



Modularity of the anthropoid dentition: Implications for the evolution of the hominin canine honing complex



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ARTICLE INFO

Article history:

Received 5 May 2013

Accepted 3 July 2015

Available online 11 August 2015

Keywords:

Morphological integration

Constraint

Canine reduction

Australopithecus

ABSTRACT

In most anthropoid primates, the maxillary canine, mandibular canine, and mesial mandibular premolar form a functional complex that hones the canines. Characters in functional complexes are predicted to covary genetically, which constrains their evolutionary independence. As a result of substantial changes to canine and honing premolar size and shape, hominins are characterized by the apomorphic loss of canine honing. In early hominins, changes in canine and 'honing' premolar size and shape appear to have been uncoordinated, which is unexpected if there is strong genetic covariation coupling these teeth. Using the pattern and magnitude of phenotypic dental size covariation in extant anthropoids, results of this study indicate that certain dimensions of the anthropoid honing complex are characterized by strong size covariation within species and that canine and honing premolar size have evolved in a coordinated manner in both males and females, which undermines arguments that the complex is selectively important only in males. Further, there is no evidence for negative or strong positive covariance between canine and either incisor or postcanine size. If patterns of phenotypic covariation reflect genetic covariation, this suggests that canine reduction was unlikely to have been a dependent change associated with the development of postcanine megadontia or incisor reduction.

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1. Introduction

The canine honing complex is a nearly ubiquitous functional complex in the nonhuman anthropoid dentition. During early hominin evolution, the canines and honing premolar were altered in size and shape, which resulted in the loss of functional canine honing and a shift to apically-dominated canine wear. Fossils attributed to *Ardipithecus* and the earliest species of *Australopithecus* suggest that maxillary canine height reduction preceded mandibular canine height reduction, that substantial reduction in canine heights preceded reduction in their basal sizes, and that the P₃ retained morphological relicts of its honing past long after the maxillary canine was reduced and the function of canine honing was lost (Haile-Selassie, 2001; Haile-Selassie et al., 2004, 2009; Semaw et al., 2005; Kimbel and Delezene, 2009; Suwa et al., 2009; Ward et al., 2010; Delezene and Kimbel, 2011; Manthi et al., 2012). Thus, the fossil record currently points to a mosaic transformation of the hominin 'honing' complex (Ward et al., 2010; Manthi et al., 2012). As the canines and honing premolar form a functional

complex in extant anthropoids, a hypothesis of morphological integration predicts that the size and shape of these teeth should covary as a result of genetic and/or developmental factors and that they should have evolved in a coordinated manner (e.g., Wagner et al., 2007; Klingenberg, 2008). Therefore, their evolutionary independence in early hominins indicates that either the elements of the complex are not coupled genetically in extant nonhuman anthropoids or that selection was particularly strong on only some aspects of the complex and acted upon genetic variance not shared among all dimensions of the canines and mesial mandibular premolar.

In most nonhuman anthropoid primates, canines are used in visual threat displays and occasionally as weapons, especially during intraspecific conflicts (e.g., Walker, 1984; McGraw et al., 2002; Leigh et al., 2008; Galbany et al., 2015). Many anthropoid primates have tall, projecting canines; however, canine size varies between sexes and among species. Anthropoid species characterized by high intensity and frequency of agonism have larger relative canine size than species with less frequent and less intense agonism (Kay et al., 1988; Plavcan and van Schaik, 1992; Plavcan, 1993, 1998, 2001; Thoren et al., 2006). This pattern holds in both males and females (Plavcan et al., 1995); however, since male–male

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competition for mates results in greater variance in reproductive success than female competition for resources, selection is stronger for large, hypertrophied male canines (Plavcan et al., 1995).

In addition to crown height, other aspects of anthropoid canines suggest that selection has shaped their use as weapons. For example, though many male (and some female) canine crowns are quite tall, they are as resistant to bending stresses as are carnivore canines, which is perhaps an adaptation to resist breakage during conflicts involving the canines (Plavcan and Ruff, 2008). Additionally, as it slides against the labial face of the maxillary canine (C^1) during occlusion, the mandibular canine (C_1) is honed along its distal face. At the same time, occlusion between the distolingual surface of the C^1 and the mesiobuccal surface of the mesial-most mandibular premolar (P_2 in platyrrhines, P_3 in catarrhines) hones the C^1 , sharpening its distal crest from the apex towards the cervix of the tooth (Zingesser, 1969; Walker, 1984).

The honing premolar, be it P_3 or P_2 , is specialized for its function as a honing device and is morphologically distinct from more distal premolars, which Greenfield and Washburn (1992) describe as premolar heteromorphy. Though the honing premolars may not be homologous in platyrrhines and catarrhines, they share a suite of anatomical features that reflects their function as a hone for the C^1 . Generally, the honing premolar is unicuspid and the single cusp, the protoconid, is taller than on the more distal premolar(s). In addition, catarrhines have a mesiobuccal root that is partly covered by an enamel extension that forms the honing surface. The tall, centrally-placed protoconid, elongated mesial face, and inferior projection of enamel create a broad sloping surface that hones the C^1 (e.g., Zingesser, 1969).

Models predict that natural selection shapes genetic covariation to be strong among characters in functional complexes and to be weak between characters in different complexes (e.g., Cheverud, 1989, 1996; Wagner et al., 2007); such functionally and genetically coupled traits are said to be ‘integrated’ (Olson and Miller, 1958; Chernoff and Magwene, 1999). Genetic covariation is reflected within populations as phenotypic covariation. As a result, patterns of phenotypic covariation are predicted to reflect functional modularity so that the phenotype is divisible into variational ‘modules,’ which are “set[s] of covarying traits that vary relatively independently of other such sets of traits” (Wagner et al., 2007: 921; Wagner, 1996; Wagner and Altenberg, 1996; Klingenberg, 2008). Since the honing premolar and canines work together to complete the function of honing, a hypothesis of integration predicts that phenotypic covariation should exist within species for the elements of the canine honing complex.

The pattern of genetic variance and covariance among a series of characters is summarized by the genetic variance-covariance matrix (the **G**-matrix or, simply, **G**). Typically, **G** is estimated in pedigreed populations with large sample sizes; therefore, it is difficult to estimate in wild populations where familial relationships are uncertain (e.g., de Oliveira et al., 2009). As a result, estimates of **G** in primates have been limited to a few laboratory populations (e.g., *Papio* sp. at the Southwest National Primate Research Center [SNPRC]) (e.g., Hlusko and Mahaney, 2007a,b, 2009 Koh et al., 2010). Due to limitations in the estimation of **G**, the phenotypic variance-covariance matrix (**P**-matrix or **P**) is often used to estimate **G** in non-pedigreed samples (Cheverud, 1988a). For a wide assortment of traits and in diverse taxa, this substitution has been shown to be valid (e.g., Cheverud, 1988a; Roff, 1995; Waitt and Levin, 1998). Indeed, when dental size **P**-matrices estimated from wild-shot cercopithecoid samples were compared to the **G**-matrix of SNPRC *Papio*, both Hlusko and Mahaney (2007a) and Grieco et al. (2013) found that **P** and **G** were similar. Since **P** is affected by both genetic and environmental influences, it is desirable for the effect of the environment to be minimal. The relative effect of

additive genotypic and environmental variance on the phenotypic variance of a character is defined as its narrow-sense heritability (h^2); as h^2 approaches 1, the effect of the environment on variance is minimized. Overall, estimates of h^2 for dental size in humans and nonhuman primates are relatively high. For linear measures of dental size in *Homo sapiens*, h^2 estimates generally range from 0.6 to 0.8 (e.g., Townsend and Brown, 1978; Townsend et al., 2006), which is similar to h^2 estimates for linear and areal dimensions of the dentition in SNPRC baboons (Hlusko et al., 2002, 2011; Hlusko and Mahaney, 2007a,b). In fact, for 68 dimensions of the SNPRC baboon dentition, Hlusko et al. (2011) report an average h^2 of 0.56 after the effects of age and sex are taken into account. Thus, for the samples and elements that have been considered, primate dental size h^2 has been shown to be high.

Genetic covariation is an evolutionary constraint (Maynard Smith et al., 1985) that limits the ability of characters to evolve independently (e.g., Klingenberg, 2010; Marroig and Cheverud, 2010). In the most extreme case where characters are perfectly correlated, they must change states simultaneously when selection acts on either of them. For characters that are highly correlated but that retain some independent variance, selection tends to pull them along the major axis of covariation (termed the ‘line of least evolutionary resistance’; Schluter, 1996; Marroig and Cheverud, 2010). For genetically-coupled characters, phenotypic correlations observed among species are in part an extension of the genetic relationship that exists within species (e.g., Lande, 1979; Cheverud, 1982, 1988b, 1989, 1996).

