



Developmental Aspects of Sexual Dimorphism in Hominoid Canines

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We examined the histology of canine teeth in extant hominoids and provided a comparative database on several aspects of canine development. The resultant data augment the known pattern of differences in aspects of tooth crown formation among great apes and more importantly, enable us to determine the underlying developmental mechanisms responsible for canine dimorphism in them. We sectioned and analyzed a large sample (n = 108) of reliably-sexed great ape mandibular canines according to standard histological techniques. Using information from long- and short-period incremental markings in teeth, we recorded measurements of daily secretion rates, periodicity and linear enamel thickness for specimens of Pan troglodytes, Gorilla gorilla, Pongo pygmaeus and Homo sapiens. Modal values of periodicities in males and females, respectively, are: Pan 7/7; Gorilla 9/10; Pongo 10/10; and Homo 8/8. Secretion rates increase from the inner to the outer region of the enamel cap and decrease from the cuspal towards the cervical margin of the canine crown in all great ape species. Female hominoids tend to possess significantly thicker enamel than their male counterparts, which is almost certainly related to the presence of faster daily secretion rates near the enamel-dentine junction, especially in Gorilla and Pongo. Taken together, these results

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indicate that sexual differences in canine development are most apparent in the earlier stages of canine crown formation, while interspecific differences are most apparent in the outer crown region. When combined with results on the rate and duration of canine crown formation, the results provide essential background work for larger projects aimed at understanding the developmental basis of canine dimorphism in extant and extinct large-bodied hominoids and eventually in early hominins.

KEY WORDS: canine dimorphism; dental development; incremental lines; periodicity; secretion rates; growth and development.

INTRODUCTION

Despite more than a century of research, researchers have pinpointed few clear differences in the details of dental development among living hominoid taxa (Keith, 1895, 1899; Zuckerman, 1928; Krogman, 1930; Schultz, 1935, 1940; Bennejeant, 1940; Nissen and Riesen, 1945, 1964; Clements and Zuckerman, 1953; Kraus and Jordan, 1965, 1969; Oka and Kraus, 1969; Tarrant and Swindler, 1972; Moxham and Berkovitz, 1974; Dean and Wood, 1981; Swindler, 1985; Anemone *et al.*, 1991, 1996; Siebert and Swindler, 1991; Kuykendall *et al.*, 1992; Smith, 1994; Smith *et al.*, 1994; Winkler, 1995; Kuykendall, 1996; Kuykendall and Conroy, 1996; Dirks, 1998; Reid *et al.*, 1998; Schwartz *et al.*, 2000). In part, this is due to the inaccessibility of large samples of reliably sexed individuals in museum collections. The exception is investigations on living chimpanzees (Nissen and Riessen, 1945, 1964; Kuykendall, 1996). Recently, more details have emerged that distinguish *Pan*, *Gorilla* and *Pongo* (Schwartz and Dean, 2000; Schwartz and Dean, submitted).

Differences among species and genera of hominoids are well-documented for many morphological features of the dentition: tooth size, tooth shape, occlusal morphology and enamel thickness. However, it is only with a detailed understanding of the ontogeny of dental development that underlying growth processes responsible for final tooth form will be determined. For instance, canine size and shape have long been used as distinguishing characters in hominoid taxonomy/phylogeny (Kelley and Xu, 1991; Kelley, 1995; Waddle *et al.*, 1995; Kelley and Plavcan, 1998), but we are just beginning to uncover developmental differences that help explain the mechanisms of morphological change with respect to models of canine growth (Schwartz and Dean, submitted). While we are coming closer to elucidating the precise cellular-level developmental mechanisms responsible for final tooth form (Jernvall *et al.*, 1994, 2000; Sharpe, 1995; Ferguson *et al.*, 2000; Jernvall and Thesleff, 2000), almost nothing is known about the degree

to which any feature associated with developing teeth differs between sexes within a species of extant large-bodied hominoid.

In this study, we provide new ontogenetic data bearing on tooth development and sexual dimorphism in hominoids. We compare several aspects of the ontogeny of canine development in a sample of reliably-sexed hominoid canines. We compare the microstructure of a single tooth type among all four hominoid taxa and relate the effects of sex on the pattern of canine growth.

Several microstructural details of enamel and dentine can be used to calculate the time and timing of tooth formation precisely. The regular, periodic secretion of these tissues results in long- and short-period incremental lines in enamel and dentine, which are clearly visible in polarized light microscopy. Despite the extensive use of these histological growth markers in studies of ape and human dental development, very little is known about the variation in these structures within and among hominoids. Moreover, no data are available to determine whether males and females of a species differ from each other with respect to any of these developmental features. In this respect, our study differs slightly from some earlier comparative dental developmental investigations: We focus on the histology of developing dental hard tissues to understand how they relate to, or in fact, contribute to, sexual dimorphism in adult canine size. As part of a larger study aimed at detailing the developmental mechanism responsible for the disparity in crown height between sexes in modern hominoids, we report on the variation in long-period striae periodicity and daily secretion rates in the enamel of extant hominoids and how they may relate to adult sexual dimorphism through canine growth. A further key objective is to document any differences in linear enamel thickness among and between sexed hominoid canines to determine the nature, if any, of the relationships among this variable, daily secretion rates and canine dimorphism.

