morphology such as enamel thickness, Bornean orangutans should possess thicker enamel than Sumatran orangutans. Enamel thickness might also be expected to differ given differences in dietary breadth, as Bornean orangutans show a more varied diet than Sumatran orangutans (reviewed in Morrogh-Bernard et al., 2009). Predictions based on sex-specific ecological differences are less straightforward, as more frequent hard-object consumption in males might lead to selection for thicker enamel than in females. However, preferential consumption of bark by females, which is known to be rather stiff and tough (Vogel et al., 2011), may lead to selection for thicker enamel in females. This study aims to test these predictions by assessing two-dimensional (2D) enamel thickness within and between full dentitions of Bornean and Sumatran orangutans, including the first comparison of 2D enamel thickness indices between non-human primate sexes. Little is known about enamel thickness in congeneric great ape species aside from reports on small samples of *Pan* and *Pongo* molars, which show highly overlapping values (Smith et al., 2003, 2005). In addition to providing insight into the relationship between ecology and morphology, these data are also valuable for assessing the taxonomic significance of enamel thickness variation within small samples of fossil hominoid and hominin genera (reviewed in Smith et al., 2006b; Kunitz et al., 2007; Mahoney et al., 2007; also see Olejniczak et al., 2008b,c; Smith et al., 2009).

MATERIALS AND METHODS

Sample preparation

Enamel thickness was assessed in 238 orangutan teeth representing all tooth positions (Table 1), which were derived from 43 individuals. Of these, the sex was known for 24 individuals (yielding 172 teeth). Orangutans (mainly wild-shot) were obtained from the Harvard University Museum of Comparative Zoology (Cambridge, USA), Museum for Natural History (Berlin, Germany), Senckenberg Research Institute (Frankfurt, Germany),

Bavarian State Collection for Zoology (Munich, Germany), and the Natural History Museum (London, UK). Information on collection localities is available for a subset of the sample, which includes individuals from all three recognized subspecies of Bornean orangutans, as well as several populations of Sumatran orangutans. Two captive individuals of unknown origin were also included from the histology collections of the University of Newcastle, UK (one of which was described by Beynon et al., 1991). Both physical and virtual (micro-computed tomographic) sections were employed to assess 2D enamel thickness, which yield comparable data when similar landmarks are used to create sections (Olejniczak and Grine, 2006; Smith et al., 2010).

Fifty-six teeth were physically sectioned with an annular or peripheral saw according to established methods (detailed in Beynon et al., 1991; Smith et al., 2005). Anterior teeth (incisors and canines) were cut in a labial-lingual plane, whereas premolars and molars were cut in buccal-lingual planes across the mesial cusps. Anterior teeth and premolars were aligned during cutting to capture the cusp tips and the maximum extension of the cervical enamel. Each sectioned face or histological section was imaged with macrophotography or a stereomicroscope, and only those that appeared to capture the internal dentine horn tip(s) were included. [Data from 41 sectioned molar teeth previously published by Smith et al. (2005) are included here to maximize available samples.] The remaining 182 teeth were obtained from micro-computed tomographic (micro-CT) imaging performed with one of four micro-CT scanners: X-Tek (Metris) HMXST 225 CT scanner, Harvard University; Skyscan 1172 micro-CT, Max Planck Institute for Evolutionary Anthropology (MPI-EVA); BIR ACTIS 225/300 industrial CT system, MPI-EVA; or the BAM 225 kV micro-CT, German Federal Institute for Materials Research and Testing. Olejniczak et al. (2007) demonstrated that different micro-CT scanners yield comparable enamel thickness data, provided that scan parameters are similar. Similar operating conditions (current, energy, metallic filters) were employed for the current study, and voxel sizes ranged between 14 and 52 cubic microns, depending on whether isolated teeth or complete dentitions were scanned.

Virtual 2D section planes were generated from three-dimensional (3D) models with VG Studio MAX 2.0/2.1 software (Volume Graphics). Sectioning protocols have been previously published and illustrated (Feeney et al., 2010; Smith et al., 2010), and are only briefly reviewed here. For incisors, 2D sections were created by virtually rotating 3D models around the central mammelon to find the 2D labial-lingual plane that captured the widest bi-cervical diameter (typically the longest cervical enamel extension). Canine sections were created by rotating the 3D model to locate a labial-lingual plane through the cingulum that captured the maximum bi-cervical diameter (approximately perpendicular to the maximum mesial-distal width). For premolars, the buccal and lingual cusps of 3D models were aligned, and the dentine horn tip of the buccal cusp was set as the center of rotation. To generate a buccal-lingual 2D section along the axis of the tooth, the model was rotated to locate the plane midway between the maximum buccal-lingual bi-cervical diameter and the maximum cervical enamel extension. For molar teeth, the 3D coordinates of the two dentine horn tips and two pulpal horn tips of the mesial cusps were first found and then recorded. Molar

2D planes were located as the midpoint between the two pulp chamber horn tips and the two dentine horn tips using rotational vectors (with a dentine horn tip set as the center of rotation). This method was designed to yield a 2D plane perpendicular to the developmental axis of the crown that captures the maximum extension of cervical enamel, as is standard practice for physical sectioning.