If fitness is affected by the interaction of characters that are genetically uncorrelated, then, to maintain functional equivalence during evolutionary change, the characters must independently respond to selection. This is referred to as ‘selective covariance.’ In this case, unlike what is observed with characters that strongly covary genetically, no pattern of phenotypic covariation is expected within species even though one exists among species (e.g., Armbruster and Schwaegerle, 1996). Therefore, selection that has acted upon genetically correlated and uncorrelated traits can result in significant among-species phenotypic correlation; however, it is possible to distinguish between the two processes if both the within- and among-species patterns of covariation are examined.

Few studies have examined the hypothesis that the canine honing complex is a variational module in anthropoid primates. Both Cochard (1981) and Grieco et al. (2013) included canine basal dimensions in their examinations of cercopithecoid dental size covariation. Cochard examined *Colobus badius* males and females separately and found similar patterns of covariation. Within each arch, the observed ranges ($r^2 = 0.00–0.46$ for females; $r^2 = 0.03–0.48$ for males) and averages ($r^2 = 0.19$ for females; $r^2 = 0.15$ for males) between the canines and all other dental dimensions are similar in both sexes. Between the C^1 and C_1 bases, Cochard found covariation that ranged from $r^2 = 0.05–0.35$ and no significant differences between males and females. Grieco et al. (2013) estimated **P** for maxillary dental size in six cercopithecoid taxa and also compared these **P**-matrices to estimates of **P** and **G** in SNPRC baboons. They found that **P** is similar among samples and similar to **G** in the SNPRC sample. Among all samples, phenotypic covariation between canine and incisor size ($r^2 = 0.02–0.62$, average $r^2 = 0.21$) and canine and postcanine size ($r^2 = 0.00–0.64$, average $r^2 = 0.16$) are similar. Observed covariation between the length and width of the maxillary canine, though, is stronger ($r^2 = 0.13–0.90$; average $r^2 = 0.53$). The Cochard and Grieco et al. studies suggest that the pattern of covariation is similar among cercopithecoids, is similar in males and females, and that canine basal size covaries with the size of teeth outside the complex, though generally at a lower absolute value than between the basal dimensions of the canines. However,

neither canine heights nor the length of the premolar honing surface were included in the Cochard and Grieco et al. studies.

Among species, Greenfield and Washburn (1992; Greenfield, 1992) assessed the correlation between canine and honing premolar size in a broad sample of anthropoid primates. They found a significant correlation between male C¹ projection (they did not measure C¹ crown height) and the length of the mandibular premolar honing surface; however, a statistically significant correlation was not observed in females. Greenfield (1992) interpreted this difference to reflect the selective importance of the honing complex in males and its relative unimportance in females, which supported his dual selection hypothesis for canine morphology (e.g., Greenfield, 1992, 1993; critiqued by Plavcan and Kelley, 1996). Plavcan (1993) questioned the functional relevance of their metric, which does not include the entire crown height; indeed, the honing facet on the C¹ extends above the postcanine occlusal plane (Personal observation). Given that only a portion of C¹ height is represented by its projection and that females typically have a shorter C¹ than conspecific males, canine projection often captures a smaller fraction of total C¹ height in females than it does in males. As a result, it is possible that Greenfield's metric fails to capture the correlation of female C¹ height, which is the more functionally relevant measure as regards honing, and premolar honing surface length.

That males and females may express different among-species correlation patterns for C¹ height and premolar honing surface length generates hypotheses about the existence of genetic covariation among characters of the honing complex. If, in fact, the teeth have not coevolved¹ in females, then it is possible that C¹ height and the length of the premolar honing surface are not genetically coupled; thus, change into any dimension of phenotype space has been genetically unconstrained throughout anthropoid evolution. In males, the honing premolar may have independently tracked changes in C¹ height to maintain functional honing at different canine sizes; that is, the C¹ and honing premolar have selectively covaried (sensu Armbruster and Schwaegele, 1996). Alternatively, sex-specific factors may create genetic correlations in the male honing complex that do not exist in the female honing complex. As phenotypic correlations are expected to reflect genetic correlations, these alternatives can be evaluated if both the within- and among-species patterns of phenotypic covariation are estimated in both males and females, which is the strategy employed in this study.

While a modular perspective predicts minimal covariation between characters in different functional complexes, some have predicted that genetic covariation extends between the canines and the incisors and/or the postcanines. Drawing attention to similar trends in anterior dental reduction in *Theropithecus* and hominins, Jolly (1970) offered several models to explain such convergence, including one that posited selection for reduced incisor size and a pleiotropic connection between incisor and canine size. Similarly, Greenfield (1993) suggested that the canine lies at the border of two morphogenetic fields, and that, especially in females, is shaped by selection to act as an incisor. If either the Jolly (1970) or Greenfield (1993) models are correct, then canine and incisor size should positively covary within species. Others have hypothesized a developmental trade-off between the sizes of the anterior and

posterior teeth (McCollum and Sharpe, 2001). If this model is correct, then canine size should negatively covary with postcanine size within species because “it is conceivable that increasing the size of any one subunit may occur at the expense of others... the postcanine dentition may have been developmentally correlated with reduction of the canine” (McCollum and Sharpe, 2001:487).

This study evaluates several hypotheses that relate to the modularity of the anthropoid dentition. It is hypothesized that the canine honing complex is a variational module separate from the incisors and postcanines (except for the premolar honing surface length). Both within and among species, phenotypic covariation is predicted to be strong and positive between canine heights and premolar honing surface length and weaker between dimensions of the honing complex and those of the incisors and postcanines. The McCollum and Sharpe (2001) hypothesis that the anterior and posterior teeth negatively covary in size is also tested. Furthermore, if negative genetic covariation has influenced the among-species diversification of dental size, then a significant negative among-species size correlation will be observed. If Greenfield's observation that the honing complex has coevolved in males but not in females (1992; Greenfield and Washburn, 1992) accurately captures the evolution of C¹ height and premolar honing surface length, then among-species analyses should indicate significant covariation only in males. Greenfield's observations indicate two potential explanations for the among-species pattern: 1) that genetic covariation is absent among elements of the complex in both males and females, or 2) that genetic covariation exists only among dimensions of the male complex. If genetic covariation exists in either sex, then within-species phenotypic covariation will be strong. Correctly identifying the pattern of covariation among elements of the complex has implications for interpreting the mosaic pattern of character change in the early hominin ‘honing’ complex.

2. Materials

Museum collections with a high likelihood of containing an adequate sample of unworn or minimally worn canines were identified a priori. In total, data were collected from 1739 individuals from 37 anthropoid species (Table 1; Supplementary Online Material [SOM] Fig. S1). To address patterns of within-species covariation, it is necessary to minimize confounding influences (e.g., genetic drift and selection between populations) that could affect the estimated strength of phenotypic covariation if populations with varying dental sizes are pooled. Therefore, for each taxon, an attempt was made to measure individuals from as geographically limited an area as possible. Ten samples with large sample sizes identifiable to the level of subspecies were selected for investigations of intraspecific covariation (Table 1 and SOM Table 1).

3. Methods

3.1. Measurements

Using standard odontometric definitions (Swindler, 2002), the buccolingual (BL) or labiolingual (LaL) breadth and mesiodistal (MD) length were measured for all maxillary and mandibular teeth (Fig. 1). Molar breadths correspond to the trigon/trigonid breadths of Swindler (2002). The breadth and length of the honing premolar were excluded from analysis because of the low repeatability of these measures. Incisor MD lengths were measured on the lingual side as the maximum distance perpendicular to the crown's height. The height of each canine was measured from the tip of the canine to the enamel-dentin margin on the labial side of the tooth (Fig. 1). The length of the premolar hone was measured from the tip of the protoconid to the end of the mesiobuccal enamel extension, which

¹ The term ‘coevolution’ is used throughout this paper to describe the coordinated change of characters (traits) among populations or species. Coevolution is a portmanteau of ‘correlated evolution.’ The use of coevolution to describe such change should not be confused with the use of the word to describe the coadaptation of species to one another (as in host–parasite interactions). This use of coevolution is consistent with other studies (e.g., Edwards, 2006).

Table 1
Taxa analyzed.