BACKGROUND

Each of the three hard tissues that make up a tooth—(enamel, dentine and cementum)—grows incrementally. Histologically, one can view several sets of incremental markings in enamel and dentine (Owen, 1845; Andresen, 1898; von Ebner, 1902, 1906; Retzius, 1837). They can be grouped into two sets, which are visible via polarized light and confocal microscopy and occasionally in scanning electron microscopy (Fig. 1). Short-period lines are daily markings, including daily von Ebner's lines in dentine and daily cross-striations along enamel prisms. They represent the amount of enamel and dentine matrix produced by ameloblasts—(enamel-producing cells)—and

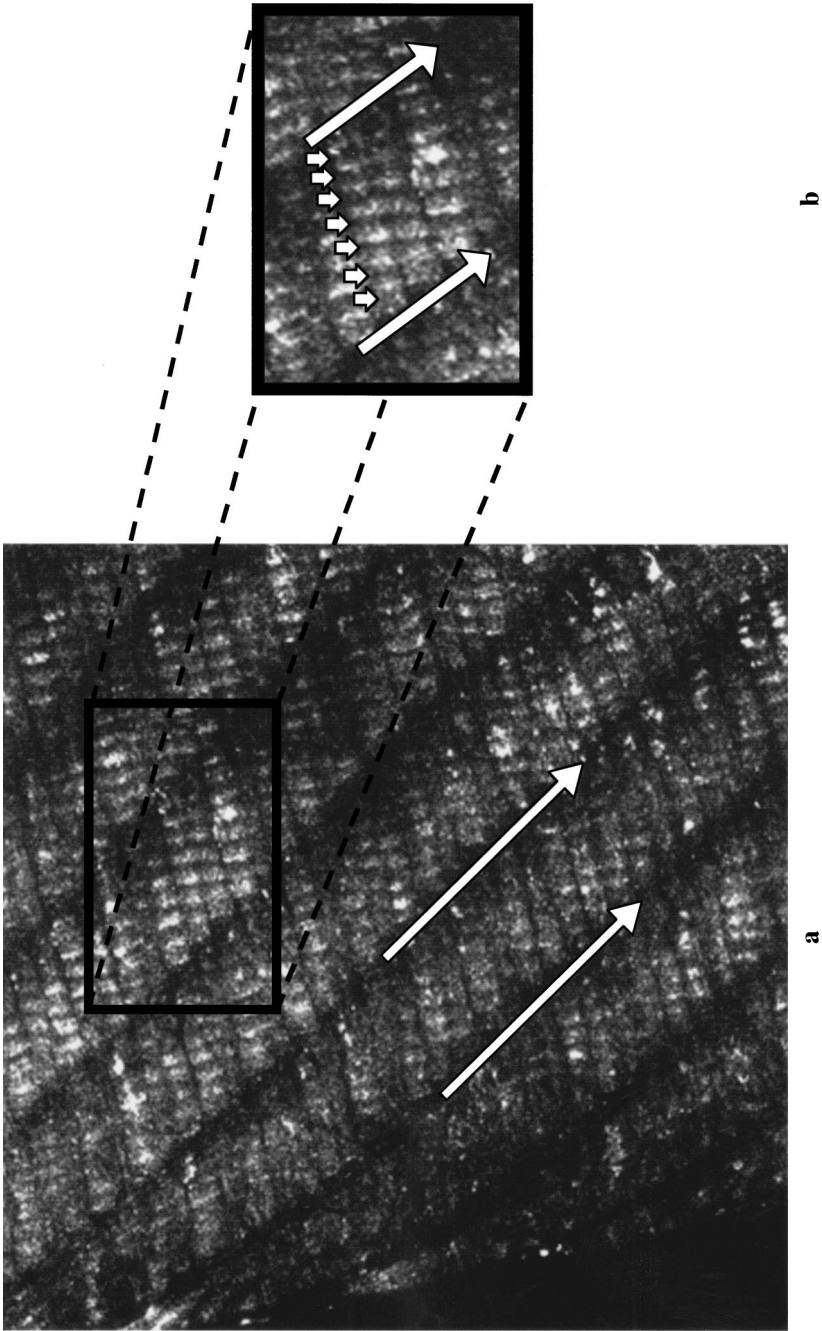


Fig. 1. a. Laser confocal micrograph of the lateral enamel in the anterior tooth of *Pongo pygmaeus*. Perikymata are to the left and are continuous with striae of Retzius internally (arrows). **b.** Detailed view of the outlines inset in Fig. 1a illustrating the daily cross—striations (small arrows) between adjacent Retzius lines (large arrows). In this specimen the periodicity is 8.

odontoblasts (dentine-producing cells). Long-period lines include Andresen lines in dentine and the regular striae of Retzius in enamel (Fig. 1a). The short-period lines (Fig. 1b) reflect the daily, or circadian, secretory cycle of enamel matrix and allow estimates of the linear daily secretion rate of enamel (the cross-striation repeat interval), i.e., the rate of enamel protein gene expression. It is both counts and measurements of these daily markings that are central to determine the precise timing of the onset of mineralization, the duration of crown formation, the rate of root growth and the overall pattern of dental development in hominoids. Though the etiology of some incremental lines are not completely understood, they have allowed paleontologists to generate a much more refined view of the cellular mechanisms contributing to the broad spectrum of tooth crown morphologies present within primates and other mammals (Asper, 1916; Gysi, 1931; Schour and Poncher, 1937; Schour and Hoffman, 1939; Okada, 1943; Massler and Schour, 1946; Fukuhara, 1959; Boyde, 1963, 1964, 1989, 1990; Newman and Poole, 1974; Shellis, 1984a, b, 1998; Beynon and Wood, 1986, 1987; Risnes, 1985, 1986; Beynon and Dean, 1987; Beynon *et al.*, 1991a, b; Bromage, 1991; Dean and Beynon, 1991; Dean, 1998; Dirks, 1998; FitzGerald, 1998; Reid *et al.*, 1998).

A general picture has emerged from these studies that clearly shows two important trends. First, daily enamel secretion rates gradually increase from inner through middle to outer areas in all regions, i.e., cuspal, lateral and cervical, of the enamel cap (Beynon *et al.*, 1991b; Macho and Wood, 1995; Reid *et al.*, 1998). Second, there is a consistent reduction in daily secretion rates from cuspal to cervical regions of the enamel cap with the lowest values towards the cervical margin. The reduction in daily secretion rates in these regions appears to be a characteristic of enamel formation in monkeys, great apes, humans and *Proconsul* (Beynon *et al.*, 1991b; Bromage, 1991; Macho and Wood, 1995; Reid *et al.*, 1998; Beynon *et al.*, 1998). Few data are available to determine whether rates of secretion differ between sexes in any hominoid.

