Morphological Integration and the Anthropoid Dentition

by

Lucas Delezene

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved June 2011 by the
Graduate Supervisory Committee:

William Kimbel, Chair
Mark Spencer
Gary Schwartz
Brian Verrelli

ARIZONA STATE UNIVERSITY

December 2011

ABSTRACT

The pattern and strength of genetic covariation is shaped by selection so that it is strong among functionally related characters and weak among functionally unrelated characters. Genetic covariation is expressed as phenotypic covariation within species and acts as a constraint on evolution by limiting the ability of linked characters to evolve independently of one another. Such linked characters are "constrained" and are expected to express covariation both within and among species. In this study, the pattern and magnitude of covariation among aspects of dental size and shape are investigated in anthropoid primates. Pleiotropy has been hypothesized to play a significant role in derivation of derived hominin morphologies. This study tests a series of hypotheses; including 1) that negative within- and among-species covariation exists between the anterior (incisors and canines) and postcanine teeth, 2) that covariation is strong and positive between the canines and incisors, 3) that there is a dimorphic pattern of within-species covariation and coevolution for characters of the canine honing complex, 4) that patterns of covariation are stable among anthropoids, and 5) that genetic constraints have been a strong bias on the diversification of anthropoid dental morphology. The study finds that patterns of variance-covariance are conserved among species. Despite these shared patterns of variance-covariance, dental diversification has frequently occurred along dimensions not aligned with the vector of genetic constraint. As regards the canine honing complex, there is no evidence for a difference in the pleiotropic organization or the coevolution of characters of the complex in males and females, which undermines arguments that the complex is selectively important only in males. Finally, there is no evidence for strong or negative pleiotropy between any dental characters, which falsifies hypotheses that predict such relationships between incisors and postcanine teeth or between the canines and the postcanine teeth.

DEDICATION

I dedicate this dissertation to my mother, Teresa Wicker, and to my grandmothers, Martha Delezene and Ruth Clark. You all have provided love, support, and guidance throughout my life. Though my path through life has been circuitous at times, your support has been unwavering.

ACKNOWLEDGMENTS

I would like to thank my family for their enduring support during graduate school. Thanks especially to my parents (Teresa and Ken Wicker) for always supporting my pursuits (I've tried to do the same for you). Thanks to my aunt Dee and uncle Bob for driving the miles to visit while I was collecting data in Cleveland and Chicago. Thanks to my grandparents, especially Grandma Martha, without whose quiet, and sometimes hidden and unrecognized, support I would have never been able to participate in graduate school. Thanks also to Rosalia Vasquez and Robert Villaseñor, your doors have always been open to me and I am forever grateful. I would like to acknowledge those who could not be here with me at the end of this phase (Stephen Delezene, Larry Delezene, Lewis Clark); I gave it my best shot.

Thanks to 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 (National Museum of Natural History), and Suzanne MacLaren (Carnegie Museum of Natural History).You all were an invaluable help and I really appreciate your assistance during my extended stays.

Thanks to the many people who shared their homes with me during my data collection travels: Perry White (Cleveland), Carrie Seltzer and Matt Grosso (Chicago), Wonny and Jenny (Boston), Wendy and Robert Teale (Birchington), Amy Llanso and Brian Villmoare (London), Julie Fritz (New York City), and Rachel Hinton, Matt Kweskin, and Jane Moisan (Washington D.C.).

Thanks to the Institute of Human Origins and its board members. IHO board members Herb and Laura Roskind deserve special thanks for donating their laptop to the IHO, which I used to collect the data for this project and to write the bulk of the dissertation. Thanks to IHO board member Jay Greene for his friendship and for sharing my home for a semester, which gave me the break I needed to hit the road.

Thanks to my Masters and PhD committee members: Dr. Bill Kimbel (chair MA and PhD committees), Dr. Gary Schwartz (PhD committee member), Dr. Mark Spencer (PhD committee member), Dr. Brian Verelli (PhD committee member), Dr. Kaye Reed (MA committee member), and Dr. Donald Johanson (MA committee member). I appreciate all of the opportunities that you all created and the doors that you opened for me. I learned a lot from you all about the science of paleoanthropology and I am quite certain that I will never again be surrounded by such a gifted collection of paleoanthropologists. I know it was not always easy, but I appreciate that you all put up with me for ten years!

And finally, I thank the Wenner-Gren Foundation and the National Science Foundation for providing the funding for my dissertation research.

TABLE OF CONTENTS

Chapter 1

INTRODUCTION

As a result of selection shaping such patterns, genetic covariation is predicted to be strong among functionally related characters and weak among functionally unrelated characters (Wagner et al., 2007). For highly heritable characters, within species genetic covariation is expressed as phenotypic covariation. Genetic covariation acts as a constraint on evolution by biasing the evolutionary trajectories of linked characters, limiting their ability to evolve independently of one another and channeling coordinated change along the major axis of genetic covariation (e.g., Klingenberg, 2010; Marroig and Cheverud, 2010). The strength of constraint is proportional to the "flexibility" of the linked traits to evolve independently of one another; as constraint increases in strength, flexibility decreases (Marroig et al., 2009).

In anthropoid primates, a variety of functions are performed by teeth (food acquisition, food processing, social signaling, and canine honing) and these functions are, in general, spatially separated and performed by distinct dental units. As primate dental variation has been shown to be highly heritable in samples where it has been estimated (e.g., Hlusko and Mahaney, 2007b; Hlusko et al., 2010), the dentition is ideal for examining the predicted correspondence of character covariation to functional relationships.

Though patterns of covariation are investigated for all dental elements, the focus of this dissertation is on understanding the role of genetic constraints on the evolution of the canine honing complex in nonhuman anthropoid primates. Extant nonhuman anthropoids, and most extinct anthropoids, have a functional complex that sharpens the canines, which are used in social signaling and less frequently as weapons (e.g., Walker, 1984; Leigh et al., 2008), while hominins have reduced canines and lost the function of

canine honing (e.g., Greenfield, 1990). During hominin evolution, the honing complex was dramatically altered morphologically and functionally, though the pace of change was not consistent for the elements that formerly comprised the honing complex. Near the base of the hominin clade, canine height reduction was unequal for the maxillary and mandibular canines, substantial reduction in canine heights preceded substantial reduction in basal size (Suwa et al., 2009; Ward et al., 2010), and the P_3 retained morphological relicts of its honing past after the function of canine honing was lost and canines were reduced (Suwa et al., 2009; Delezene and Kimbel, 2011), suggesting that many of the changes that transformed the canine honing complex were uncoordinated. The role of pleiotropy in the evolution of the canine honing complex is uncertain. Among extant nonhuman anthropoids, Greenfield and Washburn (1992; Greenfield, 1992) found that the elements of the honing complex coevolved in males but not in females, suggesting either sexual dimorphism in patterns of pleiotropy (present and strong in males and absent in females) or a lack of pleiotropy in both sexes. According to Greenfield's model, the discordant patterns among species reflect the lack of functional integration among the elements of the complex in females and selection for female canines to function as incisors, a perspective that is not generally supported (e.g., Plavcan, 1993). Greenfield's findings have implications for understanding the changes that altered the honing complex in early hominins. If the elements of the honing complex do not covary genetically in extant primates, then no pattern of character change in the hominins would be constrained. In contrast, if pleiotropy exists among the elements of the complex, then strong selective pressure would be required to generate the pattern of uncoordinated character change that is observed.

The role of genetic covariation in the reduction of the hominin canine is also uncertain. Greenfield (1993) suggested that the canine lies at the "border of two

morphogenetic fields," and that, especially in females, it is shaped by selection to act as an incisor. If true, then the canines should covary in size with the incisors within species. It has been proposed that the canines share positive genetic covariation with the incisors (e.g., Jolly, 1970; McCollum and Sharpe, 2001) and that selection for reduced incisor size caused a coordinated diminution of hominin canine size; in this model, canine reduction represents a selective trade off in tooth size mediated by pleiotropy. Studying patterns of covariation among the elements of the honing complex and adjacent teeth and the impact genetic covariation has had on dental diversification provides a test of these hypothesized relationships.

In contrast to the canines, among anthropoids the functional roles of the incisors (food acquisition) and postcanine teeth (food processing) have remained constant. Diets vary among taxa; as a result, selection has shaped the incisors and postcanine teeth to meet the mechanical demands associated with their functions (Ungar, 2010). Analyses of captive baboons indicate that incisor sizes have a positive genetic correlation with one another and that postcanine tooth sizes have a positive genetic correlation with one another. A developmental model predicts that anterior and posterior tooth size should have a negative genetic correlation (McCollum and Sharpe, 2001), which recently received limited empirical support in pedigreed baboons (Hlusko et al., 2010). If the anterior and posterior teeth covary negatively within species, then this has implications for the coordinated enlargement of the postcanine dentition and diminution of the anterior dentition that occurred in some Plio-Pleiostocene hominins and *Theropithecus* (e.g., Jolly, 1970). Evidence for negative within-species covariation has not been documented in any wild population of anthropoid primates; nor has the predicted effect of the negative genetic correlation on the evolutionary trajectories of the anterior and posterior teeth been demonstrated.

This dissertation addresses a range of issues related to the patterning and stability of character covariation among anthropoid dental characters. Questions of different specificity at different biological levels are addressed. For example, are dental functional units (incisors, canine honing complex, postcanine dentition) defined by patterns of covariation or is there strong overlapping covariation between them? Given the constancy of dental functions among species, and the constancy of the teeth performing these functions, are patterns of covariation conserved among species? As there is little theoretical expectation that dimensions of the dentition should be "absolutely constrained" (e.g., Klingenberg, 2010), does the pattern of variance-covariance within species predict the direction of character difference between species? In addition to these basic questions about the patterning of genetic covariation in systems with functional differentiation and the effect of genetic covariation on the among species behavior of linked characters, more specific questions about the strength and direction of covariation between anterior and posterior teeth and evidence for dimorphic patterns of covariation in the honing complex are also addressed.

Below, the topics of integration, pleiotropy, and modularity are reviewed. This is followed by a summary of the composition and morphology of the functional units in the dentition, evidence that selection has driven among-species diversification in dental morphology and previous research on pleiotropy in the anthropoid dentition. This chapter concludes with a series of hypotheses that will be addressed in subsequent analytical chapters.

Character Covariation Within Species

Morphological Integration: "Integration" is a common research topic in evolutionary biology; however, its meaning is variable and contextual. The term originated as the title to the 1958 book Morphological Integration, which addressed the correspondence of

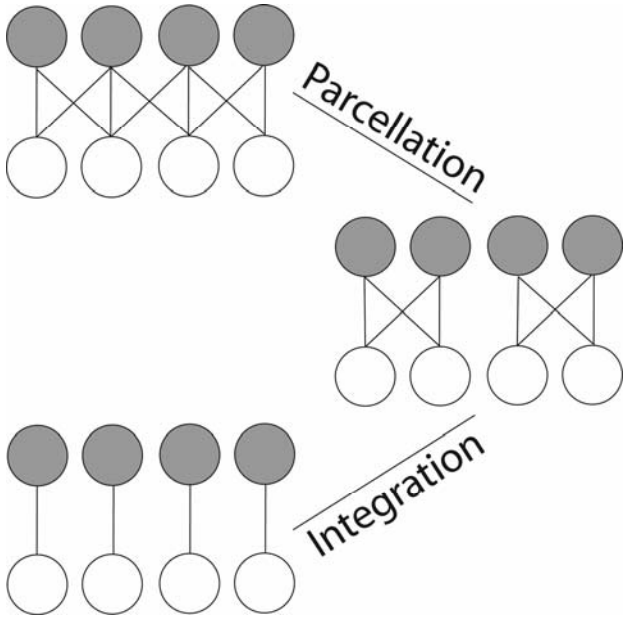

Fig. 1.1. White circles represent genes, grey circles represent phenotypic traits, and the lines link genes to the traits they affect. On the top, a system in which genes affect many traits; on the bottom, a series of one gene-one trait relationships. In the middle, a modular system. Parcellation removes genetic correlations among characters, while integration extends them. Adapted from Wagner (1996).

patterns of character covariation to functional and developmental relationships (Olson and Miller, 1958). The term was not defined in the text of the book; however, generally speaking, integration can be defined as "the observation that particular subsets of morphological traits tend to covary strongly over development and evolution, while other subsets are more weakly associated" (Magwene, 2006: 490). A perspective of integration views the phenotype as "networks of component traits connected by genetic, developmental, or functional interactions" (Santos and Cannatella, 2011: 1). The pattern and magnitudes of covariation can vary among species; thus, studies of integration aim to understand not only why certain characters covary within and among species and others do not, but also why covariation is stable or unstable over an evolutionary time scale. As will be reviewed, the pattern of variance-covariance created by genetic networks, and not

just the morphological products of genes, is shaped by evolutionary mechanisms (selection, drift, etc.).

The term "integration" is used to describe an evolutionary transformation of genetic networks to create covariation among characters and also to describe covariation that is observed within a biological population (measured for phenotypic characters with a correlation coefficient, for example). When the term is used to describe a process, integration is contrasted with "parcellation," which alters genetic networks to remove covariation among characters (Figure 1.1). Integration and parcellation are predicted to shape the genotype-phenotype map so that patterns of genetic covariation reflect those of the functional relationships among characters (e.g., Wagner, 1996; Wagner and Altenberg, 1996; Wagner et al., 2007; Hallgrimsson et al., 2009).

An organism's features can be atomized into many characters, but these characters are linked by a number of biological factors. Broadly considered, integration is observed as the "correspondence of patterns of covariation among traits to a priori or a posteriori hypotheses" (Chernoff and Magwene, 1999: 319) based on shared biological attributes. Examples of these attributes include origin in embryonic tissue, pleiotropy, function, spatial constraints, and evolutionary history, all of which are expected to impact patterns of character covariation. Character covariation can be addressed across a range of biological hierarchies: among genes, within demes, within and among populations of a species, and among species (covariation observed at higher taxonomic levels of the hierarchy may or may not be reflected in the levels below it) (e.g., Cheverud, 1996). The multitude of influences on covariation and the many biological levels at which covariation can be studied (e.g., Cheverud, 1996) partially explains the plethora of adjectives attached to "integration:" ontogenetic integration (e.g., Ackermann, 2005), developmental integration (Cheverud, 1996; Fink and Zelditch, 1996; Klingenberg,

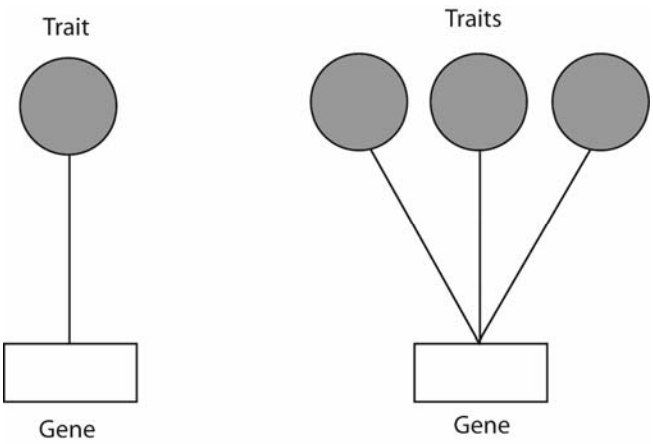

Fig. 1.2. On the left, a simple one gene-one trait relationship; on the right, a pleiotropic relationship in which a gene affects the expression of more than one trait.

2003), phenotypic integration (e.g., Cheverud, 1982; Pigliucci, 2003; Pigliucci and Preston, 2004; Arnold, 2005), evolutionary integration (e.g., Cheverud, 1996; Monteiro et al., 2005), genetic integration (e.g., Cheverud, 1982), and functional integration (e.g., Zelditch and Carmichael, 1989; Lockwood, 2007) to name a few. As Klingenberg (2008: 117) states, "overall, therefore, it is clear that no general consensus on the meaning and measurement of morphological integration has been achieved. Readers are advised to exercise caution when comparing the results from different studies." The present study of the anthropoid primate dentition addresses character covariation at two levels, the population and the clade. As will be discussed, combining these two levels of analysis permits the distinguishing of two processes that produce character coevolution: 1) natural selection acting on genetically covarying characters and 2) selective covariation, where natural selection acts on genetically independent characters.

Pleiotropy: Within a population, phenotypic covariation is affected by genetic and environmental influences. One genetic mechanism that creates phenotypic covariation is pleiotropy, where "loci involved in development participate in multiple developmental

$$G = \begin{bmatrix} \sigma^2_A(1) & \sigma_A(1,2) & \sigma_A(1,3) \\ \sigma_A(1,2) & \sigma^2_A(2) & \sigma_A(2,3) \\ \sigma_A(1,3) & \sigma_A(2,3) & \sigma^2_A(3) \end{bmatrix} \quad P = \begin{bmatrix} \sigma^2(1) & \sigma(1,2) & \sigma(1,3) \\ \sigma(1,2) & \sigma^2(2) & \sigma(2,3) \\ \sigma(1,3) & \sigma(2,3) & \sigma^2(3) \end{bmatrix}$$

Fig. 1.3. Examples of phenotypic and genetic variance-covariance matrices for three characters. $\sigma^2_A(i)$ is the additive variance for character *i* and $\sigma_A(i,j)$ is the additive covariance for characters *i* and *j*. The **G**-matrix, on the left, is the additive genetic variance-covariance matrix, while the **P**-matrix, on the right, is the observed phenotypic variance-covariance matrix.

pathways" (Figure 1.2) (e.g., Hodgkin, 1998; MacKay, 2001). In such an arrangement, allelic variants of a gene produce phenotypic covariation when measured at the population level.

The strength of a pleiotropic association of two characters can be quantified as a genetic correlation (r_G); similarly, among a suite of characters, patterns of genetic correlation are summarized by the genetic variance-covariance matrix (the **G**-matrix or, simply, **G**). The cells on the diagonal of **G** are the additive genetic variances for each character and the off-diagonal elements are the additive genetic covariances among characters (Figure 1.3). Most commonly, **G** is estimated in pedigreed samples 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, studies of genetic variance-covariance in primates have been limited to a few "laboratory" primate populations; for example, *Papio* sp. at the Southwest National Primate Research Center (SNPRC) (e.g., Hlusko et al., 2007a, 2007b; Hlusko and Mahaney, 2009; Koh et al., 2010), *Macaca mulatta* at Cayo Santiago, Puerto Rico (Cheverud, 1982), and *Saguinas fuscicollis* at the Oak Ridge Associated University Marmoset Research Center

(Cheverud, 1995). Among these samples, genetic correlations in the dentition have been studied most extensively in the SNPRC baboons (e.g., Hlusko et al., 2002, 2004, 2006; Hlusko and Mahaney, 2009; Hlusko et al., 2010).

The phenotypic variance-covariance matrix (**P**-matrix or **P**) is typically used to estimate **G** in nonpedigreed samples (Figure 1.3); however, the substitution of phenotypic values is only appropriate if certain conditions are met. Since phenotypic variance-covariance reflects both genetic and environmental influences, the effect of the environment should be minimal for the phenotypic values to reflect their genetic counterparts. The relative effect of genotypic and environmental variance on the phenotypic variance of character can be defined as the character's narrow-sense heritability ($\mathbf{h^2}$); as $\mathbf{h^2}$ approaches 1, the effect of the environment is minimized (more on the calculation of $\mathbf{h^2}$ and limitations in its estimation are provided below). Another factor to consider is sample size; as is true of all sample statistics, confidence in the estimation of the population-level phenotypic variance-covariance increases as the sample size becomes larger.

Cheverud (1988a) conducted a meta-analysis of 23 studies for which genetic- and phenotypic-correlation matrices were available (these 23 studies were conducted on a wide range of animals ("human to amphipod") and traits ("morphological to cognitive")). He demonstrated that, as sample size increases, the disparity in the estimates of genetic and phenotypic correlations becomes negligible. He concluded that the "actual population values for genetic and phenotypic correlations are quite similar," (Cheverud, 1988a: 964) which is now widely known as "Cheverud's conjecture" in the literature. Waitt and Levin (1998), in a survey of plants, and Reusch and Blanckenhorn (1998), in a study of the dung fly *Sepsis cynipsea*, each supported Cheverud's conjecture (see also, Schluter, 1996; Roff, 1997). For the size of the anthropoid maxillary dentition, Hlusko and Mahaney

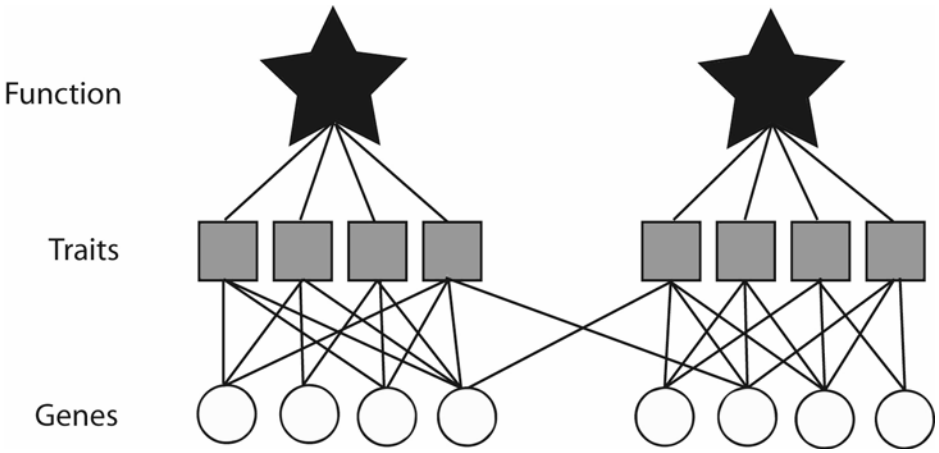

Fig. 1.4. In this example, two functional modules also represent variational modules, since pleiotropic effects are mostly confined to each module. This is an example of modular pleiotropy. Adapted from Wagner (1996) and Wang et al. (2010).

(2009) found that genetic and phenotypic correlation matrices are similar in pedigreed SNPRC *Papio* sp. and that both matrices are similar to the phenotypic correlation matrix for wild-shot *Papio anubis*. In this study, patterns of phenotypic variance-covariance are examined and are assumed to reflect genetic variance-covariance. Fortunately for this study, primate dentometric variation has been shown to be highly heritable in the samples where it has been estimated, as will be reviewed below.

Modularity: As a general principle applicable to many different biological systems, Wagner et al. (2007) define modularity as "a pattern of connectedness in which elements are grouped into highly connected subsets — that is, modules — which are more loosely connected to other such groups" (see also Cheverud et al., 1997, 2004; Leamy et al., 1999; Cheverud, 2001; Klingenberg et al., 2004; Juenger et al., 2005). To complete a function, often several phenotypic characters participate as a unit (i.e., a functional complex), which Wagner et al. (2007) define as a "functional module." Characters in a functional module tend to be linked by pleiotropy and form a "variational module,"

which is “a set of covarying traits that vary relatively independently of other such sets of traits. Variational modules are recognized by higher than average correlations among traits” (Figure 1.4) (Wagner et al., 2007: 921).

Modularity is an organizing principle and in certain models (summarized in Wagner et al., 2007) is purported to be selectively advantageous. These models rely on the principle that modularity “is selected if it ….makes adaptive phenotypes accessible that would be genetically unattainable otherwise” (Wagner et al., 2007: 926). As there are a variety of functions performed by an organism, it is not likely that all characters need to simultaneously change to meet shifting environmental conditions. If characters in functional modules are pleiotropically linked to one another and unlinked to characters outside of the module, then the functional unit can easily coevolve in response to selection and not affect the morphology/function of characters outside of the complex. Therefore, changes in one functional module do not compromise adaptations in other modules. This argument for the existence of modularity is similar to R.A. 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 pleiotropy does not exist has a high “cost of complexity,” requiring each character in a functional module to respond independently to natural selection. Wagner and Zhang (2011: 205) state, “the more independent dimensions of variation the phenotype has, the more difficult is improvement resulting from random changes. The reason is that, if there are many different ways to change a phenotype, it becomes very unlikely that a random mutation affects the right combination of traits in the right way to improve fitness.” A modular organization reduces this cost. Since pleiotropy creates this covariation, Cheverud et al. (2004; Wagner et al., 2007) refer to this model of organization as “modular pleiotropy.”

To describe the effects of modularity on the evolutionary potential of systems, Wagner and Altenberg (1996) use the "representation phenomenon" of evolvable computer algorithms, which refers to how an algorithm's code is translated into output, as an analogy. Some evolutionary algorithms fail to produce improvements in a program's success at performing tasks because mutations in the code affect the whole program and randomize the output. Modularly organized evolvable algorithms are more successful because each module has a specific task and mutational effects are confined to a single module (Hansen, 2003). For organisms, the equivalent of the representation phenomenon is the "genotype-phenotype map," which, within individuals, describes how the genotype is translated into the phenotype (Figure 1.4) and on an evolutionary scale it describes how genetic changes are reflected as phenotypic changes (Wagner, 1996; Wagner and Altenberg, 1996).

Character Covariation Among Species

Selection on Genetically Covarying Characters: Since pleiotropically linked characters are not free to vary independently of one another, each character is "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) (Figure 1.5). The strength of constraint ranges from absent (no genetic correlation; $r_G = 0$) to absolute (complete genetic correlation; $r_G = 1$ or -1). In between absent and absolute constraint, characters are relatively constrained (Figure 1.5). Beldade and Brakefield (2003: 119) noted, "there is no real dichotomy between absolute and relative constraints but rather, as so often in biology, a continuum of constraints (limitations/biases) of different strengths." There is little evidence that absolute

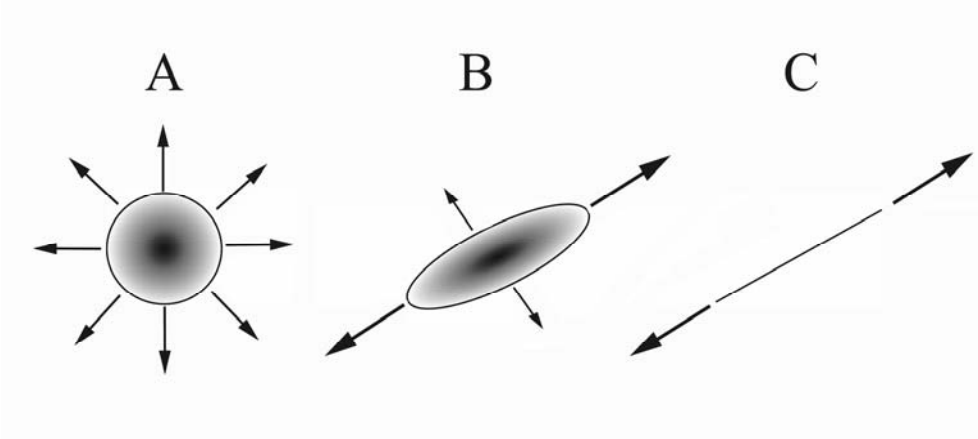

Fig. 1.5. In A, the two characters do not covary within a population; therefore, each character is equally free to evolve in any direction of phenotypic space. In B, the two characters are relatively constrained; limited change is possible perpendicular to the major axis of covariation, though most change is predicted to be channeled along the major axis. In C, the two characters are absolutely constrained and are not free to vary independently of one another; no change is possible away from the major axis. Adapted from Klingenberg (2010).

constraints exist, as most pleiotropically-linked characters have some heritable variation that is not shared with other characters (Klingenberg, 2008; 2010). Within species, pleiotropy is revealed by a pattern of character covariation and, among populations, pleiotropy channels character change along the major axis of genetic covariation; less change is possible perpendicular to the major axis. Therefore, the major axis of genetic covariation represents the "line of least evolutionary resistance" along which characters can evolve (Figures 1.5 and 1.6) (Schluter, 1996; Klingenberg, 2010; Marroig and Cheverud, 2010).

To maintain functional equivalence, characters in functional complexes are expected to coevolve as a result of natural selection acting on the complex and several processes can generate such a pattern.[1] When selection acts on pleiotropically linked

[1] Throughout this dissertation, the term "coevolution" is used to describe the coordinated change of characters (traits) among populations or species. Coevolution is a portmanteau of "correlated

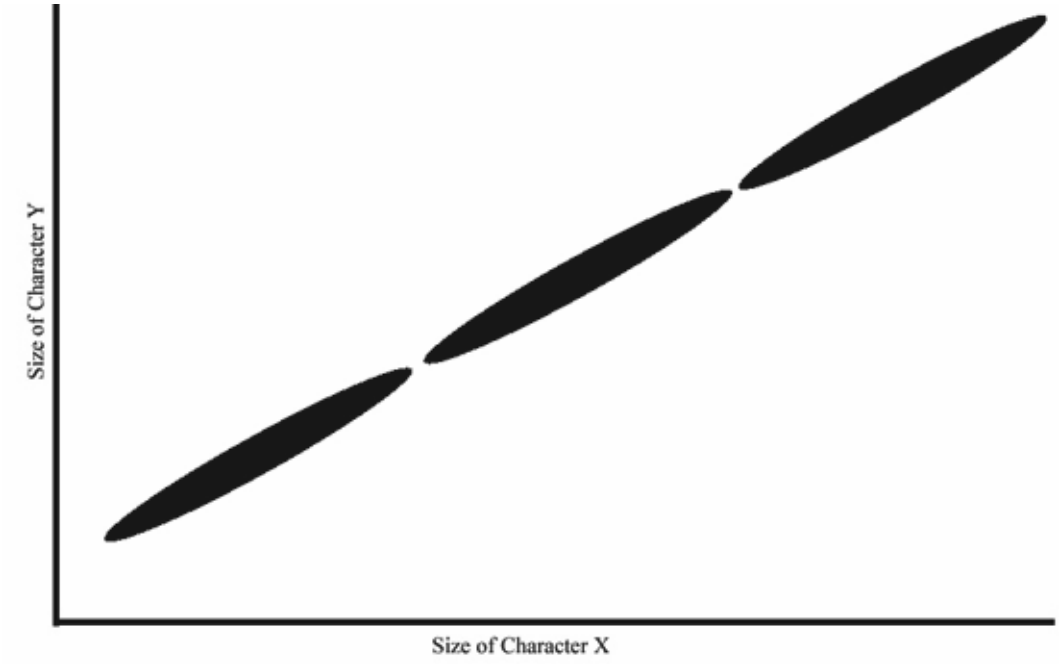

Fig. 1.6. In this example, the sizes of two characters are plotted for three species. The 95% confidence ellipses are estimated as an ellipse for each species. The two characters are characterized by a high degree of covariation (represented by highly elongated ellipses) within samples and are relatively constrained. Among the samples, the two characters have evolved along the major axis of genetic covariation (i.e., the line of least evolutionary resistance).

characters, it tends to pull them along the major axis of covariation; in this case, coevolution, observed among species, is in part an extension of the genetic relationship that exists within species (e.g., Cheverud, 1982, 1988b, 1989, 1996). Pleiotropically linked characters are expected to express phenotypic covariation both within and among species (when measured using species means, for example) (Figure 1.6).

The response of a single character to natural selection is expressed by the breeder's equation: $\mathbf{\Delta z = h^2 S}$, where $\mathbf{\Delta z}$ is the change in the mean value of the character of interest, $\mathbf{h^2}$ is the narrow-sense heritability of the character, and $\mathbf{S}$ is the strength of

---

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).

selection. The multivariate selection model, $\mathbf{\Delta z} = \mathbf{G\beta}$, is an extension of the breeder's equation and demonstrates how coevolution, observed phenotypically, can be produced as the result of selection acting within populations on genetically correlated traits (e.g., Lande, 1979; Cheverud, 1982). In the multivariate selection model, **G** is the **G**-matrix, **β** is the selection vector, where each β_i reflects the strength of selection acting on each character *i*, and **Δz** is the vector of change in mean value for each character. Selection on genetically correlated traits, which occurs at the population level, will cause them to coevolve.

For a suite of traits, the major axis of genetic covariation ($\mathbf{g_{max}}$) is quantified as the "linear combination...that displays the maximum within-population variance (first principal component)" (Marroig and Cheverud, 2010: 1471, see also, Schluter, 1996; Klingenberg, 2010). As change between populations in directions not aligned with $\mathbf{g_{max}}$ is relatively constrained, then population divergence (**Δz)** should be strongly correlated with $\mathbf{g_{max}}$. (Note that this is not the same as saying the change can *only* happen along $\mathbf{g_{max}}$.) In Figure 1.6, all three populations share the same $\mathbf{g_{max}}$ and **Δz** between all populations occurred along the shared $\mathbf{g_{max}}$. The extent to which lines of least evolutionary resistance are shared among taxa and the correspondence of among-species change to them can be empirically determined (see Chapter 2) (e.g., Marroig and Cheverud, 2005). It is unknown if $\mathbf{g_{max}}$ for anthropoid dental traits is shared among species and if dental diversification is principally aligned with it.

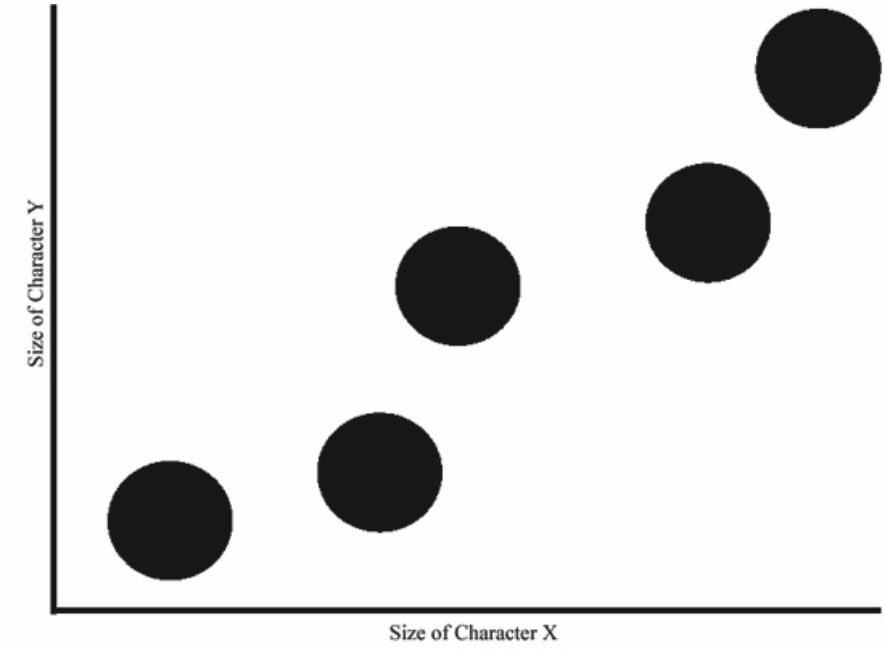

Fig. 1.7. In this example, within-species covariation is estimated for five samples. The 95% confidence ellipses form circles for each species, indicating that the two characters do not covary and are therefore unconstrained; however, among species the species means are correlated. This is the expected pattern if selective or drift covariance occurred.

Selective and Drift Covariance: If fitness is determined 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 pleiotropically linked characters, no pattern of phenotypic covariation is expected within species, even though one exists among species (Figure 1.7) (Armbruster and Schwaegerle, 1996). Thus, selection acting on genetically correlated and uncorrelated traits can produce a 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 (compare Figures 1.6 and 1.7). The failure to recognize that pleiotropy is not a prerequisite for among-species covariation has led some

to infer pleiotropic constraints when only among-species patterns have been analyzed (e.g., Jolly, 1970), as will be discussed below.

Natural selection is not the only evolutionary mechanism that can produce significant covariation when measured among samples. Genetic drift can mimic the pattern produced by natural selection if "drift covariance" occurred (Armbruster and Schwaegerle, 1996). In this case, a pattern of among-sample covariation is the artifact of population structure, genetic drift, and phylogenetic history. As outlined in Chapter 2, the careful choice of samples for data collection and the use of appropriate analyses can limit the influence of drift covariance on observed levels of covariation both within and among species.

Functional and Variational Modules in the Anthropoid Dentition

Teeth are responsible for acquiring and processing food (Ungar, 2010). However, teeth do more than interact with food; among anthropoids, canines are rarely used in diet-related functions, but are instead used in visual displays and as weapons in conflicts. Expectedly, their diversification has been strongly driven by sexual selection (e.g., Plavcan, 2001). In both the maxilla and mandible of the adult dentition of anthropoid primates, four classes of teeth are recognized: incisor, canine, premolar, and molar. Though distinctions in shape, size, and nonmetric morphology are observed within each class, each class is easily distinguishable from the others. Theories that explain the discreteness of tooth class (field theory, clone theory, etc.) have a long history (e.g., Butler, 1939; Dahlberg, 1945). More recent analyses have placed dental covariation within the framework of morphological integration and modularity and have compared patterns of covariation in the primate dentition to that of murine model organisms in

*TABLE 1.1 Narrow sense heritability (**h^2**) estimates for dental features. Sources are as follows: 1) Dempsey et al. (1995), 2) Townsend and Brown (1978), 3) Hughes et al. (2007), 4) Hlusko and Mahaney (2003), 5) Hlusko and Mahaney (2009), 6) Hlusko et al. (2004b), 7) Hlusko and Mahaney (2007a), 8) Hlusko et al. (2004a), 9) Koh et al. (2010), 10) Hlusko et al. (2007b)*

Taxon	Character	h^2	Source
Homo sapiens (South Australian Twins)	Mandibular and Maxillary Incisor MD and BL	♂ = 0.84–0.89 ♀ = 0.81–0.91	1
Homo sapiens (Australian Twins)	I^2 emergence time	♂ = 0.82–0.94 ♀ = 0.71–0.96	3
Homo sapiens (Yuendumu Aborigines)	Permanent tooth size (half-sib, full-sib, parent-offspring)	MD = 0.63, 0.72, 0.64 BL = 0.66, 0.81, 0.57	2
Papio sp. (SNPRC)	Maxillary and Mandibular Cingular Remnant	0.33–0.73 $\bar{x}$ = 0.49	4
Papio sp. (SNPRC)	I^1 size (right, left)	MD = 0.58, 0.65 BL = 0.61, 0.45	5
Papio sp. (SNPRC)	I^2 size (right, left)	MD = 0.61, 0.45 BL = 0.64, 0.60	5
Papio sp. (SNPRC)	P^3 size (right, left)	MD = 0.32, 0.24 BL = 0.66, 0.29	5
Papio sp. (SNPRC)	P^4 size (right, left)	MD = 0.68, 0.48 BL = 0.59, 0.61	5
Papio sp. (SNPRC)	M^1 size (right, left)	MD = 0.66, 0.75 BL = 0.67, 0.72	5
Papio sp. (SNPRC)	M^2 size (right, left)	MD = 0.76, 0.85 BL = 0.54, 0.68	5
Papio sp. (SNPRC)	M^3 size(right, left)	MD = 0.45, 0.23 BL = 0.56, 0.23	5
Papio sp. (SNPRC)	$M^{1–3}$ loph angles	0.32–0.43	6
Papio sp. (SNPRC)	M_2 size	MD = 0.67 BL = 0.73	7
Papio sp. (SNPRC)	M_2 area	MD*BL = 0.85 planimetric = 0.83	7
Papio sp. (SNPRC)	M_2 enamel thickness (right, left)	0.44, 0.32	8
Papio sp. (SNPRC)	M^{1-3} hypocone area	0.11–0.54	9
Papio sp. (SNPRC)	M^{1-3} protocone area	0.15–0.42	9
Papio sp. (SNPRC)	M^{1-3} paracone area	0.09–0.55	9
Papio sp. (SNPRC)	M^{1-3} metacone area	0.10–0.59	9
Papio sp. (SNPRC)	$M_{1–3}$ loph angles	0.24–0.68	6
Papio sp. (SNPRC)	$M_{1–3}$ metaconid area	0.45–0.59	10
Papio sp. (SNPRC)	$M_{1–3}$ entoconid area	0.29–0.44	10
Papio sp. (SNPRC)	$M_{1–3}$ protoconid area	0.11–0.25	10
Papio sp. (SNPRC)	$M_{1–3}$ hypoconid area	0.28–0.57	10

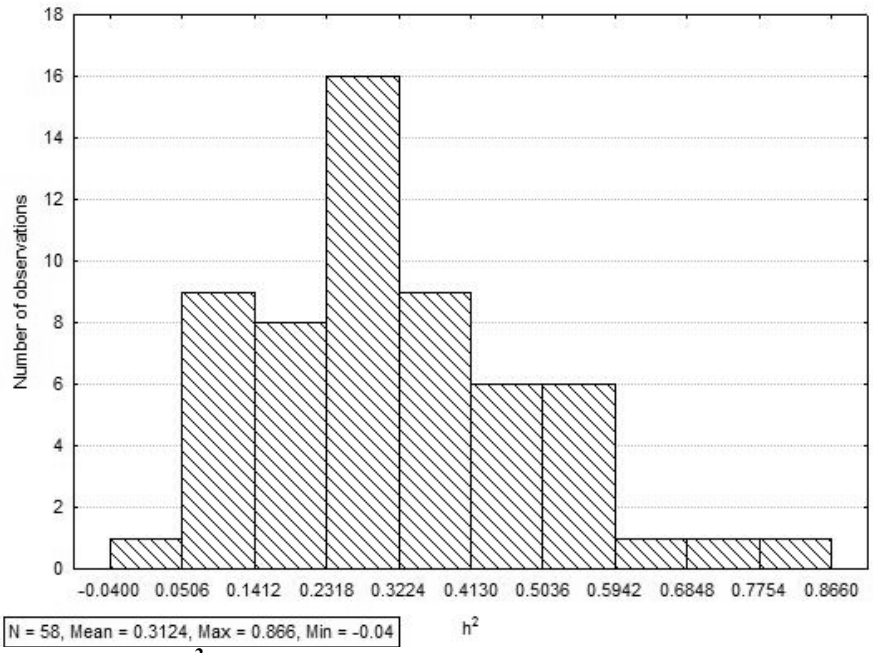

Fig 1.8. Histogram of $\mathbf{h^2}$ estimates for 58 linear measurements of the cranium, derived from the from the Cayo Santiago *Macaca mulatta* sample (Cheverud, 1982).

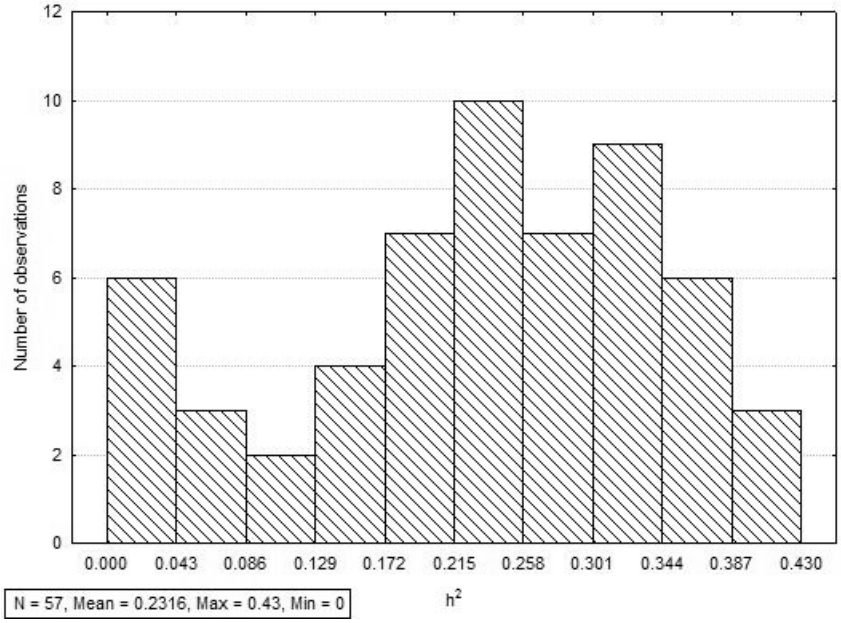

Fig. 1.9. Histogram of $\mathbf{h^2}$ estimates for 57 linear measurements of the ectocranium, derived from the Hallstatt, Austria skeletal collection (Martínez-Abadías et al., 2008). that variational modules do not exist in the dentition. Recent molecular work has shown

which odontogenesis has been studied extensively (Hlusko and Mahaney, 2009; Hlusko et al., 2010).

Dental field theory and clone theory each suggest that teeth are meristic structures; that is, like vertebrae and ribs, they are serially homologous (e.g., Butler, 1939, 1967; Lombardi, 1975). The premise of these theories is that within each class dental development is controlled by shared genes; however, an alternative perspective suggests that each tooth is genetically independent and that similarities in form arose because teeth that share functions independently converged on similar morphologies (see Butler, 1967). Field and clone theory would predict that dental classes are both functional and variational modules (*sensu* Wagner et al., 2007), while the alternative would suggest that variational modules do not exist in the dentition. Recent molecular work has shown that teeth are indeed meristic structures (e.g., Kangas et al., 2004) and that enamel knots (the site of future cusps) themselves form as a result of "repeated activation of the same molecular machinery" (i.e., developmental module) (Jernvall and Hungl, 2000: 183), indicating that the dentition is developmentally integrated. Below, the evidence for dental functional and variational modules is reviewed.

Heritability of Dental Variation: It is an assumption of this study that phenotypic variance-covariance in dental characters, observed within species, reflects underlying genetic variance-covariance; dental variation must have high heritability. Narrow-sense heritability measures the relative effect of genotypic and environmental variance on the phenotypic variance of a trait. It is defined as $\mathbf{h^2 = \sigma^2_G/\sigma^2_P}$, where $\mathbf{\sigma^2_G}$ is the additive genetic variance and $\mathbf{\sigma^2_P}$ is the phenotypic variance. As $\mathbf{h^2}$ approaches 1, the effect of the environment approaches 0; therefore, for highly heritable characters (i.e., $\mathbf{h^2}$ close to 1), the influence of the environment on phenotypic variance is small.

Overall, estimates of $\mathbf{h^2}$ for dental characters in human and nonhuman primates are relatively high. In general, estimates of $\mathbf{h^2}$ for linear measures of dental size in *Homo sapiens* range from 0.6–0.8 (Townsend and Brown, 1978; Townsend et al., 2006), which is similar to $\mathbf{h^2}$ estimates for linear and areal dimensions of the dentition in SNPRC baboons (Table 1.1) (Hlusko et al., 2002; Hlusko and Mahaney, 2007b; Hlusko et al., 2010). For 68 dimensions of the SNPRC baboon dentition, Hlusko et al. (2010) report an average $\mathbf{h^2}$ of 0.56 after the effects of age and sex are accounted for. The relatively high $\mathbf{h^2}$s observed for primate dentometric variation can be seen by contrasting them with those observed for craniometrics. For example, Cheverud (1982) estimated $\mathbf{h^2}$ for 58 linear dimensions of the cranium in pedigreed *Macaca mulatta* at Cayo Santiago; in that sample, $\mathbf{h^2}$ estimates range from 0.04–0.89 with a mean of 0.31 (Figure 1.8). Martínez-Abadías et al. (2009) estimated $\mathbf{h^2}$ for 58 linear dimensions of the cranium in a pedigreed sample of Austrian *Homo sapiens* and reported a range of 0.00–0.43 and a mean of 0.23 (Figure 1.9). Even relative to other anatomical regions that have been frequent subjects for studies of integration and modularity (e.g. Cheverud, 1982; Cheverud, 1995; Ackermann, 2009; Marroig and Cheverud, 2010), the primate dentition is characterized by high $\mathbf{h^2}$s; in the two studies of primate cranial size heritability cited here, few $\mathbf{h^2}$s approach the values observed for linear and areal dimensions of the dentition. In fact, in the two studies combined, only 3 of 115 $\mathbf{h^2}$ estimates exceed 0.60 (Figures 1.8 and 1.9), a value that is frequently exceeded in estimates of tooth size in *Homo sapiens* and SNPRC *Papio* sp. (Table 1.1).

Comparisons of $\mathbf{h^2}$ between studies and among populations must keep certain factors in mind. For example, there are a variety of ways that pedigree information is used to generate estimates of $\mathbf{h^2}$; estimates may be derived from regressions of phenotypic values of mother-offspring, father-offspring, midparent-offspring,

TABLE 1.2. Summary statistics for M^2 length and breadth in the SNPRC Papio and wild shot Papio anubis. Data are from Hlusko and Mahaney (2007a).

		LM^2			RM^2		
		MD	Mesial Breadth	Distal Breadth	MD	Mesial Breadth	Distal Breadth
Wild *Papio anubis*	*n*	91	89	88	94	88	88
	$\bar{x}$	12.25	11.47	10.40	12.22	11.38	10.38
	s	0.84	0.75	0.69	0.87	0.79	0.71
	CV	6.86	6.54	6.63	7.12	6.94	6.84
Total Captive SNPRC	*n*	649	647	637	643	638	623
	$\bar{x}$	12.51	10.12	9.13	12.43	10.09	9.07
	s	0.84	0.87	0.832	0.84	0.87	0.83
	CV	6.71	8.60	9.11	6.76	8.62	9.15
SNPRC Founders	*n*	60	57	57	59	59	58
	$\bar{x}$	12.13	9.60	8.70	12.09	9.57	8.76
	s	0.57	0.59	0.58	0.57	0.52	0.52
	CV	4.70	6.15	6.67	4.71	5.43	5.94
SNPRC Descendents	*n*	589	590	580	584	579	565
	$\bar{x}$	12.55	10.17	9.17	12.46	10.14	9.10

monozygotic twins, dizygotic twins, full sibling, half sibling, etc., which produces estimates that are not necessarily equivalent (Table 1.1). In addition to these simple pedigree estimates, complex pedigrees that include distantly related kin are also used to estimate $\mathbf{h^2}$. It is from more complex pedigrees that $\mathbf{h^2}$ estimates have been derived for pedigreed SNPRC *Papio* sp. (e.g., Hlusko et al., 2004a, 2004b, 2006; Hlusko and Maheney, 2009).

Though the study of SNPRC baboons suggests high $\mathbf{h^2}$s for the anthropoid dentition, some have expressed doubts that $\mathbf{h^2}$ estimates in laboratory populations reflect their values in wild populations. Because founding laboratory populations tend to be quite small, their founding likely involves a loss of genetic variation due to genetic drift

TABLE 1.3. Summary statistics for M_2 length and breadth in SNPRC Papio and wild shot Papio anubis. Data are from Hlusko and Mahaney (2007).

		LM_2			RM_2	
		MD	Mesial Breadth	Distal Breadth	MD	Mesial Breadth	Distal Breadth
Wild *Papio anubis*	*n*	87	86	85	87	89	86
	$\bar{x}$	12.12	10.09	9.93	12.20	10.09	9.86
	s	0.82	0.74	0.74	0.83	0.7	0.65
	CV	6.77	7.33	7.45	6.79	6.94	6.59
Total Captive SNPRC	*n*	590	581	572	593	585	575
	$\bar{x}$	12.29	9.35	8.79	12.30	9.35	8.79
	s	0.82	0.77	0.83	0.79	0.74	0.77
	CV	6.67	8.24	9.44	6.40	7.91	8.76
SNPRC Founders	*n*	52	51	51	54	54	53
	$\bar{x}$	11.96	8.94	8.38	12.00	9.04	8.45
	s	0.54	0.49	0.54	0.54	0.51	0.42
	CV	4.52	5.48	6.44	4.50	5.64	4.97
SNPRC Descendents	*n*	538	530	521	539	531	522
	$\bar{x}$	12.32	9.39	8.83	12.38	9.38	8.82

(founder effect), which should lower $\mathbf{h^2}$ relative to wild populations. Though the founder effect may lower $\mathbf{h^2}$, admixture of separate biological populations and a reduction of environmental variance are predicted to elevate $\mathbf{h^2}$ in the laboratory setting (Weigensberg and Roff, 1996). These concerns can be illustrated in the SNPRC baboon sample. Hlusko and Maheney (2007a) reported summary statistics for 12 measurements of the M^2 and M_2 in the SNPRC founding population, the total SNPRC sample, and a wild-shot sample of *Papio anubis*. For 11 of 12 measures, the SNPRC founding population has the lowest standard deviation (*s*) and coefficient of variation (CV) (Tables 1.2 and 1.3), likely indicating a founder effect. The CVs for the total sample (which includes the founding

individuals) are similar to those of the wild-shot *Papio anubis* sample, suggesting an elevation of phenotypic variance subsequent to the SNPRC population's founding. Admixture is also evident in the SNPRC baboons; though the founding sample comprised mostly *Papio anubis* individuals, some *Papio hamadryas* and *Papio cynocephalus* individuals were founders and the descendents include hybrids of these biologically distinct populations (Hlusko and Mahaney, 2007a, 2009). Tooth size has also evolved over time in the SNPRC baboon sample, as all 12 dimensions of the second molars have larger means ($\bar{x}$) in the descendent sample than in the founding sample (Tables 1.2 and 1.3)

To address the correspondence of $\mathbf{h^2}$ estimates in laboratory and wild populations, Weigensberg and Roff (1996) performed a meta-analysis and found that in the populations they studied $\mathbf{h^2}$ estimates are not significantly different for the same populations in wild and captive settings. Contrary to their expectations, they found that $\mathbf{h^2}$ estimates in wild populations are usually higher than in laboratory populations. It is an assumption of this study that $\mathbf{h^2}$s are high for the dental characters; however, without estimating $\mathbf{h^2}$ in all wild populations included in this analysis, it is impossible to know if they are similar to those observed in SNPRC *Papio* sp. or *Homo sapiens*.

Acquisition (Incisal) Module: In anthropoids, the incisors primarily function to acquire food. Examples of acquisition behaviors include fracturing items into smaller fragments, which can then be introduced into the mouth for further processing, isolating edible from inedible items, cropping and stripping leaves from branches, gouging trees to release exudates, peeling fruits, separating the fleshy endocarp of fruits from the dense seeds within (Ungar, 2010; Ungar and Lucas, 2010) and, rarely, to "rip and tear skin from the cadaver," as observed in *Pan troglodytes* (Pickford, 2005: 28).

TABLE 1.4: Coefficients of Determination (r^2) among dimensions of maxillary incisor size (Hlusko and Mahaney, 2009).

SNPRC *Papio* Genetic (n = 358–576)

	I^1MD	I^2LL	I^2MD
I^1LL	0.10	0.80	0.74
I^1MD	—	0.10	0.20
I^2LL		—	0.66

SNPRC *Papio* Phenotypic (n = 151–487)

	I^1MD	I^2LL	I^2MD
I^1LL	0.05	0.28	0.16
I^1MD	—	0.04	0.07
I^2LL		—	0.18

wild-shot *Papio anubis* (n = 113–132)

	I^1MD	I^2LL	I^2MD
I^1LL	0.45	0.51	0.34
I^1MD	—	0.34	0.31
I^2LL		—	0.31

wild-shot *Presbytis* (n = 25)

	I^1MD	I^2LL	I^2MD
I^1LL	-0.26	0.65	-0.31
I^1MD	—	-0.39	0.72
I^2LL		—	-0.39

Anthropoid taxa vary in their incisal use and not all taxa frequently perform all behaviors listed in the previous paragraph. Among species, there is considerable diversity in incisor size (in absolute size, relative to body size, relative to the size of postcanine dentition, and even relative to the size of one another) and shape (ranging from broad and spatulate to narrow and styliform), which is believed to reflect "adaptations to meet the mechanical demands of food acquisition" (Ungar and Lucas, 2010: 519; Ang et al. 2006; Agrawal et al. 2008; Anapol and Lee, 1994; Eaglen, 1984; Norconk et al., 2009; Ungar, 2010). An example illustrates the relationship between incisal form and function. Among

closely related anthropoid species, the length of the incisal row has been shown to covary positively with body size; in this general scaling relationship, positive residuals (i.e., larger than expected incisor size) are associated with frugivorous diets, which require frequent incisal preparation, and negative residuals are associated with folivorous diets (Hylander 1975; Ungar, 1994; Ungar, 2010; Ungar and Lucas, 2010; Eaglen, 1984; Ungar, 1996). Among anthropoids, some of the most morphologically derived and functionally specialized incisors are seen in pitheciines (*Pithecia*, *Chiropotes*, *Cacajao*), which have tall, narrow and procumbent incisors (Anapol and Lee, 1994; Kinzey, 1992; Rosenberger, 1992; Rosenberger and Strier, 1989) that are used in piercing fruit husks and scraping mesocarp from hard nuts, and also in prying resistant seeds from fruits (Kinzey and Norconk, 1990; Anapol and Lee, 1994).

While it is evident that incisors form a functional module and that selection has shaped them to acquire food, there is far less evidence that they form a variational module and that pleiotropy is a strong constraint on their evolution. Hlusko and Mahaney (2009) investigated modularity in the maxillary dentition of the SNPRC baboon sample and wild-shot samples of *Papio anubis* and *Presbytis* (species unspecified). As regards incisor size covariation, their results are not easily interpretable (Table 1.4). Though a Mantel test of correlation matrix similarity for the entire dental set (incisors + postcanine) indicated pattern similarity for all samples, this is not evident when incisor covariation is considered in isolation. For example, the SNPRC genetic correlation matrix indicates that the labiolingual (LL) and mesiodistal (MD) dimensions are essentially independent for the I^1 ($r^2 = 0.10$ for I^1MD-I^1LL) but not so for the I^2 ($r^2 = 0.66$ for I^2MD-I^2LL); moreover, the LL breadths of the maxillary incisors show high magnitude genetic covariation ($r^2 = 0.80$ for I^1LL-I^2LL) but the MD lengths do not ($r^2 = 0.20$ for I^1MD-I^2MD), suggesting that levels of covariation are drastically different for the LL and MD dimensions between

incisors. For the SNPRC genetic correlations, the second highest level of covariation was observed for I^1LL-I^2MD (r^2 = 0.74), suggesting a substantially tighter pleiotropic linkage between I^1LL and I^2MD than between I^1LL and I^1MD. In contrast, the SNPRC phenotypic correlation matrix indicates weak covariation among all incisal pairs (the highest, r^2 = 0.28, is observed for I^1LL-I^2LL); the I^1LL-I^2MD r^2 is 0.58 less in the SNPRC phenotypic matrix than in the genetic matrix, the I^1LL-I^2LL r^2 is 0.52 less, and the I^2MD-I^2LL r^2 is 0.48 less (Table 1.4; note that sample sizes vary between the samples being compared). The wild-shot *Papio anubis* data set differs from both SNPRC baboon correlation matrices in that the MD length and LL breadth of the I^1 highly covary (r^2 = 0.45), while covariation between LL breadths is only slightly higher (r^2 = 0.51). For wild-shot *Papio anubis*, the second highest magnitude of covariation is between I^1MD-I^1LL; however, in the SNPRC matrices, the magnitude of covariation between the LL breadths is far greater than between I^1MD and I^1LL. The wild-shot *Presbytis* sample is the most distinctive of all; the LL breadths and the MD lengths of the maxillary incisors show similarly strong magnitudes of covariation (r^2 = 0.65 and 0.72, respectively), but all comparisons between MD length and LL breadth show moderate levels of *negative* covariation (between r^2 = -0.26 and -0.39; the negative sign indicates that the correlation coefficient (r) is negative). About the only commonality among the four correlation matrices is that the LL breadths of the maxillary incisors are typically the most highly covarying character pair.