Taxon	♂	♀	Taxon	♂	♀
<i>Ateles geoffroyi vellerosus</i> ▲	44	42	<i>Macaca mulatta mulatta</i>	5	0
<i>Callicebus cupreus discolor</i>	9	6	<i>Macaca nemestrina nemestrina</i>	12	14
<i>Cebus libidinosus libidinosus</i> ▲	47	46	<i>Macaca nigra</i>	15	8
<i>Chlorocebus aethiops hilgerti</i>	7	15	<i>Macaca sinica</i>	25	20
<i>Cercopithecus cephus cephus</i> ▲	48	31	<i>Miopithecus ogouensis</i>	9	12
<i>Cercopithecus nictitans nictitans</i> ▲	50	38	<i>Nomascus concolor</i>	10	5
<i>Cercopithecus pogonias grayi</i> ▲	42	32	<i>Pan troglodytes schweinfurthii</i>	12	10
<i>Colobus badius powelli</i>	0	7	<i>Pan troglodytes troglodytes</i> ▲	54	57
<i>Colobus guereza caudatus</i>	13	14	<i>Pithecia monachus monachus</i>	11	0
<i>Colobus satanas</i> ▲	26	27	<i>Pongo abelii</i>	15	12
<i>Erythrocebus patas</i>	12	10	<i>Pongo pygmaeus</i>	50	45
<i>Gorilla beringei</i>	20	14	<i>Presbytis entellus thersites</i>	0	7
<i>Gorilla gorilla gorilla</i> ▲	76	58	<i>Presbytis rubicunda</i>	28	27
<i>Hoolock hoolock</i>	47	25	<i>Presbytis vetulus</i>	7	18
<i>Hylobates klossii</i>	23	15	<i>Pygathrix nemaesus nigripes</i>	13	0
<i>Hylobates lar carpenteri</i> ▲	52	55	<i>Rhinopithecus roxellana</i>	0	7
<i>Lagothrix cana</i>	20	30	<i>Symphalangus syndactylus syndactylus</i>	16	18
<i>Lagothrix poeppigi</i>	26	24	<i>Theropithecus gelada</i>	14	6
<i>Macaca fascicularis fascicularis</i> ▲	66	60			

A ▲ indicates a sample assessed in intraspecific analyses.

corresponds to the same measurement in Greenfield and Washburn (1992). All measurements were collected using fine-point Mitutoyo digital calipers and recorded to the nearest one-tenth of a millimeter.

3.2. Sample size criteria

For all intraspecific analyses, except for those involving canine heights, a sample size of $n = 20$ was deemed minimal. This threshold is arbitrary, but given the inconsistency of estimates of variance-covariance at small sample sizes (e.g., Ackermann, 2009), it was necessary to restrict analyses to those samples that are reasonably well represented. As canines (especially the C^1) wear (Walker, 1984; Leigh et al., 2008; Galbany et al., 2015) and often

break at their apices, there were fewer adequately-sized samples available for their analysis within species; therefore, the sample size criterion was relaxed for C^1 height in a few cases. The smallest C^1 height sample size accepted was $n = 15$. For the interspecific analyses of covariation, which were conducted on species means, smaller sample sizes were permitted; however, no sample with fewer than five individuals was included.

3.3. Estimating intraspecific covariation

Because of the interest in potential sexual differences in patterns of covariation, males and females were considered separately. The % boot macro (<http://support.sas.com/kb/24/982.html>) was used within SAS v9.1.3 for the UNIX system to estimate covariation

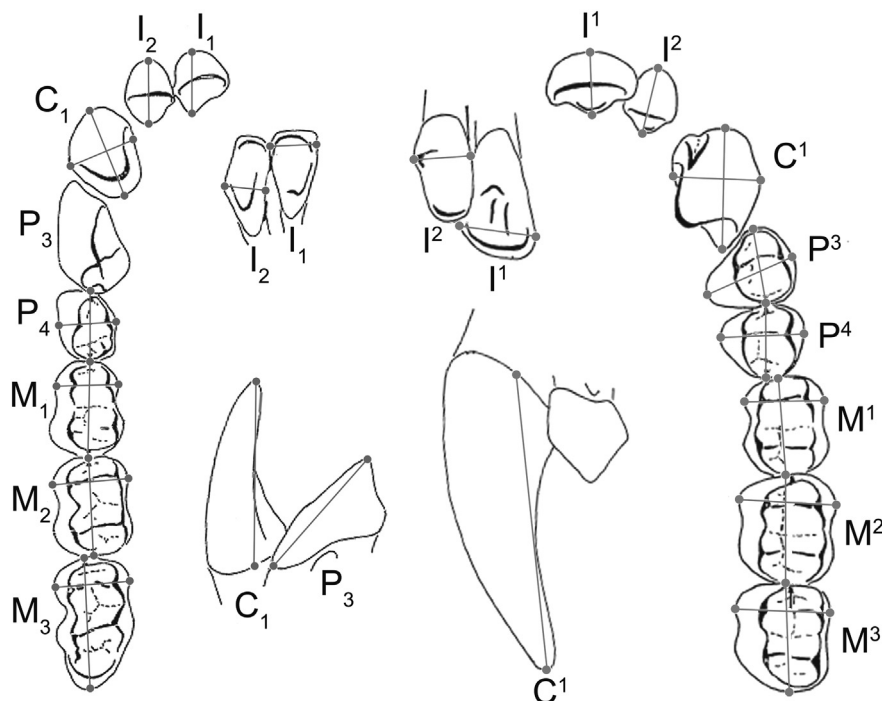


Figure 1. The measurements considered as depicted on the dentition of *Nasalis larvatus* (figure modified from Plavcan [1990]). See text for more description.

within species, which is reported as the coefficient of determination (r^2). The bootstrapping procedure used 10,000 iterations and the bias-corrected mean was reported as the sample estimate and the bias-corrected confidence interval was used to determine statistical significance. Instances of negative covariation (i.e., where the sample Pearson's correlation coefficient is negative) are indicated in (SOM Tables 2–15).

3.4. Estimating interspecific covariation

Because species means violate the assumption of independence among data points, inherent in statistical testing, their use has been criticized for analyses of interspecific correlations. Following other studies of character coevolution (e.g., Edwards, 2006), among-species correlations were assessed using phylogenetically-independent contrasts (e.g., Felsenstein, 1985; Garland et al., 1992; Pagel, 1992; Nunn and Barton, 2000; Barton, 2006), which were computed using PDTREE within Phenotypic Diversity Analysis Programs (PDAP, <http://www.biology.ucr.edu/people/faculty/Garland/PDAP.html>; Garland et al., 1999; Garland and Ives, 2000). The following molecular studies were used as references to create the phylogeny (SOM Fig. 1) from which independent contrasts were calculated: Platyrrhini (Opazo et al., 2006; Wildman et al., 2009), Hylobatidae (Whittaker et al., 2007; Matsudaira and Ishida, 2010; Thinh et al., 2010), Cercopithecinae (Tosi et al., 2004; Li et al., 2009), and Colobinae (Ting, 2008). The general consensus tree from 10kTrees (<http://10kTrees.fas.harvard.edu>; Arnold et al., 2010) was also used as a reference for constructing the phylogeny. Complications arise because some taxa included in this analysis were not analyzed in recent molecular phylogenies. For example, *Cercopithecus pogonias* could not be located in a molecular phylogeny, so its phylogenetic placement was based on phenotypic data that group *C. pogonias* and *Cercopithecus mona* in the 'mona group' of guenons (Groves, 2003). Branches were scaled using Pagel's (1992) branch length transformation (SOM Fig. 1).

4. Results

4.1. Canine dimensions within species

For C_1 height, 19 within-species comparisons were made with C_1 LaL and 19 were made with C_1 MD. Of these 38 comparisons, 24 are significantly different from zero and all are positive in direction (SOM Table 2). For C^1 height, 13 within-species comparisons were made with both C^1 LaL and C^1 MD. Of these 26 comparisons, 11 are significantly different from zero and all estimates are positive (SOM Table 3). Average covariation for heights and MD and LaL dimensions range from $r^2 = 0.14$ – 0.20 and are only slightly higher if basal size is calculated as $\sqrt{(C_1\text{LaL} \cdot C_1\text{MD})}$ (Table 2, SOM Tables 2 and 3). In males and females of all taxonomic groups, positive covariation, which is generally less than $r^2 = 0.20$, is observed between canine heights and basal sizes.

