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## Developmental processes and canine dimorphism in primate evolution

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### Abstract

Understanding the evolutionary history of canine sexual dimorphism is important for interpreting the developmental biology, socioecology and phylogenetic position of primates. All current evidence for extant primates indicates that canine dimorphism is achieved through bimaturism rather than via differences in rates of crown formation time. Using incremental growth lines, we charted the ontogeny of canine formation within species of Eocene *Cantius*, the earliest known canine-dimorphic primate, to test whether canine dimorphism via bimaturism was developmentally canalized early in primate evolution. Our results show that canine dimorphism in *Cantius* is achieved primarily through different rates of crown formation in males and females, not bimaturism. This is the first demonstration of rate differences resulting in canine dimorphism in any primate and therefore suggests that canine dimorphism is not developmentally homologous across Primates. The most likely interpretation is that canine dimorphism has been selected for at least twice during the course of primate evolution. The power of this approach is its ability to identify underlying developmental processes behind patterns of morphological similarity, even in long-extinct primate species.

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### Introduction

Members of the genus *Cantius* (Notharctidae, Adapiformes, Primates) preserve the earliest

evidence of sexual dimorphism in the primate fossil record (Gingerich, 1995). Sexual dimorphism is defined as an intraspecific difference between males and females in some aspect of their

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non-reproductive anatomy (e.g., body size, tooth size, pelage color) and, to some degree, is related to sexual selection (Darwin, 1871). Understanding one particular type of dimorphism, canine sexual dimorphism (CSD), is critical for interpreting the developmental biology, socioecology and phylogenetic position of primate groups. Simply stated, CSD is defined as males of a species having larger canines than females. The phenomenon is widespread among extant anthropoids and absent to weak in extant prosimians (Leutenegger and Kelley, 1977; Plavcan and van Schaik, 1992, 1997; Kappeler, 1993, 1996; Plavcan et al., 1995). The magnitude of CSD is strongly correlated with patterns of intrasexual aggression, competition, group size, body size, and demography though the precise mechanisms underlying its evolution are complex (Leutenegger and Kelley, 1977; Plavcan and van Schaik, 1992, 1997). Identifying the ontogenetic trajectories underlying canine dimorphism is therefore critical for better understanding the links among function, development, phylogeny and the evolutionary mechanisms regulating the expression of this complex morphological feature.

In principle, CSD can be achieved through alterations of either the duration or rate of crown formation. Previous work across a wide range of extant primate taxa has demonstrated the role of bimaturism in body size dimorphism within anthropoid primates (Leigh, 1992). Bimaturism is the process of males and females growing at the same rate, but with males growing for a longer period of time (Jarman, 1983). Bimaturism is the dominant process responsible for CSD in most anthropoids for which data exist, and the only process responsible for CSD in the extant apes, *Pan*, *Gorilla* and *Pongo* (Schwartz and Dean, 2000; Leigh et al., in press). Generally, strepsirrhines are not body size dimorphic nor do they display large degrees of canine dimorphism. This is apparently related, at least in some cases, to the unique ecogeography of Madagascar and patterns of strepsirrhine social hierarchy, seasonality and reproductive synchrony (Kappeler, 1993; Leigh and Terranova, 1998; Wright, 1999; Richard et al., 2002).

Given that most extant primates for which data are available achieve CSD through bimaturism, we tested the hypothesis that it would also be the

dominant development process regulating male and female canine growth in the earliest known sexually dimorphic primate, *Cantius*.