While support for strong covariation among incisal pairs within species is ambiguous; in support of the hypothesis of dental modularity, Hlusko and Mahaney (2009) found that incisor size and postcanine size do not covary strongly. For the SNPRC genetic correlations, out of 52 correlations between incisor and postcanine size, the highest observed value is r^2 = 0.64 (for I^1LL-P^3MD), which is probably aberrantly high,

as the second highest value is only $r^2 = 0.21$ (for I^1LL-M^1MD). For the SNPRC phenotypic correlations, the highest observed value is $r^2 = 0.06$ (for I^1LL-P^3MD), for the wild-shot *Papio anubis* sample, levels of covariation were typically higher, with 10 out of 52 correlations having an $r^2 \geq 0.40$ (the highest is $r^2 = 0.49$ for I^2MD-M^3 distal breadth), and for the wild-shot *Presbytis* sample the highest observed value was $r^2 = 0.29$ (for I^1MD-M^1 mesial breadth). The low level of size covariance among incisors and postcanine teeth is consistent with the expression domains of genes involved in dental development. In mice, the genes Msx1 and Msx2 are expressed in the tissues that produce incisors, while Dlx1, Dlx2, and Barx1 are expressed in the tissues that produce molars. The genes Lhx6 and Lhx7 are expressed in both regions (Hlusko et al., 2010).

In Hlusko and Mahaney (2009), all genetic correlations between the incisors and postcanine teeth are positive; however, in a subsequent study of the SNPRC baboons, Hlusko et al. (2010) found that some dimensions of incisor and postcanine size are negatively correlated. These negative correlations are spread among both maxillary and mandibular dental size. For the mandible, 24 of 53 significant genetic correlations are negative for the left side and 19 of 53 significant correlations are negative for the right side; for the maxilla, 14 of 53 significant correlations are negative for the left side and 22 of 55 significant correlations are significant for the right side. They state that the "evolutionary implications could be quite interesting and important" (Hlusko et al., 2010: 46); specifically, they cite the among-species differences in *Australopithecus* and *Paranthropus* tooth size, relative to extant apes, that indicate an enlargement of the postcanine dentition and concurrent diminution of the anterior dentition. They are implicating constraints, imposed by the genetic architecture, in the evolution of hominin dental size. Such a negative genetic correlation has been predicted to exist by McCollum and Sharpe (2001), as will be discussed later.

While the evidence for the magnitude and direction of incisor size covariation is not consistent among cercopithecid species (Hlusko and Mahaney, 2009), it suggests limited support for the hypothesis that the incisors are a variational module; however, there is little evidence that the incisors have coevolved as a unit. To date, no study has examined the coevolution of incisor size or the extent to which incisor diversification in either size or shape has followed $\mathbf{g}_{\mathbf{max}}$. A cursory examination among species suggests that the incisors are not strongly constrained. Kelly et al. (1995) report mean maxillary incisor size for *Pongo abelii* (I^1MD: 13.9 mm; I^2MD: 7.7 mm: I^1MD/I^2MD: 1.78), *Pongo pygmaeus* (I^1MD: 13.7 mm; I^2MD: 8.8 mm; I^1MD/I^2MD: 1.55), *Gorilla gorilla* (I^1MD: 12.5 mm; I^2MD: 9.1mm; I^1MD/I^2MD: 1.38), and *Pan troglodytes* (I^1MD: 11.5 mm; I^2MD: 9.0 mm; I^1MD/I^2MD: 1.29). Compared to *Pongo*, the *Gorilla gorilla* I^1MD is more than 1.0 mm less than either *Pongo* species, but its I^2MD is larger (1.4 mm greater than *Pongo abelii* and 0.3 mm greater than *Pongo pygmaeus*). Such a pattern of difference among taxa would only be expected if the sizes of the maxillary incisors are not strongly linked pleiotropically or if the sizes of the teeth have a negative correlation. The same is true to a more exaggerated extent when maxillary incisor size is compared between *Pan troglodytes* and *Pongo*; in this comparison, the *Pan* I^1MD is more than 2.0 mm smaller than either *Pongo* species but its I^2MD mean is larger (1.3 mm larger than *Pongo abelii* and 0.2 mm larger than *Pongo pygmaeus*). Not surprisingly, *Pongo* incisor size heteromorphy is far greater than in *Pan.* If only the 4 hominid taxa mentioned are considered, then an r^2 = -0.48 is observed for the MD lengths of the maxillary incisors, which indicates a negative correlation (i.e., as the central incisor becomes larger, the lateral becomes smaller and vice versa). This seems unlikely when incisor size in Miocene hominoids and extant hylobatids are also considered, as many of these taxa have both smaller I^1MD and I^2MD lengths than any of the extant hominids (see data in Kelley

TABLE 1.5. Coefficients of Determination (r^2s) among some dimensions of maxillary postcanine size (from Hlusko and Mahaney (2009)).

	P^4MD-M^1MD	M^1MD-M^2MD	M^2MD-M^3MD	P^4BL-M^1BL	M^1BL-M^2BL	M^2BL-M^3BL
SNPRC *Papio* Genetic (*n* = 358–576)	0.32	0.84	0.90	0.28	0.75	0.84
SNPRC *Papio* Phenotypic (*n* = 151–487)	0.16	0.49	0.23	0.18	0.34	0.22
wild-shot *Papio anubis* (*n* = 113–132)	0.24	0.35	0.37	0.25	0.70	0.72
wild-shot *Presbytis* (*n* = 25)	0.37	0.74	0.53	0.71	0.80	0.88

et al., 1995; personal observations). The negative correlation for hominid MD length is not predicted from the SNPRC baboon correlation matrices (Table 1.4) (Hlusko and Mahaney, 2009; Hlusko et al., 2010). Instead of a negative genetic correlation, it is more likely that the MD lengths of the maxillary incisors are not tightly constrained by pleiotropy and are capable of quite divergent evolutionary trajectories.

Processing (Postcanine) Module: After food items are acquired, they are processed (masticated) by the postcanine dentition (premolars and molars). At the most basic level, the postcanine teeth fracture food into smaller pieces by "compression as the lowers approach opposing uppers with food items between them" (Ungar, 2010: 155). Food processing is intimately linked to the maxillary and mandibular postcanine teeth functioning as a unit.

The relationship between form and function has been studied extensively for the postcanine teeth (especially so for molars). Among species, molar size has been related to fracture mechanics of the food items masticated. Lucas (2004) suggested that, in order to increase the probability of fracture, smaller food particles select for larger tooth size, as do foods that form thin sheets. In addition to tooth size, substantial interspecific variation in cusp relief and shearing crest development has been related to variation in the material properties of the foods most frequently masticated, so that primates that consume "hard, brittle foods with stress-limited defenses" have low blunt cusped teeth, while primates that routinely consume "tough leaves or other plant parts, or insects with tough exoskeletons, typically have long...shearing crests" (Kay, 1977; Ungar 1998; Kay and Hylander, 1978; Kay and Covert, 1984; Strait 1993; Ungar and Lucas, 2010: 521). Selection has clearly driven the evolution of postcanine morphology.

As compared to the incisors, there is more evidence to indicate that the postcanine dentition forms a variational module; however, even here the extent to which patterns of pleiotropy (**G**-matrix and $\mathbf{g}_{max}$) are shared among species and the extent to which these parameters influence among-species diversification are unknown. For cercopithecid primates, Hlusko and Mahaney (2009) found that maxillary molars have high covariation among many dimensions (Table 1.5); in fact, they indicated that some dimensions of the maxillary postcanine dentition are characterized by complete pleiotropy in the SNPRC genetic correlation matrix (i.e., the observed r_G is not significantly different from 1). They also found that premolar size covaries with molar size, but not nearly as strongly as molars covary in size with one another (Table 1.5), proposing that premolars and molars are "quasi-independent" modules with overlapping pleiotropic effects, which implies that not all variance is shared between molars and premolars. In humans, several studies have suggested that premolars form an independent

unit (Dahlberg, 1945; Suarez and Williams, 1973; Townsend and Brown, 1981; Scott and Turner, 1997; Stefan, 2006), which supports the conclusion of Hlusko and Mahaney (2009). That premolar size is partially independent from molar size may be important for interpreting the evolution of premolar molarization and the enlargement of the premolars in some hominin lineages (e.g., Suwa, 1988; Kimbel and Delezene, 2009).

McCollum and Sharpe (2001) hypothesized that the sizes of the postcanine teeth and the anterior teeth (incisors and canine) should have a negative genetic correlation due to competition among the precursor cells of each tooth type for limited space in the jaw. According to this model, for hominins of the genera *Australopithecus* and *Paranthropus*, the selective advantage of having relatively large postcanine teeth outweighed the advantage of having relatively large canines and incisors; therefore, as a result of selection driving an enlargement of postcanine tooth size, the anterior teeth were reduced in size. In SNPRC baboons, as stated, Hlusko et al. (2010) have provided the first empirical support for this developmental relationship. Outside of the pedigreed baboon population, there is no evidence for negative within-species covariation between the anterior and posterior teeth and there is no examination of the predicted effects of such a negative correlation on the among species relationship between anterior and posterior tooth size. These hypothesized within- and among-species relationships can be easily tested by comparing the within- and among-species patterns of covariation in wild primate populations.

***Canine Honing Module*:** Unlike incisors and postcanine teeth, the elements of the canine honing complex (mandibular canine, maxillary canine, mesial mandibular premolar) mostly perform nondietary functions (pitheciines are a notable exception) (Rosenberger, 1992; Norconk, 2007). The complex is present in all extant nonhuman anthropoids

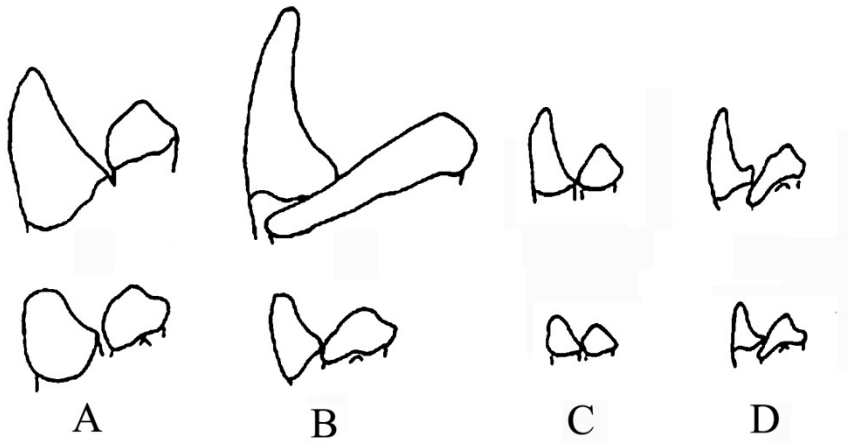

Fig. 1.10. Line drawings of mandibular canines and honing premolars in males and females of four anthropoid species. For each species the male is depicted above the female. A=*Pan troglodytes*, B=*Mandrillus leucophaeus*, C=*Alouatta seniculus*, D=*Macaca mulatta*. Figure is adapted from Plavcan (2001).

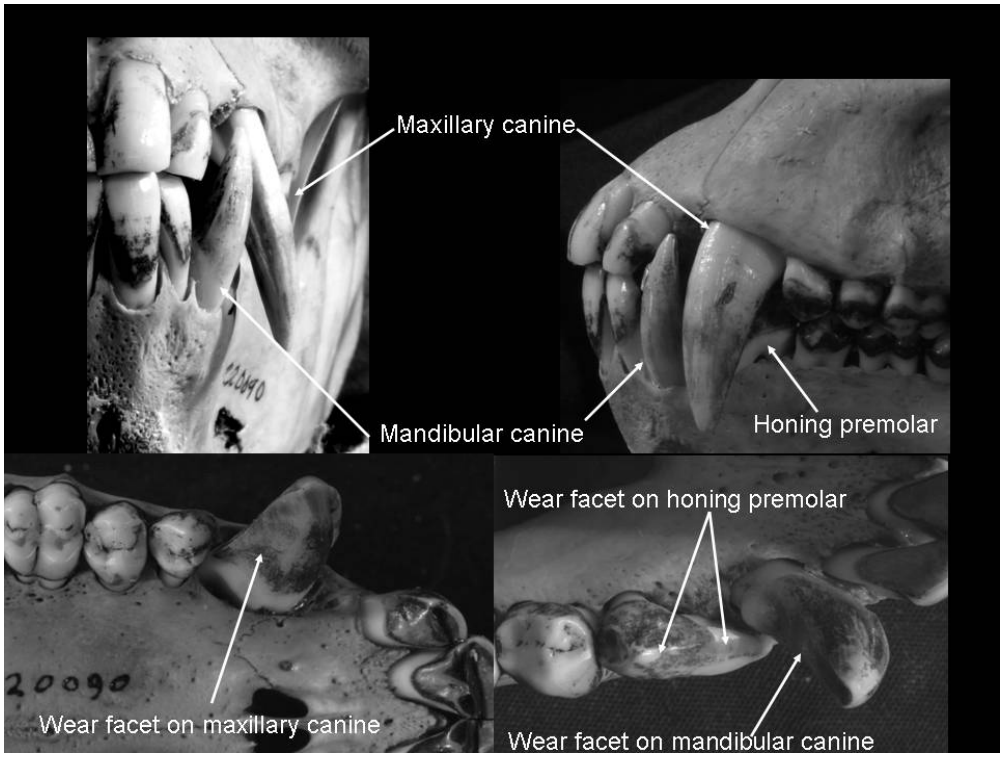

Fig. 1.11. The canine honing complex of *Cercocebus torquatus*.

(Ryan, 1979; Greenfield and Washburn 1991, 1992) and is evident in late Eocene taxa from the Fayum, such as the stem catarrhine *Catopithecus* and the parapithecids *Apidium* and *Parapithecus*, which represent the earliest evidence for canine honing in anthropoids (geologically younger Fayum catarrhines, like *Aegyptopithecus*, *Oligopithecus*, and *Propliopithecus* also had canine honing complexes) (Simons, 1989, 1992; Greenfield, 1995; Gunnell and Miller, 2001). It is unknown if the common ancestor of platyrrhines and catarrhines possessed a honing complex but its presence in parapithecids and stem catarrhines suggests that this is likely.

Typically, in extant nonhuman anthropoids the maxillary and mandibular canines project beyond the occlusal plane of the postcanine dentition (Figures 1.10 and 1.11); however, the degree of projection varies between sexes and among species (discussed later). Large honing canines are used in visual threat displays and also as weapons during intraspecific conflicts, usually in polygynous social settings (e.g., Walker, 1984; McGraw et al., 2002; Leigh et al., 2008). Relative canine size covaries with the intensity and amount of agonistic intrasexual behavior within a species; species with high intensity and frequency of agonism are characterized by larger relative canine size than species with less frequent and less intense agonism (Kay et al., 1988; Plavcan, 1993, 1998, 2001; Thoren et al., 2006). This pattern holds for both males and females; however, since males *typically* experience more frequent and intense encounters, predictably, they normally possess larger canines than do conspecific females (Figure 1.10). This model (e.g., Plavcan et al., 2005; Plavcan, 1997, 2001) even explains the nearly monomorphic large canines of male and female hylobatids; Plavcan and van Schaik (1997: 362) state, "hylobatids aggressively defend territories from both male and female conspecifics, and show consistent ritual displays consistent with agonistic intrasexual competition in both

sexes." Thus, sexual selection explains both interspecific differences in relative canine size and canine size mono-/dimorphism within species.

Further evidence for the role of sexual selection on canine size is provided by an ontogenetic study of maxillary canine height in mandrills, *Mandrillus sphinx*, by Leigh et al. (2008). They found that male mandrill reproductive fitness is intimately linked to the height of the maxillary canine. Males that successfully sired offspring had taller canines than nonsires and as the canine wore down during a male's lifetime his reproductive fitness also decreased. In their sample, 94% of offspring were sired by males with canine heights greater than 2/3 of maximum height. They suggested that the timing of the eruption of the maxillary canine is closely linked to the period of maximum reproductive potential and that, due to attrition of the canine's height, the canine is only useful as a weapon in intrasexual conflicts for a short period of the male's lifetime (about 4 years of a 20-year lifespan).

In addition to crown height, other aspects of the complex suggest that selection has favored the use of the canines as weapons. For example, primate canine crowns are as resistant to bending stresses as are carnivore canines, 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 during occlusion, the mandibular canine is honed along its distal face. At the same time, occlusion between the distolingual surface of the maxillary canine and the mesiobuccal surface of the mesial-most mandibular premolar (P_2 in platyrrhines, P_3 in catarrhines) hones the maxillary canine, sharpening the distal crest from its apex towards the cervix of the tooth (Figure 1.11; Walker, 1984). It seems likely that sharpening the canines helps to weaponize them (Walker, 1984).

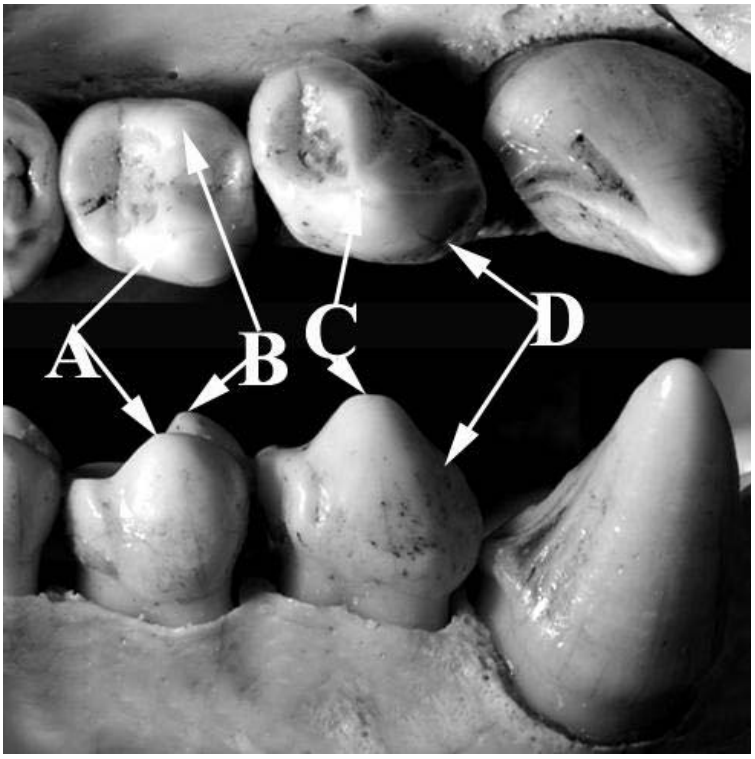

Fig. 1.12. Mandibular premolar heteromorphy in *Pan*. Top, occlusal view, and bottom, buccal view of canine, P_3, and P_4. A is the protoconid of the P_4, B is the metaconid of the P_4, C is the protoconid of the P_3, and D is the broad mesiobuccal face of the P_3, which is where honing occurs. The P_3 is derived for its functional role as a honing device and it is the accumulation of honing related features that creates premolar heteromorphy.

Maxillary canine honing does not occur because of incidental contact; the honing premolar, be it P_3 or P_2, is derived to function as a honing device and is morphologically distinct from that of more distal premolars, which Greenfield and Washburn (1992) describe as "premolar heteromorphy." Generally, the honing premolar is unicuspid and the single cusp, the protoconid, is taller than on the more distal premolar(s) (Figure 1.12). Unlike more distal premolars, which typically have a straight enamel-dentine junction (i.e., cervical margin), the honing premolar may have an enamel extension that covers a portion of the mesiobuccal root (this is especially true of catarrhines). The tall, centrally placed protoconid, elongated mesial face, and inferior projection of enamel create a broad

sloping surface that occludes with and hones the maxillary canine (Figure 1.12). To match their taller canines, males typically have a longer honing surface than do females (Figure 1.10). And, among species, the size of this surface varies in extent; among catarrhines, the honing surface is the most expansive in cercopithecids and is less exaggerated in hominoids (Figure 1.10). In contrast to the honing premolar, nonhoning mandibular premolars are typically bicuspid (i.e., have well developed metaconid that is more nearly equal in height and area to the protoconid) and lack the mesial elongation and mesiobuccal enamel extension. Within platyrrhines and hominoids, heteromorphy is evident; however, it is most pronounced in cercopithecids (Figures 1.10, 1.11, 1.12) (Greenfield and Washburn, 1992).

The strong evidence that canine size varies among species as a result of sexual selection and the evidence for morphological specialization within the complex suggest that the canine honing complex, a functional module, should form a pleiotropically linked variational module. Few studies of covariation within species have examined this hypothesis. When analyses have been performed within species, they have mostly focused on canine basal areas (e.g., Cochard, 1981; Scott, 2010) and not their heights. Cochard (1981) examined correlations among the LL breadths and MD lengths of all teeth in *Colobus badius*. For both males and females, he found moderate levels of covariation for canine basal dimensions and all dimensions of incisor and postcanine size. Within each arch, the female range is $r^2 = 0.00$ (C_1MD-I_1MD) to $r^2 = 0.46$ (C^1MD-P^4MD) and the average level of covariation between the canines and all other dental dimensions is $r^2 = 0.19$. For males the range is $r^2 = 0.03$ (C_1LL-I_2LL and C_1MD-M_3MD) to $r^2 = 0.48$ (C^1LL-M^3BL) and the average level of covariation between the canines and all other dental dimensions is $r^2 = 0.15$. Between the maxillary and mandibular canine basal sizes, Cochard found low to moderate levels of covariation ($r^2 = 0.35$ for ♂C^1LL-C_1LL, r^2 =

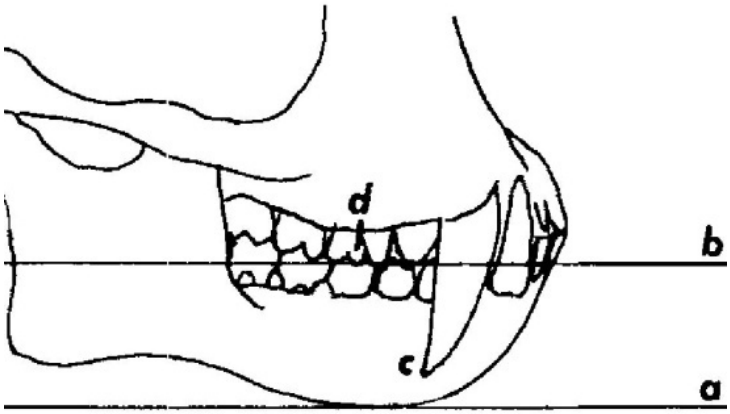

Fig. 1.13. Greenfield (1992) and Greenfield and Washburn (1992) measured projected canine height as the distance between line b and point c, point d is the paracone of the M^1. Figure adapted from Greenfield and Washburn (1991, 1992).

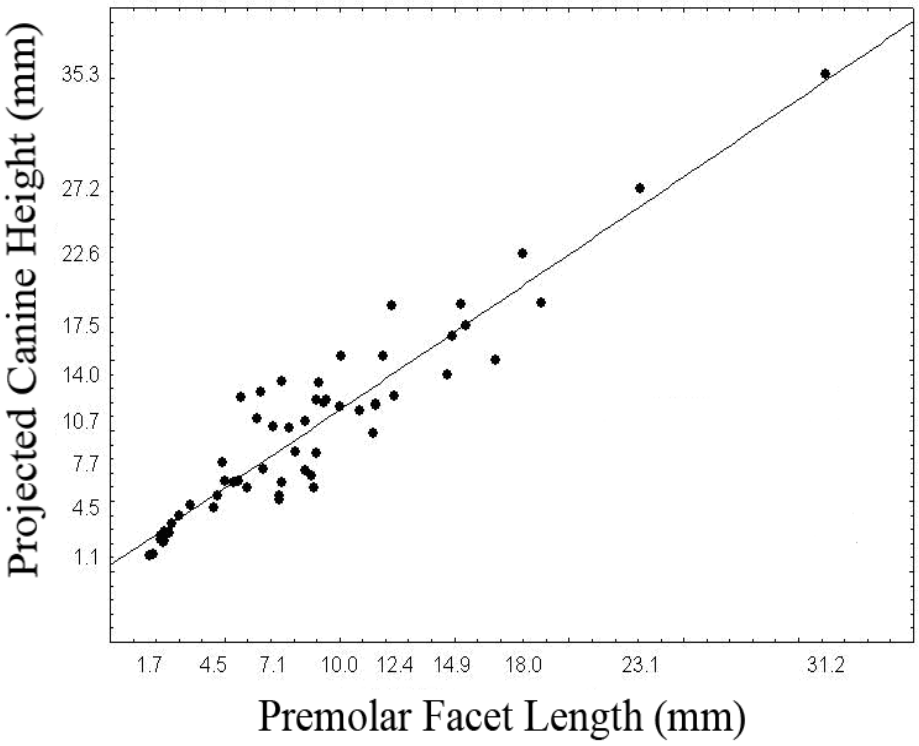

Fig. 1.14. Projected canine height and premolar honing surface length among male anthropoids ($r^2 = 0.88$; $p < 0.0001$). Data are taken from Greenfield (1992) and Greenfield and Washburn (1992).

0.24 for ♀C^1LL-C_1LL, $r^2 = 0.05$ for ♂C^1MD-C_1MD, and $r^2 = 0.13$ for ♀C^1MD-C_1MD) and no significant differences in the magnitude of covariation between males and females. Cochard's study suggests that the pattern of covariation is similar in males and females, that not all dimensions of the canines are tightly linked, and that the sizes of the canines positively covary with other dental elements, though generally at a low absolute value. However, Cochard's study is incomplete, as canine heights were not investigated, the honing premolar was not included in his analysis because of measurement error, and only correlations between homologous measures were reported; levels of covariation between the LL and MD dimensions of the canines were not reported.

Additional evidence that the canines share at least some overlapping pleiotropic effects with adjacent teeth is provided by Garn et al. (1966), who found among anthropoids that teeth adjacent to the canines (I2 and mesial premolar) express higher indices of dimorphism (male mean/female mean) than nonadjacent teeth. Similarly, Plavcan (1990) found indices of dimorphism were elevated for the honing premolar over other noncanine teeth. This pattern can be explained if the canine and honing premolar are pleiotropically linked so that both canine height and honing premolar size are larger in males than females.

Among species, Greenfield and Washburn (1992; Greenfield, 1992) assessed patterns of correlation between canines and honing premolars in a broad sample of anthropoid primates. They found a significant correlation between male canine projection (Figures 1.13 and 1.14) (they did not measure crown height) and the length of the mandibular premolar honing surface; a statistically significant correlation did not characterize females. Greenfield (1992) interpreted this difference between males and females to indicate the selective importance of the honing complex in males and its relative unimportance in females, which supported his dual selection hypothesis for

canine morphology in anthropoid primates (e.g., Greenfield, 1992; 1993; Plavcan and Kelley, 1996). Plavcan (1993) questioned the functional relevance of their metric; though designed to capture the "weapon-related" portion of the canine's height, canine projection does not even include the entire height of the honed portion of the maxillary canine, which extends above the occlusal plane (personal observation). Given that only a portion of the canine's height is represented by its projection beyond the occlusal plane and that females typically have shorter canines than conspecific males, canine projection captures a smaller fraction of total canine height in females than in males. As a result, it is possible that Greenfield's metric fails to capture the coevolutionary behavior of female canine *height* and premolar honing surface length.

That males and females may differ in a pattern of character coevolution between maxillary canine height and premolar honing surface length raises questions about the existence of pleiotropy among characters of the honing complex. As reviewed above, characters can coevolve in the absence of pleiotropy if natural selection independently favors change in each character. If the among-species pattern is different for males and females, then it is possible that maxillary canine height and the size of the premolar honing surface are not pleiotropically linked; in males, the honing premolar may independently track changes in canine height to maintain functional honing at different canine sizes (as in Figure 1.7). Alternatively, sex-specific factors may create genetic correlations in the male honing complex that do not exist in the female honing complex. This hypothesis can be tested if both the within- and among-species patterns of covariation are estimated for both males and females, which is the strategy employed in this study.

In early hominins, the maxillary canine was substantially reduced in height before the mandibular canine height was reduced (e.g., Suwa et al., 2009), the height of

the canines were reduced before the sizes of the canine bases were reduced (e.g., Suwa et al., 2009; Ward et al., 2010), and the P_3 retained many relicts of its honing past long after the function of canine honing was lost (e.g., the tooth is unicuspid, has a principal cusp that is taller than on the distal premolar, and the main axis is often set obliquely to the postcanine axis, so that premolar heteromorphy is pronounced in early hominins) (Suwa et al., 2009; Delezene and Kimbel, 2011). The pattern of changes that resulted in the morphological and functional transformation of the complex did not happen in a coordinated fashion. If characters of the honing complex are not linked pleiotropically, then change into any dimension of phenotypic space is genetically unconstrained. If pleiotropy does exist among the characters, then strong selection, especially on maxillary canine height, would be necessary to produce the hominin pattern of character state change. Studying patterns of character change in extant anthropoids in relation to the pattern and strength of constraint will reveal how unique the hominin pattern is.

Pleiotropy has been implicated in the reduction of hominin canine size. Such models rely on a hypothesized developmental trade-off between the sizes of the anterior and posterior teeth (e.g., Jolly, 1970; McCollum and Sharpe, 2001). In some lineages (e.g., Plio-Pleiostocene *Theropithecus* and the hominins *Australopithecus* and *Paranthropus*), the posterior teeth became megadont, while the anterior teeth (both incisors and canines) reduced in size. If these models are correct, then the canines should share positive covariation with the incisors and negative covariation with the postcanine teeth 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). There is limited empirical support for negative covariance between incisors and postcanine teeth (reviewed above) and none for the canines and postcanine teeth.

Proposals for broad scale genetic correlations among the masticatory complex, such as McCollum and Sharpe (2001), address the concern that many of the supposed "independent" character changes that occurred during hominin evolution, and that are used to reconstruct cladistic relationships, are actually part of single functional and developmental module (e.g., Strait and Grine, 1998; Strait, 2001; McCollum and Sharpe, 2001; Lockwood, 2007; Strait et al., 2007). While selective tradeoffs among tooth sizes may have happened in certain cases, it is not necessary for genetic correlations to exist for such a pattern to occur (e.g., Figure 1.7). That characters that are genetically independent can change state simultaneously has been recognized by others (e.g., Lockwood, 2007). The extent of covariation within and between functional units of the dentition, and their impact on dental diversification are easily quantified.

Hypotheses

By combining empirical evidence from studies of genetic correlations among teeth (e.g., Hlusko and Mahaney, 2009; Hlusko et al., 2010), theoretical predictions of integration and modularity (e.g., Wagner et al., 2007), and the functional relationships among teeth, several hypotheses are addressed. The findings will be used to inform a discussion about the role of constraints and selection on anthropoid dental evolution, especially as it regards hominin dental evolution and mosaicism in the evolution of the hominin "honing" complex. Below, the hypotheses that are addressed in this study are enumerated; all statistical tests are described in Chapter 2.

It is hypothesized that the functional modules of the dentition are variational modules. **The proposed modules are: an acquisition module (incisors), a social signaling and honing module (canines and mesial portion of honing premolar), and a processing module (molars, nonhoning premolars). Both within and among**

species, phenotypic covariation is predicted to be high within each module and low between modules. Therefore, there are two criteria that can be used to reject the hypothesis of modularity: 1) low magnitude covariation among characters within a hypothesized module, or 2) similar magnitudes of covariation between characters in different modules.

Hlusko and Mahaney (2009) reported that premolars and molars covary in size, but not as strongly as they covary with one another. They suggested that the variation in magnitude of genetic covariation between premolar and molar size indicated that premolars have unique pleiotropic connections that are not shared with molars. **If true, then premolars should share significant partial covariation when molar size is held constant.** This hypothesis will be rejected if premolars do not share partial covariation.

This study focuses on understanding the relationship between among- and within-species patterns of covariation. **Given that the functions and the dental elements performing the functions are common among species, then it is predicted that patterns of variance-covariance (reflected by similar $\mathbf{p}_{max}$s and P-matrices) will be stable among species.** To test the commonality of patterns of correlation, the Mantel test is used. The null hypothesis for this test is no similarity, so a rejection of the null hypothesis indicates that correlation matrices are similar among species. To test the commonality of the **P**-matrix among species, the random skewers test is used. The null hypothesis for this test is also no similarity, so a rejection of the null hypothesis indicates that **P**-matrices are similar. To test the commonality of lines of least evolutionary resistance (estimated as $\mathbf{p}_{max}$), angles ($\boldsymbol{\Theta}$) between $\mathbf{p}_{max}$**s** are calculated among species. The null hypothesis for this test is $\boldsymbol{\Theta} = 0$, so a rejection of the null hypothesis indicates that $\mathbf{p}_{max}$**s** are not similar.

If dental diversification has been strongly channeled by genetic constraints, then among species diversification (Δz) will have occurred along p_{max}. This hypothesis is tested by assessing the deviations of $\mathbf{\Delta z}$, the vector of mean differences between samples, from species estimates of $\mathbf{p}_{max}$. The null hypothesis for this test is $\mathbf{\Theta} = 0$; a rejection of the null hypothesis indicates that among species differences did not accumulate along $\mathbf{p}_{max}$.

The ability of characters to evolve independently of one another is proportional to the strength of constraint among them (Marroig et al., 2009). **Therefore, those characters with the highest magnitude of within-species covariation are predicted to be the most constrained among species; that is, the magnitude of covariation within species should be reflected in the magnitude of covariation among species**. This hypothesis is informally tested by comparing magnitudes of phenotypic covariation within species to those derived among species from independent contrasts.

Jolly (1970) and McCollum and Sharpe (2001) have hypothesized that the anterior and posterior teeth have a negative genetic covariation, which has recently received some empirical support (Hlusko et al., 2010). **If true, then the anterior and posterior teeth should have negative phenotypic covariation within species.** This hypothesis will be rejected if covariation is either absent or positive in direction between the incisors and postcanine teeth. **Furthermore, if covariation is negative within species and has influenced the among-species diversification of dental size, then a significant negative among-species correlation will be observed.** This hypothesis will be rejected if covariation among species between incisor and postcanine size is either absent or positive in direction. The hypothesized negative covariation between anterior and posterior teeth has been hypothesized to be reflected for canine basal size as well (Jolly, 1970). **If true, then canine basal size should covary negatively with postcanine**

size within species and positively with incisor size within species. This hypothesis will be rejected if covariation is low in magnitude between canine basal size and dimensions and other functional modules, if covariation is positive between canine and postcanine size, or if covariation between canine and incisor size is negative.

Among species, Greenfield (1992; Greenfield and Washburn, 1992) indicated that canine projection and premolar honing surface length coevolved in male but not female anthropoids. As discussed, canine projection does not capture the entire height of the canine and does even capture then entire height of the honed surface of the canine, which extends nearly to the cervix. Therefore, coevolution of the canine honing complex is investigated for canine crown heights and the length of the premolar honing surface. **If Greenfield's observation accurately captures the coevolutionary behavior of canine height and premolar honing surface length, then independent contrasts among species should indicate significant covariation only in male anthropoids**. This hypothesis will be rejected if significant covariation exists in both sexes. Greenfield's observations indicate two potential explanations within-species for the among-species pattern: **1) that pleiotropy is absent among elements of the complex in both males and females, or 2) that pleiotropy only exists in the male complex**. **If pleiotropy exists in either sex, then within-species covariation should be strong.** The absence of pleiotropy will be rejected if covariation is significantly different from zero.

Chapter 2

MATERIALS AND METHODS

Materials

Choice of Samples: Since analyses of the canine honing complex are important in this study, it was necessary *a priori* to identify museum collections with a high likelihood of containing an adequate sample of unworn or minimally worn canines. A similar selection criterion was utilized by Plavcan (1990) in his study of sexual selection and canine dimorphism, so his specimen list was used a general guide to choose taxa and to target individual specimens within the study species. The sample used here overlaps that of Plavcan (1990), but does not include all species or specimens analyzed by him and includes measurements from taxa (e.g., *Gorilla beringei*) and specimens that were not included in his analysis. In total, data were collected from 1768 individuals from 37 species of anthropoid primates (Table 2.1).Summary information about the museums at which specimens are housed, collection localities, and notes on taxonomy are available upon request.

For the interspecific analyses, species were chosen to ensure that the overall sample was broad taxonomically, in body size, dental size, and social organization. To address patterns of pleiotropy within species, 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 distinct populations are pooled. Therefore, for each taxon an attempt was made to measure individuals from as geographically limited an area as possible. Ideally, true biological populations would be sampled; unfortunately, museum collections rarely fit this stringent criterion. In order to fully identify the phylogenetic distribution of patterns of pleiotropy and their consistency among species, each species included in the interspecific analysis should also be included

TABLE 2.1: Species included in this analysis. A ▲indicates a sample that will be analyzed in intraspecific analyses. Explanations for why other well represented samples are excluded from intraspecific analyses are provided in Appendix A.

Species	♂	♀	?	**Species**	♂	♀	?
Ateles geoffroyi vellerosus▲	44	42		*Macaca mulatta mulatta*	5		
Callicebus cupreus discolor	9	6		*Macaca nemestrina nemestrina*	12	14	
Cebus libidinosus libidinosus▲	47	46		*Macaca nigra*	15	8	
Chlorocebus aethiops hilgerti	7	15		*Macaca sinica*	25	20	
Cercopithecus cephus cephus▲	48	31	1	*Miopithecus ogouensis*	9	12	1
Cercopithecus nictitans nictitans▲	50	38		*Nomascus concolor*	10	5	
Cercopithecus pogonias grayi▲	42	32		*Pan troglodytes schweinfurthii*	12	10	2
Colobus badius powelli	2	7		*Pan troglodytes troglodytes*▲	54	57	
Colobus guereza caudatus	13	14	1	*Pithecia monachus monachus*	11		
Colobus satanas▲	26	27		*Pongo abelii*	15	12	7
Erythrocebus patas	12	10		*Pongo pygmaeus*	50	45	2
Gorilla beringei	20	14	1	*Presbytis entellus thersites*		7	
Gorilla gorilla▲	76	58	5	*Presbytis rubicunda*	28	27	
Hoolock hoolock	47	25		*Presbytis vetulus*	7	18	
Hylobates klosii	23	15		*Pygathrix nemaeus nigripes*	13	3	
Hylobates lar carpenteri▲	52	55		*Rhinopithecus roxellana*		7	
Lagothrix lagothricha cana	20	30		*Symphalanges syndactulus syndactulus*	16	18	
Lagothrix lagothricha poeppiggi	26	24	2	*Theropithecus gelada*	14	6	
Macaca fascicularis fascicularis▲	66	60	2				

in intraspecific analyses (see introduction to Hlusko and Maheney (2009)), but it was rarely possible to achieve adequately large sample sizes that fit the criteria established above. Therefore, intraspecific analyses were restricted to ten taxa that are numerically well represented, are from geographically restricted areas, and are confidently assigned to subspecies. The ten taxa deemed appropriate for analyses of within-species covariation are indicated in Table 2.1. For some species, subspecies were pooled to calculate a species mean.

Sample Size Criteria: For all characters except for canine heights, a sample size of $n = 20$ was deemed minimal for intraspecific or interspecific analyses. This threshold is arbitrary, but given the reduction in statistical power (Sokal and Rohlf, 1995) and the inconsistency of estimates of variance-covariance at small sample sizes (e.g., Ackerman, 2009), it was necessary to restrict analyses to those samples that are reasonably well represented. Given the tendency for canines to normally wear away (Walker, 1984; Leigh et al., 2008) or break at their apices (especially the maxillary), there were fewer adequately-sized samples available for their analysis within species; therefore, the minimum sample size for canine heights used for intraspecific analysis was $n = 15$. Even for canine heights, several samples exceed $n = 20$, so the strength of covariation observed in the smaller samples can be compared to the larger samples. Though some species are represented by small sample sizes, no sample with fewer than 5 individuals was included in the interspecific analysis.

Other studies of canine covariation within and among species (e.g., Plavcan, 1990; Scott, 2010) have included moderately worn canines in their analyses. In the case of Plavcan, who was more concerned with indices of dimorphism and among-species differences in mean canine size and relative canine size, it is unclear if the inclusion of

worn canines affected his height measures. As a result of these concerns, when Suwa (2009) used Plavcan's database of canine measurements he explicitly excluded measures of worn canine heights. Scott (2010) addressed questions of pleiotropy and functional constraints on canine size and included moderately worn canines in his data set. He used a statistical manipulation of the raw data to identify outliers, deleting the smallest canine heights until the sample coefficient of variation (CV) was ≤ 10. As a result, no sample of canine heights was larger than 24 for males and 23 for females. Scott (2010) did not examine intraspecific covariation for canine heights; his intraspecific analyses of covariation were based on canine basal dimensions. Even in intraspecific analyses of canine basal area correlations, Scott (2010: 106) reported that "the median sample size for male great apes is n = 12 (range: n = 5–19)." It is unlikely that such small sample sizes accurately capture the magnitude of within-species covariation. As stated in Chapter 1, absolute constraints are rare, therefore identifying statistically significant correlations (i.e., $r > 0.00$) reveals little about the expected dependence or independence of among-species diversification, which has been shown to be proportional to the *magnitude* of covariation (Marroig et al., 2009). Scott (2010) did analyze canine height correlations among species, but, as discussed in Chapter 1, there are multiple pathways to achieving significant among-species correlation, and not all rely on the existence of pleiotropy among characters (Figure 1.7). The current sample of canine heights is composed largely of juvenile specimens, which have incompletely erupted canines and, therefore, are not represented in the Scott and Plavcan datasets. Because wear does not affect the size of the basal dimensions (except for the MD length of the maxillary canine at advanced wear stages), canine basal areas were measured from specimens with worn canines,

TABLE 2.2: Dental characters.

MEASUREMENT	ELEMENT
Height from Cervix to Apex	Maxillary Canine and Mandibular Canine
Labiolingual (LL) Breadth	Maxillary and Mandibular Incisors and Canines
Mesiodistal (MD) Length	All Maxillary and Mandibular Teeth, Excluding Honing Premolar
Buccolingual (BL) Breadth Across Mesial Cusps	Mandibular Molars and Nonhoning Premolars
Maximum Crown Breadth Perpendicular to MD axis	Maxillary Postcanine Teeth
Honing Surface Length	Honing Premolar
Oblique Length	Honing Premolar
Midcrown Breadth Perpendicular to Oblique Length,	Honing Premolar
Mesiocervical Enamel Extension	Mesial-Most Maxillary Premolar
Crown Shape (MD/BL)	Incisors and Postcanine Teeth

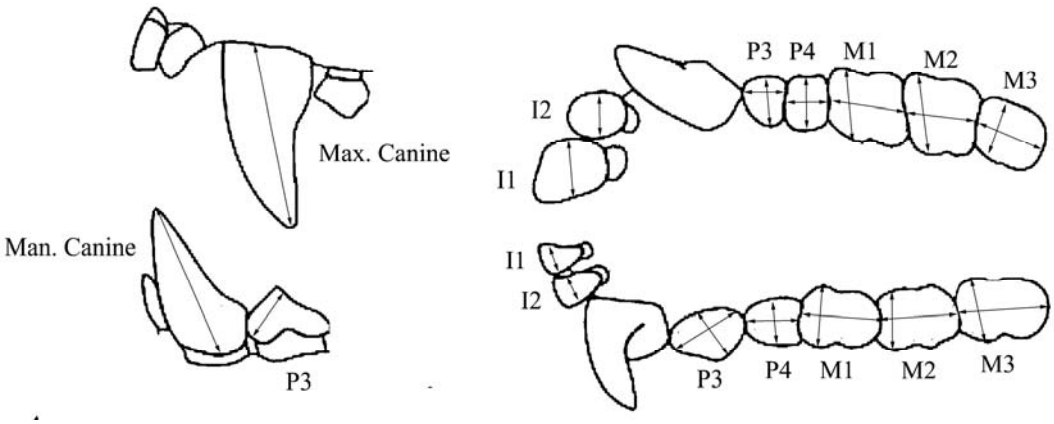

Fig. 2.1. Upper left: maxillary canine height. Upper right: mesiodistal and labio-buccolingual dimensions of the maxillary incisors and postcanine teeth. Lower right: mesiodistal and labio- buccolingual dimensions of the mandibular incisors and postcanine teeth. Lower left: mandibular canine height and premolar honing surface length.

Characters: Measurements of the dentition were chosen to capture the size and shape of each tooth. Measures of mesiodistal (MD) length and buccolingual (BL) and labiolingual (LL) breadth were considered and were also used to create ratios describing shape (Table 2.2 and Figure 2.1).

Methods

Data collection: Linear measurements were collected using fine-point Mitutoyo digital calipers with a foot pedal used as a data entry tool. Measurements were recorded to the nearest one-tenth of a millimeter.

Data Quality: The overlap between the specimens included in this analysis and those in Plavcan's (1990) sample permitted comparisons of interobserver error. Plavcan (1990) measured all dental metrics with a calibrated reticle, while the current study used digital calipers. Therefore, some difference is expected as a result of instrumentation effects; however, instances where the absolute difference between the current study and Plavcan's (1990) study exceeded 4% of the mean values were investigated to ensure that the measurement was accurately assessed in the current study.

Since the current data set does not wholly overlap that of Plavcan (1990), data quality was also assessed other ways. While at the museum, outliers were investigated to ensure that they were accurately measured. Additionally, given that many measurements are correlated, bivariate plots were created and visually inspected for many character pairs. Outlying measurements and those that leverage regressions were then investigated to ensure accuracy.

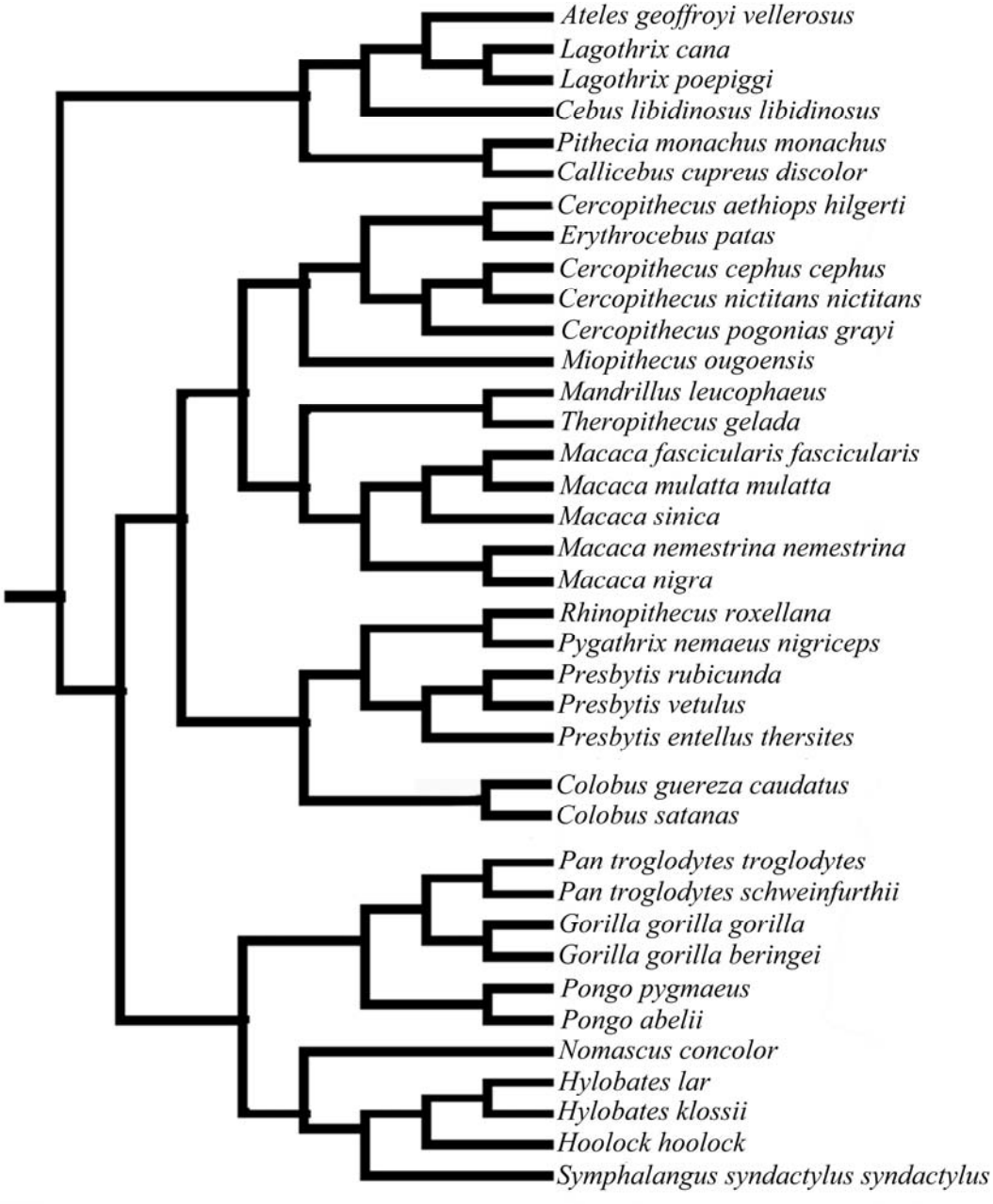

Fig. 2.2. Phylogeny of taxa included in this analysis. In this figure, all branches are equal.

Independent Contrasts: 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; Garamszegi et al., 2002), among-species correlations were assessed using phylogenetically independent contrasts (e.g., Felsenstein, 1985; Garland et al., 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). Since independent contrasts are calculated as the difference between sister taxa, they essentially assess the amount of evolutionary change that has occurred since a cladogenic event; therefore, if drift covariance occurred during cladogenesis, then it will be expected to affect only the calculation of a single independent contrast, reducing the potential confounding effect of drift covariance.

The following molecular phylogenies were used to create the phylogeny used to calculate independent contrasts (Figure 2.2): 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); Colibinae (Ting, 2008). The general consensus tree derived from the 10kTrees website (http//10kTrees.fas. harvard.edu; Arnold et al., 2010) was also used as a reference for constructing the phylogeny.

Unfortunately, there is disagreement about the placement of some taxa within the phylogeny. Notably, generic level relationships within the Hylobatidae are poorly resolved; for example, *Hoolock* is variably placed as the sister taxon to the remaining hylobatid genera (*Nomascus*, *Symphalangus*, and *Hylobates*) (Whittaker et al., 2007) or as the sister taxon to only *Hylobates* (Purvis, 1995; Thinh et al., 2010), with

Symphalangus and *Nomascus* more distantly related. *Symphalangus* and *Nomascus* form a clade to the exclusion of *Hylobates* and *Hoolock* in the Whittaker et al. (2007) phylogeny, but in both Chaterjee (2006) and Thinh et al. (2010), *Nomascus* is the sister taxon to the clade *Symphalangus+Hoolock+Hylobates*. With no obvious method for determining which of these phylogenies is correct, the most recent hylobatid phylogeny as determined by Thinh (2010) is used in this analysis. Other 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 *Cercopithecus pogonias* and *Cercopithecus mona* in the "*mona* group" of guenons (e.g., Groves, 2001).

Independent contrasts incorporate branch lengths in their calculation and several methods are available for branch length estimation. For example, divergence dates among taxa, based on genetic distances and calibration with the fossil record, can be used. However, assigning ages to nodes for a sample as broad as the one used in this study is not without complications; for example, no study of divergence dates includes all of the taxa that are included in this study. The results from smaller scale studies can be combined to generate estimates for many nodes in the phylogeny but that leaves dates for some nodes unassigned (for example, by combining Thinh et al. (2010), Stepler et al. (2004), and Opazo et al. (2006)). There is also a second problem; often, where divergence dates are estimated for the same node in different studies, the estimated divergence dates are quite different. This occurs because assumptions about rates of neutral evolutionary change, effective population sizes, and calibration points based on the fossil record differ among the studies. Other studies of among-species covariation in dental size pooled estimated dates of divergence from multiple sources (e.g., Scott, 2010); it is unclear what effect this has. Since it was not possible to accurately reconstruct branch lengths, results

of independent contrasts were reported for equal branch lengths (branch lengths all equal to 1).

Phenotypic Covariation Within Species: Given dimorphism in size for many measures, the male and female distributions largely overlap; however, the means slightly differ. If males and females are pooled, this would exaggerate the estimated strength of covariation above its true biological value (males and females were pooled in Hlusko and Mahaney (2009), for example). This effect was noted by Plavcan and Daegling (2006) in their study of dental and mandibular size covariation and by Scott (2010) in his study of canine correlations. In the most extreme case, where male and female distributions minimally overlap (as for highly size-dimorphic characters, like canine crown heights), this has the effect of creating a two point regression. To avoid this, for all characters outside of the canine honing complex, the male mean was adjusted to equal the female mean and then males and females were pooled into a single analysis. Males and females were pooled without adjusting means in analyses of shape.

The %boot macro (http://support.sas.com/kb/24/982.html) was used within SAS v9.1.3 for the UNIX system to estimate the strength of covariation, which is reported here as the coefficient of determination (r^2). The bootstrapping procedure used 10,000 iterations and the bias-corrected mean r^2 was reported as the sample estimate. When an outlier is present in the raw data, the bootstrap distribution is often skewed. Bias correction adjusts the estimate of r^2 to remove the leverage of the outlying estimates in such a distribution. In most cases considered in this study, the bootstrap distribution was approximately normal and no bias correction was necessary. With sample sizes as large as they are for most characters in this study, the bootstrapped estimate of r^2 rarely deviated from the estimate produced from standard methods (personal observation).

TABLE 2.3: Categorizing the strength of r^2.

Value of r^2	Categorical Description
$0.00 < r^2 \leq 0.20$	Very Low
$0.20 < r^2 \leq 0.40$	Low
$0.40 < r^2 \leq 0.60$	Moderate
$0.60 < r^2 \leq 0.80$	High
$0.80 < r^2 \leq 1.00$	Very High

Where bootstrapping proved useful was in calculating confidence intervals for the sample r^2 estimate. Several options are available for estimating the confidence intervals from the bootstrap distribution (e.g., Percentile, Bias Corrected, Bias Corrected Accelerated, Efron's, Hybrid, T) (see Manly (2001) for a discussion of this topic); in this study, the Bias Corrected (BC) confidence interval was used to determine the statistical significance of each reported r^2.

Other studies of integration and pleiotropy often report not coefficients of determination, but Pearson's correlation coefficients (r) (e.g., Hlusko and Maheney, 2009; Scott, 2010); readers are urged to consider this difference when comparing the magnitude of covariation between studies. In addition to more easily interpreting the meaning of r^2, there is an additional advantage over r; r^2 is an additive parameter while r is not. Therefore, the average is a defined quantity for r^2 but not for r, which allows for the calculation of the average magnitude of covariation (e.g., de Oliveira et al., 2009).

While values of r^2 were used for hypothesis testing, a protocol for referring to the relative strength of r^2 was used throughout this study (Table 2.3). The use of categorical descriptors to capture differences in the magnitude of covariation has been employed by others (e.g., Devore and Farnum, 2005); however, there are no firm guidelines or

accepted terms for categorical descriptors. In this study, units of covariation were divided into 5 categories of equal size. Given that r^2 is calculated as the square of the correlation coefficient (r), it cannot have a negative value. To indicate instances where a negative correlation exists between two variables, a negative sign (-) is placed before the r^2 value.

Given that the premolars and molars are indicated to have both unique and shared pleiotropic effects (e.g., Hlusko and Mahaney, 2009), partial correlations were used to investigate this hypothesis. Partial correlations reflect the correlation between two variables when correlation with a third variable is held constant. If premolar size retains significant partial correlation when molar size is held constant, then the hypothesis of quasi-independence is supported. For example, for variables X, Y, and Z, the partial correlation for X and Y, with Z held constant, is quantified by first regressing X against Z and then Y against Z. The residuals for each analysis are calculated and the partial correlation coefficient between X and Y, with Z held constant, is the correlation between the residuals. The %boot macro was used within SAS v9.1.3 for the UNIX system (using 10,000 iterations) to calculate partial correlations and their confidence intervals.

Patterns of Covariation Among Species: The similarity of patterns of covariation among species was assessed using both correlation and variance-covariance matrices. In studies of integration, the Mantel test has been commonly employed to test correlation matrix similarity (e.g., Cheverud, 1995; Hlusko and Mahaney, 2009); in this study, Mantel tests were conducted using the POPTOOLS v3.1.0 add-in for Microsoft Excel (http://www.cse.csiro.au/poptools/). The Mantel test generates two test statistics for estimating the strength of similarity between two matrices, the matrix correlation coefficient (r_M), which allows for two-tailed tests of significance, and the cross-product value (Z), which allows for a one-tailed test of significance. The null hypothesis for the

Mantel test is no similarity, so a statistically significant result indicates that the correlation matrices are similar. Statistical significance was determined using a randomization procedure (10,000 iterations).