Enamel thickness quantification and statistical analyses

Several variables were quantified on micrographs of each section using a digitizing tablet interfaced with SigmaScan software (SPSS Science). Following Martin (1983, 1985), these variables include the area of the enamel cap (c), the length of the enamel-dentine junction (e), and the area of the coronal dentine enclosed by the enamel cap (b) (illustrated in Smith et al., 2005: Fig. 1, p. 579). Average enamel thickness (AET) is calculated as $[c/e]$, yielding the average straight-line distance (mm units), or thickness, from the enamel-dentine junction to the outer enamel surface. Given that orangutans are known to be highly sexually dimorphic in tooth size and body mass (Mahler, 1973; Smith and Jungers, 1997), AET was scaled for comparisons between sexes by calculation of RET: $[100 \times [c/e]/\text{sq. rt. } b]$. Martin (1983) originally proposed this dimensionless RET index for comparisons among different sized hominoids.

When physical or virtual sections demonstrated light to moderate wear, the outer enamel surface and dentine horn tips were manually reconstructed prior to quantification based on the profiles of unworn teeth, which show relatively low morphological variation. Assessments of alternative reconstructions revealed that small changes in the crown profile make little difference for the calculation of enamel area (or enamel thickness indices). Corrections were also made when small areas of cervical enamel were missing based on the curvature and orientation of the outer enamel surface relative to the enamel-dentine junction. Sections with heavy wear, or with both cervices missing, were excluded. When multiple physical planes of section were available for a single tooth, the one with the lowest RET was chosen for analysis (to minimize potential effects of planar obliquity).

Previous studies have revealed significant differences in hominoid enamel thickness among tooth positions and between maxillary and mandibular rows (Smith et al., 2005, 2006b, 2008), thus tooth positions were assessed separately for initial statistical comparisons between species. The Mann-Whitney U test was employed where sample sizes of each tooth position were four or greater to examine differences in enamel thickness indices and components between orangutan species, between maxillary and mandibular rows, between sexes for the entire sample, and between sexes of known-species affiliation. The Jonckheere-Terpstra test (reviewed in Smith et al., 2005) was employed to test the significance of trends in AET across the dentition; maxillary and mandibular rows were tested separately.

RESULTS

AET values for wild Bornean and Sumatran orangutan dentitions are given in Table 2 and Figure 1. No significant differences in AET were found between species (Table 3), thus the two species were pooled for subsequent analyses (and 27 teeth of unknown species affiliation