## Materials and methods

A total of 18 mandibular and maxillary canines of *Cantius* (*C. ralstoni*, *C. trigonodus*, and *C. mckennai*) were selected (Table 1). Sex determinations were assigned prior to our study and were based on differential canine height and canine base dimensions (Fig. 1A). This is possible because in notharctines (including *Cantius* and *Notharctus*), differences in male-female canine height are significantly greater than that in both canine monomorphic (*Aotus*) and dimorphic (*Saimiri*, *Cebus*) extant primates (Gingerich, 1995). In all species of *Cantius* for which canines are known, there is a bimodal distribution of canine size. In notharctines that are closely related to *Cantius* (such as *Notharctus* and *Smilodectes*) a similar bimodal distribution is present with larger canines being associated with more robust crania possessing large sagittal and nuchal crests, while those specimens with smaller canines possess more gracile skulls with less cresting (Krishtalka et al., 1990; Alexander, 1994). While crania of *Cantius* are extremely rare, similar canine bimodality suggests that, if known, crania of *Cantius* would resemble those of other notharctines in dimorphic features. The canines used here were isolated specimens and were identified as male or female based on comparisons with canines associated with gnathic remains and known size ranges of species-specific canines.

Specimens were embedded in epoxy resin to minimize the risk of fragmentation. Using a Microslice™ annular blade saw, one 180–200µm thick longitudinal ground section was removed from the midline axial plane such that each section included both the cusp tip (and dentine horn) and the entire buccal aspect of the crown, thereby encompassing the entire period of crown formation. Each section was polished on a Logitech™ lapping machine with a diamond suspension paste, cleaned in an ultrasonic bath to remove surface debris, dehydrated through a graded series of ethanol baths,

Table 1

*Cantius* canines examined. Age given as biochronological zone of the Wasatchian (early Eocene) North American Land Mammal Age (oldest = Wa0, youngest = Wa7). Abbreviations: UM = University of Michigan; SC = University of Michigan Sand Coulee locality; MP = University of Michigan McCullough Peaks locality; L = left, R = right. Specimens in bold preserved incremental features in enamel and dentine and were used in analyses.

Specimen	Species	Description	Locality	Age	Sex
UM 91444	<i>Cantius abditus</i>	L maxillary canine	MP-72	Wa6	Male
UM 73878	<i>Cantius mckennai</i>	Maxillary canine	SC-192	Wa3	Male
<b>UM 76736</b>	" "	<b>L maxillary canine</b>	<b>SC-3</b>	<b>Wa3</b>	<b>Female</b>
UM 77013	" "	Maxillary canine	SC-54	Wa2	Female
UM 79004	" "	Mandibular canine	SC-34	Wa3	Male
UM 85192	" "	R mandibular canine	SC-54	Wa2	Male
UM 85195	" "	R mandibular canine	SC-213	Wa2	Female
UM 85196	" "	L mandibular canine	SC-213	Wa2	Male
UM 85215	" "	L maxillary canine	SC-54	Wa2	Male
<b>UM 85216</b>	" "	<b>L maxillary canine</b>	<b>SC-54</b>	<b>Wa2</b>	<b>Female</b>
UM 85232	" "	L maxillary canine	SC-64	Wa4	Female
<b>UM 85189</b>	<i>Cantius ralstoni</i>	<b>R mandibular canine</b>	<b>SC-210</b>	<b>Wa1</b>	<b>Male</b>
UM 85191	" "	L mandibular canine	SC-161	Wa1	Female
<b>UM 85207</b>	" "	<b>R maxillary canine</b>	<b>SC-4</b>	<b>Wa1</b>	<b>Male</b>
UM 66811	<i>Cantius trigonodus</i>	Maxillary canine	SC-112	Wa4	Male
<b>UM 72947</b>	" "	<b>Maxillary canine</b>	<b>SC-64</b>	<b>Wa4</b>	<b>Female</b>
UM 73186	" "	Maxillary canine	SC-255	Wa4	Female
<b>UM 79953</b>	" "	<b>R maxillary canine</b>	<b>SC-113</b>	<b>Wa4</b>	<b>Male</b>

cleared in HistoClear™ and mounted with cover slips in DPX™ mounting medium.

