

Intra- and Interspecific Variation in Macaque Molar Enamel Thickness

Akiko Kato,^{1,2} Nancy Tang,¹ Carola Borries,³ Amanda M. Papakyrikos,⁴ Katie Hinde,¹ Ellen Miller,⁵ Yutaka Kunimatsu,⁶ Eishi Hirasaki,⁷ Daisuke Shimizu,^{6,8} and Tanya M. Smith^{1*}

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

²Department of Oral Anatomy, School of Dentistry, Aichi Gakuin University, Nagoya 4648650, Japan

³Department of Anthropology, Stony Brook University, Stony Brook, NY 11794

⁴Department of Biological Sciences, Wellesley College, Wellesley, MA 02481

⁵Department of Anthropology, Wake Forest University, Winston-Salem, NC 27106

⁶Graduate School of Science, Kyoto University, Kyoto 6068502, Japan

⁷Primate Research Institute, Kyoto University, Inuyama 4848506, Japan

⁸Japan Monkey Center, Inuyama 4840081, Japan

KEY WORDS dental morphology; dietary ecology; functional morphology; primate ecogeography; relative enamel thickness

ABSTRACT Enamel thickness has played an important role in studies of primate taxonomy, phylogeny, and functional morphology, although its variation among hominins is poorly understood. Macaques parallel hominins in their widespread geographic distribution, relative range of body sizes, and radiation during the last five million years. To explore enamel thickness variation, we quantified average and relative enamel thickness (AET and RET) in *Macaca arctoides*, *Macaca fascicularis*, *Macaca fuscata*, *Macaca mulatta*, *Macaca nemestrina*, and *Macaca sylvanus*. Enamel area, dentine area, and enamel-dentine junction length were measured from mesial sections of 386 molars scanned with micro-computed tomography, yielding AET and RET indices. Intraspecific sex differences were not found in AET or RET. *Macaca fuscata* had the highest AET and RET, *M. fascicularis* showed the lowest AET, and *M. arctoides*

had the lowest RET. The latitudinal distribution of macaque species was associated with AET for these six species. Temperate macaques had thicker molar enamel than did tropical macaques, suggesting that thick enamel may be adaptive in seasonal environments. Additional research is needed to determine if thick enamel in temperate macaques is a response to intensified hard-object feeding, increased abrasion, and/or a broader diet with a greater range of food material properties. The extreme ecological flexibility of macaques may prohibit identification of consistent trends between specific diets and enamel thickness conditions. Such complications of interpretation of ecological variability, dietary diversity, and enamel thickness may similarly apply for fossil *Homo* species. *Am J Phys Anthropol* 155:447–459, 2014. © 2014 Wiley Periodicals, Inc.

Primate enamel thickness, assessed in numerous studies of fossil hominins and hominoids, is reported to provide phylogenetic, taxonomic, and functional information (reviewed in Smith et al., 2003, 2006; Olejniczak et al., 2008a; Alba et al., 2010; Benazzi et al., 2011; Smith et al., 2012a). However, considerable variation in enamel thickness is increasingly evident within genera (Dumont, 1995; Beynon et al., 1998; Mackiewicz et al., 2010; Smith et al., 2011, 2012a,b). Temporal and geographic variation in enamel thickness has been documented in comparisons between fossil and living orangutans (Smith et al., 2011), as well as among members of the Miocene hominoid genus *Proconsul* (Andrews and Martin, 1991; Beynon et al., 1998), and fossil cave bear species (Mackiewicz et al., 2010). This variation is particularly apparent among species of *Homo*, which range from the intermediate thickness of Neanderthals to the extremely thick enamel of some early *Homo* fossils from eastern and southern Africa (Schwartz, 1997; Olejniczak et al., 2008b; Smith et al., 2012a).

Recent work has reinvigorated functional explanations for primate enamel thickness variation (Vogel et al., 2008; Constantino et al., 2009; Rabenold and Pearson, 2011; McGraw et al., 2012; Mahoney, 2013; Pampush et al., 2013). A number of studies posit a relationship

between enamel thickness and the mechanics of tooth wear or fracturing, while others assess the relationship between enamel thickness and diet (preferred and/or fallback foods) (reviewed in Smith et al., 2012b). Information on the material properties of hominoid dietary items has also guided functional hypotheses (Lucas et al., 1994; Vogel et al., 2008; Constantino et al., 2009),

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

Grant sponsors: Harvard University, National Science Foundation; Grant number: BCS-0921978; Aichi Gakuin University, Wake Forest University, Primate Research Institute Kyoto University and the Nikon Corporation (Japan).

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

Received 8 November 2013; accepted 5 August 2014

DOI: 10.1002/ajpa.22593

Published online 21 August 2014 in Wiley Online Library (wileyonlinelibrary.com).

TABLE 1. Species in order of decreasing mean latitude of northernmost distributions

	Max Latitude			Female mass (kg)	Male mass (kg)
	Fooden	IUCN	Mean used		
<i>M. fuscata</i>	42	41.5	41.75	8.0	11.0
<i>M. mulatta</i>	41	36.0	38.50	5.4	7.7
<i>M. sylvanus</i>	37	36.5	36.75	9.6	14.5
<i>M. arctoides</i>	27	29.0	28.00	8.4	12.2
<i>M. nemestrina</i> ^a	27	29.0	28.00	4.9–6.5	7.7–11.2
<i>M. fascicularis</i>	22	21.5	21.75	3.6	5.4

Maximum latitude derived from IUCN distribution maps (<http://www.iucnredlist.org>) and physical collections of specimens (Fooden, 1975, 1980, 1995, 2000, 2005, 2007). Body mass data are from Smith and Jungers (1997) and Isler et al. (2008).

^a*Macaca nemestrina* maximum latitude derived from the recently recognized species *Macaca leonina* (Ziegler et al., 2007), body mass ranges include both *M. nemestrina* and *M. leonina*.

although much less is known about the material properties of the diets of other primates. Three main hypotheses have been proposed to explain primate enamel thickness variation: (1) thick enamel is advantageous for resisting fracture due to high bite forces generated during the mastication of hard foods (e.g., Kay, 1981; Dumont, 1995; Lambert et al., 2004; Vogel et al., 2008; Constantino et al., 2011; McGraw et al., 2012, 2014); (2) thick enamel is advantageous for resisting abrasion caused by hard particles in or on food items (e.g., Jolly, 1970; Gantt, 1977; Rabenold and Pearson, 2011; Pampush et al., 2013); and/or (3) thin enamel is advantageous for shearing tough herbivorous food items (e.g., Kay, 1981; Ulhaas et al., 1999; Shimizu, 2002; Vogel et al., 2008). An additional scenario, which is not mutually exclusive from the above predictions, is that thick enamel is an adaption for expanded dietary breadth driven by increased seasonality and colonization of temperate environments (Andrews and Martin, 1991). Primates living in these environments are often required to incorporate more diverse items than ripe fruit or young leaves into their diets than primates in tropical environments (van Schaik et al., 1993; Hemingway and Bynum, 2005; Hanya et al., 2013; Tsuji et al., 2013).

Investigations of primate enamel thickness have yielded equivocal support for the above hypotheses, and several factors hinder direct tests such as the potential confounding effects of phylogenetic nonindependence, the degree of mechanical processing before ingestion, and variation in tooth size. Dumont (1995) compared enamel thickness in congeneric pairs of primates and chiropterans, reporting that relative enamel thickness (RET) values were consistently greater in hard-object feeders than in the respective soft-object feeders. Importantly these values overlapped greatly across taxa, precluding the determination of absolute ranges of enamel thickness values that predict dietary preferences. McGraw et al. (2012) recently challenged Dumont's (1995) characterization of *Cercocebus (Lophocebus) albigena* as a soft-object frugivore, arguing that all mangabeys process hard objects and have thick enamel. However, thick enamel is not necessary for hard-object feeding, as certain pitheciin primates with thin molar enamel use their anterior dentition for processing hard objects (Martin et al., 2003; also see Constantino et al. 2011 for related data on sea otters). In similarly-sized Bornean and Sumatran orangutans, the species that is presumed to feed on harder objects showed greater average enamel thickness (AET) in females but not in males

(Smith et al., 2012b). In contrast, a recent study of primate enamel thickness that statistically controlled for phylogeny concluded that thick molar enamel may have been selected to resist lifelong abrasion rather than tooth fracture (Pampush et al., 2013).

To contribute further to our understanding of the nature and magnitude of enamel thickness variation among congeneric primates, we examined molar enamel thickness in six macaque species. Our sample includes three temperate species: *Macaca fuscata* (Japanese macaque), *Macaca mulatta* (rhesus macaque), *Macaca sylvanus* (Barbary macaque); and three tropical species: *Macaca arctoides* (stump-tailed macaque), *Macaca fascicularis* (long-tailed macaque) and *Macaca nemestrina* (pig-tailed macaque). These species span an approximately twofold range of body mass values, and show considerable geographic variation (Table 1).

MACAQUE DIETS AND ENAMEL THICKNESS

Dietary studies of *M. fascicularis*, *M. fuscata*, and *M. sylvanus* are more common in the literature than are such studies for *M. nemestrina*, *M. mulatta*, and *M. arctoides* (Suzuki, 1965; Clutton-Brock and Harvey, 1977; Rodman, 1978; Ojha, 1980; Wheatley, 1980; Khan and Wahab, 1983; Goldstein, 1984; Ménard, 1985; Caldecott, 1986a, 1986b; Ménard and Vallet, 1986; Aggimarangsee, 1992; Ungar, 1992; Ahsan, 1994; Agetsuma, 1995; Yeager, 1996; Hill, 1997; Agetsuma and Nakagawa, 1998; Ménard and Qarro, 1999; Hanya, 2003, 2004; Tsuji and Takatsuki, 2004; Tsuji et al., 2006; Richter et al., 2013; Ménard et al., 2014). For *M. arctoides* we could locate only one short-term survey of provisioned groups near human habitations (Aggimarangsee, 1992). Given the apparent extreme ecological flexibility of certain macaque species, here we restrict our dietary characterizations to studies of unprovisioned, wild populations with one or more years of quantitative data on feeding behavior. On the basis of the most comprehensive studies available (Ménard, 1985; Caldecott, 1986a,b; Yeager, 1996; Hanya, 2004), *M. sylvanus* consumes the highest proportion of seeds and pods, *M. fuscata* and *M. sylvanus* are the most folivorous species, and *M. nemestrina* and *M. fascicularis* are the most frugivorous species (Fig. 1).

