

Ontogeny of Canine Dimorphism in Extant Hominoids

Gary T. Schwartz^{1,2*} and Christopher Dean³

¹*Department of Anthropology, The George Washington University, Washington, DC 20052*

²*Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560*

³*Evolutionary Anatomy Unit, Department of Anatomy and Developmental Biology, University College London, London WC1E 6JJ, UK*

ABSTRACT Many behavioral and ecological factors influence the degree of expression of canine dimorphism for different reasons. Regardless of its socioecological importance, we know virtually nothing about the processes responsible for the development of canine dimorphism. Our aim here is to describe the developmental process(es) regulating canine dimorphism in extant hominoids, using histological markers of tooth growth. Teeth preserve a permanent record of their ontogeny in the form of short- and long-period incremental markings in both enamel and dentine. We selected 52 histological sections of sexed hominoid canine teeth from a total sample of 115, from which we calculated the time and rate of cuspal enamel formation and the rate at which ameloblasts differentiate along the future enamel-dentine junction (EDJ) to the end of crown formation. Thus, we were able to reconstruct longitudinal growth curves for height attainment in male and female hominoid canines. Male hominoids consistently take longer to form canine crowns than do females (although not

significantly so for our sample of *Homo*). Male orangutans and gorillas occasionally take up to twice as long as females to complete enamel formation. The mean ranges of female canine crown formation times are similar in *Pan*, *Gorilla*, and *Pongo*. Interspecific differences between female *Pan* canine crown heights and those of *Gorilla* and *Pongo*, which are taller, result from differences in rates of growth. Differences in canine crown heights between male *Pan* and the taller, more dimorphic male *Gorilla* and *Pongo* canines result both from differences in total time taken to form enamel and from faster rates of growth in *Gorilla* and *Pongo*. Although modern human canines do not emerge as significantly dimorphic in this study, it is well-known that sexual dimorphism in canine crown height exists. Larger samples of sexed modern human canines are therefore needed to identify clearly what underlies this. *Am J Phys Anthropol* 115:269–283, 2001.

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One of the most intriguing themes in primate and human evolution is the nature of sexual dimorphism. This goes well beyond the simple observation that males are often bigger than females. It raises sociological and behavioral issues that Darwin (1871) recognized must underlie the nature of sexual selection in evolution. Now, more than ever, it begs questions about the ontogenetic mechanisms that bring about morphological differences between males and females during evolution, both within the same species and between different species.

Adult variation in canine size and its relationship with sexual selection, mating systems, predation pressure, body size dimorphism, dietary constraints, phylogeny, etc., are well-documented (e.g., Leutenegger and Kelly, 1977; Harvey et al., 1978a,b; Leutenegger, 1982; Leutenegger and Cheverud, 1982, 1985; Cheverud et al., 1985a,b; Milton, 1985; Lucas et al., 1986; Oxnard, 1987; Kay et al., 1988; Plavcan, 1998; Plavcan and Kay, 1988; Plavcan and van Schaik, 1992, 1994; Plavcan et al., 1995). Data on the ontogenetic bases of adult variation in canine size, however, are virtually nonexistent. Examining canine dimorphism from an ontogenetic framework allows insights into the adaptive and evolutionary significance of canine size variation by linking ontogenetic morphological data to certain key life-his-

tory variables (e.g., rates of growth, bimaturism) as well as to behavioral and ecological variation (e.g., Wiley, 1974; Jarman, 1983; Stearns, 1992; Leigh, 1995; Leigh and Shea, 1995, 1996). Our goal here is to provide data on the ontogeny of canine size in order to examine the developmental mechanism(s) regulating canine dimorphism in extant large-bodied hominoids. Intra- and interspecific differences in the growth processes underlying canine dimorphism are then interpreted within the context of existing models on variance dimorphism and bimaturism. When viewed in conjunction with comparative data on body size dimorphism, these findings will help build a more complete picture of the evolutionary and adaptive significance of dimorphism throughout hominoid and hominin evolution.

ONTOGENY AND DIMORPHISM

Many previous studies described the evolution of dimorphism for specific ape species (e.g., Galdikas,

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*Correspondence to: Gary T. Schwartz, Department of Anthropology, The George Washington University, 2110 G St. NW, Washington, DC 20052. E-mail: garys@gwu.edu

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1979; MacKinnon, 1979; Rodman, 1973; Rodman and Ritani, 1987; Jungers and Cole, 1992; Master-son and Leutenegger, 1992; Leutenegger and Master-son, 1989). Comparative ontogenetic data indicate that different mechanisms might underlie similar degrees of adult dimorphism (e.g., Fedigan, 1982; Leigh, 1995; Leigh and Shea, 1995; Shea, 1986). For instance, Shea (1986) and Leigh (1995) found considerable diversity in the role that differences in rate and duration play during ontogeny in the development of dimorphism among groups of closely related primate species (e.g., macaques, guenons, baboons, and African apes). For some species, similar amounts of adult dimorphism appear to result through rate differences, while differences in the timing, or duration, of the growth period give rise to dimorphism in others. As a result of these and other studies, we know a lot about the degree of variability in the ontogeny of body size dimorphism and some of the socioecological correlates (Shea, 1985, 1986; Leigh, 1992; Leigh and Shea, 1995).

Comparatively little is known about the ontogeny of canine size dimorphism, especially for the hominoids. Canine dimorphism is particularly important, not only because it has strong biological links with many socioecological variables and that many behavioral and ecological factors have been implicated in influencing its degree of expression for many different reasons (e.g., Washburn and Avis, 1958; Kinzey, 1970; Greene, 1973; Washburn and Ciochon, 1974; Leutenegger and Kelly, 1977; Clutton-Brock and Harvey, 1977; Leutenegger, 1978, 1982; Lucas, 1981; Smith, 1981; Jungers, 1985; Lucas et al., 1986; Oxnard, 1987; Kay et al., 1988; Cronin, 1991; Plavcan, 1998; Plavcan and van Schaik, 1992; Plavcan et al., 1995; reviewed in Plavcan and van Schaik, 1994), but because only with a firm understanding of intraspecific variability in canine ontogeny can we say something about the processes involved in selecting for or constraining canine size.

As yet, it remains unknown to what degree the pattern of dental growth trajectories mirrors aspects of somatic growth. Dental development is generally considered to be more conservative than somatic development (Demisch and Wartmann, 1956; Lewis and Garn, 1960; Watts, 1990). Direct comparisons of somatic and dental ontogenetic growth trajectories now allow us to ask, for example, whether species in which males and females become sexually dimorphic in body size, primarily through differences in the duration of growth, share a similar ontogenetic trajectory with respect to canine growth. They also allow us to ask if there is ontogenetic decoupling between somatic and dental growth, and whether there are cases where sexual dimorphism in body size for a species comes about through rate differences but where dimorphism in dental growth results from differences in time. The ability to chart the ontogenetic history of teeth will ultimately allow us to determine the plasticity of dental development. Whatever the mechanism responsible for its evolu-

tion, sexual dimorphism, in the very widest sense, is clearly linked to various aspects of an animal's life strategy and can therefore be used as a reliable predictor of habitat and social structure (e.g., Leutenegger and Kelly, 1977; Clutton-Brock and Harvey, 1977; Leutenegger, 1978, 1982; Jungers, 1985; Kay et al., 1988; Cronin, 1991; Plavcan and van Schaik, 1994).

ONTOGENETIC EVIDENCE FOR CANINE DIMORPHISM

While few data exist for the ontogeny of canines in apes, a mass of information exists on other aspects of dental development in great apes. Despite this, comparatively little evidence exists that points to any differences in any aspect of dental development among the three ape genera.