Short- and long period lines in both enamel (cross striations and Retzius lines, respectively) and dentine (von Ebner and Andresen lines, respectively) were used to obtain a chronology of increasing crown height throughout the entire period of canine crown formation (Schwartz and Dean, 2000) (Fig. 1B). Only a subset (n = 6; 3 males, 3 females) of these canines preserved a record of their growth in the form of incremental markings in enamel and dentine (see Table 1). Standard growth curves were generated by plotting accumulating canine height against the duration of crown formation. These curves were constructed by determining both cuspal and lateral enamel formation rates (Schwartz and Dean, 2000; Fig. 2). The duration of cuspal growth was determined by measuring daily rates of enamel secretion throughout cuspal formation. The height of the cuspal portion of the crown was measured as the linear distance from the cusp tip to the point of the enamel-dentine junction coincident with the last appositional, or cuspal, striae of Retzius (Fig. 2A-C). Together these yield the rate of attainment of

cuspal enamel height. Rate of attainment of lateral enamel was estimated by first measuring the linear distance along the buccal enamel-dentine junction at intervals of 10 long-period striae (Fig. 2D-F). The time taken to form each 10-striae segment of the crown was determined by multiplying each segment by the striae periodicity (i.e., the number of daily cross-striations between successive long-period striae; which was either 2 or 3 in the individuals in our sample). Summing the time to crown height attainment of cuspal and lateral yields a cumulative measure of the rate of increasing crown height throughout the entire period of canine crown formation, as well as the overall time of formation (Fig. 3).

## Results

Resultant longitudinal data from each canine demonstrate that CSD in *Cantius* is predominantly a product of rate differences in crown formation, with male canines growing at a faster rate than those of females (Fig. 3). If CSD in *Cantius* were the result of bimaturism, slopes of male and female