Currently, deficits in our knowledge of the dietary ecology and mechanical properties of the foods of wild-living macaques handicap direct tests of functional explanations of enamel thickness. Moreover, population-

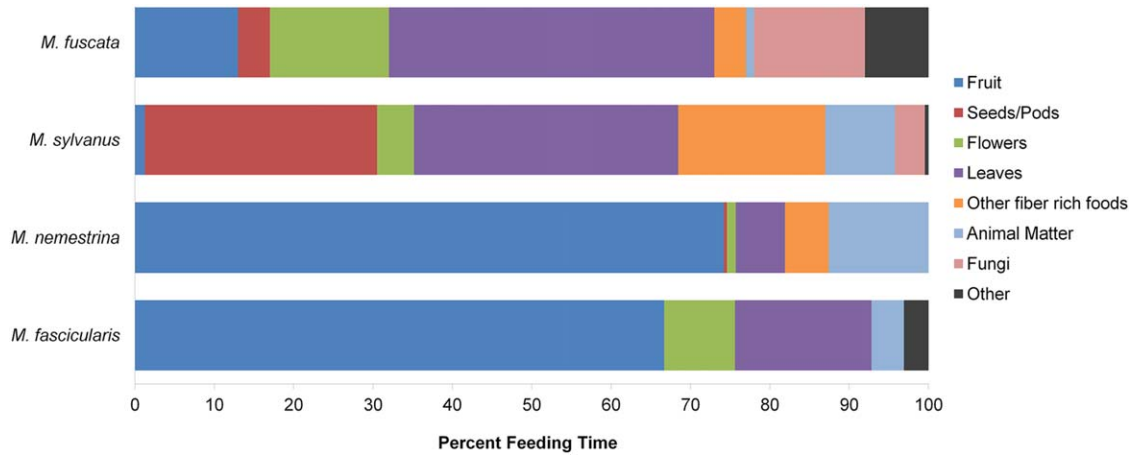


Fig. 1. Percentage of annual feeding time spent on major food categories. Species are arranged from top to bottom in decreasing mean latitude of their northernmost distribution. “Other fiber rich foods” include scapes, roots, and lichens for *M. sylvanus*; buds, stems, and palm fronds for *M. nemestrina*; bud, root, and pith for *M. fuscata*. Data on *M. fuscata* from Hanya (2004), *M. sylvanus* from Ménard (1985), *M. nemestrina* from Caldecott (1986a,b), and *M. fascicularis* from Yeager (1996). The Yakushima highland population of *M. fuscata* was employed as its environment most closely resembled the Takahama population for which enamel thickness was measured (Agetsuma, 1995; Agetsuma and Nakagawa, 1998; Tsuji et al., 2013).

TABLE 2. Sample of macaque teeth employed

Species	Sex	UM1	UM2	UM3	LM1	LM2	LM3	Total
<i>M. arctoides</i>	Female	3	4	4	5	4	4	24
	Male	4	4	2	4	3	2	19
<i>M. fascicularis</i>	Female	9	9	6	9	8	5	46
	Male	12	7	4	10	8	4	45
	Unknown	1	1	1	1	1	1	6
<i>M. fuscata</i>	Female	7	8	1	5	8	1	30
	Male	7	11	7	5	9	7	46
<i>M. mulatta</i>	Female	9	6	1	9	6	2	33
	Male	9	8	3	9	8	3	40
	Unknown	1	0	1	0	0	2	4
<i>M. nemestrina</i>	Female	6	7	4	5	6	4	32
	Male	6	3	1	5	3	1	19
	Unknown	2	3	2	2	3	2	14
<i>M. sylvanus</i>	Female	3	3	3	1	2	3	15
	Male	2	0	0	2	0	0	4
	Unknown	2	2	1	1	2	1	9

U, maxillary; L, mandibular; M1, first molar; M2, second molar; M3, third molar.

specific feeding data may not reflect general species trends. For example, Pampush et al. (2013) followed others in categorizing *M. mulatta* as “highly folivorous” based on a field study from an environment modified by human activity in Pakistan (Goldstein and Richard, 1989). However, other studies in Pakistan, India, and Bangladesh suggest a more omnivorous or frugivorous diet for *M. mulatta* (Lindburg, 1976, 1977; Ojha, 1980; Ahsan, 1994; Sengupta et al., in press), which is in keeping with characteristic cercopithecine dental and digestive anatomy (Chivers and Hladik, 1980; Lambert, 1998; Swindler, 2002; Fleagle, 2013). Importantly, there are no year-round, quantitative feeding data available for *M. mulatta* or *M. arctoides* from undisturbed environments or unprovisioned populations. As such we have omitted these two species from quantitative dietary comparisons.

Gantt (1977) hypothesized that differences in enamel thickness among macaque species would reflect dietary variation or differences in body mass. However, he did not find significant differences among elements of the

posterior dentition (also see Molnar and Gantt, 1977). Subsequent studies of macaques have employed limited samples of worn or physically sectioned teeth (Kay, 1981; Shellis et al., 1998; Shimizu, 2002), or micro-computed tomographic (micro-CT) scans (Olejniczak et al., 2008a; Horvath et al., 2012). Here we employ a more robust sample in order to better explore enamel thickness variation within and among closely-related species, and to consider the extent to which these results are consistent with hypothesized explanations for enamel thickness variation, although definitive understanding awaits information on the mechanical properties of specific foods (e.g., Lambert et al., 2004; Vogel et al., 2008; McGraw et al., 2014). Lastly, if thick enamel is advantageous in environments characterized by greater seasonal variation, temperate species (*M. fuscata*, *M. mulatta*, and *M. sylvanus*) should show thicker enamel than more tropical species (*M. arctoides*, *M. fascicularis*, and *M. nemestrina*). These hypotheses, which are not mutually exclusive, are considered below in light of novel data on macaque enamel thickness.

MATERIALS AND METHODS

Sample

Enamel thickness was quantified in 386 molars from 109 individuals of six species: *M. arctoides*, *M. fascicularis*, *M. fuscata*, *M. mulatta*, *M. nemestrina*, and *M. sylvanus* (Table 2). Sex was known for 353 of the 386 molars. Macaque crania were obtained from the Harvard University Museum of Comparative Zoology (Cambridge, MA), American Museum of Natural History (New York, NY), Wake Forest University Primate Center (Winston-Salem, NC), California National Primate Research Center (Davis, CA), Alpha Genesis, Inc. (Yemassee, SC), University of Washington Regional Primate Research Center (Seattle, WA), University at Buffalo (Buffalo, NY), Kyoto University Primate Research Institute (Inuyama, Japan), and Japan Monkey Center (Inuyama, Japan). The majority of individuals were captive; those

with signs of severe skeletal or dental pathology were excluded. The *M. nemestrina* sample was broadly defined to include the former subspecies *Macaca nemestrina nemestrina*, *Macaca nemestrina leonina*, and *Macaca nemestrina pagensis*, as a number of crania from museum collections and captive facilities designated as “*Macaca nemestrina*” are of unknown origin (see Ziegler et al., 2007 for a recent revision of this taxon).

Intact dentitions and a few isolated molars were scanned with one of two micro-CT scanners (Harvard University Center for Nanoscale Systems X-Tek HMXST 225 CT, Nikon Corporation X-Tek XT H225 CT) with voxel sizes between 17 and 43 cubic microns, depending on specimen size and whether isolated teeth or complete dentitions were scanned. We employed standard operating conditions (current, energy, and metallic filters) following established protocols (Olejniczak et al., 2007, 2008a,b; Feeney et al., 2010; Smith et al., 2012a,b). Virtual two-dimensional (2D) sections were generated from three-dimensional (3D) models with VG Studio MAX 2.1/2.2 software (Volume Graphics GmbH) (Supporting Information Fig. 1). Sectioning protocols have been previously described (Feeney et al., 2010; Smith et al., 2010, 2011, 2012a,b), and are only briefly reviewed here. The 3D coordinates of the dentine and pulp horn tips of the mesial molar cusps were first found and recorded. Molar 2D plane position was calculated 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, as is standard practice for physical sectioning.

Enamel thickness quantification and statistical analyses

Following Martin (1983, 1985), several variables were quantified on 2D section planes using a digitizing tablet and SigmaScan Pro software (Systat Software), including 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) (Supporting Information Fig. 1). AET was calculated as $[c/e]$, yielding the average straight-line distance (mm units), or thickness, from the enamel-dentine junction to the outer enamel surface. This index was scaled for interspecific comparisons by calculation of RET: $[100 \times [c/e]/\text{sq. rt. b}]$. When virtual sections demonstrated light to moderate wear, the outer enamel surface and dentine horn tips were manually reconstructed prior to quantification by visually projecting the profiles of unworn teeth (as illustrated in Smith et al., 2012a; Supporting Information Fig. 1). 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. We excluded sections with heavy wear and/or both cervices missing. When both left and right molars were available, the side with the lowest RET was used (following Martin, 1983; Smith et al., 2005).