Covariance between LaL and MD dimensions of each canine is stronger, on average, than between heights and basal size. Average covariation is similar for the C_1 and the C^1 ($r^2 = 0.32$ and 0.34 , respectively) (Table 2, SOM Tables 2 and 3). The basal dimensions of each canine covary more strongly on average in platyrrhines ($r^2 = 0.51$ for $C_1\text{LaL}$ – $C_1\text{MD}$ and $r^2 = 0.36$ for $C^1\text{LaL}$ – $C^1\text{MD}$) and hominoids ($r^2 = 0.43$ for $C_1\text{LaL}$ – $C_1\text{MD}$ and $r^2 = 0.36$ for $C^1\text{LaL}$ – $C^1\text{MD}$) than in cercopithecids ($r^2 = 0.22$ for $C_1\text{LaL}$ – $C_1\text{MD}$ and $r^2 = 0.21$ for $C^1\text{LaL}$ – $C^1\text{MD}$) (SOM Tables 2 and 3).

In all taxonomic groups and in both sexes, stronger covariation is observed between homologous dimensions of the upper and lower canines than between heights and basal size of each canine. Between the C^1 and C_1 basal sizes (calculated as $\sqrt{[\text{MD} \cdot \text{LaL}]}$) and heights both

Table 2

Weighted average within-species covariation for mandibular and maxillary canine size for samples listed in Table 1.

	C_1 MD	C_1 LaL	C_1 base
C_1 height	$\delta r^2 = 0.23$ $\varphi r^2 = 0.17$	$\delta r^2 = 0.23$ $\varphi r^2 = 0.18$	$\delta r^2 = 0.27$ $\varphi r^2 = 0.21$
C_1 MD	–	$\delta r^2 = 0.42$ $\varphi r^2 = 0.31$	–
	C^1 MD	C^1 LaL	C^1 base
C^1 height	$\delta r^2 = 0.21$ $\varphi r^2 = 0.18$	$\delta r^2 = 0.22$ $\varphi r^2 = 0.11$	$\delta r^2 = 0.20$ $\varphi r^2 = 0.16$
C^1 MD	–	$\delta r^2 = 0.41$ $\varphi r^2 = 0.23$	–
	C_1 height	C^1 base	C_1 base
C^1 height	$\delta r^2 = 0.71$ $\varphi r^2 = 0.51$	C^1 base	$\delta r^2 = 0.65$ $\varphi r^2 = 0.49$

covary on average around $r^2 = 0.55$ (Table 2 and SOM Table 4). As outlined in the Methods, the minimum sample size for analyses of canine heights was set at $n = 15$; as a result, only a single male cercopithecoid sample (*Cercopithecus cephus*) and a single platyrrhine male sample (*Cebus libidinosus*) were included in the analysis of canine height covariation (though three hominoid samples are included). In both *C. libidinosus* and *C. cephus* males, the estimate is greater than $r^2 = 0.60$. Taxonomic coverage is much better for females; all female taxonomic averages for C^1 height– C_1 height are between $r^2 = 0.40$ and 0.60 (SOM Table 4). The anthropoid average values for both C_1 height– C^1 height and $\sqrt{(C_1\text{MD} \cdot C_1\text{LaL})} - \sqrt{(C^1\text{MD} \cdot C^1\text{LaL})}$ are more than twice the average magnitude of covariation observed between the height and basal size of each canine.

4.2. Canine, incisor, and postcanine size within species

Within species, 141 comparisons of incisor and canine basal size were assessed. Of these, only 77 are significantly different from zero and all significant correlations are positive in direction (SOM Tables 5–8). For incisor dimensions compared to canine basal size, all have an anthropoid average $r^2 < 0.25$. The highest averages, observed for $C^1\text{LaL}$ – $I^1\text{LaL}$ (hominoid average $r^2 = 0.30$; platyrrhine average $r^2 = 0.31$) and $C^1\text{MD}$ – $I^2\text{MD}$ (hominoid average $r^2 = 0.36$; platyrrhine average $r^2 = 0.28$), are with dimensions of the maxillary incisors (Table 3). A similar pattern is observed for canine basal and postcanine size. Of 224 within-species comparisons, 143 are significantly different from zero and all significant correlations are positive in direction (SOM Tables 5–8). The highest average covariation is only $r^2 = 0.21$ (Table 3). Though weak on average (Fig. 1), the covariance between canine basal and postcanine size is positive in direction.

Similar magnitudes of covariation are observed for canine heights and incisor and postcanine size (Table 4). Of 126 within-species comparisons of canine height to incisor size, only 41 are significantly different from zero and all significant correlations are positive in direction (SOM Tables 9–12). Of 143 within-species comparisons of canine heights to postcanine size, only 56 are significantly different from zero and all significant correlations are positive in direction (SOM Tables 9–12). The highest observed average is $r^2 = 0.14$ for C^1 height– $M^1\text{MD}$ (Table 4). In summary, magnitudes of covariation between functional modules do not approach those observed for homologous dimensions of the canine honing complex (Fig. 1; Table 2).

4.3. Canine height and premolar honing surface length within species

Both C^1 height–premolar hone and C_1 height–premolar hone covary on average around $r^2 = 0.45$ (Table 5). All comparisons of C^1

Table 3

Weighted average within-species covariation for mandibular and maxillary canine size for samples listed in Table 1.

	I ₁ MD	I ₂ MD	P ₄ MD	M ₁ MD	M ₂ MD
C ₁ MD	♂ $r^2 = 0.11$ ♀ $r^2 = 0.08$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.06$	♂ $r^2 = 0.20$ ♀ $r^2 = 0.18$	♂ $r^2 = 0.18$ ♀ $r^2 = 0.10$	♂ $r^2 = 0.25$ ♀ $r^2 = 0.13$
	I ₁ LaL	I ₂ LaL	P ₄ BL	M ₁ BL	M ₂ BL
C ₁ LaL	♂ $r^2 = 0.15$ ♀ $r^2 = 0.20$	♂ $r^2 = 0.22$ ♀ $r^2 = 0.20$	♂ $r^2 = 0.20$ ♀ $r^2 = 0.21$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.16$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.16$
	I ¹ MD	I ² MD	P ⁴ MD	M ¹ MD	M ² MD
C ¹ MD	♂ $r^2 = 0.17$ ♀ $r^2 = 0.18$	♂ $r^2 = 0.21$ ♀ $r^2 = 0.23$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.17$	♂ $r^2 = 0.15$ ♀ $r^2 = 0.12$	♂ $r^2 = 0.17$ ♀ $r^2 = 0.17$
	I ¹ LaL	I ² LaL	P ⁴ BL	M ¹ BL	M ² BL
C ¹ LaL	♂ $r^2 = 0.22$ ♀ $r^2 = 0.24$	♂ $r^2 = 0.15$ ♀ $r^2 = 0.18$	♂ $r^2 = 0.21$ ♀ $r^2 = 0.16$	♂ $r^2 = 0.12$ ♀ $r^2 = 0.14$	♂ $r^2 = 0.18$ ♀ $r^2 = 0.17$

Table 4

Weighted average within-species covariation for mandibular and maxillary canine size for samples listed in Table 1.

	I ₁ MD	I ₂ MD	P ₄ MD	M ₁ MD	M ₂ MD
C ₁ height	♂ $r^2 = 0.12$ ♀ $r^2 = 0.12$	♂ $r^2 = 0.15$ ♀ $r^2 = 0.08$	♂ $r^2 = 0.08$ ♀ $r^2 = 0.08$	♂ $r^2 = 0.09$ ♀ $r^2 = 0.10$	♂ $r^2 = 0.11$ ♀ $r^2 = 0.10$
	I ₁ LaL	I ₂ LaL	P ₄ BL	M ₁ BL	M ₂ BL
C ₁ height	♂ $r^2 = 0.12$ ♀ $r^2 = 0.14$	♂ $r^2 = 0.12$ ♀ $r^2 = 0.13$	♂ $r^2 = 0.19$ ♀ $r^2 = 0.08$	♂ $r^2 = 0.13$ ♀ $r^2 = 0.10$	♂ $r^2 = 0.18$ ♀ $r^2 = 0.09$
	I ¹ MD	I ² MD	P ⁴ MD	M ¹ MD	M ² MD
C ¹ height	♂ $r^2 = 0.15$ ♀ $r^2 = 0.09$	♂ $r^2 = 0.03$ ♀ $r^2 = 0.14$	♂ $r^2 = 0.04$ ♀ $r^2 = 0.09$	♂ $r^2 = 0.20$ ♀ $r^2 = 0.10$	♂ $r^2 = 0.07$ ♀ $r^2 = 0.10$
	I ¹ LaL	I ² LaL	P ⁴ BL	M ¹ BL	M ² BL
C ¹ height	♂ $r^2 = 0.12$ ♀ $r^2 = 0.10$	♂ $r^2 = 0.09$ ♀ $r^2 = 0.11$	♂ $r^2 = 0.16$ ♀ $r^2 = 0.11$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.03$	♂ $r^2 = 0.06$ ♀ $r^2 = 0.08$

height and premolar hone length are significantly different from zero and only one sample, female *C. cephus*, evinces a nonsignificant correlation between C₁ height and premolar hone (SOM Table 13). This sample warrants further investigation to determine if covariation is indeed absent or if the result is simply an outlier given the large number of comparisons that were made. Thus, the observed covariances between canine heights and premolar honing surface length are weaker on average than those observed between homologous dimensions of the canines. However, covariation between canine heights and premolar honing surface length is of a greater magnitude than observed between canine heights and incisor and postcanine size (Fig. 2; Table 4).