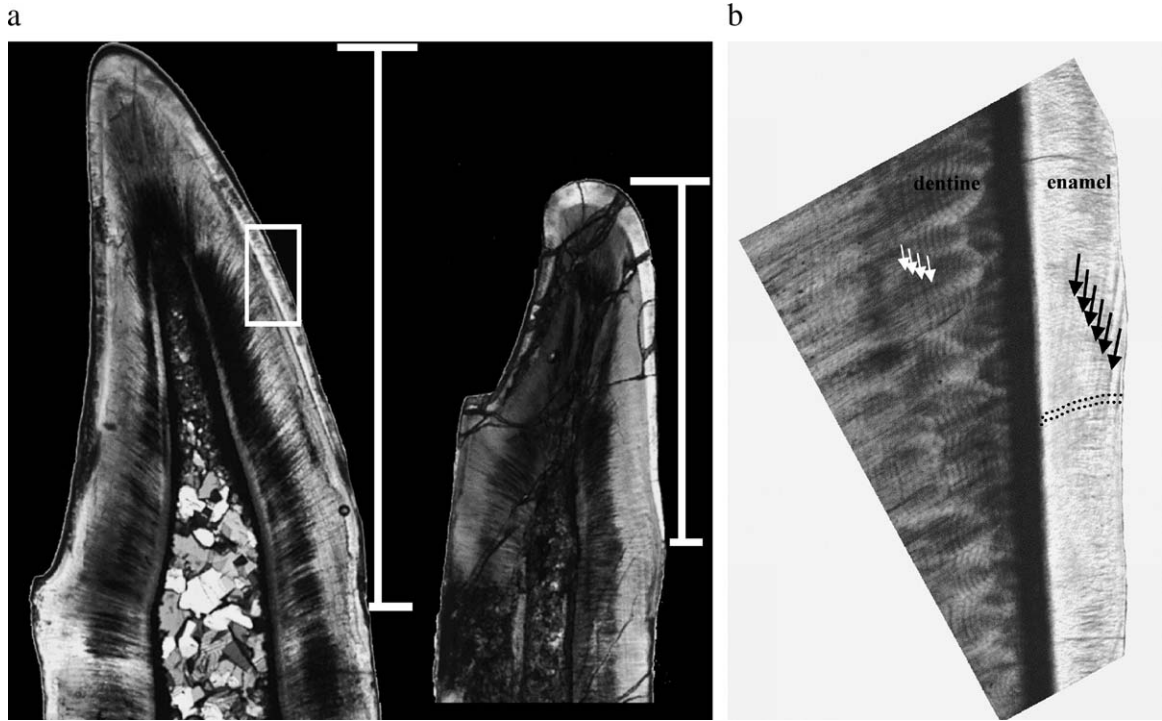


Fig. 1. (A) Low-magnification (x4) photograph of a section through a male (left; specimen UM 85189) and female (right; specimen UM 85191) canine crown of *Cantius ralstoni* illustrating dimorphism in canine crown height (white bar). White box indicates the area highlighted in Fig. 1B. (B) Higher magnification (x20) view of the enamel and dentine in the lateral enamel of UM 85189 showing the various incremental features used in our analysis. Striae of Retzius are indicated by black arrows in enamel while Andresen lines are indicated by the white arrows in dentine. Both are long-term incremental markings and displayed a periodicity of either 2 or 3 days in our sample of *Cantius*. Periodicities were easily measured by counting the number of daily growth lines (or cross striations) along enamel prisms (indicated by dotted lines) between adjacent Retzius lines.

canine growth trajectories would be identical. Modeling growth profiles using ordinary least squares regression (OLS) of canine height (y) on time of formation (x) (Leigh et al., in press) supports this significantly faster growth rate in males (Figs. 3, 4).

Two potentially confounding variables in our study are: 1) the mixed sample of maxillary and mandibular canines; 2) the inclusion of only one sex for two of the three included species. At least in apes and humans, there is no evidence to date suggesting that processes regulating canine crown formation differ between dental arcades (Schwartz

and Dean, 2000). This appears to be the case in *Cantius* as well, as shown by the shared ontogenetic trajectory for the maxillary and mandibular canines of *C. ralstoni* (see Fig. 3A). Also, for the species that is represented by both sexes, *C. trigonodus*, the pattern of ontogeny mirrors that of the mixed species sample as a whole (Fig. 4).<sup>1</sup>

## Discussion and conclusions

Longitudinal data are robust even for reduced samples, suggesting that sex-related differences in

<sup>1</sup> CSD is predominantly the result of rate differences, not bimaturism, in particular for *C. trigonodus*. Further studies may find, however, that bimaturism is a contributing factor when both males and females from other canine-dimorphic adapiform primate species are analyzed.