Previous studies have revealed significant differences in hominoid enamel thickness among tooth positions and between maxillary and mandibular rows (Smith et al., 2005, 2006, 2008, 2012b). Therefore, tooth positions were assessed separately for initial statistical comparisons between species. The Mann–Whitney *U* test was employed when categories were represented by four or

TABLE 3. Average and relative enamel thickness (AET and RET) values in macaque molars

Tooth	Species	N	AET	Range	RET	Range
UM1	<i>M. arctoides</i>	7	0.50	0.41–0.56	9.35	7.54–11.55
	<i>M. fascicularis</i>	22	0.45	0.39–0.51	11.64	10.13–13.20
	<i>M. fuscata</i>	14	0.60	0.49–0.65	13.08	10.83–14.68
	<i>M. mulatta</i>	19	0.57	0.47–0.63	12.16	9.65–13.49
	<i>M. nemestrina</i>	14	0.50	0.43–0.55	10.84	8.44–13.37
UM2	<i>M. sylvanus</i>	7	0.56	0.49–0.66	11.42	9.80–13.75
	<i>M. arctoides</i>	8	0.61	0.53–0.66	10.31	8.50–13.27
	<i>M. fascicularis</i>	17	0.53	0.38–0.74	11.95	8.86–16.21
	<i>M. fuscata</i>	19	0.74	0.64–0.80	13.53	11.32–15.01
	<i>M. mulatta</i>	14	0.65	0.55–0.75	12.28	10.75–14.53
UM3	<i>M. nemestrina</i>	13	0.57	0.47–0.66	11.22	8.81–13.44
	<i>M. sylvanus</i>	5	0.74	0.66–0.83	12.86	11.95–14.22
	<i>M. arctoides</i>	6	0.66	0.57–0.75	12.11	9.99–16.28
	<i>M. fascicularis</i>	11	0.55	0.48–0.71	13.16	10.77–18.27
	<i>M. fuscata</i>	8	0.80	0.68–0.89	14.25	11.39–16.99
LM1	<i>M. mulatta</i>	5	0.67	0.60–0.76	12.55	11.32–14.36
	<i>M. nemestrina</i>	7	0.63	0.53–0.72	12.86	10.20–16.18
	<i>M. sylvanus</i>	4	0.76	0.72–0.89	13.21	10.69–15.35
	<i>M. arctoides</i>	9	0.48	0.44–0.51	10.18	8.89–11.87
	<i>M. fascicularis</i>	20	0.44	0.38–0.49	12.12	10.69–14.45
LM2	<i>M. fuscata</i>	10	0.59	0.55–0.64	13.85	12.67–15.40
	<i>M. mulatta</i>	18	0.54	0.48–0.60	13.16	10.03–16.18
	<i>M. nemestrina</i>	12	0.47	0.39–0.53	10.61	8.00–12.79
	<i>M. sylvanus</i>	4	0.53	0.50–0.56	11.51	10.06–12.78
	<i>M. arctoides</i>	7	0.57	0.48–0.62	9.81	7.62–13.06
LM3	<i>M. fascicularis</i>	17	0.52	0.45–0.72	12.15	10.80–16.49
	<i>M. fuscata</i>	17	0.71	0.61–0.80	13.91	12.13–15.61
	<i>M. mulatta</i>	14	0.67	0.59–0.75	13.10	10.77–15.31
	<i>M. nemestrina</i>	12	0.55	0.47–0.68	10.73	8.76–14.57
	<i>M. sylvanus</i>	4	0.67	0.57–0.72	11.93	10.43–13.56
LM3	<i>M. arctoides</i>	6	0.63	0.51–0.71	11.64	8.77–15.46
	<i>M. fascicularis</i>	10	0.56	0.47–0.78	14.09	11.65–20.96
	<i>M. fuscata</i>	8	0.80	0.72–0.88	15.21	13.33–17.85
	<i>M. mulatta</i>	7	0.70	0.61–0.78	14.10	11.79–16.50
	<i>M. nemestrina</i>	7	0.62	0.54–0.72	12.61	10.56–17.02
	<i>M. sylvanus</i>	4	0.73	0.68–0.79	12.88	12.60–13.39

See Table 2 legend for explanation of tooth positions. AET values are in mm. RET is a dimensionless index.

more teeth to examine differences in enamel thickness indices and components between maxillary and mandibular rows, between sexes, and between macaque species. The Jonckheere–Terpstra test was employed to examine trends in AET from first to third molars; maxillary and mandibular rows were tested separately for each species. This test was also employed to examine the significance of trends in AET and the latitude of each species’ northernmost distribution; tests were run for each maxillary and mandibular molar position separately. We used the Jonckheere–Terpstra test because the number of species was not sufficient for regression analyses. Statistical tests were performed with SPSS software (v. 21, IBM Corp.).

RESULTS

Average enamel thickness (AET) and RET values are given in Table 3. Comparisons of maxillary and mandibular molars revealed a number of significant differences in the components of enamel thickness indices (enamel cap area, dentine area, and enamel-dentine junction length) (Table 4). These differences were largely because of greater values in maxillary teeth, except for RET in *M. mulatta* first molars and enamel-dentine junction length in *M. nemestrina* second molars, which showed greater values in mandibular teeth. The Jonckheere–Terpstra test showed a significant increasing trend in

TABLE 4. Results of Mann–Whitney U tests for comparisons of enamel thickness components and indices between maxillary and mandibular molars

Tooth	Species	Stat	c	e	AET	b	RET
M1	<i>M. arctoides</i>	Z	-1.641	-2.064	-0.900	-2.699	-1.429
		P value	0.114	0.042	0.408	0.005	0.174
	<i>M. fascicularis</i>	Z	-1.133	-1.335	-0.579	-2.367	-1.410
		P value	0.257	0.182	0.562	0.018	0.158
	<i>M. fuscata</i>	Z	-1.698	-2.049	-1.054	-3.513	-1.464
		P value	0.096	0.042	0.312	0.000	0.154
	<i>M. mulatta</i>	Z	-3.555	-3.950	-2.021	-4.497	-2.340
		P value	0.000	0.000	0.042	0.000	0.019
	<i>M. nemestrina</i>	Z	-1.723	-0.926	-1.672	-1.800	-0.463
		P value	0.085	0.374	0.095	0.076	0.667
	<i>M. sylvanus</i>	Z	-1.701	-0.945	-1.231	-1.701	-0.378
		P value	0.109	0.412	0.230	0.109	0.788
M2	<i>M. arctoides</i>	Z	-0.694	-0.694	-1.504	-0.231	-0.810
		P value	0.536	0.536	0.152	0.867	0.463
	<i>M. fascicularis</i>	Z	-0.396	-1.188	-0.603	-1.188	-0.396
		P value	0.708	0.245	0.563	0.245	0.708
	<i>M. fuscata</i>	Z	-2.171	-1.252	-1.933	-3.216	-1.220
		P value	0.030	0.219	0.052	0.001	0.232
	<i>M. mulatta</i>	Z	-0.230	-0.551	-0.781	-1.287	-1.562
		P value	0.839	0.603	0.454	0.210	0.125
	<i>M. nemestrina</i>	Z	-0.054	-2.176	-0.734	-0.761	-0.761
		P value	0.979	0.030	0.470	0.470	0.470
	<i>M. sylvanus</i>	Z	-0.735	-0.245	-0.980	-0.490	-1.225
		P value	0.556	0.905	0.413	0.730	0.286
M3	<i>M. arctoides</i>	Z	-0.160	-0.801	-0.641	-0.160	-0.641
		P value	0.937	0.485	0.589	0.937	0.589
	<i>M. fascicularis</i>	Z	-0.352	-1.197	-0.035	-1.479	-1.127
		P value	0.756	0.251	0.973	0.152	0.282
	<i>M. fuscata</i>	Z	-0.210	-0.315	-0.053	-1.680	-1.050
		P value	0.878	0.798	0.959	0.105	0.328
	<i>M. mulatta</i>	Z	-0.244	-1.543	-0.731	-1.705	-1.543
		P value	0.876	0.149	0.530	0.106	0.149
	<i>M. nemestrina</i>	Z	-0.831	-1.086	-0.319	-0.064	-0.064
		P value	0.456	0.318	0.805	1.000	1.000
	<i>M. sylvanus</i>	Z	-0.577	-0.577	-0.581	-0.289	-0.866
		P value	0.686	0.686	0.686	0.886	0.486

c, area of enamel cap; e, enamel-dentine junction length; AET, average enamel thickness; b, area of coronal dentine; RET, relative enamel thickness. Significant differences are in bold.

AET from first to the third molars in both maxillary and mandibular rows of all species ($p < 0.01$). Therefore tooth row and type were examined separately in analyses of sex and species-level differences. Comparisons of known-sex individuals revealed no significant intraspecific sexual dimorphism in AET or RET values (Table 5). In several instances males showed significantly greater enamel-dentine junction length and dentine area. Given that AET and RET did not significantly differ between sexes, all samples were subsequently combined to assess differences between macaque species.

Both AET and RET differed significantly among species for all tooth positions (Tables 6 and 7), although fewer significant differences were found in comparisons of third molars, which was likely due to insufficient statistical power from limited sample sizes. The most marked differences in AET were found between species that showed the lowest AET (*M. fascicularis* and *M. nemestrina*) and those that showed the highest AET (*M. sylvanus* and *M. fuscata*) (Fig. 2). The Jonckheere–Terpstra test revealed a significant increasing trend in AET with the latitude of northernmost species’ distributions for each maxillary and mandibular molar position ($p < 0.001$) (Fig. 3). Comparisons of RET revealed different interspecific trends than comparisons of AET, due in part to the relatively thin enamel in *M. arctoides* and

the relatively thick enamel of *M. fascicularis* (Fig. 4). *Macaca fuscata* showed the relatively thickest enamel of all six species.