The Mantel test only accounts for the pattern of the magnitudes of covariation among characters. As an alternative to the Mantel test, in studies of genetic variance-covariance (or studies where phenotypic values are substituted for genetic), a procedure known as "random skewers" uses the multivariate selection model ($\mathbf{\Delta z = G\beta}$) to investigate the similarity of variance-covariance matrices (e.g., Cheverud, 1996; Cheverud and Marroig, 2007). To do so, a random $\mathbf{\beta}$ (the random skewer) is multiplied with each variance-covariance matrix to generate a $\mathbf{\Delta z}$, assessing the evolutionary response of each variance-covariance matrix to randomly generated selection vectors. The procedure is repeated several times and the vector correlation between the resulting $\mathbf{\Delta z}$s is computed. As with the Mantel test, the null hypothesis for the random skewers procedure is no similarity, so a statistically significant result indicates that matrices are similar. In this study, the phenotypic variance-covariance matrix (**P**) was substituted for the genetic variance-covariance matrix (**G**). To determine statistical significance, 10,000 iterations of the random skewers procedure were performed using the program "skewers," available from Dr. Liam Revell (http://anolis.oeb.harvard.edu/~liam/programs/).

The Line Of Least Evolutionary Resistance and Evolutionary Divergence: Several methods were used to visualize and demonstrate constraints on the evolution of linked traits and to assess the correspondence of evolutionary change to the line of least evolutionary resistance (discussed in Chapter 1). To that end, 95% confidence ellipses

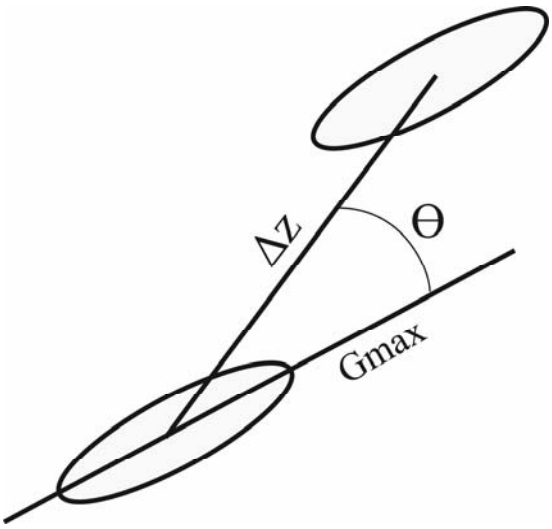

Fig. 2.3. Confidence ellipses are used to describe the orientation and strength of covariation for two characters. **Δz** is the vector that describes the direction of difference between the means of the two samples. $\mathbf{g}_{max}$ is the maximum vector of genetic covariation and describes the line of least evolutionary resistance for the two characters to evolve along. Θ is the angle between the sample $\mathbf{g}_{max}$ and **Δz**. In this study $\mathbf{p}_{max}$ is substituted for $\mathbf{g}_{max}$.

were generated, using Statistica version 7.1, to graphically display the magnitude and orientation of covariation for two characters. For a group of characters, the line of least evolutionary resistance ($\mathbf{g}_{max}$) is the principle axis of genetic covariation among the characters. In this study, which focuses exclusively on the phenotype, $\mathbf{p}_{max}$, the eigenvector associated with the first principal component of the phenotypic values (e.g., Schluter, 1996; Marroig and Cheverud, 2010), was substituted for $\mathbf{g}_{max}$. If $\mathbf{p}_{max}$ is similar between two taxa, then the angle between their vectors ($\mathbf{\Theta p}_{max}\mathbf{-p}_{max}$) should be approximately zero and the vector correlation should be nearly one. Similarly, **Δz** is a vector that describes the magnitude and direction of difference between species; therefore, if it is aligned with $\mathbf{p}_{max}$, then the angle between **Δz** and $\mathbf{p}_{max}$ ($\mathbf{\Theta \Delta z\text{-}p}_{max}$) should be approximately zero and the correlation between the vectors should be nearly one (Figure 2.3). Before calculating angles between vectors and vector correlations, all

vectors were converted to unit length (i.e., length of 1). In such cases, $\boldsymbol{\Theta} = \arccos \mathbf{a}\cdot\mathbf{b}$; $\boldsymbol{\Theta}$, in radians, is the inverse cosine of the dot product of the unit vectors **a** and **b**. The vector correlation is defined as $r_{\boldsymbol{\Theta}} = \cos \boldsymbol{\Theta}$. The calculation of these parameters is explained more fully in Schluter (1996) and Marroig and Cheverud (2010). Eigenvectors were calculated using SAS for the UNIX system and the statistical significance of $\boldsymbol{\Theta}\mathbf{p}_{\mathbf{max}}\text{-}\mathbf{p}_{\mathbf{max}}$ and $\boldsymbol{\Theta}\boldsymbol{\Delta}\mathbf{z}\text{-}\mathbf{p}_{\mathbf{max}}$ was determined using a bootstrapping procedure outlined in Berner (2009). The bootstrapped eigenvectors were generated using the bootpca macro for SAS, written by Dr. Steve Tonsor (http://www.pitt.edu/~tonsor/downloads/programs/ bootpca.html), which has been used by other researchers investigating genetic variance-covariance and constraints (e.g., Caruso et al., 2005). The null hypothesis for these tests is $\boldsymbol{\Theta} = 0$; a rejection of the null hypothesis indicates that the vectors are not aligned. This method for hypothesis testing differs from that of Marroig and Cheverud (2010), who used the "broken sticks" approach originally described by Schluter (1996), to test similar hypotheses. The broken sticks procedure generates random vectors (broken sticks) of unit length and then assesses the correlation of these random vectors with a fixed vector (all components of the vector are the same value) of unit length. The standard deviation of the resulting vector correlations is used to generate confidence intervals for hypothesis testing. Since the bootstrapping procedure used in this study incorporates error in the estimates of all vectors, but the broken sticks procedure does not, these two approaches potentially yield different confidence intervals for statistical testing. The author is unaware of any study that has compared the statistical power of either approach or their rates of Type I and Type II error.

Chapter 3

INCISOR MODULARITY

As reviewed in Chapter 1, the incisors form a functional module and are hypothesized to form a variational module in which characters are linked by pleiotropy. The incisors are predicted to express high magnitude covariation (calculated as the phenotypic r^2) with one another and low magnitude covariation with characters outside the complex (i.e., r^2 nearly zero). This hypothesis will be rejected if either the incisors covary weakly with one another (i.e., r^2 nearly zero) or if covariation is nearly equal in magnitude with characters in other functional modules. The hypothesis of negative covariation between incisor and postcanine size (e.g., Jolly, 1970; McCollum and Sharpe, 2001; Hlusko et al., 2010) is also tested. This hypothesis will be rejected if covariation between incisor and postcanine size is either weak (i.e., r^2 nearly zero) or significant and positive in direction. Lastly, the expectation that levels of constraint, calculated within species, influence the independence of characters among species is investigated by comparing the magnitude of within-species phenotypic covariation (r^2) to that among-species (r^2 derived from independent contrasts). The similarity of covariation within and among species is not set up as a formal hypothesis, but is used to frame the discussion of the role of constraints in among species diversification. For a subset of species, incisor $\mathbf{p}_{max}$ and the correspondence of incisor $\mathbf{\Delta z}$ to $\mathbf{p}_{max}$ will be formally analyzed in Chapter 6.

*TABLE 3.1. The magnitude of covariation between the length and breadth of each incisor (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I_1MD-I_1LL	I_2MD-I_2LL	I^1MD-I^1LL	I^2MD-I^2LL
Gorilla Gorilla	$r^2 = 0.22$** $n = 61$	$r^2 = 0.18$** $n = 74$	$r^2 = 0.08$* $n = 64$	$r^2 = 0.36$*** $n = 64$
Pan Troglodytes	$r^2 = 0.13$* $n = 77$	$r^2 = 0.14$** $n = 79$	$r^2 = 0.07$* $n = 72$	$r^2 = 0.30$** $n = 71$
Hylobates Lar	$r^2 = 0.15$* $n = 68$	$r^2 = 0.21$*** $n = 76$	$r^2 = 0.15$* $n = 47$	$r^2 = 0.22$** $n = 49$
Cercopithecus Cephus	$r^2 = 0.23$*** $n = 69$	$r^2 = 0.16$*** $n = 75$	$r^2 = 0.31$*** $n = 69$	$r^2 = 0.20$*** $n = 67$
Cercopithecus Nictitans	$r^2 = 0.12$* $n = 70$	$r^2 = 0.20$*** $n = 77$	$r^2 = 0.22$** $n = 63$	$r^2 = 0.25$*** $n = 70$
Cercopithecus Pogonias	$r^2 = 0.08$* $n = 50$	$r^2 = 0.22$*** $n = 61$	$r^2 = 0.36$*** $n = 46$	$r^2 = 0.27$*** $n = 55$
Macaca fascicularis	$r^2 = 0.12$* $n = 65$	$r^2 = 0.19$* $n = 67$	$r^2 = 0.29$*** $n = 60$	$r^2 = 0.04$ $n = 73$
Colobus Satanas	$r^2 = 0.09$* $n = 49$	$r^2 = 0.05$ $n = 46$	$r^2 = 0.25$*** $n = 49$	$r^2 = 0.14$* $n = 46$
Ateles Geoffroyi	$r^2 = 0.10$** $n = 67$	$r^2 = 0.21$** $n = 67$	$r^2 = 0.37$*** $n = 61$	$r^2 = 0.42$*** $n = 61$
Cebus libidinosus	$r^2 = 0.21$*** $n = 68$	$r^2 = 0.27$*** $n = 86$	$r^2 = 0.17$*** $n = 87$	$r^2 = 0.08$* $n = 82$
Weighted Anthropoid Average	$r^2 = 0.15$	$r^2 = 0.19$	$r^2 = 0.22$	$r^2 = 0.22$
Weighted Hominoid Average	$r^2 = 0.16$	$r^2 = 0.18$	$r^2 = 0.09$	$r^2 = 0.30$
Weighted Cercopithecid Average	$r^2 = 0.13$	$r^2 = 0.17$	$r^2 = 0.28$	$r^2 = 0.18$
Weighted Platyrrhine Average	$r^2 = 0.16$	$r^2 = 0.24$	$r^2 = 0.27$	$r^2 = 0.25$
Significantly different from zero ($p < \alpha = 0.01$)	4/10	8/10	7/10	7/10

TABLE 3.2. The average magnitude of covariation between maxillary and mandibular incisor breadth and length.

	I^1LL-I^2MD	I^1LL-I_1MD	I^1LL-I_2MD	I^2LL-I^1MD
Hominoid Average	$r^2 = 0.17$	$r^2 = 0.15$	$r^2 = 0.16$	$r^2 = 0.08$
Cercopithecid Average	$r^2 = 0.12$	$r^2 = 0.12$	$r^2 = 0.07$	$r^2 = 0.24$
Platyrrhine Average	$r^2 = 0.16$	$r^2 = 0.24$	$r^2 = 0.16$	$r^2 = 0.19$
Anthropoid Average	$r^2 = 0.14$	$r^2 = 0.16$	$r^2 = 0.12$	$r^2 = 0.18$
Significantly different from zero ($p < \alpha = 0.01$)	7/10	8/10	6/10	8/10

	I^2LL-I_1MD	I_2LL-I^1MD	I_1LL-I^1MD	I_1LL-I^2MD
Hominoid Average	$r^2 = 0.10$	$r^2 = 0.14$	$r^2 = 0.15$	$r^2 = 0.20$
Cercopithecid Average	$r^2 = 0.08$	$r^2 = 0.13$	$r^2 = 0.16$	$r^2 = 0.12$
Platyrrhine Average	$r^2 = 0.17$	$r^2 = 0.08$	$r^2 = 0.10$	$r^2 = 0.15$
Anthropoid Average	$r^2 = 0.11$	$r^2 = 0.12$	$r^2 = 0.14$	$r^2 = 0.15$
Significantly different from zero ($p < \alpha = 0.01$)	6/10	8/10	8/10	8/10

	I_1LL-I_2MD	I^2LL-I_2MD	I_2LL-I^2MD	I_2LL-I_1MD
Hominoid Average	$r^2 = 0.15$	$r^2 = 0.12$	$r^2 = 0.27$	$r^2 = 0.18$
Cercopithecid Average	$r^2 = 0.09$	$r^2 = 0.08$	$r^2 = 0.12$	$r^2 = 0.12$
Platyrrhine Average	$r^2 = 0.13$	$r^2 = 0.21$	$r^2 = 0.19$	$r^2 = 0.18$
Anthropoid Average	$r^2 = 0.12$	$r^2 = 0.12$	$r^2 = 0.18$	$r^2 = 0.15$
Significantly different from zero ($p < \alpha = 0.01$)	8/10	6/10	8/10	9/10

RESULTS

***Incisor Size Covariation Within Species*:** All estimates of covariation between the MD length and LL breadth of each incisor are positive in direction, though estimates are quite variable among species (Table 3.1). The range among species for I_1MD-I_1LL is r^2 = 0.08–0.23, for I_2MD-I_2LL it is r^2 = 0.05–0.27, for I^1MD-I^1LL it is r^2 = 0.07–0.37, and for I^2MD-I^2LL it is r^2 = 0.04–0.42. Most estimates of r^2 for the MD length and LL breadth of each incisor are below r^2 = 0.25 (10 out of 10 estimates for I_1MD-I_1LL, 9 out of 10 estimates for I_2MD-I_2BL, 4 out 10 estimates for I^1MD-I^1BL, and 5 out of 10 estimates for I^2MD-I^2BL). The magnitude of covariation is consistent for all incisors; for both maxillary incisors, the anthropoid average is r^2 = 0.22 (Table 3.1) and for the mandibular incisors the anthropoid averages are lower at r^2 = 0.15 (I_1) and r^2 = 0.19 (I_2). Following the criteria outlined in Table 2.4, these r^2s are categorized as very low to low in magnitude. The hominoid, cercopithecid, and platyrrhine average r^2s are similar, indicating that this weak level of covariation is a common feature for anthropoids. Many of the r^2s for the MD length and LL breadth of each incisor are significantly different from zero at $\alpha = 0.05$ (38 out of 40 estimates), but fewer are significant at more restrictive α values (26 out of 40 estimates are significant at $p = 0.01$). The MD and LL dimensions of each incisor largely vary independently of one another within species.

As when the incisors were considered in isolation, the MD and LL dimensions of different incisors also express low to very low magnitude covariation (Table 3.2). Though weak in strength, all estimates of covariation for comparisons of MD length and LL breadth among incisors are positive in direction. Compared with MD length and LL breadth of a single incisor (Table 3.1), analyses that pair measurements of different incisors have anthropoid averages that are slightly lower; average estimates are routinely below r^2 = 0.20 and as low as r^2 = 0.07. As covariation is consistently weak for all

*TABLE 3.3. The magnitude of covariation among incisor breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I^1LL-I^2LL	I_1LL-I_2LL	I^1LL-I_1LL
Gorilla gorilla	$r^2 = 0.19^{**}$ $n = 72$	$r^2 = 0.70^{***}$ $n = 85$	$r^2 = 0.44^{***}$ $n = 69$
Pan troglodytes	$r^2 = 0.58^{***}$ $n = 84$	$r^2 = 0.81^{***}$ $n = 84$	$r^2 = 0.47^{***}$ $n = 78$
Hylobates lar	$r^2 = 0.24^{**}$ $n = 45$	$r^2 = 0.62^{***}$ $n = 82$	$r^2 = 0.40^{***}$ $n = 49$
Cercopithecus cephus	$r^2 = 0.07^{**}$ $n = 74$	$r^2 = 0.60^{***}$ $n = 75$	$r^2 = 0.37^{***}$ $n = 71$
Cercopithecus nictitans	$r^2 = 0.24^{***}$ $n = 69$	$r^2 = 0.58^{***}$ $n = 75$	$r^2 = 0.54^{***}$ $n = 68$
Cercopithecus pogonias	$r^2 = 0.17^{*}$ $n = 53$	$r^2 = 0.48^{***}$ $n = 63$	$r^2 = 0.24^{***}$ $n = 52$
Macaca fascicularis	$r^2 = 0.37^{***}$ $n = 72$	$r^2 = 0.63^{***}$ $n = 71$	$r^2 = 0.52^{***}$ $n = 63$
Colobus satanas	$r^2 = 0.26^{***}$ $n = 43$	$r^2 = 0.21^{*}$ $n = 45$	$r^2 = 0.13^{*}$ $n = 47$
Ateles geoffroyi	$r^2 = 0.47^{***}$ $n = 65$	$r^2 = 0.70^{***}$ $n = 74$	$r^2 = 0.24^{***}$ $n = 66$
Cebus libidinosus	$r^2 = 0.24^{***}$ $n = 83$	$r^2 = 0.62^{***}$ $n = 87$	$r^2 = 0.22^{***}$ $n = 87$
Weighted Anthropoid Average	$r^2 = 0.29$	$r^2 = 0.62$	$r^2 = 0.36$
Weighted Hominoid Average	$r^2 = 0.36$	$r^2 = 0.71$	$r^2 = 0.44$
Weighted Cercopithecid Average	$r^2 = 0.22$	$r^2 = 0.53$	$r^2 = 0.38$
Weighted Platyrrhine Average	$r^2 = 0.34$	$r^2 = 0.66$	$r^2 = 0.23$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	9/10	9/10

*TABLE 3.4 The magnitude of covariation among incisor breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I^2LL-I_2LL	I^1LL-I_2LL	I_1LL-I^2LL
Gorilla gorilla	$r^2 = 0.44^{***}$ $n = 75$	$r^2 = 0.36^{***}$ $n = 68$	$r^2 = 0.28^{***}$ $n = 72$
Pan troglodytes	$r^2 = 0.56^{***}$ $n = 84$	$r^2 = 0.59^{***}$ $n = 78$	$r^2 = 0.58^{***}$ $n = 83$
Hylobates lar	$r^2 = 0.11^{*}$ $n = 64$	$r^2 = 0.28^{***}$ $n = 49$	$r^2 = 0.12^{*}$ $n = 61$
Cercopithecus cephus	$r^2 = 0.26^{***}$ $n = 74$	$r^2 = 0.31^{***}$ $n = 72$	$r^2 = 0.22^{***}$ $n = 72$
Cercopithecus nictitans	$r^2 = 0.27^{***}$ $n = 75$	$r^2 = 0.29^{***}$ $n = 69$	$r^2 = 0.24^{**}$ $n = 72$
Cercopithecus pogonias	$r^2 = 0.34^{***}$ $n = 57$	$r^2 = 0.07$ $n = 53$	$r^2 = 0.36^{***}$ $n = 57$
Macaca fascicularis	$r^2 = 0.57^{***}$ $n = 69$	$r^2 = 0.46^{***}$ $n = 65$	$r^2 = 0.34^{***}$ $n = 68$
Colobus satanas	$r^2 = 0.42^{***}$ $n = 44$	$r^2 = 0.08^{*}$ $n = 43$	$r^2 = 0.05$ $n = 44$
Ateles geoffroyi	$r^2 = 0.38^{***}$ $n = 71$	$r^2 = 0.32^{***}$ $n = 66$	$r^2 = 0.38^{***}$ $n = 70$
Cebus libidinosus	$r^2 = 0.43^{***}$ $n = 83$	$r^2 = 0.09^{*}$ $n = 89$	$r^2 = 0.43^{***}$ $n = 81$
Weighted Anthropoid Average	$r^2 = 0.38$	$r^2 = 0.30$	$r^2 = 0.32$
Weighted Hominoid Average	$r^2 = 0.39$	$r^2 = 0.43$	$r^2 = 0.35$
Weighted Cercopithecid Average	$r^2 = 0.37$	$r^2 = 0.26$	$r^2 = 0.26$
Weighted Platyrrhine Average	$r^2 = 0.41$	$r^2 = 019$	$r^2 = 0.41$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	7/10	8/10

taxonomic groups, incisor MD length and LL breadth largely vary independently of one another both within a single incisor and among incisors.

In contrast to the low and very low magnitude of covariation observed for pairings of MD length and LL breadth, stronger covariation is observed for comparisons of LL breadth between incisors, with some LL breadths expressing moderate to high levels of covariation (Tables 3.3 and 3.4). The estimated magnitude of covariation is highest between the LL breadths of I_1 and I_2 (the anthropoid average is $r^2 = 0.62$); with one notable exception (*Colobus satanas*, $r^2 = 0.21$), all species have estimated levels of covariation for I_1LL-I_2LL $\geq r^2 = 0.48$. The low level observed in *Colobus satanas* is stands out from other species estimates and may be explained by the fact that the sample size is the smallest for any taxon included in the analysis and is, therefore, more easily influenced by outliers. The estimates of r^2 for I_1LL-I_2LL are significantly different from zero not only at $\alpha = 0.05$ (10 out of 10 samples), but also at more restrictive levels of significance (9 out of 10 are significant at $\alpha = 0.001$); however, the null hypothesis of complete pleiotropy (i.e., $r^2 = 1$) is also rejected, as the 95, 99, and 99.9% confidence intervals do not include $r^2 = 1$ for any of the ten taxa.

All other estimates of covariation among incisor LL breadths are lower than between the mandibular incisors, with anthropoid averages falling in the range $r^2 = 0.29$–0.38 (Tables 3.3 and 3.4). Following the LL breadths of the mandibular incisors in strength, the next highest level of covariation is for I_2LL-I^2LL (anthropoid average $r^2 = 0.38$) and then for the I_1LL-I^1LL (anthropoid average $r^2 = 0.36$), which are combinations of characters in equivalent positions in the opposite arch. Notably, the magnitude of covariation between maxillary incisor breadths (anthropoid average is $r^2 = 0.29$) is on average no higher than that seen between the I_2LL-I^1LL (anthropoid average $r^2 = 0.30$) and the I_1LL-I^2LL (anthropoid average $r^2 = 0.32$), indicating that maxillary incisors share

far less variation in common than do the mandibular incisors. The magnitudes of covariation between the LL breadths are higher than between pairings of MD length and LL breadths, but, with the exception of the mandibular incisors, the majority of variation in each dimension is not shared with any other dimensions; there is substantial independent variation for selection to act upon.

For most comparisons of LL breadth, the level of covariation observed in cercopithecids is lower than that observed in platyrrhines and hominoids (Tables 3.3 and 3.4). This difference is especially pronounced for I^1LL-I^2LL (the cercopithecid average r^2 is 0.14 less than hominoid average and 0.12 less than the platyrrhine average) and for I_1LL-I_2LL (the cercopithecid average r^2 is 0.18 less than the hominoid average and 0.13 less than the platyrrhine average). The low cercopithecid averages are in part a reflection of the low r^2s in *Colobus satanas*; however, excluding *Colobus satanas* still results in lower averages for cercopithecids than in the other taxonomic groups.

The comparisons of incisor LL breadths highlight three features of incisor size covariation: first, that covariation is much stronger between the breadths of the mandibular incisors than between the breadths of the maxillary incisors; second, that between arches, incisors of similar position tend to covary more strongly with one another (I_1 with I^1, I_2 with I^2) than they do with the incisor in the opposite position (I_1 with I^2, I_2 with I^1); and third, that the incisor breadths of cercopithecids do not covary as strongly as they do in platyrrhines and hominoids. The underlying morphological explanation for these patterns will be given at the end of the chapter.

In general, the magnitudes of covariation for incisor MD lengths are lower than for LL breadths (Tables 3.5 and 3.6); however, variation in the strength of covariation for the MD lengths follows a similar pattern to that of the LL breadths. Covariation

*TABLE 3.5. The magnitude of covariation among incisor lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I^1MD-I^2MD	I_1MD-I_2MD	I^1MD-I_1MD
Gorilla gorilla	$r^2 = 0.23$* $n = 55$	$r^2 = 0.26$*** $n = 54$	$r^2 = 0.29$*** $n = 50$
Pan troglodytes	$r^2 = 0.40$*** $n = 65$	$r^2 = 0.52$*** $n = 74$	$r^2 = 0.35$*** $n = 69$
Hylobates lar	$r^2 = 0.03$ $n = 32$	$r^2 = 0.55$*** $n = 65$	$r^2 = 0.64$*** $n = 41$
Cercopithecus cephus	$r^2 = 0.12$** $n = 61$	$r^2 = 0.35$*** $n = 69$	$r^2 = 0.28$*** $n = 62$
Cercopithecus nictitans	$r^2 = 0.21$*** $n = 63$	$r^2 = 0.15$* $n = 71$	$r^2 = 0.18$* $n = 62$
Cercopithecus pogonias	$r^2 = 0.50$*** $n = 43$	$r^2 = 0.19$** $n = 48$	$r^2 = 0.14$* $n = 41$
Macaca fascicularis	$r^2 = 0.03$ $n = 64$	$r^2 = 0.34$*** $n = 74$	$r^2 = 0.46$*** $n = 67$
Colobus satanas	$r^2 = 0.11$ $n = 43$	$r^2 = 0.00$ $n = 46$	$r^2 = 0.13$* $n = 46$
Ateles geoffroyi	$r^2 = 0.24$** $n = 57$	$r^2 = 0.67$*** $n = 62$	$r^2 = 0.29$*** $n = 60$
Cebus libidinosus	$r^2 = 0.20$*** $n = 81$	$r^2 = 0.46$*** $n = 67$	$r^2 = 0.46$*** $n = 68$
Weighted Anthropoid Average	$r^2 = 0.21$	$r^2 = 0.36$	$r^2 = 0.33$
Weighted Hominoid Average	$r^2 = 0.26$	$r^2 = 0.46$	$r^2 = 0.41$
Weighted Cercopithecid Average	$r^2 = 0.18$	$r^2 = 0.22$	$r^2 = 0.26$
Weighted Platyrrhine Average	$r^2 = 0.22$	$r^2 = 0.56$	$r^2 = 0.38$
Significantly different from zero ($p < \alpha = 0.01$)	6/10	8/10	7/10

*TABLE 3.6. The magnitude of covariation among maxillary and mandibular incisor lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I^2MD-I_2MD	I^1MD-I_2MD	I_1MD-I^2MD
Gorilla gorilla	$r^2 = 0.40^{***}$ $n = 53$	$r^2 = 0.22^{**}$ $n = 52$	$r^2 = 0.17^{*}$ $n = 46$
Pan troglodytes	$r^2 = 0.36^{***}$ $n = 68$	$r^2 = 0.34^{***}$ $n = 68$	$r^2 = 0.42^{***}$ $n = 65$
Hylobates lar	$r^2 = 0.07^{*}$ $n = 48$	$r^2 = 0.33^{***}$ $n = 42$	$r^2 = 0.07$ $n = 47$
Cercopithecus cephus	$r^2 = 0.16^{***}$ $n = 66$	$r^2 = 0.18^{***}$ $n = 68$	$r^2 = 0.11^{*}$ $n = 59$
Cercopithecus nictitans	$r^2 = 0.09$ $n = 69$	$r^2 = 0.15^{*}$ $n = 65$	$r^2 = 0.16^{*}$ $n = 64$
Cercopithecus pogonias	$r^2 = 0.08$ $n = 51$	$r^2 = 0.14^{*}$ $n = 44$	$r^2 = 0.01$ $n = 45$
Macaca fascicularis	$r^2 = 0.13^{**}$ $n = 70$	$r^2 = 0.15^{*}$ $n = 63$	$r^2 = 0.05$ $n = 70$
Colobus satanas	$r^2 = 0.07^{*}$ $n = 44$	$r^2 = 0.12^{*}$ $n = 45$	$r^2 = 0.03$ $n = 43$
Ateles geoffroyi	$r^2 = 0.32^{**}$ $n = 55$	$r^2 = 0.28^{***}$ $n = 60$	$r^2 = 0.27^{***}$ $n = 56$
Cebus libidinosus	$r^2 = 0.12^{**}$ $n = 82$	$r^2 = 0.29^{***}$ $n = 84$	$r^2 = 0.15^{*}$ $n = 64$
Weighted Anthropoid Average	$r^2 = 0.18$	$r^2 = 0.22$	$r^2 = 0.15$
Weighted Hominoid Average	$r^2 = 0.29$	$r^2 = 0.30$	$r^2 = 0.24$
Weighted Cercopithecid Average	$r^2 = 0.11$	$r^2 = 0.15$	$r^2 = 0.08$
Weighted Platyrrhine Average	$r^2 = 0.20$	$r^2 = 0.29$	$r^2 = 0.21$
Significantly different from zero ($p < \alpha = 0.01$)	6/10	6/10	2/10

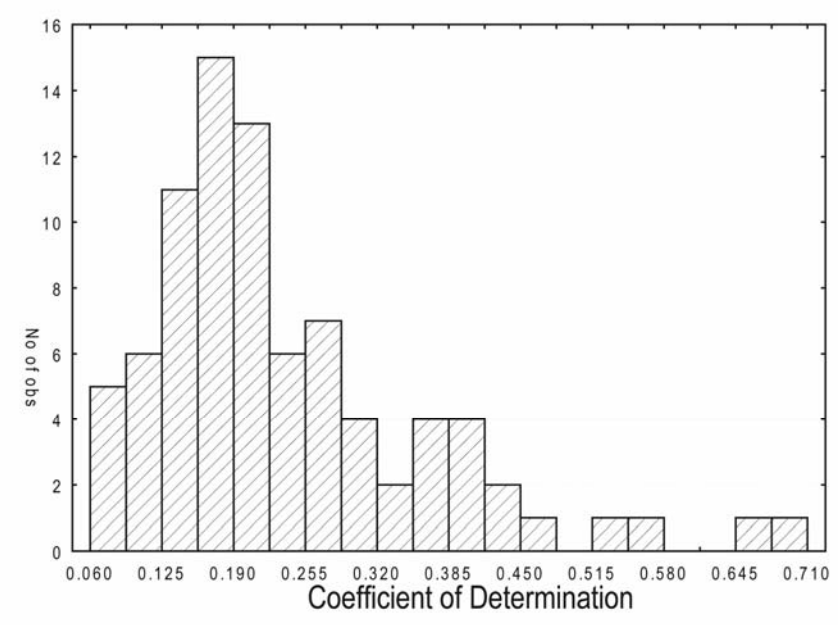

Fig. 3.1. Histogram of incisor size average r^2s for platyrrhines, hominoids, and cercopithecids.

among MD lengths is highest between I_1MD-I_2MD (the anthropoid average is $r^2 = 0.36$) and I_1MD-I^1MD (the anthropoid average is $r^2 = 0.33$) and lower in strength for all other combinations. Covariation among MD lengths departs from the pattern observed for LL breadths in one important way; the I^2MD does not covary strongly with any other measure of MD length. For all pairings, as observed for LL breadths, the cercopithecid average is lower than the hominoid and platyrrhine averages. In fact, the discrepancy in levels of covariation for incisor MD lengths is more pronounced than it is for LL breadths. The average r^2 for I_1MD-I_2MD in cercopithecids ($r^2 = 0.22$) is 0.24 less than the hominoid average ($r^2 = 0.46$) and 0.34 less than the platyrrhine average ($r^2 = 0.56$). For the I_1MD-I^1MD, the cercopithecid average ($r^2 = 0.26$) is 0.12 less than the platyrrhine average ($r^2 = 0.38$) and 0.15 less than the hominoid average (r^2 =0.41). The weaker r^2

estimates in cercopithecids likely indicate that incisor size coevolution will behave differently among cercopithecids than it does among hominoids or platyrrhines.

Variation in the strength of incisal size covariation can be seen when the platyrrhine, cercopithecid, and hominoid average r^2s for all incisal character pairs are placed in a histogram (Figure 3.1). Most character pairs express only very low or low magnitude covariation (principally pairs of LL breadth and MD length). The character pairs that stand out from the rest for their moderate to high levels of covariation include, in order of strength, the hominoid I_1LL-I_2LL (0.71), platyrrhine I_1LL-I_2LL (0.66), platyrrhine I_1MD-I_2MD (0.56), cercopithecid I_1LL-I_2LL (0.53), and hominoid I_1MD-I_2MD (0.46), which are all pairings of homologous dimensions of the mandibular incisors.[2] In strength, there is another cluster of characters that covary between 0.35–0.45; these include the hominoid and platyrrhine I^2LL-I^1LL, cercopithecid I_1LL-I^1LL, the I^2LL-I_2LL of all taxonomic groups, the hominoid I^1LL-I_2LL, the hominoid and platyrrhine I_1LL-I^2LL, and the hominoid I_1MD-I^1MD. (Tables 3.1–3.6) This second cluster of characters includes measures of homologous dimensions in either the maxilla or between the maxilla and mandible. Incisor size does not form a module characterized by consistent, high magnitude covariation among all elements.

At the surface, the low level of covariation among most pairs of incisal crown-size metrics suggests that the incisors do not form a variational module. It is clear, however, that the pattern of covariation is not random. In fact, the data are consistent with the existence of two incisor variational modules, a LL module and a MD module, with each module having overlapping pleiotropic effects with the other. The one dimension of the complex that lies mostly outside of the MD variational module is I^2MD. Using the

[2] Throughout this dissertation the term "homologous dimension" is used to refer to pairings of labio- and buccolingual breadths, mesiodistal lengths, and heights with one another. The use of this term follows from Cochard (1981).

hominoid, cercopithecid, and platyrrhine averages, all characters, with the exception of the I^2MD, can be linked to at least one other character at $r^2 \geq 0.40$. For I^2MD, its highest observed taxonomic average is $r^2 = 0.30$ for I^2MD-I^2LL in hominoids. If pleiotropy channels among-species change in incisor size, then I^2MD length should exhibit the greatest independence.

In summary, for all analyses of incisor size, estimates of covariation are frequently significantly different from zero and all significant correlations are positive. This contrasts with the findings of Hlusko and Mahaney (2009) in which the LL breadth and MD length of the *Presbytis* maxillary incisors were estimated to have a negative phenotypic correlation. For many comparisons, estimated levels of incisor covariation show substantial variation among species. This inconsistency is also seen in the Hlusko and Mahaney (2009) analysis and is not easily explained. However, the overall pattern of covariation is consistent among species.

Incisor-Postcanine Size Covariation Within Species: The hypothesis of modular pleiotropy also predicts that characters in different functional modules belong to different variational modules; the magnitude of covariation should be nearly zero between dimensions of the incisors and dimensions of the other functional modules. Additionally, within and among species is predicted to be negative between the anterior and posterior teeth. To test these hypotheses, the covariation of incisor size with the size of dimensions of the honing complex and the postcanine dentition was also investigated. Covariation with the honing complex will be discussed in Chapter 5; here, the discussion is confined to covariation between postcanine and incisal characters. Eight incisor dimensions, 20 catarrhine postcanine dimensions, and 24 platyrrhine postcanine dimensions were considered in this study, which yields 160 possible character-pairs of incisor and

*TABLE 3.7. The magnitude of covariation between the breadths of the I1 and postcanine teeth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I1LL-P2, P3BL	I1LL-P4BL	I1LL-M1BL	I1LL-M2BL
Gorilla gorilla	$r^2_{max} = 0.22^{***}$ $n = 73$ $r^2_{mand} = 0.23^{**}$ $n = 81$	$r^2_{max} = 0.26^{***}$ $n = 71$ $r^2_{mand} = 0.24^{***}$ $n = 82$	$r^2_{max} = 0.14^{**}$ $n = 74$ $r^2_{mand} = 0.10^{*}$ $n = 77$	$r^2_{max} = 0.20^{***}$ $n = 75$ $r^2_{mand} = 0.17^{***}$ $n = 84$
Pan troglodytes	$r^2_{max} = 0.35^{***}$ $n = 83$ $r^2_{mand} = 0.26^{***}$ $n = 84$	$r^2_{max} = 0.38^{***}$ $n = 83$ $r^2_{mand} = 0.32^{***}$ $n = 82$	$r^2_{max} = 0.21^{***}$ $n = 85$ $r^2_{mand} = 0.15^{***}$ $n = 82$	$r^2_{max} = 0.23^{***}$ $n = 84$ $r^2_{mand} = 0.35^{***}$ $n = 86$
Hylobates lar	$r^2_{max} = 0.21^{*}$ $n = 39$ $r^2_{mand} = 0.25^{***}$ $n = 62$	$r^2_{max} = 0.27^{*}$ $n = 42$ $r^2_{mand} = 0.34^{***}$ $n = 70$	$r^2_{max} = 0.12^{*}$ $n = 52$ $r^2_{mand} = 0.19^{*}$ $n = 60$	$r^2_{max} = 0.15^{*}$ $n = 45$ $r^2_{mand} = 0.22^{***}$ $n = 76$
Cercopithecus cephus	$r^2_{max} = 0.18^{**}$ $n = 74$ $r^2_{mand} = 0.18^{***}$ $n = 73$	$r^2_{max} = 0.13^{**}$ $n = 75$ $r^2_{mand} = 0.13^{***}$ $n = 75$	$r^2_{max} = 0.17^{*}$ $n = 74$ $r^2_{mand} = 0.28^{***}$ $n = 74$	$r^2_{max} = 0.15^{**}$ $n = 75$ $r^2_{mand} = 0.31^{***}$ $n = 75$
Cercopithecus nictitans	$r^2_{max} = 0.05$ $n = 68$ $r^2_{mand} = 0.08^{*}$ $n = 71$	$r^2_{max} = 0.19^{***}$ $n = 69$ $r^2_{mand} = 0.13^{*}$ $n = 72$	$r^2_{max} = 0.11^{*}$ $n = 70$ $r^2_{mand} = 0.14^{*}$ $n = 68$	$r^2_{max} = 0.09^{*}$ $n = 69$ $r^2_{mand} = 0.16^{***}$ $n = 73$
Cercopithecus pogonias	$r^2_{max} = 0.16^{*}$ $n = 53$ $r^2_{mand} = 0.17^{***}$ $n = 60$	$r^2_{max} = 0.16^{*}$ $n = 53$ $r^2_{mand} = 0.13^{*}$ $n = 60$	$r^2_{max} = 0.05$ $n = 55$ $r^2_{mand} = 0.14^{*}$ $n = 63$	$r^2_{max} = 0.15^{*}$ $n = 53$ $r^2_{mand} = 0.17^{**}$ $n = 63$
Macaca fascicularis	$r^2_{max} = 0.27^{***}$ $n = 68$ $r^2_{mand} = 0.10^{*}$ $n = 66$	$r^2_{max} = 0.22^{***}$ $n = 67$ $r^2_{mand} = 0.06^{*}$ $n = 69$	$r^2_{max} = 0.13^{***}$ $n = 73$ $r^2_{mand} = 0.05$ $n = 70$	$r^2_{max} = 0.10^{*}$ $n = 73$ $r^2_{mand} = 0.11^{*}$ $n = 72$
Colobus satanas	$r^2_{max} = 0.04^{*}$ $n = 44$ $r^2_{mand} = 0.00$ $n = 45$	$r^2_{max} = 0.23^{***}$ $n = 44$ $r^2_{mand} = 0.03$ $n = 45$	$r^2_{max} = 0.12^{*}$ $n = 49$ $r^2_{mand} = 0.01$ $n = 50$	$r^2_{max} = 0.20^{*}$ $n = 49$ $r^2_{mand} = 0.10^{*}$ $n = 50$
Ateles geoffroyi	$r^2_{max} = 0.44^{***}$ $n = 58$ $r^2_{mand} = 0.29^{***}$ $n = 63$	$r^2_{max} = 0.19^{***}$ $n = 58$ $r^2_{mand} = 0.27^{***}$ $n = 62$	$r^2_{max} = 0.25^{**}$ $n = 61$ $r^2_{mand} = 0.46^{***}$ $n = 53$	$r^2_{max} = 0.17^{***}$ $n = 61$ $r^2_{mand} = 0.37^{***}$ $n = 57$
Cebus libidinosus	$r^2_{max} = 0.26^{***}$ $n = 76$ $r^2_{mand} = 0.21^{**}$ $n = 75$	$r^2_{max} = 0.18^{***}$ $n = 78$ $r^2_{mand} = 0.24^{***}$ $n = 74$	$r^2_{max} = 0.17^{***}$ $n = 77$ $r^2_{mand} = 0.12^{*}$ $n = 86$	$r^2_{max} = 0.17^{***}$ $n = 88$ $r^2_{mand} = 0.18^{**}$ $n = 80$
Weighted Anthropoid Average	$r^2_{max} = 0.23$ $r^2_{mand} = 0.18$	$r^2_{max} = 0.22$ $r^2_{mand} = 0.20$	$r^2_{max} = 0.15$ $r^2_{mand} = 0.16$	$r^2_{max} = 0.16$ $r^2_{mand} = 0.22$

*TABLE 3.8. The magnitude of covariation between the breadths of the I2 and postcanine teeth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I2LL-P2, P3BL	I2LL-P4BL	I2LL-M1BL	I2LL-M2BL
Gorilla gorilla	$r^2_{max} = 0.22^{***}$ $n = 81$ $r^2_{mand} = 0.31^{***}$ $n = 95$	$r^2_{max} = 0.23^{***}$ $n = 79$ $r^2_{mand} = 0.35^{***}$ $n = 94$	$r^2_{max} = 0.13^{***}$ $n = 81$ $r^2_{mand} = 0.25^{***}$ $n = 89$	$r^2_{max} = 0.18^{**}$ $n = 82$ $r^2_{mand} = 0.25^{***}$ $n = 100$
Pan troglodytes	$r^2_{max} = 0.28^{***}$ $n = 89$ $r^2_{mand} = 0.28^{***}$ $n = 87$	$r^2_{max} = 0.31^{***}$ $n = 89$ $r^2_{mand} = 0.32^{***}$ $n = 85$	$r^2_{max} = 0.20^{***}$ $n = 90$ $r^2_{mand} = 0.13^{***}$ $n = 84$	$r^2_{max} = 0.30^{***}$ $n = 89$ $r^2_{mand} = 0.33^{***}$ $n = 87$
Hylobates lar	$r^2_{max} = 0.30^{***}$ $n = 56$ $r^2_{mand} = 0.27^{***}$ $n = 67$	$r^2_{max} = 0.28^{***}$ $n = 61$ $r^2_{mand} = 0.26^{**}$ $n = 72$	$r^2_{max} = 0.11^{*}$ $n = 61$ $r^2_{mand} = 0.17^{*}$ $n = 60$	$r^2_{max} = 0.28^{***}$ $n = 64$ $r^2_{mand} = 0.25^{***}$ $n = 78$
Cercopithecus cephus	$r^2_{max} = 0.24^{***}$ $n = 76$ $r^2_{mand} = 0.25^{***}$ $n = 75$	$r^2_{max} = 0.24^{***}$ $n = 77$ $r^2_{mand} = 0.23^{***}$ $n = 77$	$r^2_{max} = 0.10^{**}$ $n = 76$ $r^2_{mand} = 0.32^{***}$ $n = 76$	$r^2_{max} = 0.17^{**}$ $n = 77$ $r^2_{mand} = 0.30^{***}$ $n = 77$
Cercopithecus nictitans	$r^2_{max} = 0.13^{*}$ $n = 73$ $r^2_{mand} = 0.14^{***}$ $n = 75$	$r^2_{max} = 0.17^{*}$ $n = 74$ $r^2_{mand} = 0.16^{***}$ $n = 76$	$r^2_{max} = 0.06^{*}$ $n = 74$ $r^2_{mand} = 0.16^{***}$ $n = 72$	$r^2_{max} = 0.08$ $n = 75$ $r^2_{mand} = 0.17^{***}$ $n = 77$
Cercopithecus pogonias	$r^2_{max} = 0.41^{***}$ $n = 56$ $r^2_{mand} = 0.18^{***}$ $n = 61$	$r^2_{max} = 0.30^{**}$ $n = 56$ $r^2_{mand} = 0.19^{***}$ $n = 61$	$r^2_{max} = 0.07^{*}$ $n = 58$ $r^2_{mand} = 0.14^{*}$ $n = 63$	$r^2_{max} = 0.14^{*}$ $n = 56$ $r^2_{mand} = 0.26^{***}$ $n = 64$
Macaca fascicularis	$r^2_{max} = 0.26^{***}$ $n = 74$ $r^2_{mand} = 0.25^{***}$ $n = 65$	$r^2_{max} = 0.20^{***}$ $n = 72$ $r^2_{mand} = 0.13^{*}$ $n = 68$	$r^2_{max} = 0.19^{**}$ $n = 78$ $r^2_{mand} = 0.07^{*}$ $n = 71$	$r^2_{max} = 0.16^{*}$ $n = 79$ $r^2_{mand} = 0.21^{**}$ $n = 72$
Colobus satanas	$r^2_{max} = 0.16^{*}$ $n = 46$ $r^2_{mand} = 0.04$ $n = 45$	$r^2_{max} = 0.29^{***}$ $n = 46$ $r^2_{mand} = 0.15^{*}$ $n = 45$	$r^2_{max} = 0.16^{*}$ $n = 46$ $r^2_{mand} = 0.12^{*}$ $n = 46$	$r^2_{max} = 0.19^{**}$ $n = 46$ $r^2_{mand} = 0.12^{*}$ $n = 46$
Ateles geoffroyi	$r^2_{max} = 0.37^{***}$ $n = 63$ $r^2_{mand} = 0.27^{***}$ $n = 63$	$r^2_{max} = 0.23^{***}$ $n = 60$ $r^2_{mand} = 0.44^{***}$ $n = 62$	$r^2_{max} = 0.32^{***}$ $n = 62$ $r^2_{mand} = 0.46^{***}$ $n = 53$	$r^2_{max} = 0.28^{***}$ $n = 63$ $r^2_{mand} = 0.44^{***}$ $n = 57$
Cebus libidinosus	$r^2_{max} = 0.15^{*}$ $n = 74$ $r^2_{mand} = 0.22^{***}$ $n = 77$	$r^2_{max} = 0.20^{***}$ $n = 76$ $r^2_{mand} = 0.21^{***}$ $n = 76$	$r^2_{max} = 0.23^{***}$ $n = 75$ $r^2_{mand} = 0.19^{**}$ $n = 88$	$r^2_{max} = 0.19^{***}$ $n = 83$ $r^2_{mand} = 0.23^{**}$ $n = 83$
Weighted Anthropoid Average	$r^2_{max} = 0.25$ $r^2_{mand} = 0.23$	$r^2_{max} = 0.24$ $r^2_{mand} = 0.25$	$r^2_{max} = 0.16$ $r^2_{mand} = 0.20$	$r^2_{max} = 0.20$ $r^2_{mand} = 0.26$

*TABLE 3.9. The magnitude of covariation between the lengths of the I1 and postcanine teeth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I1MD-P2, P3Oblique	I1MD-P4MD	I1MD-M1MD	I1MD-M2MD
Gorilla gorilla	r^2_{max} = 0.06* n = 51	r^2_{max} = 0.16* n = 58	r^2_{max} = 0.22*** n = 63	r^2_{max} = 0.11* n = 62
	r^2_{mand} = 0.30*** n = 49	r^2_{mand} = 0.20** n = 56	r^2_{mand} = 0.13* n = 58	r^2_{mand} = 0.16* n = 56
Pan troglodytes	r^2_{max} = 0.04 n = 67	r^2_{max} = 0.08* n = 72	r^2_{max} = 0.19*** n = 75	r^2_{max} = 0.14* n = 74
	r^2_{mand} = 0.17* n = 71	r^2_{mand} = 0.07* n = 75	r^2_{mand} = 0.08* n = 76	r^2_{mand} = 0.07* n = 79
Hylobates lar	r^2_{max} = 0.11 n = 24	r^2_{max} = 0.18* n = 35	r^2_{max} = 0.03 n = 48	r^2_{max} = 0.02 n = 40
	r^2_{mand} = 0.01 n = 52	r^2_{mand} = 0.24*** n = 55	r^2_{mand} = 0.09* n = 61	r^2_{mand} = 0.06* n = 64
Cercopithecus cephus	r^2_{max} = 0.06 n = 57	r^2_{max} = 0.09* n = 69	r^2_{max} = 0.26*** n = 69	r^2_{max} = 0.13* n = 69
	r^2_{mand} = 0.05 n = 68	r^2_{mand} = 0.22** n = 69	r^2_{mand} = 0.11* n = 68	r^2_{mand} = 0.14* n = 69
Cercopithecus nictitans	r^2_{max} = 0.06 n = 57	r^2_{max} = 0.13* n = 66	r^2_{max} = 0.20* n = 67	r^2_{max} = 0.08* n = 66
	r^2_{mand} = 0.00 n = 66	r^2_{mand} = 0.03 n = 68	r^2_{mand} = 0.06 n = 67	r^2_{mand} = 0.02 n = 69
Cercopithecus pogonias	r^2_{max} = 0.01 n = 40	r^2_{max} = 0.21* n = 44	r^2_{max} = 0.28** n = 47	r^2_{max} = 0.22* n = 45
	r^2_{mand} = 0.00 n = 46	r^2_{mand} = 0.00 n = 46	r^2_{mand} = 0.05 n = 49	r^2_{mand} = 0.04 n = 49
Macaca fascicularis	r^2_{max} = 0.09* n = 56	r^2_{max} = 0.26** n = 58	r^2_{max} = 0.24*** n = 71	r^2_{max} = 0.31*** n = 66
	r^2_{mand} = 0.11* n = 63	r^2_{mand} = 0.38*** n = 70	r^2_{mand} = 0.20** n = 81	r^2_{mand} = 0.26*** n = 78
Colobus satanas	r^2_{max} = 0.07 n = 44	r^2_{max} = 0.17* n = 44	r^2_{max} = 0.09* n = 49	r^2_{max} = 0.07* n = 49
	r^2_{mand} = -0.01 n = 44	r^2_{mand} = 0.12 n = 44	r^2_{mand} = 0.04 n = 49	r^2_{mand} = 0.01 n = 49
Ateles geoffroyi	r^2_{max} = 0.40*** n = 53	r^2_{max} = 0.23** n = 61	r^2_{max} = 0.18* n = 63	r^2_{max} = 0.31*** n = 59
	r^2_{mand} = 0.00 n = 55	r^2_{mand} = 0.34*** n = 61	r^2_{mand} = 0.25** n = 64	r^2_{mand} = 0.17* n = 62
Cebus libidinosus	r^2_{max} = 0.29*** n = 70	r^2_{max} = 0.20*** n = 75	r^2_{max} = 0.14* n = 75	r^2_{max} = 0.18*** n = 85
	r^2_{mand} = 0.03 n = 54	r^2_{mand} = 0.10* n = 57	r^2_{mand} = 0.09* n = 67	r^2_{mand} = 0.20** n = 60
Weighted Anthropoid Average	r^2_{max} = 0.13	r^2_{max} = 0.17	r^2_{max} = 0.19	r^2_{max} = 0.16
	r^2_{mand} = 0.07	r^2_{mand} = 0.18	r^2_{mand} = 0.11	r^2_{mand} = 0.12

*TABLE 3.10. The magnitude of covariation between the lengths of the I2 and postcanine teeth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	I2MD-P2, P3MD	I2MD-P4MD	I2MD-M1MD	I2MD-M2MD
Gorilla gorilla	r^2_{max} = 0.11* n = 54 r^2_{mand} = 0.33*** n = 62	r^2_{max} = 0.20** n = 61 r^2_{mand} = 0.12* n = 68	r^2_{max} = 0.23*** n = 64 r^2_{mand} = 0.05 n = 71	r^2_{max} = 0.07 n = 63 r^2_{mand} = 0.12** n = 72
Pan troglodytes	r^2_{max} = 0.24** n = 66 r^2_{mand} = 0.16** n = 77	r^2_{max} = 0.13* n = 71 r^2_{mand} = 0.12* n = 79	r^2_{max} = 0.09* n = 73 r^2_{mand} = 0.12* n = 78	r^2_{max} = 0.18** n = 71 r^2_{mand} = 0.07* n = 80
Hylobates lar	r^2_{max} = 0.25** n = 31 r^2_{mand} = 0.07* n = 60	r^2_{max} = 0.24** n = 44 r^2_{mand} = 0.23** n = 66	r^2_{max} = 0.26*** n = 49 r^2_{mand} = 0.07* n = 66	r^2_{max} = 0.31*** n = 49 r^2_{mand} = 0.16*** n = 74
Cercopithecus cephus	r^2_{max} = 0.06 n = 56 r^2_{mand} = 0.20*** n = 76	r^2_{max} = 0.21*** n = 67 r^2_{mand} = 0.17*** n = 77	r^2_{max} = 0.19** n = 67 r^2_{mand} = 0.15** n = 76	r^2_{max} = 0.21*** n = 67 r^2_{mand} = 0.21*** n = 77
Cercopithecus nictitans	r^2_{max} = 0.00 n = 59 r^2_{mand} = 0.05 n = 72	r^2_{max} = 0.12* n = 70 r^2_{mand} = 0.04* n = 74	r^2_{max} = 0.07* n = 72 r^2_{mand} = 0.04 n = 73	r^2_{max} = 0.04 n = 71 r^2_{mand} = 0.02 n = 75
Cercopithecus pogonias	r^2_{max} = 0.06 n = 45 r^2_{mand} = 0.01 n = 57	r^2_{max} = 0.24** n = 52 r^2_{mand} = 0.02 n = 58	r^2_{max} = 0.31** n = 55 r^2_{mand} = 0.07* n = 59	r^2_{max} = 0.25** n = 53 r^2_{mand} = 0.03 n = 61
Macaca fascicularis	r^2_{max} = 0.05* n = 65 r^2_{mand} = 0.06* n = 59	r^2_{max} = 0.03 n = 69 r^2_{mand} = 0.06* n = 66	r^2_{max} = 0.04 n = 76 r^2_{mand} = 0.11* n = 75	r^2_{max} = 0.04 n = 75 r^2_{mand} = 0.06* n = 73
Colobus satanas	r^2_{max} = 0.36** n = 44 r^2_{mand} = 0.03 n = 45	r^2_{max} = 0.42*** n = 44 r^2_{mand} = 0.07 n = 45	r^2_{max} = 0.18* n = 46 r^2_{mand} = 0.10* n = 48	r^2_{max} = 0.17* n = 46 r^2_{mand} = 0.07 n = 48
Ateles geoffroyi	r^2_{max} = 0.56*** n = 50 r^2_{mand} = 0.00 n = 57	r^2_{max} = 0.41*** n = 54 r^2_{mand} = 0.32** n = 63	r^2_{max} = 0.38*** n = 60 r^2_{mand} = 0.21*** n = 62	r^2_{max} = 0.39*** n = 66 r^2_{mand} = 0.15* n = 60
Cebus libidinosus	r^2_{max} = 0.32*** n = 70 r^2_{mand} = 0.02 n = 73	r^2_{max} = 0.06* n = 75 r^2_{mand} = 0.13** n = 76	r^2_{max} = 0.09* n = 75 r^2_{mand} = 0.04 n = 85	r^2_{max} = 0.15** n = 82 r^2_{mand} = 0.05* n = 78
Weighted Anthropoid Average	r^2_{max} = 0.19 r^2_{mand} = 0.10	r^2_{max} = 0.19 r^2_{mand} = 0.13	r^2_{max} = 0.17 r^2_{mand} = 0.09	r^2_{max} = 0.17 r^2_{mand} = 0.09

postcanine size for catarrhines and 192 possible character-pairs for platyrrhines. To reduce the number of comparisons, while providing adequate representation of the pattern of covariation between incisor and postcanine size, comparisons were restricted to homologous dimensions of I1, I2, P2 (platyrrhines only), P3 (catarrhines only), P4, M1, and M2 within an arch (Tables 3.7, 3.8, 3.9, and 3.10).

For the breadths of the incisors and postcanine dentition (Tables 3.7 and 3.8), anthropoid averages range from $r^2 = 0.16–0.26$. Most estimates of r^2 are significantly different from zero (159 out of 160 estimates within species) and no estimate of covariation is negative in direction; that is, larger incisors are associated with larger premolars and molars within all species. Many r^2 estimates are significantly different from zero at $\alpha = 0.05$ (153 out 160 within species estimates) and at more restrictive values (107 out of 160 estimates are significant at $p \leq 0.01$), which reflects the large sample sizes for each character pair, as the r^2s are low in absolute value. The anthropoid averages indicate that very low to low levels of positive covariation exist between incisor and postcanine breadth.

Compared to measures of breadth, covariation among the incisor and postcanine MD lengths is weaker in strength (Tables 3.9 and 3.10). The range of anthropoid average r^2s is 0.07–0.19. As a result, fewer r^2 estimates are significantly different from zero at $\alpha = 0.05$ (117 out of 160) and far fewer are significantly different from zero at $\alpha = 0.01$ (52 out of 160) than was observed for breadths. As with the breadths of the incisors and postcanine dentition, with one exception (I_1MD-P_3Oblique in *Colobus satanas,* $r^2 = -0.01$), all estimates of incisor and postcanine MD length covariation that are not zero are positive in direction. This contrasts with the McCollum and Sharpe (2001) model, which predicts negative covariation, and the reported negative genetic correlations in Hlusko et al. (2010).