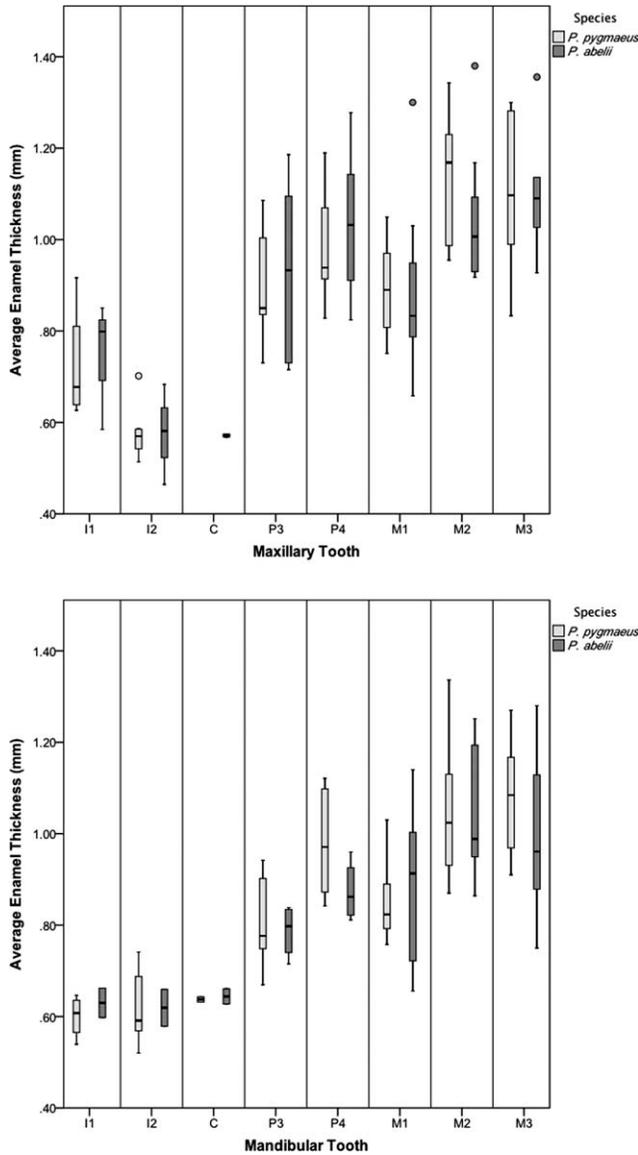


Fig. 1. Comparisons of AET in mm between orangutan species. Standard box and whisker plot revealing the interquartile range (25th–75th percentiles: bars), 1.5 interquartile ranges (whiskers), and the median values (black line). Outliers are signified by circles and extreme values are indicated with asterisks.

were added). Comparisons between maxillary and mandibular teeth revealed a number of significant differences in the components of enamel thickness indices (enamel cap area, enamel-dentine junction length, dentine area; Table 4). Significant differences in these components and indices are due to greater values in maxillary teeth, except for lateral incisors (which show greater values in mandibular analogs). The Jonckheere–Terpstra test revealed a significant increasing trend in AET from anterior to posterior teeth (central incisors to third molars) in both maxillary and mandibular rows ($P < 0.001$), thus tooth type and row were considered separately in analyses of sex differences. Maxillary central incisors appeared as an exception to this trend, showing markedly greater enamel thickness values than lateral incisors.

Comparisons of known-sex individuals in the lumped-species sample revealed that males typically have larger

TABLE 2. Mean AET (in mm) in orangutan dentitions

Tooth	Species	N	AET	Range	CV
UI1	<i>P. abelii</i>	3	0.75	0.58–0.85	18.91
	<i>P. pygmaeus</i>	4	0.72	0.63–0.92	18.22
UI2	<i>P. abelii</i>	3	0.58	0.46–0.68	18.97
	<i>P. pygmaeus</i>	7	0.58	0.51–0.70	10.66
UC	<i>P. abelii</i>	2	0.57	0.57–0.57	–
	<i>P. pygmaeus</i>	–	–	–	–
UP3	<i>P. abelii</i>	6	0.93	0.72–1.19	21.23
	<i>P. pygmaeus</i>	9	0.89	0.73–1.09	13.38
UP4	<i>P. abelii</i>	7	1.03	0.82–1.28	16.11
	<i>P. pygmaeus</i>	9	0.98	0.83–1.19	11.32
UM1	<i>P. abelii</i>	9	0.89	0.66–1.30	21.23
	<i>P. pygmaeus</i>	13	0.90	0.75–1.05	11.72
UM2	<i>P. abelii</i>	7	1.05	0.92–1.38	16.13
	<i>P. pygmaeus</i>	12	1.13	0.95–1.34	11.83
UM3	<i>P. abelii</i>	6	1.10	0.93–1.36	13.04
	<i>P. pygmaeus</i>	11	1.11	0.83–1.30	15.10
LI1	<i>P. abelii</i>	2	0.63	0.60–0.66	–
	<i>P. pygmaeus</i>	4	0.60	0.54–0.65	7.75
LI2	<i>P. abelii</i>	2	0.62	0.58–0.66	–
	<i>P. pygmaeus</i>	5	0.62	0.52–0.74	14.52
LUC	<i>P. abelii</i>	2	0.64	0.63–0.66	–
	<i>P. pygmaeus</i>	2	0.64	0.63–0.64	–
LP3	<i>P. abelii</i>	4	0.79	0.72–0.84	7.38
	<i>P. pygmaeus</i>	7	0.81	0.67–0.94	12.67
LP4	<i>P. abelii</i>	4	0.87	0.81–0.96	7.62
	<i>P. pygmaeus</i>	8	0.98	0.84–1.12	11.93
LM1	<i>P. abelii</i>	7	0.88	0.66–1.14	20.76
	<i>P. pygmaeus</i>	14	0.86	0.76–1.03	10.22
LM2	<i>P. abelii</i>	9	1.05	0.86–1.25	14.81
	<i>P. pygmaeus</i>	14	1.05	0.87–1.34	13.36
LM3	<i>P. abelii</i>	7	1.00	0.75–1.28	19.25
	<i>P. pygmaeus</i>	11	1.08	0.91–1.27	12.14
LM4	<i>P. abelii</i>	–	–	–	–
	<i>P. pygmaeus</i>	1	1.07	–	–

U, upper; L, lower. See Table 1 legend for explanation of tooth positions. CVs were not calculated for sample sizes <3.