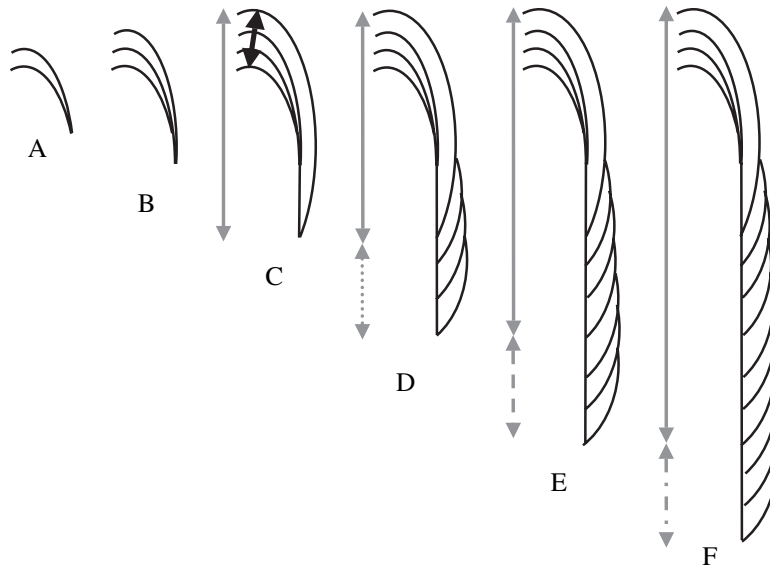


Fig. 2. Canine growth curves were generated by plotting accumulating canine height against the duration of crown formation. Each growth profile was generated by determining the time it takes to form both cuspal and lateral enamel. The rate of attainment of cuspal enamel height was determined by plotting the time taken to form cuspal enamel thickness (black arrow; A-C). The height of the cuspal portion of the crown associated with the time to form cuspal enamel was measured as the linear distance from the cusp tip to the point along the enamel-dentine junction with the last appositional, or cuspal, striae of Retzius (solid grey arrow; C). Rate of attainment of lateral enamel was estimated by first measuring the linear distance along the buccal enamel-dentine junction at known intervals of 10 long-period striae (dotted grey arrow; D). The time taken to form each 10-striae segment of the crown was determined by multiplying each segment by the striae periodicity. This process was repeated for the next 10-striae segment of the crown (dashed grey arrow; E), and so on (dash-dot grey arrow; F) until the full height of the canine was reached (adapted from Schwartz and Dean, 2000).

rates of canine growth are indeed present in at least some Eocene notharctine primates. Given the complex associations among canine dimorphism, rates of canine growth, size, intrasexual competition, etc., that exist across Primates, it is not yet possible to link the novel developmental pathway exhibited by *Cantius* to any explicit life history strategy. Furthermore, it is unclear whether selection targeted male or female growth rates, though each scenario would have important implications for reconstructing life history strategies.

The key to interpreting variation in the ontogeny of CSD lies in understanding that natural selection targets phenotype. Our results indicate that the phenotype of larger male canines is an important enough morphological feature that it has been selected for at least twice during course of primate evolution: once via rate differences, as in *Cantius*, and once via bimaturism, as in extant anthropoids.

In anthropoids, the presence and magnitude of CSD are strongly associated with levels of intermale and interfemale competition, and so are used as anatomical correlates of social organization in living and fossil primates (Leutenegger and Kelley, 1977; Rosenberger et al., 1985; Krishtalka et al., 1990; Plavcan and van Schaik, 1992, 1997; Kappeler, 1993; Plavcan et al., 1995; Simons et al., 1999). Slight to moderate levels of CSD are present in several extant strepsirrhines but are unrelated to differences in body size, mating system or frequency of aggression (Kappeler, 1990, 1996). Levels of CSD in species of Eocene *Cantius*, however, exceed those of extant strepsirrhines and even some canine-dimorphic anthropoids (Plavcan and van Schaik, 1992; Gingerich, 1995; Plavcan et al., 1995; Kappeler, 1996) suggesting a moderate degree of intermale competition perhaps in concert with low levels of female competition.