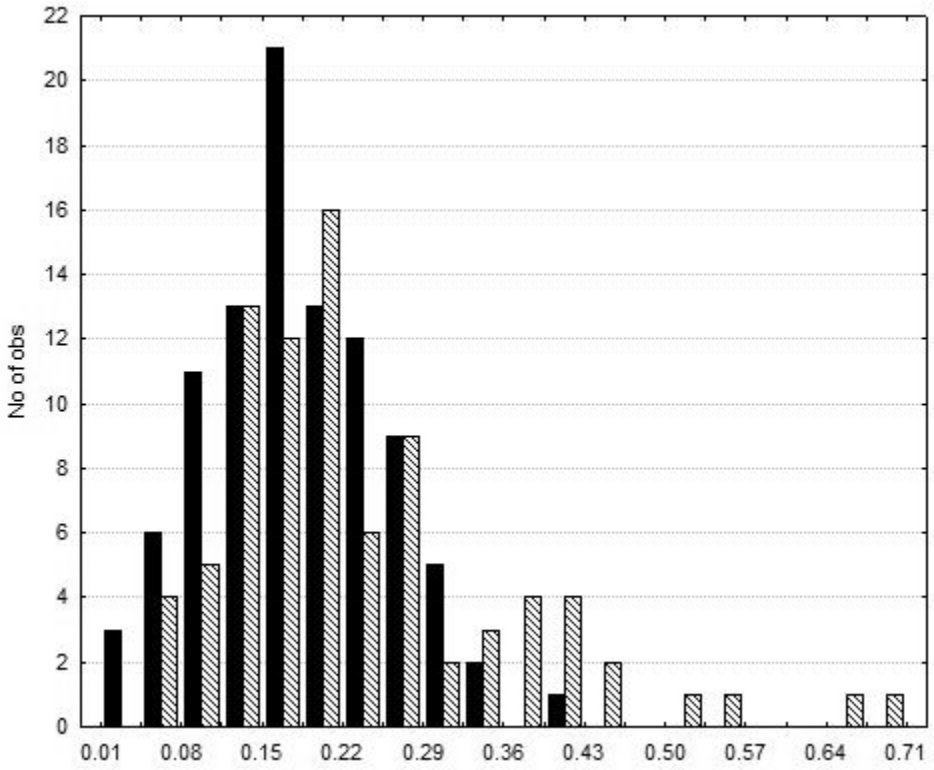

Fig. 3.2. Histogram of r^2 values for platyrrhine, cercopithecid, and hominoid average values. Values between the size of homologous dimensions of the incisors and postcanine dentitions are in black and values between all incisor sizes are in diagonal stripes.

When the r^2 values for homologous dimensions of the incisors and postcanine teeth are compared to those for all incisal pairs (Figure 3.2), incisor size consistently covaries with postcanine size at a very low to low level, similar to that observed between many comparisons of incisor size (principally comparisons between incisor MD length and LL breadth), which further supports the conclusion that the sizes of the incisors are not all tightly linked by pleiotropy. There are fifteen examples of covariation between incisor size that exceed those between the incisors and postcanine dentition: I_1LL-I_2LL, I^1LL-I^2LL, I^1LL-I_1LL, I^2LL-I_2LL, I^1LL-I_2LL, I_1LL-I^2LL, I_1MD-I_2MD, and I_1MD-I^1MD, again highlighting the nonrandom pattern of character covariation among incisor size. When the sizes of the incisors and postcanine teeth are considered, the

TABLE 3.11. The magnitude of covariation among species for incisor size, equal branch lengths. All r^2s are significantly different from zero at $p < \alpha = 0.0001$. $n = 35$ for both males and females; however, the taxonomic composition is slightly different for males and females.

	I_1LL	I_1MD	I_2LL	I_2MD	I^1LL	I^1MD	I^2LL
I_1MD	♂ $r^2 = 0.84$ ♀ $r^2 = 0.84$	—	—	—	—	—	—
I_2LL	♂ $r^2 = 0.88$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.79$ ♀ $r^2 = 0.84$	—	—	—	—	—
I_2MD	♂ $r^2 = 0.61$ ♀ $r^2 = 0.72$	♂ $r^2 = 0.82$ ♀ $r^2 = 0.81$	♂ $r^2 = 0.87$ ♀ $r^2 = 0.81$	—	—	—	—
I^1LL	♂ $r^2 = 0.88$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.78$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.82$ ♀ $r^2 = 0.81$	♂ $r^2 = 0.69$ ♀ $r^2 = 0.65$	—	—	—
I^1MD	♂ $r^2 = 0.79$ ♀ $r^2 = 0.71$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.77$ ♀ $r^2 = 0.79$	♂ $r^2 = 0.70$ ♀ $r^2 = 0.66$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.82$	—	—
I^2LL	♂ $r^2 = 0.65$ ♀ $r^2 = 0.76$	♂ $r^2 = 0.56$ ♀ $r^2 = 0.61$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.64$ ♀ $r^2 = 0.63$	♂ $r^2 = 0.66$ ♀ $r^2 = 0.65$	♂ $r^2 = 0.43$ ♀ $r^2 = 0.56$	—
I^2MD	♂ $r^2 = 0.46$ ♀ $r^2 = 0.68$	♂ $r^2 = 0.57$ ♀ $r^2 = 0.57$	♂ $r^2 = 0.57$ ♀ $r^2 = 0.69$	♂ $r^2 = 0.60$ ♀ $r^2 = 0.71$	♂ $r^2 = 0.41$ ♀ $r^2 = 0.51$	♂ $r^2 = 0.46$ ♀ $r^2 = 0.45$	♂ $r^2 = 0.66$ ♀ $r^2 = 0.45$

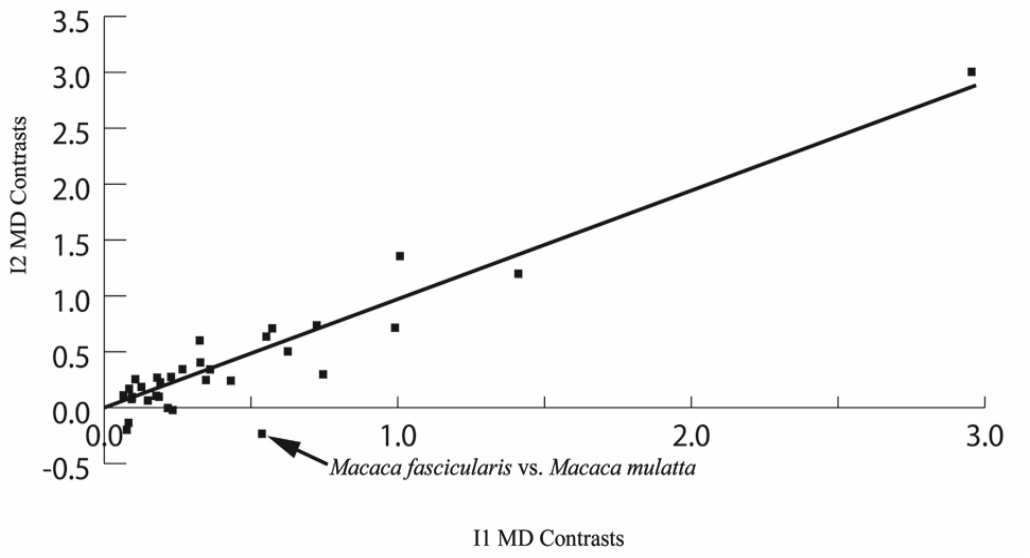

Fig. 3.3. Independent Contrasts for ♂I_1MD-I_2MD, branch lengths equal. The line represents the RMA Regression Line. The contrast with the largest residual value, between *Macaca fascicularis* and *Macaca mulatta*, is indicated with an arrow.

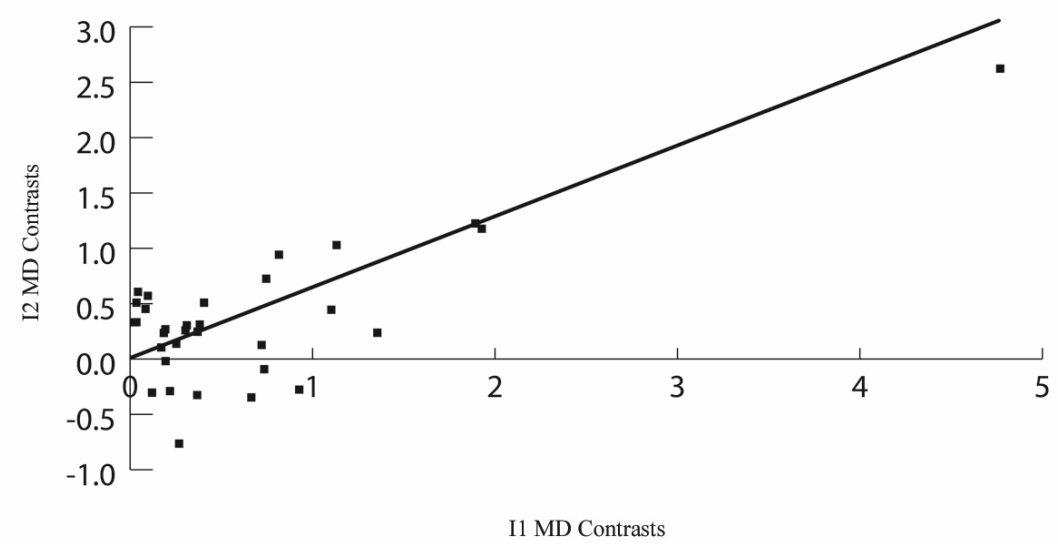

Fig. 3.4. Independent Contrasts for ♂I^1MD-I^2MD, branch lengths equal. In contrast to the relationship among mandibular incisor lengths, there is a poorer fit of the of the maxillary incisor length independent contrasts to the RMA regression line. Maxillary incisor lengths demonstrate more flexibility to evolve independently of one another among species than do the mandibular incisor lengths.

.

hypothesis of pleiotropic modularity is supported with some revision. The separation between the postcanine dentition and the incisors is not complete, as there is weak, but consistent, positive covariation between modules.

***Incisor Size Covariation Among Species*:** As reviewed in Chapter 2, both selection acting on pleiotropically linked characters and selective covariance create among-species covariation. In this section, evaluation of independent contrasts is used to determine if variation in the magnitude of covariation within species is reflected in variation in the magnitude of covariation between characters among species. Those characters that covary most strongly within species should be the most constrained (i.e., show the highest levels of among-species covariation).

All among-species r^2s for incisor size are significantly different from zero (Table 3.11). Though most r^2s are ≥ 0.65 (42 out of 56 estimates), the range of estimates is quite broad. When the male and female values are pooled to compute an average r^2 for each incisal dimension (I_1MD: 0.75, I_1LL: 0.75, I_2MD: 0.71, I_2LL: 0.80, I^1MD: 0.69, I^1LL: 0.73, I^2MD: 0.56, I^2LL: 0.64), it is evident that the I^2, the I^2MD especially, expresses the lowest level of among-species covariation. The relative independence of the I^2MD is also evidenced by the fact that of the 14 estimates of r^2 that are less than 0.65, 10 involve the I^2MD. Bivariate plots of incisor size independent contrasts highlight the weaker covariance of maxillary incisor size than mandibular incisor size (Figures 3.3 and 3.4). For example, contrasts of mandibular incisors show a single notable outlier (the contrast between *Macaca fascicularis* and *Macaca mulatta*), while the remainder of the contrasts fall near the Reduced Major Axis (RMA) regression line. The weak among-species r^2 for maxillary incisor size is not the result of outlying contrasts that leverage the model; there is simply a poorer overall correspondence of their sizes among species (Figure 3.4).

The magnitudes of among-species covariation between MD lengths and LL breadths, which do not covary strongly within species, is nearly as strong as it is for homologous dimensions that express higher levels of covariation within species. This is easily explained if natural selection has often acted to cause coordinated change in each character. Recall the multivariate selection model, $\mathbf{\Delta z = G\beta}$. Since all size covariation within species is positive, if each incisor ("*i*") experiences a β that favors change in the same direction, then the characters will coevolve regardless of their magnitude of covariation within species (as in Figure 1.7). What the among-species analysis of incisor size shows is that in most cases each dimension of the incisors has experienced a β_i that favored change in the same direction. However, as the large contrasts for I^2MD length indicate, characters that covary weakly within species retain substantial ability to change independently of one another. As a result, the most weakly covarying character pairs within species are also the most weakly covarying among species and, conversely, the most strongly covarying character pairs within species are the mostly strongly covarying among species. However, it is evident that there is no simple relationship between the magnitudes of within- and among-species covariation. The high level of covariation among species for character pairs that demonstrate low levels of within-species covariation suggests that it is unwise to assume tight pleiotropic linkages for characters that have coevolved. This finding will be discussed below in relation to among-species covariation in incisor and postcanine size and further elaborated in Chapter 7.

Incisor-Postcanine Size Covariation Among Species: Within species, it was shown that homologous dimensions of the incisors and postcanine dentition express statistically significant, but very low to low levels of covariation (Tables 3.7–3.10). Furthermore, within-species levels of covariation between incisor and postcanine size are similar to

TABLE 3.12. The magnitude of among-species covariation for incisor and postcanine size, equal branch lengths. All r^2s are significantly different from zero at $p < \alpha = 0.001$. n = 35 taxa for all independent contrasts.

	I_1MD	I_1LL	I_2MD	I_2LL
P_4MD	♂r^2 = 0.46 ♀r^2 = 0.43	♂r^2 = 0.49 ♀r^2 = 0.47	♂r^2 = 0.38 ♀r^2 = 0.31	♂r^2 = 0.60 ♀r^2 = 0.53
P_4BL	♂r^2 = 0.56 ♀r^2 = 0.57	♂r^2 = 0.58 ♀r^2 = 0.56	♂r^2 = 0.51 ♀r^2 = 0.47	♂r^2 = 0.72 ♀r^2 = 0.68
M_1MD	♂r^2 = 0.43 ♀r^2 = 0.42	♂r^2 = 0.47 ♀r^2 = 0.49	♂r^2 = 0.40 ♀r^2 = 0.35	♂r^2 = 0.62 ♀r^2 = 0.56
M_1BL	♂r^2 = 0.54 ♀r^2 = 0.54	♂r^2 = 0.55 ♀r^2 = 0.57	♂r^2 = 0.52 ♀r^2 = 0.45	♂r^2 = 0.71 ♀r^2 = 0.67
M_2MD	♂r^2 = 0.33 ♀r^2 = 0.30	♂r^2 = 0.38 ♀r^2 = 0.37	♂r^2 = 0.29 ♀r^2 = 0.23	♂r^2 = 0.51 ♀r^2 = 0.42
M_2BL	♂r^2 = 0.52 ♀r^2 = 0.48	♂r^2 = 0.57 ♀r^2 = 0.50	♂r^2 = 0.49 ♀r^2 = 0.36	♂r^2 = 0.71 ♀r^2 = 0.59
M_3MD	♂r^2 = 0.26 ♀r^2 = 0.24	♂r^2 = 0.31 ♀r^2 = 0.30	♂r^2 = 0.21 ♀r^2 = 0.17	♂r^2 = 0.39 ♀r^2 = 0.30
M_3BL	♂r^2 = 0.43 ♀r^2 = 0.45	♂r^2 = 0.48 ♀r^2 = 0.47	♂r^2 = 0.41 ♀r^2 = 0.33	♂r^2 = 0.64 ♀r^2 = 0.57
Average	r^2 = 0.44	r^2 = 0.47	r^2 = 0.37	r^2 = 0.58

	I^1MD	I^1LL	I^2MD	I^2LL
P^4MD	♂r^2 = 0.52 ♀r^2 = 0.54	♂r^2 = 0.48 ♀r^2 = 0.51	♂r^2 = 0.45 ♀r^2 = 0.39	♂r^2 = 0.64 ♀r^2 = 0.49
P^4BL	♂r^2 = 0.63 ♀r^2 = 0.59	♂r^2 = 0.64 ♀r^2 = 0.55	♂r^2 = 0.52 ♀r^2 = 0.40	♂r^2 = 0.71 ♀r^2 = 0.53
M^1MD	♂r^2 = 0.47 ♀r^2 = 0.46	♂r^2 = 0.45 ♀r^2 = 0.43	♂r^2 = 0.40 ♀r^2 = 0.38	♂r^2 = 0.63 ♀r^2 = 0.49
M^1BL	♂r^2 = 0.49 ♀r^2 = 0.49	♂r^2 = 0.47 ♀r^2 = 0.47	♂r^2 = 0.46 ♀r^2 = 0.44	♂r^2 = 0.58 ♀r^2 = 0.46
M^2MD	♂r^2 = 0.39 ♀r^2 = 0.28	♂r^2 = 0.30 ♀r^2 = 0.27	♂r^2 = 0.28 ♀r^2 = 0.22	♂r^2 = 0.48 ♀r^2 = 0.33
M^2BL	♂r^2 = 0.50 ♀r^2 = 0.45	♂r^2 = 0.46 ♀r^2 = 0.40	♂r^2 = 0.43 ♀r^2 = 0.34	♂r^2 = 0.55 ♀r^2 = 0.39
M^3MD	♂r^2 = 0.25 ♀r^2 = 0.25	♂r^2 = 0.23 ♀r^2 = 0.25	♂r^2 = 0.27 ♀r^2 = 0.17	♂r^2 = 0.43 ♀r^2 = 0.29
M^3BL	♂r^2 = 0.43 ♀r^2 = 0.41	♂r^2 = 0.42 ♀r^2 = 0.39	♂r^2 = 0.41 ♀r^2 = 0.31	♂r^2 = 0.54 ♀r^2 = 0.38
Average	r^2 = 0.45	r^2 = 0.42	r^2 = 0.37	r^2 = 0.50

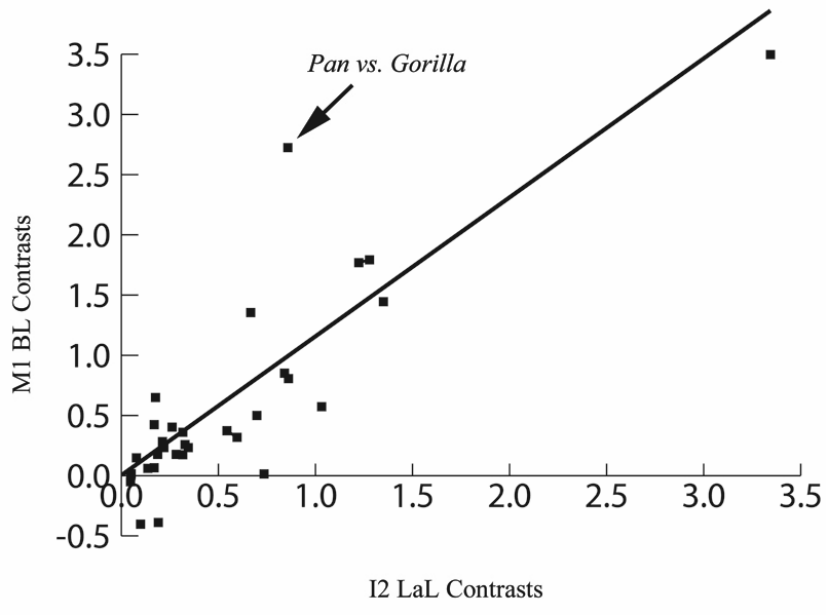

Fig. 3.5. Independent contrasts between I_2LL and M_1BL. The largest contrast, between *Pan* and *Gorilla*, is indicated with an arrow.

those between the MD length and LL breadth of incisor pairs, which suggests that the incisors and postcanine teeth have weak, overlapping pleiotropic effects.

Among-species covariation between incisor and postcanine tooth size is always significantly different from zero (even at restrictive α levels) and positive in direction (Table 3.12). Average among-species r^2s for incisor-postcanine size range between r^2 = 0.37–0.58, which is lower than estimates for incisor pairs (except for some comparisons of I^2 size) (Table 3.11). As Figure 3.5 shows, there is a strong association among species for some incisor and postcanine dimensions. At a broad level, incisor and postcanine sizes covary, but there is little to suggest that the sizes of the incisors and postcanine teeth are considerably constrained to evolve in a single direction. For example, in Figure 3.5 the largest outlying contrast is between *Pan* and *Gorilla*, where the M_1BL size difference between them is greater than expected for their I_2LL difference (relative to M_1BL, the

Pan I_2 is broader), indicating that incisor and postcanine size can change independently of one another even between closely related species.

In summary, as all among-species correlations between incisor and postcanine size are statistically significant and positive in direction. The Jolly (1970) and McCollum and Sharpe (2001) hypotheses that predict trade-offs in anterior and posterior tooth size are rejected. There is no evidence that the negative genetic correlation among incisor and postcanine size reported in SNPRC baboons played an "important" role (Hlusko et al., 2010: 46) in channeling the among-species evolution of incisor and postcanine tooth size. This does not indicate that there was not a selective tradeoff between the anterior and posterior teeth in some hominin species, only that is was not mediated by pleiotropy.

Incisor Shape Covariation Within Species: As anthropoid taxa vary in the shape of their incisors, incisor shape covariation was also investigated within and among species. Levels of incisor shape covariation do not approach the highest levels observed for incisor size (Tables 3.13 and 3.14). For size, the highest levels of covariation are between the mandibular incisors; not surprisingly, the shapes of the mandibular incisors are shown to covary significantly, while all other incisor pairs do not. For both the LL breadths and MD lengths, cercopithecid mandibular incisors do not covary as strongly as do hominoids and platyrrhines (especially true for MD lengths). Expectedly, moderate covariation between mandibular incisor shapes is seen in hominoids (average $r^2 = 0.42$) and platyrrhines (average $r^2 = 0.46$), but not in cercopithecids (average $r^2 = 0.18$). As will be discussed, the hominoid and platyrrhine taxa examined in this study are characterized by homomorphic mandibular incisors, while the cercopithecid mandibular incisors are heteromorphic. As for incisor size covariation, the discrepancy in incisor shape covariation observed between taxa suggests that if cercopithecid incisor morphology

*TABLE 3.13. The magnitude of covariation among incisor shapes (*** p-value < 0.0001, ** p-value < 0.001, * p-value < 0.05).*

	I_1-I_2	I^1-I^2	I_1-I^1
Gorilla gorilla	$r^2 = 0.40$*** $n = 50$	$r^2 = 0.04$ $n = 53$	$r^2 = 0.23$* $n = 50$
Pan troglodytes	$r^2 = 0.41$*** $n = 70$	$r^2 = 0.25$*** $n = 62$	$r^2 = 0.17$*** $n = 67$
Hylobates lar	$r^2 = 0.45$*** $n = 63$	$r^2 = 0.00$ $n = 30$	$r^2 = 0.07$ $n = 38$
Cercopithecus cephus	$r^2 = 0.19$* $n = 69$	$r^2 = -0.01$ $n = 61$	$r^2 = 0.15$*** $n = 62$
Cercopithecus nictitans	$r^2 = 0.20$*** $n = 70$	$r^2 = 0.11$* $n = 59$	$r^2 = 0.08$* $n = 60$
Cercopithecus grayi	$r^2 = 0.14$* $n = 48$	$r^2 = 0.08$ $n = 43$	$r^2 = 0.05$ $n = 39$
Macaca fascicularis	$r^2 = 0.31$*** $n = 63$	$r^2 = 0.13$** $n = 58$	$r^2 = 0.26$*** $n = 50$
Colobus satanas	$r^2 = 0.04$ $n = 44$	$r^2 = 0.04$ $n = 43$	$r^2 = 0.04$ $n = 46$
Ateles geoffroyi	$r^2 = 0.58$*** $n = 62$	$r^2 = 0.04$ $n = 54$	$r^2 = 0.06$ $n = 55$
Cebus libidinosus	$r^2 = 0.34$*** $n = 67$	$r^2 = 0.07$* $n = 81$	$r^2 = 0.08$* $n = 68$
Weighted Anthropoid Average	$r^2 = 0.31$	$r^2 = 0.08$	$r^2 = 0.12$
Weighted Hominoid Average	$r^2 = 0.42$	$r^2 = 0.10$	$r^2 = 0.16$
Weighted Cercopithecid Average	$r^2 = 0.18$	$r^2 = 0.07$	$r^2 = 0.12$
Weighted Platyrrhine Average	$r^2 = 0.46$	$r^2 = 0.06$	$r^2 = 0.07$
Significantly different from zero ($p < \alpha = 0.01$)	7/10	2/10	3/10

*TABLE 3.14. The magnitude of covariation among incisor shapes (*** p-value < 0.0001, ** p-value < 0.001, * p-value < 0.05).*

	I_1-I^2	I_2-I^1	I_2-I^2
Gorilla gorilla	$r^2 = 0.17$* $n = 46$	$r^2 = 0.00$ $n = 51$	$r^2 = 0.39$*** $n = 51$
Pan troglodytes	$r^2 = 0.21$*** $n = 62$	$r^2 = 0.26$*** $n = 65$	$r^2 = 0.10$* $n = 66$
Hylobates lar	$r^2 = 0.00$ $n = 45$	$r^2 = 0.04$ $n = 40$	$r^2 = 0.00$ $n = 48$
Cercopithecus cephus	$r^2 = 0.00$ $n = 59$	$r^2 = 0.05$* $n = 67$	$r^2 = 0.02$ $n = 35$
Cercopithecus nictitans	$r^2 = 0.25$*** $n = 63$	$r^2 = 0.07$* $n = 63$	$r^2 = 0.15$* $n = 68$
Cercopithecus	$r^2 = 0.00$ $n = 45$	$r^2 = 0.06$ $n = 43$	$r^2 = 0.00$ $n = 51$
Macaca fascicularis	$r^2 = 0.08$ $n = 60$	$r^2 = 0.16$* $n = 52$	$r^2 = 0.21$** $n = 63$
Colobus satanas	$r^2 = 0.04$ $n = 43$	$r^2 = 0.03$ $n = 43$	$r^2 = 0.00$ $n = 44$
Ateles geoffroyi	$r^2 = 0.03$ $n = 56$	$r^2 = 0.06$ $n = 56$	$r^2 = 0.00$ $n = 55$
Cebus libidinosus	$r^2 = 0.07$* $n = 64$	$r^2 = 0.12$* $n = 84$	$r^2 = 0.08$* $n = 82$
Weighted Anthropoid Average	$r^2 = 0.09$	$r^2 = 0.08$	$r^2 = 0.10$
Weighted Hominoid Average	$r^2 = 0.13$	$r^2 = 0.10$	$r^2 = 0.16$
Weighted Cercopithecid Average	$r^2 = 0.08$	$r^2 = 0.09$	$r^2 = 0.10$
Weighted Platyrrhine Average	$r^2 = 0.05$	$r^2 = 0.09$	$r^2 = 0.04$
Significantly different from zero ($p < \alpha = 0.01$)	2/10	1/10	2/10

evolved from a platyrrhine- or hominoid-like condition, then the pattern and strength of pleiotropy was altered to parcel out the mandibular lateral incisor from that of the mandibular central incisor (as in Figure 1.1). In line with observations of maxillary incisor size covariation, the maxillary incisors covary more weakly in shape than do the mandibular. Measures of shape incorporate measurement error in both the MD and LL dimensions, so some diminution of the estimated strength of shape covariation from its true population value is likely, as an estimate of r^2 is affected by the measurement error of four dimensions (2 for each incisor); however, the difference in the magnitudes of covariation between mandibular and maxillary incisors cannot be explained as a result of measurement error. In summary, for shapes, it is only the mandibular incisors of platyrrhines and hominoids that share substantial variation in shape. All other pairs of incisor shapes vary independently of one another.

Incisor Shape Among Species: For incisor size, all among-species r^2s exceeded their values within species; all incisor dimensions were shown to covary strongly among species. In contrast, there is far less evidence that incisor shapes have coevolved (Table 3.17). As was true of levels of incisor shape covariation within species, the highest level of among-species covariation is for the shapes of the mandibular incisors, but even this is quite (unexpectedly) low. The low level of among-species covariation for mandibular incisor shape largely results from the presence of large outlying contrasts (Figure 3.7). The large contrasts for mandibular incisor shape capture well established differences in incisor morphology. For example, the *Pan* I_2 is much longer MD, relative to the LL breadth, than is the *Gorilla* I_2 (Kelley et al., 1995; Pickford, 2005), so that large contrast is easily explained. In addition, the contrast between incisor shapes in *Callicebus* and *Pithecia* likely relate to functional differences in the use of the pitheciine incisors in

*TABLE 3.17. The magnitude of incisor shape covariation among species, equal branch lengths. (*** p-value < 0.0001, ** p-value < 0.001, * p-value < 0.05). n = 34 taxa for all comparisons.*

	I_1	I_2	I^1
I_2	$r^2 = 0.23$***	—	—
I^1	$r^2 = 0.21$	$r^2 = 0.06$*	—
I^2	$r^2 = 0.00$	$r^2 = 0.06$*	$r^2 = 0.07$

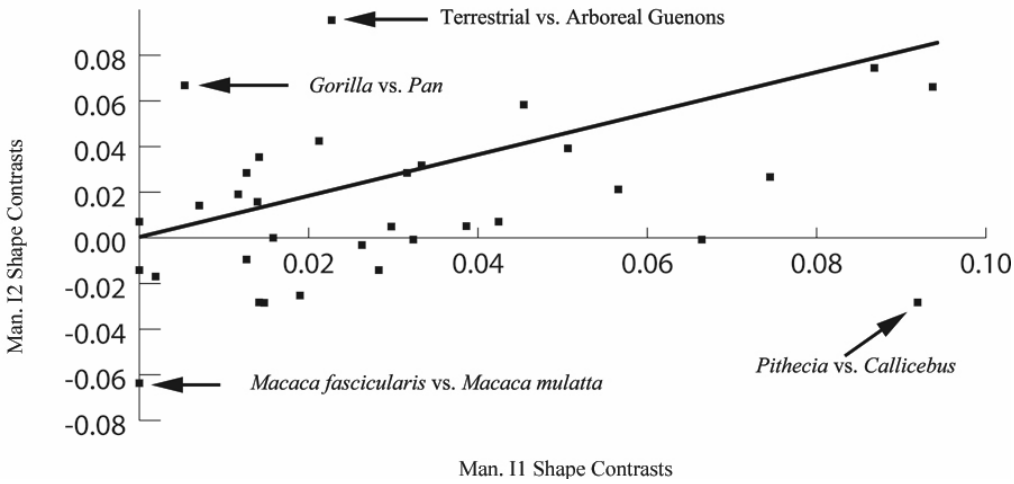

Fig 3.7. Independent Contrasts for mandibular incisor shape, branch lengths equal. The line represents the Reduced Major Axis Regression Line. The contrasts with the largest residual values are indicated with arrows.

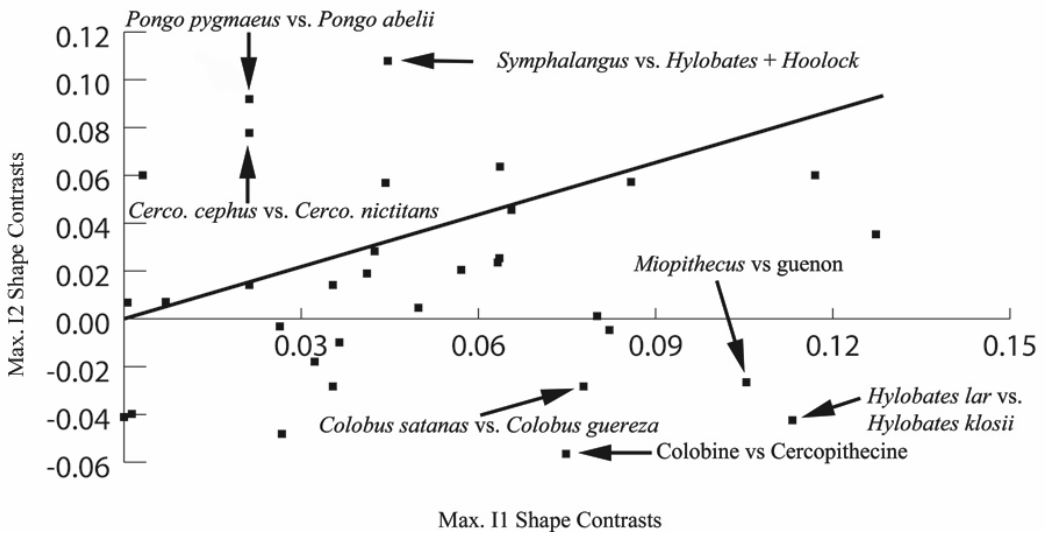

Fig. 3.8. Independent Contrasts for maxillary incisor shape, branch lengths equal. The line represents the Reduced Major Axis Regression Line. Notably large contrasts are highlighted.

gouging and husking behaviors, which are absent in *Callicebus* (Kinzey, 1992; Rosenberger, 1992). The contrast between *Macaca fascicularis* and *Macaca mulatta* is more difficult to explain. *Macaca mulatta* is not numerically well represented in this study, but this contrast is not due to error associated with small sample size, as the same dichotomy in shapes is also evident in the larger sample published in Plavcan (1990). The low level of covariation between maxillary incisor shapes (Figure 3.8) results from the combination of a low overall correspondence in shape among species and the presence of many large outlying contrasts. These large contrasts include intrageneric contrasts (*Cercopithecus nictitans* vs. *Cercopithecus cephus*, *Colobus guereza* vs. *Colobus satanas*, *Pongo pygmaeus* vs. *Pongo abelii*, *Hylobates lar* vs. *Hylobates klossii*), which are not obviously associated with any dietary differences, and contrasts between deeper nodes (*Miopithecus* vs. guenons, colobine vs. cercopithecine, *Symphalangus* vs. other hylobatids), which may reflect dietary differences. Among species, the shapes of the

incisors do not covary strongly. The shapes of the mandibular incisors express moderate levels of among-species covariation, while the maxillary incisors do not.

Discussion and Summary

For certain incisal dimensions, covariation is strong within and among species. Covariation is weak between the incisors and postcanine teeth within species. The hypothesis of variational modularity is supported for the incisors; however, it is evident that the strength of covariation is highly variable among character pairs. For incisor size, MD and LL dimensions do not strongly covary within species; however, homologous dimensions (with the exception of I^2MD) covary strongly with one another. Levels of size covariation are generally higher between homologous mandibular dimensions than between homologous maxillary dimensions and, for both sets of characters, covariation is generally lower in cercopithecids than in hominoids and platyrrhines. Among all anthropoids, the maxillary incisors are more heteromorphic in size and shape than are the mandibular and, among species, the cercopithecid mandibular incisors are more heteromorphic than are their platyrrhine and hominoid counterparts (personal observation). The lower levels of covariation among maxillary incisors than among mandibular incisors and the lower levels of cercopithecid incisor covariation compared to hominoids and platyrrhines capture these differences in heteromorphy. Covariation is expected to channel among species change and to facilitate the rapid response of functionally linked characters to changing environmental conditions (e.g., Marroig and Cheverud, 2010). The analyses of incisor size and shape indicate that there is considerable "flexibility" (e.g., Marroig et al., 2009) in the system, which allows incisal characters to change independently of one another (especially so for maxillary incisor size and shape). The analyses of independent contrasts indicate that there are multiple

adaptive combinations of size and shape, which is to say that $\mathbf{p}_{max}$ among incisor traits is often not aligned with fitness peaks on an adaptive landscape (Arnold et al., 2001), which will be addressed in Chapter 6.

The separation of incisor and postcanine size is not complete. The highest levels of within-species covariation between incisor and postcanine size do not, however, approach the highest levels among homologous incisor dimensions. Low levels of positive covariation characterize the incisors and postcanine teeth within species (*contra* Jolly, 1970; McCollum and Sharpe, 2001; Hlusko et al., 2010) and moderate levels of covariation were observed among species. This positive correlation among species did not result from selection acting on characters strongly linked by pleiotropy and is best explained as an example of selective covariance (Chapter 1; Figure 1.7). Jolly (1970) hypothesized the within species relationship between incisor and postcanine size from two convergent cases of incisal reduction and postcanine enlargement (*Theropithecus* and *Australopithecus/Paranthropus*) that occurred during the Plio-Pliestocene. The general trend among anthropoids is for larger incisors to be associated with larger postcanine teeth. That characters that covary weakly within species routinely express moderate covariation among species indicates that the pattern and magnitude of within-species covariation cannot be accurately predicted from an examination of among-species patterns.

The McCollum and Sharpe (2001) model is based on a hypothetical developmental relationship, which has limited empirical support (Hlusko et al., 2010). The contrast with the direction of covariation observed in Hlusko et al. (2010) is not easily dismissed, but it bears noting that estimates of incisor and postcanine genetic correlations in the same sample published only one year earlier (Hlusko and Mahaney, 2009) presented only positive genetic correlations between incisor and postcanine size.

Why the captive SNPRC baboons are anomalous in their pattern relative to all wild populations examined in this study is unknown.

The incisors and postcanine teeth perform different functions and are not united by strong covariation. Selection has been free to act upon the abundant independent phenotypic variance in each functional unit. Any change in absolute or relative size that occurred during hominin evolution should be considered independent changes.

Chapter 4

POSTCANINE MODULARITY

In this chapter, two hypotheses are tested. The postcanine teeth are hypothesized to form a variational module. If this hypothesis is true then the postcanine teeth will covary strongly within and among species (calculated using phenotypic r^2s within species and r^2s of independent contrasts among species) and covariation with characters outside of the module will be weak (i.e., r^2 nearly zero). This hypothesis will be rejected if covariation among postcanine dimensions is weak or if it is nearly equal in magnitude with that of the other functional modules. Second, the hypothesis that the postcanine dentition is divisible into two subunits (the premolars and molars) is tested. If the hypothesis is true, then partial correlations of premolar size, with molar size held constant, will be significantly different from zero. If no partial correlation remains among premolars after accounting for molar size, then this hypothesis will be rejected. The relationship between the strength of constraint and flexibility is informally investigated by comparing the magnitudes of covariation within species to that among species. The similarity of postcanine $\mathbf{p}_{max}$ among species and the correspondence of $\mathbf{\Delta z}$ and $\mathbf{p}_{max}$ are investigated in Chapter 6 for a subset of species.

Results

***Covariation of Premolar Size Within Species*:** As described in Chapter 1, the mandibular premolars are distinctive morphologically and functionally (Figure 1.12). Here, two measures of the honing premolar (oblique length and breadth perpendicular to the oblique axis across the protoconid) are considered, while MD length and BL breadth are

*TABLE 4.1. The magnitude of covariation for the length and breadth of each catarrhine premolar (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_3Oblique-P_3BL	P_4MD-P_4BL	P^3MD-P^3BL	P^4MD-P^4BL
Gorilla gorilla	r^2 = 0.46*** n = 102	r^2 = 0.25*** n = 118	r^2 = 0.08* n = 97	r^2 = 0.33*** n = 119
Pan troglodytes	r^2 = 0.14** n = 93	r^2 = 0.13*** n = 95	r^2 = 0.03 n = 85	r^2 = 0.33*** n = 93
Hylobates lar	r^2 = 0.24*** n = 62	r^2 = 0.32*** n = 74	r^2 = 0.25* n = 39	r^2 = 0.46*** n = 75
Cercopithecus cephus	r^2 = 0.21*** n = 78	r^2 = 0.22*** n = 81	r^2 = 0.38*** n = 64	r^2 = 0.21*** n = 81
Cercopithecus nictitans	r^2 = 0.33*** n = 78	r^2 = 0.16*** n = 80	r^2 = 0.10* n = 65	r^2 = 0.20*** n = 83
Cercopithecus pogonias	r^2 = 0.17*** n = 66	r^2 = 0.25*** n = 68	r^2 = 0.21*** n = 57	r^2 = 0.19*** n = 68
Macaca fascicularis	r^2 = 0.33*** n = 77	r^2 = 0.34*** n = 83	r^2 = 0.13* n = 71	r^2 = 0.32*** n = 80
Colobus satanas	r^2 = 0.17* n = 46	r^2 = 0.26* n = 46	r^2 = 0.12* n = 47	r^2 = 0.08 n = 47
Weighted Catarrhine Average	r^2 = 0.27	r^2 = 0.24	r^2 = 0.15	r^2 = 0.28
Weighted Hominoid Average	r^2 = 0.29	r^2 = 0.23	r^2 = 0.12	r^2 = 0.37
Weighted Cercopithecid Average	r^2 = 0.25	r^2 = 0.25	r^2 = 0.19	r^2 = 0.21
Significantly different from zero ($p < \alpha = 0.01$)	7/8	7/8	2/8	7/8

considered for all other premolars (Table 2.2 and Figure 2.1). Given that platyrrhines and catarrhines differ in premolar number and that the honing premolar is adjacent to the P_4in catarrhines but spatially separated from the P_4 in platyrrhines, it is inappropriate to directly compare patterns of covariation between these groups; therefore, results are presented separately for each anthropoid infraorder.

Statistically significant, but low to very low magnitude, positive covariation characterizes the MD length and BL breadth of each premolar. In catarrhines, the MD length and BL breadth of the P_4, P_3, and P^4 express low average levels of covariation (r^2 =

*TABLE 4.2. The magnitude of covariation for the length and breadth of each platyrrhine premolar (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_2Oblique-P_2BL	P_3MD-P_3BL	P_4MD-P_4BL
Ateles geoffroyi	$r^2 = 0.62$*** $n = 61$	$r^2 = 0.29$** $n = 57$	$r^2 = 0.34$** $n = 60$
Cebus libidinosus	$r^2 = 0.08$* $n = 75$	$r^2 = 0.07$ $n = 73$	$r^2 = 0.29$*** $n = 75$
Weighted Platyrrhine Average	$r^2 = 0.32$	$r^2 = 0.17$	$r^2 = 0.31$

	P^2MD-P^2BL	P^3MD-P^3BL	P^4MD-P^4BL
Ateles geoffroyi	$r^2 = 0.50$*** $n = 53$	$r^2 = 0.19$*** $n = 58$	$r^2 = 0.16$** $n = 59$
Cebus libidinosus	$r^2 = 0.01$ $n = 72$	$r^2 = 0.06$* $n = 78$	$r^2 = 0.10$** $n = 77$
Weighted Platyrrhine Average	$r^2 = 0.22$	$r^2 = 0.12$	$r^2 = 0.13$

0.24–0.28); for the catarrhine P^3, the level is very low (average $r^2 = 0.15$) (Table 4.1). With a few exceptions (relatively high estimate for P_3Oblique-P_3BL in *Gorilla gorilla*, relatively high estimate for P^4MD-P^4BL in *Hylobates lar*, and relatively low estimate for P^4MD-P^4BL in *Colobus satanas*), there is little variation in the magnitude of estimates among catarrhine taxa and no obvious distinctions in strength between cercopithecids and hominoids (Table 4.1).

For platyrrhines, the range of r^2s is broader (average $r^2 = 0.12$–0.32) and three premolars (P_3, P^3, and P^4) have an average $r^2 < 0.20$ (Table 4.2). There is a considerable difference in the magnitude of covariation within the P2s in *Ateles geoffroyi* and *Cebus libidinosus*. The mesial premolars of *Ateles geoffroyi* have r^2s ≥ 0.50, while in *Cebus libidinosus* the values are < 0.10. This discrepancy is not easily explained, as an investigation of the data reveals that estimates of r^2 are not influenced by outlying measurements.

TABLE 4.3. The average magnitude of covariation among premolar breadths and lengths.

	P^3BL-P^4MD	P^3BL-P_4MD	P^3BL-P_3oblique	P^4BL-P^3MD	P^4BL-P_4MD
Weighted Hominoid Average	$r^2 = 0.24$	$r^2 = 0.14$	$r^2 = 0.29$	$r^2 = 0.23$	$r^2 = 0.23$
Weighted Cercopithecid Average	$r^2 = 0.18$	$r^2 = 0.17$	$r^2 = 0.22$	$r^2 = 0.16$	$r^2 = 0.31$
Weighted Catarrhine Average	$r^2 = 0.21$	$r^2 = 0.15$	$r^2 = 0.25$	$r^2 = 0.19$	$r^2 = 0.28$
Significantly different from zero ($p < \alpha = 0.01$)	7/8	7/8	8/8	6/8	8/8

	P^4BL-P_3oblique	P_4BL-P^3MD	P_4BL-P^4MD	P_4BL-P_3oblique
Weighted Hominoid Average	$r^2 = 0.25$	$r^2 = 0.24$	$r^2 = 0.33$	$r^2 = 0.28$
Weighted Cercopithecid Average	$r^2 = 0.15$	$r^2 = 0.15$	$r^2 = 0.28$	$r^2 = 0.16$
Weighted Catarrhine Average	$r^2 = 0.19$	$r^2 = 0.19$	$r^2 = 0.30$	$r^2 = 0.21$
Significantly different from zero ($p < \alpha = 0.01$)	6/8	6/8	8/8	7/8

	P^2BL-P_2Oblique	P^2BL-P_3MD	P^2BL-P_4MD	P^2BL-P^3MD	P^2BL-P^4MD
Weighted Platyrrhine Average	$r^2 = 0.14$	$r^2 = 0.13$	$r^2 = 0.17$	$r^2 = 0.13$	$r^2 = 0.16$
Significantly different from zero ($p < \alpha = 0.01$)	1/2	½	1/2	1/2	2/2

	P^3BL-P_2Oblique	P^3BL-P_3MD	P^3BL-P_4MD	P^3BL-P^2MD	P^3BL-P^4MD
Weighted Platyrrhine Average	$r^2 = 0.23$	$r^2 = 0.20$	$r^2 = 0.20$	$r^2 = 0.18$	$r^2 = 0.13$
Significantly different from zero ($p < \alpha = 0.01$)	2/2	2/2	2/2	1/2	2/2

	P^4BL-P_2Oblique	P^4BL-P_3MD	P^4BL-P_4MD	P^4BL-P^2MD	P^4BL-P^3MD
Weighted Platyrrhine Average	$r^2 = 0.17$	$r^2 = 0.13$	$r^2 = 0.20$	$r^2 = 0.12$	$r^2 = 0.06$
Significantly different from zero ($p < \alpha = 0.01$)	2/2	½	2/2	1/2	0/2

	P_2BL-P_3MD	P_2BL-P_4MD	P_2BL-P^2MD	P_2BL-P^3MD	P_2BL-P^4MD
Weighted Platyrrhine Average	$r^2 = 0.09$	$r^2 = 0.07$	$r^2 = 0.14$	$r^2 = 0.13$	$r^2 = 0.12$
Significantly different from zero ($p < \alpha = 0.01$)	1/2	0/2	2/2	1/2	2/2

(cont.)

TABLE 4.3 continued.

	P_3BL-P_2Oblique	P_3BL-P_4MD	P_3BL-P^2MD	P_3BL-P^3MD	P_3BL-P^4MD
Weighted Platyrrhine Average	$r^2 = 0.20$	$r^2 = 0.16$	$r^2 = 0.19$	$r^2 = 0.15$	$r^2 = 0.18$
Significantly different from zero ($p < \alpha = 0.01$)	2/2	½	2/2	2/2	2/2

	P_4BL-P_2Oblique	P_4BL-P_3MD	P_4BL-P^2MD	P_4BL-P^3MD	P_4BL-P^4MD
Weighted Platyrrhine Average	$r^2 = 0.23$	$r^2 = 0.18$	$r^2 = 0.15$	$r^2 = 0.27$	$r^2 = 0.22$
Significantly different from zero ($p < \alpha = 0.01$)	2/2	2/2	1/2	2/2	2/2

In Chapter 3, it was found that incisor MD and LL dimensions covary weakly within an incisor (the anthropoid averages for each incisor are $r^2 = 0.15$–0.23 (Table 3.1)). Similarly, premolar lengths and breadths do not express substantial levels of covariation. The range of catarrhine and platyrrhine premolar average r^2s largely overlaps, but is sometimes slightly higher than what was observed for the incisors.

Premolar length and breadth are not only mostly independent within a premolar, but also among them (Table 4.3). Though very low and low in absolute value, for both platyrrhines and catarrhines, covariation between premolar MD length and BL breadth is always positive in direction and often significantly different from zero at $\alpha = 0.05$. Within catarrhines, the average level of covariation for MD length-BL breadth ranges from very low ($r^2 = 0.15$ for P^3BL-P_4MD) to low ($r^2 = 0.30$ for P_4BL-P^4MD). The levels observed in cercopithecids and hominoids are similar, though the hominoid average is higher for seven out of nine pairs of measurements. For platyrrhines, length and breadth among premolars have r^2 estimates that range from very low ($r^2 = 0.08$ for P^4BL-P^3MD) to low ($r^2 = 0.39$ for P_3BL-P_2Oblique). Eighteen out of 30 platyrrhine pairings have an $r^2 \leq 0.25$. As for the MD and BL dimensions of each premolar, the highest platyrrhine r^2s are for

*TABLE 4.4. The magnitude of covariation among catarrhine premolar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_3Oblique-P_4MD	P^3MD-P^4MD	P_3Oblique-P^3MD	P_4MD-P^4MD
Gorilla gorilla	r^2 = 0.26*** n = 100	r^2 = 0.48*** n = 93	r^2 = 0.21*** n = 85	r^2 = 0.54*** n = 119
Pan troglodytes	r^2 = 0.31*** n = 89	r^2 = 0.26*** n = 81	r^2 = 0.24*** n = 78	r^2 = 0.59*** n = 87
Hylobates lar	r^2 = 0.26*** n = 62	r^2 = 0.35** n = 40	r^2 = 0.38*** n = 35	r^2 = 0.48*** n = 68
Cercopithecus cephus	r^2 = 0.17*** n = 80	r^2 = 0.48*** n = 64	r^2 = 0.20*** n = 63	r^2 = 0.59*** n = 81
Cercopithecus nictitans	r^2 = 0.33*** n = 79	r^2 = 0.36*** n = 65	r^2 = 0.10* n = 62	r^2 = 0.56*** n = 81
Cercopithecus pogonias	r^2 = 0.11* n = 67	r^2 = 0.38*** n = 57	r^2 = 0.16** n = 56	r^2 = 0.63*** n = 66
Macaca fascicularis	r^2 = 0.23*** n = 75	r^2 = 0.35*** n = 70	r^2 = 0.07 n = 61	r^2 = 0.64*** n = 77
Colobus satanas	r^2 = 0.19* n = 46	r^2 = 0.35* n = 47	r^2 = 0.22* n = 46	r^2 = 0.29* n = 46
Weighted Catarrhine Average	r^2 = 0.24	r^2 = 0.38	r^2 = 0.19	r^2 = 0.55
Weighted Hominoid Average	r^2 = 0.28	r^2 = 0.37	r^2 = 0.25	r^2 = 0.54
Weighted Cercopithecid Average	r^2 = 0.21	r^2 = 0.39	r^2 = 0.15	r^2 = 0.56
Significantly different from zero ($p < \alpha = 0.01$)	6/8	7/8	5/8	7/8

comparisons with either P_2Oblique length or P_2BL breadth and, again, this is driven by a distinction between the values observed in *Ateles geoffroyi*, where the r^2 estimates are high, and *Cebus libidinosu*s, where the estimates are very low in absolute value and not significantly different from zero. The data indicate that the difference between the taxa is not due to the presence of outliers or levers in either taxon. It is unclear whether or not the difference in strength between these two taxa reflects underlying biological differences, or if the discrepancy is merely due to stochastic effects associated with data collection. Other *Ateles* and *Cebus* species should be examined to determine if these values are typical of their respective genera.

*TABLE 4.5. The magnitude of covariation among platyrrhine premolar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_2Oblique-P_3MD	P_2Oblique-P_4MD	P_2Oblique-P^2MD	P_2Oblique-P^3MD
Ateles geoffroyi	$r^2 = 0.10$* $n = 58$	$r^2 = 0.07$* $n = 58$	$r^2 = 0.15$* $n = 47$	$r^2 = 0.24$* $n = 54$
Cebus libidinosus	$r^2 = 0.09$* $n = 73$	$r^2 = 0.05$* $n = 73$	$r^2 = 0.08$* $n = 70$	$r^2 = 0.04$ $n = 75$
Weighted Platyrrhine Average	$r^2 = 0.09$	$r^2 = 0.06$	$r^2 = 0.11$	$r^2 = 0.12$

	P_2Oblique-P^4MD	P_3MD-P_4MD	P_3MD-P^2MD	P_3MD-P^3MD
Ateles geoffroyi	$r^2 = 0.14$* $n = 55$	$r^2 = 0.55$*** $n = 67$	$r^2 = 0.41$*** $n = 54$	$r^2 = 0.40$*** $n = 62$
Cebus libidinosus	$r^2 = 0.03$ $n = 75$	$r^2 = 0.41$*** $n = 75$	$r^2 = 0.19$*** $n = 71$	$r^2 = 0.26$*** $n = 72$
Weighted Platyrrhine Average	$r^2 = 0.08$	$r^2 = 0.48$	$r^2 = 0.29$	$r^2 = 0.32$

	P_3MD-P^4MD	P^2MD-P^3MD	P^2MD-P^4MD	P^3MD-P^4MD
Ateles geoffroyi	$r^2 = 0.52$*** $n = 63$	$r^2 = 0.23$** $n = 53$	$r^2 = 0.36$*** $n = 54$	$r^2 = 0.40$*** $n = 64$
Cebus libidinosus	$r^2 = 0.13$** $n = 75$	$r^2 = 0.15$** $n = 72$	$r^2 = 0.12$* $n = 72$	$r^2 = 0.55$*** $n = 78$
Weighted Platyrrhine Average	$r^2 = 0.31$	$r^2 = 0.18$	$r^2 = 0.22$	$r^2 = 0.48$

	P_4MD-P^2MD	P_4MD-P^3MD	P_4MD-P^4MD
Ateles geoffroyi	$r^2 = 0.50$*** $n = 54$	$r^2 = 0.33$*** $n = 64$	$r^2 = 0.43$*** $n = 65$
Cebus libidinosus	$r^2 = 0.13$* $n = 71$	$r^2 = 0.27$*** $n = 76$	$r^2 = 0.31$*** $n = 76$
Weighted Platyrrhine Average	$r^2 = 0.29$	$r^2 = 0.30$	$r^2 = 0.37$

*TABLE 4.6. The magnitude of covariation among catarrhine premolar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P^3BL-P^4BL	P_3BL-P_4BL	P_3BL-P^3BL	P_4BL-P^4BL
Gorilla gorilla	$r^2 = 0.60$*** $n = 124$	$r^2 = 0.45$*** $n = 110$	$r^2 = 0.18$*** $n = 116$	$r^2 = 0.41$*** $n = 114$
Pan troglodytes	$r^2 = 0.56$*** $n = 95$	$r^2 = 0.40$*** $n = 91$	$r^2 = 0.20$** $n = 93$	$r^2 = 0.60$*** $n = 89$
Hylobates lar	$r^2 = 0.47$*** $n = 74$	$r^2 = 0.32$*** $n = 61$	$r^2 = 0.37$*** $n = 65$	$r^2 = 0.42$*** $n = 75$
Cercopithecus cephus	$r^2 = 0.46$*** $n = 80$	$r^2 = 0.38$*** $n = 78$	$r^2 = 0.46$*** $n = 77$	$r^2 = 0.47$*** $n = 81$
Cercopithecus nictitans	$r^2 = 0.50$*** $n = 81$	$r^2 = 0.54$*** $n = 79$	$r^2 = 0.24$*** $n = 78$	$r^2 = 0.48$*** $n = 79$
Cercopithecus pogonias	$r^2 = 0.37$*** $n = 70$	$r^2 = 0.48$*** $n = 67$	$r^2 = 0.34$*** $n = 69$	$r^2 = 0.29$*** $n = 68$
Macaca fascicularis	$r^2 = 0.48$*** $n = 83$	$r^2 = 0.40$*** $n = 81$	$r^2 = 0.34$*** $n = 81$	$r^2 = 0.50$*** $n = 77$
Colobus satanas	$r^2 = 0.36$*** $n = 47$	$r^2 = 0.14$* $n = 46$	$r^2 = 0.01$ $n = 46$	$r^2 = 0.18$* $n = 46$
Weighted Catarrhine Average	$r^2 = 0.49$	$r^2 = 0.41$	$r^2 = 0.27$	$r^2 = 0.44$
Weighted Hominoid Average	$r^2 = 0.55$	$r^2 = 0.40$	$r^2 = 0.23$	$r^2 = 0.47$
Weighted Cercopithecid Average	$r^2 = 0.44$	$r^2 = 0.41$	$r^2 = 0.30$	$r^2 = 0.41$
Significantly different from zero ($p < \alpha = 0.01$)	8/8	7/8	7/8	7/8

In contrast to pairings of premolar MD length and BL breadth, higher levels of covariation are observed when MD lengths are compared to one another, both within an arch and between arches. In catarrhines, the MD lengths of the mandibular premolars (P_3Oblique length and P_4MD length) express an average level of covariation ($r^2 = 0.24$) that is lower than that seen between the MD lengths of the maxillary premolars ($r^2 = 0.38$) (Table 4.4). Between the arches, the highest level of covariation is observed between the lengths of the P4s ($r^2 = 0.55$); that is, the P4 lengths covary with each other more strongly than they do with the length of the adjacent premolar in their respective arch. The same cannot be said of covariation for P_3Oblique-P^3MD, which averages $r^2 =$

*TABLE 4.7. The magnitude of covariation among platyrrhine premolar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_2BL-P_3BL	P_2BL-P_4BL	P_2BL-P^2BL	P_2BL-P^3BL
Ateles geoffroyi	$r^2 = 0.07$* $n = 54$	$r^2 = 0.16$* $n = 55$	$r^2 = 0.08$* $n = 57$	$r^2 = 0.21$*** $n = 56$
Cebus libidinosus	$r^2 = 0.21$*** $n = 74$	$r^2 = 0.32$*** $n = 75$	$r^2 = 0.06$* $n = 76$	$r^2 = 0.13$* $n = 77$
Weighted Platyrrhine Average	$r^2 = 0.15$	$r^2 = 0.25$	$r^2 = 0.07$	$r^2 = 0.16$

	P_2BL-P^4BL	P_3BL-P_4BL	P_3BL-P^2BL	P_3BL-P^3BL
Ateles geoffroyi	$r^2 = 0.18$* $n = 55$	$r^2 = 0.66$*** $n = 53$	$r^2 = 0.38$*** $n = 55$	$r^2 = 0.30$*** $n = 55$
Cebus libidinosus	$r^2 = 0.11$* $n = 76$	$r^2 = 0.56$*** $n = 72$	$r^2 = 0.21$*** $n = 73$	$r^2 = 0.22$*** $n = 74$
Weighted Platyrrhine Average	$r^2 = 0.14$	$r^2 = 0.60$	$r^2 = 0.28$	$r^2 = 0.25$

	P_3BL-P^4BL	P^2BL-P^3BL	P^2BL-P^4BL	P^3BL-P^4BL
Ateles geoffroyi	$r^2 = 0.22$*** $n = 54$	$r^2 = 0.69$*** $n = 59$	$r^2 = 0.44$*** $n = 58$	$r^2 = 0.66$*** $n = 60$
Cebus libidinosus	$r^2 = 0.13$** $n = 74$	$r^2 = 0.57$*** $n = 76$	$r^2 = 0.40$*** $n = 75$	$r^2 = 0.77$*** $n = 77$
Weighted Platyrrhine Average	$r^2 = 0.17$	$r^2 = 0.62$	$r^2 = 0.42$	$r^2 = 0.72$

	P_4BL-P^2BL	P_4BL-P^3BL	P_4BL-P^4BL
Ateles geoffroyi	$r^2 = 0.33$*** $n = 57$	$r^2 = 0.33$*** $n = 58$	$r^2 = 0.37$*** $n = 56$
Cebus libidinosus	$r^2 = 0.25$*** $n = 74$	$r^2 = 0.43$*** $n = 76$	$r^2 = 0.44$*** $n = 75$
Weighted Platyrrhine Average	$r^2 = 0.28$	$r^2 = 0.39$	$r^2 = 0.41$

0.19. As observed for the incisors, it is the most heteromorphic elements of a dental class that exhibit the lowest magnitude covariation with other members.