It is well-known that great ape canines begin to mineralize shortly after birth and, together with third molars, are among the last of the permanent teeth to emerge into the mouth, usually before 11 years of age in all male and female apes (e.g., Kraus and Jordan, 1965; Oka and Kraus, 1969; Moxham and Berkovitz, 1974; Dean and Wood, 1981; Swindler, 1985; Beynon et al., 1991; Siebert and Swindler, 1991; Winkler et al., 1991; Smith et al., 1994; Winkler, 1995; Reid et al., 1998). The most reliable studies documenting aspects of canine initiation and rate of growth focus on our closest relative among the extant apes, the common chimpanzee (Anemone et al., 1991, 1996; Kuykendall, 1996; Kuykendall and Conroy, 1996; Reid et al., 1998). These studies reveal that, in general, male and female chimps initiate mineralization of mandibular canines at approximately 0.45 years for males and 0.40–0.52 years for females (Kuykendall, 1996; Reid et al., 1998). The ranges for male and female mandibular canine crown formation times (in years) are reported to be between 6.37–8.20 ($n = 2$) for males and 5.60–7.69 ($n = 8$) for females, with midpoint ages of attainment¹ greater in males (6.71 and 5.44 years for males and females; Kuykendall, 1996). Though this study provided much needed data on sexual differences in aspects of dental development in chimpanzees, the number of male individuals whose canines reached the crown complete stage was not large enough to allow statistical comparisons. Excellent data are also available on the variability in gingival emergence times for certain teeth of chimpanzees (e.g., Kuykendall et al., 1992), though interestingly, differences in canine emergence times are not evident in this one tooth that differs most in size between the two sexes.

The first study to clearly document biologically meaningful sex differences between developing min-

¹"Midpoint age of attainment" is generally younger than "mean ages." The former approximates the typical age at attainment of a given developmental stage, while the latter is the average age of all individuals *already exhibiting* a particular stage of development (see Kuykendall, 1996).

eralization stages of male and female chimpanzee canines was that of Kuykendall (1996). Median age of attainment was shown to differ significantly between sexes, but only at the points in time where enamel formation is complete at the occlusal surface, where root length is less than crown height, and where root length equaled crown height; i.e., relative to females, male canine crown and root formation was prolonged by approximately 1.4 years. Other stages of canine development, however, showed smaller, but less significant, differences between sexes. Importantly, Kuykendall (1996) also noted that in absolute terms, human and chimpanzee canines take an equivalent time to form, but suggested that relatively less of that time is devoted to root formation in the chimpanzee. Taken together, these data seem to indicate that no significant differences exist between males and females in age at initiation and in total *period* of canine tooth formation (i.e., enamel cusp to root apex) in chimps. Whether or not this holds for other apes is unknown, as unfortunately few data are available on the absolute ages of male and female canine crown formation in gorillas and orangutans. With this finding in *Pan*, however, together with the observation that male great ape canines are markedly larger in almost every metric aspect, it would not be unreasonable to assume that female and male canine teeth grow at different *rates*. Preliminary work has suggested some overall similarity between chimpanzees and orangutans, though to date only a few specimens of each have been examined; but even these few data lend some partial support to the notion that male and female Asian great apes exhibit sexual dimorphism in dental development (Beynon et al., 1991; Winkler et al., 1991). Despite all we know about the pattern, chronology, and timing of dental development in modern apes, it is still somewhat surprising that not one piece of evidence points to any clear difference in any aspect of dental development among hominoid species, and in particular, for canine development.

DEVELOPMENTAL BASES OF CANINE DIMORPHISM

Regardless of the adaptive, social, or behavioral basis of canine dimorphism, it is clear is that the important morphological variable to be considered is canine projection above the gingival margin (i.e., clinical crown height, which closely approximates anatomical canine crown height in this case). Despite the many previous histological studies of great ape tooth growth, none has presented data for males or females of known sex, and none has provided a clear idea about the degree of sexual dimorphism in the timing of canine tooth development. This is in stark contrast to the many metric studies of teeth where the degree of dimorphism in crown height or crown base area, or where simple measures of mesial and distal diameter, have been documented in detail on large samples of known sex (e.g., Oxnard et

al., 1985; Swindler, 1985; Wood et al., 1991; Plavcan and van Schaik, 1992; Plavcan, 1993, 1998; Greenfield, 1992a,b,c).

Canine teeth in primates grow from their cusps to their root apices over a period of some 10–12 years (Dean and Wood, 1981; Anemone et al., 1991, 1996; Beynon et al., 1991; Kuykendall, 1996; Kuykendall and Conroy, 1996). In essence, measurements of rates of growth of canine height through time reflect rates of secretion of enamel in the cuspal regions, and rates and duration of cell proliferation in the noncuspal, or lateral, enamel of the crown. Several metrical studies of canine dimorphism presented data for unworn canine height in primates, and effectively provided information about adult canine crown size at completion of growth (e.g., Kelley and Xu, 1991; Wood et al., 1991; Kelley, 1995; Waddle et al., 1995), but none provided longitudinal data on canine crown formation.

In some of the most searching studies of sexual dimorphism in primate canine teeth, canine base measurements (mesiodistal length and buccolingual breadth) were used as a measure of canine size (Oxnard et al., 1985; Oxnard, 1987; Wood et al., 1991). Oxnard (1987) detected differences in dispersion (of canine base measurements) between males and females in a large sample of certain great ape taxa, as well as significant dimorphism between mean values for canine size in some of these groups. In both orangutans and humans, Oxnard (1987) detected size dimorphism but no difference in the dispersion of measurements of the canine base between males and females. However, in gorillas and especially in chimpanzees, there was not only size dimorphism but a greater dispersion in the measurements of male canine bases than in females. This important finding points, potentially, to underlying differences in the mechanisms by which canines may grow in male and female apes and humans. Wood et al. (1991) were, however, unable to detect any significant differences in dispersion of male and female canine crown measurements, though these were present to some extent in *Gorilla*.

Differences in rate or duration of growth between males and females, or between different taxa, are thought to result in different degrees of dispersion of size measurements. Leutenegger and Cheverud (1982, 1985), in a quantitative genetic modeling exercise, drew attention to the fact that if male variance of characters is higher than that of females, then sexual dimorphism will increase simply as a consequence of increase in overall body size, and this seems to be the case in African apes and the Papionini. However, Plavcan and Kay (1988) and Plavcan (2000) found no systematic differences between male and female variances for a variety of dental measurements across a wide range of primate species. Regardless of the role of variance dimorphism, it is unclear whether these metric differences between male and female great ape canines result from alterations in the total period of crown forma-

TABLE 1. Sample of hominoid canines used in this study

Species	Sex	N	Collections
<i>Pan troglodytes</i>	Female	6	Anthropologisches Institut, Universität Zürich; Evolutionary Anatomy Unit, UCL; Odontological Museum, Royal College of Surgeons.
	Male	6	
<i>Gorilla gorilla</i>	Female	7	Anthropologisches Institut, Universität Zürich; Evolutionary Anatomy Unit, UCL; Odontological Museum, Royal College of Surgeons.
	Male	8	
<i>Pongo pygmaeus</i>	Female	7	Anthropologisches Institut, Universität Zürich; Evolutionary Anatomy Unit, UCL; Odontological Museum, Royal College of Surgeons.
	Male	8	
<i>Homo sapiens</i>	Female	5	University of Witwatersrand.
	Male	5	

tion, the rate at which the crown forms, or some combination thereof. Such questions can be addressed by using information from incremental lines in teeth, as these allow us to reconstruct longitudinal data from each canine and thus the total period of crown formation and the rate at which crown formation proceeds.