DISCUSSION

Enamel thickness patterns in macaques and other primates

Enamel thickness patterns within the macaque dentition were similar in many ways to hominoid patterns (Smith et al., 2005, 2006, 2008, 2012b). Maxillary molars typically showed greater values for the components of enamel thickness than did mandibular molars. This is reflective of tooth size patterns, as macaque maxillary molars have larger buccal-lingual dimensions than do mandibular molars (Swindler, 2002). Similarly, a significant trend of increasing AET values from first to third molars has now been documented in macaques, great apes, and humans, which is due to increases in enamel cap area and/or reductions in enamel-dentine junction length. Our data do not support the idea that increasing enamel thickness in posterior molars is due to reduction in tooth size (Grine, 2005; Grine et al., 2005), as macaques show increases in both enamel thickness and tooth size from first to third molars. Considerable debate exists about the biomechanical significance of this

TABLE 5. Results of Mann–Whitney *U* tests for comparisons of enamel thickness components and indices between sexes

Tooth	Species	Stat	c	e	AET	b	RET
UM1	<i>M. fascicularis</i>	<i>Z</i>	-0.569	-0.569	-0.604	-0.569	-0.213
		<i>P value</i>	0.602	0.602	0.554	0.602	0.862
	<i>M. fuscata</i>	<i>Z</i>	-0.575	-0.575	-1.086	-0.703	-1.597
		<i>P value</i>	0.620	0.620	0.318	0.535	0.128
	<i>M. mulatta</i>	<i>Z</i>	-1.015	-0.486	-0.883	-0.486	-0.177
		<i>P value</i>	0.340	0.666	0.387	0.666	0.863
<i>M. nemestrina</i>	<i>Z</i>	-0.160	-1.281	-0.641	-0.480	-0.961	
	<i>P value</i>	0.937	0.240	0.589	0.699	0.394	
UM2	<i>M. arctoides</i>	<i>Z</i>	-0.577	-0.577	-0.577	-1.155	-0.577
		<i>P value</i>	0.686	0.686	0.686	0.343	0.686
	<i>M. fascicularis</i>	<i>Z</i>	-0.688	-1.852	-0.370	-2.382	-1.323
		<i>P value</i>	0.536	0.071	0.758	0.016	0.210
	<i>M. fuscata</i>	<i>Z</i>	-0.413	-1.321	-0.620	-2.477	-1.569
		<i>P value</i>	0.717	0.206	0.545	0.012	0.129
<i>M. mulatta</i>	<i>Z</i>	-0.387	-0.258	-0.129	-0.904	-0.645	
	<i>P value</i>	0.755	0.852	0.950	0.414	0.573	
UM3	<i>M. fascicularis</i>	<i>Z</i>	-0.853	-1.492	-0.426	-1.279	-0.426
LM1	<i>M. arctoides</i>	<i>Z</i>	-1.715	-1.715	-0.735	-0.980	-1.470
		<i>P value</i>	0.111	0.111	0.556	0.413	0.190
<i>M. fascicularis</i>	<i>Z</i>	-1.470	-1.796	-0.858	-1.061	-0.653	
	<i>P value</i>	0.156	0.079	0.400	0.315	0.549	
<i>M. fuscata</i>	<i>Z</i>	-0.731	-1.358	-0.313	-1.776	-0.940	
	<i>P value</i>	0.548	0.222	0.841	0.095	0.421	
<i>M. mulatta</i>	<i>Z</i>	-0.927	-0.309	-0.795	-0.927	-0.486	
	<i>P value</i>	0.387	0.796	0.436	0.387	0.666	
<i>M. nemestrina</i>	<i>Z</i>	-0.522	-0.313	-0.104	-0.104	-0.104	
	<i>P value</i>	0.690	0.841	1.000	1.000	1.000	
LM2	<i>M. fascicularis</i>	<i>Z</i>	-0.840	-2.100	-0.315	-1.575	-1.155
		<i>P value</i>	0.442	0.038	0.798	0.130	0.279
<i>M. fuscata</i>	<i>Z</i>	-0.674	-0.192	-0.241	-0.577	-0.962	
	<i>P value</i>	0.541	0.888	0.815	0.606	0.370	
<i>M. mulatta</i>	<i>Z</i>	-0.645	-0.904	-0.516	-1.291	-0.129	
	<i>P value</i>	0.573	0.414	0.662	0.228	0.950	
LM3	<i>M. fascicularis</i>	<i>Z</i>	-0.980	0.000	-1.225	-0.735	-0.490
		<i>P value</i>	0.413	1.000	0.286	0.556	0.730

See Table 4 legend for explanation of tooth positions and components. Significant differences are in bold. Statistical tests were not applied for sample sizes less than four (which are not shown).

pattern in primates, which is explored further in Schwartz (2000), Grine (2005), Grine et al. (2005) and Mahoney (2010, 2013).

The lack of significant sex differences in AET or RET within macaque species differed from orangutans and humans, where females showed greater AET and/or RET values than males (Smith et al., 2006; Feeney et al., 2010; Smith et al., 2012b). However, macaque females typically had smaller enamel-dentine junction length and dentine area values, resulting in nonsignificantly greater enamel thickness indices. Given that several macaque species show sex differences in molar tooth size, particularly in buccal-lingual dimensions (Swindler, 2002), an expanded sample may reveal significant sex differences.

The current study represents the largest analysis of molar enamel thickness within a nonhuman primate genus. Gantt (1977) first examined enamel thickness in 43 molar teeth from four macaque species (*Macaca cyclopis*, *M. fascicularis*, *M. mulatta*, and *M. nemestrina*), concluding that enamel thickness does not significantly differ among macaque species. In contrast, we found numerous significant differences between species, particularly in comparisons of first and second molars (for which sample sizes were the largest). Differences were detected most often between the species with the least

and greatest AET, *M. fascicularis* and *M. fuscata*, respectively, but significant differences were also found between all species pairs for one or more molar positions (save for comparisons of *M. arctoides* and *M. nemestrina*). These patterns are explored in relation to frequently-invoked functional hypotheses in the following section.

Gantt (1977) also hypothesized that differences in enamel thickness among macaque species may be expected given differences in body mass. While size may partially explain differences in AET between *M. fascicularis* and *M. fuscata*, comparisons of AET in the similarly-sized species *M. arctoides* and *M. fuscata* revealed significant differences for each molar position (Table 6). Martin (1983) originally proposed the dimensionless RET index for comparisons among different-sized primates represented by isolated teeth (where body mass was unknown) (Smith et al., 2005). After finding a positive association between molar dentine area and body mass in hominoids, he scaled AET by the square root of dentine area to yield the RET index. Dumont (1995) subsequently examined the relationship between the components of enamel thickness and body mass, and concluded that Martin's RET index "eliminates some, although not all, of the size component inherent in measurements of enamel volume" (p. 1133). Grine (2005)

TABLE 6. Results of Mann-Whitney U test for comparisons of average enamel thickness between species

	M1						M2						M3					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
M1 <i>M. arctoides</i>	-2.269*	-3.059***	-2.804**	-0.224	-2.236*	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. fascicularis</i>	-2.750**	-4.885***	-5.282***	-3.570***	-3.772***	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. fuscata</i>	-3.674**	-4.400***	-2.532**	-3.952***	-2.313*	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. mulatta</i>	-3.292***	-5.147***	-3.844***	-0.752	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. nemestrina</i>	-0.071	-2.200*	-3.956***	-3.536***	-2.537*	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. sylvanus</i>	-2.315*	-3.100***	-2.336*	-0.724	-2.183*	-	-	-	-	-	-	-	-	-	-	-	-	-
M2 <i>M. arctoides</i>	-	-	-	-	-	-	-2.796**	-3.718***	-1.775	-1.413	-2.781*	-	-	-	-	-	-	-
<i>M. fascicularis</i>	-	-	-	-	-	-	-2.509*	-4.685***	-4.010***	-1.528	-3.173***	-	-	-	-	-	-	-
<i>M. fuscata</i>	-	-	-	-	-	-	-3.653***	-3.844***	-4.586***	-1.102	-	-	-	-	-	-	-	-
<i>M. mulatta</i>	-	-	-	-	-	-	-3.172***	-2.144*	-2.888**	-2.563*	-	-	-	-	-	-	-	-
<i>M. nemestrina</i>	-	-	-	-	-	-	-0.803	-1.373	-4.340***	-3.600***	-3.105***	-	-	-	-	-	-	-
<i>M. sylvanus</i>	-	-	-	-	-	-	-1.89	-2.687**	-1.075	-2.304*	-	-	-	-	-	-	-	-
M3 <i>M. arctoides</i>	-	-	-	-	-	-	-	-	-	-	-	-2.715**	-2.582**	-0.365	-0.93	1.288	-	-
<i>M. fascicularis</i>	-	-	-	-	-	-	-	-	-	-	-	-2.061*	-3.470***	-2.778**	-2.401*	-2.877**	-	-
<i>M. fuscata</i>	-	-	-	-	-	-	-	-	-	-	-	-3.098***	-2.662***	-2.342*	-2.893**	-0.679	-	-
<i>M. mulatta</i>	-	-	-	-	-	-	-	-	-	-	-	-1.571	-2.785**	-	-0.893	-0.984	-	-
<i>M. nemestrina</i>	-	-	-	-	-	-	-	-	-	-	-	-0.429	-3.125**	-1.981	-0.893	-2.462*	-	-
<i>M. sylvanus</i>	-	-	-	-	-	-	-	-	-	-	-	-2.132*	-1.868	-0.756	-2.268*	-	-	-

Legend: Species order is the same on both sides of the matrix (i.e., 1 = *M. arctoides*, 2 = *M. fascicularis*, 3 = *M. fuscata*, 4 = *M. mulatta*, 5 = *M. nemestrina*, and 6 = *M. sylvanus*). Upper right half, maxillary molars; lower left half, mandibular molars. Significance of Z score indicated as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 7. Results of Mann-Whitney U test for comparisons of relative enamel thickness between species

	M1						M2						M3					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
M1 <i>M. arctoides</i>	-3.415***	-3.506***	-3.498***	-2.014*	-2.492*	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. fascicularis</i>	-3.394***	-3.505***	-1.909	-2.012*	-0.714	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. fuscata</i>	-3.674**	-3.652***	-2.586**	-3.538***	-2.313*	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. mulatta</i>	-3.806***	-2.543*	-1.39	-3.844***	-1.474	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. nemestrina</i>	-0.924	-2.803*	-3.824***	-3.725***	-0.746	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. sylvanus</i>	-2.006	-0.468	-2.546**	-1.873	-0.97	-	-	-	-	-	-	-	-	-	-	-	-	-
M2 <i>M. arctoides</i>	-	-	-	-	-	-	-2.890**	-2.621**	-3.717***	-3.071***	-1.521	-2.489*	-	-	-	-	-	-
<i>M. fascicularis</i>	-	-	-	-	-	-	-3.461***	-3.703***	-3.375***	-0.873	-1.109	-1.606	-	-	-	-	-	-
<i>M. fuscata</i>	-	-	-	-	-	-	-3.059***	-2.104*	-1.627	-2.768**	-3.626***	-1.102	-	-	-	-	-	-
<i>M. mulatta</i>	-	-	-	-	-	-	-1.014	-2.125*	-3.764***	-3.086**	-2.888**	-0.926	-	-	-	-	-	-
<i>M. nemestrina</i>	-	-	-	-	-	-	-1.89	-0.179	-2.418*	-1.593	-1.334	-1.725	-	-	-	-	-	-
<i>M. sylvanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-1.508	-1.936	-0.913	-0.571	-1.066	-
M3 <i>M. arctoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-1.735	-1.404	-0.736	-0.589	-0.131	-
<i>M. fascicularis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-2.324*	-1.777	-1.903	-1.157	-0.679	-
<i>M. fuscata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-1.857	-0.39	-1.273	-0.893	-0.735	-
<i>M. mulatta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-0.714	-1.659	-2.430*	-1.597	-0.567	-
<i>M. nemestrina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-1.066	-0.99	-2.378*	-0.756	-0.567	-
<i>M. sylvanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

See Table 6 legend for explanation of species order, tooth positions, and significance of Z scores.