As was observed for the catarrhine honing premolar oblique length, in platyrrhines, all comparisons of P_2Oblique length to other premolar MD lengths have very low r^2 estimates (the highest average is $r^2 = 0.12$) and no comparison involving the P_2Oblique length is significantly different from zero at $\alpha = 0.01$ (Table 4.5). Also shared with catarrhines, the length of the mesial maxillary premolar, P^2MD, covaries weakly with other premolars; the highest estimate is $r^2 = 0.29$ for both P^2MD-P_3MD and P^2MD-P_4MD. At the other end of the spectrum, the MD lengths of the distal premolars show moderate levels of covariation; the average for both P_3MD-P_4MD and P^3MD-P^4MD is $r^2 = 0.48$. Between the arches, the highest average covariance is between the P_4MD-P^4MD ($r^2 = 0.37$), which is slightly higher than that observed between P_3MD-P^3MD ($r^2 = 0.32$). The magnitude of covariation between MD lengths in platyrrhines is variable among taxa, with *Ateles geoffroyi* typically expressing higher levels of covariation than *Cebus*.

In catarrhines, when premolar BL breadths are compared, a similar pattern is observed to that among premolar MD lengths (Table 4.6). The average level of covariation between the P_3BL and P_4BL ($r^2 = 0.41$) is slightly lower than that between P^3BL-P^4BL ($r^2 = 0.49$). Between the arches, the catarrhine P4BL breadths covary at $r^2 = 0.41$, while the P3BL breadths covary weakly (average $r^2 = 0.27$). The P4BL average is affected by low estimates in *Cercopithecus pogonias* and *Colobus satanas*. Levels of covariation observed between the BL breadths tend to be higher than that observed between the MD lengths (though not in every case, as the estimate of r^2 for P4MD lengths is slightly higher than for their breadths).

A similar pattern is observed for the platyrrhine premolar breadths (Table 4.7). The P_2BL breadth covaries weakly with other premolars; the highest estimate is $r^2 = 0.25$

for P_2BL-P_4BL. In contrast, all adjacent maxillary premolars express high levels (r^2 > 0.60) of covariation between their BL breadths, as do the P_3 and P_4. Between the arches, very low to moderate levels of covariation are observed for the nonhoning premolars; r^2 estimates range from $r^2 = 0.17$ (P_3BL-P^4BL) to $r^2 = 0.41$ (P_4BL-P^4BL).

In summary, premolar size covariation is not consistently strong among all dimensions. In both platyrrhines and catarrhines, MD lengths and BL breadths express weak levels of covariation with one another, while pairings of homologous dimensions covary more strongly. Premolar breadth covariation tends to be higher in magnitude than among lengths and, for both dimensions, the mesial-most premolars covary weakly with other premolars. The highest levels of size covariation are between adjacent premolars in the same arch and, between arches, the P4s in both catarrhines and platyrrhines. As inferred for the incisors, the pattern of premolar covariation is consistent with MD lengths and BL breadths forming mostly separate modules.

There is an apparent morphological explanation for the low magnitude covariation observed for the mesial premolars. As described in Chapter 1, premolar heteromorphy characterizes both the mandibular and maxillary premolars (Figure 1.11 and Figure 4.1), which is more pronounced in catarrhines than in platyrrhines. In catarrhines, there is a prominent mesiocervical enamel extension on the P^3 that occludes with the distal protoconid crest and protoconid of the P_3. Additionally, the P^3 paracone is more projecting than on more distal premolar(s) and, lingually, the P^3 protocone is smaller than the paracone in area, which creates an asymmetric crown with a shorter lingual than buccal profile (Figure 4.1). This contrasts with the P^4, which has a more symmetric crown with shorter and more equally developed cusps. Thus, as a result of accommodating the specialized morphology of the honing premolar, premolar heteromorphy also characterizes maxillary premolars. For the $P^{2,3}$, it is the MD dimension

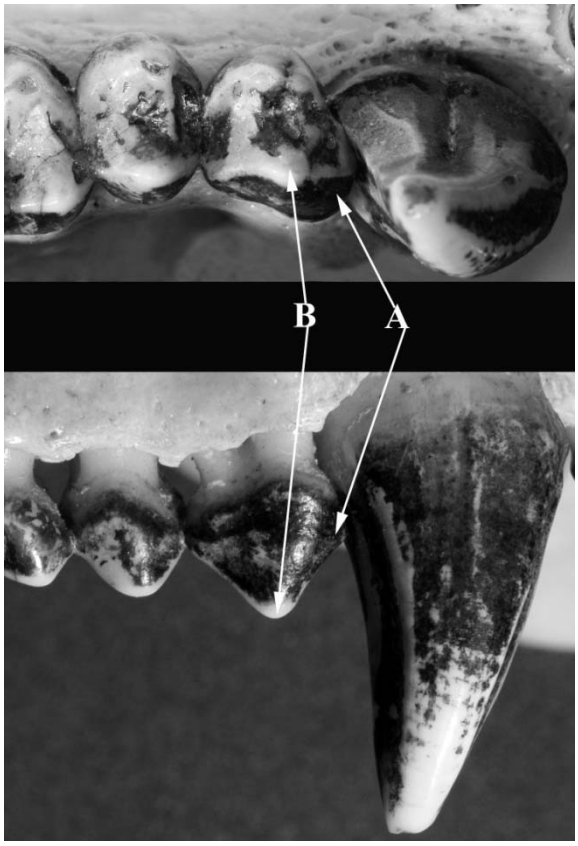

Fig. 4.1. Maxillary premolar heteromorphy in a male *Pan troglodytes*. Above, occlusal view of maxillary premolars and canines (mesial to the right, lingual to the top). On the bottom, buccal view of the maxillary premolars and canine. Point **A** is the mesiocervical enamel extension of the P^3 and point **B** is the principle cusp, the paracone, which is taller and larger in area that the minor cusp, the protocone. The P^3 protocone is also taller than the P^4 protocone. The elongated mesiocervical face of the P^3 occludes with the distal face of the P3 protoconid along the distal protoconid crest.

that is most distinct from the distal premolar(s) (Figure 4.1). Levels of MD covariation between the mesial and distal maxillary premolar(s) are typically lower than for BL widths. Variation in magnitudes of covariation apparently reflects this heteromorphy in length. For the mandibular mesial premolar, its heteromorphy relative to distal premolars was outlined in Chapter 1 and its weak covariation with other premolars follows the principle outlined here. In Chapter 3, it was also noted that degrees of incisor heteromorphy between arches and among species are reflected as differences in the

*TABLE 4.8. The magnitude of covariation among mandibular premolar and molar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_4MD-M_1MD	P_4MD-M_2MD	P_4MD-M_3MD
Gorilla gorilla	$r^2 = 0.35$*** $n = 117$	$r^2 = 0.53$*** $n = 120$	$r^2 = 0.31$*** $n = 102$
Pan troglodytes	$r^2 = 0.28$*** $n = 93$	$r^2 = 0.39$*** $n = 95$	$r^2 = 0.28$*** $n = 78$
Hylobates lar	$r^2 = 0.36$*** $n = 62$	$r^2 = 0.38$*** $n = 76$	$r^2 = 0.34$*** $n = 56$
Cercopithecus cephus	$r^2 = 0.43$*** $n = 80$	$r^2 = 0.41$*** $n = 81$	$r^2 = 0.39$*** $n = 73$
Cercopithecus nictitans	$r^2 = 0.55$*** $n = 74$	$r^2 = 0.54$*** $n = 81$	$r^2 = 0.51$*** $n = 74$
Cercopithecus pogonias	$r^2 = 0.44$*** $n = 63$	$r^2 = 0.41$*** $n = 67$	$r^2 = 0.40$*** $n = 61$
Macaca fascicularis	$r^2 = 0.43$*** $n = 83$	$r^2 = 0.57$*** $n = 86$	$r^2 = 0.49$*** $n = 69$
Colobus satanas	$r^2 = 0.23$*** $n = 46$	$r^2 = 0.14$** $n = 46$	$r^2 = 0.08$ $n = 44$
Ateles geoffroyi	$r^2 = 0.39$*** $n = 65$	$r^2 = 0.44$*** $n = 62$	$r^2 = 0.35$*** $n = 42$
Cebus libidinosus	$r^2 = 0.36$*** $n = 76$	$r^2 = 0.34$*** $n = 75$	$r^2 = 0.19$* $n = 66$
Weighted Anthropoid Average	$r^2 = 0.38$	$r^2 = 0.43$	$r^2 = 0.34$
Weighted Hominoid Average	$r^2 = 0.33$	$r^2 = 0.45$	$r^2 = 0.31$
Weighted Cercopithecid Average	$r^2 = 0.43$	$r^2 = 0.44$	$r^2 = 0.40$
Weighted Platyrrhine Average	$r^2 = 0.37$	$r^2 = 0.39$	$r^2 = 0.25$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	8/10

*TABLE 4.9. The magnitude of covariation among mandibular premolar and molar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_4BL-M_1BL	P_4BL-M_2BL	P_4BL-M_3BL
Gorilla gorilla	$r^2 = 0.46$*** $n = 103$	$r^2 = 0.54$*** $n = 113$	$r^2 = 0.37$*** $n = 99$
Pan troglodytes	$r^2 = 0.48$*** $n = 90$	$r^2 = 0.67$*** $n = 90$	$r^2 = 0.28$*** $n = 80$
Hylobates lar	$r^2 = 0.42$*** $n = 51$	$r^2 = 0.42$*** $n = 75$	$r^2 = 0.33$** $n = 63$
Cercopithecus cephus	$r^2 = 0.38$*** $n = 80$	$r^2 = 0.51$*** $n = 81$	$r^2 = 0.39$*** $n = 73$
Cercopithecus nictitans	$r^2 = 0.42$*** $n = 71$	$r^2 = 0.47$*** $n = 79$	$r^2 = 0.40$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.25$*** $n = 66$	$r^2 = 0.25$*** $n = 68$	$r^2 = 0.21$** $n = 61$
Macaca fascicularis	$r^2 = 0.54$*** $n = 79$	$r^2 = 0.62$*** $n = 84$	$r^2 = 0.62$*** $n = 67$
Colobus satanas	$r^2 = 0.25$** $n = 46$	$r^2 = 0.32$** $n = 46$	$r^2 = 0.22$* $n = 44$
Ateles geoffroyi	$r^2 = 0.51$*** $n = 44$	$r^2 = 0.38$*** $n = 50$	$r^2 = 0.18$* $n = 47$
Cebus libidinosus	$r^2 = 0.35$*** $n = 76$	$r^2 = 0.49$*** $n = 75$	$r^2 = 0.33$*** $n = 69$
Weighted Anthropoid Average	$r^2 = 0.41$	$r^2 = 0.49$	$r^2 = 0.34$
Weighted Hominoid Average	$r^2 = 0.46$	$r^2 = 0.55$	$r^2 = 0.33$
Weighted Cercopithecid Average	$r^2 = 0.38$	$r^2 = 0.45$	$r^2 = 0.38$
Weighted Platyrrhine Average	$r^2 = 0.41$	$r^2 = 0.45$	$r^2 = 0.27$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	9/10	8/10

*TABLE 4.10. The magnitude of covariation among maxillary premolar and molar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P^4MD-M^1MD	P^4MD-M^2MD	P^4MD-M^3MD
Gorilla gorilla	$r^2 = 0.37$*** $n = 119$	$r^2 = 0.51$*** $n = 121$	$r^2 = 0.34$*** $n = 104$
Pan troglodytes	$r^2 = 0.32$*** $n = 92$	$r^2 = 0.36$*** $n = 91$	$r^2 = 0.28$*** $n = 75$
Hylobates lar	$r^2 = 0.42$*** $n = 72$	$r^2 = 0.50$*** $n = 74$	$r^2 = 0.31$** $n = 57$
Cercopithecus cephus	$r^2 = 0.36$*** $n = 81$	$r^2 = 0.34$*** $n = 81$	$r^2 = 0.19$** $n = 71$
Cercopithecus nictitans	$r^2 = 0.56$*** $n = 83$	$r^2 = 0.61$*** $n = 83$	$r^2 = 0.40$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.54$*** $n = 67$	$r^2 = 0.63$*** $n = 68$	$r^2 = 0.25$*** $n = 60$
Macaca fascicularis	$r^2 = 0.53$*** $n = 79$	$r^2 = 0.64$*** $n = 82$	$r^2 = 0.55$*** $n = 61$
Colobus satanas	$r^2 = 0.27$*** $n = 47$	$r^2 = 0.34$*** $n = 47$	$r^2 = 0.09$ $n = 45$
Ateles geoffroyi	$r^2 = 0.28$** $n = 65$	$r^2 = 0.39$*** $n = 61$	$r^2 = 0.21$** $n = 51$
Cebus libidinosus	$r^2 = 0.19$** $n = 78$	$r^2 = 0.09$* $n = 78$	$r^2 = 0.01$ $n = 61$
Weighted Anthropoid Average	$r^2 = 0.39$	$r^2 = 0.45$	$r^2 = 0.27$
Weighted Hominoid Average	$r^2 = 0.37$	$r^2 = 0.46$	$r^2 = 0.31$
Weighted Cercopithecid Average	$r^2 = 0.47$	$r^2 = 0.52$	$r^2 = 0.31$
Weighted Platyrrhine Average	$r^2 = 0.23$	$r^2 = 0.22$	$r^2 = 0.10$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	9/10	8/10

*TABLE 4.11. The magnitude of covariation among maxillary premolar and molar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P^4BL-M^1BL	P^4BL-M^2BL	P^4BL-M^3BL
Gorilla gorilla	r^2 = 0.37*** n = 116	r^2 = 0.48*** n = 120	r^2 = 0.28*** n = 104
Pan troglodytes	r^2 = 0.33*** n = 95	r^2 = 0.49*** n = 94	r^2 = 0.23*** n = 79
Hylobates lar	r^2 = 0.39*** n = 74	r^2 = 0.41*** n = 82	r^2 = 0.38*** n = 68
Cercopithecus cephus	r^2 = 0.39*** n = 80	r^2 = 0.59*** n = 81	r^2 = 0.47*** n = 72
Cercopithecus nictitans	r^2 = 0.49*** n = 79	r^2 = 0.56*** n = 83	r^2 = 0.58*** n = 75
Cercopithecus pogonias	r^2 = 0.33*** n = 69	r^2 = 0.44*** n = 70	r^2 = 0.37*** n = 62
Macaca fascicularis	r^2 = 0.41*** n = 80	r^2 = 0.61*** n = 84	r^2 = 0.48*** n = 58
Colobus satanas	r^2 = 0.50*** n = 47	r^2 = 0.61*** n = 47	r^2 = 0.38*** n = 43
Ateles geoffroyi	r^2 = 0.31*** n = 56	r^2 = 0.51*** n = 57	r^2 = 0.36*** n = 47
Cebus libidinosus	r^2 = 0.28*** n = 77	r^2 = 0.39*** n = 77	r^2 = 0.20*** n = 64
Weighted Anthropoid Average	r^2 = 0.38	r^2 = 0.50	r^2 = 0.37
Weighted Hominoid Average	r^2 = 0.36	r^2 = 0.46	r^2 = 0.29
Weighted Cercopithecid Average	r^2 = 0.42	r^2 = 0.56	r^2 = 0.47
Weighted Platyrrhine Average	r^2 = 0.29	r^2 = 0.44	r^2 = 0.27
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	10/10

magnitudes of observed covariation. In Chapter 5, covariation between the length of the honing surface of the mesial mandibular premolar and the length of the mesiocervical extension of the maxillary premolar will be investigated. As hypothesized for heteromorphy in incisors, the hypothesis that the mesial premolars were parceled out of the postcanine variational module as they evolved from a homomorphic ancestral condition deserves attention.

***Premolar-Molar Size Covariation Within Species*:** Hlusko and Mahaney (2009) found that maxillary premolars and molars covary in size and suggested that the premolars and molars are quasi-independent modules. As the P4 is the only premolar for which the function is comparable in platyrrhines and catarrhines, the covariation of P4 and molar size is here investigated. Covariation of honing premolar and molar size will be investigated in depth in Chapter 5. In this section, not all possible pairs of premolar and molar size were investigated; analyses were restricted to comparisons of homologous dimensions between premolars and molars in the same arch.

Levels of covariation among all homologous dimensions of the P4 and molars are positive and significantly different from zero at $\alpha = 0.05$ (Tables 4.8, 4.9, 4.10, 4.11). Covariation between P4 and molar size is, however, not constant in magnitude among all molar positions. For example, in the mandible covariation is consistently highest between the P_4 and M_2 (anthropoid average r^2s = 0.43(MD) and 0.49(BL)), intermediate for the P_4 and M_1 (anthropoid average r^2s = 0.38(MD) and 0.41(BL)), and lowest between the P_4 and M_3 (anthropoid average r^2s = 0.34(MD) and 0.34(BL)). The difference in strength is subtle, but it is repeated again in the maxilla, where the highest average covariation is

between the P^4 and M^2 (anthropoid average r^2s = 0.45(MD) and 0.50(BL)), a lower magnitude is observed for the P^4 and M^1 (anthropoid average r^2s = 0.39(MD) and 0.38(BL)), and the lowest is between the P^4 and M^3 (anthropoid average r^2s = 0.27(MD) and 0.37(BL)). The average covariation between P4-molar BL breadths is slightly, but consistently, higher than average MD covariation; the average BL covariation exceeds average MD covariation by 0.00-0.07 for all tooth positions. The discrepancy in the strength of covariation between the MD and BL breadths of the P^4 and M^3 is in part a reflection of the exceptionally low estimates for r^2 between the MD lengths of these teeth in platyrrhines; unlike catarrhine primates, where the M^3 is a relatively well developed tooth, in the platyrrhine taxa included in this analysis (*Cebus* and *Ateles*) the M^3 is a fairly small ovular tooth. M^3MD length is less tightly linked with the premolars than is its BL breadth. The low magnitude covariation for the platyrrhine M^3 is not simply a function of it being more variable than in catarrhine primates. Coefficients of variation for M^3MD length in the ten taxa (*Ateles geoffroyi:* 10.2, *Cebus libidinosus*: 7.9, *Cercopithecus cephus*: 9.1, *Cercopithecus nictitans*: 9.0, *Cercopithecus pogonias*: 7.0, *Colobus satanas*: 4.3, *Gorilla gorilla*: 7.2, *Hylobates lar*: 8.7, *Macaca fascicularis*: 6.0, *Pan troglodytes*: 8.3) show that the taxon that stands out from the rest is *Colobus satanas* for its exceptionally low level of variation.

To determine if the premolars share pleiotropic connections that are not shared with the molars, partial correlations of premolar size, holding molar size constant, are investigated. The results of the analysis are not trivial. During hominin evolution the sizes of the premolars relative to the molars show variation among species; for example, premolars are enlarged relative to molar size in *Paranthropus* (Suwa, 1988). If premolars express unique size covariation, relative to the molars, then this would demonstrate a possible pathway for selection to affect premolar size independently of molar size.

*TABLE 4.12. Partial correlations of catarrhine premolar size, holding M2 size constant (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_3oblique-P_4MD	P_3BL-P_4BL	P^3MD-P^4MD	P^3BL-P^4BL
Gorilla gorilla	$r^2 = 0.01$ $n = 98$	$r^2 = 0.25$*** $n = 103$	$r^2 = 0.29$** $n = 92$	$r^2 = 0.36$*** $n = 120$
Pan troglodytes	$r^2 = 0.20$*** $n = 88$	$r^2 = 0.09$* $n = 85$	$r^2 = 0.08$* $n = 81$	$r^2 = 0.48$*** $n = 91$
Hylobates lar	$r^2 = 0.11$* $n = 62$	$r^2 = 0.11$* $n = 59$	$r^2 = 0.16$* $n = 40$	$r^2 = 0.22$** $n = 73$
Cercopithecus cephus	$r^2 = 0.01$ $n = 80$	$r^2 = 0.14$ $n = 78$	$r^2 = 0.34$*** $n = 64$	$r^2 = 0.37$** $n = 80$
Cercopithecus nictitans	$r^2 = 0.20$*** $n = 78$	$r^2 = 0.32$*** $n = 78$	$r^2 = 0.14$* $n = 65$	$r^2 = 0.30$*** $n = 81$
Cercopithecus pogonias	$r^2 = 0.03$ $n = 66$	$r^2 = 0.40$*** $n = 67$	$r^2 = 0.20$*** $n = 57$	$r^2 = 0.19$* $n = 70$
Macaca fascicularis	$r^2 = 0.13$*** $n = 75$	$r^2 = 0.14$* $n = 80$	$r^2 = 0.06$* $n = 70$	$r^2 = 0.24$*** $n = 83$
Colobus satanas	$r^2 = 0.11$ $n = 46$	$r^2 = 0.13$* $n = 46$	$r^2 = 0.24$* $n = 47$	$r^2 = 0.18$* $n = 47$
Weighted Hominoid Average	$r^2 = 0.10$	$r^2 = 0.16$	$r^2 = 0.19$	$r^2 = 0.36$
Weighted Cercopithecid Average	$r^2 = 0.10$	$r^2 = 0.23$	$r^2 = 0.19$	$r^2 = 0.26$
Weighted Catarrhine Average	$r^2 = 0.10$	$r^2 = 0.20$	$r^2 = 0.19$	$r^2 = 0.31$
Significantly different from zero ($p < \alpha = 0.01$)	3/8	3/8	3/8	6/8

*TABLE 4.13. Partial correlations of platyrrhine premolar size, holding M2 size constant (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_2oblique-P_3MD	P_2oblique -P_4MD	P_3MD-P_4MD	P_2BL-P_3BL
Ateles geoffroyi	r^2 = 0.00 *n* = 54	r^2 = -0.01 *n* = 53	r^2 = 0.26*** *n* = 61	r^2 = 0.01 *n* = 47
Cebus libidinosus	r^2 = 0.04 *n* = 72	r^2 = 0.01 *n* = 72	r^2 = 0.28*** *n* = 74	r^2 = 0.08* *n* = 73
Weighted Platyrrhine Average	r^2 = 0.02	r^2 = 0.00	r^2 = 0.27	r^2 = 0.05

	P_2BL-P_4BL	P_3BL-P_4BL	P^2MD-P^3MD	P^2MD-P^4MD
Ateles geoffroyi	r^2 = 0.10* *n* = 47	r^2 = 0.47*** *n* = 45	r^2 = 0.01 *n* = 50	r^2 = 0.10 *n* = 51
Cebus libidinosus	r^2 = 0.12* *n* = 74	r^2 = 0.40*** *n* = 71	r^2 = 0.12* *n* = 72	r^2 = 0.08* *n* = 72
Weighted Platyrrhine Average	r^2 = 0.11	r^2 = 0.43	r^2 = 0.07	r^2 = 0.09

	P^3MD-P^4MD	P^2BL-P^3BL	P^2BL-P^4BL	P^3BL-P^4BL
Ateles geoffroyi	r^2 = 0.10* *n* = 58	r^2 = 0.56*** *n* = 56	r^2 = 0.21*** *n* = 55	r^2 = 0.43*** *n* = 57
Cebus libidinosus	r^2 = 0.52*** *n* = 78	r^2 = 0.31*** *n* = 76	r^2 = 0.15** *n* = 75	r^2 = 0.63*** *n* = 77
Weighted Platyrrhine Average	r^2 = 0.34	r^2 = 0.42	r^2 = 0.18	r^2 = 0.54

If no partial correlation remains after controlling for molar size, then the hypothesis of quasi-autonomy is rejected. As P4 size was shown to covary most strongly with M2 size among the molars, M2 size was selected as the variable to hold constant. For comparisons of maxillary premolar MD length covariation, M^2MD length was held constant; for comparisons of maxillary premolar BL breadth, M^2BL breadth was held constant; for comparisons of mandibular premolar MD length, M_2MD length was held constant; and for comparisons of mandibular premolar BL breadth, M_2BL breadth was held constant.

For the catarrhines, premolar size covariation is significantly affected by controlling for M2 size. For P^3MD, little covariation with P^4MD length remains after controlling for M^2MD length (average catarrhine partial $r^2 = 0.19$) (Table 4.12). Maxillary premolar breadths retain nearly twice as much covariation after controlling for M^2BL breadth (average catarrhine partial $r^2 = 0.36$), indicating that there are unique premolar breadth pleiotropic effects. For the mandibular premolars, there is virtually no covariance remaining for P_3Oblique-P_4MD (average catarrhine partial $r^2 = 0.10$) or for P_3BL-P_4BL (average catarrhine partial $r^2 = 0.20$). When covariation among the dimensions of the premolars was considered (above), it was seen that the catarrhine mandibular premolars share low levels of covariation for both dimensions and the maxillary premolars share little for their MD lengths but more for the BL breadths. The analyses of partial correlations show the same pattern and highlight that the sizes of catarrhine mandibular premolars and the P^3MD share few unique pleiotropic connections. What little variation they do share appears to arise from pleiotropic effects that are also shared with the molars.

The platyrrhine premolars exhibit a similar pattern of partial correlation (Table 4.13), with virtually no covariance remaining between the P_2 and the other mandibular premolars or between the P^2MD and other maxillary premolar lengths. In contrast, in the

mandible, both the MD length (partial $r^2 = 0.27$) and BL breadth (partial $r^2 = 0.43$) of the P_3 and P_4 retain higher levels of partial correlation, especially for the BL breadths. In the maxilla, substantial partial covariation remains among all BL breadths (except for P^2BL-P^4BL) and the comparison of P^3MD-P^4MD (Table 4.13).

In summary, the analyses of partial correlation in both platyrrhines and catarrhines further highlight the isolation of the mesial mandibular premolar and the MD length of the mesial maxillary premolar from the pleiotropic effects that link the distal premolar(s). This is an important observation, for the mesial premolars of hominins underwent significant morphological change in size and shape, which resulted in a reduction of premolar heteromorphy for both the maxillary and mandibular premolars (e.g., Kimbel and Delezene, 2009; Delezene and Kimbel, 2011). Based on the pattern of covariation observed in extant anthropoids, there is little reason to expect that these changes occurred as a consequence of selection acting on other characters that are pleiotropically linked to the on mesial premolar dimensions, which have been shown to share little variation with other postcanine teeth. The Hlusko and Mahaney (2009) hypothesis of quasi-independence for premolar and molar size is supported, especially for the distal premolars of platyrrhines and the BL breadths of the catarrhine maxillary premolars. That there are unique pleiotropic effects among the premolars, not shared with the molars, implies that there are developmental pathways on which selection can act to drive independent changes in premolar and molar morphology.

*TABLE 4.14. The magnitude of covariation between the length and breadth of each mandibular molar (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M_1MD-M_1BL	M_2MD-M_2BL	M_3MD-M_3BL
Gorilla gorilla	$r^2 = 0.50$*** $n = 112$	$r^2 = 0.52$*** $n = 120$	$r^2 = 0.39$*** $n = 99$
Pan troglodytes	$r^2 = 0.35$*** $n = 98$	$r^2 = 0.25$*** $n = 98$	$r^2 = 0.29$*** $n = 82$
Hylobates lar	$r^2 = 0.56$*** $n = 66$	$r^2 = 0.50$*** $n = 84$	$r^2 = 0.38$*** $n = 55$
Cercopithecus cephus	$r^2 = 0.33$*** $n = 79$	$r^2 = 0.32$*** $n = 81$	$r^2 = 0.55$*** $n = 73$
Cercopithecus nictitans	$r^2 = 0.20$** $n = 77$	$r^2 = 0.27$*** $n = 83$	$r^2 = 0.39$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.09$* $n = 67$	$r^2 = 0.29$*** $n = 72$	$r^2 = 0.26$*** $n = 64$
Macaca fascicularis	$r^2 = 0.43$*** $n = 112$	$r^2 = 0.35$*** $n = 93$	$r^2 = 0.44$*** $n = 72$
Colobus satanas	$r^2 = 0.20$* $n = 52$	$r^2 = 0.28$** $n = 51$	$r^2 = 0.20$** $n = 44$
Ateles geoffroyi	$r^2 = 0.33$*** $n = 52$	$r^2 = 0.52$*** $n = 53$	$r^2 = 0.62$*** $n = 38$
Cebus libidinosus	$r^2 = 0.14$** $n = 89$	$r^2 = 0.14$** $n = 78$	$r^2 = 0.38$*** $n = 68$
Weighted Anthropoid Average	$r^2 = 0.33$	$r^2 = 0.35$	$r^2 = 0.39$
Weighted Hominoid Average	$r^2 = 0.46$	$r^2 = 0.43$	$r^2 = 0.35$
Weighted Cercopithecid Average	$r^2 = 0.27$	$r^2 = 0.31$	$r^2 = 0.39$
Weighted Platyrrhine Average	$r^2 = 0.21$	$r^2 = 0.29$	$r^2 = 0.47$
Significantly different from zero ($p < \alpha = 0.01$)	8/10	10/10	10/10

*TABLE 4.15. The magntidue of covariation between the length and breadth of each maxillary molar (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M^1MD-M^1BL	M^2MD-M^2BL	M^3MD-M^3BL
Gorilla gorilla	$r^2 = 0.46^{***}$ $n = 124$	$r^2 = 0.30^{***}$ $n = 124$	$r^2 = 0.19^{***}$ $n = 101$
Pan troglodytes	$r^2 = 0.17^{***}$ $n = 100$	$r^2 = 0.24^{***}$ $n = 100$	$r^2 = 0.19^{**}$ $n = 82$
Hylobates lar	$r^2 = 0.50^{***}$ $n = 83$	$r^2 = 0.56^{***}$ $n = 86$	$r^2 = 0.39^{***}$ $n = 64$
Cercopithecus cephus	$r^2 = 0.30^{***}$ $n = 80$	$r^2 = 0.64^{***}$ $n = 81$	$r^2 = 0.47^{***}$ $n = 71$
Cercopithecus nictitans	$r^2 = 0.27^{***}$ $n = 84$	$r^2 = 0.46^{***}$ $n = 84$	$r^2 = 0.27^{***}$ $n = 75$
Cercopithecus pogonias	$r^2 = 0.07^{*}$ $n = 71$	$r^2 = 0.21^{***}$ $n = 71$	$r^2 = 0.14^{*}$ $n = 63$
Macaca fascicularis	$r^2 = 0.35^{***}$ $n = 114$	$r^2 = 0.48^{***}$ $n = 94$	$r^2 = 0.41^{***}$ $n = 61$
Colobus satanas	$r^2 = 0.26^{**}$ $n = 53$	$r^2 = 0.26^{***}$ $n = 52$	$r^2 = 0.08^{*}$ $n = 43$
Ateles geoffroyi	$r^2 = 0.33^{***}$ $n = 68$	$r^2 = 0.40^{***}$ $n = 62$	$r^2 = 0.35^{**}$ $n = 49$
Cebus libidinosus	$r^2 = 0.22^{***}$ $n = 88$	$r^2 = 0.35^{***}$ $n = 81$	$r^2 = 0.22^{**}$ $n = 62$
Weighted Anthropoid Average	$r^2 = 0.30$	$r^2 = 0.39$	$r^2 = 0.27$
Weighted Hominoid Average	$r^2 = 0.38$	$r^2 = 0.35$	$r^2 = 0.24$
Weighted Cercopithecid Average	$r^2 = 0.26$	$r^2 = 0.43$	$r^2 = 0.29$
Weighted Platyrrhine Average	$r^2 = 0.27$	$r^2 = 0.37$	$r^2 = 0.28$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	10/10	8/10

TABLE 4.16. The average magnitude of covariation among molar lengths and breadths.

	M^1BL-M_1MD	M^1BL-M_2MD	M^1BL-M_3MD	M^1BL-M^2MD	M^1BL-M^3MD
Weighted Anthropoid Average	$r^2 = 0.26$	$r^2 = 0.23$	$r^2 = 0.13$	$r^2 = 0.22$	$r^2 = 0.10$
Weighted Hominoid Average	$r^2 = 0.28$	$r^2 = 0.23$	$r^2 = 0.09$	$r^2 = 0.16$	$r^2 = 0.10$
Weighted Cercopithecid Average	$r^2 = 0.25$	$r^2 = 0.21$	$r^2 = 0.14$	$r^2 = 0.29$	$r^2 = 0.12$
Weighted Platyrrhine Average	$r^2 = 0.22$	$r^2 = 0.27$	$r^2 = 0.19$	$r^2 = 0.18$	$r^2 = 0.06$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	8/10	7/10	9/10	5/10
	M^2BL-M_1MD	M^2BL-M_2MD	M^2BL-M_3MD	M^2BL-M^1MD	M^2BL-M^3MD
Weighted Anthropoid Average	$r^2 = 0.21$	$r^2 = 0.31$	$r^2 = 0.19$	$r^2 = 0.26$	$r^2 = 0.15$
Weighted Hominoid Average	$r^2 = 0.19$	$r^2 = 0.33$	$r^2 = 0.17$	$r^2 = 0.28$	$r^2 = 0.15$
Weighted Cercopithecid Average	$r^2 = 0.24$	$r^2 = 0.29$	$r^2 = 0.20$	$r^2 = 0.26$	$r^2 = 0.17$
Weighted Platyrrhine Average	$r^2 = 0.17$	$r^2 = 0.31$	$r^2 = 0.19$	$r^2 = 0.22$	$r^2 = 0.10$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	10/10	7/10	9/10	6/10
	M^3BL-M_1MD	M^3BL-M_2MD	M^3BL-M_3MD	M^3BL-M^1MD	M^3BL-M^2MD
Weighted Anthropoid Average	$r^2 = 0.16$	$r^2 = 0.24$	$r^2 = 0.25$	$r^2 = 0.18$	$r^2 = 0.28$
Weighted Hominoid Average	$r^2 = 0.08$	$r^2 = 0.19$	$r^2 = 0.18$	$r^2 = 0.14$	$r^2 = 0.18$
Weighted Cercopithecid Average	$r^2 = 0.24$	$r^2 = 0.29$	$r^2 = 0.31$	$r^2 = 0.25$	$r^2 = 0.37$
Weighted Platyrrhine Average	$r^2 = 0.10$	$r^2 = 0.20$	$r^2 = 0.19$	$r^2 = 0.12$	$r^2 = 0.29$
Significantly different from zero ($p < \alpha = 0.01$)	5/10	9/10	8/10	8/10	8/10
	M_1BL-M_2MD	M_1BL-M_3MD	M_1BL-M^1MD	M_1BL-M^2MD	M_1BL-M^3MD
Weighted Anthropoid Average	$r^2 = 0.24$	$r^2 = 0.14$	$r^2 = 0.34$	$r^2 = 0.27$	$r^2 = 0.13$
Weighted Hominoid Average	$r^2 = 0.26$	$r^2 = 0.16$	$r^2 = 0.47$	$r^2 = 0.26$	$r^2 = 0.19$
Weighted Cercopithecid Average	$r^2 = 0.22$	$r^2 = 0.14$	$r^2 = 0.29$	$r^2 = 0.27$	$r^2 = 0.12$
Weighted Platyrrhine Average	$r^2 = 0.25$	$r^2 = 0.08$	$r^2 = 0.24$	$r^2 = 0.26$	$r^2 = 0.03$
Significantly different from zero ($p < \alpha = 0.01$)	8/10	4/10	10/10	9/10	4/10

(cont.)

TABLE 4.16 continued.

	M_2BL-M_1MD	M_2BL-M_3MD	M_2BL-M^1MD	M_2BL-M^2MD	M_2BL-M^3MD
Weighted Anthropoid Average	$r^2 = 0.27$	$r^2 = 0.35$	$r^2 = 0.28$	$r^2 = 0.38$	$r^2 = 0.16$
Weighted Hominoid Average	$r^2 = 0.31$	$r^2 = 0.42$	$r^2 = 0.35$	$r^2 = 0.38$	$r^2 = 0.20$
Weighted Cercopithecid Average	$r^2 = 0.25$	$r^2 = 0.30$	$r^2 = 0.23$	$r^2 = 0.41$	$r^2 = 0.16$
Weighted Platyrrhine Average	$r^2 = 0.23$	$r^2 = 0.29$	$r^2 = 0.28$	$r^2 = 0.34$	$r^2 = 0.09$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	10/10	10/10	10/10	7/10

	M_3BL-M_1MD	M_3BL-M_2MD	M_3BL-M^1MD	M_3BL-M^2MD	M_3BL-M^3MD
Weighted Anthropoid Average	$r^2 = 0.23$	$r^2 = 0.31$	$r^2 = 0.23$	$r^2 = 0.34$	$r^2 = 0.27$
Weighted Hominoid Average	$r^2 = 0.20$	$r^2 = 0.34$	$r^2 = 0.22$	$r^2 = 0.30$	$r^2 = 0.27$
Weighted Cercopithecid Average	$r^2 = 0.26$	$r^2 = 0.33$	$r^2 = 0.25$	$r^2 = 0.39$	$r^2 = 0.29$
Weighted Platyrrhine Average	$r^2 = 0.23$	$r^2 = 0.20$	$r^2 = 0.21$	$r^2 = 0.30$	$r^2 = 0.22$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	9/10	10/10	9/10	7/10

*TABLE 4.17. The magntidue of covariation among maxillary molar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M^1BL-M^2BL	M^1BL-M^3BL	M^2BL-M^3BL
Gorilla gorilla	$r^2 = 0.54$*** $n = 118$	$r^2 = 0.29$*** $n = 100$	$r^2 = 0.50$*** $n = 104$
Pan troglodytes	$r^2 = 0.46$*** $n = 102$	$r^2 = 0.14$*** $n = 83$	$r^2 = 0.51$*** $n = 83$
Hylobates lar	$r^2 = 0.57$*** $n = 77$	$r^2 = 0.23$** $n = 60$	$r^2 = 0.41$*** $n = 69$
Cercopithecus cephus	$r^2 = 0.65$*** $n = 80$	$r^2 = 0.45$*** $n = 71$	$r^2 = 0.66$*** $n = 72$
Cercopithecus nictitans	$r^2 = 0.62$*** $n = 80$	$r^2 = 0.49$*** $n = 71$	$r^2 = 0.68$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.73$*** $n = 69$	$r^2 = 0.27$*** $n = 61$	$r^2 = 0.47$*** $n = 63$
Macaca fascicularis	$r^2 = 0.64$*** $n = 89$	$r^2 = 0.63$*** $n = 57$	$r^2 = 0.76$*** $n = 61$
Colobus satanas	$r^2 = 0.61$*** $n = 52$	$r^2 = 0.31$** $n = 43$	$r^2 = 0.55$*** $n = 43$
Ateles geoffroyi	$r^2 = 0.65$*** $n = 59$	$r^2 = 0.33$*** $n = 48$	$r^2 = 0.50$*** $n = 48$
Cebus libidinosus	$r^2 = 0.53$*** $n = 81$	$r^2 = 0.20$*** $n = 65$	$r^2 = 0.38$*** $n = 66$
Weighted Anthropoid Average	$r^2 = 0.59$	$r^2 = 0.33$	$r^2 = 0.54$
Weighted Hominoid Average	$r^2 = 0.52$	$r^2 = 0.22$	$r^2 = 0.48$
Weighted Cercopithecid Average	$r^2 = 0.65$	$r^2 = 0.44$	$r^2 = 0.63$
Weighted Platyrrhine Average	$r^2 = 0.58$	$r^2 = 0.26$	$r^2 = 0.43$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	10/10

*TABLE 4.18. The magnitude of covariation among mandibular molar breadths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M_1BL-M_2BL	M_1BL-M_3BL	M_2BL-M_3BL
Gorilla gorilla	$r^2 = 0.73^{***}$ $n = 105$	$r^2 = 0.44^{***}$ $n = 89$	$r^2 = 0.53^{***}$ $n = 99$
Pan troglodytes	$r^2 = 0.48^{***}$ $n = 95$	$r^2 = 0.24^{***}$ $n = 82$	$r^2 = 0.52^{***}$ $n = 81$
Hylobates lar	$r^2 = 0.69^{***}$ $n = 56$	$r^2 = 0.43^{***}$ $n = 41$	$r^2 = 0.63^{***}$ $n = 65$
Cercopithecus cephus	$r^2 = 0.64^{***}$ $n = 80$	$r^2 = 0.51^{***}$ $n = 72$	$r^2 = 0.76^{***}$ $n = 73$
Cercopithecus nictitans	$r^2 = 0.60^{***}$ $n = 74$	$r^2 = 0.35^{***}$ $n = 67$	$r^2 = 0.72^{***}$ $n = 76$
Cercopithecus pogonias	$r^2 = 0.68^{***}$ $n = 70$	$r^2 = 0.46^{***}$ $n = 62$	$r^2 = 0.62^{***}$ $n = 64$
Macaca fascicularis	$r^2 = 0.54^{***}$ $n = 85$	$r^2 = 0.56^{***}$ $n = 62$	$r^2 = 0.72^{***}$ $n = 71$
Colobus satanas	$r^2 = 0.56^{***}$ $n = 51$	$r^2 = 0.40^{***}$ $n = 44$	$r^2 = 0.37^{**}$ $n = 44$
Ateles geoffroyi	$r^2 = 0.76^{***}$ $n = 45$	$r^2 = 0.51^{***}$ $n = 38$	$r^2 = 0.53^{***}$ $n = 45$
Cebus libidinosus	$r^2 = 0.61^{***}$ $n = 81$	$r^2 = 0.33^{***}$ $n = 70$	$r^2 = 0.48^{***}$ $n = 71$
Weighted Anthropoid Average	$r^2 = 0.62$	$r^2 = 0.41$	$r^2 = 0.60$
Weighted Hominoid Average	$r^2 = 0.63$	$r^2 = 0.36$	$r^2 = 0.55$
Weighted Cercopithecid Average	$r^2 = 0.60$	$r^2 = 0.46$	$r^2 = 0.66$
Weighted Platyrrhine Average	$r^2 = 0.66$	$r^2 = 0.39$	$r^2 = 0.50$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	10/10

TABLE 4.19. The average magntidue of covariation among the breadth of the maxillary and mandibular molars.

	M_1BL-M^1BL	M_1BL-M^2BL	M_1BL-M^3BL
Weighted Anthropoid Average	$r^2 = 0.50$	$r^2 = 0.34$	$r^2 = 0.19$
Weighted Hominoid Average	$r^2 = 0.47$	$r^2 = 0.30$	$r^2 = 0.15$
Weighted Cercopithecid Average	$r^2 = 0.55$	$r^2 = 0.36$	$r^2 = 0.24$
Weighted Platyrrhine Average	$r^2 = 0.41$	$r^2 = 0.34$	$r^2 = 0.16$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	9/10
	M_2BL-M^1BL	M_2BL-M^2BL	M_2BL-M^3BL
Weighted Anthropoid Average	$r^2 = 0.43$	$r^2 = 0.53$	$r^2 = 0.33$
Weighted Hominoid Average	$r^2 = 0.37$	$r^2 = 0.47$	$r^2 = 0.24$
Weighted Cercopithecid Average	$r^2 = 0.47$	$r^2 = 0.58$	$r^2 = 0.43$
Weighted Platyrrhine Average	$r^2 = 0.46$	$r^2 = 0.48$	$r^2 = 0.23$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	9/10
	M_3BL-M^1BL	M_3BL-M^2BL	M_3BL-M^3BL
Weighted Anthropoid Average	$r^2 = 0.30$	$r^2 = 0.42$	$r^2 = 0.47$
Weighted Hominoid Average	$r^2 = 0.18$	$r^2 = 0.36$	$r^2 = 0.36$
Weighted Cercopithecid Average	$r^2 = 0.38$	$r^2 = 0.49$	$r^2 = 0.58$
Weighted Platyrrhine Average	$r^2 = 0.30$	$r^2 = 0.35$	$r^2 = 0.37$
Significantly different from zero ($p < \alpha = 0.01$)	9/10	10/10	9/10

Molar Size Covariation Within Species: The average r^2 for the MD length and BL breadth of each molar ranges from 0.33–0.40 (Tables 4.14 and 4.15). The magnitude of covariation between the MD and BL dimensions of the M^3 is slightly lower than seen for other molars; otherwise, covariation is approximately equal for all maxillary and mandibular molars. The covariation between the MD and BL dimensions of the molars is higher than was observed for comparisons of breadth and length for each incisor (anthropoid average r^2 = 0.15–0.23, Table 3.1) and each premolar (catarrhine and platyrrhine average r^2 = 0.12–0.32, Tables 4.1 and 4.2). The levels observed for each molar do not, however, approach the highest levels of covariation observed between comparisons of homologous dimensions for incisor and premolar size. As for the premolars and incisors, when breadths and lengths are compared among the molars, the average level of covariation is lower than for comparisons of any single tooth. Among the molars, the anthropoid range for average MD-BL covariation is r^2 = 0.10 (M^1BL-M^3MD) to r^2 = 0.38 (M_2BL-M^2MD) (Table 4.16). Apparently, the lengths and breadths of all anthropoid teeth share very low to low levels of covariation.

Expectedly, moderate and high levels of covariation are observed among the BL breadths of the molars (Tables 4.17 and 4.18). For the maxillary molars, the highest magnitude is between the M^1 and M^2 (anthropoid average r^2 = 0.60), an intermediate level is observed for the M^2 and M^3 (anthropoid average r^2 = 0.54), and the lowest level is between the M^1 and M^3 (anthropoid average r^2 = 0.35) (Table 4.18). This pattern is also observed in the mandible, where the highest level of covariation is between the M_1 and M_2 (anthropoid average r^2 = 0.63); it is slightly lower for the M_2 and M_3 (anthropoid average r^2 = 0.58) and lowest between the M_1 and M_3 (anthropoid average r^2 = 0.41) (Table 4.17). The strength of covariation between the BL breadths of M1 and M2, M1

*TABLE 4.20. The magnitude of covariation among mandibular molar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M_1MD-M_2MD	M_1MD-M_3MD	M_2MD-M_3MD
Gorilla gorilla	$r^2 = 0.55$*** $n = 120$	$r^2 = 0.33$*** $n = 99$	$r^2 = 0.48$*** $n = 102$
Pan troglodytes	$r^2 = 0.46$*** $n = 97$	$r^2 = 0.27$*** $n = 80$	$r^2 = 0.49$*** $n = 81$
Hylobates lar	$r^2 = 0.54$*** $n = 73$	$r^2 = 0.28$* $n = 46$	$r^2 = 0.48$*** $n = 58$
Cercopithecus cephus	$r^2 = 0.59$*** $n = 80$	$r^2 = 0.61$*** $n = 72$	$r^2 = 0.63$*** $n = 73$
Cercopithecus nictitans	$r^2 = 0.68$*** $n = 77$	$r^2 = 0.59$*** $n = 68$	$r^2 = 0.77$*** $n = 74$
Cercopithecus pogonias	$r^2 = 0.52$*** $n = 66$	$r^2 = 0.40$*** $n = 59$	$r^2 = 0.53$*** $n = 64$
Macaca fascicularis	$r^2 = 0.71$*** $n = 91$	$r^2 = 0.52$*** $n = 67$	$r^2 = 0.58$*** $n = 71$
Colobus satanas	$r^2 = 0.59$*** $n = 51$	$r^2 = 0.07$ $n = 44$	$r^2 = 0.13$* $n = 44$
Ateles geoffroyi	$r^2 = 0.56$*** $n = 65$	$r^2 = 0.53$*** $n = 44$	$r^2 = 0.59$*** $n = 45$
Cebus libidinosus	$r^2 = 0.62$*** $n = 77$	$r^2 = 0.30$*** $n = 67$	$r^2 = 0.29$*** $n = 65$
Weighted Anthropoid Average	$r^2 = 0.58$	$r^2 = 0.40$	$r^2 = 0.51$
Weighted Hominoid Average	$r^2 = 0.52$	$r^2 = 0.30$	$r^2 = 0.48$
Weighted Cercopithecid Average	$r^2 = 0.63$	$r^2 = 0.47$	$r^2 = 0.56$
Weighted Platyrrhine Average	$r^2 = 0.59$	$r^2 = 0.39$	$r^2 = 0.41$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	8/10	9/10

*TABLE 4.21. The magntidue of covariation among maxillary molar lengths (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M^1MD-M^2MD	M^1MD-M^3MD	M^2MD-M^3MD
Gorilla gorilla	$r^2 = 0.56$*** $n = 124$	$r^2 = 0.27$*** $n = 102$	$r^2 = 0.41$*** $n = 105$
Pan troglodytes	$r^2 = 0.47$*** $n = 95$	$r^2 = 0.29$*** $n = 78$	$r^2 = 0.49$*** $n = 82$
Hylobates lar	$r^2 = 0.43$*** $n = 82$	$r^2 = 0.23$*** $n = 58$	$r^2 = 0.27$** $n = 63$
Cercopithecus cephus	$r^2 = 0.46$*** $n = 81$	$r^2 = 0.31$*** $n = 71$	$r^2 = 0.44$*** $n = 71$
Cercopithecus nictitans	$r^2 = 0.62$*** $n = 84$	$r^2 = 0.32$*** $n = 75$	$r^2 = 0.49$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.55$*** $n = 68$	$r^2 = 0.21$*** $n = 60$	$r^2 = 0.35$*** $n = 63$
Macaca fascicularis	$r^2 = 0.65$*** $n = 90$	$r^2 = 0.46$*** $n = 62$	$r^2 = 0.59$*** $n = 66$
Colobus satanas	$r^2 = 0.47$*** $n = 52$	$r^2 = 0.16$* $n = 45$	$r^2 = 0.08$ $n = 45$
Ateles geoffroyi	$r^2 = 0.52$*** $n = 65$	$r^2 = 0.24$* $n = 53$	$r^2 = 0.32$* $n = 51$
Cebus libidinosus	$r^2 = 0.31$*** $n = 81$	$r^2 = 0.00$ $n = 61$	$r^2 = 0.15$* $n = 61$
Weighted Anthropoid Average	$r^2 = 0.51$	$r^2 = 0.26$	$r^2 = 0.38$
Weighted Hominoid Average	$r^2 = 0.50$	$r^2 = 0.27$	$r^2 = 0.40$
Weighted Cercopithecid Average	$r^2 = 0.56$	$r^2 = 0.30$	$r^2 = 0.41$
Weighted Platyrrhine Average	$r^2 = 0.40$	$r^2 = 0.11$	$r^2 = 0.23$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	7/10	8/10

TABLE 4.22. The average magntidue of covariation among maxillary and mandibular molar lengths.

	M_1MD-M^1MD	M_1MD-M^2MD	M_1MD-M^3MD
Weighted Anthropoid Average	$r^2 = 0.58$	$r^2 = 0.42$	$r^2 = 0.26$
Weighted Hominoid Average	$r^2 = 0.61$	$r^2 = 0.39$	$r^2 = 0.26$
Weighted Cercopithecid Average	$r^2 = 0.65$	$r^2 = 0.50$	$r^2 = 0.30$
Weighted Platyrrhine Average	$r^2 = 0.32$	$r^2 = 0.26$	$r^2 = 0.16$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	8/10
	M_2MD-M^1MD	M_2MD-M^2MD	M_2MD-M^3MD
Weighted Anthropoid Average	$r^2 = 0.45$	$r^2 = 0.61$	$r^2 = 0.35$
Weighted Hominoid Average	$r^2 = 0.43$	$r^2 = 0.61$	$r^2 = 0.34$
Weighted Cercopithecid Average	$r^2 = 0.52$	$r^2 = 0.71$	$r^2 = 0.42$
Weighted Platyrrhine Average	$r^2 = 0.34$	$r^2 = 0.34$	$r^2 = 0.18$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	10/10	8/10
	M_3MD-M^1MD	M_3MD-M^2MD	M_3MD-M^3MD
Weighted Anthropoid Average	$r^2 = 0.28$	$r^2 = 0.40$	$r^2 = 0.46$
Weighted Hominoid Average	$r^2 = 0.24$	$r^2 = 0.40$	$r^2 = 0.44$
Weighted Cercopithecid Average	$r^2 = 0.35$	$r^2 = 0.46$	$r^2 = 0.53$
Weighted Platyrrhine Average	$r^2 = 0.17$	$r^2 = 0.23$	$r^2 = 0.30$
Significantly different from zero ($p < \alpha = 0.01$)	8/10	8/10	9/10

and M3, and M2 and M3 are approximately equal in both arches, suggesting a similar pattern of pleiotropic linkage among the molars in each arch. Hlusko and Mahaney (2009) and Hlusko et al. (2010) indicated than many postcanine dimensions in the pedigreed SNPRC baboon sample are characterized by complete pleiotropy (i.e., r_G not significantly different from 1). Although they are among the most strongly covarying characters in the anthropoid dentition, the null hypothesis for complete pleiotropy is rejected for all pairs of BL breadth in all 10 species in both the maxilla and mandible, as no 95, 99, or 99.99% confidence intervals contain $r^2 = 1.0$.

Between the arches, all pairs of molar BL breadth express statistically significant levels of covariation, with anthropoid averages ranging from very low, $r^2 = 0.19$ (M_1BL-M^3BL), to moderate, $r^2 = 0.53$ (M_2BL-M^2BL and M_3BL-M^3BL), (Table 4.19). The highest levels of covariation between arches are only slightly lower in magnitude than in the most strongly covarying pairs within an arch (Tables 4.17 and 4.18). For all taxonomic groups, the average levels of covariation between arches express an interesting pattern. For any molar, the highest level of covariation is always with the molar in the equivalent position in the opposite arch ($M_1$with M^1, M_2 with M^2, and M_3 with M^3). There is also an apparent taxonomic distinction. Cercopithecids show substantially higher levels of covariation for M_3BL-M^3BL and for all other comparisons involving M3BL. In cercopithecids, the BL breadths of the M3s are more tightly linked to one another and to the other molars than is true of hominoids and platyrrhines (Tables 4.17, 4.18, and 4.19). Many of the cercopithecids analyzed in this study have well developed M3s. For the M_3, there is often a prominent distal heel formed by the hypoconulid (personal observation, Ungar, 2010). In some sense, the variation in the magnitude of covariation observed for the M3s between platyrrhines and cercopithecids reflect the relative size of the teeth compared to the other molars. The relatively small platyrrhine M^3 covaries weakly with

the other molars; the relatively large and well developed cercopithecid M3s covary more strongly with the other molars.

As observed for molar BL breadths, levels of covariation among molar MD lengths are statistically significant and strong, but not consistent between molar pairs (Tables 4.20 and 4.21). For the mandibular molars, the highest level of covariation is between the M_1 and M_2 (anthropoid average $r^2 = 0.58$), an intermediate level is observed for the M_2 and M_3 (anthropoid average $r^2 = 0.49$), and lowest between the M_1 and M_3 (anthropoid average $r^2 = 0.39$). The same pattern is observed for the maxillary molars. The highest level is between the M^1 and M^2 (anthropoid average $r^2 = 0.51$), an intermediate level for the M^2 and M^3 (anthropoid average $r^2 = 0.37$), and the lowest level is between the M^1 and M^3 (anthropoid average $r^2 = 0.25$). Levels of covariation between the first and second molars are similar for the maxilla and mandible, but levels of covariation with M^3MD are substantially lower than observed in the mandible (the anthropoid average is 0.14 less for M^1MD-M^3MD than for M_1MD-M_3MD and 0.13 less lower magnitudes of covariation for the M^3MD comparisons, but the discrepancy is largest in platyrrhines (Tables 4.20 and 4.21). The M^3MD length is the most independent dimension of molar size, a point that will be revisited below in the among-species analysis.

For MD lengths between the arches, the anthropoid averages range from low, $r^2 = 0.28$ (M_3MD-M^1MD), to high, $r^2 = 0.61$ (M_2MD-M^2MD), (Table 4.22). As for the BL breadths, the highest level of covariation is always between molars in the same position in the opposite arch. Covariation between teeth in the same position is as high as between those of adjacent teeth in the same arch, indicating substantial amounts of shared variation in both cases.

When levels of covariation among the premolars, among the molars, and between the homologous dimensions of the premolars and molars are considered (Figure 4.1) the range of r^2 estimates is approximately equal for comparisons among premolar sizes and among molar sizes (the average among the molar sizes is slightly higher). This likely results from the fact that the BL and oblique dimensions of the mesial mandibular premolar and the MD length of the mesial maxillary premolar share little covariation with the other premolars. The pairing of homologous measures of premolar-molar size in each arch also significantly covary, but these magnitudes do not approach the highest levels observed within the premolars or within the molars. With r^2 values approaching and exceeding 0.50 and as high as 0.70 in some taxa, the homologous dimensions of the molars are among the most highly covarying characters observed in the anthropoid dentition.