As for somatic growth trajectories, the works of Shea (1983a,b) and Leigh (1992, 1995) have gone a long way in documenting details of the ontogeny of body size dimorphism in extant apes. While these and other penetrating studies have provided much of the needed groundwork for interpreting and comparing the ontogeny of dimorphism, they "may lead to controversy because they cannot account for the different ways in which development produces similar levels of adult dimorphism" (Leigh, 1995:340; e.g., Leigh, 1992; Fedigan, 1982; Martin et al., 1984; Shea, 1985, 1986; Watts, 1986; Willner and Martin, 1984; Ralls, 1977; Jarman, 1983). In other words, identical levels of adult dimorphism (documented for body size in the aforementioned studies) can be produced through quite distinct ontogenetic trajectories. Our study provides a unique opportunity to document this important aspect of hominoid biology and, at the same time, allow intra- and interspecific comparisons of variation in the way ontogeny produces body size and canine dimorphism in the same species.

AIMS AND OBJECTIVES

The principal aim of this study was to identify (using well-established histological methods) the developmental mechanisms that determine how male canine teeth in living great apes come to grow bigger than the canine teeth of females of the same species. Our present histological analysis of the ontogenetic mechanisms underlying canine dimorphism explores the developmental and evolutionary mechanisms that bring about morphological differences between males and females, both within and between species. As such, it provides the first comparative and developmental framework for examining this feature in early hominins. The data presented here are potentially an important adjunct to other studies that seek to determine whether samples of fossil Miocene ape teeth contain two species, one large and one small, or two sexes, one large and one small. With this comparative developmental foundation, we will then be in a position to explore the

developmental mechanisms in fossil ape and hominid canine teeth.

Teeth preserve a permanent record of their ontogeny in the form of short- and long-period incremental lines in both enamel and dentine (e.g., Boyde, 1963, 1989; Beynon and Dean, 1988; FitzGerald, 1998). From histological sections of teeth, it is therefore possible to retrieve information not only about the rate of apposition of cuspal enamel (Dean, 1998) during the earliest stages of mineralization, but also about the rate at which new ameloblasts and odontoblasts differentiate along the enamel-dentine junction (EDJ) throughout the whole period of crown formation (Boyde, 1963, 1989; Shellis, 1984, 1987; Macho and Wood, 1995). The combined rate at which both these occur (enamel apposition in the cusp, and differentiation of ameloblasts at the developing cervical loop) is directly responsible for cumulative increases in crown height. The accumulation of crown height in this manner can thus be measured over the total period of canine crown formation.

The specific objectives of this study were 1) to determine the total time taken to form both cuspal and lateral enamel in male and female canine crowns belonging to *Pan*, *Gorilla*, *Pongo*, and *Homo*; 2) to determine whether time or rate differences (or both) in tooth growth contribute to sexual dimorphism in canine crown height within each of these taxa; 3) to determine to what extent interspecific differences in canine crown height can be accounted for by differences in rate or duration of growth (or both); 4) to document the degree of dispersion (i.e., variance) in crown height among males and females of these taxa during different periods of growth of the whole crown from initial mineralization to the end of crown formation; and 5) to interpret our findings within the larger context of dimorphism, bimaturation, and life-history theory.

MATERIALS AND METHODS

In all, 52 great ape and human mandibular canines of known sex were used in this study. A summary of the specimens used in this study and their provenance appear in Table 1. Great ape specimens used were: *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*. Sexed modern human teeth (of Black South African origin) were collected, with consent, following dental and oral surgery. For consistency, right canines of great apes were preferentially chosen over lefts where possible. However, no canine

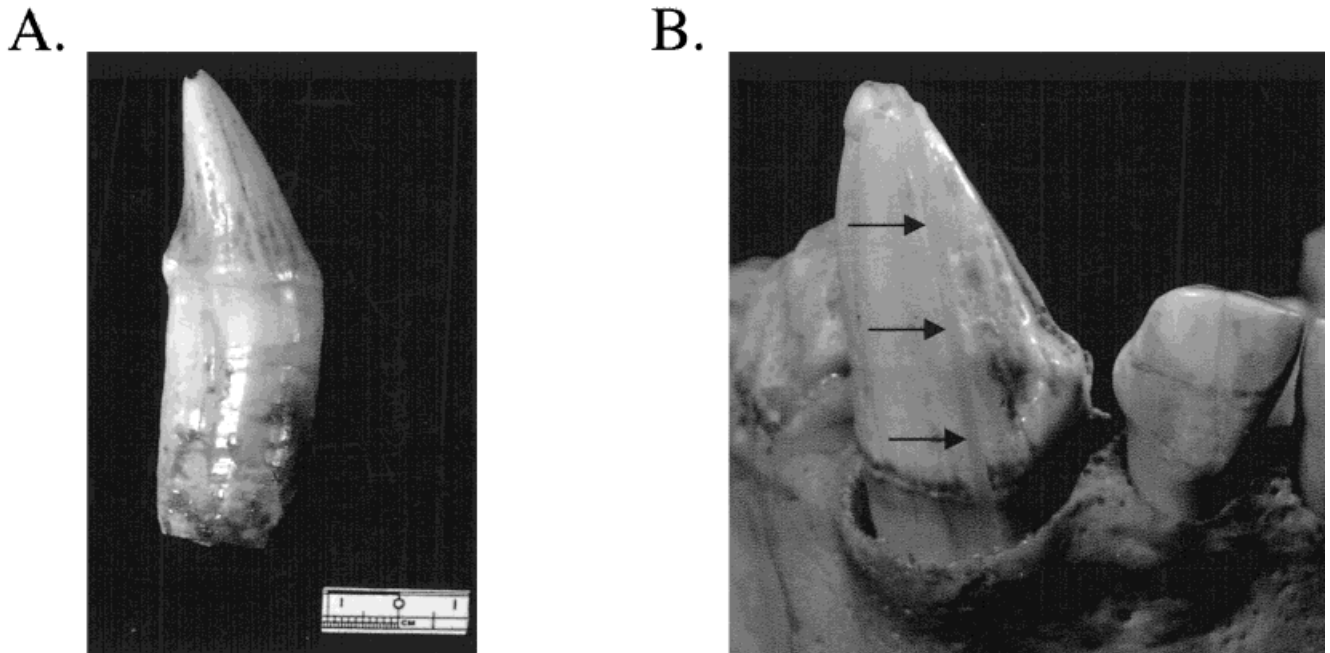


Fig. 1. Photographic series of a great ape canine (A) prior to sectioning and (B) after the canine was reconstructed to its original dimensions (see text), showing the approximately 500- μm area where the thin section was removed (arrows). Pictures not at same scale.

tooth was ever sectioned from a museum collection unless an antimere was present and in good condition. Each great ape canine was extracted from the mandible, cleaned, and replicated (i.e., a cast made) using Coltene™ silicon medium body putty and an epoxy resin casting medium. Prior to sectioning, each canine was coated in cyanoacrylate to minimize the risk of fragmentation of dried or cracked tooth tissues. A Buehler™ Isomet diamond wafering blade saw was used to cut 180–200- μm -thick longitudinal ground sections from each tooth. These were cut from the midline axial plane such that each section included both the cusp tip (and dentine horn) and the entire buccal aspect of each canine crown, thereby encompassing the entire period of crown formation. Sections were then lapped to a final thickness of 100–120 μm , polished with 3- μm aluminum powder, placed in an ultrasonic bath to remove surface debris, dehydrated through a graded series of alcohol baths, cleared in HistoClear™, and mounted with cover slips in DPX™ mounting medium. The remaining halves of the canines were then placed back into the Coltene putty molds, reconstructed to their original dimensions using tooth-colored dental wax, and placed back into their parent mandibles (Fig. 1).