TABLE 3. Results of Mann–Whitney *U* test for comparisons of AET between orangutan species

Tooth	Z	P value
UP3	–0.236	0.814
UP4	–0.688	0.491
UM1	–0.668	0.504
UM2	–1.353	0.176
UM3	–0.101	0.920
LP3	–0.567	0.571
LP4	–1.698	0.089
LM1	–0.075	0.941
LM2	–0.441	0.659
LM3	–1.042	0.297

Samples were too small for comparisons of anterior teeth between species.

enamel cap areas, enamel-dentine junction lengths, and dentine areas; these differences are often significant for the latter two variables (Table 5). Females typically show greater RET values than males across the dentition (Fig. 2), which are significantly different for maxillary lateral incisors and third molars, and mandibular third and fourth premolars. To control for the potential confounding effects of sexual dimorphism on interspecific contrasts, we conducted a post hoc comparison of enamel thickness between males and females of each species. AET was employed, as sex-specific body masses are approximately equal between species (Smith and Jungers, 1997). Although samples are too small for statistical comparisons,

TABLE 4. Results of Mann-Whitney U test for comparisons of enamel thickness components and indices between orangutan maxillary and mandibular dentitions (both species combined)

Tooth	Stat	c	e	AET	b	RET
I1	Z	-2.626	-2.521	-2.205	-2.941	-0.630
	P value	0.009	0.012	0.027	0.003	0.529
I2	Z	-2.629	-2.701	-0.426	-2.345	-1.421
	P value	0.009	0.007	0.670	0.019	0.155
P3	Z	-0.984	-0.858	-1.528	-1.779	-2.239
	P value	0.325	0.391	0.127	0.075	0.025
P4	Z	-2.568	-2.657	-1.240	-2.391	-0.576
	P value	0.010	0.008	0.215	0.017	0.565
M1	Z	-1.948	-1.269	-1.456	-0.670	-0.750
	P value	0.051	0.205	0.145	0.503	0.453
M2	Z	-1.751	-1.194	-1.194	-0.892	-0.167
	P value	0.080	0.233	0.233	0.372	0.867
M3	Z	-2.079	-0.594	-1.172	-0.297	-0.660
	P value	0.038	0.552	0.241	0.766	0.509

Canine samples were too small for comparisons between maxillary and mandibular dentitions. c, area of enamel cap; e, enamel-dentine junction length; AET, average enamel thickness; b, area of coronal dentine; RET, relative enamel thickness.

TABLE 5. Results of Mann-Whitney U test for comparisons of enamel thickness components and indices between orangutan sexes (both species combined)

Tooth	Stat	c	e	AET	b	RET
UI2	Z	-2.021	-2.309	-0.866	-2.309	-2.021
	P value	0.043	0.021	0.386	0.021	0.043
UP3	Z	-1.543	-2.842	-0.893	-2.842	-1.705
	P value	0.123	0.004	0.372	0.004	0.088
UP4	Z	-1.543	-2.680	-1.218	-2.680	-1.218
	P value	0.123	0.007	0.223	0.007	0.223
UM1	Z	-1.952	-2.830	-0.586	-2.928	-0.976
	P value	0.051	0.005	0.558	0.003	0.329
UM2	Z	-0.118	-1.886	-1.121	-2.003	-1.828
	P value	0.906	0.059	0.262	0.045	0.068
UM3	Z	-0.617	-2.315	-2.472	-2.469	-2.469
	P value	0.537	0.021	0.013	0.014	0.014
LI2	Z	-1.443	-2.309	0.000	-2.309	-1.732
	P value	0.149	0.021	1.000	0.021	0.083
LP3	Z	-0.490	-1.960	-1.225	-1.715	-2.449
	P value	0.624	0.050	0.221	0.086	0.014
LP4	Z	-0.104	-2.193	-1.149	-2.402	-2.611
	P value	0.917	0.028	0.251	0.016	0.009
LM1	Z	-0.926	-0.810	-0.579	-2.083	-0.926
	P value	0.355	0.418	0.563	0.037	0.355
LM2	Z	-1.073	-2.395	-0.165	-2.395	-1.569
	P value	0.283	0.017	0.869	0.017	0.117
LM3	Z	-0.586	-1.610	-0.880	-1.171	-1.464
	P value	0.558	0.107	0.379	0.242	0.143

Central incisor and canine samples were too small for comparisons between sexes. See Table 4 legend for an explanation of variables tested.