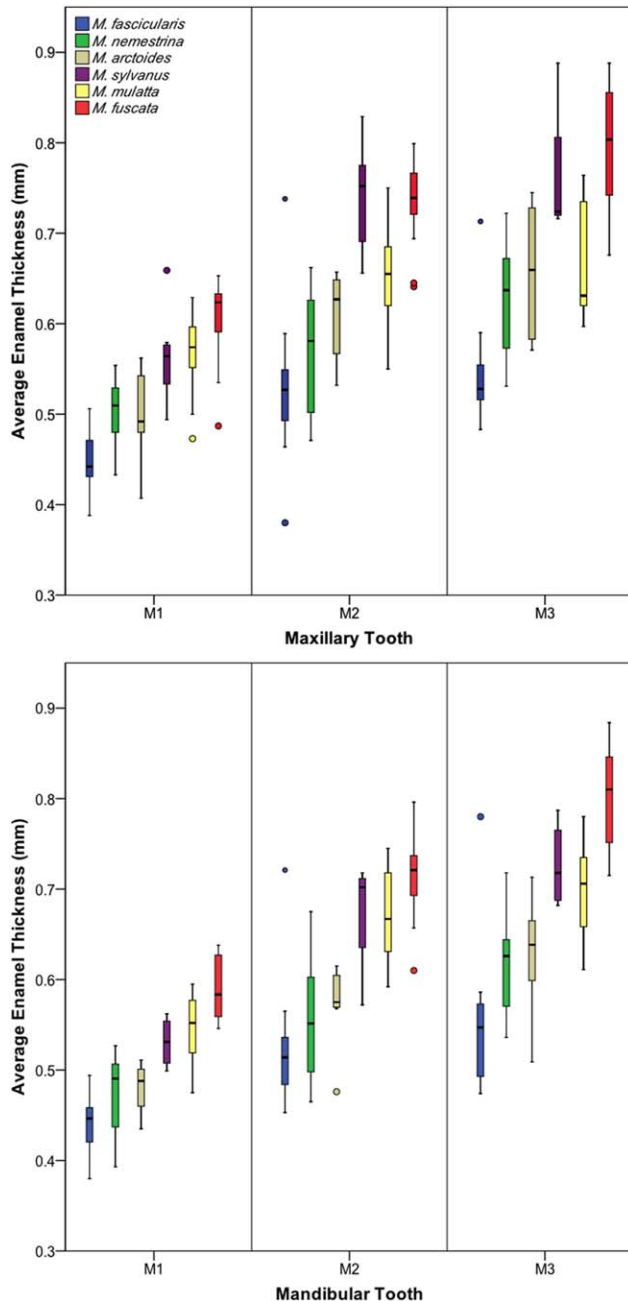


Fig. 2. Average enamel thickness in the molars of six macaque species. Species in order of increasing mean latitude of northernmost distributions. Standard box and whisker plot revealing the interquartile range (25th–75th percentiles: bars), 1.5 interquartile ranges (whiskers), and the median values (black line). Outliers are signified by circles. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

advocated dividing AET by the bicervical width of the tooth, although this index showed nearly identical trends to RET. For the dataset presented here, comparisons of AET between similarly-sized species and comparisons of RET between different-sized species revealed numerous significant differences, indicating that enamel thickness variation among macaque species is not solely due to differences in body mass.

The six macaque species examined in this study show a range of RET values that overlap with “thin” and

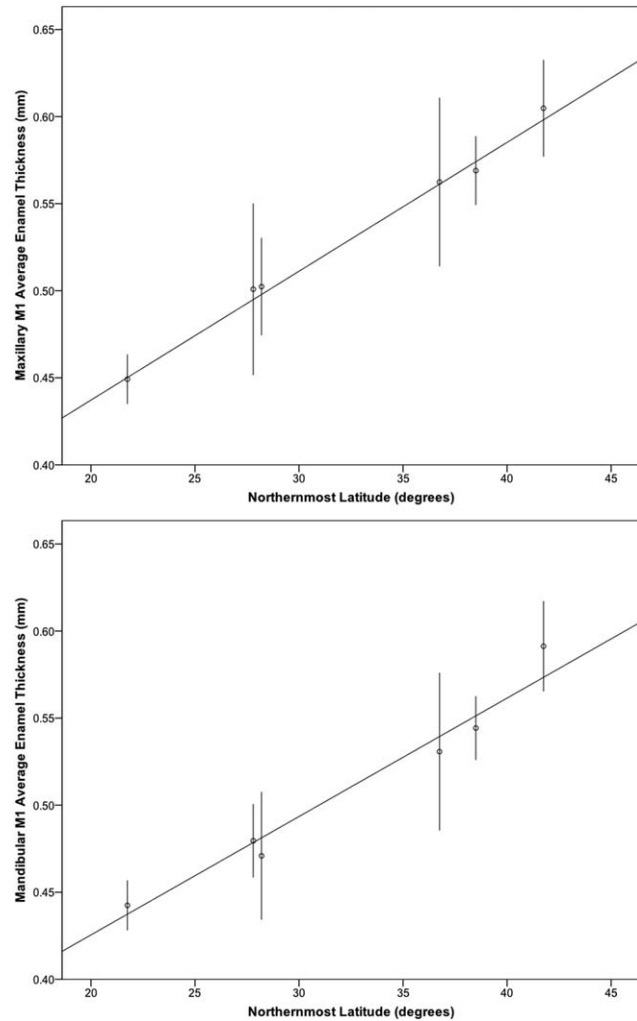


Fig. 3. Relationship between first molar average enamel thickness and northernmost latitude. Vertical lines represent 95% confidence intervals and circles represent mean values. Note the two species that fall at 28° latitude are artificially offset by $\pm 0.2^\circ$ (as they would otherwise overlap completely). The regression line refers to the original condition (both species at 28°). See Tables 1 and 3 for individual species' values.

“intermediate-thick” hominoids *Pan*, *Gorilla*, and *Pongo* (Martin, 1983; Smith et al., 2005, 2008, 2012b), but are on average distinctively thinner than *Homo sapiens* and most fossil hominins (Grine and Martin, 1988; Grine, 2005; Smith et al., 2006, 2012a). Cercopithecines are known to show RET values that span all of Martin's (1985) quantitative enamel thickness categories (Dumont, 1995; Ulhaas et al., 1999; Olejniczak et al., 2008b; McGraw et al., 2012; this study). Martin (1983) originally suggested that hominoid molar RET values reflected phylogenetic relationships, which has been called into question by genetic evidence (Ruvolo, 1997) and subsequent studies of enamel thickness (e.g., Smith et al., 2003, 2005, 2008). Whether closely-related macaques show more similar RET values than distantly-related species remains an empirical question, although unfortunately the number of species employed here are insufficient for phylogenetic analyses (e.g., Nunn, 2011).

Evolutionarily, *M. sylvanus* is believed to be the first species to diverge within the macaque lineage around

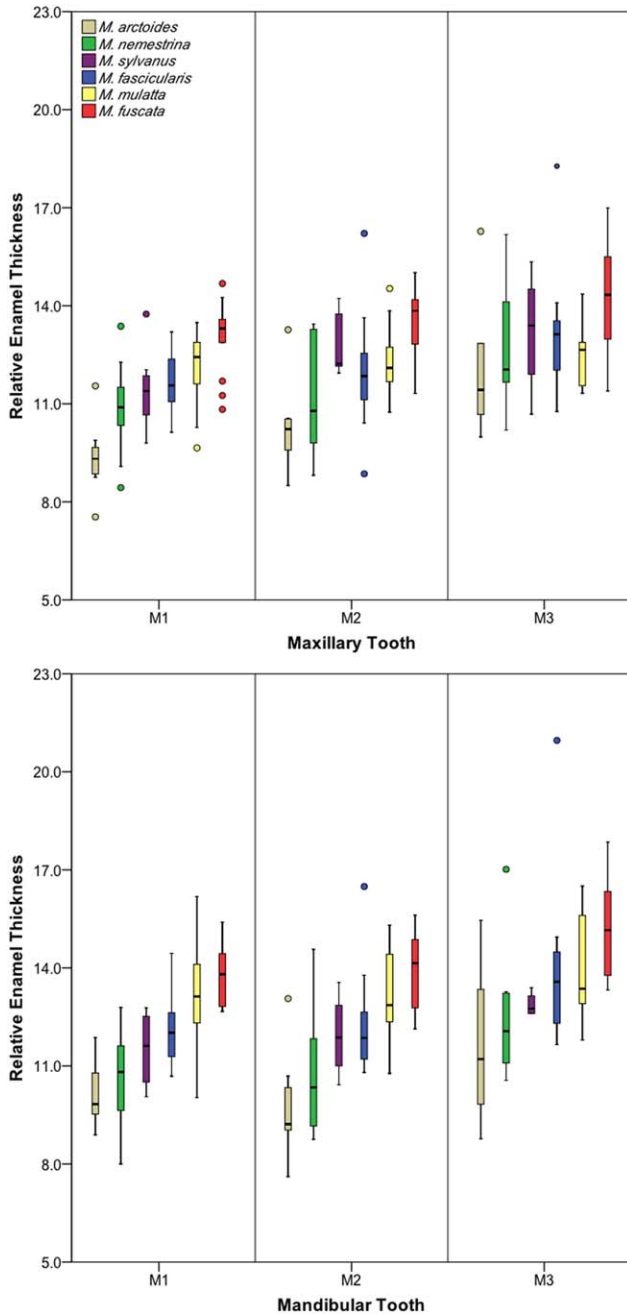


Fig. 4. Relative enamel thickness (RET) in the molars of six macaque species. Species in order of increasing RET values. See Figure 2 for description of graph. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

five million years ago, which was subsequently followed by the divergence of the “silenus group,” including *M. nemestrina* (Delson, 1980; Fooden, 1980; Fa, 1989; Tosi et al., 2000, 2003; Ziegler et al., 2007; Li et al., 2009). The relationships of the remaining four species in this study have been variably reconstructed, although *M. mulatta* and *M. fuscata* are generally considered to be the most closely related (Fa, 1989; Li et al., 2009: Fig. 2, p. 245). These evolutionary relationships are not consistently supported by RET patterns (Table 7, Fig. 4). *Macaca arctoides* had the thinnest RET of all six species

and is most similar to *M. nemestrina*, which would not be expected given its closer relationship to *M. fascicularis*, *M. mulatta*, and *M. fuscata* than to *M. nemestrina* and *M. sylvanus*. *Macaca mulatta* and *M. fuscata* did cluster together (along with *M. fascicularis*), but showed significantly different RET values for maxillary first and second molars. Although our preliminary results are consistent with the lack of phylogenetic signals in hominoid enamel thickness values, the inclusion of additional macaque species would provide further clarification.