The sections were examined using routine polarized light microscopy and photomontages ($\times 250$) were constructed of the buccal aspect of each tooth crown. To construct longitudinal growth curves of tooth height against time for each tooth, it was first necessary to estimate both cuspal and lateral enamel formation rates. The time to form the first increments of enamel apposition in the cusp was

TABLE 2. Ordinary least squares polynomial regression equations and coefficients of determination (R^2) in a total of 12 hominoid canines and used to predict cuspal enamel growth¹

Species	N	Regression equation	R^2	P-value
<i>Pan</i>	2	$y = 0.41 + 0.31x - 0.0008x^2$	0.991	<0.0001
<i>Gorilla</i>	3	$y = 1.44 + 0.29x - 0.0005x^2$	0.983	<0.0001
<i>Pongo</i>	2	$y = 11.3 + 0.37x - 0.0001x^2$	0.962	<0.0001
<i>Homo</i>	5	$y = -3.63 + 0.42x - 0.00008x^2$	0.992	<0.0001

¹ Each regression is cuspal enamel thickness vs. cuspal formation time in a mixed-sex sample for canines of each extant large-bodied hominoid species.

either 1) estimated directly from counts of daily cross striations along enamel prisms that extend from the dentine horn to the cusp tips (as in Dean, 1998), as was possible in only 12 of the 115 teeth sectioned, or 2) predicted from a series of species-specific polynomial regressions of cuspal enamel thickness against time of cuspal formation based on data from the 12 sections studied in detail (Table 2, Fig. 2).² Tooth heights for the imbricational components of each crown were measured along the buccal EDJ at intervals of 20 long-period striae (Fig. 2). Other studies focusing on crown height variation in great apes (e.g., Kelley and Xu, 1991; Kelley, 1995; Waddle et al., 1995; Kelley and Plavcan, 1998; Plavcan, 2000) recorded a linear measurement of adult buccal crown height from cusp tip to buccal enamel cervix (however defined). It should be noted that in

²The polynomial regressions possessed higher coefficients of determination (i.e., R^2) than linear regression models, and were thus more appropriate for predicting cuspal times in slightly worn specimens.

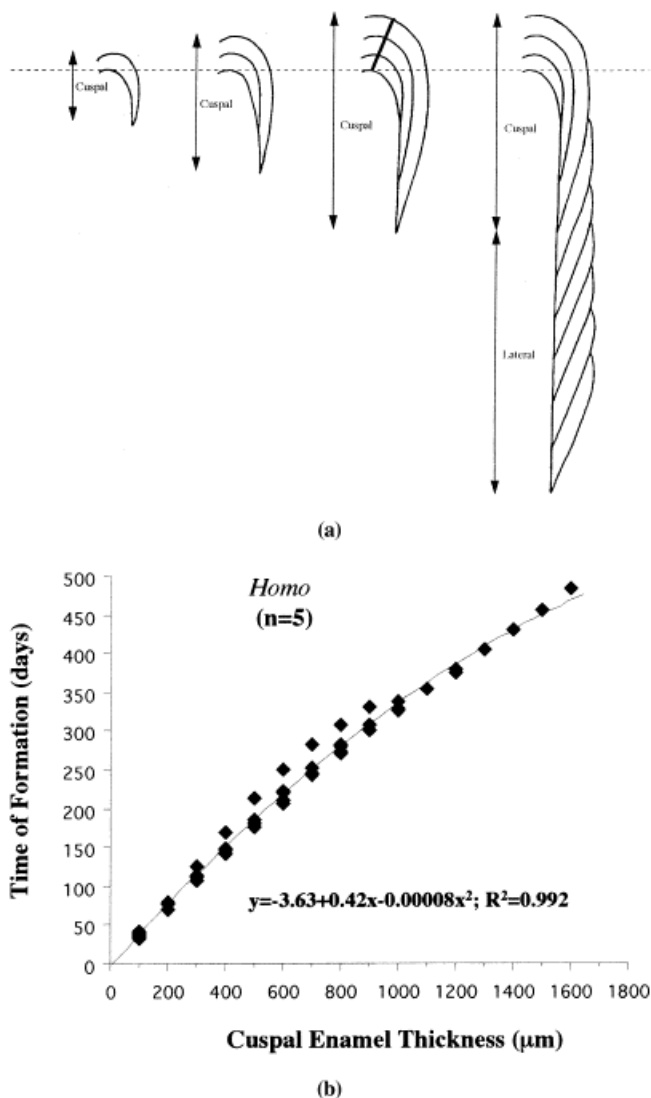


Fig. 2. **a:** Diagram of a series of longitudinal sections through the buccal aspect of a tooth germ at four stages of development. Dotted line is drawn through the dentine horns. Cuspal (or appositional) enamel increases thickness of enamel here, and as a result the tooth germ grows in height above this line. Proliferation of ameloblasts at the cervical loop of the inner enamel epithelium also contributes to an increase in height of the developing tooth below dotted line. This proliferation of ameloblasts continues during lateral enamel formation, after cuspal enamel is complete. Long-period incremental markings are represented in the lateral enamel and illustrate how appositional enamel formation below the cuspal portion contributes to thickness of the buccal enamel only and not to the height of the growing tooth crown. Line drawn from dentine horn to surface of the cusp represents the path of prisms, counted through zones, each 100 µm of cuspal enamel thickness. **b:** Only canines were used where each daily increment (cross striation) could be seen from dentine horn to cusp tip, so that polynomial regressions (see Table 2) are generated for each taxon relating cuspal enamel thickness (abscissa) to time of formation in days (ordinate).

this study, cumulative increases in tooth height were measured along the EDJ. Since this may undulate and is often sinuous, especially in regions where hypoplasias have affected the tooth, total measures of crown height measured in these two

different ways are not directly comparable and tend to be greater on average in this study than in others. The times taken to form lateral enamel formation were determined by multiplying each 20-striae interval by the periodicity. This was calibrated in each individual tooth by counting the number of daily incremental markings (cross striations) between successive long-period striae of Retzius. Periodicities remained constant in any one individual in this study, but varied considerably between individuals of a species. This was in agreement with other studies reviewed by FitzGerald (1998). It is important to note that measurements between striae at the surface of the enamel (or perikymata) cannot be used to reconstruct growth of the crown along the EDJ, as such counts do not reflect true enamel extension rates at the EDJ. Furthermore, marked differences in enamel thickness between taxa, and the tendency for striae to diverge unpredictably as they course through it from the EDJ towards the enamel surface, render estimates of crown height attainment using perikymata inaccurate. When cuspal crown height attainment is summed with lateral crown height attainment, a cumulative measure of increasing crown height throughout the entire period of canine crown formation can be plotted against time into tooth formation. These data are effectively longitudinal growth curves for each of the canine teeth used in the study. In reality, the times of initiation of each tooth would have varied during the first few months after birth. For ease of comparison, each of the longitudinal growth curves was plotted here as if initial mineralization began at birth.

RESULTS

Regression equations for predicting the time taken to form any given thickness of cuspal enamel in each taxon are listed in Table 2. Statistical comparisons of cuspal enamel formation within and among hominoid genera are listed in Table 3, while female and male canine crown formation times and heights are reported in Table 4. From the data reported here, it is clear that sexual dimorphism in canine crown height within any one species of extant great apes results primarily from differences in duration of growth, where males grow enamel for a longer period of time. Differences between great ape taxa result from a combination of both differences in duration and rates of growth.