Bornean females show greater AET than Sumatran females at most tooth positions (Fig. 3, Supporting Information Table 1). Samples of known-species male teeth are more limited, showing an opposite trend in AET and smaller interspecific differences than in females (Fig. 4).

DISCUSSION

Enamel thickness variation within hominoid dentitions

Data on tooth crown size and shape are available for large samples of great apes (e.g., Pilbeam, 1969; Mahler,

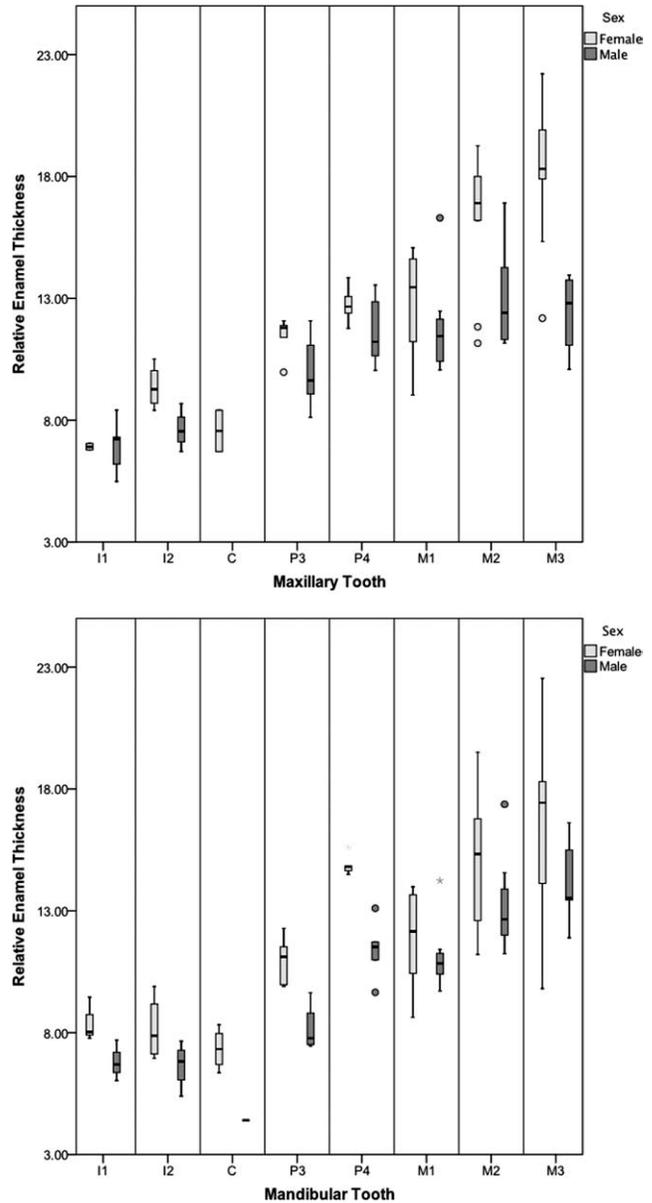


Fig. 2. Comparisons of RET between male and female orangutans (lumped species). See legend of Figure 1 for description of graph.

1973; Uchida, 1998a,b; Swindler, 2002; Pilbrow, 2006), which have been sought for their insight into hominin and hominoid evolution. In one of the most comprehensive studies to date, Uchida (1998a) found that interspecific differences in orangutan crown size or shape did not exceed differences within species. Less is known about the proportions of enamel and dentine that comprise tooth crowns. The expanded sample employed in this study supports the preliminary finding that 2D AET does not differ between mixed-sex samples of Bornean and Sumatran orangutans (Smith et al., 2005), which is explored further below. Thus aspects of both external and internal orangutan tooth morphology do not appear to show species-specific size, shape, or enamel thickness values that may be used to diagnose the affiliation of unassociated teeth (potentially including thousands of