The long-period incremental lines in enamel and dentine occur at more widely spaced intervals and represent isochronous positions of the forming enamel and dentine front, respectively, during crown formation. It is now clear that the number of daily cross-striations between successive striae, i.e., the periodicity, does not vary within or between teeth of the same individual (Beynon, 1992; FitzGerald, 1998). However, it varies among individuals within populations and among populations (FitzGerald, 1998). The extent to which the long-period striae periodicity varies within primate populations has never before been documented for large numbers of individuals. Some researchers have reported periodicities that mirror good data for humans and cite a modal value of 8 or 9 in living nonhuman hominoids (Fukuhara,

1959; Newman and Poole, 1974; Shellis and Poole, 1977; Shellis, 1984a, b; Bromage and Dean, 1985; Dean, 1987; Dean and Scandrett, 1995, 1996; Reid *et al.*, 1998). In most monkeys, long-period lines in enamel are reported to be 4 or 5 days apart, and prosimians appear to have periodicities of 2 or 3 (Okada, 1943; Fukuhara, 1959; pers. observ.). This seems to suggest some broad link between periodicity and body size (or related parameters such as metabolic rate or neonatal brain mass). A more fundamental question that remains unanswered, however, is whether periodicity values differ systematically between sexes within or even among hominoid species.

SPECIFIC OBJECTIVES

We provide descriptive statistics on long-period striae periodicities and daily secretion rates for a large sample of reliably sexed hominoid canines to serve as a baseline data set for future comparative studies on extant and extinct primates. We also test a series of hypotheses relevant to understanding whether noticeable patterns of sexual dimorphism and/or interspecific variation are evidenced in enamel secretion, i.e., daily secretion rates and periodicities. The null hypotheses are that:

1. Periodicities do not differ significantly between sexes of each hominoid species.
2. Periodicities do not differ significantly among hominoid species.
3. Daily secretion rates do not differ significantly between canines of male and female hominoid species at homologous regions of the crown.
4. Daily secretion rates do not differ between inner and outer regions of the canine crown and exhibit no clear sexual and/or taxonomic pattern.
5. Sexual differences in linear enamel thickness are absent within hominoid canines.

MATERIALS AND METHOD

We examined a total of 108 great ape and human mandibular canines of known sex (Table I). This represents the largest reliably-sexed sample of teeth used in a histological analysis to date. The great ape canines are from both wild-shot and captive individuals from the following collections: Department of Anatomy, University College London; Anthropologisches Institut, Universität Zürich-Irchel, Switzerland; The Odontological Museum,

Table I. The sample of great ape and human mandibular canines used and descriptive statistics for values of periodicity

	Sex	N	Mean	S.D.	Range	Mode	<i>p</i> -value*
<i>Pan troglodytes</i>	M	10	7.00	0.93	6.00–9.00	7.00	0.2294
	F	10	6.90	0.57	6.00–8.00	7.00	
<i>Gorilla gorilla</i>	M	18	8.78	0.55	8.00–10.00	9.00	0.6925
	F	18	8.63	1.09	7.00–10.00	8.00	
<i>Pongo pygmaeus</i>	M	12	9.67	0.78	8.00–11.00	10.00	0.4884
	F	12	9.42	0.90	8.00–11.00	10.00	
<i>Homo sapiens</i>	M	19	8.37	0.96	7.00–11.00	8.00	0.3016
	F	9	9.00	1.41	7.00–11.00	8.00	

*Results from Mann-Whitney U tests for differences in periodicity between males and females.

The Royal College of Surgeons of England. The human sample is from specimens collected over the years in the Department of Oral Biology, Newcastle upon Tyne Dental School, UK, and from dental clinics in Johannesburg and Pietmaritzberg, South Africa. We used right canines preferentially over left ones. In all cases, sectioning of the ape specimens was carried out only when antimeres were present and in reasonable condition. We extracted ape canines from the mandible, cleaned them, and prepared molds using Coltene™ silicon medium body putty. Before sectioning, we coated each canine in cyanoacrylate to reduce the risk of splintering. Using a Buehler™ Isomet diamond wafering blade saw, we prepared 180–200 μm longitudinal ground sections from the midline axial plane such that each section traversed both the cusp tip (and dentine horn) and the entire buccal aspect of each canine crown. We lapped the sections to a final thickness of 100–120 μm , polished them with a 3 μm aluminum powder, placed them in an ultrasonic bath to remove surface debris, dehydrated them through a graded series of alcohol baths, cleared them in Histoclear™ and mounted them with cover slips in xylene-based DPX™ mounting medium. We sectioned human canines in the same manner. We will return all ape sections the museums to serve as a reference sample. We examined the sections via routine polarized light microscopy and constructed photomontages ($\times 250$) of the cusp tip and buccal aspect of each tooth crown.

Daily Secretion Rate

We determined the linear rate of enamel secretion per day in two ways. From the montages, it was easy to find areas in all regions of the canine crown where many cross-striations were visible. We measured across six cross-striations along a single prism (thereby representing 5 days secretion) and

divided by five, to produce a daily linear secretion rate (DSR): Dean, 1998. We repeated this procedure many times in the inner and outer areas of the cuspal, lateral and cervical regions of all specimens. The values in the Tables III–V are means. In total, $n = 1,363$ separate measurements of DSR for the entire sample of canines. Alternative methods of estimating DSRs require knowledge of the periodicity. In areas where it is difficult to resolve cross-striations, one can measure the linear distance along a prism between adjacent long-period striae of Retzius. Dividing that distance by the periodicity yields an estimate of the DSR in μm per day.

In previous studies on primate dental histology, researchers divided the enamel cap into three areas—(inner, middle and outer)—and the crown into three distinct regions—(cuspal, lateral and cervical)—to facilitate comparisons within any one tooth and across teeth attributed to different species (Beynon *et al.*, 1991a, b; Reid *et al.*, 1998). Because they mainly focused on the developing enamel on posterior teeth and because enamel is so much thinner on anterior teeth, we have modified this convention to include only the inner and outer areas of the cuspal, lateral and cervical regions of canines crowns.