Differences in cuspal enamel formation times are evident among all hominoid taxa, with *Pan* taking 4.8–8.1 months; *Gorilla* taking 6.6–10.1 months; *Pongo* taking 9.5–12.3 months; and *Homo* taking 10.2–15.8 months to complete cuspal enamel formation (Table 3). Cuspal formation times for these taxa represent approximately 6–9% of the total enamel formation time in canine crowns in *Pan*, 8–16% in *Gorilla*, 8–21% in *Pongo*, and 14–31% in *Homo*. Interestingly, no differences were present between sexes of each species with respect to cuspal formation times (Table 3). These times are longest in the

TABLE 3. Species and sex differences in hominoid cuspal enamel formation times¹

Interspecific analyses	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Homo</i>
<i>Pan</i> (12)				
<i>Gorilla</i> (15)	<0.0001			
<i>Pongo</i> (15)	<0.0001	<0.0001		
<i>Homo</i> (10)	<0.0001	<0.0001	<0.0001	
Intraspecific analyses	Sex	Mean (days ± 1 SD)	Range	P-value
<i>Pan</i>	Male (6)	190.5 ± 39.6	146–242	0.2663
	Female (6)	171.8 ± 7.29	166–182	
<i>Gorilla</i>	Male (8)	278.4 ± 9.38	267–291	0.4231
	Female (7)	256.5 ± 38.4	199–302	
<i>Pongo</i>	Male (8)	337.9 ± 26.6	284–369	0.8969
	Female (7)	337.6 ± 20.4	308–368	
<i>Homo</i>	Male (5)	400.1 ± 53.3	307–473	0.7454
	Female (5)	407.8 ± 29.4	380–449	

¹ Probability values based on Mann-Whitney U tests. Sample sizes are in parentheses. Cuspal enamel formation varied between 4.8–8.1 months in *Pan*; 6.6–10.1 months in *Gorilla*; 9.5–12.3 months in *Pongo*; and 10.2–15.8 months in *Homo*, and represents approximately 6–9% of total enamel formation time in canine crowns in *Pan*; 8–16% in *Gorilla*; 8–21% in *Pongo*; and 14–31% in *Homo*, respectively.

TABLE 4. Mean canine crown formation times (in years ± 1 SD) and mean canine crown heights (in mm ± 1 SD), separated by sex for each hominoid species

Species	Sex	Mean	Range
Crown formation times			
<i>Pan</i> *	Male	6.81 ± 0.56	5.91–7.58
	Female	5.85 ± 0.51	5.28–6.49
<i>Gorilla</i> **	Male	8.54 ± 0.83	7.43–9.78
	Female	5.64 ± 0.94	4.63–7.58
<i>Pongo</i> *	Male	8.73 ± 0.86	7.18–9.64
	Female	5.47 ± 0.73	4.59–6.37
<i>Homo</i>	Male	4.58 ± 0.48	4.17–5.27
	Female	3.98 ± 0.45	3.55–4.56
Canine crown height ¹			
<i>Pan</i> *	Male	20.6 ± 1.73	18.3–22.5
	Female	15.4 ± 0.62	14.7–16.4
<i>Gorilla</i> **	Male	36.7 ± 3.42	33.1–42.3
	Female	22.4 ± 1.57	20.4–24.9
<i>Pongo</i> *	Male	32.9 ± 3.16	28.9–36.4
	Female	19.5 ± 1.43	17.8–21.8
<i>Homo</i>	Male	13.9 ± 2.17	11.9–15.9
	Female	12.5 ± 1.84	10.5–14.8

¹ Canine crown heights measured along the sinuous buccal EDJ, as in this study, are not equivalent to buccal crown heights as measured in some other studies of primate canines (e.g., Kelley, 1995). Results for Mann-Whitney U tests are for differences between sexes of each species.

* $P < 0.01$.

** $P < 0.001$.

cusps of *Pongo* and *Homo*, and are related to the presence of thicker enamel in these species. Modern humans, when compared to all other hominoids, emerge as unique in possessing a significantly higher proportion of cuspal enamel formation relative to total crown formation time (Fig. 3). *Pongo* canines also possess relatively large ratios of cuspal: imbricational enamel formation times, and show some overlap with the range expressed in modern humans. Interestingly, all females possess proportionally (and significantly) more cuspal enamel relative to imbricational enamel than do males, except in *Pan* (see Fig. 3).

Cuspal enamel formation times, imbricational formation times produce added total crown formation

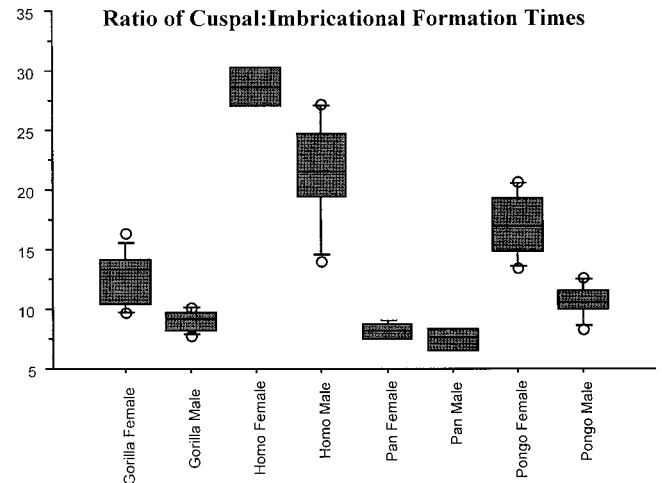
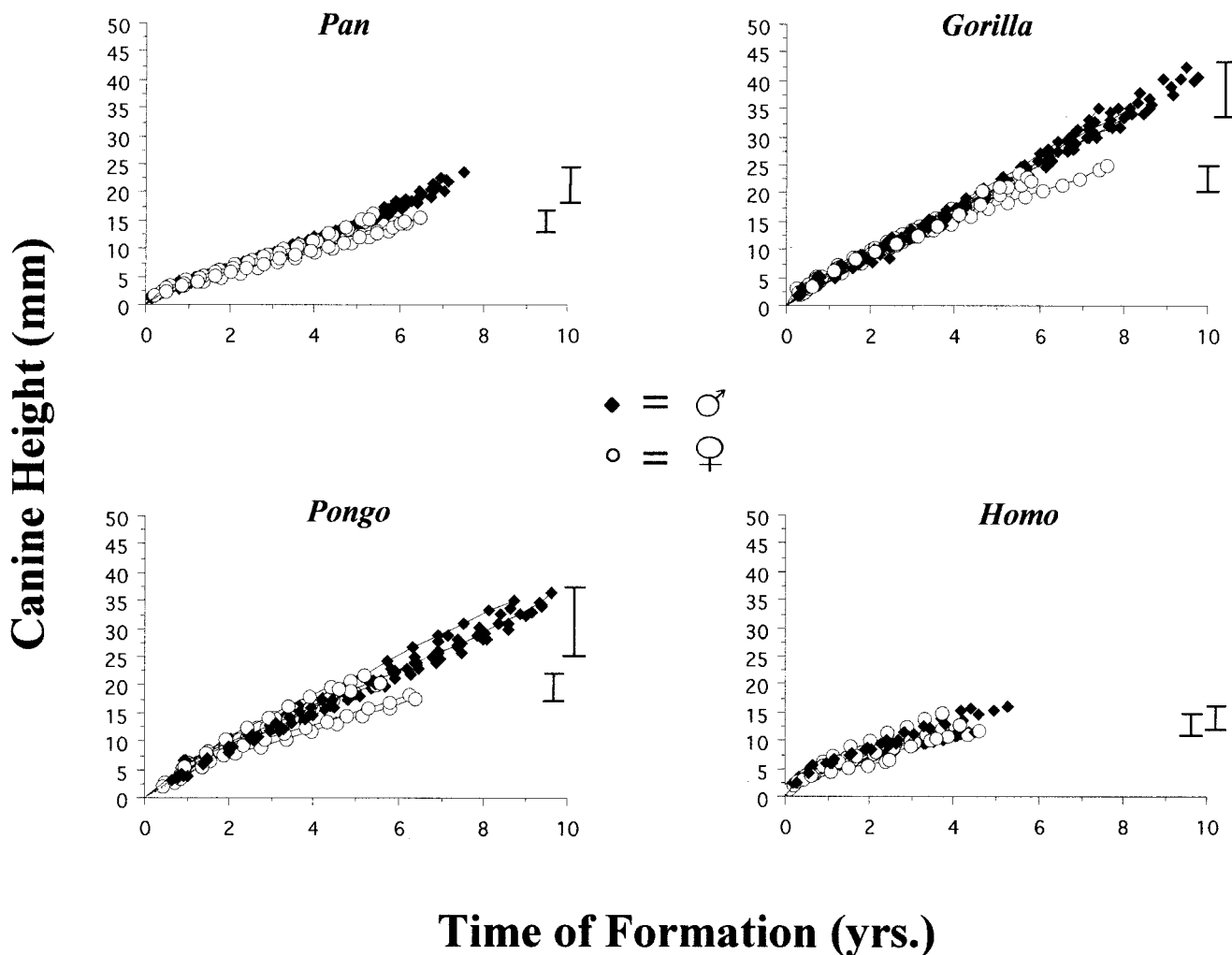