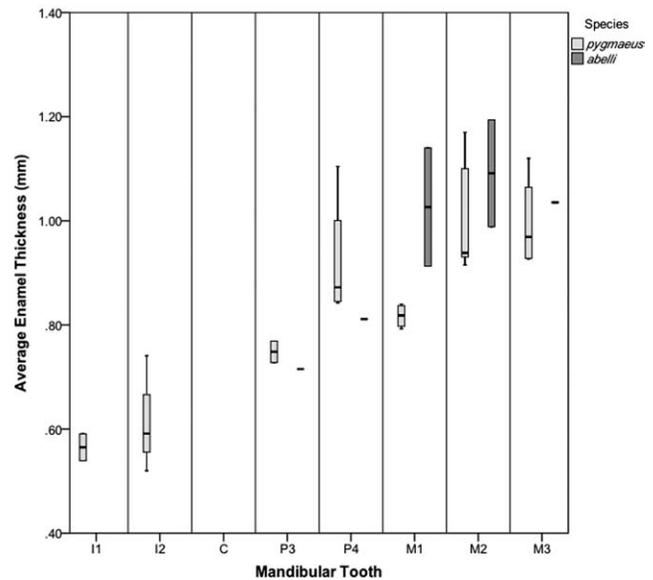
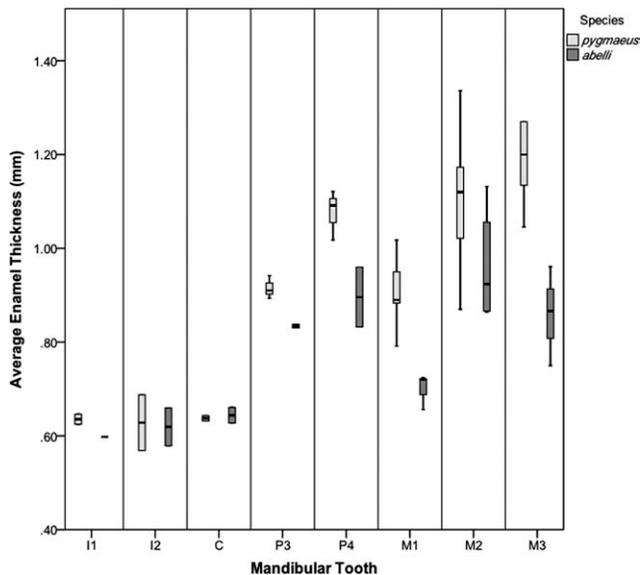
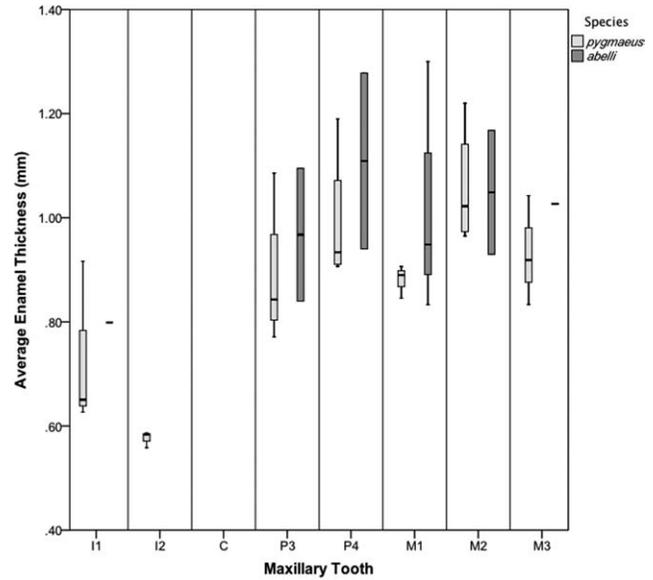
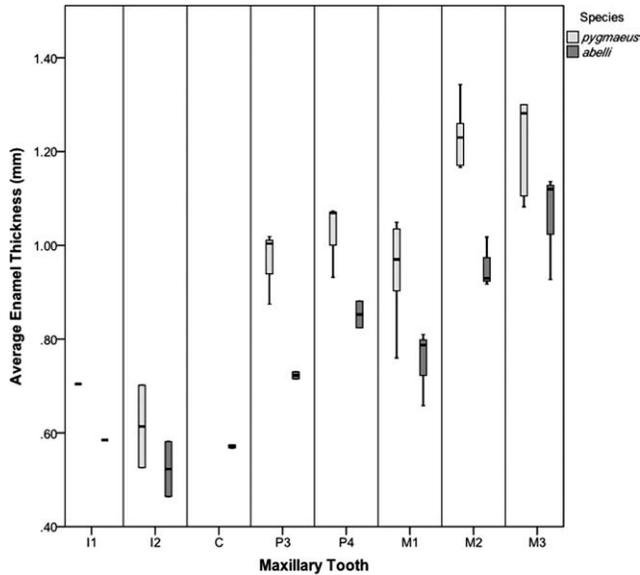


Fig. 3. Comparisons of AET between females of each orangutan species. See legend of Figure 1 for description of graph.