4.4. Premolar honing surface length and incisor and postcanine size within species

Covariation between premolar hone length and incisor and postcanine size is much weaker than that observed between

premolar hone length and canine heights. Of 77 within-species comparisons made for premolar hone and mandibular incisor size, only 22 are significantly different from zero and all 22 are positive in direction (SOM Tables S14 and S15). Of 114 within-species comparisons between premolar hone length and the dimensions of the mandibular postcanine dentition, 54 are significantly different from zero and all 54 are positive (SOM Tables S14 and S15). For premolar hone length and incisor and postcanine size, the highest observed average covariation is $r^2 = 0.14$ for premolar hone-M₂ MD (Table 5).

4.5. Dimensions of the honing complex among species

Among-species covariation was assessed for canine heights, canine basal size ($\sqrt{[LaL*MD]}$), and length of the premolar honing surface. In short, all elements of the complex express statistically significant high magnitude among-species covariation in both males and females (Table 6).

Females do, in fact, express weaker covariation for C¹ height-premolar hone and for the comparisons of canine heights to canine basal areas (Table 6). The lower level of covariation for C¹ height-premolar hone results from large outlying contrasts between major primate clades, which are evident when bivariate plots of independent contrasts are compared. In females, two contrasts stand out relative to the reduced major axis (RMA) regression line: the contrast between hylobatids and hominids and the contrast between cercopithecids and hominoids (Fig. 3). In males, the hylobatid versus hominid comparison also stands out; however, the cercopithecoid versus hominoid comparison does not. These contrasts capture well documented distinctions in canine and honing premolar size and shape and are discussed below.

4.6. The honing complex, incisors, and postcanines among species

Among species, all dimensions of the canines and honing premolar covary positively with incisor and postcanine size (Tables 7 and 8); however, there are substantial differences in the average magnitudes of covariation. Covariation between C₁ height and incisor and postcanine size (average $r^2 = 0.52$) is higher than that for C¹ height (average $r^2 = 0.37$). Among species, canine basal size ($\sqrt{[MD*LaL]}$), for both the C¹ and C₁, covaries more strongly with incisor and postcanine size than do canine heights (average $r^2 = 0.75$ for C₁ base and $r^2 = 0.76$ for C¹ base). The length of the premolar honing surface also covaries more weakly with incisor and postcanine size (average $r^2 = 0.53$) than does canine basal size. In summary, canine basal sizes track overall dental size more closely than do canine heights and premolar honing surface length.

5. Discussion

5.1. Modularity of the canine honing complex

A modular genetic organization is argued to be selectively advantageous. As there are many functions performed by an

Table 5

Weighted average within-species covariation for mandibular and maxillary canine size for samples listed in Table 1.

	C ¹ height	C ₁ height	I ₁ MD	I ₁ LaL	I ₂ MD	I ₂ LaL
P _{2,3} hone length	♂ $r^2 = 0.45$ ♀ $r^2 = 0.42$	♂ $r^2 = 0.46$ ♀ $r^2 = 0.46$	♂ $r^2 = 0.10$ ♀ $r^2 = 0.05$	♂ $r^2 = 0.10$ ♀ $r^2 = 0.12$	♂ $r^2 = 0.08$ ♀ $r^2 = 0.09$	♂ $r^2 = 0.11$ ♀ $r^2 = 0.14$
	P ₄ MD	P ₄ BL	M ₁ MD	M ₁ BL	M ₂ MD	M ₂ BL
P _{2,3} hone length	♂ $r^2 = 0.12$ ♀ $r^2 = 0.11$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.12$	♂ $r^2 = 0.09$ ♀ $r^2 = 0.13$	♂ $r^2 = 0.12$ ♀ $r^2 = 0.09$	♂ $r^2 = 0.15$ ♀ $r^2 = 0.11$	♂ $r^2 = 0.14$ ♀ $r^2 = 0.11$

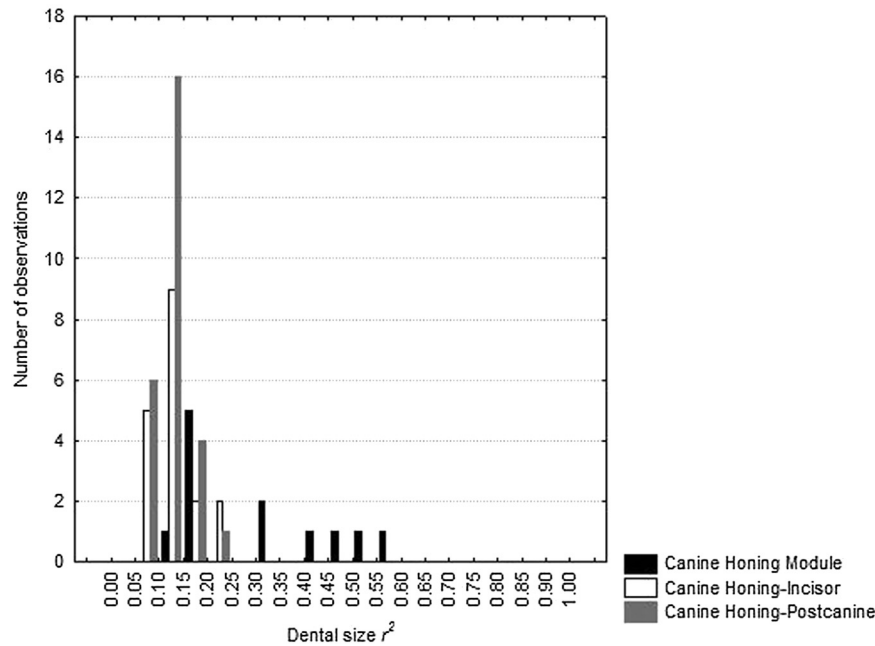


Figure 2. Summary of r^2 values for character pairs within the canine honing complex, between honing complex and incisor size, and between honing complex and postcanine size. Here, anthropoid average values are plotted for males and females separately. The highest values of covariance are all for homologous dimension of the canines, the second highest are for the heights of the canines and the length of the premolar honing surface, and the lowest are for dimensions of the honing complex and those of the incisors and postcanines.

organism, it is not likely that all characters need to change simultaneously in order to meet shifting environmental conditions. If characters in functional modules are coupled by genetic factors (e.g., genetic linkage or pleiotropy) and not coupled with characters outside the module, then the functional unit can easily coevolve in response to selection and not affect the morphology/function of characters outside the complex (e.g., Wagner et al., 2007). Therefore, change in one functional module does not compromise adaptations in others. This selective argument is similar to Fisher's Geometric Model that noted that mutations with large widespread effects on the phenotype are not likely to be adaptive (Fisher, 1930; Wang et al., 2010; Wagner and Zhang, 2011). Conversely, a system in which genetic covariation does not exist has a high cost of complexity, requiring each character in a functional complex to respond independently to selection; as a result, "it becomes very unlikely that a random mutation affects the right combination of traits in the right way to improve fitness" (Wagner and Zhang, 2011:205). A modular organization reduces this cost.

Genetically covarying characters are 'constrained' (Maynard Smith et al., 1985); that is, each character has "reduc[ed] evolvability in at least some directions of the phenotype space" (Klingenberg, 2005:220, 2010; see also Pigliucci, 2003). However, it is important to consider that genetic covariation, and by extension

the constraint it creates, is not an all or none phenomenon (see review in Klingenberg, 2008). Genetic covariation ranges from absent (no genetic correlation; $r_G = 0$) to absolute (complete genetic correlation; $r_G = \pm 1$ or -1). Values between $r_G = \pm 1$ and $= 0$ are only relatively constrained and each character retains some unshared genetic variance. As Beldade and Brakefield (2003) noted, absolute and relative constraints should not be treated dichotomously, but, rather, viewed as existing along a continuum of strengths. Therefore, characters that are relatively constrained retain some evolutionary independence.