Fig. 3. Box plots of ratio of cuspal to imbricational enamel formation times for males and females of each hominoid species. Ratio calculated as: [(Cuspal formation time/Total crown formation time) × 100].

time (CFT). Differences between the sexes among each hominoid taxa with respect to CFT reflect differences in canine height (Table 4), although as noted above, these are not exactly equivalent to buccal crown heights as measured in some other studies of primate canines, e.g., Kelley (1995). Overall, total CFTs in hominoids span a wide range of ages, with this small sample of female humans taking just 3.5 years, as opposed to male gorillas taking just under 10 years (Table 4).

Estimates of cuspal and lateral (or imbricational) enamel formation rates were used to construct longitudinal growth curves of cumulative increase in canine crown heights plotted against total crown formation time (in days) for each of the taxa studied here (Fig. 4). Significant differences in crown formation times between sexes are apparent in all ape species, and noticeably absent in modern humans. This pattern is also mirrored in the results for canine heights, as defined in this study (Table 4).

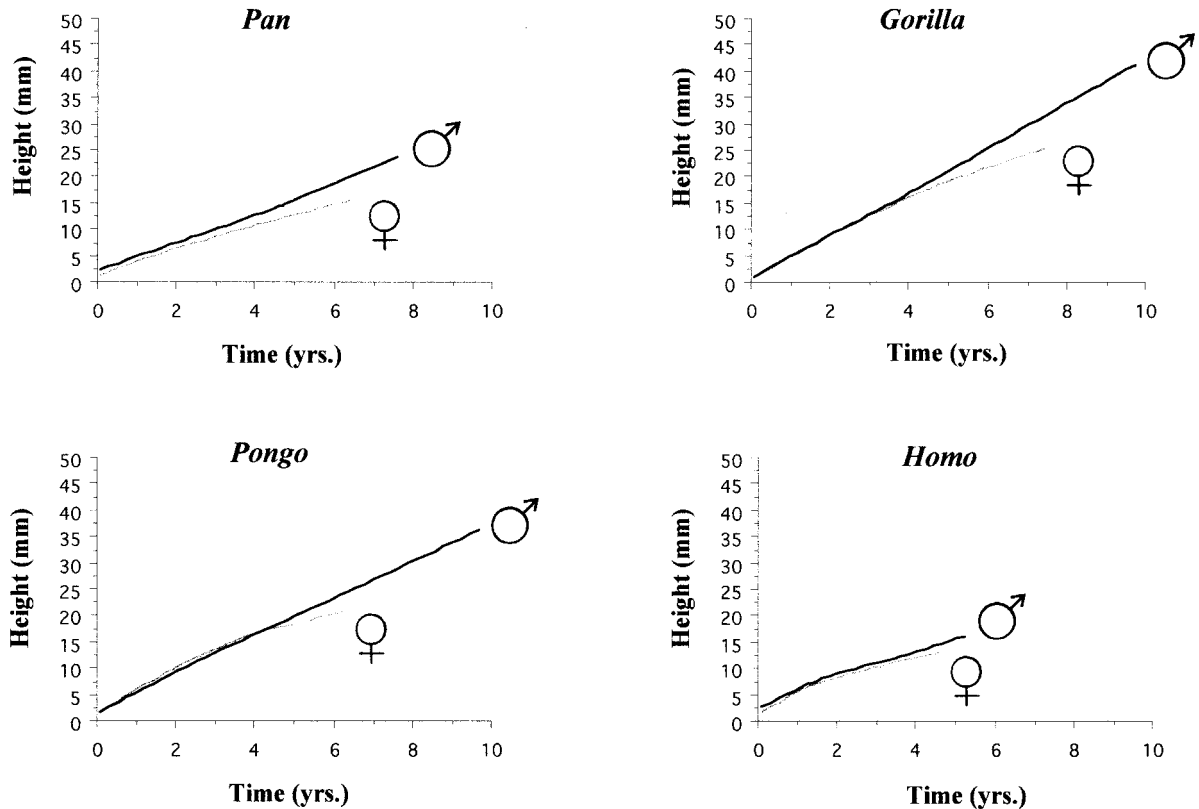


(b)

Fig. 4. a: Longitudinal growth trajectories for male and female hominoid taxa. Canine heights for imbricational components of each crown were measured along the buccal EDJ at intervals of 20 long-period striae (striae of Retzius), and when added to the cuspal component of crown height, provided a cumulative measure of increasing crown height over total period of canine crown formation. Ranges in canine height are indicated to right of graphs, as bars. Total times of formation are determined by multiplying each 20-striae interval by stria periodicity, which was calibrated in each individual tooth by counting the periodicity, or total number of daily incremental markings (cross striations) between successive long-period striae of Retzius (periodicities remain constant in any one individual, but may vary between individuals of a species). **b:** Lowess regressions of longitudinal growth trajectories for males and females for each hominoid species. Lowess regressions are nonparametric, locally weighted, least squares regressions. This technique fits a line through small portions of a bivariate normal distribution of points, and is analogous to the calculation of moving averages in a time series analysis (see Cleveland, 1979; Cleveland and Devlin, 1988; Efron and Tibshirani, 1991; Leigh, 1992).

The highly dimorphic male canine teeth of *Gorilla* and *Pongo* grow for approximately 3–4 years longer than the female canine crowns (Table 4; Fig. 4). The same pattern is evident in *Pan*, though to a much lesser degree; on average, male chimp crowns grow for only a year longer. It is important to note, however, that considerable overlap in male and female crown formation times exists in *Pan*, seeming to mirror the overlap in crown heights. In *Gorilla* and *Pongo*, there is little overlap in canine heights, especially in *Gorilla*. Interestingly, male ape canines exhibit much larger ranges of variation in height than females. Human male and female canines not only share a similar range of variation in crown

height, but also exhibit near-complete overlap in the range for crown formation times; traits which distinguish them from other hominoids. Though neither canine heights nor crown formation times in the sample of modern humans used here differed significantly, mean values of each are greater in males. There is, however, no clear evidence from this sample of teeth that male canines might take longer to form than female canines. Larger samples of reliably sexed modern human canines may provide the basis for a more satisfactory analysis, since it is clear from the literature that when large samples of human teeth are measured, male canines are on the order of 6% taller than female canines (e.g., Kieser, 1990).



(b)

Fig. 4. (continued)

DISCUSSION

Much of the work on sexual dimorphism in great apes over the past few years has focused on the ontogenetic mechanisms underlying adult body size dimorphism (e.g., Leigh, 1992; Leigh and Shea, 1995; Shea, 1985, 1986). This variable is tightly correlated with aspects of reproductive biology and social behavior, and especially with levels of male-male competition (e.g., Plavcan and van Schaik, 1992, 1994, 1997; Plavcan, 1998; Plavcan et al., 1995). A few studies have also documented the levels of sexual dimorphism in adult canine height, either in the context of masticatory function or in diagnosing and sexing samples of fossil hominoids (Washburn and Avis, 1958; Kinzey, 1970; Greene, 1973; Washburn and Ciochon, 1974; Smith, 1981; Lucas et al., 1986; Wood et al., 1991; Kelley, 1995). To date, however, no study has focused on the ontogenetic process(es) responsible for canine dimorphism. The advantage of an ontogenetic perspective is the ability to interpret the processes regulating the development of this feature within the larger framework of life history, behavioral ecology, social structure, etc. The sample size of great ape canines available to us for this study is small; however, it represents the largest existing collection of histological material derived from reliably sexed great apes. More importantly, data derived from each sample of males and

females are longitudinal and therefore sufficient to allow us to meet the aims and objectives of this study.