Periodicity

As with DSRs, periodicities can be determined by two complementary methods. In most sections, it is possible to count the number of cross-striations between adjacent long-period lines (Fig. 1b). In areas where cross-striations are not easily discerned, periodicities can be directly estimated by dividing the linear distance along the length of a prism between adjacent Retzius lines by the mean DSR in that region of the canine for hominoid species. Each of us estimated periodicities via both methods: the interobserver error is less than 3%.

Enamel Thickness

We recorded linear enamel thickness measurements on each section by averaging two measurements: one at the most occlusal portion of the buccal lateral enamel, i.e., at the point where the last appositional component meets the EDJ and begins the imbricational component of the crown, and another 5 mm from the first measure towards the cervix. This provides a reasonable assessment of overall buccal enamel thickness in canine teeth and avoids problems such as obliquity of section and gnarled enamel associated with measuring enamel thickness at the cusp tip.

RESULTS

Results for periodicities are in Tables I and II. They fail to falsify the first null hypothesis; modal values for periodicity are similar in males and females in each of the large-bodied hominoids, and there is no statistically significant difference between sexes (Table I). However, the second null hypothesis relating to periodicity values between species is falsified. In pooled-sex samples, all hominoids differ significantly from one another with the exception of *Gorilla* vs. *Homo* (Table IIa). The same pattern of differences is evident when only males are considered (Table IIb) though this does not hold true for females (Table IIc); female *Pongo* possess periodicity values similar to females of *Gorilla* and *Homo*, whereas male *Pongo* have significantly

Table IIa. Matrix of results from statistical comparisons (*p*-values)* for differences in periodicity values among hominoid genera

	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>	<i>Homo sapiens</i>
<i>Pan troglodytes</i>	–			
<i>Gorilla gorilla</i>	<0.0001	–		
<i>Pongo pygmaeus</i>	<0.0001	0.0048	–	
<i>Homo sapiens</i>	<0.0001	0.9811	0.0027	–

*Reported *p*-values are from Scheffé's tests, which we used here to test for significant groupings within the hominoid sample. This statistical test is equivalent to a Student's *t*-test when comparing two means, however, when more than two means are present, Scheffé's test has the advantage of maintaining the probability of finding an erroneous significant result—Type I error—below 0.05.

Table IIb. Matrix of results from statistical comparisons (*p*-values)* for differences in periodicity values between males

	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>	<i>Homo sapiens</i>
<i>Pan troglodytes</i>	–			
<i>Gorilla gorilla</i>	<0.0001	–		
<i>Pongo pygmaeus</i>	<0.0001	0.0242	–	
<i>Homo sapiens</i>	0.0008	0.6105	0.0007	–

*Same as in Table IIa.

Table IIc. Matrix of results from statistical comparisons (*p*-values)* for differences in periodicity values between females

	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>	<i>Homo sapiens</i>
<i>Pan troglodytes</i>	–			
<i>Gorilla gorilla</i>	0.0014	–		
<i>Pongo pygmaeus</i>	<0.0001	0.2221	–	
<i>Homo sapiens</i>	0.0007	0.8286	0.8320	–

*Same as in Table IIa.

Table IIIa. Descriptive statistics for daily secretion rate (DSR, in μm) in pooled, i.e. mixed sex, samples at the level of the EDJ area in each region of the crown in each hominoid genus

		DSR at the level of the EDJ area				
		N	Mean	Std. dev.	Range	<i>p</i> -value ^a
<i>Pan:</i>	Cuspal	54	3.37	0.29	2.69–4.34	<0.0001
	Lateral	120	3.03	0.25	2.28–3.46	
	Cervical	107	2.66	0.32	2.06–3.37	
<i>Gorilla:</i>	Cuspal	210	3.08	0.29	2.34–3.99	<0.0001
	Lateral	206	2.83	0.41	2.08–4.63	
	Cervical	42	2.64	0.55	2.06–4.14	
<i>Pongo:</i>	Cuspal	31	3.90	0.41	3.23–4.45	<0.0001 ^b
	Lateral	102	2.85	0.29	2.06–3.36	
	Cervical	60	2.76	0.29	1.99–3.40	
<i>Homo:</i>	Cuspal	19	2.68	0.23	2.19–2.99	0.0006 ^c
	Lateral	19	2.74	0.22	2.39–2.98	
	Cervical	19	2.46	0.20	2.18–2.78	

^a*p*-values from an ANOVA testing for differences in DSR among regions of the canine crown at the level of the EDJ for each species of hominoid. Results from Scheffé's post hoc tests.

^bThe cuspal region differs significantly from both lateral and cervical regions ($p < 0.0001$ in both cases); however, the difference between lateral and cervical regions is not statistically significant ($p = 0.2728$).

^cCervical values for modern humans differ from both the cuspal and lateral regions ($p = 0.0127$ and 0.0012 , respectively); however, the cuspal and lateral regions do not differ significantly from each other ($p = 0.7127$).

N = number of measurements at each region of the crown.

greater periodicity values than both of the other genera, despite overall similarities in modal values for males and females in all three genera (Tables I and II).

Descriptive statistics for, and an evaluation of sexual dimorphism in, DSRs at both the EDJ and the outer area of the canine crown are in Tables IIIa and IIIb, respectively, for each hominoid genus. Like many earlier studies on a broad range of primates, our data support the pattern of a significant decrease in DSRs from cuspal through lateral to cervical regions of the enamel cap within each species (Fig. 2). There is also a strong and significant trend for DSRs to increase from the inner to outer areas in each hominid species. DSRs at the level of the EDJ in the cuspal region of all great apes exhibit a similar range, from just under $3.5 \mu\text{m}$ to nearly $4.5 \mu\text{m}$ per day, but differ in other regions.