The hypothesis of variation modularity predicts low or no covariation between functional modules. When postcanine r^2s are compared to those among homologous measures of the incisors and postcanine teeth (Figure 4.2), it is evident that there are consistent but low levels of positive covariation between the modules, as discussed in Chapter 3. The level of covariation between the modules does not approach the highest levels observed within the postcanine module. The hypothesis that postcanine dentition is a variational module is supported by these observations.

Among-Species Covariation for Postcanine Size: Covariation among species was estimated for all molars and the P4. Expectedly, all elements of the postcanine dentition show a high level of covariation in both males and females (Tables 4.23, 4.24, 4.25, 4.26). Though among-species r^2s are typically higher than the values observed within

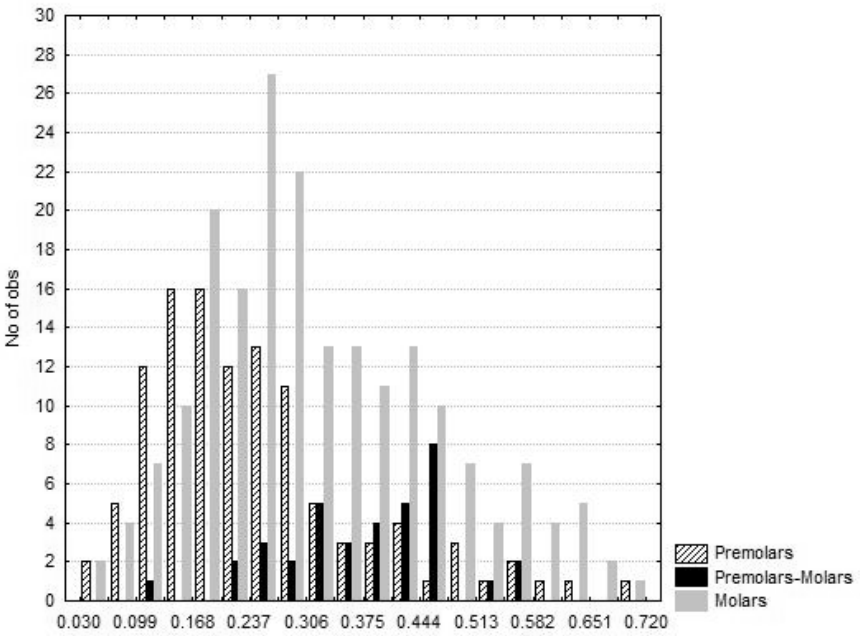

Fig 4.1. Histogram of r^2 estimates for postcanine tooth size. r^2 estimates are for platyrrhine, cercopithecid, and hominoid averages. Note that this histogram does not represent all possible correlations among character pairs. The values in this Figure are those presented in the tables in this chapter.

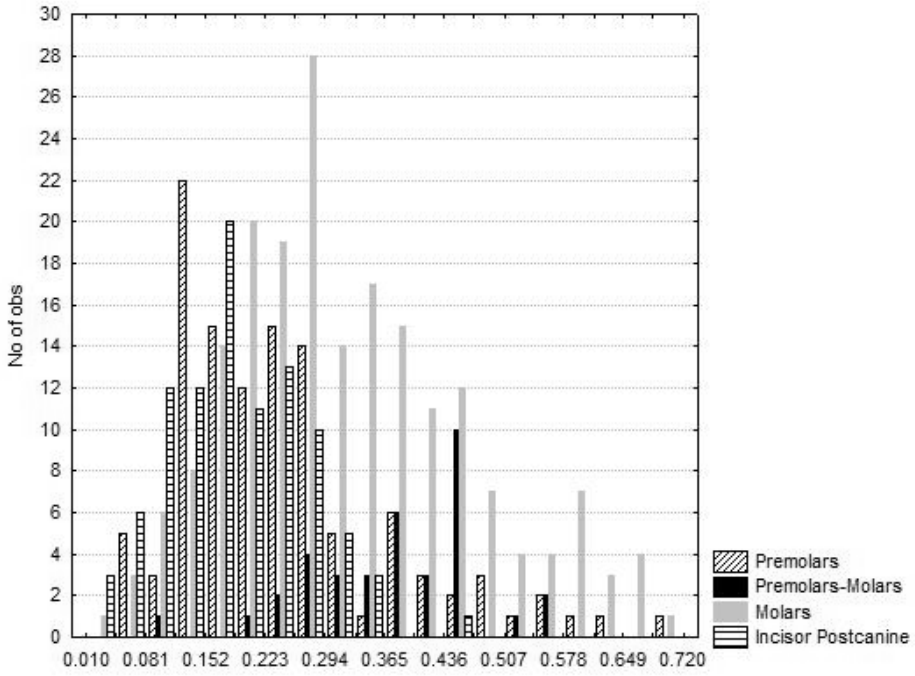

Fig 4.2. Histogram of r^2 estimates for postcanine tooth size and incisor size. r^2 estimates are for platyrrhine, cercopithecid, and hominoid averages. Note that this histogram does not represent all possible correlations among character pairs. The values in this Figure are those presented in the tables in this chapter.

TABLE 4.23. Among-species covariation for maxillary postcanine size, equal branch lengths. All correlations are significantly different from zero at $p < 0.0001$. $n = 35$ for all comparisons, though the taxonomic conformation of the males and females differs slightly.

	P^4MD	P^4BL	M^1MD	M^1BL	M^2MD	M^2BL	M^3MD
P^4BL	♂ $r^2 = 0.92$ ♀ $r^2 = 0.93$	—	—	—	—	—	—
M^1MD	♂ $r^2 = 0.92$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.81$	—	—	—	—	—
M^1BL	♂ $r^2 = 0.87$ ♀ $r^2 = 0.83$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.80$ ♀ $r^2 = 0.76$	—	—	—	—
M^2MD	♂ $r^2 = 0.86$ ♀ $r^2 = 0.82$	♂ $r^2 = 0.74$ ♀ $r^2 = 0.69$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.74$ ♀ $r^2 = 0.67$	—	—	—
M^2BL	♂ $r^2 = 0.90$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.90$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.78$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.79$ ♀ $r^2 = 0.85$	—	—
M^3MD	♂ $r^2 = 0.82$ ♀ $r^2 = 0.79$	♂ $r^2 = 0.69$ ♀ $r^2 = 0.66$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.67$ ♀ $r^2 = 0.58$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.90$	♂ $r^2 = 0.72$ ♀ $r^2 = 0.68$	—
M^3BL	♂ $r^2 = 0.91$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.84$ ♀ $r^2 = 0.82$	♂ $r^2 = 0.86$ ♀ $r^2 = 0.76$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.90$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.98$	♂ $r^2 = 0.79$ ♀ $r^2 = 0.73$

TABLE 4.24. Among-species covariation for mandibular postcaninesize, equal branch lengths. All correlations are significantly different from zero at $p < 0.0001$. $n = 35$ for all comparisons, though the taxonomic conformation of the males and females differs slightly.

	P_4MD	P_4BL	M_1MD	M_1BL	M_2MD	M_2BL	M_3MD
P_4BL	♂ $r^2 = 0.90$ ♀ $r^2 = 0.89$	—	—	—	—	—	—
M_1MD	♂ $r^2 = 0.94$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.89$ ♀ $r^2 = 0.87$	—	—	—	—	—
M_1BL	♂ $r^2 = 0.92$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.98$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.94$	—	—	—	—
M_2MD	♂ $r^2 = 0.91$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.78$	♂ $r^2 = 0.98$ ♀ $r^2 = 0.97$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.88$	—	—	—
M_2BL	♂ $r^2 = 0.94$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.95$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.96$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.92$	—	—
M_3MD	♂ $r^2 = 0.85$ ♀ $r^2 = 0.77$	♂ $r^2 = 0.73$ ♀ $r^2 = 0.64$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.79$ ♀ $r^2 = 0.75$	♂ $r^2 = 0.95$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.81$	—
M_3BL	♂ $r^2 = 0.94$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.91$	♂ $r^2 = 0.98$ ♀ $r^2 = 0.98$	♂ $r^2 = 0.89$ ♀ $r^2 = 0.83$

TABLE 4.25. Among-species covariation for mandibular and maxillary postcanine size, equal branch lengths. All correlations are significantly different from zero at $p < 0.0001$. $n = 35$ for all comparisons, though the taxonomic conformation of the males and females differs slightly.

	P_4MD	P_4BL	M_1MD	M_1BL	M_2MD	M_2BL	M_3MD	M_3BL
P^4MD	♂ $r^2 = 0.98$ ♀ $r^2 = 0.98$	♂ $r^2 = 0.93$ ♀ $r^2 = 0.91$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.90$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.85$ ♀ $r^2 = 0.79$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.95$
P^4BL	♂ $r^2 = 0.89$ ♀ $r^2 = 0.90$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.97$	♂ $r^2 = 0.86$ ♀ $r^2 = 0.86$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.91$	♂ $r^2 = 0.81$ ♀ $r^2 = 0.78$	♂ $r^2 = 0.95$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.72$ ♀ $r^2 = 0.66$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.91$
M^1MD	♂ $r^2 = 0.90$ ♀ $r^2 = 0.87$	♂ $r^2 = 0.86$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.98$ ♀ $r^2 = 0.97$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.96$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.91$
M^1BL	♂ $r^2 = 0.87$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.90$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.85$ ♀ $r^2 = 0.80$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.76$ ♀ $r^2 = 0.68$	♂ $r^2 = 0.86$ ♀ $r^2 = 0.82$
M^2MD	♂ $r^2 = 0.85$ ♀ $r^2 = 0.80$	♂ $r^2 = 0.76$ ♀ $r^2 = 0.70$	♂ $r^2 = 0.94$ ♀ $r^2 = 0.92$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.82$	♂ $r^2 = 0.97$ ♀ $r^2 = 0.97$	♂ $r^2 = 0.87$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.90$ ♀ $r^2 = 0.86$
M^2BL	♂ $r^2 = 0.90$ ♀ $r^2 = 0.86$	♂ $r^2 = 0.87$ ♀ $r^2 = 0.80$	♂ $r^2 = 0.89$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.82$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.88$	♂ $r^2 = 0.81$ ♀ $r^2 = 0.77$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.90$
M^3MD	♂ $r^2 = 0.81$ ♀ $r^2 = 0.76$	♂ $r^2 = 0.70$ ♀ $r^2 = 0.64$	♂ $r^2 = 0.90$ ♀ $r^2 = 0.84$	♂ $r^2 = 0.77$ ♀ $r^2 = 0.74$	♂ $r^2 = 0.93$ ♀ $r^2 = 0.90$	♂ $r^2 = 0.81$ ♀ $r^2 = 0.80$	♂ $r^2 = 0.96$ ♀ $r^2 = 0.95$	♂ $r^2 = 0.85$ ♀ $r^2 = 0.83$
M^3BL	♂ $r^2 = 0.91$ ♀ $r^2 = 0.93$	♂ $r^2 = 0.83$ ♀ $r^2 = 0.89$	♂ $r^2 = 0.91$ ♀ $r^2 = 0.83$	♂ $r^2 = 0.86$ ♀ $r^2 = 0.78$	♂ $r^2 = 0.92$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.90$ ♀ $r^2 = 0.85$	♂ $r^2 = 0.88$ ♀ $r^2 = 0.80$	♂ $r^2 = 0.93$ ♀ $r^2 = 0.89$

TABLE 4.26: Average magnitude of among-species covariation for P4–M3 size.

P_4MD	P_4BL	M_1MD	M_1BL	M_2MD	M_2BL	M_3MD	M_3BL
$r^2 = 0.89$	$r^2 = 0.85$	$r^2 = 0.91$	$r^2 = 0.87$	$r^2 = 0.90$	$r^2 = 0.91$	$r^2 = 0.83$	$r^2 = 0.91$

P^4MD	P^4BL	M^1MD	M^1BL	M^2MD	M^2BL	M^3MD	M^3BL
$r^2 = 0.90$	$r^2 = 0.85$	$r^2 = 0.89$	$r^2 = 0.83$	$r^2 = 0.85$	$r^2 = 0.86$	$r^2 = 0.80$	$r^2 = 0.87$

species, variation in the strength of covariation observed among species closely conforms to the pattern observed within species. For both the maxillary and mandibular molars, with few exceptions, homologous dimensions among molars always covary more strongly with one another than with nonhomologous dimensions. The length and breadth of each molar do not covary to the same degree as the homologous measures among molars. For the P4, high levels of covariation are observed with all dimensions of the molars; unlike for the molars, it is not necessarily the homologous dimensions of the P4 that covary the most strongly with the molars among species. Within species, the M^3MD is the most weakly covarying dimension with other molar dimensions. Among species, the lowest level of average covariation is for M^3MD ($r^2 = 0.80$) (Table 4.26). The lower level of M^3MD covariation within species is reflected in its relative independence among species.

Premolar Shape Covariation Within Species: Compared to the magnitudes of covariation observed for premolar sizes, the covariation of maxillary premolar shapes is

*TABLE 4.27: The magnitude of covariation among maxillary premolar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P^3-P^4	P^2-P^3	P^2-P^4	P^3-P^4
Gorilla gorilla	$r^2 = 0.19$*** $n = 92$	NA	NA	NA
Pan troglodytes	$r^2 = 0.04$ $n = 79$	NA	NA	NA
Hylobates lar	$r^2 = 0.02$ $n = 39$	NA	NA	NA
Cercopithecus cephus	$r^2 = 0.28$*** $n = 64$	NA	NA	NA
Cercopithecus nictitans	$r^2 = 0.33$*** $n = 65$	NA	NA	NA
Cercopithecus pogonias	$r^2 = 0.19$** $n = 57$	NA	NA	NA
Macaca fascicularis	$r^2 = 0.12$** $n = 68$	NA	NA	NA
Colobus satanas	$r^2 = 0.07$ $n = 47$	NA	NA	NA
Ateles geoffroyi	NA	$r^2 = 0.16$** $n = 48$	$r^2 = 0.26$*** $n = 49$	$r^2 = 0.44$*** $n = 56$
Cebus libidinosus	NA	$r^2 = 0.20$*** $n = 72$	$r^2 = 0.06$* $n = 72$	$r^2 = 0.54$*** $n = 77$
Weighted Hominoid Average	$r^2 = 0.10$	NA	NA	NA
Weighted Cercopithecid Average	$r^2 = 0.20$	NA	NA	NA
Weighted Platyrrhine Average	NA	$r^2 = 0.18$	$r^2 = 0.14$	$r^2 = 0.50$
Significantly different from zero ($p < \alpha = 0.01$)	5/8	2/2	½	2/2

*TABLE 4.28. The magntidue of covariation among mandibular premolar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

.

	P_3-P_4	P_2-P_3	P_2-P_4	P_3-P_4
Gorilla gorilla	$r^2 = 0.01$ $n = 94$	NA	NA	NA
Pan troglodytes	$r^2 = 0.09$** $n = 86$	NA	NA	NA
Hylobates lar	$r^2 = 0.02$ $n = 50$	NA	NA	NA
Cercopithecus cephus	$r^2 = 0.04$ $n = 78$	NA	NA	NA
Cercopithecus nictitans	$r^2 = 0.16$*** $n = 76$	NA	NA	NA
Cercopithecus pogonias	$r^2 = 0.00$ $n = 66$	NA	NA	NA
Macaca fascicularis	$r^2 = 0.00$ $n = 73$	NA	NA	NA
Colobus satanas	$r^2 = 0.05$ $n = 46$	NA	NA	NA
Ateles geoffroyi	NA	$r^2 = -0.04$ $n = 48$	$r^2 = 0.00$ $n = 48$	$r^2 = 0.32$*** $n = 51$
Cebus libidinosus	NA	$r^2 = 0.00$ $n = 71$	$r^2 = 0.00$ $n = 72$	$r^2 = 0.27$*** $n = 72$
Weighted Hominoid Average	$r^2 = 0.04$	NA	NA	NA
Weighted Cercopithecid Average	$r^2 = 0.05$	NA	NA	NA
Weighted Platyrrhine Average	NA	$r^2 = -0.02$	$r^2 = 0.00$	$r^2 = 0.29$
Significantly different from zero ($p < \alpha = 0.01$)	2/8	0/2	0/2	2/2

*TABLE 4.29. The magnitude of covariation among maxillary and mandibular premolar shapes in catarrhines (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_3-P^3	P_3-P^4	P_4-P^3	P_4-P^4
Gorilla gorilla	r^2 = 0.00 n = 84	r^2 = -0.01 n = 97	r^2 = 0.02 n = 88	r^2 = 0.18*** n = 110
Pan troglodytes	r^2 = 0.00 n = 77	r^2 = 0.01 n = 82	r^2 = 0.04 n = 81	r^2 = 0.25*** n = 83
Hylobates lar	r^2 = 0.04 n = 29	r^2 = 0.01 n = 53	r^2 = 0.03 n = 35	r^2 = 0.16** n = 66
Cercopithecus cephus	r^2 = 0.01 n = 62	r^2 = 0.00 n = 78	r^2 = 0.06 n = 64	r^2 = 0.28*** n = 81
Cercopithecus nictitans	r^2 = 0.01 n = 61	r^2 = -0.02 n = 77	r^2 = 0.21*** n = 64	r^2 = 0.15*** n = 79
Cercopithecus pogonias	r^2 = 0.01 n = 55	r^2 = -0.02 n = 64	r^2 = 0.14** n = 56	r^2 = 0.24*** n = 66
Macaca fascicularis	r^2 = 0.01 n = 60	r^2 = 0.00 n = 69	r^2 = 0.07* n = 68	r^2 = 0.29*** n = 74
Colobus satanas	r^2 = -0.07 n = 46	r^2 = -0.27*** n = 46	r^2 = 0.06 n = 46	r^2 = -0.01 n = 46
Weighted Catarrhine Average	r^2 = 0.00	r^2 = -0.02	r^2 = 0.05	r^2 = 0.19
Weighted Hominoid Average	r^2 = 0.01	r^2 = 0.00	r^2 = 0.03	r^2 = 0.20
Weighted Cercopithecid Average	r^2 = 0.00	r^2 = -0.05	r^2 = 0.11	r^2 = 0.21
Significantly different from zero ($p < \alpha = 0.01$)	0/8	1/8	2/8	7/8

*TABLE 4.30. The magnitude of covariation among platyrrhine mandibular and maxillary premolar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_2-P^2	P_2-P^3	P_2-P^4
Ateles geoffroyi	r^2 = -0.10* n = 43	r^2 = -0.03 n = 48	r^2 = -0.03 n = 49
Cebus libidinosus	r^2 = 0.00 n = 70	r^2 = -0.03 n = 75	r^2 = -0.03 n = 74
Weighted Platyrrhine Average	r^2 = -0.04	r^2 = -0.03	r^2 = -0.03
Significantly different from zero ($p < \alpha = 0.01$)	0/2	0/2	0/2

	P_3-P^2	P_3-P^3	P_3-P^4
Ateles geoffroyi	r^2 = 0.10* n = 45	r^2 = 0.08* n = 51	r^2 = 0.11* n = 51
Cebus libidinosus	r^2 = 0.06* n = 69	r^2 = 0.02 n = 73	r^2 = 0.02 n = 73
Weighted Platyrrhine Average	r^2 = 0.08	r^2 = 0.04	r^2 = 0.06
Significantly different from zero ($p < \alpha = 0.01$)	0/2	0/2	0/2

	P_4-P^2	P_4-P^3	P_4-P^4
Ateles geoffroyi	r^2 = 0.14** n = 47	r^2 = 0.03 n = 55	r^2 = 0.15** n = 53
Cebus libidinosus	r^2 = 0.06* n = 70	r^2 = 0.11** n = 75	r^2 = 0.13** n = 75
Weighted Platyrrhine Average	r^2 = 0.09	r^2 = 0.04	r^2 = 0.14
Significantly different from zero ($p < \alpha = 0.01$)	½	1/2	2/2

minimal, with one exception. The catarrhine maxillary premolars share almost no covariation within any species (Table 4.27). For the platyrrhines, the P^2 does not covary strongly with either the P^3 or P^4 (Table 4.27). In contrast, the distal platyrrhine maxillary premolars share substantial covariation in shape in both *Cebus libidinosus* and *Ateles geoffroyi*.

Among the mandibular premolars, the catarrhine P_3 and P_4 share no shape covariation within species (Table 4.28). For the platyrrhine mandibular premolars, the P_2 does not covary in shape with either the P_3 or the P_4. As with the maxillary premolars, the platyrrhine distal mandibular premolars share a higher level of covariation; though, the level observed for the platyrrhine mandibular premolars is lower than observed for the maxillary premolars (Table 4.28). Premolar shape covariation is highest between adjacent premolars that are not heteromorphic in shape, again suggesting that the heteromorphic mesial premolars were parceled out of the variational module when heteromorphy developed.

Between the arches, unsurprisingly, the only pairs of premolars that share significant levels of shape covariation are the catarrhine P_4 and P^4 (Table 4.29) and the platyrrhine P_4 and P^4 (Table 4.30). In both cases, the level of covariation is low compared to the magnitude observed for the sizes of the premolars between the arches (Tables 4.3–4.7). The magnitude of shape covariation is highest between occluding premolars, but shape covariation between the arches does not approach the moderate level observed between the platyrrhine maxillary premolars.

Premolar-Molar Shape Covariation Within Species: For shape, the P_4 expresses low levels of covariation with the molars in both the maxilla and mandible (Table 4.31 and 4.32). Though absolute magnitudes are low and differences in magnitude between molars

*TABLE 4.31. The magnitude of covariation among maxillary P4 and molar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P^4-M^1	P^4-M^2	P^4-M^3
Gorilla gorilla	$r^2 = 0.15$** $n = 109$	$r^2 = 0.26$*** $n = 113$	$r^2 = 0.15$** $n = 95$
Pan troglodytes	$r^2 = 0.19$** $n = 87$	$r^2 = 0.19$*** $n = 88$	$r^2 = 0.29$*** $n = 72$
Hylobates lar	$r^2 = 0.00$ $n = 65$	$r^2 = 0.08$* $n = 74$	$r^2 = 0.04$ $n = 57$
Cercopithecus cephus	$r^2 = 0.24$*** $n = 79$	$r^2 = 0.27$*** $n = 81$	$r^2 = 0.06$* $n = 73$
Cercopithecus nictitans	$r^2 = 0.21$** $n = 79$	$r^2 = 0.41$*** $n = 83$	$r^2 = 0.20$** $n = 75$
Cercopithecus pogonias	$r^2 = 0.39$*** $n = 67$	$r^2 = 0.45$*** $n = 68$	$r^2 = 0.20$** $n = 60$
Macaca fascicularis	$r^2 = 0.26$*** $n = 76$	$r^2 = 0.36$*** $n = 80$	$r^2 = 0.20$*** $n = 54$
Colobus satanas	$r^2 = 0.25$*** $n = 47$	$r^2 = 0.32$*** $n = 47$	$r^2 = 0.28$*** $n = 43$
Ateles geoffroyi	$r^2 = 0.09$ $n = 55$	$r^2 = 0.27$*** $n = 54$	$r^2 = 0.12$* $n = 44$
Cebus libidinosus	$r^2 = 0.06$ $n = 77$	$r^2 = 0.02$ $n = 77$	$r^2 = 0.02$ $n = 60$
Weighted Anthropoid Average	$r^2 = 0.18$	$r^2 = 0.26$	$r^2 = 0.15$
Weighted Hominoid Average	$r^2 = 0.13$	$r^2 = 0.19$	$r^2 = 0.17$
Weighted Cercopithecid Average	$r^2 = 0.27$	$r^2 = 0.36$	$r^2 = 0.18$
Weighted Platyrrhine Average	$r^2 = 0.07$	$r^2 = 0.12$	$r^2 = 0.06$
Significantly different from zero ($p < \alpha = 0.01$)	7/10	8/10	6/10

*TABLE 4.32. The magnitude of covariation among mandibular P4 and molar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_4-M_1	P_4-M_2	P_4-M_3
Gorilla gorilla	$r^2 = 0.20$*** $n = 96$	$r^2 = 0.18$*** $n = 109$	$r^2 = 0.12$* $n = 92$
Pan troglodytes	$r^2 = 0.25$*** $n = 87$	$r^2 = 0.38$*** $n = 89$	$r^2 = 0.19$** $n = 74$
Hylobates lar	$r^2 = 0.11$* $n = 47$	$r^2 = 0.15$** $n = 72$	$r^2 = 0.13$* $n = 52$
Cercopithecus cephus	$r^2 = 0.23$*** $n = 79$	$r^2 = 0.24$*** $n = 81$	$r^2 = 0.16$** $n = 73$
Cercopithecus nictitans	$r^2 = 0.32$*** $n = 70$	$r^2 = 0.38$*** $n = 78$	$r^2 = 0.39$*** $n = 73$
Cercopithecus pogonias	$r^2 = 0.16$** $n = 63$	$r^2 = 0.14$** $n = 67$	$r^2 = 0.22$** $n = 61$
Macaca fascicularis	$r^2 = 0.16$** $n = 78$	$r^2 = 0.28$*** $n = 82$	$r^2 = 0.18$*** $n = 66$
Colobus satanas	$r^2 = 0.01$ $n = 46$	$r^2 = 0.03$ $n = 44$	$r^2 = 0.01$ $n = 46$
Ateles geoffroyi	$r^2 = 0.21$* $n = 40$	$r^2 = 0.29$* $n = 45$	$r^2 = 0.06$ $n = 36$
Cebus libidinosus	$r^2 = 0.06$* $n = 75$	$r^2 = 0.10$* $n = 73$	$r^2 = 0.02$ $n = 65$
Weighted Anthropoid Average	$r^2 = 0.18$	$r^2 = 0.23$	$r^2 = 0.16$
Weighted Hominoid Average	$r^2 = 0.20$	$r^2 = 0.24$	$r^2 = 0.15$
Weighted Cercopithecid Average	$r^2 = 0.19$	$r^2 = 0.24$	$r^2 = 0.21$
Weighted Platyrrhine Average	$r^2 = 0.11$	$r^2 = 0.17$	$r^2 = 0.03$
Significantly different from zero ($p < \alpha = 0.01$)	6/10	7/10	5/10

are subtle, the pattern of covariation for mandibular premolar-molar shape is the same as for size: the highest level is between the P4 and M2 (anthropoid average $r^2 = 0.24$ (Mandible) and 0.26 (Maxillary)), intermediate for the P4-M1 (anthropoid average r^2s = 0.18 (Mandible) and 0.18 (Maxillary)), and lowest for the P4-M3 (anthropoid average r^2s = 0.15 (Mandible) and 0.16 (Maxillary)). This is true not only of the anthropoid average, but for the cercopithecid, hominoid, and platyrrhine averages.

There appears to be a taxonomic difference in levels of covariation between mandibular premolars and molars. Platyrrhines express the lowest levels of covariation and cercopithecids the highest; though, again, these differences are rather subtle. Despite substantial sample sizes, only 60% (P_4-M_1), 70% (P_4-M_2), and 50% (P_4-M_3) of species estimates are significantly different from zero at $\alpha = 0.01$ (no platyrrhine estimates for mandibular premolar-molar shape covariation are significant at the more restrictive level). The same pattern is observed in the maxilla; in fact, the observed average levels of covariation between the P^4 and maxillary molars are almost identical to that observed between the P_4 and mandibular molars. Again, the magnitude of covariation is highest for the P^4 and M^2, intermediate for P^4 and M^1, and lowest for P^4 and M^3. As for mandibular premolar-molar shape, levels of covariation for maxillary premolar shape are highest for the cercopithecids and lowest for the platyrrhines (Table 4.32).

In summary, given the low magnitude of the covariation between P4 and molar shape, the shape of the P4 is only subtly linked to that of the mandibular molars. Premolar crown shape can be affected by altering the relative sizes of its component parts (e.g., cusps, anterior fovea, and talonid). Such changes in relative size occurred during hominin evolution (e.g., Suwa, 1988). Given the low magnitude of covariation that exists between premolar and molar shape, such changes in hominin premolar shape probably do

not reflect the outcome of selection acting on set of traits that are united pleiotropically linked to the molars.

Molar Shape Covariation Within Species: Significant covariation is observed among mandibular molar shapes (Table 4.27). The highest level of shape covariation is between the M_1 and M_2 (anthropoid average $r^2 = 0.46$), lower for M_2 and M_3 (anthropoid average $r^2 = 0.37$), and lowest between the M_1 and M_3 (anthropoid average $r^2 = 0.29$), which is also the pattern for homologous dimensions of mandibular molar size. The strength of covariation is similar between taxonomic groups, though cercopithecids tend to express higher levels than either hominoids or platyrrhines. The low hominoid value for M_1-M_3 results partly from an exceptionally low estimate in *Hylobates lar*. An examination of the *Hylobates lar* data indicates that this is not an artifact of outliers in the data set; given that no other hylobatid was included in the analysis, it is unclear whether this represents a real distinction from the hominids or if it is an aberrantly low estimate for shape covariation. A similar pattern is observed among the shapes of the maxillary molars, where moderate levels of covariation characterize the M^1 and M^2 (anthropoid average $r^2 = 0.39$), a lower level is expressed for the M^2 and M^3 (anthropoid average $r^2 = 0.29$), and the lowest is for the M^1 and M^3 (anthropoid average $r^2 = 0.20$) (Table 4.28). Again, the same pattern observed for the size of the homologous dimensions of the maxillary molars and for the shapes of the mandibular molars. Average levels of covariation are similar for platyrrhines, hominoids, and cercopithecids for the M^1-M^2, though all comparisons with the M^3 shape are lower in platyrrhines. As discussed for molar size, the MD length of the platyrrhine M^3 expresses significantly lower levels of covariation with the lengths of the M^1 and M^2 than is observed in catarrhine taxa. The analysis of shape covariation

*TABLE 4.33. The magnitude of covariation among mandibular molar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M_1-M_2	M_1-M_3	M_2-M_3
Gorilla gorilla	$r^2 = 0.43$*** $n = 100$	$r^2 = 0.25$*** $n = 81$	$r^2 = 0.38$*** $n = 91$
Pan troglodytes	$r^2 = 0.56$*** $n = 92$	$r^2 = 0.23$*** $n = 75$	$r^2 = 0.30$** $n = 76$
Hylobates lar	$r^2 = 0.36$*** $n = 55$	$r^2 = 0.02$ $n = 33$	$r^2 = 0.22$** $n = 53$
Cercopithecus cephus	$r^2 = 0.40$*** $n = 79$	$r^2 = 0.31$*** $n = 71$	$r^2 = 0.45$*** $n = 71$
Cercopithecus nictitans	$r^2 = 0.68$*** $n = 73$	$r^2 = 0.48$*** $n = 64$	$r^2 = 0.61$*** $n = 70$
Cercopithecus pogonias	$r^2 = 0.65$*** $n = 66$	$r^2 = 0.64$*** $n = 59$	$r^2 = 0.63$*** $n = 64$
Macaca fascicularis	$r^2 = 0.37$*** $n = 82$	$r^2 = 0.28$*** $n = 60$	$r^2 = 0.42$*** $n = 67$
Colobus satanas	$r^2 = 0.38$*** $n = 51$	$r^2 = 0.15$** $n = 44$	$r^2 = 0.21$* $n = 44$
Ateles geoffroyi	$r^2 = 0.35$*** $n = 40$	$r^2 = 0.32$* $n = 27$	$r^2 = 0.27$* $n = 35$
Cebus libidinosus	$r^2 = 0.42$*** $n = 76$	$r^2 = 0.26$*** $n = 67$	$r^2 = 0.18$** $n = 64$
Weighted Anthropoid Average	$r^2 = 0.47$	$r^2 = 0.31$	$r^2 = 0.38$
Weighted Hominoid Average	$r^2 = 0.46$	$r^2 = 0.20$	$r^2 = 0.31$
Weighted Cercopithecid Average	$r^2 = 0.50$	$r^2 = 0.38$	$r^2 = 0.48$
Weighted Platyrrhine Average	$r^2 = 0.40$	$r^2 = 0.28$	$r^2 = 0.21$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	8/10	8/10

*TABLE 4.34. The magnitude of covariation among maxillary molar shapes (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	M^1-M^2	M^1-M^3	M^2-M^3
Gorilla gorilla	$r^2 = 0.43$*** $n = 113$	$r^2 = 0.24$*** $n = 90$	$r^2 = 0.55$*** $n = 96$
Pan troglodytes	$r^2 = 0.46$*** $n = 91$	$r^2 = 0.32$*** $n = 74$	$r^2 = 0.46$*** $n = 77$
Hylobates lar	$r^2 = 0.21$*** $n = 74$	$r^2 = 0.01$ $n = 51$	$r^2 = 0.01$ $n = 63$
Cercopithecus cephus	$r^2 = 0.32$*** $n = 80$	$r^2 = 0.21$*** $n = 67$	$r^2 = 0.06$* $n = 71$
Cercopithecus nictitans	$r^2 = 0.44$*** $n = 80$	$r^2 = 0.19$*** $n = 71$	$r^2 = 0.38$*** $n = 75$
Cercopithecus pogonias	$r^2 = 0.64$*** $n = 68$	$r^2 = 0.36$*** $n = 60$	$r^2 = 0.45$*** $n = 63$
Macaca fascicularis	$r^2 = 0.35$*** $n = 86$	$r^2 = 0.28$*** $n = 54$	$r^2 = 0.46$*** $n = 61$
Colobus satanas	$r^2 = 0.24$** $n = 52$	$r^2 = 0.23$** $n = 43$	$r^2 = 0.30$*** $n = 43$
Ateles geoffroyi	$r^2 = 0.37$*** $n = 54$	$r^2 = 0.12$* $n = 45$	$r^2 = 0.23$** $n = 44$
Cebus libidinosus	$r^2 = 0.40$*** $n = 81$	$r^2 = 0.05$* $n = 61$	$r^2 = 0.01$ $n = 61$
Weighted Anthropoid Average	$r^2 = 0.39$	$r^2 = 0.20$	$r^2 = 0.29$
Weighted Hominoid Average	$r^2 = 0.37$	$r^2 = 0.19$	$r^2 = 0.34$
Weighted Cercopithecid Average	$r^2 = 0.40$	$r^2 = 0.25$	$r^2 = 0.33$
Weighted Platyrrhine Average	$r^2 = 0.39$	$r^2 = 0.09$	$r^2 = 0.12$
Significantly different from zero ($p < \alpha = 0.01$)	10/10	7/10	7/10

TABLE 4.35. The average magnitude of covariation between maxillary and mandibular molar shapes.

	M^1-M_1	M^1-M_2	M^1-M_3
Weighted Anthropoid Average	$r^2 = 0.22$	$r^2 = 0.16$	$r^2 = 0.11$
Weighted Hominoid Average	$r^2 = 0.16$	$r^2 = 0.09$	$r^2 = 0.09$
Weighted Cercopithecid Average	$r^2 = 0.31$	$r^2 = 0.24$	$r^2 = 0.16$
Weighted Platyrrhine Average	$r^2 = 0.12$	$r^2 = 0.09$	$r^2 = 0.03$
Significantly different from zero ($p < \alpha = 0.01$)	8/10	7/10	5/10

	M^2-M_1	M^2-M_2	M^2-M_3
Weighted Anthropoid Average	$r^2 = 0.14$	$r^2 = 0.21$	$r^2 = 0.16$
Weighted Hominoid Average	$r^2 = 0.13$	$r^2 = 0.14$	$r^2 = 0.15$
Weighted Cercopithecid Average	$r^2 = 0.19$	$r^2 = 0.30$	$r^2 = 0.19$
Weighted Platyrrhine Average	$r^2 = 0.03$	$r^2 = 0.06$	$r^2 = 0.07$
Significantly different from zero ($p < \alpha = 0.01$)	5/10	7/10	7/10

	M^3-M_1	M^3-M_2	M^3-M_3
Weighted Anthropoid Average	$r^2 = 0.14$	$r^2 = 0.16$	$r^2 = 0.21$
Weighted Hominoid Average	$r^2 = 0.09$	$r^2 = 0.10$	$r^2 = 0.15$
Weighted Cercopithecid Average	$r^2 = 0.17$	$r^2 = 0.22$	$r^2 = 0.26$
Weighted Platyrrhine Average	$r^2 = 0.13$	$r^2 = 0.07$	$r^2 = 0.16$
Significantly different from zero ($p < \alpha = 0.01$)	4/10	5/10	8/10

TABLE 4.36. The magnitude of among-species covariation for P4 and molar shapes, branch lengths equal. All correlations significant at $p < 0.0001$.

	P^4	M^1	M^2
M^1	$r^2 = 0.54$ $n = 34$	—	—
M^2	$r^2 = 0.60$ $n = 34$	$r^2 = 0.75$ $n = 34$	—
M^3	$r^2 = 0.50$ $n = 34$	$r^2 = 0.75$ $n = 34$	$r^2 = 0.70$ $n = 34$

	P_4	M_1	M_2
M_1	$r^2 = 0.51$ $n = 34$	—	—
M_2	$r^2 = 0.37$ $n = 34$	$r^2 = 0.73$ $n = 34$	—
M_3	$r^2 = 0.34$ $n = 34$	$r^2 = 0.46$ $n = 34$	$r^2 = 0.54$ $n = 34$

	P^4	M^1	M^2	M^3
P_4	$r^2 = 0.59$ $n = 34$	$r^2 = 0.44$ $n = 34$	$r^2 = 0.28$ $n = 34$	$r^2 = 0.29$ $n = 34$
M_1	$r^2 = 0.44$ $n = 34$	$r^2 = 0.57$ $n = 34$	$r^2 = 0.47$ $n = 34$	$r^2 = 0.29$ $n = 34$
M_2	$r^2 = 0.48$ $n = 34$	$r^2 = 0.44$ $n = 34$	$r^2 = 0.61$ $n = 34$	$r^2 = 0.34$ $n = 34$
M_3	$r^2 = 0.35$ $n = 34$	$r^2 = 0.56$ $n = 34$	$r^2 = 0.62$ $n = 34$	$r^2 = 0.70$ $n = 34$

indicates, again, that the platyrrhine M^3 is more weakly connected by pleiotropy with the other maxillary molars than is typical in catarrhine primates.

Among-Species Postcanine Shape: Among species, premolar shape shows significant covariation with molar shape (Table 4.30). For the P_4, the level of covariation with mandibular molar shape is lower than is seen among the molars themselves, which is consistent with the magnitudes of covariation observed within species. Within species, it was observed that the P_4 covaries in shape most strongly with the M_2, less so with the M_1, least for the M_3. Among species, the pattern is slightly different, with the highest level of covariation existing between P_4-M_1, a lower level for P_4-M_2, and the lowest level for P_4-M_3. The pattern for the maxillary premolars is slightly different in magnitude. Overall, P^4 shape covaries more strongly with maxillary molar shape than was observed among the mandibular premolars and molars (especially so for comparisons with M^2 and M^3). This is unexpected given similarities in levels of covariation observed within species. Variation in the magnitude of covariation between P^4 and maxillary molar shape reflects that observed within species; it is highest between P^4-M^2, intermediate for P^4-M^1, and lowest for P^4-M^3.

Among species, mandibular molar shape covariation is similar in its pattern to that observed within species; molar shape covariation is stronger than observed with premolar shape and the pattern of magnitude differences is the same as observed for shape within species. Among-species covariation is highest for M_1-M_2 ($r^2 = 0.74$), intermediate for M_2-M_3 ($r^2 = 0.54$), and the lowest level for M_1-M_3 ($r^2 = 0.46$) (Table 4.36). Among species, maxillary molars covary more strongly in shape with one another than they do with the P^4. Expectedly, the highest level of covariation is between M^1-M^2

($r^2 = 0.75$); however, unexpectedly, the level of covariation between M^1-M^3 is equal to that between M^1-M^2 ($r^2 = 0.75$), and the lowest level is between M^2-M^3 ($r^2 = 0.70$).

Between arches the highest levels of covariation are seen between molars in similar positions in the opposite arch. The one exception is for the M^2, in which the covariation with the M_3 ($r^2 = 0.62$) is slightly higher than with the M_2 ($r^2 = 0.61$). This pattern is the same as observed within species, in which teeth in the same position in the opposite arch were the most highly covarying character pairs when shapes were compared between arches (Table 4.29). As food processing requires the interaction of the maxillary and mandibular postcanine teeth, it is not surprising that the shapes of the maxillary and mandibular teeth have coevolved.

Discussion and Summary

Covariation among postcanine size is strong within and among species, while covariation of postcanine and incisor size is weak. The postcanine teeth form both a functional and a variational module that shares only weak pleiotropic connections with the incisors. As with the incisors, covariation among sizes is strongest between homologous dimensions of adjacent teeth and slightly lower between teeth in the same position in the opposite arch. For shapes, the highest covariation is between neighbors of the same class in the same arch and between teeth in the same class in the same position in the opposite arch. The postcanine variational module is best characterized as a having two subdivisions, premolars and molars, that are not completely independent of each other. These quasi-autonomous modules correspond to the premolars and molars.

Within species, dimensions of three teeth are noted for sharing the least covariation with other members of the postcanine variational module ($P^{2,3}$MD, M^3MD, and all dimensions of the $P_{2,3}$). If the honing premolar evolved from a nonhoning ancestor

that was not characterized by premolar heteromorphy, then the honing premolar was likely parceled out of the postcanine variational module (as in Figure 1.1). This parcellation must have occurred before the divergence of platyrrhines and catarrhines. As a result of the functional and morphological specialization of the honing premolar, its occlusal partner, the mesial maxillary premolar, also evolved specialized morphology. The MD length of the mesial maxillary premolar was also likely parceled out of the remainder of the maxillary premolars. Lower magnitude covariation for the M^3MD, especially in platyrrhines where it is reduced in size relative to its catarrhine counterparts, may indicate that the first step towards significant reductions in relative M3 size also required a change of the covariance structure, which "individualized" the M3 (e.g., Stock, 2001).

As regards the mesial mandibular premolar, there is substantial variation in the degree of heteromorphy, shape, and occlusal morphology among extant anthropoids. During hominin evolution, subsequent to the loss of canine honing, the P_3 was morphologically transformed by adding an additional cusp lingually, closing the anterior fovea, altering its shape so it is no longer obliquely set in the postcanine row, and changing the orientation of the transverse crest to expand the posterior fovea (e.g., Delezene and Kimbel, 2011). As a result of these changes, premolar heteromorphy is significantly reduced in most hominins. Though not tested, the results of this study suggest that there is little reason to suspect that such a transformation reflects a coordinated response to selection acting on other postcanine traits that are pleiotropically linked to the P_3. If hominin sample sizes were sufficient, then it would be possible to determine if the P_3 became "integrated" with the P_4 as the premolars became more homomorphic (as in Figure 1.1)

Chapter 5

CANINE HONING COMPLEX MODULARITY

The honing complex is hypothesized to form a variational module. Both within and among species, covariation is predicted to be high in magnitude among the elements that comprise the complex and weak with characters in other functional modules. This hypothesis will be rejected if covariation is weak in magnitude among characters of the honing complex or if covariation is equal in magnitude between characters of the honing complex and the incisors and postcanine teeth. Following the developmental model of McCollum and Sharpe (2001) and the pleiotropy model of Jolly (1970), the hypothesis that within-species covariation is negative between the basal size of the canines and the size of the postcanine teeth is also tested. This hypothesis will be rejected if covariation with the postcanine dentition is either weak in magnitude or positive in direction. The hypothesis will also be rejected if covariation is negative or weak between the canines and the incisors. Following from the among-species analyses of Greenfield and Washburn (1992) and Greenfield (1992), the hypothesis that the honing complex coevolved in males but not females is tested. Using correlations of independent contrasts, Greenfield's hypothesis will be rejected if the canine honing complex significantly covaries among species in both males and females. Unlike in the previous chapters, in which males and females were pooled for analysis, males and females are considered separately in this chapter. The similarity of canine honing complex $\mathbf{p}_{max}$ between species and the correspondence of $\mathbf{\Delta z}$ and $\mathbf{p}_{max}$ will be investigated in Chapter 6 for a subset of species.

*TABLE 5.1. The magnitude of covarition for imensions of the mandibular canine (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1height–C_1MD	C_1height–C_1LL	C_1height–C_1base	C_1MD–C_1LL
Gorilla gorilla ♀	$r^2 = 0.06$ $n = 32$	$r^2 = 0.00$ $n = 34$	$r^2 = 0.01$ $n = 30$	$r^2 = 0.42$*** $n = 44$
Gorilla gorilla ♂	$r^2 = 0.21$** $n = 32$	$r^2 = 0.26$*** $n = 33$	$r^2 = 0.32$** $n =32$	$r^2 = 0.65$*** $n = 59$
Pan troglodytes ♀	$r^2 = 0.09$ $n = 36$	$r^2 = 0.08$ $n = 38$	$r^2 = 0.10$ $n = 36$	$r^2 = 0.33$*** $n = 46$
Pan troglodytes ♂	$r^2 = 0.28$** $n = 28$	$r^2 = 0.21$* $n = 24$	$r^2 = 0.20$* $n = 24$	$r^2 = 0.63$*** $n = 34$
Hylobates carpenteri ♀	$r^2 = 0.39$*** $n = 25$	$r^2 = 0.29$** $n = 24$	$r^2 = 0.36$** $n = 23$	$r^2 = 0.53$*** $n = 38$
Hylobates carpenteri ♂	$r^2 = 0.20$* $n = 19$	$r^2 = 0.30$** $n = 19$	$r^2 = 0.33$** $n = 19$	$r^2 = 0.32$*** $n = 41$
Cercopithecus cephus ♀	$r^2 = 0.25$* $n = 25$	$r^2 = 0.27$** $n = 22$	$r^2 = 0.31$** $n = 23$	$r^2 = 0.21$* $n = 28$
Cercopithecus cephus ♂	$r^2 = 0.15$ $n = 36$	$r^2 = 0.24$** $n = 37$	$r^2 = 0.23$* $n = 36$	$r^2 = 0.17$ $n = 49$
Cercopithecus nictitans ♀	$r^2 = 0.02$ $n = 25$	$r^2 = 0.04$ $n = 25$	$r^2 = 0.04$ $n = 25$	$r^2 = 0.05$ $n = 31$
Cercopithecus nictitans ♂	$r^2 = 0.33$*** $n = 38$	$r^2 = 0.26$*** $n = 37$	$r^2 = 0.38$*** $n = 37$	$r^2 = 0.35$*** $n = 47$
Cercopithecus pogonias ♀	$r^2 = 0.05$ $n = 21$	$r^2 = 0.31$* $n = 20$	$r^2 = 0.20$* $n = 20$	$r^2 = 0.29$** $n = 31$
Cercopithecus pogonias ♂	$r^2 = 0.04$ $n = 25$	$r^2 = 0.06$ $n = 22$	$r^2 = 0.08$ $n = 22$	$r^2 = 0.23$** $n = 33$
Macaca fascicularis ♀	$r^2 = 0.34$* $n = 26$	$r^2 = 0.06$ $n = 26$	$r^2 = 0.29$** $n = 26$	$r^2 = 0.08$ $n = 43$
Macaca fascicularis ♂	$r^2 = 0.30$** $n = 21$	$r^2 = 0.24$ $n = 18$	$r^2 = 0.33$* $n = 18$	$r^2 = 0.41$*** $n = 31$
Colobus satanas ♀	$r^2 = 0.22$* $n = 20$	$r^2 = 0.47$** $n = 19$	$r^2 = 0.52$*** $n = 19$	$r^2 = 0.23$* $n = 21$
Colobus satanas ♂	$n = 12$	$n = 12$	$n = 12$	$r^2 = 0.13$ $n = 20$
Ateles vellerosus ♀	$r^2 = 0.24$** $n = 29$	$r^2 = 0.19$* $n = 29$	$r^2 = 0.23$** $n = 29$	$r^2 = 0.49$*** $n = 36$
Ateles vellerosus ♂	$r^2 = 0.37$** $n = 20$	$r^2 = 0.37$** $n = 20$	$r^2 = 0.40$** $n = 20$	$r^2 = 0.74$*** $n = 28$
Cebus libidinosus ♀	$r^2 = 0.10$ $n = 30$	$r^2 = 0.28$** $n = 29$	$r^2 = 0.22$* $n = 29$	$r^2 = 0.35$*** $n = 35$
Cebus libidinosus ♂	$r^2 = 0.23$** $n = 29$	$r^2 = 0.13$ $n = 29$	$r^2 = 0.20$* $n = 29$	$r^2 = 0.50$*** $n = 37$
Hom. ♂ Avg.	$r^2 = 0.23$	$r^2 = 0.25$	$r^2 = 0.28$	$r^2 = 0.54$
Hom. ♀ Avg.	$r^2 = 0.16$	$r^2 = 0.10$	$r^2 = 0.14$	$r^2 = 0.42$
Cerc. ♂ Avg.	$r^2 = 0.21$	$r^2 = 0.21$	$r^2 = 0.27$	$r^2 = 0.26$
Cerc. ♀ Avg.	$r^2 = 0.18$	$r^2 = 0.21$	$r^2 = 0.26$	$r^2 = 0.16$
Plat. ♂ Avg.	$r^2 = 0.29$	$r^2 = 0.23$	$r^2 = 0.28$	$r^2 = 0.60$
Plat. ♀ Avg.	$r^2 = 0.17$	$r^2 = 0.24$	$r^2 = 0.23$	$r^2 = 0.42$

*TABLE 5.2. The magnitude of covariation for dimensions of the maxillary canine (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C^1height–C^1MD	C^1height–C^1LL	C^1height–C^1base	C^1MD–C^1LL
Gorilla gorilla ♀	$r^2 = 0.38$*** $n = 33$	$r^2 = 0.15$* $n = 34$	$r^2 = 0.34$*** $n =33$	$r^2 = 0.31$*** $n = 46$
Gorilla gorilla ♂	$r^2 = 0.36$** $n = 25$	$r^2 = 0.45$*** $n = 28$	$r^2 = 0.30$** $n =25$	$r^2 = 0.60$*** $n = 43$
Pan troglodytes ♀	$r^2 = 0.08$ $n = 34$	$r^2 = 0.01$ $n = 36$	$r^2 = 0.06$ $n = 33$	$r^2 = 0.22$** $n = 49$
Pan troglodytes ♂	$r^2 = 0.00$ $n = 20$	$r^2 = 0.00$ $n = 22$	$r^2 = 0.00$ $n = 19$	$r^2 = 0.44$*** $n = 36$
Hylobates carpenteri ♀	$n = 14$	$n = 13$	$n = 13$	$r^2 = 0.56$*** $n = 25$
Hylobates carpenteri ♂	$n = 12$	$n = 14$	$n = 12$	$r^2 = 0.55$*** $n = 24$
Cercopithecus cephus ♀	$r^2 = 0.39$** $n = 21$	$r^2 = 0.35$*** $n = 21$	$r^2 = 0.31$** $n = 21$	$r^2 = 0.11$ $n = 27$
Cercopithecus cephus ♂	$r^2 = 0.25$ $n = 15$	$r^2 = 0.20$ $n = 15$	$r^2 = 0.27$* $n = 15$	$r^2 = 0.41$*** $n = 32$
Cercopithecus nictitans ♀	$r^2 = 0.06$ $n = 22$	$r^2 = 0.09$ $n = 21$	$r^2 = 0.01$ $n = 21$	$r^2 = 0.02$ $n = 31$
Cercopithecus nictitans ♂	$n = 11$	$n = 10$	$n = 10$	$r^2 = 0.27$ $n = 24$
Cercopithecus pogonias ♀	$r^2 = 0.12$ $n = 19$	$r^2 = 0.22$* $n = 19$	$r^2 = 0.27$* $n = 19$	$r^2 = 0.06$ $n = 30$
Cercopithecus pogonias ♂	$n = 10$	$n = 10$	$n = 10$	$r^2 = 0.39$** $n = 21$
Macaca fascicularis ♀	$r^2 = 0.18$* $n = 22$	$r^2 = 0.06$ $n = 22$	$r^2 = 0.15$ $n = 22$	$r^2 = 0.04$ $n = 41$
Macaca fascicularis ♂	$n = 9$	$n = 9$	$n = 9$	$r^2 = 0.46$*** $n = 20$
Colobus satanas ♀	$r^2 = 0.07$ $n = 21$	$r^2 = 0.02$ $n = 21$	$r^2 = 0.06$ $n = 21$	$r^2 = 0.36$** $n = 22$
Colobus satanas ♂	$n = 4$	$n = 4$	$n = 4$	$n = 17$
Ateles vellerosus ♀	$r^2 = 0.27$* $n = 20$	$r^2 = 0.13$ $n = 20$	$r^2 = 0.23$* $n = 20$	$r^2 = 0.55$*** $n = 35$
Ateles vellerosus ♂	$n = 11$	$n = 11$	$n = 11$	$r^2 = 0.27$** $n = 26$
Cebus libidinosus ♀	$r^2 = 0.09$ $n = 28$	$r^2 = 0.07$ $n = 28$	$r^2 = 0.00$ $n = 28$	$r^2 = 0.14$* $n = 36$
Cebus libidinosus ♂	$r^2 = 0.20$* $n = 26$	$r^2 = 0.17$* $n = 27$	$r^2 = 0.22$* $n = 26$	$r^2 = 0.47$*** $n = 34$
Anthropoid Avg.	$r^2 = 0.20$	$r^2 = 0.14$	$r^2 = 0.17$	$r^2 = 0.32$
Hominoid ♂ Avg.	$r^2 = 0.20$	$r^2 = 0.25$	$r^2 = 0.17$	$r^2 = 0.53$
Hominoid ♀ Avg.	$r^2 = 0.26$	$r^2 = 0.07$	$r^2 = 0.20$	$r^2 = 0.33$
Cercopithecid ♂ Avg.	$r^2 = 0.25$	$r^2 = 0.20$	$r^2 = 0.27$	$r^2 = 0.38$
Cercopithecid ♀ Avg.	$r^2 = 0.16$	$r^2 = 0.15$	$r^2 = 0.16$	$r^2 = 0.10$
Platyrrhine ♂ Avg.	$r^2 = 0.20$	$r^2 = 0.17$	$r^2 = 0.22$	$r^2 = 0.38$
Platyrrhine ♀ Avg.	$r^2 = 0.17$	$r^2 = 0.10$	$r^2 = 0.10$	$r^2 = 0.34$

Results

Canine Dimensions Within Species: For both the maxillary and mandibular canines, basal dimensions do not strongly covary with canine heights. For mandibular canine height, 39 within-species comparisons were made with LL and MD dimensions; of these comparisons, 24 are significantly different from zero and all are positive (Table 5.1). The anthropoid average covariation (male and female r^2s pooled) for both C_1height-C_1MD and C_1height-C_1LL is $r^2 = 0.19$. If C_1 crown basal size is calculated as √(LL*MD), the average magnitude of covariation for C_1height-C_1base is $r^2 = 0.24$. For the maxillary canine height; of 26 within-species comparisons with LL and MD dimensions, 11 are significantly different from zero and all are positive. The anthropoid average covariation is $r^2 = 0.20$ for C^1height-C^1MD and $r^2 = 0.14$ for C^1height-C_1LL (Table 5.2). When covariation is considered for C^1height and the C^1 basal size is calculated as √(LL*MD), the average covariation for C^1height-C^1base is $r^2 = 0.17$. For males and females of all taxonomic groups, very low to low average levels of covariation are observed between canine height and basal size (Tables 5.1 and 5.2), which indicates that canine-crown height and basal size are not strongly linked by pleiotropy.

Basal dimensions moderately covary with one another for the mandibular canine (anthropoid average $r^2 = 0.37$ for C_1LL-C_1MD) (Table 5.1) and for the maxillary canine (anthropoid average $r^2 = 0.32$ for C^1LL-C^1MD) (Table 5.2). The basal dimensions of each canine covary more strongly in platyrrhines ($r^2 = 0.51$ for C_1LL-C_1MD and $r^2 = 0.36$ for C^1LL-C^1MD) and hominoids ($r^2 = 0.43$ for C_1LL-C_1MD and $r^2 = 0.36$ for C^1LL-C^1MD) than in cercopithecids ($r^2 = 0.22$ for C_1LL-C_1MD and $r^2 = 0.21$ for C^1LL-C^1MD). For the platyrrhines and hominoids, covariation between the dimensions of the canine bases slightly exceeds that between length and width of each incisor and postcanine tooth; the values in cercopithecids are similar (Chapters 3 and 4); however,

*TABLE 5.3. The magnitude of covariation between the heights and basal sizes of the maxillary and mandibular canines (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1height-C^1height	C_1base-C^1base
Gorilla gorilla ♀	$r^2 = 0.57$*** $n = 26$	$r^2 = 0.62$*** $n = 44$
Gorilla gorilla ♂	$r^2 = 0.77$*** $n = 17$	$r^2 = 0.75$*** $n = 40$
Pan troglodytes♀	$r^2 = 0.47$*** $n = 31$	$r^2 = 0.56$*** $n = 43$
Pan troglodytes ♂	$r^2 = 0.43$*** n = 15	$r^2 = 0.73$*** $n = 30$
Hylobates carpenteri ♀	$n = 14$	$r^2 = 0.57$*** $n = 24$
Hylobates carpenteri ♂	$n = 10$	$r^2 = 0.41$** $n = 23$
Cercopithecus cephus ♀	$r^2 = 0.36$*** $n = 19$	$r^2 = 0.67$*** $n = 24$
Cercopithecus cephus ♂	$r^2 = 0.87$*** $n = 15$	$r^2 = 0.74$*** $n = 32$
Cercopithecus nictitans ♀	$r^2 = 0.46$*** $n = 19$	$r^2 = 0.44$*** $n = 30$
Cercopithecus nictitans ♂	$n = 11$	$r^2 = 0.65$*** $n = 23$
Cercopithecus pogonias ♀	$r^2 = 0.68$*** $n = 17$	$r^2 = 0.28$** $n = 28$
Cercopithecus pogonias ♂	$n = 10$	$n = 19$
Macaca fascicularis ♀	$n = 11$	$r^2 = 0.39$*** $n = 39$
Macaca fascicularis ♂	$n = 8$	$n = 16$
Colobus satanas ♀	$r^2 = 0.41$** $n = 19$	$r^2 = 0.34$** $n = 21$
Ateles vellerosus ♀	$r^2 = 0.21$* $n = 19$	$r^2 = 0.65$*** $n = 33$
Ateles vellerosus ♂	$n = 9$	$n = 17$
Cebus libidinosus ♀	$r^2 = 0.81$*** $n = 26$	$r^2 = 0.30$** $n = 34$
Cebus libidinosus ♂	$r^2 = 0.74$*** $n = 22$	$r^2 = 0.53$*** $n = 34$
W. Hom. ♂ Avg.	$r^2 = 0.61$	$r^2 = 0.66$
W. Hom. ♀ Avg.	$r^2 = 0.52$	$r^2 = 0.59$
W. Cerco. ♂ Avg.	$r^2 = 0.87$	$r^2 = 0.70$
W. Cerco. ♀ Avg.	$r^2 = 0.47$	$r^2 = 0.42$
W.Plat. ♂ Avg.	$r^2 = 0.74$	$r^2 = 0.53$
W.Plat. ♀ Avg.	$r^2 = 0.56$	$r^2 = 0.47$

the magnitude of covariation does not approach that observed among homologous dimensions of the incisors or of the postcanine dentition in any taxonomic group.