It has in the past been easier to identify similarities in dental development among living great apes than differences between them. It seems, for example, that all three apes possess the same overall sequence, or “pattern,” of dental developmental stages for each tooth type and even equivalent molar crown formation times (see references in Introduction). The data presented in this study for permanent canines show for the first time that there are clear interspecific differences in both the time (or duration) of enamel formation and in rates of enamel extension. These differences relate not only to both the total duration of canine formation and the rate at which formation proceeds, but to the relative amount of time devoted to cuspal enamel formation.

Cuspal enamel formation

Cuspal enamel formation times are greatest in *Homo* and *Pongo* canines, where enamel thickness is known to be thicker than in *Gorilla* and *Pan* (Schwartz et al., 2001). Cuspal enamel formation times constitute an important component of total crown formation times, especially when crown formation times are short. The combination of a short

crown formation time and thick cuspal enamel distinguishes modern human canines from those of great apes. As early hominin canines resemble modern human canines in their size and morphology, it can be hypothesized that canines of australopithecines should also possess thicker cuspal enamel and shorter crown formation times than canines of great apes. Histological data for one early hominin canine confirm this and suggests that cusp formation is more similar to that of modern humans than of chimpanzees (Dean et al., 1993).

No significant differences in cuspal enamel formation times exist between males or females in any of the species sampled here. This implies that the basis for sexual dimorphism in canine size lies wholly in the rate and/or duration of lateral enamel formation.

Intraspecific differences in total crown formation times

Few data on canine crown formation times in apes are available in the literature, with the exception of those for *Pan*. As noted previously, crown formation times for chimpanzee males and females have been documented on reasonably large samples of captive animals X-rayed at regularly spaced time intervals (Kuykendall, 1996; Kuykendall and Conroy, 1996), but the data for canines, in particular, at key stages of development are sparse. In conjunction with other observations on age at initial mineralization of the canine crown, it appeared from those studies that few clear statistical differences exist in the total time of enamel formation between male and female chimpanzee canines. Those data therefore suggest that differences in rate might account for the disparity in adult canine crown height. In a previous attempt to describe the ontogenetic basis of differences between male and female chimpanzee canine teeth, Dean and Beynon (1991) relied solely on surface perikymata counts in a single male and a single female canine. Results from that study suggested that male canine teeth grow at a rate different from that of females within the same period of time. It is now clear that differences in perikymata spacing result from differences in periodicity of the long-period incremental markings, and since these diverge as they approach the surface, from differences in enamel thickness (Schwartz et al., 2001). The present study was designed to overcome these problems by projecting measurements of increase in tooth crown height back to the EDJ. Measurements of tooth height made in this way are therefore homologous with those made directly from developing human tooth germs belonging to individuals of known age (Liversidge et al., 1993).

The data presented here for *Pan* on enamel formation times differ slightly from those of Kuykendall (1996) and Kuykendall and Conroy (1996), and are based on larger numbers of individual canine teeth. Histological estimates of canine enamel formation times consistently yield greater crown for-

mation times than those from radiographic studies, which may be due to the difficulties in scoring dental stages from plain-film radiographs (see Beynon et al., 1998; Kuykendall, 2001). From our results, it is now clear that differences in rates of enamel formation do not entirely account for adult canine dimorphism in chimps, but that male chimps grow enamel for a greater period of time.

The data for male and female *Gorilla* and *Pongo* canine crown formation times are the first reliable data available on sexed samples, and demonstrate clearly that males achieve taller canine crown heights than females by growing canine crowns for a longer duration in both species. This is also true for *Pan*, but the more sexually dimorphic *Gorilla* and *Pongo* males form enamel for much longer periods of time than do *Pan* males. This finding is an interesting parallel with that for increase in weight in common chimpanzees (Gavin, 1953) and for somatic growth for some ape species (Shea, 1985, 1986; Leigh and Shea, 1995, 1996).

Interspecific differences in ontogenetic processes

As comparative data have been lacking for most hominoid species, few studies have been able to pinpoint any clear differences among hominoids in the details of dental development. It can be seen from Table 4 that the mean times taken for male and female hominoids to form enamel are calculated, respectively, as 6.8 and 5.9 years in *Pan*, 8.4 and 5.6 years in *Gorilla*, 7.3 and 5.5 years in *Pongo*, and 4.5 and 4.0 years in *Homo*. Males consistently take a longer period of time to form enamel than do females. While male chimpanzees only exceed females by 1–3 years in enamel formation times, male orangutans and gorillas exceed females by greater amounts of time and occasionally take up to twice as long as females to complete enamel formation (the range of enamel formation times in our sample of *Gorilla* males was 7.4–9.8 years, and in *Pongo* males, 7.2–9.6 years). In this sample, the difference between modern human males and females is not significant, but it is clear that such a small degree of sexual dimorphism as exists between human male and female canines (6% or so in larger sexed samples; see Kieser, 1990) cannot be detected with so few individuals. It is far easier to distinguish male and female great apes and to identify differences between *Pan*, *Gorilla*, and *Pongo*.

Differences in canine crown heights between male *Pan* and the taller, more dimorphic male *Gorilla* and *Pongo* canines result both from differences in total time taken to form enamel, and from faster rates of growth in *Gorilla* and *Pongo* (Fig. 5a). The mean ranges of female canine crown formation times are similar in *Pan*, *Gorilla*, and *Pongo*. However, interspecific differences between female *Pan* canine crown heights and those of *Gorilla* and *Pongo*, which are taller, result primarily from differences in rates of growth (Fig. 5b). It is therefore a combination of

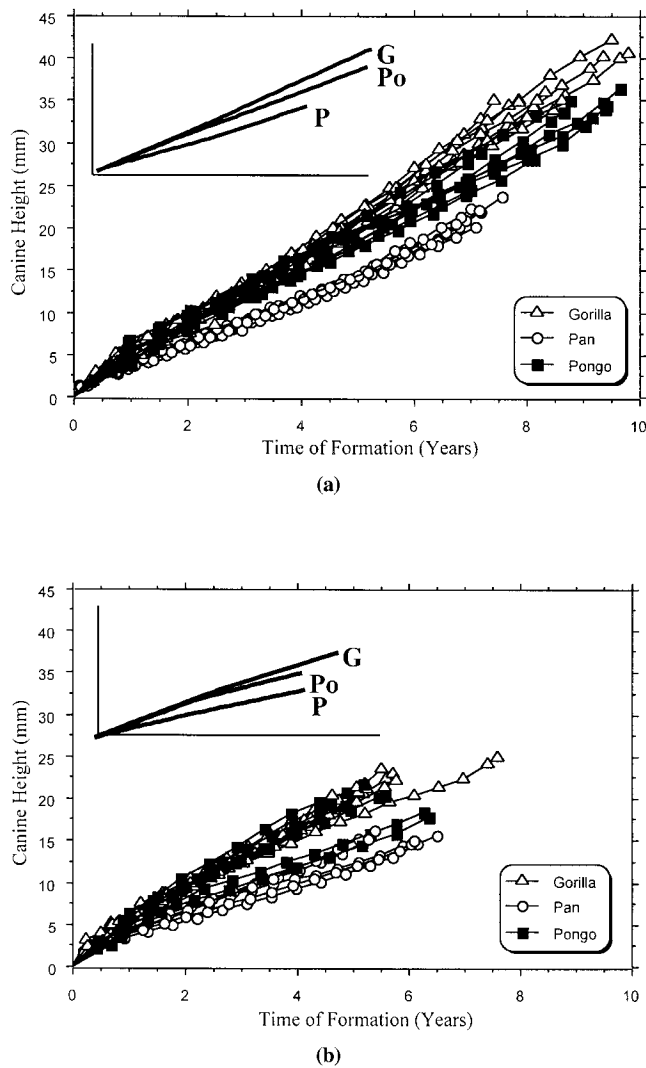


Fig. 5. Interspecific comparisons of canine ontogeny for (a) male and (b) female hominoids. Insets depict Lowess regression lines by sex for gorillas (G), orangutans (Po), and chimpanzees (P).

duration and rate differences that accounts for disparity in canine crown heights among different species of living great apes.