In humans, DSRs maintain a similar range regardless of crown region (Table IIIa). The rates decrease in all taxa towards the lateral region, except in *Gorilla*, in which some specimens have higher rates than occur in the cuspal region of the crown (Table IIIa). At the outer level of the outer

Table IIIb. Descriptive statistics for daily secretion rate (DSR, in μm) in pooled, i.e. mixed sex, samples at the outer enamel area in each region of the crown in each hominoid genus

		DSR at the level of outer area				
		N	Mean	Std. dev.	Range	<i>p</i> -value ^a
<i>Pan:</i>	Cuspal	4	4.39	0.70	3.75–5.29	0.0104^b
	Lateral	39	4.12	0.40	3.33–5.01	
	Cervical	16	3.74	0.55	2.50–4.65	
<i>Gorilla:</i>	Cuspal	64	5.74	0.41	4.82–6.75	<0.0001
	Lateral	84	4.73	0.40	3.61–5.43	
	Cervical	25	3.96	0.41	3.17–4.60	
<i>Pongo:</i>	Cuspal	23	5.19	0.29	4.60–5.72	<0.0001
	Lateral	43	4.39	0.44	3.29–5.10	
	Cervical	19	3.40	0.26	3.05–4.00	
<i>Homo:</i>	Cuspal	19	4.92	0.42	4.18–5.77	<0.0001
	Lateral	19	4.38	0.32	3.98–4.97	
	Cervical	19	3.43	0.30	2.99–3.98	

^a*p*-values from an ANOVA testing for differences in DSR among regions of the canine crown at the level of the outer area of the enamel cap for each species of hominoid. Results from Scheffé's post hoc tests.

^bOnly the lateral and cervical regions are significantly different from each other ($p = 0.0318$); the differences between the cuspal and both the lateral and cervical regions are not statistically significant ($p = 0.5270$ and 0.0508 , respectively).

N = number of measurements at each region of the crown.

enamel surface, DSRs increase markedly in all species and can reach well over $6 \mu\text{m}$ per day in the cuspal region of *Gorilla* (Table IIIb; Fig. 3).

When compared interspecifically, hominoid species exhibit a complicated pattern of similarities and differences in DSRs, thereby falsifying the third null hypothesis (Table IV). When sexes are pooled, all taxa differ significantly from one another at the level of the EDJ in the cuspal region. These differences become increasingly less evident towards the cervical region of the canine crown such that only canines of *Pan* differ from those of *Gorilla*, *Pongo* and *Homo* in the lateral region of crown, while only *Pongo* and *Homo* differ from each other in the cervical region. In the outer level of the crown, the canines of *Gorilla* are unique, differing significantly from all other hominoids at both the cuspal and lateral regions of the crown, and from only *Homo* and *Pongo* in the cervical region of the canine crown. Canines of *Pan* also differ significantly from those of *Pongo*, but in the cuspal and lateral regions of the crown only (Table IV).

Differences in rates of enamel growth are present between sexes especially in the thick-enameled apes, thus falsifying the fourth null hypothesis. However, rate differences only exist at the level of the EDJ and not at the

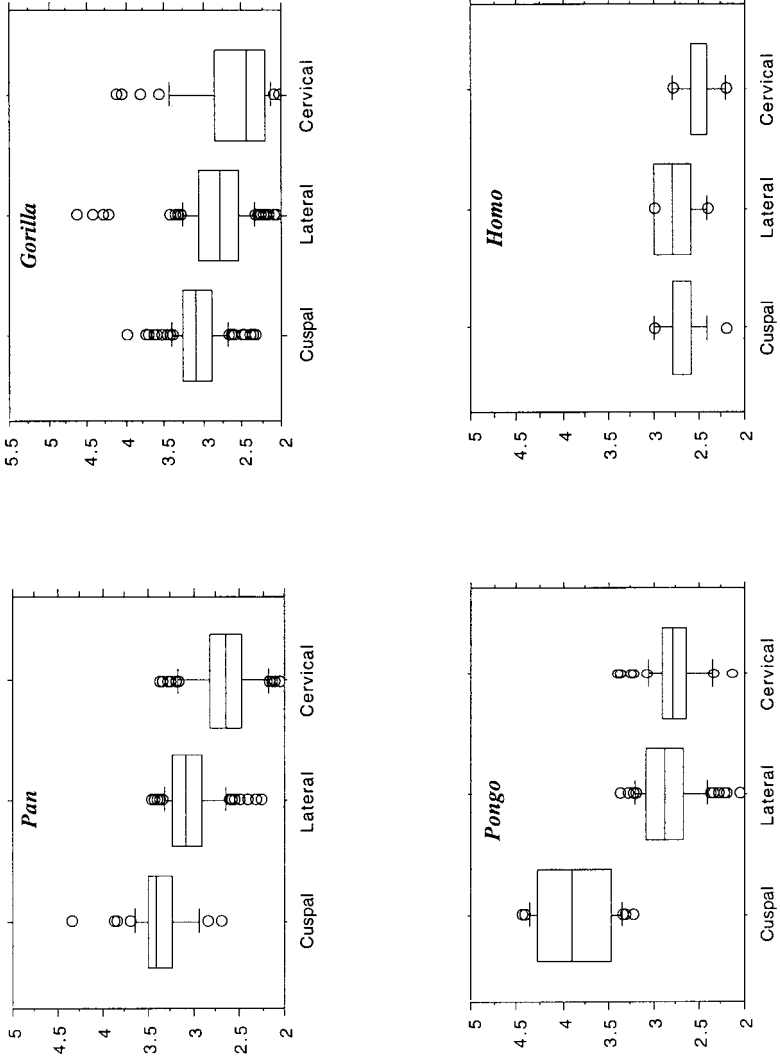


Fig. 2. Box plots of daily secretion rates (μm) at the level of the EDJ.