Between the maxillary and mandibular canines, basal size (calculated as √(MD*LL)) covaries moderately (anthropoid average $r^2 = 0.56$) (Table 5.3), which is comparable to the magnitude observed among homologous dimensions of the incisors and postcanine teeth. All 16 comparisons of basal size within species are significantly different from zero at $\alpha = 0.05$ and $\alpha = 0.01$; 12 are significantly different from zero at $\alpha = 0.001$. Moderate to high levels of covariation characterize the canine basal areas of all taxonomic groups and sexes (Table 5.3). The average magnitude of covariation between the canine bases is higher than that observed by Cochard (1981) (($r^2 = 0.35$ for ♂C^1LL-C_1LL, $r^2 = 0.24$ for ♀C^1LL-C_1LL, $r^2 = 0.05$ for ♂C^1MD-C_1MD, and $r^2 = 0.13$ for ♀C^1MD-C_1MD). The basal areas of the mandibular and maxillary canines are strongly linked by pleiotropy and thus are expected to coevolve among species.

As maxillary canine heights are not adequately represented in all samples, a restricted set was analyzed. For maxillary and mandibular canine crown heights, moderate to very high levels of covariation are observed for all taxonomic groups and sexes (Table 5.3), with an anthropoid average (male and female r^2s pooled) of $r^2 = 0.56$. All 12 comparisons of canine heights are significantly different from zero at $\alpha = 0.05$; 11 are significantly different from zero at $\alpha = 0.01$; and 10 are significantly different from zero at $\alpha = 0.001$. As discussed in Chapter 2, the minimum sample size for analyses of canine heights was set at $n = 15$. As a result, only a single male cercopithecid sample (*Cercopithecus cephus*) and a single platyrrhine male sample (*Cebus libidinosus*) were included in the analysis of canine height covariation. For both of these male samples, the estimate of r^2 is very high (i.e., > 0.60). It is unwarranted to assume that such strong covariation characterizes all platyrrhine and cercopithecid male samples; future data

collection and analysis will reveal whether this is true or not. Taxonomic coverage is much better for females; all taxonomic averages display moderate levels (i.e., $0.40 < r^2 \leq 0.60$) of covariation between the arches.

In summary, as with other functional modules in the dentition, not all dimensions of the canines covary equally. Canine basal dimensions and heights do not covary strongly within species. Between the arches, canine basal areas strongly covary with one another, as do canine heights in a limited sample. Therefore, the evolution of canine heights and basal areas are not likely to have constrained one another during primate evolution; however, evolutionary change in canine heights should be strongly constrained, as should changes in canine basal areas. These points that will be revisited below in the among-species analysis and in Chapter 7 when the evolution of the hominin canine honing complex is discussed. The independence of canine height and basal size can also be seen in indices of dimorphism for various canine dimensions. Though all dimensions of the canine have larger means in males than females, the heights of the canines tend to be much more dimorphic than bases (see Table 1 in Plavcan and van Schaik, 1992), which suggests that genetic networks responsible for the generation of larger canine heights in males are not extensively shared with other canine dimensions.

Covariation of the Canines with the Incisors and Postcanine Dentition Within Species: Canine basal dimensions vary independently of the breadths and lengths of the incisors and postcanine teeth. This is true for both the MD (Table 5.4) and LL (Table 5.5) dimensions of the mandibular canine and for MD (Table 5.6) and LL (Table 5.7) dimensions of the maxillary canine. The average magnitudes of covariation are very low to low; of the 20 incisor and postcanine dimensions compared to canine basal size, 15 have an average $r^2 < 0.20$. The comparisons with the highest average r^2 include the

*TABLE 5.4. The magnitude of covariation between mandibular canine and incisor and postcanine length (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1MD - I_1MD	C_1MD - I_2MD	C_1MD- P_4MD	C_1MD- M_1MD	C_1MD- M_2MD
Gorilla gorilla ♂	$r^2 = 0.18$ $n = 20$	$r^2 = 0.26$** $n = 27$	$r^2 = 0.11$** $n = 63$	$r^2 = 0.12$** $n = 60$	$r^2 = 0.27$*** $n = 62$
Gorilla gorilla ♀	$r^2 = 0.19$* $n = 29$	$r^2 = 0.05$ $n = 35$	$r^2 = 0.16$** $n = 46$	$r^2 = 0.09$* $n = 45$	$r^2 = 0.16$** $n = 47$
Pan troglodytes ♂	$r^2 = 0.20$* $n = 27$	$r^2 = 0.26$** $n = 29$	$r^2 = 0.26$** $n = 35$	$r^2 = 0.12$* $n = 37$	$r^2 = 0.18$** $n = 38$
Pan troglodytes ♀	$r^2 = 0.09$ $n = 41$	$r^2 = 0.10$* $n = 43$	$r^2 = 0.11$* $n = 50$	$r^2 = 0.06$ $n = 48$	$r^2 = 0.05$ $n = 49$
Hylobates carpenteri ♂	$r^2 = 0.18$* $n = 27$	$r^2 = 0.26$** $n = 34$	$r^2 = 0.22$** $n = 34$	$r^2 = 0.14$* $n = 31$	$r^2 = 0.10$ $n = 39$
Hylobates carpenteri ♀	$r^2 = -0.04$ $n = 25$	$r^2 = -0.02$ $n = 29$	$r^2 = 0.18$* $n = 34$	$r^2 = 0.17$* $n = 29$	$r^2 = 0.15$* $n = 36$
Cercopithecus cephus ♂	$r^2 = 0.02$ $n = 45$	$r^2 = 0.05$ $n = 48$	$r^2 = 0.10$* $n = 50$	$r^2 = 0.11$* $n = 49$	$r^2 = 0.28$*** $n = 50$
Cercopithecus cephus ♀	$r^2 = 0.11$ $n = 24$	$r^2 = 0.11$ $n = 28$	$r^2 = 0.12$ $n = 30$	$r^2 = 0.18$* $n = 30$	$r^2 = 0.21$* $n = 30$
Cercopithecus nictitans ♂	$r^2 = 0.04$ $n = 39$	$r^2 = 0.14$* $n = 43$	$r^2 = 0.36$*** $n = 49$	$r^2 = 0.47$*** $n = 44$	$r^2 = 0.42$*** $n = 48$
Cercopithecus nictitans ♀	$r^2 = -0.01$ $n = 28$	$r^2 = 0.02$ $n = 30$	$r^2 = 0.10$ $n = 32$	$r^2 = 0.00$ $n = 29$	$r^2 = 0.02$ $n = 32$
Cercopithecus pogonias ♂	$r^2 = -0.01$ $n = 18$	$r^2 = 0.08$ $n = 29$	$r^2 = 0.09$ $n = 36$	$r^2 = 0.06$ $n = 32$	$r^2 = 0.19$** $n = 35$
Cercopithecus pogonias ♀	$r^2 = 0.00$ $n = 29$	$r^2 = 0.00$ $n = 29$	$r^2 = 0.12$ $n = 31$	$r^2 = 0.06$ $n = 31$	$r^2 = 0.08$ $n = 32$
Macaca fascicularis ♂	$r^2 = 0.33$** $n = 22$	$n = 19$	$r^2 = 0.42$*** $n = 35$	$r^2 = 0.25$** $n = 34$	$r^2 = 0.38$*** $n = 35$
Macaca fascicularis ♀	$r^2 = 0.10$ $n = 39$	$r^2 = 0.02$ $n = 39$	$r^2 = 0.38$*** $n = 42$	$r^2 = 0.07$ $n = 41$	$r^2 = 0.17$** $n = 43$
Colobus satanas ♂	$r^2 = -0.06$ $n = 20$	$r^2 = 0.03$ $n = 20$	$r^2 = 0.00$ $n = 20$	$r^2 = 0.08$ $n = 20$	$r^2 = 0.00$ $n = 20$
Colobus satanas ♀	$r^2 = 0.09$ $n = 20$	$r^2 = 0.10$ $n = 21$	$r^2 = 0.37$** $n = 22$	$r^2 = 0.27$* $n = 22$	$r^2 = 0.26$* $n = 22$
Ateles vellerosus ♂	$r^2 = 0.02$ $n = 25$	$r^2 = 0.11$ $n = 26$	$r^2 = 0.45$*** $n = 29$	$r^2 = 0.23$** $n = 28$	$r^2 = 0.24$** $n = 27$
Ateles vellerosus ♀	$r^2 = 0.04$ $n = 32$	$r^2 = 0.15$* $n = 33$	$r^2 = 0.26$** $n = 34$	$r^2 = 0.19$* $n = 34$	$r^2 = 0.28$** $n = 33$
Cebus libidinosus ♂	$r^2 = 0.28$** $n = 28$	$r^2 = 0.11$* $n = 38$	$r^2 = 0.04$ $n = 38$	$r^2 = 0.17$** $n = 39$	$r^2 = 0.22$** $n = 37$
Cebus libidinosus ♀	$r^2 = 0.24$* $n = 25$	$r^2 = 0.05$ $n = 34$	$r^2 = 0.00$ $n = 34$	$r^2 = 0.02$ $n = 34$	$r^2 = 0.03$ $n = 35$
Weighted Hom. Avg.	$r^2 = 0.11$	$r^2 = 0.11$	$r^2 = 0.14$	$r^2 = 0.10$	$r^2 = 0.15$
Weighted Cercopith. Avg.	$r^2 = 0.06$	$r^2 = 0.06$	$r^2 = 0.22$	$r^2 = 0.16$	$r^2 = 0.22$
Weighted Plat. Avg.	$r^2 = 0.14$	$r^2 = 0.10$	$r^2 = 0.17$	$r^2 = 0.15$	$r^2 = 0.19$
Wghted Avg.	$r^2 = 0.10$	$r^2 = 0.10$	$r^2 = 0.19$	$r^2 = 0.14$	$r^2 = 0.19$

*TABLE 5.5. The magnitude of covariation between mandibular canine and incisor and postcanine breadth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1LL - I_1LL	C_1LL - I_2LL	C_1LL - P_4BL	C_1LL- M_1BL	C_1LL- M_2BL
Gorilla gorilla ♂	$r^2 = 0.24^{**}$ $n = 37$	$r^2 = 0.15^{**}$ $n = 45$	$r^2 = 0.06$ $n = 56$	$r^2 = 0.09^{*}$ $n = 51$	$r^2 = 0.09^{*}$ $n = 58$
Gorilla gorilla ♀	$r^2 = 0.18^{**}$ $n = 40$	$r^2 = 0.32^{***}$ $n = 47$	$r^2 = 0.33^{***}$ $n = 47$	$r^2 = 0.16^{**}$ $n = 41$	$r^2 = 0.16^{**}$ $n = 47$
Pan troglodytes ♂	$r^2 = 0.29^{**}$ $n = 26$	$r^2 = 0.28^{**}$ $n = 27$	$r^2 = 0.18^{*}$ $n = 31$	$r^2 = 0.02$ $n = 0.505$	$r^2 = 0.10$ $n = 31$
Pan troglodytes ♀	$r^2 = 0.27^{***}$ $n = 41$	$r^2 = 0.28^{***}$ $n = 43$	$r^2 = 0.10^{*}$ $n = 44$	$r^2 = 0.11^{*}$ $n = 46$	$r^2 = 0.10^{*}$ $n = 44$
Hylobates carpenteri ♂	$r^2 = 0.07$ $n = 35$	$r^2 = 0.10$ $n = 36$	$r^2 = 0.32^{***}$ $n = 33$	$r^2 = 0.28^{**}$ $n = 24$	$r^2 = 0.41^{***}$ $n = 35$
Hylobates carpenteri ♀	$r^2 = 0.09$ $n = 31$	$r^2 = 0.07$ $n = 34$	$r^2 = 0.21^{**}$ $n = 33$	$r^2 = 0.33^{**}$ $n = 22$	$r^2 = 0.13^{*}$ $n = 34$
Cercopithecus cephus ♂	$r^2 = 0.01$ $n = 47$	$r^2 = 0.13^{*}$ $n = 47$	$r^2 = 0.21^{***}$ $n = 49$	$r^2 = 0.12^{*}$ $n = 49$	$r^2 = 0.12^{*}$ $n = 49$
Cercopithecus cephus ♀	$r^2 = 0.32^{**}$ $n = 26$	$r^2 = 0.42^{***}$ $n = 27$	$r^2 = 0.10$ $n = 28$	$r^2 = 0.25^{**}$ $n = 27$	$r^2 = 0.16^{*}$ $n = 28$
Cercopithecus nictitans ♂	$r^2 = 0.15^{*}$ $n = 39$	$r^2 = 0.24^{***}$ $n = 42$	$r^2 = 0.20^{**}$ $n = 45$	$r^2 = 0.31^{***}$ $n = 40$	$r^2 = 0.24^{***}$ $n = 46$
Cercopithecus nictitans ♀	$r^2 = 0.25^{**}$ $n = 29$	$r^2 = 0.26^{**}$ $n = 30$	$r^2 = 0.25^{**}$ $n = 31$	$r^2 = 0.03$ $n = 28$	$r^2 = 0.03$ $n = 31$
Cercopithecus pogonias ♂	$r^2 = 0.06$ $n = 27$	$r^2 = 0.28^{**}$ $n = 28$	$r^2 = 0.31^{***}$ $n = 33$	$r^2 = 0.17^{*}$ $n = 32$	$r^2 = 0.05$ $n = 34$
Cercopithecus pogonias ♀	$r^2 = 0.21^{**}$ $n = 30$	$r^2 = 0.11$ $n = 30$	$r^2 = 0.32^{***}$ $n = 31$	$r^2 = 0.04$ $n = 31$	$r^2 = 0.05$ $n = 32$
Macaca fascicularis ♂	$r^2 = 0.23^{*}$ $n = 21$	$r^2 = 0.54^{***}$ $n = 20$	$r^2 = 0.21^{**}$ $n = 30$	$r^2 = 0.09$ $n = 30$	$r^2 = 0.17^{*}$ $n = 32$
Macaca fascicularis ♀	$r^2 = 0.07$ $n = 38$	$r^2 = 0.07$ $n = 38$	$r^2 = 0.18^{**}$ $n = 43$	$r^2 = 0.07$ $n = 39$	$r^2 = 0.09^{*}$ $n = 42$
Colobus satanas ♂	$r^2 = 0.00$ $n = 20$	$r^2 = -0.03$ $n = 20$	$r^2 = 0.03$ $n = 20$	$r^2 = 0.00$ $n = 20$	$r^2 = 0.01$ $n = 20$
Colobus satanas ♀	$r^2 = 0.28^{*}$ $n = 20$	$r^2 = 0.06$ $n = 20$	$r^2 = 0.12$ $n = 21$	$r^2 = 0.48^{***}$ $n = 21$	$r^2 = 0.49^{***}$ $n = 21$
Ateles vellerosus ♂	$r^2 = 0.44^{***}$ $n = 28$	$r^2 = 0.61^{***}$ $n = 29$	$r^2 = 0.55^{***}$ $n = 23$	$n = 14$	$n = 16$
Ateles vellerosus ♀	$r^2 = 0.15^{*}$ $n = 32$	$r^2 = 0.21^{**}$ $n = 32$	$r^2 = 0.30^{**}$ $n = 29$	$r^2 = 0.19^{*}$ $n = 28$	$r^2 = 0.26^{**}$ $n = 29$
Cebus libidinosus ♂	$r^2 = 0.07$ $n = 36$	$r^2 = 0.05$ $n = 38$	$r^2 = 0.09$ $n = 38$	$r^2 = 0.04$ $n = 38$	$r^2 = 0.05$ $n = 37$
Cebus libidinosus ♀	$r^2 = 0.24^{**}$ $n = 34$	$r^2 = 0.15^{*}$ $n = 35$	$r^2 = 0.19^{*}$ $n = 32$	$r^2 = 0.19^{*}$ $n = 33$	$r^2 = 0.24^{**}$ $n = 35$
Weighted Hom. Avg.	$r^2 = 0.18$	$r^2 = 0.19$	$r^2 = 0.16$	$r^2 = 0.14$	$r^2 = 0.12$
Weighted Cerco. Avg.	$r^2 = 0.14$	$r^2 = 0.20$	$r^2 = 0.20$	$r^2 = 0.15$	$r^2 = 0.14$
Weighted Plat. Avg.	$r^2 = 0.21$	$r^2 = 0.24$	$r^2 = 0.25$	$r^2 = 0.13$	$r^2 = 0.18$
Weighted Anthro. Avg.	$r^2 = 0.17$	$r^2 = 0.21$	$r^2 = 0.21$	$r^2 = 0.15$	$r^2 = 0.15$

*TABLE 5.6: The magnitude of covariation between maxillary canine and incisor and postcanine length (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C^1MD-I^1MD	C^1MD-I^2MD	C^1MD-P^4 MD	C^1MD-M^1MD	C^1MD-M^2MD
Gorilla gorilla ♂	$r^2 = 0.10$ $n = 23$	$r^2 = 0.44$*** $n = 22$	$r^2 = 0.24$*** $n = 42$	$r^2 = 0.17$** $n = 42$	$r^2 = 0.18$** $n = 42$
Gorilla gorilla ♀	$r^2 = 0.32$** $n = 23$	$r^2 = 0.42$*** $n = 26$	$r^2 = 0.35$*** $n = 45$	$r^2 = 0.25$** $n = 42$	$r^2 = 0.13$* $n = 45$
Pan troglodytes ♂	$r^2 = 0.33$** $n = 22$	$r^2 = 0.43$*** $n = 22$	$r^2 = 0.20$** $n = 33$	$r^2 = 0.26$** $n = 34$	$r^2 = 0.14$* $n = 37$
Pan troglodytes ♀	$r^2 = 0.02$ $n = 40$	$r^2 = 0.24$*** $n = 40$	$r^2 = 0.05$ $n = 47$	$r^2 = 0.03$ $n = 48$	$r^2 = 0.04$ $n = 48$
Hylobates carpenteri ♂	$n = 12$	$n = 19$	$r^2 = 0.01$ $n = 23$	$r^2 = 0.01$ $n = 22$	$r^2 = 0.00$ $n = 23$
Hylobates carpenteri ♀	$n = 14$	$n = 13$	$r^2 = 0.35$** $n = 25$	$r^2 = 0.14$ $n = 25$	$r^2 = 0.35$*** $n = 26$
Cercopithecus cephus ♂	$r^2 = 0.13$ $n = 30$	$r^2 = 0.08$ $n = 28$	$r^2 = 0.26$** $n = 34$	$r^2 = 0.19$* $n = 34$	$r^2 = 0.35$*** $n = 34$
Cercopithecus cephus ♀	$r^2 = 0.13$ $n = 25$	$r^2 = 0.13$ $n = 25$	$r^2 = 0.08$ $n = 27$	$r^2 = 0.38$*** $n = 27$	$r^2 = 0.34$** $n = 27$
Cercopithecus nictitans ♂	$r^2 = 0.15$ $n = 22$	$r^2 = 0.05$ $n = 22$	$r^2 = 0.06$ $n = 25$	$r^2 = 0.13$ $n = 25$	$r^2 = 0.11$ $n = 25$
Cercopithecus nictitans ♀	$r^2 = 0.23$** $n = 27$	$r^2 = 0.07$ $n = 30$	$r^2 = 0.20$* $n = 31$	$r^2 = 0.01$ $n = 31$	$r^2 = 0.08$ $n = 31$
Cercopithecus pogonias ♂	$n = 12$	$n = 14$	$n = 19$	$n = 19$	$r^2 = 0.29$* $n = 21$
Cercopithecus pogonias ♀	$r^2 = 0.21$* $n = 24$	$r^2 = 0.13$ $n = 26$	$r^2 = 0.14$* $n = 30$	$r^2 = 0.04$ $n = 30$	$r^2 = 0.19$* $n = 30$
Macaca fascicularis ♂	$n = 15$	$n = 19$	$n = 19$	$n = 19$	$n = 19$
Macaca fascicularis ♀	$r^2 = 0.13$* $n = 30$	$r^2 = 0.01$ $n = 39$	$r^2 = 0.08$ $n = 40$	$r^2 = 0.03$ $n = 40$	$r^2 = 0.09$ $n = 41$
Colobus satanas ♂	$n = 17$	$n = 17$	$n = 17$	$n = 17$	$n = 17$
Colobus satanas ♀	$r^2 = 0.15$ $n = 20$	$r^2 = 0.41$*** $n = 22$	$r^2 = 0.27$* $n = 22$	$r^2 = 0.05$ $n = 22$	$r^2 = 0.11$ $n = 22$
Ateles vellerosus ♂	$n = 14$	$n = 15$	$n = 18$	$n = 18$	$n = 17$
Ateles vellerosus ♀	$r^2 = 0.22$** $n = 31$	$r^2 = 0.51$*** $n = 29$	$r^2 = 0.21$** $n = 30$	$r^2 = 0.39$*** $n = 30$	$r^2 = 0.60$*** $n = 29$
Cebus libidinosus ♂	$r^2 = 0.18$* $n = 35$	$r^2 = 0.12$* $n = 35$	$r^2 = 0.00$ $n = 36$	$r^2 = 0.10$ $n = 36$	$r^2 = 0.12$* $n = 36$
Cebus libidinosus ♀	$r^2 = 0.24$** $n = 34$	$r^2 = 0.26$** $n = 34$	$r^2 = 0.04$ $n = 36$	$r^2 = 0.00$ $n = 36$	$r^2 = 0.00$ $n = 36$
Weighted Hom. Avg.	$r^2 = 0.16$	$r^2 = 0.36$	$r^2 = 0.20$	$r^2 = 0.15$	$r^2 = 0.13$
Weighted Cerco. Avg.	$r^2 = 0.16$	$r^2 = 0.11$	$r^2 = 0.15$	$r^2 = 0.11$	$r^2 = 0.19$
Weighted Plat. Avg.	$r^2 = 0.21$	$r^2 = 0.28$	$r^2 = 0.08$	$r^2 = 0.15$	$r^2 = 0.22$
Weighted Anthro. Avg.	$r^2 = 0.18$	$r^2 = 0.22$	$r^2 = 0.16$	$r^2 = 0.13$	$r^2 = 0.17$

*TABLE 5.7: The magnitude of covariation between maxillary canine and incisor and postcanine breadth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C^1LL - I^1LL	C^1LL - I^2LL	C^1LL - P^4BL	C^1LL- M^1BL	C^1LL- M^2BL
Gorilla gorilla ♂	$r^2 = 0.21$* $n = 29$	$r^2 = 0.36$*** $n = 33$	$r^2 = 0.07$ $n = 55$	$r^2 = 0.10$* $n = 53$	$r^2 = 0.10$* $n = 52$
Gorilla gorilla ♀	$r^2 = 0.36$*** $n = 33$	$r^2 = 0.18$* $n = 31$	$r^2 = 0.20$** $n = 32$	$r^2 = 0.15$* $n = 34$	$r^2 = 0.24$** $n = 35$
Pan troglodytes ♂	$r^2 = 0.25$** $n = 28$	$r^2 = 0.29$** $n = 31$	$r^2 = 0.15$* $n = 34$	$r^2 = 0.10$ $n = 37$	$r^2 = 0.03$ $n = 39$
Pan troglodytes ♀	$r^2 = 0.34$*** $n = 46$	$r^2 = 0.08$ $n = 48$	$r^2 = 0.14$** $n = 52$	$r^2 = 0.03$ $n = 53$	$r^2 = 0.00$ $n = 51$
Hylobates carpenteri♂	$n = 18$	$r^2 = 0.21$* $n = 27$	$r^2 = 0.22$* $n = 29$	$r^2 = 0.18$* $n = 26$	$r^2 = 0.25$** $n = 29$
Hylobates carpenteri ♀	$n = 15$	$r^2 = 0.30$** $n = 22$	$r^2 = 0.18$* $n = 27$	$r^2 = 0.05$ $n = 25$	$r^2 = 0.15$* $n = 28$
Cercopithecus cephus ♂	$r^2 = 0.27$*** $n = 36$	$r^2 = 0.13$* $n = 37$	$r^2 = 0.34$*** $n = 38$	$r^2 = 0.23$** $n = 38$	$r^2 = 0.31$*** $n = 38$
Cercopithecus cephus ♀	$r^2 = 0.44$*** $n = 27$	$r^2 = 0.17$* $n = 27$	$r^2 = 0.18$* $n = 29$	$r^2 = 0.19$* $n = 28$	$r^2 = 0.25$** $n = 29$
Cercopithecus nictitans ♂	$r^2 = 0.00$ $n = 29$	$r^2 = 0.04$ $n = 31$	$r^2 = 0.15$* $n = 35$	$r^2 = 0.05$ $n = 33$	$r^2 = 0.14$* $n = 35$
Cercopithecus nictitans ♀	$r^2 = 0.04$ $n = 29$	$r^2 = 0.03$ $n = 30$	$r^2 = 0.11$ $n = 33$	$r^2 = 0.14$* $n = 31$	$r^2 = 0.06$ $n = 33$
Cercopithecus pogonias ♂	$n = 19$	$n = 18$	$r^2 = -0.01$ $n = 28$	$r^2 = 0.00$ $n = 27$	$r^2 = 0.00$ $n = 28$
Cercopithecus pogonias ♀	$r^2 = -0.01$ $n = 28$	$r^2 = 0.05$ $n = 29$	$r^2 = 0.03$ $n = 33$	$r^2 = 0.00$ $n = 33$	$r^2 = 0.00$ $n = 33$
Macaca fascicularis ♂	$r^2 = 0.16$ $n = 20$	$r^2 = 0.00$ $n = 23$	$r^2 = 0.25$** $n = 26$	$r^2 = 0.05$ $n = 26$	$r^2 = 0.15$* $n = 27$
Macaca fascicularis ♀	$r^2 = 0.19$** $n = 39$	$r^2 = 0.29$*** $n = 40$	$r^2 = 0.26$*** $n = 40$	$r^2 = 0.22$** $n = 40$	$r^2 = 0.21$** $n = 42$
Colobus satanas ♂	$n = 19$	$r^2 = 0.10$ $n = 20$	$r^2 = 0.29$* $n = 20$	$r^2 = 0.22$* $n = 20$	$r^2 = 0.26$* $n = 20$
Colobus satanas ♀	$r^2 = 0.21$* $n = 20$	$r^2 = 0.22$* $n = 22$	$r^2 = 0.21$* $n = 22$	$r^2 = 0.07$ $n = 22$	$r^2 = 0.28$* $n = 22$
Ateles vellerosus ♂	$n = 18$	$r^2 = 0.08$ $n = 22$	$n = 16$	$n = 17$	$n = 16$
Ateles vellerosus ♀	$r^2 = 0.30$*** $n = 31$	$r^2 = 0.42$*** $n = 32$	$r^2 = 0.10$ $n = 30$	$r^2 = 0.11$ $n = 30$	$r^2 = 0.17$* $n = 32$
Cebus libidinosus♂	$r^2 = 0.36$*** $n = 37$	$r^2 = 0.09$ $n = 37$	$r^2 = 0.47$*** $n = 36$	$r^2 = 0.17$* $n = 37$	$r^2 = 0.38$*** $n = 37$
Cebus libidinosus♀	$r^2 = 0.26$*** $n = 36$	$r^2 = 0.14$* $n = 34$	$r^2 = 0.21$** $n = 36$	$r^2 = 0.44$*** $n = 36$	$r^2 = 0.48$*** $n = 36$
Weighted Hom. Avg.	$r^2 = 0.30$	$r^2 = 0.22$	$r^2 = 0.15$	$r^2 = 0.09$	$r^2 = 0.11$
Weighted Cerco. Avg.	$r^2 = 0.16$	$r^2 = 0.12$	$r^2 = 0.18$	$r^2 = 0.20$	$r^2 = 0.16$
Weighted Plat. Avg.	$r^2 = 0.31$	$r^2 = 0.19$	$r^2 = 0.27$	$r^2 = 0.25$	$r^2 = 0.35$
Weighted Anthro. Avg.	$r^2 = 0.23$	$r^2 = 0.17$	$r^2 = 0.18$	$r^2 = 0.13$	$r^2 = 0.18$

*TABLE 5.8. The magnitude of covariation between mandibular canine height and incisor and postcanine length (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1height - I_1MD	C_1height - I_2MD	C_1height - P_4 MD	C_1height - M_1MD	C_1height - M_2MD
Gorilla gorilla ♂	$n = 10$	$r^2 = 0.11$ $n = 15$	$r^2 = 0.00$ $n = 34$	$r^2 = -0.02$ $n = 31$	$r^2 = 0.00$ $n = 34$
Gorilla gorilla ♀	$r^2 = 0.02$ $n = 23$	$r^2 = 0.06$ $n = 27$	$r^2 = 0.00$ $n = 29$	$r^2 = 0.08$ $n = 30$	$r^2 = 0.00$ $n = 30$
Pan troglodytes ♂	$r^2 = 0.32$* $n = 18$	$r^2 = 0.25$* $n = 18$	$r^2 = 0.06$ $n = 24$	$r^2 = 0.06$ $n = 25$	$r^2 = 0.22$* $n = 26$
Pan troglodytes ♀	$r^2 = 0.04$ $n = 35$	$r^2 = 0.00$ $n = 37$	$r^2 = 0.09$ $n = 38$	$r^2 = 0.10$ $n = 37$	$r^2 = 0.03$ $n = 38$
Hylobates carpenteri ♂	$r^2 = 0.04$ $n = 16$	$r^2 = 0.02$ $n = 19$	$r^2 = 0.00$ $n = 17$	$r^2 = 0.10$ $n = 16$	$r^2 = 0.04$ $n = 20$
Hylobates carpenteri ♀	$r^2 = -0.14$ $n = 18$	$r^2 = -0.03$ $n = 21$	$r^2 = 0.10$ $n = 21$	$r^2 = 0.02$ $n = 18$	$r^2 = -0.04$ $n = 22$
Cercopithecus cephus ♂	$r^2 = 0.05$ $n = 34$	$r^2 = 0.16$* $n = 36$	$r^2 = 0.05$ $n = 37$	$r^2 = 0.06$ $n = 37$	$r^2 = 0.09$ $n = 37$
Cercopithecus cephus ♀	$r^2 = 0.18$* $n = 22$	$r^2 = 0.20$* $n = 25$	$r^2 = 0.03$ $n = 25$	$r^2 = 0.17$* $n = 25$	$r^2 = 0.09$ $n = 25$
Cercopithecus nictitans ♂	$r^2 = 0.05$ $n = 31$	$r^2 = 0.18$* $n = 35$	$r^2 = 0.23$** $n = 38$	$r^2 = 0.25$** $n = 36$	$r^2 = 0.14$* $n = 38$
Cercopithecus nictitans ♀	$r^2 = 0.18$* $n = 23$	$r^2 = 0.02$ $n = 25$	$r^2 = 0.00$ $n = 25$	$r^2 = 0.02$ $n = 23$	$r^2 = 0.12$ $n = 25$
Cercopithecus pogonias ♂	$r^2 = 0.02$ $n = 17$	$r^2 = 0.02$ $n = 25$	$r^2 = -0.01$ $n = 25$	$r^2 = -0.08$ $n = 24$	$r^2 = 0.00$ $n = 25$
Cercopithecus pogonias ♀	$r^2 = 0.27$* $n = 21$	$r^2 = 0.07$ $n = 21$	$r^2 = 0.22$* $n = 21$	$r^2 = 0.22$* $n = 21$	$r^2 = 0.40$* $n = 21$
Macaca fascicularis ♂	$r^2 = 0.19$ $n = 19$	$r^2 = 0.38$** $n = 18$	$r^2 = 0.08$ $n = 22$	$r^2 = 0.19$* $n = 22$	$r^2 = 0.14$ $n = 22$
Macaca fascicularis ♀	$r^2 = 0.22$* $n = 25$	$r^2 = 0.20$* $n = 24$	$r^2 = 0.18$* $n = 26$	$r^2 = 0.12$ $n = 26$	$r^2 = 0.13$ $n = 26$
Colobus satanas ♂	$n = 12$	$n = 12$	$n = 12$	$n = 12$	$n = 12$
Colobus satanas ♀	$r^2 = 0.03$ $n = 18$	$r^2 = 0.11$ $n = 19$	$r^2 = 0.07$ $n = 20$	$r^2 = 0.14$ $n = 20$	$r^2 = 0.13$ $n = 20$
Ateles vellerosus ♂	$r^2 = 0.22$ $n = 17$	$r^2 = 0.06$ $n = 17$	$r^2 = 0.13$ $n = 19$	$r^2 = 0.22$* $n = 19$	$r^2 = 0.31$* $n = 19$
Ateles vellerosus ♀	$r^2 = 0.24$* $n = 24$	$r^2 = 0.16$ $n = 24$	$r^2 = 0.21$* $n = 25$	$r^2 = 0.21$* $n = 25$	$r^2 = 0.31$** $n = 25$
Cebus libidinosus ♂	$r^2 = 0.16$ $n = 23$	$r^2 = 0.15$* $n = 30$	$r^2 = 0.10$ $n = 30$	$r^2 = 0.06$ $n = 30$	$r^2 = 0.11$ $n = 30$
Cebus libidinosus ♀	$r^2 = 0.16$* $n = 24$	$r^2 = 0.01$ $n = 30$	$r^2 = -0.01$ $n = 30$	$r^2 = -0.04$ $n = 30$	$r^2 = -0.03$ $n = 30$
Weighted Hom. Avg.	$r^2 = 0.05$	$r^2 = 0.05$	$r^2 = 0.04$	$r^2 = 0.06$	$r^2 = 0.04$
Weighted Cerco. Avg.	$r^2 = 0.13$	$r^2 = 0.15$	$r^2 = 0.10$	$r^2 = 0.12$	$r^2 = 0.13$
Weighted Plat. Avg.	$r^2 = 0.19$	$r^2 = 0.10$	$r^2 = 0.10$	$r^2 = 0.10$	$r^2 = 0.15$
Weighted Anthro. Avg.	$r^2 = 0.12$	$r^2 = 0.11$	$r^2 = 0.08$	$r^2 = 0.10$	$r^2 = 0.11$

*TABLE 5.9. The magnitude of covariation between mandibular canine height and incisor and postcanine breadth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C_1height - I_1LL	C_1height - I_2LL	C_1height - P_4BL	C_1height - M_1BL	C_1height - M_2BL
Gorilla gorilla ♂	r^2 = 0.25* *n* = 19	r^2 = 0.09 *n* = 24	r^2 = 0.01 *n* = 32	r^2 = 0.02 *n* = 28	r^2 = 0.02 *n* = 33
Gorilla gorilla ♀	r^2 = 0.11 *n* = 27	r^2 = 0.02 *n* = 29	r^2 = 0.15* *n* = 29	r^2 = 0.07 *n* = 23	r^2 = 0.06 *n* = 30
Pan troglodytes ♂	r^2 = 0.35** *n* = 19	r^2 = 0.28* *n* = 20	r^2 = 0.38** *n* = 24	r^2 = 0.03 *n* = 24	r^2 = 0.24* *n* = 24
Pan troglodytes ♀	r^2 = 0.08 *n* = 37	r^2 = 0.08 *n* = 37	r^2 = 0.09 *n* = 35	r^2 = 0.14* *n* = 37	r^2 = 0.08 *n* = 38
Hylobates carpenteri♂	r^2 = -0.04 *n* = 19	r^2 = -0.05 *n* = 19	r^2 = -0.02 *n* = 18	*n* = 13	r^2 = 0.05 *n* = 17
Hylobates carpenteri ♀	r^2 = 0.12 *n* = 20	r^2 = 0.16 *n* = 21	r^2 = 0.02 *n* = 21	r^2 = 0.02 *n* = 15	r^2 = 0.00 *n* = 22
Cercopithecus cephus ♂	r^2 = 0.10 *n* = 35	r^2 = 0.08 *n* = 35	r^2 = 0.15* *n* = 37	r^2 = 0.25** *n* = 37	r^2 = 0.34*** *n* = 37
Cercopithecus cephus ♀	r^2 = 0.31* *n* = 23	r^2 = 0.17* *n* = 25	r^2 = 0.08 *n* = 25	r^2 = 0.13 *n* = 24	r^2 = 0.02 *n* = 25
Cercopithecus nictitans ♂	r^2 = 0.03 *n* = 32	r^2 = 0.14** *n* = 35	r^2 = 0.24** *n* = 37	r^2 = 0.17* *n* = 35	r^2 = 0.21** *n* = 37
Cercopithecus nictitans ♀	r^2 = 0.04 *n* = 24	r^2 = -0.01 *n* = 25	r^2 = 0.00 *n* = 25	r^2 = -0.04 *n* = 23	r^2 = 0.01 *n* = 25
Cercopithecus pogonias ♂	r^2 = 0.07 *n* = 24	r^2 = 0.21* *n* = 25	r^2 = 0.03 *n* = 25	r^2 = 0.07 *n* = 24	r^2 = 0.08 *n* = 25
Cercopithecus pogonias ♀	r^2 = 0.11 *n* = 21	r^2 = 0.09 *n* = 21	r^2 = 0.28* *n* = 21	r^2 = 0.05 *n* = 21	r^2 = 0.16 *n* = 21
Macaca fascicularis ♂	r^2 = 0.00 *n* = 19	r^2 = 0.13 *n* = 19	r^2 = 0.45*** *n* = 22	r^2 = 0.17 *n* = 20	r^2 = 0.32** *n* = 22
Macaca fascicularis ♀	r^2 = 0.22 *n* = 26	r^2 = 0.37** *n* = 24	r^2 = 0.03 *n* = 26	r^2 = 0.14 *n* = 25	r^2 = 0.11 *n* = 25
Colobus satanas ♂	*n* = 12	*n* = 12	*n* = 12	*n* = 12	*n* = 12
Colobus satanas ♀	r^2 = 0.15 *n* = 19	r^2 = 0.13 *n* = 19	r^2 = 0.14 *n* = 20	r^2 = 0.36** *n* = 20	r^2 = 0.37** *n* = 20
Ateles vellerosus ♂	r^2 = 0.36** *n* = 19	r^2 = 0.20 *n* = 20	r^2 = 0.37* *n* = 16	*n* = 9	*n* = 13
Ateles vellerosus ♀	r^2 = 0.28** *n* = 25	r^2 = 0.32** *n* = 25	r^2 = 0.07 *n* = 24	r^2 = 0.13 *n* = 22	r^2 = 0.15 *n* = 24
Cebus libidinosus♂	r^2 = 0.05 *n* = 29	r^2 = 0.05 *n* = 30	r^2 = 0.16* *n* = 30	r^2 = 0.15* *n* = 30	r^2 = 0.13 *n* = 29
Cebus libidinosus♀	r^2 = 0.05 *n* = 30	r^2 = 0.01 *n* = 30	r^2 = -0.02 *n* = 29	r^2 = 0.00 *n* = 30	r^2 = 0.01 *n* = 30
Weighted Hom. Avg.	r^2 = 0.13	r^2 = 0.09	r^2 = 0.11	r^2 = 0.07	r^2 = 0.07
Weighted Cerco. Avg.	r^2 = 0.11	r^2 = 0.14	r^2 = 0.15	r^2 = 0.15	r^2 = 0.18
Weighted Plat. Avg.	r^2 = 0.16	r^2 = 0.13	r^2 = 0.12	r^2 = 0.09	r^2 = 0.09
Weighted Anthro. Avg.	r^2 = 0.13	r^2 = 0.12	r^2 = 0.13	r^2 = 0.11	r^2 = 0.13

*TABLE 5.10. The magnitude of covariation between maxillary canine height and incisor and postcanine length (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C^1 height - I^1MD	C^1 height - I^2MD	C^1 height - P^4MD	C^1 height - M^1MD	C^1 height - M^2MD
Gorilla gorilla ♂	r^2 = -0.02 n = 15	n = 14	r^2 = 0.02 n = 28	r^2 = 0.09 n = 28	r^2 = 0.02 n = 29
Gorilla gorilla ♀	r^2 = 0.04 n = 24	r^2 = 0.17* n = 25	r^2 = 0.09 n = 35	r^2 = 0.10 n = 33	r^2 = 0.01 n = 35
Pan troglodytes ♂	r^2 = 0.00 n = 19	r^2 = 0.00 n = 17	r^2 = -0.09 n = 22	r^2 = -0.01 n = 23	r^2 = 0.00 n = 23
Pan troglodytes ♀	r^2 = 0.00 n = 36	r^2 = 0.00 n = 34	r^2 = 0.10 n = 36	r^2 = 0.02 n = 37	r^2 = 0.01 n = 35
Hylobates carpenteri ♂	n = 10	n = 14	r^2 = 0.33* n = 15	r^2 = 0.49** n = 15	r^2 = 0.08 n = 15
Hylobates carpenteri ♀	n = 9	n = 9	n = 12	n = 13	n = 13
Cercopithecus cephus ♂	r^2 = 0.30* n = 15	r^2 = 0.06 n = 15	r^2 = 0.03 n = 15	r^2 = 0.35* n = 15	r^2 = 0.23* n = 15
Cercopithecus cephus ♀	r^2 = 0.08 n = 20	r^2 = 0.15 n = 19	r^2 = 0.09 n = 21	r^2 = 0.41* n = 21	r^2 = 0.24* n = 21
Cercopithecus nictitans ♂	n = 11	n = 11	n = 11	n = 11	n = 11
Cercopithecus nictitans ♀	r^2 = 0.19* n = 21	r^2 = 0.01 n = 22	r^2 = 0.06 n = 22	r^2 = 0.04 n = 22	r^2 = 0.01 n = 22
Cercopithecus pogonias ♂	n = 6	n = 8	n = 10	n = 10	n = 10
Cercopithecus pogonias ♀	r^2 = 0.26* n = 16	r^2 = 0.16 n = 18	r^2 = 0.14 n = 19	r^2 = 0.10 n = 19	r^2 = 0.20 n = 19
Macaca fascicularis ♂	n = 8	n = 9	n = 9	n = 9	n = 9
Macaca fascicularis ♀	r^2 = 0.00 n = 18	r^2 = 0.00 n = 21	r^2 = 0.00 n = 21	r^2 = 0.04 n = 22	r^2 = 0.05 n = 22
Colobus satanas ♂	n = 4	n = 4	n = 4	n = 4	n = 4
Colobus satanas ♀	r^2 = 0.02 n = 19	r^2 = 0.24 n = 21	r^2 = 0.12 n = 21	r^2 = 0.07 n = 21	r^2 = 0.16 n = 21
Ateles vellerosus ♂	n = 9	n = 10	n = 10	n = 10	n = 10
Ateles vellerosus ♀	r^2 = 0.25* n = 17	r^2 = 0.49** n = 17	r^2 = 0.24* n = 17	r^2 = 0.27* n = 17	r^2 = 0.44** n = 17
Cebus libidinosus ♂	r^2 = 0.25** n = 28	r^2 = 0.03 n = 28	r^2 = 0.01 n = 28	r^2 = 0.26** n = 28	r^2 = 0.09 n = 28
Cebus libidinosus ♀	r^2 = 0.11 n = 27	r^2 = 0.21* n = 28	r^2 = 0.01 n = 28	r^2 = 0.01 n = 28	r^2 = 0.00 n = 28
Weighted Hom. Avg.	r^2 = 0.01	r^2 = 0.06	r^2 = 0.08	r^2 = 0.10	r^2 = 0.02
Weighted Cerco. Avg.	r^2 = 0.13	r^2 = 0.10	r^2 = 0.07	r^2 = 0.16	r^2 = 0.14
Weighted Plat. Avg.	r^2 = 0.20	r^2 = 0.21	r^2 = 0.06	r^2 = 0.17	r^2 = 0.14
Weighted Anthro. Avg.	r^2 = 0.11	r^2 = 0.12	r^2 = 0.07	r^2 = 0.14	r^2 = 0.09

*TABLE 5.11. The magnitude of covariation between maxillary canine height and incisor and postcanine breadth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	C^1 height - I^1LL	C^1 height - I^2LL	C^1 height - P^4BL	C^1 height - M^1BL	C^1 height - M^2BL
Gorilla gorilla ♂	$r^2 = 0.04$ $n = 18$	$r^2 = 0.01$ $n = 17$	$r^2 = 0.02$ $n = 29$	$r^2 = 0.00$ $n = 28$	$r^2 = 0.00$ $n = 28$
Gorilla gorilla ♀	$r^2 = 0.14$* $n = 29$	$r^2 = 0.19$* $n = 30$	$r^2 = 0.11$* $n = 35$	$r^2 = 0.15$* $n = 34$	$r^2 = 0.11$ $n = 34$
Pan troglodytes ♂	$r^2 = 0.02$ $n = 19$	$r^2 = 0.01$ $n = 20$	$r^2 = -0.02$ $n = 22$	$r^2 = 0.00$ $n = 21$	$r^2 = 0.04$ $n = 23$
Pan troglodytes ♀	$r^2 = 0.11$ $n = 36$	$r^2 = 0.11$* $n = 37$	$r^2 = 0.15$* $n = 36$	$r^2 = 0.05$ $n = 37$	$r^2 = 0.12$* $n = 36$
Hylobates carpenteri♂	$n = 13$	$n = 14$	$r^2 = 0.51$** $n = 15$	$r^2 = 0.45$** $n = 15$	$r^2 = 0.17$ $n = 15$
Hylobates carpenteri ♀	$n = 9$	$n = 12$	$n = 12$	$n = 12$	$n = 13$
Cercopithecus cephus ♂	$r^2 = 0.18$ $n = 15$	$r^2 = 0.14$ $n = 15$	$r^2 = 0.04$ $n = 15$	$r^2 = 0.12$ $n = 15$	$r^2 = 0.18$ $n = 15$
Cercopithecus cephus ♀	$r^2 = 0.34$* $n = 21$	$r^2 = 0.01$ $n = 20$	$r^2 = 0.19$ $n = 21$	$r^2 = 0.08$ $n = 21$	$r^2 = 0.15$ $n = 21$
Cercopithecus nictitans ♂	$n = 9$	$n = 9$	$n = 11$	$n = 11$	$n = 11$
Cercopithecus nictitans ♀	$r^2 = 0.03$ $n = 22$	$r^2 = -0.04$ $n = 22$	$r^2 = 0.08$ $n = 22$	$r^2 = 0.01$ $n = 22$	$r^2 = 0.04$ $n = 22$
Cercopithecus pogonias ♂	$n = 9$	$n = 8$	$n = 10$	$n = 10$	$n = 10$
Cercopithecus pogonias ♀	$r^2 = 0.07$ $n = 18$	$r^2 = 0.22$* $n = 19$	$r^2 = 0.01$ $n = 19$	$r^2 = 0.00$ $n = 19$	$r^2 = 0.02$ $n = 19$
Macaca fascicularis ♂	$n = 8$	$n = 9$	$n = 9$	$n = 9$	$n = 9$
Macaca fascicularis ♀	$r^2 = -0.01$ $n = 21$	$r^2 = 0.04$ $n = 22$	$r^2 = 0.02$ $n = 21$	$r^2 = 0.00$ $n = 22$	$r^2 = 0.01$ $n = 22$
Colobus satanas ♂	$n = 4$	$n = 4$	$n = 4$	$n = 4$	$n = 4$
Colobus satanas ♀	$r^2 = 0.04$ $n = 19$	$r^2 = 0.04$ $n = 21$	$r^2 = 0.43$** $n = 21$	$r^2 = 0.07$ $n = 21$	$r^2 = 0.23$* $n = 21$
Ateles vellerosus ♂	$n = 9$	$n = 10$	$n = 10$	$n = 10$	$n = 9$
Ateles vellerosus ♀	$r^2 = 0.19$ $n = 16$	$r^2 = 0.36$* $n = 17$	$r^2 = 0.20$ $n = 16$	$r^2 = 0.08$ $n = 17$	$r^2 = 0.09$ $n = 17$
Cebus libidinosus♂	$r^2 = 0.22$* $n = 28$	$r^2 = 0.18$* $n = 28$	$r^2 = 0.31$** $n = 28$	$r^2 = 0.23$** $n = 28$	$r^2 = 0.03$ $n = 28$
Cebus libidinosus♀	$r^2 = 0.01$ $n = 28$	$r^2 = 0.08$ $n = 28$	$r^2 = -0.17$* $n = 28$	$r^2 = -0.16$* $n = 28$	$r^2 = -0.03$ $n = 28$
Weighted Hom. Avg.	$r^2 = 0.09$	$r^2 = 0.10$	$r^2 = 0.12$	$r^2 = 0.10$	$r^2 = 0.08$
Weighted Cerco. Avg.	$r^2 = 0.11$	$r^2 = 0.06$	$r^2 = 0.13$	$r^2 = 0.04$	$r^2 = 0.10$
Weighted Plat. Avg.	$r^2 = 0.13$	$r^2 = 0.18$	$r^2 = 0.10$	$r^2 = 0.05$	$r^2 = 0.02$
Weighted Anthro. Avg.	$r^2 = 0.11$	$r^2 = 0.10$	$r^2 = 0.12$	$r^2 = 0.07$	$r^2 = 0.08$

C^1LL-I^1LL (hominoid average $r^2 = 0.30$; platyrrhine average $r^2 = 0.31$) and C^1MD-I^2MD (hominoid average $r^2 = 0.36$; platyrrhine average $r^2 = 0.28$). These comparisons are the exceptions, rather than the rule, for the magnitude of covariation with characters outside the honing complex.

The pleiotropy hypotheses of Jolly (1970) and McCollum and Sharpe (2001) predict a tradeoff between anterior tooth size and postcanine tooth size. Thus, the expectation is a negative covariation between canine crown size and postcanine crown size within species. This expectation is not born out here. Not only is the level of covariation weak between the canines and postcanine dentition, but it is in the direction *opposite* that predicted by the pleiotropy hypothesis. Of 224 within-species comparisons of canine basal size with the size of the postcanine dentition, 143 are significantly different from zero and all have an absolute value of > 0.00. Though weak, the pleiotropy between the basal canine dimensions and the postcanine teeth is positive in direction. For the incisors and canine basal size, of 141 within-species comparisons, 77 are significantly different from zero and all are positive in direction. Contra the pleiotropy hypotheses of Jolly (1970) and McCollum and Sharpe (2001), the basal dimensions of the canines do not covary strongly with either the incisors or the postcanine dentition. Coordinated changes in canine and either incisor or postcanine size observed in hominins are not likely to have been mediated by a pleiotropic linkage (contra Jolly, 1970).

Canine crown heights do not strongly covary with the dimensions of the incisor or postcanine crowns (Tables 5.8, 5.9, 5.10, and 5.11). The highest anthropoid average is $r^2 = 0.14$ for C^1 height-M^1MD. Of 143 within-species comparisons of canine height to the dimensions of the postcanine dentition, only 56 are significantly different from zero, and all are positive in direction. Of 126 within-species comparisons of canine height to the

dimensions of the incisors, 41 are significantly different from zero and all are positive in direction.

The low and very low levels of covariation between canine crown height and the basal dimensions of teeth in other functional modules (this study; Cochard, 1981) are not surprising given the pattern of results observed throughout this study. Namely, it always homologous dimensions within and between arches in functional modules that express the highest levels of covariation. For example, between the arches canine heights covary strongly with one another, as do basal areas, but basal areas and canine heights do not strongly covary with one another within a tooth. For the incisors and postcanine teeth, the breadths covary strongly with one another and the lengths covary strongly with one another, but breadths and lengths covary only weakly (Chapters 3 and 4). Therefore, a pleiotropic relationship between canine *heights* and any basal dimension of the incisors and postcanine dentition is not likely to exist.

Canine Height and Premolar Honing Surface Length Within Species: Above, it was shown that homologous dimensions of the canines significantly covary with one another within species. The other element of the canine honing complex is the mesial-most mandibular premolar. The distal edge of the maxillary canine is honed along the mesiobuccal surface of the honing premolar, which extends from the protoconid along the mesiobuccal root (Chapter 1, Figure 1.11).