Variance dimorphism and canine formation

Some have argued that variance in samples of males exceeds that in samples of females when sexually dimorphic characters are measured in adults (Oxnard et al., 1985; Cronin, 1991; Kelley, 1995; Martin and Andrews, 1993). In each of the longitudinal growth plots, male canines in each taxon appear to be more tightly grouped, especially at earlier ages, than those for females (Table 5; Figs. 4, 5). In other words, the growth curves for male great ape canines seem to follow a tighter trajectory. Female great apes appear to be spread over a greater range of high and low rates of growth throughout their total duration of canine formation. Coefficients of variation calculated for crown heights within three

different age categories and at crown completion do not support the variance dimorphism model for any hominoid species. It is possible that small sample sizes of males and females and differences in the distribution of individuals within each of the age categories, as defined here, might be important underlying factors. Nonetheless, the general observation that seems to hold, at least visually, contributes little to the debate about how differences in distributions of measurements of adult canine variables made by Oxnard et al. (1985) might have arisen during ontogeny.

Comparative perspectives on size dimorphism, canine dimorphism, and bimaturation

In a series of studies, Shea (1985, 1986), Leigh (1992, 1995), and Leigh and Shea (1995, 1996) explored the ontogenetic bases of body size dimorphism in primates. In the context of earlier studies (Wiley, 1974; Ralls, 1977; Jarman, 1983), they showed that several different developmental pathways exist to attain sexual dimorphism in apes and explained how these processes are related to the evolution of sexual size dimorphism. In general, males can either grow for longer periods of time than females, males and females can grow for similar periods of time with males growing at faster rates, or a combination of rate and duration differences between sexes can exist. The exact process by which a species achieves dimorphism is strongly linked to sexual selection and a variety of social, behavioral, and ecological variables (e.g., Clutton-Brock et al., 1977; Plavcan and van Schaik, 1997; Leigh, 1995). For instance, protracted growth (slow rates over a longer duration) in males serves as a risk avoidance strategy: deferring maturation avoids competition between males (Wiley, 1974; Jarman, 1983; Janson and van Schaik, 1993). Over time, this results in bimaturation, or the extension of the male growth period relative to that of the female. Instances also exist where size dimorphism is developed through sex differences in rates of growth with limited bimaturation (Shea, 1986). Reducing growth periods overall precludes the evolution of sexual dimorphism through bimaturation, and this characterizes extant lemurs (Leigh and Terranova, 1998).

Evidence for body size dimorphism through bimaturation as a risk aversion strategy for juvenile male apes is somewhat equivocal. For instance, hylobatids exhibit no sexual differences in either rate or duration of body weight growth, and are therefore not dimorphic. Both pygmy chimpanzees and gorillas become dimorphic primarily through sex differences in the duration of body weight growth (i.e., bimaturation), but sex differences in the rate of growth accounts for the majority of dimorphism in common chimpanzees. Orangutans, on the other hand, attain dimorphism through a unique pattern (at least among apes) of indeterminate male growth. Variations in ontogenetic processes leading to body size dimorphism are seen as evolutionary responses

TABLE 5. Coefficients of variation for canine height at three different age intervals during time of crown formation and at completion of canine crown height in total sexed sample of extant hominoid canines

Species	Sex	Coefficient of variation			
		1.5–2.5 years	3.5–4.5 years	4.5–5.5 years	Complete
<i>Pan</i>	Male	0.151	0.101	0.181	0.084
	Female	0.149	0.133	0.120	0.040
<i>Gorilla</i>	Male	0.165	0.121	0.083	0.093
	Female	0.138	0.117	0.080	0.070
<i>Pongo</i>	Male	0.197	0.112	0.084	0.096
	Female	0.213	0.170	0.147	0.073
<i>Homo</i>	Male	0.118	0.147	0.142	0.155
	Female	0.219	0.130	0.171	0.147

to a number of factors including territoriality, mate competition, and resource distribution. These factors, plus complicated interactions with other factors, may therefore be more important than mediating risk aversion in some ape species. Given the role of canines as a weapon and their use in threat displays and agonistic behavior (Plavcan and van Schaik, 1992; Plavcan, 1993), it may be more reasonable to expect canine dimorphism to develop through delayed male maturation, i.e., bimaturism. All of the ape species examined here follow the pattern of canine dimorphism through bimaturism (see Fig. 4). Slight rate differences do exist, especially towards the terminal end of the growth period, and this fits well with available data for body size dimorphism that suggest the presence of a “female component” to dimorphism (Leigh and Shea, 1995).

The selective pressures leading to the development of canine dimorphism through bimaturism may not be entirely clear, but do suggest a testable theoretical framework for future studies. For instance, data on the ontogeny of canine formation in the monomorphic hylobatids should mimic that for body size dimorphism and not show any sexual differences in rates or duration of growth.

Our study shows that ontogenetic processes regulating canine dimorphism are not the same as those responsible for dimorphism in body size for certain hominoid species. Dental growth is often considered more conservative than somatic growth (Demisch and Wartmann, 1956; Lewis and Garn, 1960; Watts, 1990), though our results suggest that some underlying mechanisms responsible for dimorphism, in the widest sense, may be more intimately related than previously thought. Wood et al. (1991) and Humphrey et al. (1999) demonstrated that modern human mandibles are more dimorphic than those of *Pan*, and yet the canine teeth of *Pan* are clearly more dimorphic than those of modern humans. Many early hominin mandibles are also more sexually dimorphic than both those of modern humans and *Pan*, but their canine teeth are less dimorphic than those of any living great ape. This all suggests that whatever controls tooth growth is, at least to some degree, independent of whatever controls bone growth. Thus, future studies should focus on integrating comparative ontogenetic data on both somatic and dental growth.

CONCLUSIONS

Unlike the case for body size dimorphism, canine dimorphism in all extant large-bodied apes is the result of bimaturism, i.e., male hominoids consistently take longer to form canine crowns than do females of the same species. On the contrary, modern humans exhibit no differences in either rate or duration of canine crown, thus explaining the limited size dimorphism in this one tooth. Male orangutans and gorillas occasionally take up to twice as long as females to complete enamel formation, while female canine crown formation times are similar in *Pan*, *Gorilla*, and *Pongo*. Interspecific differences in canine size, however, are due primarily to rate differences during ontogeny.

Based on our findings, it seems clear that a more extensive histological study of canine growth in primates would make a major contribution to unraveling the important findings of previous metrical studies and help with the diagnosis and interpretation of fossil hominoid material. For instance, there is considerable debate about the sex and/or number of species represented at many fossil localities and how these might be diagnosed (Kelley and Xu, 1991; Waddle et al., 1995; Kelley and Plavcan, 1998; Kelley and Alpagut, 1999). Importantly, the new data presented here provide a developmental framework with which to supplement morphometric methods designed to sort mixed samples of sexually dimorphic fossil ape teeth. Another key question that can now be addressed is how the growth processes in early fossil hominin canine crowns compare with those now known for modern human and chimpanzee canines. It may turn out that quantifying differences in growth processes is as useful as quantifying differences in size when trying to distinguish early fossil hominins from hominoids.

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