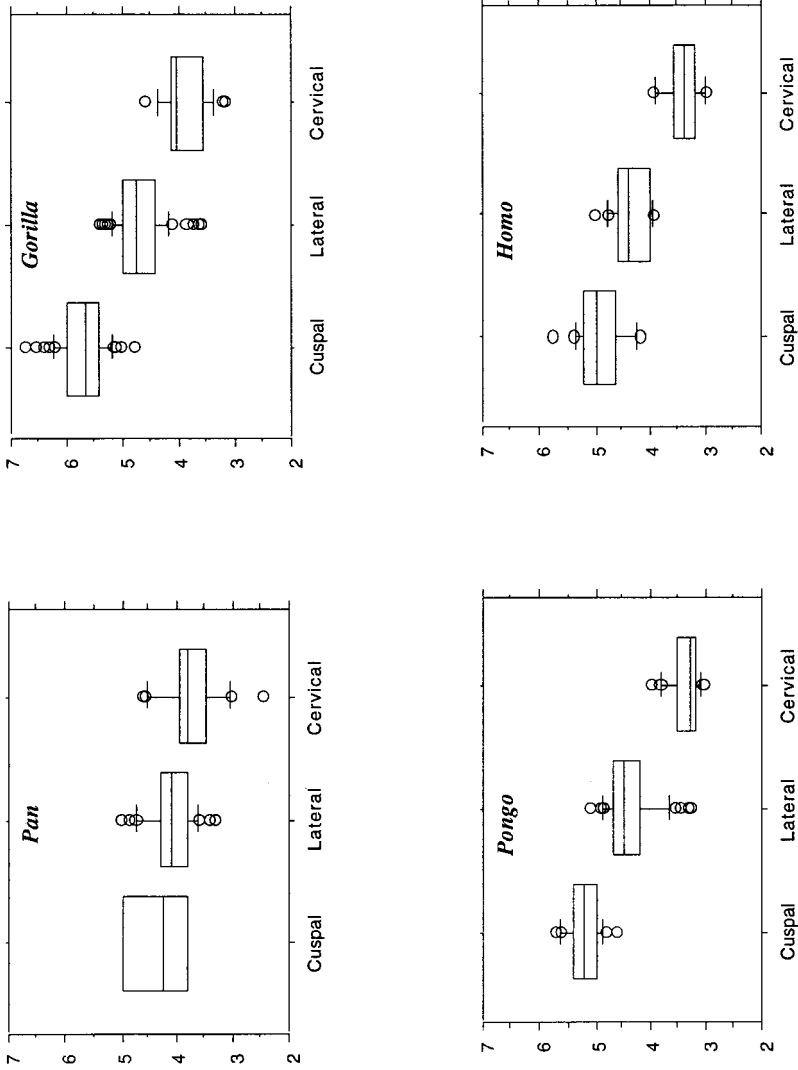


Fig. 3. Box plots of daily secretion rates (μm) at the outer level.

Table IV. Interspecific comparisons of canine DSRs (in μm) among hominoid taxa. We include only pairwise comparisons that differ significantly ($p < 0.05$) from one another. (p-values are from Scheffé's post hoc tests generated from an ANOVA testing for differences in DSR in each region of the canine crown at the level of both the EDJ and outer area of the enamel cap)

Cuspal		Lateral		Cervical	
Inner (EDJ)					
<i>Homo v. Pan</i>	<0.0001	<i>Pan v. Gorilla</i>	<0.0001	<i>Homo v. Pongo</i>	0.0206
<i>Homo v. Pongo</i>	<0.0001	<i>Pan v. Homo</i>	0.0060		
<i>Gorilla v. Homo</i>	<0.0001	<i>Pan v. Pongo</i>	0.0007		
<i>Gorilla v. Pan</i>	<0.0001				
<i>Gorilla v. Pongo</i>	<0.0001				
<i>Pan v. Pongo</i>	<0.0001				
Outer					
<i>Gorilla v. Homo</i>	<0.0001	<i>Gorilla v. Homo</i>	<0.0001	<i>Gorilla v. Homo</i>	0.0005
<i>Gorilla v. Pan</i>	<0.0001	<i>Gorilla v. Pan</i>	<0.0001	<i>Gorilla v. Pongo</i>	0.0002
<i>Gorilla v. Pongo</i>	<0.0001	<i>Gorilla v. Pongo</i>	<0.0001		
<i>Pan v. Pongo</i>	0.0052	<i>Pan v. Pongo</i>	0.0270		

outer enamel surface (Fig. 4; Table V). Additionally, it is always females that possess significantly greater rates than those of males when differences are present. Differences in DSR are absent in the outer enamel area of all great ape species. It is predominantly canines of *Gorilla* and *Pongo* that possess marked sexual dimorphism in rates of growth at the EDJ in all three regions of the crown. Male and female *Pan* differ from each other, but this difference is only significant in the cuspal region (Table V).

Descriptive statistics for linear enamel thickness measurements are in Table VI. Values for enamel thickness in anterior teeth mimic those in posterior teeth: *Pan* < *Gorilla* < *Pongo* < *Homo*. Only the thick-enamelled hominoids are sexually dimorphic in canine enamel thickness, thus falsifying the fifth null hypothesis (Fig. 5).

DISCUSSION

Much of what we know about the ontogeny of sexual dimorphism in great apes and humans stems from work on somatic development (Gavin, 1953; Shea, 1985, 1986; Leigh, 1992; Leigh and Shea, 1995). Comparatively little is known about the ontogeny of dimorphism in dental development, especially for canines.