Fig. 4. Comparisons of AET between males of each orangutan species. See legend of Figure 1 for description of graph.

fossil orangutan teeth recovered in southeast Asia: Hoijer, 1948; Harrison, 2000).

The patterning of enamel thickness indices (and their components) between orangutan maxillary and mandibular teeth is similar to other great apes and humans (Smith et al., 2005, 2006b, 2008; Feeney et al., 2010). Smith et al. (2005) noted that hominoid maxillary teeth tend to be broader in a buccal-lingual dimension than mandibular molars, leading to greater cross-sectional areas. This study also demonstrated a trend for AET to increase from anterior to posterior teeth, as was found in chimpanzees and humans (Smith et al., 2008). We suggest that the unusually thick enamel found in orangutan maxillary central incisors may relate to bark gouging or incisal biting of mechanically demanding foods (Rodman, 1988; Taylor, 2006), which is uncommon in other great apes. Knott (1999) reported that juvenile orangutans rely on their mothers in order to consume

bark, as they are unable to initiate bark stripping from trees directly. The relationship between anterior tooth use and enamel thickness deserves further exploration, as certain pitheciine primates employ their anterior teeth to process hard seed coats in order to masticate soft seeds with thin-enameled molars (reviewed in Martin et al., 2003; Vogel et al., 2009).

Orangutan dentitions are known to be highly sexually dimorphic (Mahler, 1973; Scott et al., 2009), which is largely due to significantly greater dentine cores (and likely overall tooth root sizes) in males. The sex differences documented in this study are also broadly similar to human patterns (Smith et al., 2006b; Feeney et al., 2010), although enamel cap areas in male orangutans were found to be greater than or equal to female values, which is less common in human molars (Schwartz and Dean, 2005; Smith et al., 2006b). Human and orangutan males have proportionately more dentine and longer

enamel-dentine junction lengths than females, resulting in relatively thinner enamel than females. Smith et al. (2006b) reviewed human genetic studies that indicate that sex chromosome gene expression may be at least partially responsible for differences in dental tissue proportions. Unfortunately, little is known about the genetic basis of enamel thickness in non-human primates (but see work on baboons by Hlusko et al., 2004).

Broader functional, ecological, and taxonomic implications

The lack of differences in AET between mixed-sex Bornean and Sumatran orangutan species is surprising given differences in fallback foods, dietary material properties, dietary breadth, and mandibular morphology (Taylor, 2006; Morrogh-Bernard et al., 2009; Harrison and Marshall, 2011; Vogel et al., 2011). Although there is a great deal of variation in the diets of orangutans, the average dietary differences between *P. pygmaeus* and *P. abelii* are greater than the differences found among sites within each island (Taylor, 2006; Russon et al., 2009). This is consistent with data showing that the overall forest structure and phenological patterns between the two islands are significantly different, with Sumatran forests being more productive and experiencing fewer periods of food shortage (Marshall et al., 2009; Wich et al., 2011). With respect to bark, in particular, the difference in the maximum amount of time spent eating bark between two subspecies of Bornean orangutan (52.8% and 42.1% for *P. p. morio* and *P. p. wurmbii*, respectively) is far less than the difference between Bornean and Sumatran orangutans (2.4% for *P. abelii*; Taylor, 2006). Thus, it is unlikely that we failed to find differences in enamel thickness between orangutan species due to patterns of intraspecific ecological variation.

Following Lambert et al. (2004), Constantino et al. (2009) argued that patterns of enamel thickness and tooth size can be explained through consideration of the material properties of fallback food items. They suggested that thick enamel in orangutans (relative to other great apes) might be an adaptation for masticating hard seeds. However, Harrison and Marshall (2011) note that certain seeds consumed by orangutans are actually preferred food items, and tougher foods such as bark or leaves are consumed when fruit or seeds are unavailable (see Taylor, 2006; Vogel et al., 2009). Our results suggest that differences in the consumption of fallback items such as tough bark and/or leaves may not result in marked selection for a disparate degree of enamel thickness in orangutan species. Similarly, there is no evidence that species-level differences in the material properties of common dietary items (Vogel et al., 2011) have led to thicker enamel in Bornean orangutans as a whole (although comparisons of females may suggest otherwise). While additional research may be warranted to clarify the status of orangutan preferred versus fallback foods, as well as the material properties of foods in each category, our results for the mixed-sex sample do not support ecological predictions that Bornean orangutans have thicker enamel than Sumatran orangutans.