Assuming dental phenotypic covariation reflects genetic covariation (e.g., Cheverud, 1988a; Hlusko and Mahaney, 2007a; Grieco et al., 2013), the results of this study suggest, unsurprisingly, that no character pairs of the canine honing complex have an $r_G = 1$ (Tables 2 and 5) and, further, that dimensions of the honing complex show some covariation with incisor and postcanine size (Tables 3–5). Thus, phenotypic size covariation cannot be used simply to divide the dentition into units where covariation is either absolute or absent; however, when the magnitudes of covariation within the complex are compared with that of dimensions outside the complex (Fig. 1), it is clear that the pattern is not random and that the honing complex is a variational module in both males and females. Between the C_1 and C^1 , covariation among homologous dimensions (C_1 base- C^1 base; C_1 height- C^1 height) is strongest and covariation between canine heights and premolar honing surface length is weaker (Tables 2 and 5). Such magnitudes of covariation are not observed with dimensions outside the complex (Tables 3–5; Fig. 1). That said, even within the complex, nonhomologous dimensions do not covary as strongly as do homologous dimensions. The average phenotypic covariation observed in this study between functional modules is in agreement with the values reported by Cochard (1981) and Grieco et al. (2013), which both found that covariation between the sizes of the canine bases, incisors, and postcanines averaged between $r^2 = 0.15$ – 0.25 . As canine heights, especially those of the C^1 , are represented by some of the smallest sample sizes in this study, the fact remains that some of

Table 6

Covariation among species for dimensions of the canine honing complex (*** p -value < 0.0001, ** p -value < 0.001, * p -value < 0.05).

	C^1 height	C^1 basal size	C_1 height	C_1 basal size
C^1 Basal Size	$\delta r^2 = 0.65^{***}$ $\varphi r^2 = 0.43^{***}$	–	–	–
C_1 Height	$\delta r^2 = 0.85^{***}$ $\varphi r^2 = 0.72^{***}$	$\delta r^2 = 0.75^{***}$ $\varphi r^2 = 0.60^{***}$	–	–
C_1 Basal Size	$\delta r^2 = 0.59^{***}$ $\varphi r^2 = 0.40^{***}$	$\delta r^2 = 0.97^{***}$ $\varphi r^2 = 0.90^{***}$	$\delta r^2 = 0.74^{***}$ $\varphi r^2 = 0.64^{***}$	–
Premolar Hone	$\delta r^2 = 0.82^{***}$ $\varphi r^2 = 0.51^{***}$	$\delta r^2 = 0.70^{***}$ $\varphi r^2 = 0.68^{***}$	$\delta r^2 = 0.81^{***}$ $\varphi r^2 = 0.65^{***}$	$\delta r^2 = 0.62^{***}$ $\varphi r^2 = 0.58^{***}$

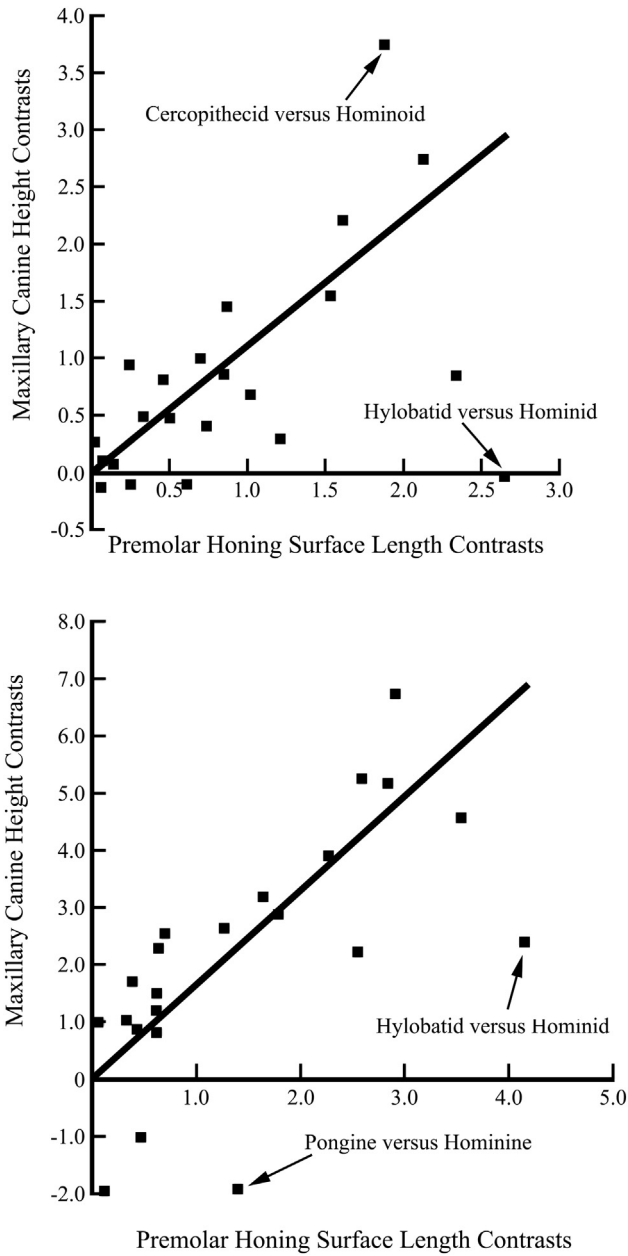


Figure 3. Above, independent contrasts for maxillary canine height and premolar honing surface length in females. Below, independent contrasts for maxillary canine height and premolar honing surface length in males. For both graphs, the solid line is the Reduced Major Axis regression line.

the weak covariation observed between canine heights and other dimensions is simply an artifact of the small sample sizes available for analysis.

5.2. The evolution of the honing complex in anthropoids

Even though intraspecific phenotypic covariation, which is assumed to reflect genetic covariation, exists among dimensions of the honing complex, the expectation that characters that are only relatively constrained should evolve in lockstep is overly restrictive, especially when one considers that the anthropoid species considered in this analysis last shared a common ancestor more than 40 million years ago (Steiper and Young, 2006). Given distinct differences in honing premolar and canine morphology observed

Table 7
Covariation among species for the mandibular canine and honing premolar and dimensions of the incisors and postcanine dentition (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).

	C ₁ height	C ₁ basal size	Premolar hone
I ₁ LaL	♂ r ² = 0.75*** ♀ r ² = 0.31***	♂ r ² = 0.68*** ♀ r ² = 0.68***	♂ r ² = 0.56*** ♀ r ² = 0.35***
I ₁ MD	♂ r ² = 0.64*** ♀ r ² = 0.40***	♂ r ² = 0.66*** ♀ r ² = 0.69***	♂ r ² = 0.42*** ♀ r ² = 0.45***
I ₂ LaL	♂ r ² = 0.76*** ♀ r ² = 0.27***	♂ r ² = 0.80*** ♀ r ² = 0.75***	♂ r ² = 0.54*** ♀ r ² = 0.30***
I ₂ MD	♂ r ² = 0.57*** ♀ r ² = 0.31**	♂ r ² = 0.62*** ♀ r ² = 0.68***	♂ r ² = 0.36*** ♀ r ² = 0.28***
P ₄ MD	♂ r ² = 0.66*** ♀ r ² = 0.42***	♂ r ² = 0.88*** ♀ r ² = 0.73***	♂ r ² = 0.69*** ♀ r ² = 0.66***
P ₄ BL	♂ r ² = 0.61*** ♀ r ² = 0.39***	♂ r ² = 0.89*** ♀ r ² = 0.81***	♂ r ² = 0.52*** ♀ r ² = 0.55***
M ₁ MD	♂ r ² = 0.66*** ♀ r ² = 0.46***	♂ r ² = 0.89*** ♀ r ² = 0.73***	♂ r ² = 0.63*** ♀ r ² = 0.65***
M ₁ BL	♂ r ² = 0.64*** ♀ r ² = 0.41***	♂ r ² = 0.89*** ♀ r ² = 0.79***	♂ r ² = 0.55*** ♀ r ² = 0.56***
M ₂ MD	♂ r ² = 0.67*** ♀ r ² = 0.44***	♂ r ² = 0.85*** ♀ r ² = 0.63***	♂ r ² = 0.67*** ♀ r ² = 0.65***
M ₂ BL	♂ r ² = 0.64*** ♀ r ² = 0.38***	♂ r ² = 0.89*** ♀ r ² = 0.74***	♂ r ² = 0.60*** ♀ r ² = 0.57***

between major clades of anthropoids (e.g., between hominoids and cercopithecids), there must have been several episodes of selection that reshaped the elements of the complex independently of one another. Though not tested in this study, there is very little to suggest that these transformations would have required a restructuring of genetic covariation or a relaxation of constraints. Further study can address potential changes in variance-covariance structure and the generation of morphological novelty in the anthropoid canine honing complex.