Adult dimorphism in body size is not directly comparable across species (Fedigan, 1982; Leigh, 1985; Leigh and Shea, 1995; Shea, 1986). For instance,

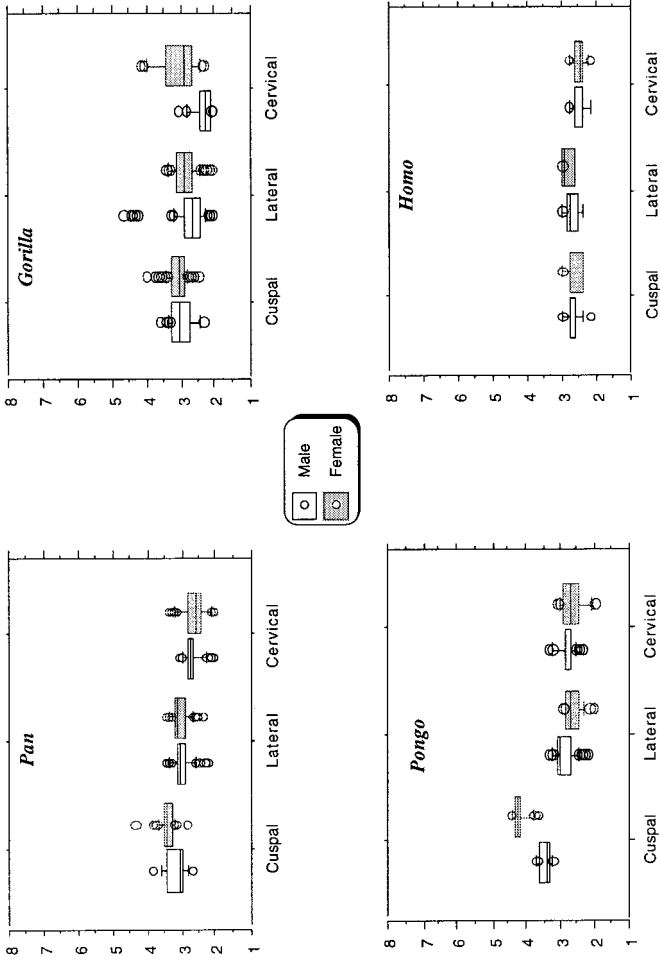


Fig. 4. Box plots of sexual dimorphism in daily secretion rates (μm) at the level of the EDJ.

Table V. An evaluation of sexual dimorphism in hominoid DSRs at both the level of the EDJ (inner) and the outer areas of the canine crown. (The *p*-values are the results from unpaired t-tests of males vs. females)

		Area of the Canine Crown					
		Inner (EDJ)			Outer		
	Region	DF	t-value	<i>P</i>	DF	t-value	<i>P</i>
<i>Pan:</i>	Cuspal	52	-3.438	0.0012*	2	-	-
	Lateral	118	-1.280	0.2029	31	0.186	0.8535
	Cervical	105	0.596	0.5523	14	-0.467	0.6479
<i>Gorilla:</i>	Cuspal	208	-2.081	0.0056*	62	-1.477	0.1448
	Lateral	204	-2.425	0.0162*	82	1.245	0.2166
	Cervical	40	-5.464	<0.0001*	23	0.308	0.7611
<i>Pongo:</i>	Cuspal	29	-9.083	<0.0001*	21	1.236	0.2302
	Lateral	100	4.178	<0.0001*	41	0.612	0.5440
	Cervical	58	2.492	0.0156*	17	0.224	0.8258
<i>Homo:</i>	Cuspal	17	-0.133	0.8959	17	-2.021	0.0593
	Lateral	17	-1.172	0.2575	17	-0.922	0.3692
	Cervical	17	-0.139	0.8909	17	-0.895	0.3830

DF = Degrees of freedom.

*Females possess significantly greater values for rates than males.

there is considerable diversity in the role that differences in rate and duration play during ontogeny in the development of body size dimorphism among groups of closely related ape species (Shea, 1985, 1986; Leigh, 1995; Leigh and Shea, 1995). For some ape species, similar amounts of adult dimorphism

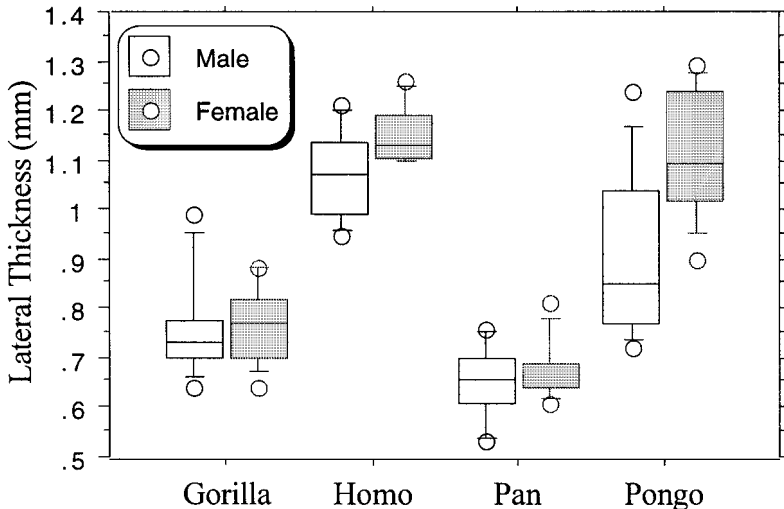


Fig. 5. Box plots of sexual dimorphism in linear enamel thickness (mm).

Table VI. Descriptive statistics for linear enamel thickness (in mm) for the sexed sample of great ape and human canines. (The *p*-values are the results from unpaired t-tests of males vs. females)

	Sex	N	Mean	Std.dev.	<i>p</i> -value ^a
<i>Pan</i>	Male	6	0.65	0.08	0.4062
	Female	11	0.68	0.06	
<i>Gorilla</i>	Male	12	0.76	0.11	0.8122
	Female	10	0.77	0.08	
<i>Pongo</i>	Male	10	0.90	0.17	0.0140
	Female	10	1.12	0.13	
<i>Homo</i>	Male	11	1.05	0.13	0.0520
	Female	7	1.16	0.06	

in body size appear to result from rate differences, while differences in the timing, or duration, of the growth period give rise to dimorphism in others. It is unknown to what degree the pattern of dental growth trajectories mirror aspects of somatic growth with respect to the development of dimorphism. Before addressing such questions, it is necessary to provide primary data on variation in periodicity, rates of secretion, and enamel thickness, and how each of them may contribute to the development of canine dimorphism within taxa.