Macaque dietary ecology and enamel thickness

Available data on macaque dietary intake and enamel thickness are not consistent with studies that suggest that thick enamel is an adaptation to protect teeth from fracture during feeding on hard objects as either a preferred or fallback food (Dumont, 1995; Lambert et al., 2004; Vogel et al., 2008; Constantino et al., 2009; Harrison and Marshall, 2011; McGraw et al., 2014). *Macaca fuscata* had the absolutely thickest enamel of our six species, but the wild population that is most ecologically similar to our sample did not consume a high proportion of foods generally characterized as “hard objects”; nuts, seeds, or pods (Agetsuma, 1995; Agetsuma and Nakagawa, 1998; Hanya, 2004; Tsuji et al., 2013). In contrast, *Macaca sylvanus*, the highest consumer of seeds and pods among species considered here, had significantly lower AET than *M. fuscata* for maxillary and mandibular first molars (despite being the largest species in this study). Consistent with the macaques, AET trends in orangutan species do not fully conform to ecological predictions (Smith et al., 2012b). Although Bornean orangutans are believed to consume more mechanically demanding foods than Sumatran orangutans, only comparisons between females revealed significant differences in AET. However, an important caveat is that data on food material properties are needed in order to directly test the hypothesized relationship between thick enamel and hard-object feeding (e.g., Lambert et al., 2004; Vogel et al., 2008; McGraw et al., 2014). For example, Vogel et al. (2008) demonstrated that the material properties of foods consumed by chimpanzees and orangutans differed as expected based on enamel thickness; thicker-enameled orangutans consumed tougher and harder foods than thinner-enameled chimpanzees.

Others have suggested that thick enamel may be an adaptive response to resist tissue loss due to abrasion (e.g., Jolly, 1970; Rabenold and Pearson, 2011; Pampush et al., 2013). Pampush et al. (2013) recently suggested that primate enamel thickness may reflect both phytolith load and the “functional life of a tooth.” However if both longevity and diet are driving enamel thickness, then the increasing pattern of AET from first to third molars is counterintuitive. First molars erupt several years before third molars (Smith et al., 1994), and are subjected to the greatest amount of attrition within the molar row. If abrasion resistance is the primary selective agent driving the evolution of thick enamel, first molars should show the absolutely thickest enamel of the molar row rather than third molars. Irrespective of this, direct assessment of the hypothesized relationship between enamel thickness and abrasion requires knowledge of dietary phytolith load and exogenous grit. Published reports on macaque diets are unsuitable for phytolith load assessment as they rarely specify the genus and species of particular food items, nor the part of the plant

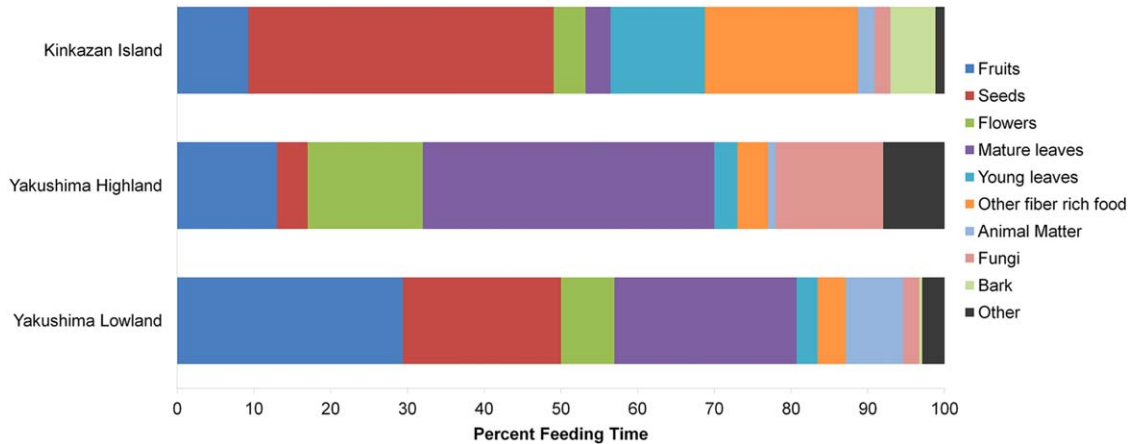


Fig. 5. Percentage of annual feeding time spent on major food categories in three populations of unprovisioned *Macaca fuscata*. Kinkazan Island data from Agetsuma and Nakagawa (1998) (minus September), Yakushima highland data from Hanya (2004), and Yakushima lowland data from Agetsuma and Nakagawa (1998) (minus January and July).

consumed, or the proportion of the total diet a specific item represents. Moreover, information on phytolith load is often only available at the family level, which can be highly variable (Piperno, 1988, 2006), and may bias the quantification of overall phytolith load.

Finally, the results of this study are not consistent with the hypothesis that thin enamel is indicative of a folivorous diet (contra Kay, 1985; Vogel et al., 2008), as the two species with the absolutely thinnest enamel, *M. nemestrina* and *M. fascicularis*, were characterized by the lowest degree of folivory. *Macaca fuscata* and *M. sylvanus*, two species with a higher degree of folivory, showed greater AET than *M. nemestrina* and *M. fascicularis*. *Macaca mulatta* has previously been characterized as highly folivorous (Goldstein and Richard, 1989), but this assessment is based on feeding data from an area that has been highly disturbed by humans. While we acknowledge that considerable variation in diet composition may exist among wild, unprovisioned populations within a species (Fig. 5), our data underscore the need for future studies of enamel thickness, feeding behavior, food mechanics, and phytolith load of dietary items within populations to conclusively determine the adaptive significance of primate enamel thickness.

Enamel thickness and geographic distribution

Enamel thickness in the six species included in this study showed a significant increasing trend between AET and geographic distribution. The species with the lowest AET (*M. fascicularis*) has the southernmost distribution, while the species with greatest AET (*M. fuscata*) has the northernmost distribution (Fig. 3). Moreover, the three species found in more temperate or seasonal environments (*M. fuscata*, *M. sylvanus*, and *M. mulatta*) have thicker enamel than the remaining three tropical species. This may be due to the greater breadth of dietary items consumed in temperate environments (Supporting Information Fig. 2), and/or the reliance on mechanically demanding foods during particular seasons (Andrews and Martin, 1991; van Schaik et al., 1993; Hemingway and Bynum, 2005; Tsuji et al., 2013). In a recent comparison of Asian temperate and tropical forests, Hanya et al. (2013) reported that temperate environments have more predictable fruiting and flushing

peaks than tropical environments, but flushing periods were relatively short, necessitating dependence on “low-quality foods” (mature leaves, buds, bark, and/or lichens) during other times of the year.

Temperate climate macaques such as *M. fuscata* show considerable seasonal variation, feeding on fruit and seeds during the spring, summer and fall, and mature leaves, buds and bark during the winter (Hanya, 2004). *Macaca fuscata* has also been reported to dig up underground plant parts during the winter and early spring (Iguchi and Izawa, 1990). *Macaca sylvanus* resides in temperate areas with comparatively few fleshy fruits, such as the evergreen and deciduous oak mountain ranges of Algeria and the cedar forests of Morocco, where structures such as acorns and cones protect seeds (Ménard and Vallet, 1986), and seasonal diet shifts are pronounced (Ménard et al., 2014). However, Fa (1984) suggested that the current North African habitat of *M. sylvanus* may not be reflective of preferred or historic habitats, which may be a reason that *M. sylvanus* does not show thicker molar enamel given its current reliance on seeds and pods. In contrast, macaques in tropical rainforest habitats (Thailand, Malaysia, Sumatra, Java, Borneo) such as *M. nemestrina* and *M. fascicularis* may consume fruit year-round. For example, a *M. fascicularis* troop in eastern Borneo was reported to feed almost exclusively on fruit (87%) throughout 18 months of investigation (Wheatley, 1980).

Macaques are characterized by a remarkable degree of adaptability among primates, as evidenced by their widespread geographic variation and diverse habitat use, eclipsed only by that of living and fossil *Homo*. Identification of species-typical macaque diets has been complicated by extensive environmental variation, as well as anthropogenic influences on geography and ecology (e.g., Fooden, 1971; Rodman, 1978; Aldrich-Blake, 1980; Fooden, 1982; Goldstein, 1984; Caldecott, 1986a,b; Richard et al., 1989; Chapman and Chapman, 1990; Fooden, 1990; Ménard, 2004; Hanya et al., 2011; Ménard et al., 2014). Certain macaques have been characterized as “weed species” that prefer to live near human habitations or in disturbed environments (Richard et al., 1989). We note that while the positive trend in AET and latitude appears to be robust in the macaques included in this study, additional investigation is needed to

determine if a similar trend exists in other primate taxa. For example, differences in enamel thickness were not detected in most comparisons of fossil orangutans from mainland Asia versus those from Indonesia (Smith et al., 2011). Similarly, Neanderthals inhabited some of the most extreme northern-most environments among fossil hominins, yet show the thinnest enamel of all fossil *Homo* species (Smith et al., 2012a).