It is possible that differences in feeding behavior between Sumatran and Bornean orangutan populations are being driven by recent changes in climate and consequent forest structure. Walsh (1996) reports that the intensity and frequency of droughts in northern Borneo has significantly increased since the 1960s. Intense

droughts in tropical forests are often associated with severe El Niño events and can lead to increased tree mortality, loss of forest due to fire, and reduction in tree growth (Wright and Calderón, 2006). These climactic patterns may be localized to small geographic areas such that forests in Borneo and Sumatra may experience varied rainfall patterns resulting in different food availability. It is also worth noting that although El Niño events have been occurring for the last 5,000 years, geological evidence suggests that they were not occurring between 5,000 and 10,000 years ago (Enfield, 1992; Walsh, 1996). This may have resulted in more consistency in food availability in tropical Asian forests during this time. Meijaard et al. (2010) have also suggested that Bornean orangutan abundance may have been greater in the recent past, potentially impacting aspects of their behavior and ecology.

Our results reveal the first significant differences in RET (and the components of this index) between non-human primate sexes, with females showing greater values than males. Although males have larger teeth, differences are mainly due to the larger dentine cores and related enamel-dentine junction lengths, which are used to scale enamel thickness. Male teeth tend also tend to show slightly greater enamel cap areas than females, which is significant for upper lateral incisors only. These differences in dental tissue proportions are somewhat difficult to interpret in light of proposed ecological models for enamel thickness. Greater AET and RET in female orangutans may be expected from their tougher and/or more diverse diet. Given that they are the ecological sex (Gaulin and Sailer, 1985), fallback foods may be more important to females, as males are larger, socially dominant, and may out-compete females at preferred feeding sites (Knott, 1999). For example, females in Borneo eat significantly more bark, which is considered to be a fallback food, in certain months than males (Knott, 1999; reviewed in Harrison and Marshall, 2011). Females, particularly those that are non-sexually active, also tend to spend more time feeding than males (Morrogh-Bernard et al., 2009; van Schaik et al., 2009). Alternatively, males may be expected to show thicker enamel due to their consumption of hard seeds. Although both species of orangutan have been observed to eat *Neesia* seeds, males eat significantly more of these seeds in Borneo (Knott, 1999; Fox et al., 2004), and while there are no sex differences in seed consumption reported in Sumatran sites, females and juveniles employ tool technology to extract the aril from the seed (Fox et al., 1999, 2004).

It is possible that the large sexual dimorphism in orangutan dentitions complicates the relationship between enamel thickness and dietary ecology. Although mixed-sex comparisons do not reveal enamel thickness differences between orangutan species, preliminary comparisons suggest that Bornean females have thicker enamel than Sumatran females. As reviewed earlier, the primary difference between Bornean and Sumatran fallback foods is in bark consumption, which is not consistent with explanatory models of thick enamel due to the mastication of hard-object fallback foods. Alternatively, sex-specific differences in enamel thickness may arise from overall differences in the material properties of Bornean and Sumatran female diets (Vogel et al., 2011), as was also found in a comparison of chimpanzees and orangutans (Vogel et al., 2008), although it is unclear why males would not follow a similar pattern. Additional

research into the dietary proportions and material properties of preferred and fallback dietary items consumed by each sex would help to clarify if thicker enamel in Bornean females is due to the incorporation of tough fallback items such as bark, or if it reflects differences in the hardness and toughness of both preferred and fallback foods.

Finally, the results of this study have important implications for ecological or taxonomic interpretations of enamel thickness in smaller samples. Comparisons of enamel thickness have revealed differences between certain non-human primate species pairs (Dumont, 1995) as well as species of *Homo* (Olejniczak et al., 2008b; Bayle et al., 2010; Smith et al., in press). Differences have also been noted for small samples of *Proconsul* and *Lufengpithecus* species (Beynon et al., 1998; Schwartz et al., 2003; Smith et al., 2003), but not for samples of *Sivapithecus* (Mahoney et al., 2007) or *Khoratpithecus* species (Chaimanee et al., 2006). We suggest that variation in highly dimorphic genera, such as *Lufengpithecus*, may be due in part to sex differences in enamel thickness. Future studies should include information on the sex of individuals when possible (for associated dentitions), which may be a confounding factor for taxonomic studies of enamel thickness in isolated dental elements (e.g., Martin, 1983; Smith et al., 2003; Kunimatsu et al., 2007).

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