Interspecific Comparisons. Great ape canines begin to mineralize shortly after birth and are (together with M3s) the last of the permanent teeth to emerge fully into the mouth, usually completely by 11 years of age in all male and female apes (Kraus and Jordan, 1965; Oka and Kraus, 1969; Moxham and Berkovitz, 1974; Dean and Wood, 1981; Swindler, 1985; Siebert and Swindler, 1991). Despite a growing amount of comparative developmental data, previous radiographic and other studies have not been able to document significant differences in the age at initial mineralization of the canine, the total period of crown formation, or the timing of canine gingival emergence among *Pan*, *Gorilla* or *Pongo*. Given differences in tooth size, diet, and life history, among hominoids, it is reasonable to expect that there are differences in some aspects of crown development, such as periodicity, daily secretion rate, and crown formation time.

For hominoids, periodicities have been known to range between 6 and 11, though larger values have been reported, especially for humans, by FitzGerald (1998). Our study shows that the modal values of long-period striae periodicity increase from 7 in *Pan*, to 8 in *Homo*, 8/9 in *Gorilla*, and 10 in *Pongo*. Overall, periodicities in humans are closest to those of *Gorilla*, not *Pan* as one might have expected given their more similar degree of canine dimorphism and closer phylogenetic relationship. Larger values for periodicity may be related to overall differences in tooth size, as *Pongo* and *Gorilla* have larger teeth than those of *Pan* and *Homo* (Swindler, 1976).

Our data confirm previous observations about DSRs increasing from the EDJ to the crown surface and decreasing from the cuspal margins to the cervix (Beynon *et al.*, 1991a; Reid *et al.*, 1998). However, the magnitude of the decrease at the EDJ, between the cusp and the cervix, is very small in all taxa so that the first-formed enamel at the EDJ in any hominoid, wherever measured, is consistently between 2.5 and 3.5 μm per day. The decreasing gradient in outer enamel between the cusp and cervix is much greater in magnitude. Differences in daily secretion rates among hominoid species are most apparent in the cuspal region (at both the level of the EDJ and the outer enamel surface) and become minimal towards the cervical crown area. It therefore seems that taxonomic differences are greatest and most apparent in the outer enamel area. This is perhaps to be expected when gross crown morphology depends so much on shorter or longer secretory lifespans of ameloblasts in conjunction with different secretory rates to produce enamel of differing thicknesses.

Studies on fossil primate teeth have often focused on enamel thickness and on the timing of dental developmental events in the context of life-history studies. Nearly all studies of enamel thickness in extant apes focus specifically on its degree of expression in posterior teeth (Martin, 1983, 1985; Grine and Martin, 1988; Macho and Berner, 1993; Shellis *et al.*, 1998; Schwartz, 2000). Our data show that enamel thickness in great ape anterior teeth mirror those known for posterior teeth. That is, the gradient of enamel thickness in posterior teeth (*Pan* < *Gorilla* < *Pongo* < *Homo*) also appears in nonfunctional anterior teeth, suggesting some systemic, regulatory mechanism mediating the expression of enamel thickness gradients (Aiello *et al.*, 1991; Macho and Wood, 1995). Since buccal enamel in canines is essentially nonfunctional during mastication one can assume that some pleiotropic effect across the whole dentition is reflected equally well in anterior teeth and perhaps is driven by an adaptation of posterior teeth to species-specific requirements of food processing (Schwartz, 2000). There is no obvious link between secretory rates and linear enamel thickness in anterior teeth. Accordingly, it appears that enamel thickness results largely, if not entirely, from the duration of ameloblast secretion rather than from rates of secretion.

Intraspecific Comparisons. Recent studies show that canine dimorphism in extant hominoids is largely a result of differences in the duration of crown formation (Schwartz *et al.*, 2000; Schwartz and Dean, submitted); however, the contributions of differences in periodicity and cell secretion rates are unknown. Our study confirms that differences in periodicity are absent between the sexes in hominoid species so that variations in this variable contribute little to the development of canine dimorphism. Whatever mechanism regulates or co-ordinates the developmental process responsible for sexual

dimorphism in growth rate or body size has no effect on long-period striae periodicity.

Differences in rate may also account in some way for the development of canine dimorphism. The pattern of differences in DSRs between sexes within each species is different from that seen among species, i.e., sexually dimorphic differences in rates of secretion are most apparent at the level of the EDJ and nonexistent in the outer enamel. Why ameloblasts with low DSRs early in secretory life should express large differences between sexes remains obscure. However, it is less likely that it reflects systemic sex hormonal levels and more likely reflects genomic imprinting and sex-chromosomal make-up. Future studies of enamel secretory rates in teeth from individuals with chromosomal aneuploidies, i.e., sex linkage disorders such as the sequence 45, XO to 46, XX to 47, XXX, may shed light on this issue as they have demonstrated the role that X and Y chromosomes play in determining thicker or thinner enamel in modern humans (Alvesalo *et al.*, 1991; Harris and Hicks, 1998; Schwartz *et al.*, in prep.). The finding that female *Homo* and *Pongo* have thicker enamel is interesting and once again may tie in with findings from sex-chromosomal studies.

CONCLUSIONS

The results of this study provide essential background for a larger project to elucidate the developmental mechanisms responsible for canine dimorphism in extant large-bodied hominoids and eventually in early hominins. When our data are viewed in conjunction with recent data on the role of rate and duration in the ontogeny of canine dimorphism, a general picture emerges suggesting that faster rates of formation in females underlies greater linear enamel thickness, though one cannot exclude a role that time differences in duration of secretion may play, whereas male canine heights result from an extension in the duration of ameloblast proliferation along the developing EDJ (Schwartz and Dean, submitted). Ultimately, these data will help to detail how sometimes subtle differences in the developmental program contribute to the marked variation in dental metrics, enamel thickness and crown formation time, in hominoid taxa. Furthermore, by understanding how sexual dimorphism in canine size develops in great apes and humans, we have a foundation for future research relating and comparing ontogenetic patterns of dimorphism between somatic and dental growth.

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