SUMMARY

Although reported dietary intake may be an imperfect solution for testing functional explanations of enamel thickness, especially in the absence of comprehensive information on the mechanical properties of ingested foods, such approaches are common in the literature (e.g., Kay, 1981; Andrews and Martin, 1991; Dumont, 1995; Constantino et al., 2009; McGraw et al., 2012). We evaluated AET and RET among six *Macaca* species in conjunction with information available on diet to explore the extent to which they were consistent with established functional hypotheses. Enamel thickness across the genus *Macaca* did not vary as would be expected if abrasive tissue loss, degree of folivory, or inferences of hard-object feeding of preferred or fallback foods served as strong selective pressures. These preliminary findings remain speculative and do not allow us to reject or support any functional hypotheses. This is because an integral component of their evaluation necessarily requires a better understanding of mechanical properties of macaque diets. Importantly, enamel thickness was strongly associated with geographic distribution; macaque species in temperate environments had thicker enamel than did macaque species with tropical distributions. Taken together these findings suggest that aspects of diet across seasons in temperate regions are likely associated with functional properties of tooth enamel in as yet unknown ways. Geographic distribution may serve as a useful proxy of such phenomena not currently captured by the paucity of systematic dietary information in the literature. Until more robust data are available to test such hypotheses further, extrapolations from enamel thickness values are unlikely to provide direct or precise information of dietary preferences in genera that exhibit marked ecological flexibility such as *Macaca* or *Homo*.

ACKNOWLEDGMENTS

The authors thank the following individuals for access to skeletal material, assistance with micro-CT scanning, and assistance with data collection: Jasmine Casart, Judy Chupasko, Allison Cleveland, Daniel Green, Eleanor Hoeger, Satoshi Kazama, T. Fettah Kosar, Joyce Sirianni, and Paul Tafforeau. Kate Carter, Andreas Koenig, Zarin Machanda, Charlie Nunn, and David Pilbeam provided helpful discussions of this project. Naoki Agetsuma and Naofumi Nakagawa are acknowledged for providing unpublished data. They appreciate the efforts of Peter Ellison, the Associate Editor, and several reviewers for their constructive comments on this manuscript.

LITERATURE CITED

- Agetsuma N. 1995. Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *Int J Primatol* 16:595-609.
- Agetsuma N, Nakagawa N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* 39:275-289.
- Aggimarangsee N. 1992. Survey for semi-tame colonies of macaques in Thailand. *Nat His Bull Siam Soc* 40:103-166.
- Ahsan MF. 1994. Feeding ecology of the primates of Bangladesh. *Curr Primatol* 1:79-86.
- Alba DM, Fortuny J, Moyà-Solà S. 2010. Enamel thickness in the Middle Miocene great apes *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*. *Proc R Soc B* 277:2237-2245.
- Aldrich-Blake FPG. 1980. Long-tailed macaques. In: Chivers DJ, editor. *Malayan forest primates: ten years' study in tropical rain forest*. New York: Plenum Press. p 147-165.
- Andrews P, Martin L. 1991. Hominoid dietary evolution. *Phil Trans R Soc Lond B* 334:199-209.
- Benazzi S, Douka K, Fornai C, Bauer CC, Kullmer O, Svoboda J, Pap I, Mallegni F, Bayle P, Coquerelle M, Condemi S, Ronchitelli A, Harvati K, Weber GW. 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479:525-528.
- Beynon AD, Dean MC, Leakey MG, Reid DJ, Walker A. 1998. Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *Am J Phys Anthropol* 35:163-209.
- Caldecott JO. 1986a. An ecological and behavioural study of the pig-tailed macaque. In: Szalay FS, editor. *Contributions to primatology*, Vol 21. Basel: Karger. p 1-259.
- Caldecott JO. 1986b. A summary of the ranging and activity patterns of the pig-tailed macaque (*Macaca n. nemestrina*) in relation to those of sympatric primates in peninsular Malaysia. In: Taub DM, King FA, editors. *Current perspectives in primate social dynamics*. New York: Van Nostrand Reinhold Company. p 152-158.
- Chapman CA, Chapman LJ. 1990. Dietary variability in primate populations. *Primates* 31:121-128.
- Chivers DJ, Hladik CM. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J Morphol* 166:337-386.
- Clutton-Brock TH, Harvey PH. 1977. Species differences in feeding and ranging behavior in primates. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes*. London: Academic Press. p 557-584.
- Constantino PJ, Lee JJ-W, Morris D, Lucas PW, Hartstone-Rose A, Lee W-K, Dominy NJ, Cunningham A, Wagner M, Lawn BR. 2011. Adaptation to hard object feeding in sea otters and hominins. *J Hum Evol* 61:89-96.
- Constantino PJ, Lucas PW, Lee JJ-W, Lawn BR. 2009. The influence of fallback foods on great ape tooth enamel. *Am J Phys Anthropol* 140:653-660.
- Delson E. 1980. Fossil macaques phyletic relationships and a scenario of development. In: Lindburg, DG, editor. *The macaques: studies in ecology behavior and evolution*. Van Nostrand Reinhold Company: New York. p 10-30.
- Dumont ER. 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. *J Mammal* 76:1127-1136.
- Fa JE. 1984. The Barbary macaque. In: Fa JE, editor. *The Barbary macaque. A case study in conservation*. New York: Plenum Press. p 3-15.
- Fa JE. 1989. The genus *Macaca*: a review of taxonomy and evolution. *Mammal Rev* 19:45-81.
- Feehey RNM, Zermeno JP, Reid DJ, Nakashima S, Sano H, Bahar A, Hublin J-J, Smith TM. 2010. Enamel thickness in Asian human canines and premolars. *Anthropol Sci* 118:191-198.
- Fleagle JG. 2013. *Primate adaptation and evolution*. California: Academic Press.
- Fooden J. 1971. Report on primates collected in Western Thailand January-April, 1967. *Fieldiana Zool* 59:1-62.
- Fooden J. 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana Zool* 67:1-169.
- Fooden J. 1980. Classification and distribution of living macaques (*Macaca* Lacepede, 1799). In: Lindburg DG, editor. *The macaques: studies in ecology, behavior and evolution*. New York: Van Nostrand Reinhold. p 1-9.

- Fooden J. 1982. Ecogeographic segregation of macaque species. *Primates* 23:574–579.
- Fooden J. 1990. The bear macaque, *Macaca arctoides*: a systematic review. *J Hum Evol* 19:607–686.
- Fooden J. 1995. Systematic review of Southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, [1821]). *Fieldiana Zool* 81:1–206.
- Fooden J. 2000. Systematic review of the rhesus macaque, *Macaca mulatta* (Zimmermann, 1780). *Fieldiana Zool* 96:1–180.
- Fooden J. 2005. Systematic review of Japanese macaques, *Macaca fuscata* (Gray, 1870). *Fieldiana Zool* 104:1–200.
- Fooden J. 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). *Fieldiana Zool* 113:1–58.
- Gantt DG. 1977. Enamel of primate teeth: its structure with reference to functional and phyletic implications [dissertation]. Saint Louis: Washington University.
- Goldstein SJ. 1984. Feeding ecology of rhesus monkeys (*Macaca mulatta*) in northwestern Pakistan [dissertation]. New Haven: Yale University.
- Goldstein SJ, Richard AF. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int J Primatol* 10: 531–567.
- Grine FE. 2005. Enamel thickness of deciduous and permanent molars in modern *Homo sapiens*. *Am J Phys Anthropol* 126: 14–31.
- Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary history of the “robust” Australopithecines. New York: Aldine de Gruyter. p 3–42.
- Grine FE, Spencer MA, Demes B, Smith HF, Strait DS, Constant DA. 2005. Molar enamel thickness in the chacma baboon, *Papio ursinus* (Kerr, 1792). *Am J Phys Anthropol* 128:812–822.
- Hanya G. 2003. Age differences in food intake and dietary selection of wild male Japanese macaques. *Primates* 44:333–339.
- Hanya G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *Int J Primatol* 25:55–71.
- Hanya G, Ménard N, Qarro M, Tattou MI, Fuse M, Vallet D, Yamada A, Go M, Takafumi H, Tsujino R, Agetsuma N, Wada K. 2011. Dietary adaptations of temperate primates: comparisons of Japanese and Barbary macaques. *Primates* 52:187–198.
- Hanya G, Tsuji Y, Grueter CC. 2013. Fruiting and flushing phenology in Asian tropical and temperate forests: implications for primate ecology. *Primates* 54:101–110.
- Harrison ME, Marshall AJ. 2011. Strategies for the use of fallback foods in apes. *Int J Primatol* 32:531–565.
- Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP, editors. Primate seasonality: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 57–104.
- Hill DA. 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *Am J Primatol* 43:305–322.
- Horvath JE, Wu C, Toler M, Fedrigo O, Pfefferle LW, Moore A, Ramachandran GL, Babbitt CC, Jernvall J, Wray GA, Wall CE. 2012. Enamel thickness in *Microcebus murinus* and *Macaca mulatta* and the evolutionary genetics of enamel matrix proteins in hominoids. *Am J Phys Anthropol Suppl* 54: 168.
- Iguchi M, Izawa K. 1990. Research Report: Digging and eating of underground plant-parts by wild Japanese monkeys (*Macaca fuscata*). *Primates* 31:621–624.
- Isler K, Kirk EC, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J Hum Evol* 55:967–978.
- Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Kay RF. 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55:141–151.
- Kay RF. 1985. Dental evidence for the diet of Australopithecus. *Ann Rev Anthropol* 14:315–341.
- Khan MAR, Wahab MA. 1983. Study of eco-ethology of the crab-eating macaque, *Macaca fascicularis* in Bangladesh. *J Asiatic Soc Bangladesh* 9:101–109.
- Lambert JE. 1998. Primate digestion: Interactions among anatomy, physiology, and feeding ecology. *Evol Anthropol* 7:8–20.
- Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecines foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am J Phys Anthropol* 125:363–368.
- Li J, Han K, Xing J, Kim H-S, Rogers J, Ryder OA, Disotell T, Yue B, Batzer MA. 2009. Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on Alu elements. *Gene* 448:242–249.
- Lindburg DG. 1976. Dietary habits of rhesus monkeys (*Macaca mulatta* Zimmermann) in Indian forests. *J Bombay Nat Hist Soc* 73:261–279.
- Lindburg DG. 1977. Feeding behavior and diet of Rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in North India. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes. London: Academic Press. p 223–249.
- Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orang-utans with their teeth in captivity and a new technique for estimating forces produced in the wild. *Am J Phys Anthropol* 94:365–378.
- Mackiewicz P, Wiszniowska T, Olejniczak AJ, Stefaniak K, Socha P, Nadachowski A. 2010. Analysis of dental enamel thickness in bears with special attention to *Ursus spelaeus* and *U. wenzensis* (= *minus*) in comparison to selected representatives of mammals. In: Nowakowski D, editor. Morphology and systematics of fossil vertebrates. Wrocław: DN Publisher. p 60–77.
- Mahoney P. 2010. Two dimensional patterns of human enamel thickness on deciduous (dm1, dm2) and permanent first (M1) mandibular molars. *Arch Oral Biol* 55:115–126.
- Mahoney P. 2013. Testing functional and morphological interpretations of enamel thickness along the deciduous tooth row in human children. *Am J Phys Anthropol* 151:518–525.
- Martin LB. 1983. The relationships of the later Miocene Hominoidea [dissertation]. London: University College London.
- Martin LB. 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314:260–263.
- Martin LB, Olejniczak AJ, Maas MC. 2003. Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyanthropus*. *J Hum Evol* 45:351–367.
- McGraw WS, Pampush JD, Daegling DJ. 2012. Brief communication: enamel thickness and durophagy in mangabeys revisited. *Am J Phys Anthropol* 147:326–333.
- McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): implications for fallback foods and dental adaptation. *Am J Phys Anthropol* 154:413–423.
- Ménard N. 1985. Le regime alimentaire de *Macaca sylvanus* dans different habitats d’Algerie: I. Regime en chenaie decidue. *Rev Ecol (Terre Vie)* 40:451–466.
- Ménard N. 2004. Do ecological factors explain variation in social organization? In: Thierry B, Singh M, Kaumanns W, editors. Macaque societies: a model for the study of social organization. Cambridge: Cambridge University Press. p 237–262.
- Ménard N, Motsch P, Delahaye A, Saintvanne A, Le Flohic G, Dupé S, Vallet D, Qarro M, Ibn Tattou M, Pierre J-S. 2014. Effect of habitat quality on diet flexibility in Barbary macaques. *Am J Primatol* 76:679–693.
- Ménard N, Qarro M. 1999. Bark stripping and water availability: a comparative study between Moroccan and Algerian Barbary macaques (*Macaca sylvanus*). *Rev Ecol (Terre Vie)* 54: 123–132.
- Ménard N, Vallet D. 1986. Le regime alimentaire de *Macaca sylvanus* dans different habitats d’Algerie: II. Regime en foret sempervirente et sur les sommets rocheux. *Rev Ecol (Terre Vie)* 41:173–192.