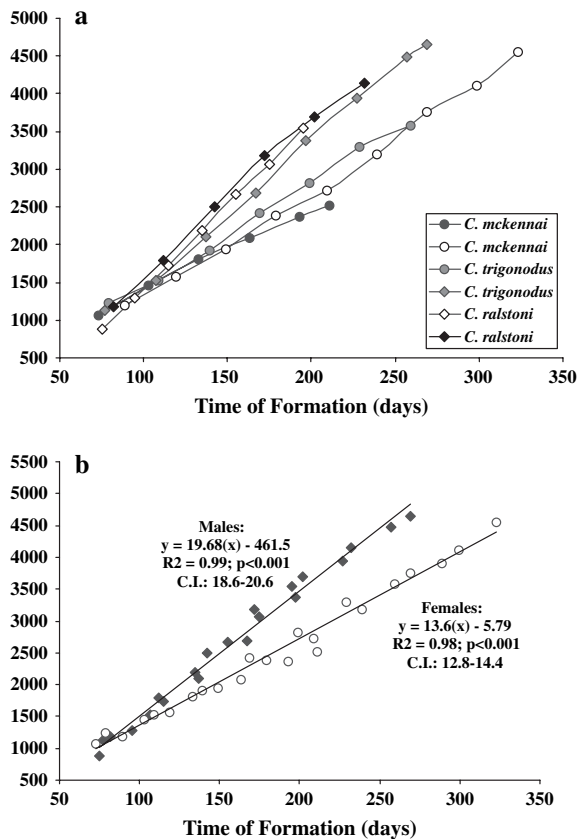


Fig. 3. Canine growth curves for Eocene *Cantius* spp. (A) Longitudinal growth curves for the ontogeny of canine crown height in males (diamond) and females (circle). Note that this is a mixed-species plot, which explains why certain male canines (e.g., the shorter *C. ralstoni*) are not taller than certain female canines (e.g., the taller *C. mckennai*). (B) OLS regression statistics including regression equation, coefficient of determination ( $R^2$ ), significance of the slope, 95% confidence intervals (CI) about the slope for both males and females. Note the coincident trajectories of the two *C. ralstoni* specimens, the mandibular canine, UM 85189, and the maxillary canine, UM 85207.

### Phylogenetic significance of CSD

Our results bear directly on arguments concerning the phylogenetic position of adapiforms relative to other primates (Kay et al., 1997). Although we examined only a single genus of notharctine adapiform, CSD has been documented within other adapiforms including other notharctines (*Notharctus*, *Smilodectes*), cercamoniines, adapids, and sivaladapids (Gingerich, 1981, 1995;

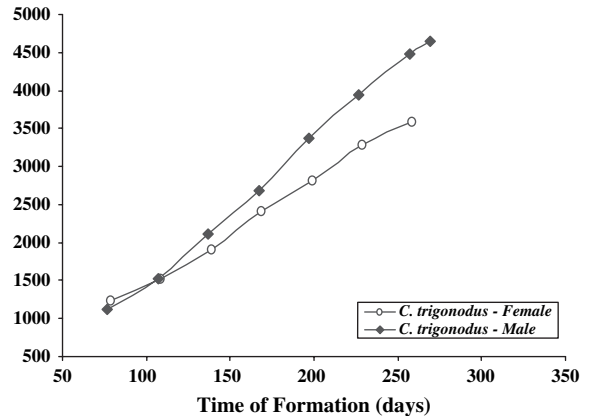


Fig. 4. Growth profiles for the male (diamond) and the female (circle) canines of *C. trigonodus*.

Gingerich and Sahni, 1984; Krishtalka et al., 1990; Rasmussen, 1994; Simons et al., 1995; Kay et al., 1997). Adapiformes have been viewed by some as potential antecedents of modern strepsirrhines (e.g., Kay et al., 1997), despite the fact that marked CSD is not a hallmark of the latter. Other studies have linked adapiforms exclusively with anthropoids (Rasmussen, 1994; Simons et al., 1995). CSD is a common feature of anthropoids but is achieved predominantly through bimaturation rather than through rate differences as documented here for *Cantius*. Our data do not support a special relationship between adapoids and anthropoids, though this conclusion is preliminary owing to the small number of adapoid specimens available for use in this initial study. Regardless of the phylogenetic position of adapoids relative to extant primate groups, our data clearly show that canine dimorphism may be functionally homologous across primates, but it is not developmentally so.

Additional ontogenetic data from other adapiformes, as well as extant strepsirrhines with low levels of CSD, will provide insights into the apparent uniqueness of achieving CSD through rate differences rather than bimaturation. It is also important to examine the developmental basis of canine dimorphism in early anthropoids, such as *Catopithecus* and *Proteopithecus* (Simons, 1995, 1997), to identify when during primate evolutionary history the anthropoid pattern of achieving CSD via bimaturation emerged, and whether the

feature is more characteristic of crown versus stem anthropoids. Likewise, it is critical to explore canine dimorphism in other groups, such as social carnivores, as variation in the ontogenetic basis of CSD is also closely linked to social, ecological, and life history variables in non-primate mammals (e.g., van Valkenberg and Sacco, 2002).

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