Among species, anthropoid canine heights and premolar honing surface lengths significantly covary in both males and females. This finding contrasts with the results of Greenfield and Washburn (Greenfield, 1992; Greenfield and Washburn, 1992), who found a significant correlation between C¹ projection and the length of the premolar honing surface in males only. The flexibility of the canine honing complex to evolve in a mosaic fashion is, in fact, expressed in subtly different ways in males and females. When the length of the premolar honing surface and C¹ height were considered in the

Table 8
Covariation among species between the maxillary canine and the incisors and postcanine teeth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).

	C ¹ height	C ¹ basal size
I ¹ LaL	♂ r ² = 0.37* ♀ r ² = 0.20*	♂ r ² = 0.65*** ♀ r ² = 0.69***
I ¹ MD	♂ r ² = 0.37** ♀ r ² = 0.22**	♂ r ² = 0.74*** ♀ r ² = 0.69***
I ² LaL	♂ r ² = 0.49** ♀ r ² = 0.14*	♂ r ² = 0.72*** ♀ r ² = 0.54***
I ² MD	♂ r ² = 0.29** ♀ r ² = 0.23**	♂ r ² = 0.54*** ♀ r ² = 0.59***
P ⁴ MD	♂ r ² = 0.55*** ♀ r ² = 0.34***	♂ r ² = 0.88*** ♀ r ² = 0.83***
P ⁴ BL	♂ r ² = 0.40** ♀ r ² = 0.24**	♂ r ² = 0.88*** ♀ r ² = 0.82***
M ¹ MD	♂ r ² = 0.57*** ♀ r ² = 0.33**	♂ r ² = 0.91*** ♀ r ² = 0.77***
M ¹ BL	♂ r ² = 0.45*** ♀ r ² = 0.29**	♂ r ² = 0.88*** ♀ r ² = 0.77***
M ² MD	♂ r ² = 0.65*** ♀ r ² = 0.35**	♂ r ² = 0.86*** ♀ r ² = 0.63***
M ² BL	♂ r ² = 0.51*** ♀ r ² = 0.31**	♂ r ² = 0.90*** ♀ r ² = 0.71***

analysis of independent contrasts, large contrasts are evident in females that are not evident in the male analysis (Fig. 2). For example, one of the contrasts with the largest residual in both male and female analyses is the contrast between hylobatids and hominids. In both cases, the direction of difference indicates that hylobatids have shorter premolar honing surfaces, relative to C¹ height, than do hominids. This is a reflection of the fact that both male and female hylobatids have tall projecting canines. In females, the contrast between cercopithecids and hominoids stands out, but, in contrast, it does not in the male analysis. Female cercopithecids have longer premolar honing surface, relative to C¹ height, than do female hominoids. As has been established by others (e.g., Greenfield, 1992; Greenfield and Washburn, 1992), the cercopithecoid female honing premolars are hypertrophied relative to either the hominoid or platyrrhine condition.

Greenfield (1992; Greenfield and Washburn, 1992) suggested that the hypertrophy of the female cercopithecoid honing premolar reflects a correlated response with the male honing premolar size and is nonadaptive. While that suggestion was not tested in this analysis, it remains possible that Greenfield is partially correct. Plavcan (1998) found that some, though not all, of the interspecific variation in female canine height can be explained as a result of a correlated response with male canine height. Specifically, he found the correlated response is evident in species in which females are not competing by using their canines, but the effect diminishes in species in which large female canine size is selected for (e.g., Plavcan et al., 1995). Therefore, it is reasonable to hypothesize that the length of the female premolar honing surface reflects, at least in part, a correlated response with the length of the premolar honing surface in males. However, the fact that the among-species analyses revealed large contrasts that were not evident in the male analysis suggests that a correlated response cannot be the sole explanation for the evolution of the female honing complex.

5.3. Patterns of character state change and the evolution of the hominin 'honing' complex

In contrast to other extant catarrhines, which have projecting canines that are honed, hominins have shorter canines that are not honed. It is most parsimonious to infer that the *Pan*-hominin last common ancestor had a functional honing complex and that the absence of honing is an apomorphy that evolved within the hominin clade; therefore, the transformation of the hominin canines and mesial mandibular premolar provides a rare opportunity to examine the refashioning of elements formerly linked in a functional complex.

Hints of the earliest phases of the transition are provided by the late Miocene *Orrorin tugenensis*, *Sahelanthropus tchadensis*, and *Ardipithecus kadabba*, which are all purported to be basal hominins (Haile-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002; Haile-Selassie et al., 2004, 2009; Semaw et al., 2005). Though sample sizes are quite limited, each has been inferred to share the lack of canine honing with Pliocene hominins, as none of the canines attributed to these taxa has a wear pattern like that seen in extant apes with a honing complex. Though functionally derived, the canines and P₃ of these taxa, where known, are quite primitive, relative those of *Australopithecus*, *Paranthropus*, and *Homo*. With the exception of C¹ height, these taxa have canines that overlap male *Pan paniscus* and female *Pan troglodytes* in size. Their C¹ heights, though, are shorter than in both sexes of *P. troglodytes* and fall between male and female *P. paniscus* (Suwa et al., 2009). The P₃ is unknown for both *Orrorin* and *Sahelanthropus*; however, the *A. kadabba* P₃ is unicuspid, has a tall protoconid, and lacks closure of the anterior fovea and, therefore, is reminiscent of the feature set seen in extant apes. Furthermore, ASK-VP-3/403, a P₃ attributed to

A. kadabba, retains a small wear facet on its mesiobuccal surface that resulted from contact with the C¹ (Haile-Selassie et al., 2004). In *Australopithecus*, *Paranthropus*, and *Homo*, P₃ wear from contact with the C¹ is predominantly along the mesial protoconid crest and not along the mesiobuccal face, which suggests more overlap between the C¹ and P₃ in *A. kadabba* than is typical of any known hominin that succeeds it temporally. If these taxa are a good guide, then hominin C¹ height reduction likely preceded C₁ height reduction, substantial reduction of C¹ basal size, and a reorganization of the P₃ crown.

The elements of the canine honing complex are well represented in *Ardipithecus ramidus* (4.4 Ma [millions of years ago]) and the morphology of the complex supports the pattern of character state change inferred from the Miocene taxa. In *A. ramidus*, absolute C₁ and C¹ basal size and C₁ height are similar to the Miocene hominins and to female *P. troglodytes* and male *P. paniscus*. Maxillary canine height, in contrast, is shorter than in both *P. troglodytes* sexes and is similar to female *P. paniscus*. In fact, Suwa et al. (2009) report that the height of the C¹ is lower than the C₁ in *A. ramidus*, which is unusual for an anthropoid. Though there is no evidence for functional canine honing in the substantial collection of *A. ramidus* canines and P₃s, the P₃ evinces many of the morphological features seen in *Pan* and *Gorilla*; for example, the P₃ is unicuspid, the crown is described as 'tall' as a result of having a projecting protoconid, and the mesiobuccal face of some specimens, though reduced compared with *Pan*, projects inferiorly to an extent not seen in *Australopithecus*, *Paranthropus*, and *Homo* (White et al., 1994; see Fig. S14 in Suwa et al., 2009). As such, premolar heteromorphy is still pronounced in *A. ramidus*.

The earliest species of *Australopithecus*, *Australopithecus anamensis* (4.2–3.9 Ma) and *Australopithecus afarensis* (3.7–3.0 Ma), capture further apomorphies of the canines and P₃ and indicate a complete shift to apically-dominated C¹ wear (Ryan and Johanson, 1989; Greenfield, 1990). As in the earlier hominins, these taxa pair a short C¹ with a C₁ that can be quite projecting and plesiomorphic in morphology and macrowear (White, 1981). In *Au. anamensis*, the honing premolar retains much of the feature set evident in extant apes, *A. kadabba*, and *A. ramidus* (the crown is unicuspid and asymmetric, the anterior fovea is open, and the protoconid is tall) so that premolar heteromorphy is pronounced (Ward et al., 2001, 2010; Deleuzene and Kimbel, 2011; Manthi et al., 2012). Compared with *Au. anamensis*, *Au. afarensis* canine crown size is not substantially smaller, though C¹ shape differs as a result of the asymmetric shoulder placement in *Au. afarensis* (Ward et al., 2001, 2010; Kimbel and Deleuzene, 2009; Manthi et al., 2012). The *Au. afarensis* P₃ sample is well known for its substantial morphological variation. Some specimens express features associated with taxa with a canine honing complex (e.g., unicuspid crowns, open anterior fovea, and crown obliquity), while others express derived traits that are fixed in *Au. africanus* and *Paranthropus* (e.g., anterior fovea closure, crown symmetry, and presence of a well-developed metaconid). However, the abundant sample of *Au. afarensis* P₃s indicates that there is not a derived package of features; instead, derived and primitive features exist in various combinations within the hypodigm (Deleuzene and Kimbel, 2011).