- Molnar S, Gantt DG. 1977. Functional implications of primate enamel thickness. *Am J Phys Anthropol* 46:447–454.
- Nunn CL. 2011. *The comparative method in evolutionary anthropology and biology*. Chicago: University Chicago Press.
- Ojha PR. 1980. The Rhesus macaque: food freeing [sic] in desert [abstract]. *Antropologia Contemporanea* 3:249.
- Olejniczak AJ, Smith TM, Feeney RNM, Macchiarelli R, Mazurier A, Bondioli L, Rosas A, Fortea J, de la Rasilla M, Garcia-Taberner A, Radovic J, Skinner MM, Toussaint M, Hublin J-J. 2008b. Dental tissue proportions and enamel thickness in Neandertal and modern human molars. *J Hum Evol* 55:12–23.
- Olejniczak AJ, Tafforeau P, Feeney RNM, Martin LB. 2008a. Three-dimensional primate molar enamel thickness. *J Hum Evol* 54:187–195.
- Olejniczak AJ, Tafforeau P, Smith TM, Temming H, Hublin J-J. 2007. Technical note: compatibility of microtomographic imaging systems for dental measurements. *Am J Phys Anthropol* 134:130–134.
- Pampush JD, Duque AC, Burrows BR, Daegling DJ, Kenney WF, McGraw WS. 2013. Homoplasy and thick enamel in primates. *J Hum Evol* 64:216–224.
- Piperno DR. 1988. *Phytolith analysis: An archaeological and geological perspective*. London: Academic Press.
- Piperno DR. 2006. *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*. Oxford: AltaMira Press.
- Rabenold D, Pearson OM. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS ONE* 6: e28379. doi:10.1371/journal.pone.0028379.
- Richard AF, Goldstein SJ, Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. *Int J Primatol* 10:569–594.
- Richter C, Taufiq A, Hodges JK, Ostner J, Schülke O. 2013. Ecology of an endemic primate species (*Macaca siberu*) on Siberut Island, Indonesia. *SpringerPlus* 2:137.
- Rodman PS. 1978. Diets, densities, and distributions of Bornean Primates. In: Montgomery GG, editor. *The ecology of arboreal folivores*. Washington: Smithsonian Institution Press. p 465–478.
- Ruvolo M. 1997. Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* 14:248–265.
- Schwartz GT. 1997. Taxonomic and functional aspects of enamel cap structure in South African Plio-Pleistocene hominids: a high-resolution computed tomographic study. Ph.D. Dissertation, Washington University.
- Schwartz GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am J Phys Anthropol* 111:221–244.
- Sengupta A, McConkey KR, Radhakrishna S. Seed dispersal by rhesus macaques *Macaca mulatta* in northern India. *Am J Primatol*, in press.
- Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. *J Hum Evol* 35: 507–522.
- Shimizu D. 2002. Functional implications of enamel thickness in the lower molars of red colobus (*Procolobus badius*) and Japanese macaque (*Macaca fuscata*). *J Hum Evol* 43:605–620.
- Smith BH, Crummett TL, Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *Yearb Phys Anthropol* 37:177–231.
- Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *J Hum Evol* 32:523–559.
- Smith TM, Bacon A-M, Demeter F, Kullmer O, Nguyen KT, Vos J de, Wei W, Zermeno JP, Zhao L. 2011. Dental tissue proportions in fossil orangutans from mainland Asia and Indonesia. *Hum Origins Res* 1:e1. doi: 10.4081/hor.2011.e1.
- Smith TM, Kupczik K, Machanda Z, Skinner MM, Zermeno JP. 2012b. Enamel thickness in Bornean and Sumatran orangutan dentitions. *Am J Phys Anthropol* 147:417–426.
- Smith TM, Martin LB, Leakey MG. 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J Hum Evol* 44:283–306.
- Smith TM, Olejniczak AJ, Martin LM, Reid DJ. 2005. Variation in hominoid molar enamel thickness. *J Hum Evol* 48:575–592.
- Smith TM, Olejniczak AJ, Reh S, Reid DJ, Hublin J-J. 2008. Brief communication: enamel thickness trends in the dental arcade of humans and chimpanzees. *Am J Phys Anthropol* 136:237–241.
- Smith TM, Olejniczak AJ, Reid DJ, Ferrell RJ, Hublin J-J. 2006. Modern human molar enamel thickness and enamel-dentine junction shape. *Arch Oral Biol* 51:974–995.
- Smith TM, Olejniczak AJ, Zermeno JP, Tafforeau P, Skinner MM, Hoffmann A, Radović J, Toussaint M, Kruszynski R, Menter C, Moggi-Cecchi J, Glasmacher UA, Kullmer O, Schrenk F, Stringer C, Hublin J-J. 2012a. Variation in enamel thickness within the genus *Homo*. *J Hum Evol* 62:395–411.
- Smith TM, Tafforeau P, Reid DJ, Pouech J, Lazzari V, Zermeno JP, Guatelli-Steinberg D, Olejniczak AJ, Hoffman A, Radovic J, Makaremi M, Toussaint M, Stringer C, Hublin J-J. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proc Natl Acad Sci U S A* 107: 20923–20928.
- Suzuki A. 1965. An ecological study of wild Japanese monkeys in the snowy areas—focused on their food habits. *Primates* 6: 31–72.
- Swindler DR. 2002. *Primate dentition: an introduction to the teeth of non-human primates*. Cambridge: Cambridge University Press.
- Tosi AJ, Morales JC, Melnick DJ. 2000. Comparison of Y chromosome and mtDNA phylogenies leads to unique inferences of macaque evolutionary history. *Mol Phylogenet Evol* 17: 133–144.
- Tosi AJ, Morales JC, Melnick DJ. 2003. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution* 57:1419–1435.
- Tsuji Y, Fujita S, Sugiura H, Saito C, Takatsuki S. 2006. Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. *Am J Primatol* 68:1068–1080.
- Tsuji Y, Hanya G, Grueter CC. 2013. Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates* 54:201–215.
- Tsuji Y, Takatsuki S. 2004. Food habits and home range use of Japanese macaques on an island inhabited by deer. *Ecol Res* 19:381–388.
- Ulhaas L, Henke W, Rothe H. 1999. Variation in molar enamel thickness in genera *Cercopithecus* and *Colobus*. *Anthropologie* 37:265–271.
- Ungar PS. 1992. *Incisor microwear and feeding behavior of four sumatran anthropoids [dissertation]*. Stony Brook: State University of New York at Stony Brook.
- van Schaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *An Rev Ecol Sys* 24:353–377.
- Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol* 55:60–74.
- Wheatley BP. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: Lindburg DG, editor. *The macaques: studies in ecology, behavior and evolution*. New York: Van Nostrand Reinhold Company. p 215–246.
- Yeager CP. 1996. Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. *Int J Primatol* 17:51–62.
- Ziegler T, Abegg C, Meijaard E, Perwitasari-Farajallah D, Walter L, Hodges JK, Roos C. 2007. Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. *Mol Phylogenet Evol* 42:807–816.