Taken together, the emerging pattern of character state change captured by the earliest hominins (*Orrorin*, *Sahelanthropus*, *Ardipithecus*) and the earliest known *Australopithecus* species (*Au. anamensis*, *Au. afarensis*) indicates that the canines and mesial premolar evolved mosaically (Ward et al., 2010; Manthi et al., 2012). This inferred pattern is the same whether *Ardipithecus*, *Orrorin*, or *Sahelanthropus* are considered basal hominins or not (e.g., Wood and Harrison, 2011). Such an evolutionary pattern could reflect a system that lacks substantial constraints imposed by genetic covariation. However, if the pattern of phenotypic covariation

observed in this study reflects that of genetic covariation, then *some* genetic constraint should have existed on the evolution of the honing complex in early hominins. This is especially true for canine heights and for canine basal areas. Therefore, given what is currently known of the hominin fossil record, the best explanation for the pattern of mosaic character change is that selection was particularly strong on C¹ height in early hominins and that the selection vector was not aligned with that of the principal axis of genetic covariation; otherwise, maxillary and mandibular canine height reductions should have coincided. The results of this study strongly support the conclusion of Ward et al. (2010) and Manthi et al. (2012) that the transformation of the honing complex from an ape-like ancestral form to a highly-derived form in younger *Australopithecus* species, *Paranthropus*, and *Homo* resulted from series of sequential selective pressures targeting different aspects of canine and premolar size and shape. Initially, selection appears to have been particularly strong only on C¹ height and only within the *Au. anamensis*–*Au. afarensis* lineage (Kimbel et al., 2006) is selection evident for the transformation of the P₃ crown (discussed in Delezene and Kimbel, 2011).

5.4. The role of covariation with incisors and postcanines in hominin canine reduction

Jolly (1970) brought attention to convergent patterns of dental evolution in hominins and *Theropithecus*. In particular, he noted similar trends for postcanine enlargement and the reduction of the anterior dentition (incisors and canines). He proffered several models to explain reduced hominin canine size. In one model, he hypothesized that there is a pleiotropic connection between the anterior teeth. Greenfield (1993) also proposed a pleiotropic connection between incisor and canine size. McCollum and Sharpe (2001) proposed a developmental model in which the dental progenitor cells compete for limited space in the developing jaw in such a way that the anterior and posterior teeth should negatively covary in size.

Within species, neither strong nor negative size covariance was observed in this study for pairings of the canine honing complex with the incisors and postcanines. Additionally, on average, covariation between the canines and either the incisors or postcanines is only about a quarter of the magnitude of the covariation observed between homologous dimensions of the canines (Fig. 2). Assessing maxillary dental size covariation in six cercopithecoid species, Grieco et al. (2013) found that the average phenotypic covariation between canine basal size and incisor size was $r^2 = 0.21$ and between maxillary canine and postcanine size was $r^2 = 0.16$, which are quite similar to the averages observed within species in this study across anthropoids (Fig. 2). In Grieco et al. (2013), none of the 24 estimates of canine and incisor size covariation was negative in direction. For covariation with the postcanine dentition, only three of 108 estimates were negative in direction and none of those estimates was significantly different from zero. Hlusko et al. (2011) also estimated genetic covariation between incisor and postcanine size in SNPRC baboons and found that the majority of correlations were positive and weak. The current study and those of Hlusko et al. (2011) and Grieco et al. (2013) all provide evidence that supports the hypothesis that genetic constraints between dental functional units are not strong. Furthermore, this study provides additional evidence that canine heights, and not just basal size, minimally covary with incisor and postcanine size.

While the Jolly (1970), Greenfield (1993), and McCollum and Sharpe (2001) models are rejected because the pattern of observed covariance does not match their predictions, tradeoffs between canine and postcanine size are unlikely to explain the initial reduction of canine height and the loss of canine honing.

That is, C¹ height reduction, and not basal size reduction, is the first substantial change noted to characterize the hominin ‘honing’ complex. If limited space in the jaw favored small canines (e.g., McCollum and Sharpe, 2001), then canine bases should have reduced either before or simultaneously with canine heights, which is not the observed pattern of character state change. In fact, canine basal size does not reduce beyond the size seen in female *P. troglodytes* near the base of the hominin clade (if *Ardipithecus* is a hominin) or even at the origin of the genus *Australopithecus* (Suwa et al., 2009; Ward et al., 2010; Manthi et al., 2012). Apparently, retaining canines with basal size like that seen in female *P. troglodytes* did not impose a cost on the earliest hominins, but maintaining a projecting C¹ did. Additionally, if overlap of the C¹ and P₃ was more substantial in the earliest hominins, as *A. kadabba* suggests (Haile-Selassie et al., 2004), then the initial loss of canine honing appears merely to be a consequence of reduced C¹ height and not because of a change in the way that the C¹ and P₃ occlude. Thus, the loss of honing and altered occlusal contact between the C¹ and P₃ was likely not the target of selection. In light of these observations, models that propose *benefits* for short maxillary canines—for example, as a reflection of reduced male–male competition (e.g., Holloway, 1967; Suwa et al., 2009) or because they “permitted molar cusps to wear more evenly” (Jolly, 1970, 2001:182), among other models—or *costs* associated with maintaining tall projecting canines—for example, tradeoffs with gape (Hylander, 2012)—are more likely to be correct than are those that see canine reduction as a byproduct of selection on genetically-coupled traits outside the complex. And, while canine height reduction in early hominins may have been the result of strong directional selection, it is also possible that stabilizing selection maintained relatively large canine basal size to strengthen the canines during use. To that end, determining the manner in which extinct hominins used their canines, if at all, in dietary and non-dietary contexts (e.g., Puech and Albertini, 1984; Ryan and Johanson, 1989; Greenfield, 1990) would provide context for determining if large canine basal size was beneficial or simply a phylogenetic relict.

6. Conclusion

The canine honing complex is a functional and variational module in both male and female anthropoids. There is no evidence for differences in either among- or within-species phenotypic covariation between male and female anthropoids, which undermines arguments that the honing complex is selectively important only in males. Despite strong covariation among certain dimensions of the canine honing complex, morphological differences among species indicate that the system retains flexibility to evolve in a mosaic fashion. The strong covariation observed between canine heights points to particularly strong selection driving their divergent reductions in early hominins. Finally, there is no evidence for negative or strong positive covariance between functional modules, which falsifies hypotheses that predict such relationships between the canines and either the incisors or postcanine teeth.

Acknowledgments

I thank the curators and collections managers at the various institutions at which I collected data: Lyman Jellema (Cleveland Museum of Natural History), Dr. William Stanley (Field Museum), Judith Chupasko and Marc Omura (Museum of Comparative Zoology), Angela Gill and Malcolm Harmon (Powell-Cotton Museum), Milly Farrell (Royal College of Surgeons), Eileen Westing (American Museum of Natural History), Linda Gordon and Darrin

Lunde (National Museum of Natural History), and Suzanne MacLaren (Carnegie Museum of Natural History). I gratefully acknowledge the Rwandan government for permission to study skeletal remains curated by the Mountain Gorilla Skeletal Project (MGSP). The MGSP is made possible by funding support from the National Science Foundation (BCS-0852866, BCS-0964944), National Geographic Society's Committee (8486-08) for Research and Exploration, and the Leakey Foundation, infrastructural support from the Dian Fossey Gorilla Fund International's (DFGFI) Karisoke Research Center, and the efforts of researchers and staff from the Rwanda Development Board's Department of Tourism and Conservation, Gorilla Doctors, DFGFI, the George Washington University, New York University College of Dentistry, and Institute of National Museums of Rwanda.

As the data and analyses presented in this study were included in my doctoral dissertation, I thank my Ph.D. committee members (Drs. Bill Kimbel, Gary Schwartz, Mark Spencer, and Brian Verrelli) for their guidance and patience. For their comments on earlier versions of the manuscript, I thank Dr. J. Michael Plavcan and Amelia Villaseñor. Furthermore, suggestions from the reviewers and editor Dr. Mark Teaford greatly improved the readability of the manuscript.

Data collection was funded by a Wenner-Gren Doctoral Dissertation Fieldwork Grant (#7884) and NSF Doctoral Dissertation Improvement Grant (BCS-0852105) under Dr. William H. Kimbel.

Appendix A. Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2015.07.001>.

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