Moderate levels of covariation are consistently observed between the heights of both canines and the length of the premolar's honing surface (Table 5.12). Only one sample, female *Cercopithecus cephus*, shows a nonsignificant correlation between mandibular canine height and premolar honing surface length. This result is likely aberrant. There are far fewer samples for which covariation can be estimated for the

*TABLE 5.12. The magnitude of covariation between canine heights and the length of the premolar honing surface (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	$P_{2,3}$ hone length-C_1 height	$P_{2,3}$ hone length-C^1 Height
Gorilla gorilla ♀	$r^2 = 0.62$*** $n = 26$	$r^2 = 0.54$*** $n = 29$
Gorilla gorilla ♂	$r^2 = 0.41$*** $n = 30$	$r^2 = 0.45$*** $n = 27$
Pan troglodytes♀	$r^2 = 0.59$*** $n = 35$	$r^2 = 0.40$*** $n = 33$
Pan troglodytes ♂	$r^2 = 0.44$*** $n = 26$	$r^2 = 0.50$*** $n = 28$
Hylobates carpenteri ♀	$r^2 = 0.54$*** $n = 20$	$n = 12$
Hylobates carpenteri ♂	$r^2 = 0.41$*** $n = 20$	$r^2 = 0.32$* $n = 15$
Cercopithecus cephus ♀	$r^2 = 0.18$ $n = 21$	$r^2 = 0.11$ $n = 19$
Cercopithecus cephus ♂	$r^2 = 0.53$*** $n = 37$	$r^2 = 0.74$*** $n = 15$
Cercopithecus nictitans ♀	$r^2 = 0.36$*** $n = 23$	$r^2 = 0.38$*** $n = 20$
Cercopithecus nictitans ♂	$r^2 = 0.59$*** $n = 38$	$n = 11$
Cercopithecus pogonias ♀	$r^2 = 0.61$*** $n = 21$	$r^2 = 0.69$*** $n = 19$
Cercopithecus pogonias ♂	$r^2 = 0.46$*** $n = 30$	$n = 10$
Macaca fascicularis ♀	$r^2 = 0.40$*** $n = 24$	$n = 14$
Macaca fascicularis ♂	$r^2 = 0.35$*** $n = 20$	$n = 9$
Colobus satanas ♀	$r^2 = 0.40$** $n = 20$	$r^2 = 0.49$*** $n = 21$
Ateles vellerosus ♀	$r^2 = 0.49$*** $n = 21$	$r^2 = 0.41$* $n = 15$
Ateles vellerosus ♂	$r^2 = 0.24$* $n = 16$	$n = 10$
Cebus libidinosus ♀	$r^2 = 0.33$** $n = 26$	$r^2 = 0.31$** $n = 23$
Cebus libidinosus ♂	$r^2 = 0.53$*** $n = 28$	$r^2 = 0.30$** $n = 26$
W. Hom. ♂ Avg.	$r^2 = 0.42$	$r^2 = 0.44$
W. Hom. ♀ Avg.	$r^2 = 0.59$	$r^2 = 0.47$
W. Cerco. ♂ Avg.	$r^2 = 0.50$	$r^2 = 0.74$
W. Cerco. ♀ Avg.	$r^2 = 0.39$	$r^2 = 0.42$
W.Plat. ♂ Avg.	$r^2 = 0.42$	$r^2 = 0.30$
W.Plat. ♀ Avg.	$r^2 = 0.40$	$r^2 = 0.35$

*TABLE 5.13. The magnitude of covariation between premolar hone length and incisor and postcanine length (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	$P_{2,3}$ hone-I_1MD	$P_{2,3}$ hone - I_2MD	$P_{2,3}$ hone-P_4MD	$P_{2,3}$ hone-M_1MD	$P_{2,3}$ hone-M_2MD
Gorilla gorilla ♂	r^2 = 0.10 n = 29	r^2 = 0.10 n = 28	r^2 = 0.23*** n = 58	r^2 = 0.13** n = 55	r^2 = 0.23*** n = 57
Gorilla gorilla ♀	r^2 = 0.10 n = 29	r^2 = 0.20** n = 34	r^2 = 0.05 n = 37	r^2 = 0.15* n = 39	r^2 = 0.12* n = 40
Pan troglodytes ♂	r^2 = 0.57*** n = 28	r^2 = 0.29** n = 29	r^2 = 0.10 n = 36	r^2 = 0.03 n = 37	r^2 = 0.18** n = 38
Pan troglodytes ♀	r^2 = 0.02 n = 39	r^2 = 0.00 n = 41	r^2 = 0.09 n = 43	r^2 = 0.10* n = 42	r^2 = 0.07 n = 42
Hylobates carpenteri ♂	r^2 = 0.18* n = 28	r^2 = 0.17* n = 32	r^2 = 0.15* n = 29	r^2 = 0.13* n = 46	r^2 = 0.17* n = 33
Hylobates carpenteri ♀	n = 16	n = 19	r^2 = 0.20* n = 22	r^2 = 0.08 n = 20	r^2 = 0.01 n = 22
Cercopithecus cephus ♂	r^2 = 0.03 n = 44	r^2 = 0.10* n = 47	r^2 = 0.03 n = 49	r^2 = 0.09* n = 48	r^2 = 0.19** n = 49
Cercopithecus cephus ♀	r^2 = 0.04 n = 23	r^2 = 0.10 n = 28	r^2 = 0.03 n = 29	r^2 = 0.02 n = 29	r^2 = 0.07 n = 29
Cercopithecus nictitans ♂	r^2 = -0.01 n = 40	r^2 = 0.02 n = 44	r^2 = 0.22*** n = 48	r^2 = 0.22** n = 44	r^2 = 0.23*** n = 47
Cercopithecus nictitans ♀	r^2 = 0.02 n = 27	r^2 = 0.07 n = 29	r^2 = 0.09 n = 30	r^2 = 0.01 n = 27	r^2 = 0.00 n = 30
Cercopithecus pogonias ♂	n = 18	r^2 = 0.02 n = 29	r^2 = 0.01 n = 36	r^2 = 0.00 n = 32	r^2 = 0.05 n = 35
Cercopithecus pogonias ♀	r^2 = 0.02 n = 27	r^2 = 0.00 n = 27	r^2 = 0.21* n = 29	r^2 = 0.23** n = 29	r^2 = 0.31** n = 29
Macaca fascicularis ♂	r^2 = 0.01 n = 26	r^2 = 0.00 n = 23	r^2 = 0.12* n = 36	r^2 = 0.06 n = 36	r^2 = 0.09 n = 36
Macaca fascicularis ♀	r^2 = 0.07 n = 36	r^2 = 0.16* n = 36	r^2 = 0.20** n = 38	r^2 = 0.22** n = 36	r^2 = 0.17** n = 38
Colobus satanas ♂	r^2 = 0.03 n = 21	r^2 = 0.04 n = 21	r^2 = 0.10 n = 21	r^2 = 0.06 n = 21	r^2 = 0.10 n = 21
Colobus satanas ♀	r^2 = -0.03 n = 22	r^2 = 0.12 n = 23	r^2 = 0.04 n = 24	r^2 = 0.23* n = 24	r^2 = 0.16* n = 24
Ateles vellerosus ♂	r^2 = 0.00 n = 23	r^2 = -0.07 n = 23	r^2 = 0.00 n = 25	r^2 = 0.00 n = 25	r^2 = 0.01 n = 24
Ateles vellerosus ♀	r^2 = 0.06 n = 21	r^2 = 0.03 n = 21	r^2 = 0.15 n = 20	r^2 = 0.29* n = 21	r^2 = 0.23* n = 21
Cebus libidinosus ♂	r^2 = 0.08 n = 29	r^2 = 0.09 n = 38	r^2 = 0.09 n = 38	r^2 = 0.09 n = 38	r^2 = 0.14* n = 37
Cebus libidinosus ♀	r^2 = 0.11 n = 23	r^2 = 0.14* n = 30	r^2 = 0.04 n = 30	r^2 = 0.00 n = 30	r^2 = 0.01 n = 30
Weighted Hom. Avg.	r^2 = 0.18	r^2 = 0.14	r^2 = 0.14	r^2 = 0.11	r^2 = 0.14
Weighted Cerco. Avg.	r^2 = 0.02	r^2 = 0.07	r^2 = 0.11	r^2 = 0.12	r^2 = 0.14
Weighted Plat. Avg.	r^2 = 0.06	r^2 = 0.06	r^2 = 0.07	r^2 = 0.08	r^2 = 0.09
Weighted Anthro. Avg.	r^2 = 0.08	r^2 = 0.09	r^2 = 0.11	r^2 = 0.11	r^2 = 0.14

*TABLE 5.14. The magnitude of covariation between premolar hone length and incisor and postcanine breadth (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	$P_{2,3}$ hone-I_1LL	$P_{2,3}$ hone-I_2LL	$P_{2,3}$ hone-P_4BL	$P_{2,3}$ hone-M_1BL	$P_{2,3}$ hone-M_2BL
Gorilla gorilla ♂	$r^2 = 0.24$** $n = 35$	$r^2 = 0.27$*** $n = 39$	$r^2 = 0.17$** $n = 56$	$r^2 = 0.32$*** $n = 51$	$r^2 = 0.23$*** $n = 55$
Gorilla gorilla ♀	$r^2 = 0.31$*** $n = 35$	$r^2 = 0.29$*** $n = 40$	$r^2 = 0.34$*** $n = 38$	$r^2 = 0.23$** $n = 35$	$r^2 = 0.29$*** $n = 38$
Pan troglodytes ♂	$r^2 = 0.32$** $n = 29$	$r^2 = 0.36$*** $n = 30$	$r^2 = 0.26$** $n = 37$	$r^2 = 0.05$ $n = 36$	$r^2 = 0.22$** $n = 36$
Pan troglodytes ♀	$r^2 = 0.07$ $n = 40$	$r^2 = 0.08$ $n = 41$	$r^2 = 0.02$ $n = 43$	$r^2 = 0.09$ $n = 42$	$r^2 = 0.08$ $n = 42$
Hylobates carpenteri ♂	$r^2 = 0.04$ $n = 31$	$r^2 = 0.04$ $n = 32$	$r^2 = 0.04$ $n = 29$	$r^2 = 0.08$ $n = 23$	$r^2 = 0.17$* $n = 30$
Hylobates carpenteri ♀	$r^2 = 0.03$ $n = 20$	$r^2 = 0.06$ $n = 21$	$r^2 = 0.18$* $n = 22$	$n = 17$	$r^2 = 0.03$ $n = 22$
Cercopithecus cephus ♂	$r^2 = 0.05$ $n = 47$	$r^2 = 0.07$ $n = 47$	$r^2 = 0.06$ $n = 49$	$r^2 = 0.12$* $n = 49$	$r^2 = 0.13$* $n = 49$
Cercopithecus cephus ♀	$r^2 = 0.02$ $n = 25$	$r^2 = 0.01$ $n = 27$	$r^2 = -0.01$ $n = 29$	$r^2 = -0.01$ $n = 28$	$r^2 = -0.04$ $n = 29$
Cercopithecus nictitans ♂	$r^2 = 0.01$ $n = 41$	$r^2 = 0.06$ $n = 44$	$r^2 = 0.21$*** $n = 46$	$r^2 = 0.13$* $n = 43$	$r^2 = 0.15$** $n = 47$
Cercopithecus nictitans ♀	$r^2 = 0.08$ $n = 28$	$r^2 = 0.03$ $n = 29$	$r^2 = 0.09$ $n = 30$	$r^2 = -0.01$ $n = 27$	$r^2 = 0.00$ $n = 30$
Cercopithecus pogonias ♂	$r^2 = 0.01$ $n = 30$	$r^2 = 0.07$ $n = 31$	$r^2 = 0.10$ $n = 36$	$r^2 = 0.17$* $n = 35$	$r^2 = 0.07$ $n = 36$
Cercopithecus pogonias ♀	$r^2 = 0.14$* $n = 28$	$r^2 = 0.11$ $n = 28$	$r^2 = 0.28$** $n = 29$	$r^2 = 0.07$ $n = 29$	$r^2 = 0.09$ $n = 29$
Macaca fascicularis ♂	$r^2 = 0.17$* $n = 27$	$r^2 = 0.08$ $n = 26$	$r^2 = 0.13$* $n = 34$	$r^2 = 0.04$ $n = 33$	$r^2 = 0.06$ $n = 36$
Macaca fascicularis ♀	$r^2 = 0.12$* $n = 36$	$r^2 = 0.17$* $n = 36$	$r^2 = 0.07$ $n = 38$	$r^2 = 0.15$* $n = 35$	$r^2 = 0.13$* $n = 37$
Colobus satanas ♂	$r^2 = 0.01$ $n = 21$	$r^2 = -0.02$ $n = 21$	$r^2 = 0.00$ $n = 21$	$r^2 = -0.31$* $n = 21$	$r^2 = -0.13$ $n = 21$
Colobus satanas ♀	$r^2 = 0.03$ $n = 23$	$r^2 = 0.31$** $n = 23$	$r^2 = 0.12$ $n = 24$	$r^2 = 0.22$* $n = 24$	$r^2 = 0.33$** $n = 24$
Ateles vellerosus ♂	$r^2 = 0.08$ $n = 25$	$r^2 = 0.00$ $n = 25$	$r^2 = 0.06$ $n = 22$	$n = 13$	$n = 17$
Ateles vellerosus ♀	$r^2 = 0.14$ $n = 21$	$r^2 = 0.21$* $n = 21$	$n = 19$	$n = 18$	$r^2 = 0.12$ $n = 20$
Cebus libidinosus ♂	$r^2 = 0.13$* $n = 37$	$r^2 = 0.10$* $n = 38$	$r^2 = 0.22$** $n = 38$	$r^2 = 0.16$* $n = 38$	$r^2 = 0.18$** $n = 37$
Cebus libidinosus ♀	$r^2 = 0.19$ $n = 30$	$r^2 = 0.08$ $n = 30$	$r^2 = 0.00$ $n = 29$	$r^2 = -0.01$ $n = 30$	$r^2 = 0.01$ $n = 30$
Weighted Hom. Avg.	$r^2 = 0.17$	$r^2 = 0.19$	$r^2 = 0.17$	$r^2 = 0.17$	$r^2 = 0.18$
Weighted Cerco. Avg.	$r^2 = 0.06$	$r^2 = 0.09$	$r^2 = 0.11$	$r^2 = 0.07$	$r^2 = 0.09$
Weighted Plat. Avg.	$r^2 = 0.14$	$r^2 = 0.09$	$r^2 = 0.11$	$r^2 = 0.09$	$r^2 = 0.11$
Weighted Anthro. Avg.	$r^2 = 0.11$	$r^2 = 0.12$	$r^2 = 0.13$	$r^2 = 0.11$	$r^2 = 0.12$

maxillary canine height than for the mandibular; however, the pattern among those samples is consistent.

The honing surface of the mandibular premolar is both functionally and pleiotropically linked to canine height in both male and female anthropoids. This result is somewhat surprising, as the maxillary canine height is worn and often broken away during an individual's lifetime (e.g., Leigh et al., 2008). As a result, over time the premolar hones a progressively shorter canine crown; therefore, the link between premolar honing surface length and maximum canine height exists for a brief period of an individual's life, suggesting that there should not be a tight functional link between honing surface length and canine height. A possible functional explanation for this phenomenon will be discussed in Chapter 7 in relation to the hyper-eruption of canines.

Premolar Honing Surface Length and Incisor and Postcanine Size Within Species: Covariation between the length of the premolar's honing surface and dimensions of the incisors and postcanine dentition was investigated. The length of the honing surface expresses only very low levels of covariation with dimensions outside the honing complex. The highest observed anthropoid average is $r^2 = 0.14$ for premolar hone-M_2MD (Tables 5.9 and 5.10). Of 77 within-species comparisons made for honing surface length with mandibular incisor size, only 22 are significantly different from zero and all 22 are positive in direction. Of 114 within-species comparisons between honing surface length and the dimensions of the mandibular postcanine dentition, 54 are significantly different from zero. Premolar honing surface length is weakly linked to the size of the incisors and postcanine dentition, further supporting the hypothesis that the canine honing complex constitutes both a functional and a variational module.

*TABLE 5.15. The magnitude of covariation between the P^3 enamel extension length and dimensions of the honing complex (***p-value < 0.0001, **p-value < 0.001, *p-value < 0.05).*

	P_3 hone - P^3 ext.	C_1 height- P^3 ext.	C^1 height- P^3 ext.
Gorilla gorilla ♂	$r^2 = 0.44$*** $n = 35$	$r^2 = 0.14$ $n = 18$	$r^2 = 0.03$ $n = 18$
Gorilla gorilla ♀	$r^2 = 0.72$*** $n = 17$	$n = 12$	$r^2 = 0.39$** $n = 16$
Pan troglodytes ♂	$r^2 = 0.57$*** $n = 30$	$r^2 = 0.13$ $n = 19$	$r^2 = 0.03$ $n = 19$
Pan. troglodytes ♀	$r^2 = 0.41$*** $n = 26$	$r^2 = 0.46$*** $n = 21$	$r^2 = 0.29$** $n = 25$
Hylobates lar ♂	$r^2 = 0.56$*** $n = 18$	$n = 12$	$n = 14$
Hylobates lar ♀	$n = 10$	$n = 9$	$n = 7$
Cercopithecus cephus ♂	$r^2 = 0.29$** $n = 28$	$r^2 = 0.29$** $n = 27$	$n = 12$
Cercopithecus cephus ♀	$r^2 = 0.51$*** $n = 26$	$r^2 = 0.14$ $n = 24$	$r^2 = 0.14$ $n = 21$
Weighted ♂ Catarrhine Avg.	$r^2 = 0.46$	$r^2 = 0.20$	$r^2 = 0.03$
Weighted ♀ Catarrhine Avg.	$r^2 = 0.52$	$r^2 = 0.29$	$r^2 = 0.27$

Maxillary Premolar Covariation with the Honing Complex Within Species: As noted in Chapter 1, premolar heteromorphy characterizes both the maxillary and mandibular premolars. Heteromorphy in the mandible is easily explained as a result of the mesial premolar functioning as a hone for the maxillary canine. Maxillary premolar heteromorphy was described in Chapter 4 (Figure 4.1). In Chapter 4, it was shown that the MD dimension of the mesial maxillary premolar covaries weakly with the MD lengths of the other maxillary premolar(s). Here, covariation of the mesio-cervical enamel extension and dimensions of the canine honing complex is investigated for four catarrhine primates (*Pan troglodytes*, *Gorilla gorilla*, *Hylobates lar,* and *Cercopithecus cephus*); covariation was assessed between the P^3 enamel extension and the canine heights and the length of the mandibular premolar honing surface (Table 5.15).

Although taxonomic representation is narrow compared to the other analyses, the results indicate that the P^3 extension strongly covaries in size with that of the P_3 honing surface (average $r^2 = 0.48$ for the six comparisons). The magnitude observed in *Cercopithecus cephus* males is low relative to the other samples. Levels of covariation between the length of the P^3 extension and canine heights are lower (average $r^2 = 0.24$ and 0.18 with the mandibular canine height and maxillary canine height, respectively). Thus, it appears that the mesial portions of the P_3 and P^3 share unique pleiotropic effects that are not shared with the canines. This does not reflect functional integration, as the P^3 extension does not occlude with the P_3 honing surface. Instead, it is probably a reflection of the increased heights of the P_3 protoconid and P^3 paracone, relative to the P4s, which contributes to the length of the P_3 honing surface (Figure 1.12) and the P^3 enamel extension (Figure 4.1).

In Chapter 4, it was hypothesized the mesial premolars became parceled out of the postcanine variational module as they evolved to be heteromorphic relative to the neighboring premolar. During hominin evolution, both mesial premolars lost many of their heteromorphic traits and became morphologically quite similar to their distal neighbor. These changes involved reductions in the height and area of the principal cusps (e.g., Kimbel and Delezene, 2009). The early hominin *Australopithecus afarensis* captures these teeth in the process of transformation, for both the mandibular and maxillary P3 of *Australopithecus afarensis* are heteromorphic relative to younger hominins, but have reduced heteromorphy relative to extant ape outgroups (Kimbel and Delezene, 2009; Delezene and Kimbel, 2011). The reduction of principal cusp heights is a good candidate for a coordinated change that was mediated by a pleiotropic relationship. Whether the mesial premolars became "integrated" into the postcanine

*TABLE 5.16. The magnitude of 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	♂r^2 = 0.63*** ♀r^2 = 0.49***	—	—	—
C_1 Height	♂r^2 = 0.80*** ♀r^2 = 0.74***	♂r^2 = 0.91*** ♀r^2 = 0.72***	—	—
C_1 Basal Size	♂r^2 = 0.55*** ♀r^2 = 0.49***	♂r^2 = 0.97*** ♀r^2 = 0.92***	♂r^2 = 0.90*** ♀r^2 = 0.77***	—
Premolar Hone	♂r^2 = 0.73*** ♀r^2 = 0.50***	♂r^2 = 0.76*** ♀r^2 = 0.75***	♂r^2 = 0.73*** ♀r^2 = 0.60***	♂r^2 = 0.69*** ♀r^2 = 0.65***

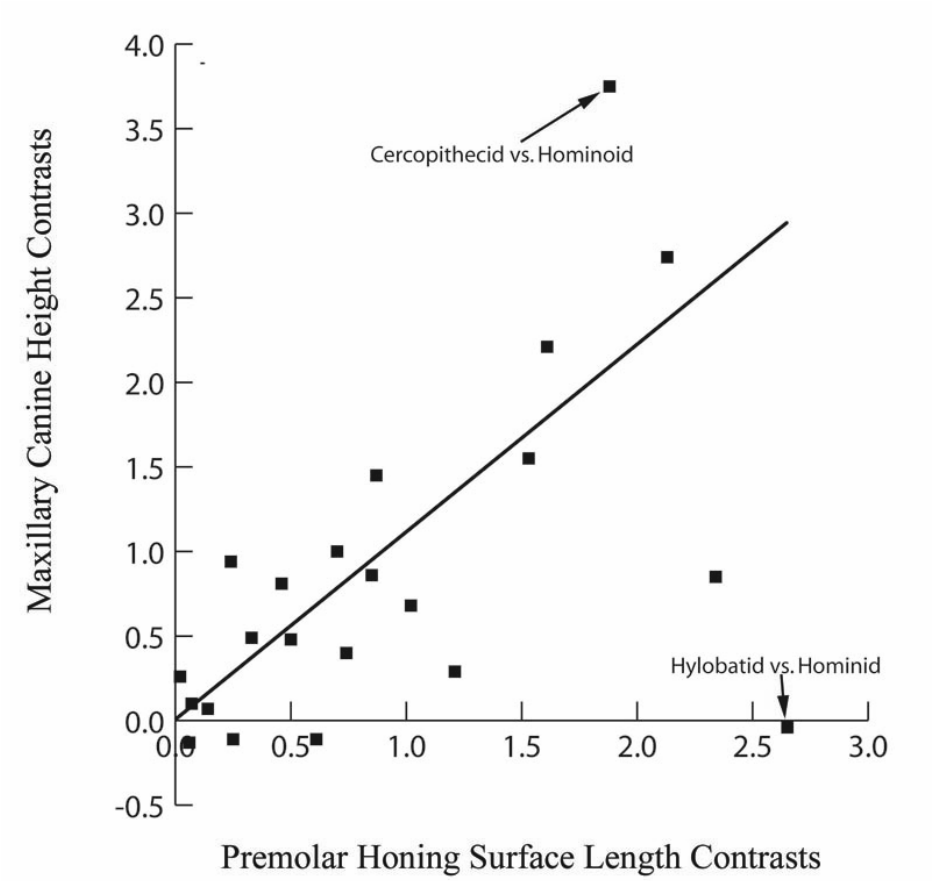

Fig. 5.1: Independent contrasts for maxillary canine height and premolar honing facet length in females. The solid line is the RMA regression line.

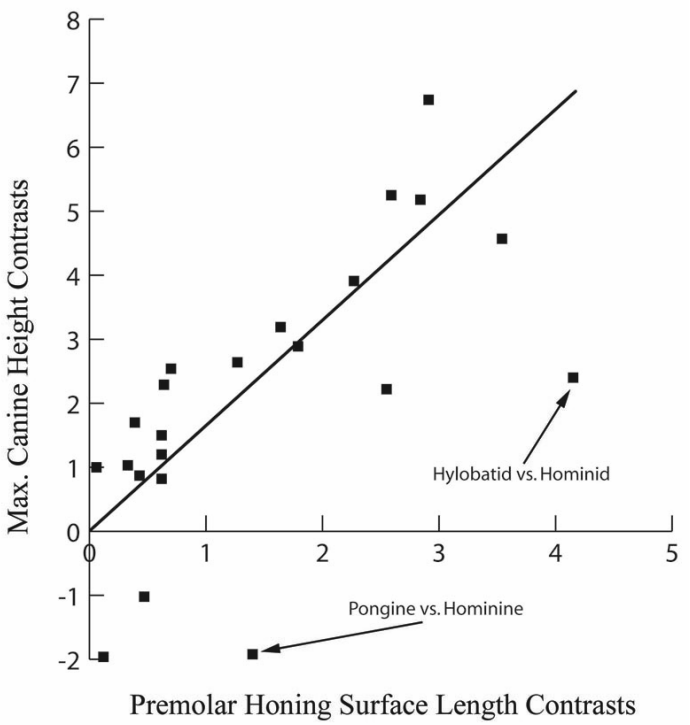

Fig. 5.2: Independent contrasts for maxillary canine height and premolar honing facet length in males. The solid line is the RMA regression line.

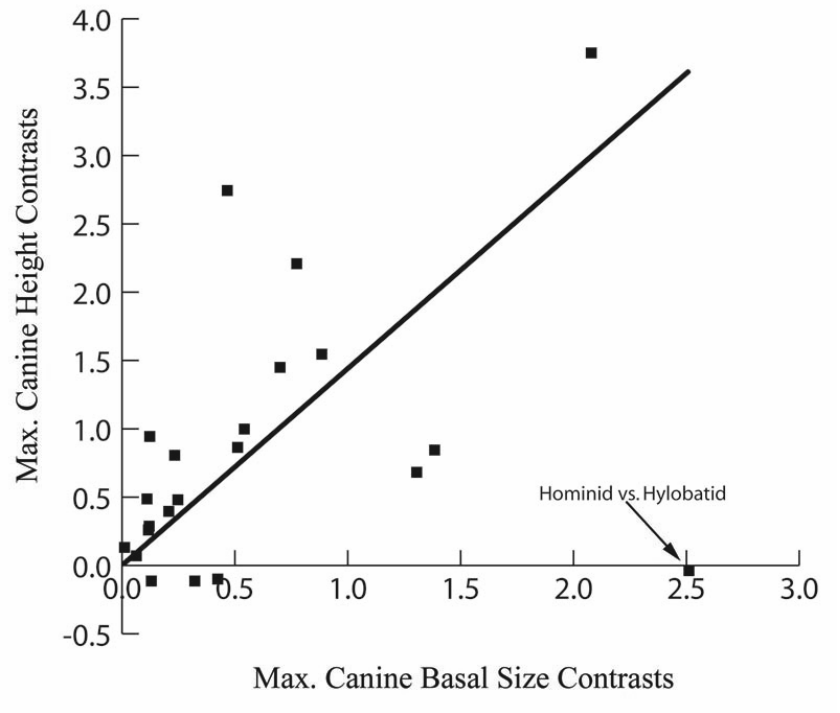

Fig 5.3. Independent contrasts of maxillary canine height and basal crown size in female anthropoid primates.

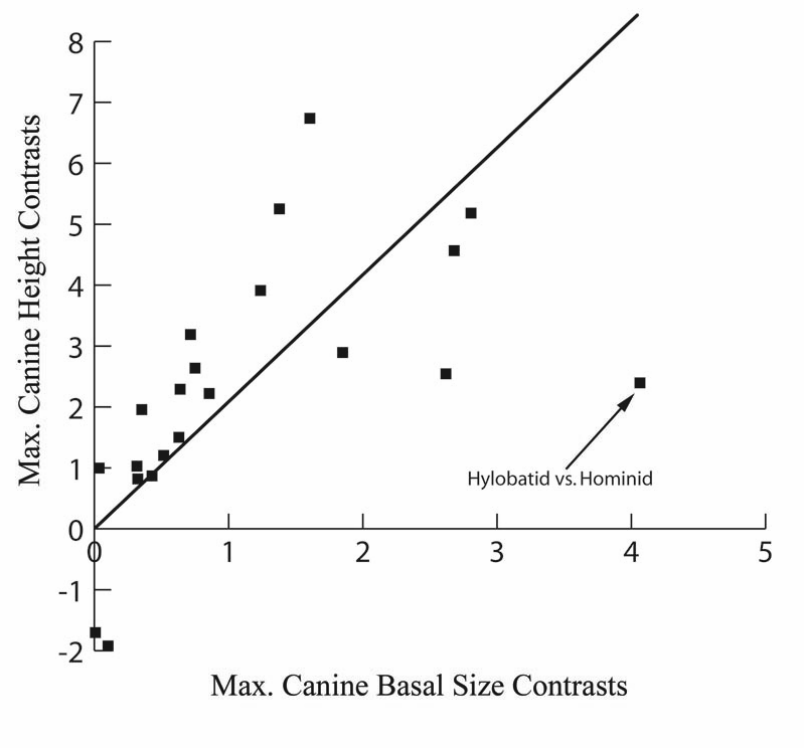

Fig. 5.4. Independent contrasts of maxillary canine height and basal size in male anthropoids.

variational module (as in Figure 1.1) as heteromorphy was reduced remains to be answered.

Dimensions of the Honing Complex Among Species: Among-species covariation was assessed for canine heights, canine basal size (√(LL*MD)), and length of the premolar's honing surface. All elements of the complex express statistically significant high levels of covariation in both males and females (Table 5.16). As covariation is significant among all elements in both sexes, Greenfield's (1992; Greenfield and Washburn, 1992) conclusion that the male complex coevolved but the female complex did not is contradicted. His results are clearly the effect of his choice of canine projection to reflect canine height (Figure 1.17). The magnitude of covariation differs between males and

females for two important comparisons. Females express lower levels of covariation for comparisons of maxillary canine height to the length of the premolar's honing surface and for the comparisons of canine height to canine basal areas.

The lower level of covariation for maxillary canine height to honing facet length in females is easily seen when bivariate plots of independent contrasts are compared (Figures 5.1 and 5.2). There is in general a poorer fit of the female contrasts to the RMA regression line (Figure 5.1) than in the male contrasts (Figure 5.2). For females, two contrasts stand out from the rest: the contrast between hylobatids and hominids and the contrast between cercopithecids and hominoids. For a given P_3 honing facet length, the hylobatid females have a taller canine than do the hominids and cercopithecids have taller canines than do hominoids. These differences were also noted by Greenfield (1992; Greenfield and Washburn, 1992). A casual comparison of the honing premolars of female cercopithecids and hominoids is sufficient to confirm that their honing premolars are quite distinct morphologically. The hominid vs. hylobatid contrast also stands out in the male analysis. The dichotomies in the honing complexes of hylobatids, hominids, and cercopithecids are addressed in Chapter 6, where among-species differences ($\mathbf{\Delta z}$) are investigated relative to $\mathbf{p}_{\mathbf{max}}$.

The female honing complex also demonstrates weaker covariation of canine basal size and height among species than do males (Figures 5.3 and 5.4). In both males and females, the contrast between hylobatids and hominids is large because the hylobatid maxillary canine is taller relative to basal size than in hominids. Within species, these characters covary weakly, so their poor correspondence among species does not indicate that selection has acted in a direction opposed by genetic constraint. Plavcan and Ruff (2008) indicated that selection has operated to make canines relatively strong (i.e., resistant to bending stresses) in primates. From a functional perspective, it might be

*TABLE 5.17. The magnitude of covariation among 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_1LL	♂r^2 = 0.69*** ♀r^2 = 0.45***	♂r^2 = 0.80*** ♀r^2 = 0.75***	♂r^2 = 0.54*** ♀r^2 = 0.47***
I_1MD	♂r^2 = 0.62*** ♀r^2 = 0.41***	♂r^2 = 0.77*** ♀r^2 = 0.74***	♂r^2 = 0.52*** ♀r^2 = 0.53***
I_2LL	♂r^2 = 0.71*** ♀r^2 = 0.43***	♂r^2 = 0.85*** ♀r^2 = 0.81***	♂r^2 = 0.52*** ♀r^2 = 0.46***
I_2MD	♂r^2 = 0.48*** ♀r^2 = 0.39**	♂r^2 = 0.82*** ♀r^2 = 0.73***	♂r^2 = 0.47*** ♀r^2 = 0.41***
P_4MD	♂r^2 = 0.81*** ♀r^2 = 0.64***	♂r^2 = 0.89*** ♀r^2 = 0.81***	♂r^2 = 0.79*** ♀r^2 = 0.82***
P_4BL	♂r^2 = 0.76*** ♀r^2 = 0.57***	♂r^2 = 0.90*** ♀r^2 = 0.88***	♂r^2 = 0.58*** ♀r^2 = 0.65***
M_1MD	♂r^2 = 0.75*** ♀r^2 = 0.62***	♂r^2 = 0.88*** ♀r^2 = 0.78***	♂r^2 = 0.70*** ♀r^2 = 0.78***
M_1BL	♂r^2 = 0.77*** ♀r^2 = 0.60***	♂r^2 = 0.90*** ♀r^2 = 0.85***	♂r^2 = 0.63*** ♀r^2 = 0.71***
M_2MD	♂r^2 = 0.75*** ♀r^2 = 0.59***	♂r^2 = 0.83*** ♀r^2 = 0.68***	♂r^2 = 0.74*** ♀r^2 = 0.78***
M_2BL	♂r^2 = 0.76*** ♀r^2 = 0.57***	♂r^2 = 0.89*** ♀r^2 = 0.80***	♂r^2 = 0.68*** ♀r^2 = 0.74***
Average	r^2 = 0.62	r^2 = 0.82	r^2 = 0.63

*TABLE 5.18. The magnitude of covariation 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^1LL	♂r^2 = 0.23* ♀r^2 = 0.25*	♂r^2 = 0.76*** ♀r^2 = 0.78***
I^1MD	♂r^2 = 0.29** ♀r^2 = 0.26**	♂r^2 = 0.81*** ♀r^2 = 0.78***
I^2LL	♂r^2 = 0.36** ♀r^2 = 0.15*	♂r^2 = 0.79*** ♀r^2 = 0.64***
I^2MD	♂r^2 = 0.36** ♀r^2 = 0.29**	♂r^2 = 0.84*** ♀r^2 = 0.68***
P^4MD	♂r^2 = 0.47*** ♀r^2 = 0.40***	♂r^2 = 0.89*** ♀r^2 = 0.86***
P^4BL	♂r^2 = 0.36** ♀r^2 = 0.32**	♂r^2 = 0.89*** ♀r^2 = 0.90***
M^1MD	♂r^2 = 0.45*** ♀r^2 = 0.36**	♂r^2 = 0.88*** ♀r^2 = 0.77***
M^1BL	♂r^2 = 0.40*** ♀r^2 = 0.36**	♂r^2 = 0.88*** ♀r^2 = 0.82***
M^2MD	♂r^2 = 0.53*** ♀r^2 = 0.36**	♂r^2 = 0.82*** ♀r^2 = 0.63***
M^2BL	♂r^2 = 0.44*** ♀r^2 = 0.36**	♂r^2 = 0.89*** ♀r^2 = 0.78***
Average	r^2 = 0.35	r^2 = 0.80

expected that heights and basal areas would have coevolved to maintain strength. Perhaps selection is weaker on female canine strength than on male canine strength.

Dimensions of the Honing Complex and of the Incisors and Postcanine Dentition Among Species: Among species, the elements of the canine honing complex covary positively with dimensions of the incisors and postcanine teeth (Tables 5.17 and 5.18). The levels of covariation between mandibular canine height and incisors (average r^2 = 0.62) and postcanine dimensions for maxillary canine height (average r^2 = 0.35). Among species, canine basal size (√(MD*LL)) covaries more strongly with the incisors and postcanine teeth than do canine heights (average r^2 = 0.82 for C_1 basal size and r^2 = 0.80 for C^1 basal size). For the length of the premolar honing surface, the average (r^2 = 0.63) is similar to that observed for the mandibular canine height.

Discussion and Summary

The results of this chapter robustly support the conclusion that the canine honing complex is both a variational and functional module in males and females. Between the mandibular and maxillary canines, covariation among homologous dimensions is strong as is covariation between canine heights and premolar honing surface length. Characters of the complex have coevolved because selection acted on pleiotropically linked sets of traits (the strong selection that has acted on the canine honing complex was reviewed in Chapter 1 (e.g., Plavcan, 1993; Plavcan, 2001; Leigh et al., 2008)) in both males and females. There is some flexibility in the system; though the length of the premolar honing surface and the height of the maxillary canine have coevolved in both sexes, there are large contrasts among species in the female analysis that are not evident in the male analysis. In addition, canine heights and basal areas demonstrate some independence

among species, which has potential implications for selection acting on canine strength (e.g., Plavcan and Ruff, 2008). Given that canine heights are among the most strongly covarying characters observed in the anthropoid dentition, this implies that selection must have been especially strong (e.g., Klingenberg, 2010) in order to drive the differential rates of canine height reduction observed in early hominins such as *Ardipithecus ramidus* (reviewed in Chapter 1; Suwa et al., 2009).

Covariation with dimensions of the honing complex and those of the incisors and postcanine dentition is weak and positive within species. The pleiotropy hypothesis (*sensu* Jolly (1970)) predicts a tradeoff between the size of the canines and the postcanine teeth and significant positive covariation between canine and incisor size. When the results of the among-species analysis are combined with the within-species analyses, it is clear that the pleiotropy hypothesis is rejected. Larger-bodied primates tend to have taller canines with larger basal dimensions, larger incisors, and larger postcanine teeth. Covariation between the canines and incisors and postcanine teeth among species is not strong; the canines retain substantial flexibility to evolve independently of the incisors and postcanine teeth. Two observations indicate that the canines are pleiotropically isolated from all teeth, except for the mesial mandibular premolar, in both males and females. First, in the within-species analyses, the magnitude of covariation between the sizes of canines and incisors and postcanine teeth is weak (see also, Cochard, 1981). Second, within species, whatever the underlying genetic cause for larger canine size in males, it does not translate into substantially larger postcanine or incisor size; all dimensions of the canines have indices of sexual dimorphism that are greater than for the incisors and postcanine teeth (Plavcan, 1990).

For the hominins, though the pattern of character state change indicates that reductions in canine size and incisor size occurred as the postcanine teeth were enlarging,

this pattern resulted from selection targeting each of the functional units individually. Jolly (1970) and McCollum and Sharpe (2001) largely inferred the within-species pattern of covariation by examining the among-species hominin pattern, which, as stressed in earlier chapters, is unwarranted. Significant among-species correlations need not arise from selection operating on traits linked by pleiotropy. This is not to say that there was not a selective tradeoff between the sizes of the anterior and posterior teeth during hominin and theropith evolution for the reasons outlined by Jolly (1970). The changes in the absolute and relative sizes of each of the dental functional complexes that occurred during hominin evolution are independent of one another.

Chapter 6

STABILITY OF PATTERNS OF CORRELATION AND VARIANCE-COVARIANCE AMONG SPECIES AND THE CORRESPONDENCE OF AMONG SPECIES DIVERSIFICATION TO LINES OF LEAST RESISTANCE

Given that dental functions, and the teeth performing them, are constant among anthropoids, then it is hypothesized that the pattern of genetic (and by extension phenotypic) covariance should be similar among species (e.g., Marroig and Cheverud, 2005; de Oliveira et al., 2009). This hypothesis is tested using the Mantel test and the random skewers test. The Mantel test only addresses the similarity of patterns of correlation, while the random skewers test addresses variance-covariance, as it tests for responses to randomly simulated selection vectors (see Chapter 2 for a description of these tests). For both tests, the null hypothesis is no similarity, so a significant result indicates that correlation or variance-covariance matrices are similar. In Chapters 3–5, the pattern and strength of covariation for character pairs was noted to be similar for all taxonomic groups. Potential taxonomic differences were also highlighted; for example, cercopithecids were noted to have lower levels of covariation among incisor MD lengths than either platyrrhines or hominoids, platyrrhines were shown to express the lowest level of M^3MD covariation, and cercopithecids were shown to express higher levels of covariance between all M3 dimensions and other postcanine teeth. If these differences are significant, then they should be revealed in the results of the Mantel and random skewers tests. Constraints can also be represented by $\mathbf{p}_{max}$. It is hypothesized that anthropoids should share a common $\mathbf{p}_{max}$ for each functional module, which would indicate that patterns of constraint have been constant and stable throughout anthropoid dental evolution. This hypothesis is testing by quantifying the angle between estimates of $\mathbf{p}_{max}$ for each species and then assessing statistical significance using a bootstrapping

procedure outlined in Berner (2009) (see Methods in Chapter 2). For this test, the null hypothesis is $\boldsymbol{\Theta} = 0$, so a rejection of the null hypothesis indicates that $\mathbf{p_{max}s}$ are not the same (Chapter 2). If constraints, represented by $\mathbf{p_{max}}$, are a strong influence on among species diversification ($\boldsymbol{\Delta z}$), then the angle between $\mathbf{p_{max}}$ and $\boldsymbol{\Delta z}$ should be nearly zero. This hypothesis is tested using a bootstrapping procedure. Again, a rejection of the null hypothesis indicates that among species diversification did not occur along $\mathbf{p_{max}}$.

Results

***Similarity of Correlation and Variance-Covariance Among Species*:** In Chapters 3 and 4, males and females were pooled to calculate covariance within species for incisors and the postcanine dentition. As aspects of the canine honing complex are highly size-dimorphic, males and females were not pooled in Chapter 5. So that the entire dentition could be considered in the Mantel and random skewers tests, the most highly size-dimorphic variables, canine heights, were excluded. Canine basal dimensions and premolar honing surface length were included and the male mean was adjusted to match the female mean, as for all other characters. As platyrrhines and catarrhines differ in premolar number, it was not possible to directly compare the pattern of correlation/variance-covariance between them. To make them comparable, the platyrrhine P2 was compared to the catarrhine P3 and the platyrrhine P3 was excluded from the analyses. As a result, the Mantel and random skewers tests were conducted on 33 dimensions of the incisors (LL and MD dimensions of all four incisors), canines (LL and MD dimensions of both canines), and postcanine dentition (BL and MD dimensions of P4–M3 and mesial-most maxillary premolar; oblique length, midcrown breadth, and honing surface length of the mesial-most mandibular premolar).

TABLE 6.1. Mantel tests for 33 dimensions of incisor, canine, and postcanine dental size.

	Cercopithecus cephus	*Cercopithecus pogonias*	*Cercopithecus nictitans*	*Macaca fascicularis*	*Colobus satanas*
Cercopithecus pogonias	$r_M = 0.50$ $p < 0.0001$ $Z = 88.0$ $p < 0.0001$	—			
Cercopithecus nictitans	$r_M = 0.64$ $p < 0.0001$ $Z = 95.5$ $p < 0.0001$	$r_M = 0.64$ $p < 0.0001$ $Z = 80.9$ $p < 0.0001$	—		
Macaca fascicularis	$r_M = 0.53$ $p < 0.0001$ $Z = 108.4$ $p < 0.0001$	$r_M = 0.47$ $p < 0.0001$ $Z = 89.7$ $p < 0.0001$	$r_M = 0.68$ $p < 0.0001$ $Z = 99.1$ $p < 0.0001$	—	
Colobus satanas	$r_M = 0.34$ $p < 0.0001$ $Z = 67.3$ $p = 0.0001$	$r_M = 0.37$ $p < 0.0001$ $Z = 57.1$ $p < 0.0001$	$r_M = 0.45$ $p < 0.0001$ $Z = 62.2$ $p < 0.0001$	$r_M = 0.35$ $p < 0.0001$ $Z = 69.3$ $p = 0.0001$	—
Gorilla gorilla	$r_M = 0.52$ $p < 0.0001$ $Z = 104.6$ $p < 0.0001$	$r_M = 0.51$ $p < 0.0001$ $Z = 87.0$ $p < 0.0001$	$r_M = 0.57$ $p < 0.0001$ $Z = 93.2$ $p < 0.0001$	$r_M = 0.49$ $p < 0.0001$ $Z = 106.4$ $p < 0.0001$	$r_M = 0.43$ $p < 0.0001$ $Z = 67.8$ $p < 0.0001$
Pan troglodytes	$r_M = 0.47$ $p < 0.0001$ $Z = 95.9$ $p < 0.0001$	$r_M = 0.56$ $p < 0.0001$ $Z = 81.2$ $p < 0.0001$	$r_M = 0.51$ $p < 0.0001$ $Z = 85.6$ $p < 0.0001$	$r_M = 0.41$ $p < 0.0001$ $Z = 97.1$ $p < 0.0001$	$r_M = 0.33$ $p < 0.0001$ $Z = 61.3$ $p < 0.0001$
Hylobates lar	$r_M = 0.56$ $p < 0.0001$ $Z = 105.4$ $p < 0.0001$	$r_M = 0.46$ $p < 0.0001$ $Z = 86.8$ $p < 0.0001$	$r_M = 0.54$ $p < 0.0001$ $Z = 93.2$ $p < 0.0001$	$r_M = 0.49$ $p < 0.0001$ $Z = 106.9$ $p < 0.0001$	$r_M = 0.47$ $p < 0.0001$ $Z = 63.8$ $p < 0.0001$
Cebus libidinosus	$r_M = 0.40$ $p < 0.0001$ $Z = 84.7$ $p < 0.0001$	$r_M = 0.34$ $p < 0.0001$ $Z = 70.0$ $p < 0.0001$	$r_M = 0.42$ $p < 0.0001$ $Z = 75.1$ $p < 0.0001$	$r_M = 0.45$ $p < 0.0001$ $Z = 87.3$ $p < 0.0001$	$r_M = 0.33$ $p < 0.0001$ $Z = 54.7$ $p < 0.0001$
Ateles geoffroyi	$r_M = 0.51$ $p < 0.0001$ $Z = 122.3$ $p < 0.0001$	$r_M = 0.47$ $p < 0.0001$ $Z = 101.0$ $p < 0.0001$	$r_M = 0.47$ $p < 0.0001$ $Z = 101.0$ $p < 0.0001$	$r_M = 0.26$ $p = 0.0068$ $Z = 121.3$ $p = 0.0070$	$r_M = 0.29$ $p = 0.0004$ $Z = 76.7$ $p = 0.0004$

(cont.)

TABLE 6.1 continued.

	Gorilla gorilla	*Pan troglodytes*	*Hylobates lar*	*Cebus libidinosus*
Pan troglodytes	$r_M = 0.63$ $p < 0.0001$ $Z = 96.7$ $p < 0.0001$	—	—	—
Hylobates lar	$r_M = 0.51$ $p < 0.0001$ $Z = 103.5$ $p < 0.0001$	$r_M = 0.42$ $p < 0.0001$ $Z = 93.3$ $p < 0.0001$	—	—
Cebus libidinosus	$r_M = 0.42$ $p < 0.0001$ $Z = 84.0$ $p < 0.0001$	$r_M = 0.41$ $p < 0.0001$ $Z = 77.3$ $p < 0.0001$	$r_M = 0.36$ $p < 0.0001$ $Z = 83.4$ $p < 0.0001$	—
Ateles geoffroyi	$r_M = 0.32$ $p < 0.0001$ $Z = 118.6$ $p < 0.0001$	$r_M = 0.40$ $p < 0.0001$ $Z = 109.8$ $p < 0.0001$	$r_M = 0.42$ $p < 0.0001$ $Z = 120.0$ $p < 0.0001$	$r_M = 0.29$ $p < 0.0001$ $Z = 121.9$ $p < 0.0001$

For the Mantel tests of correlation matrix similarity, all 45 one- and two-way comparisons are significantly different from zero at $\alpha = 0.0001$ (Table 6.1). As the null hypothesis for the Mantel test is no relationship, the results indicate that all 10 anthropoid taxa have a similar pattern of correlation among the 33 characters. Though all comparisons indicate statistical similarity, three taxa have the lowest absolute matrix correlation values (r_M): *Colobus satanas*, *Ateles geoffroyi*, and *Cebus libidinosus*. No matrix correlation for *Colobus satanas* is greater than $r_M = 0.47$, no comparison involving *Cebus libidinosus* is greater than $r_M = 0.45$, and no comparison involving *Ateles geoffroyi*

TABLE 6.2. Random Skewers Test for 33 dimensions of incisor, canine, and postcanine dental size.

	Cercopithecus cephus	*Cercopithecus pogonias*	*Cercopithecus nictitans*	*Macaca fascicularis*	*Colobus satanas*
Cercopithecus pogonias	$r_{RS} = 0.86$ $p < 0.0001$	—			
Cercopithecus nictitans	$r_{RS} = 0.89$ $p < 0.0001$	$r_{RS} = 0.84$ $p < 0.0001$	—		
Macaca fascicularis	$r_{RS} = 0.86$ $p < 0.0001$	$r_{RS} = 0.79$ $p < 0.0001$	$r_{RS} = 0.86$ $p < 0.0001$	—	
Colobus satanas	$r_{RS} = 0.73$ $p < 0.0001$	$r_{RS} = 0.74$ $p < 0.0001$	$r_{RS} = 0.73$ $p < 0.0001$	$r_{RS} = 0.68$ $p < 0.0001$	—
Gorilla gorilla	$r_{RS} = 0.81$ $p < 0.0001$	$r_{RS} = 0.81$ $p < 0.0001$	$r_{RS} = 0.78$ $p < 0.0001$	$r_{RS} = 0.75$ $p < 0.0001$	$r_{RS} = 0.73$ $p < 0.0001$
Pan troglodytes	$r_{RS} = 0.77$ $p < 0.0001$	$r_{RS} = 0.81$ $p < 0.0001$	$r_{RS} = 0.74$ $p < 0.0001$	$r_{RS} = 0.73$ $p < 0.0001$	$r_{RS} = 0.74$ $p < 0.0001$
Hylobates lar	$r_{RS} = 0.78$ $p < 0.0001$	$r_{RS} = 0.81$ $p < 0.0001$	$r_{RS} = 0.74$ $p < 0.0001$	$r_{RS} = 0.73$ $p < 0.0001$	$r_{RS} = 0.74$ $p < 0.0001$
Cebus libidinosus	$r_{RS} = 0.45$ $p = 0.0041$	$r_{RS} = 0.42$ $p = 0.0072$	$r_{RS} = 0.39$ $p = 0.0123$	$r_{RS} = 0.43$ $p = 0.0054$	$r_{RS} = 0.35$ $p = 0.0245$
Ateles geoffroyi	$r_{RS} = 0.65$ $p < 0.0001$	$r_{RS} = 0.62$ $p < 0.0001$	$r_{RS} = 0.57$ $p = 0.0001$	$r_{RS} = 0.61$ $p < 0.0001$	$r_{RS} = 0.54$ $p = 0.0002$

	Gorilla gorilla	*Pan troglodytes*	*Hylobates lar*	*Cebus libidinosus*
Pan troglodytes	$r_{RS} = 0.87$ $p < 0.0001$	—	—	—
Hylobates lar	$r_{RS} = 0.87$ $p < 0.0001$	$r_{RS} = 0.99$ $p < 0.0001$	—	—
Cebus libidinosus	$r_{RS} = 0.47$ $p = 0.0027$	$r_{RS} = 0.47$ $p = 0.0025$	$r_{RS} = 0.47$ $p = 0.0025$	—
Ateles geoffroyi	$r_{RS} = 0.66$ $p < 0.0001$	$r_{RS} = 0.68$ $p < 0.0001$	$r_{RS} = 0.68$ $p < 0.0001$	$r_{RS} = 0.78$ $p < 0.0001$

is greater than $r_M = 0.51$ (Table 6.1). Explanations for these lower values are given at the end of this section.

The results of the random skewers tests support those of the Mantel tests. All 45 comparisons of variance-covariance among anthropoids are significantly different from $r_{RS} = 0$ at $\alpha = 0.0001$ (Table 6.2). As for the Mantel test, the null hypothesis for the random skewers test is no similarity. All ten anthropoid taxa have similar variance-covariance structure for the 33 included characters. The same three taxa (*Colobus satanas*, *Cebus libidinosus*, and *Ateles geoffroyi*) that have low r_Ms also express the lowest absolute values of r_{RS}.

The *Colobus satanas* sample is numerically the smallest sample included in the analysis and the lower level of similarity to other samples reflects the uncertainty of correlation estimates at smaller sample sizes. *Colobus satanas* was noted to have aberrantly low r^2 estimates for some character pairs in earlier chapters; for example, it has exceptionally low estimates for homologous dimensions of mandibular incisor size (Tables 3.3 and 3.5) and for comparisons of P_4MD-P_4BL (Table 4.1) and among mandibular molar MD length (Table 4.20). The lower level of similarity for both platyrrhines in comparison to the catarrhines suggests some divergence of correlation/variance-covariance structure between anthropoid infraorders. That variance-covariance diverges over time simply due to the accumulation of neutral changes has been demonstrated in other studies of anthropoid covariance. de Oliveira et al. (2009) found that the magnitude of divergence in variance-covariance structure for cranial size traits was positively correlated with the time of divergence between taxa (see also, Schluter, 1996). The results of this study are consistent with that relationship, though it was not tested. It is also possible that the choice to treat the platyrrhine P2 and the catarrhine P3 as homologs in comparisons to other teeth affected these results. It was

noted in chapter 4 that platyrrhines have lower levels of covariation for M^3MD length than the catarrhines, which should also be reflected in the results of these tests. The low absolute value for the comparison of *Ateles geoffroyi* and *Cebus libidinosus* is not unexpected as well; in the analyses of Chapter 4, it was shown that *Cebus libidinosus* has relatively low estimates for premolar size covariation, while *Ateles geoffroyi* has high values for these comparisons. There is no apparent biological reason why those estimates of covariation should be so divergent in the two platyrrhine taxa.

Not surprisingly, given the results of Chapters 3–5, the Mantel and random skewers tests indicate a strong conservation of dental variance-covariance and correlation structure among anthropoid primates. The hypothesis that constraints have been stable during anthropoid evolution is supported.

The impact of pleiotropy on the evolution of characters

In Chapters 3–5, the covariation of independent contrasts among species was investigated for a large sample of anthropoid primates as an informal test of the hypothesis that magnitudes of within species covariation affect the independence of characters among species. In this section, evidence for shared patterns of constraint and their impact on among species diversification are tested for a smaller sample of species. Pleiotropy is predicted to channel among-species character change along the line of least evolutionary resistance ($\mathbf{g}_{max}$), which is estimated in this analysis as the eigenvector associated with the first principal component of dental size ($\mathbf{p}_{max}$) (see Methods in Chapter 2). Patterns of variance-covariance have been shown to be similar among species (see above and Chapters 3–5), though some distinctions in the strength of covariance among characters were noted, which should be reflected as differences in $\mathbf{p}_{max}$ among taxa. If character change ($\mathbf{\Delta z}$) between species occurred along a shared $\mathbf{p}_{max}$, then $\mathbf{\Delta z}$ and

TABLE 6.3. $\boldsymbol{\Theta p_{max}}$-$\boldsymbol{p_{max}}$ *and the vector correlation, in parentheses, for all measures of incisor size. The comparisons that are significantly different from* $\boldsymbol{\Theta} = 0$ *are shaded grey.*

	Cercopithecus nictitans	*Cercopithecus cephus*	*Macaca fascicularis*	*Colobus satanas*	*Gorilla gorilla*	*Pan troglodytes*	*Hylobates lar*	*Ateles geoffroyi*	*Cebus libidinosus*
Cerco. pogonias	$\boldsymbol{\Theta} = 14.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0947$	$\boldsymbol{\Theta} = 18.4$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0075$	$\boldsymbol{\Theta} = 31.0$ $r_{\boldsymbol{\Theta}} = 0.86$ $p = 0.0004$	$\boldsymbol{\Theta} = 19.2$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.2408$	$\boldsymbol{\Theta} = 17.1$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0356$	$\boldsymbol{\Theta} = 16.8$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0327$	$\boldsymbol{\Theta} = 24.5$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0956$	$\boldsymbol{\Theta} = 18.9$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0052$	$\boldsymbol{\Theta} = 17.4$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0225$
Cerco. nictitans		$\boldsymbol{\Theta} = 13.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.1017$	$\boldsymbol{\Theta} = 24.0$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0077$	$\boldsymbol{\Theta} = 25.6$ $r_{\boldsymbol{\Theta}} = 0.90$ $p = 0.2311$	$\boldsymbol{\Theta} = 14.8$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0788$	$\boldsymbol{\Theta} = 13.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.1072$	$\boldsymbol{\Theta} = 18.8$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.2310$	$\boldsymbol{\Theta} = 14.7$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0410$	$\boldsymbol{\Theta} = 10.1$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.2406$	
Cerco. cephus			$\boldsymbol{\Theta} = 23.9$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0011$	$\boldsymbol{\Theta} = 29.6$ $r_{\boldsymbol{\Theta}} = 0.87$ $p = 0.0446$	$\boldsymbol{\Theta} = 24.2$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0678$	$\boldsymbol{\Theta} = 16.0$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.1546$	$\boldsymbol{\Theta} = 21.8$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.1789$	$\boldsymbol{\Theta} = 17.8$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0015$	$\boldsymbol{\Theta} = 18.0$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0027$		
Macaca fascicularis				$\boldsymbol{\Theta} = 45.4$ $r_{\boldsymbol{\Theta}} = 0.70$ $p = 0.0043$	$\boldsymbol{\Theta} = 32.5$ $r_{\boldsymbol{\Theta}} = 0.84$ $p = 0.0001$	$\boldsymbol{\Theta} = 30.0$ $r_{\boldsymbol{\Theta}} = 0.087$ $p = 0.0058$	$\boldsymbol{\Theta} = 20.9$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.1587$	$\boldsymbol{\Theta} = 28.0$ $r_{\boldsymbol{\Theta}} = 0.88$ $p = 0.0001$	$\boldsymbol{\Theta} = 18.8$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0060$			
Colobus satanas					$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.1677$	$\boldsymbol{\Theta} = 71.8$ $r_{\boldsymbol{\Theta}} = 0.31$ $p < 0.0001$	$\boldsymbol{\Theta} = 36.1$ $r_{\boldsymbol{\Theta}} = 0.81$ $p = 0.0477$	$\boldsymbol{\Theta} = 27.1$ $r_{\boldsymbol{\Theta}} = 0.89$ $p = 0.0730$	$\boldsymbol{\Theta} = 31.8$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0330$				
Gorilla gorilla						$\boldsymbol{\Theta} = 13.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.1253$	$\boldsymbol{\Theta} = 18.7$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.1668$	$\boldsymbol{\Theta} = 17.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0106$	$\boldsymbol{\Theta} = 16.0$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0137$				
Pan troglodytes							$\boldsymbol{\Theta} = 15.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.3120$	$\boldsymbol{\Theta} = 9.12$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.2314$	$\boldsymbol{\Theta} = 15.5$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0489$				
Hylobates lar								$\boldsymbol{\Theta} = 14.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2860$	$\boldsymbol{\Theta} = 12.6$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.3742$				
Ateles geoffroyi									$\boldsymbol{\Theta} = 14.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0141$				

$\mathbf{p_{max}}$ should exhibit a high vector correlation (i.e., $\mathbf{\Theta p_{max}\text{-}\Delta z} = 0°$) (see Chapter 2). The hypothesis will be rejected if $\mathbf{\Theta p_{max}\text{-}\Delta z}$ is significantly different from $\mathbf{\Theta} = 0°$.These hypotheses are examined separately for dental size for each of the three functional/variational modules identified in Chapters 3–5 (incisors, postcanine, canine honing complex). The hypothesis that $\mathbf{p_{max}}$ is shared (i.e., $\mathbf{\Theta p_{max}\text{-}p_{max}} = 0°$) will be rejected if $\mathbf{\Theta p_{max}\text{-}p_{max}}$ is significantly different from $\mathbf{\Theta} = 0°$.

Incisor $\mathbf{p_{max}}$ ***and*** $\boldsymbol{\Delta z}$***:*** The hypothesis that anthropoids share a common incisor $\mathbf{p_{max}}$ (i.e., $\mathbf{\Theta p_{max}\text{-}p_{max}} = 0$ for pairwise comparisons) is tested using the LL breadths and MD lengths of all four incisors (Table 6.3). For these eight measures, the hypothesis that $\mathbf{p_{max}}$ is constant among species is rejected in 22 out of 45 comparisons (49% of all comparisons). Several samples are distinctive among the 10 species analyzed; six of nine comparisons involving *Cercopithecus pogonias* are statistically different from $\mathbf{\Theta} = 0°$, eight of nine comparisons involving *Macaca fascicularis* are significantly different; four of nine *Gorilla gorilla* comparisons are significantly different; four of nine *Colobus satanas* comparisons are significantly different; and five of nine comparisons for both *Cebus libidinosus* and *Ateles geoffroyi* are significantly different. Estimates of $\mathbf{p_{max}}$ are quite variable in cercopithecid primates and often significantly different from other cercopithecids and from platyrrhines and hominoids; in contrast, between hominoids and between platyrrhines, $\mathbf{p_{max}}$ estimates are relatively stable, No comparisons between the hominoid species are significantly different from $\mathbf{\Theta} = 0°$. The comparison between the two platyrrhine taxa is significant, but the angle between them (14.0°) is small. Though many comparisons are significantly different from zero, many of the significant contrasts have small $\mathbf{\Theta}$ values; only 18 of 45 comparisons have a $\mathbf{\Theta} > 20°$, which suggests that the bootstrapping procedure is a powerful test for detecting deviations from $\mathbf{\Theta} = 0$. The

TABLE 6.4. Number of individuals from which incisor size $\mathbf{p}_{max}$ was estimated.

Taxon	Individuals preserving all 8 incisor measurements
Gorilla gorilla	36
Pan troglodytes	59
Hylobates lar	28
Cercopithecus cephus	56
Cercopithecus nictitans	57
Cercopithecus pogonias	37
Macaca fascicularis	50
Colobus satanas	37
Ateles geoffroyi	48
Cebus libidinosus	64

largest **Θ**s are not observed between catarrhines and platyrrhines, but rather in comparisons of cercopithecids to one another and comparisons of cercopithecids to both platyrrhines and hominoids. Cercopithecid $\mathbf{p}_{max}$ estimates are exceptionally variable.

In the analysis of incisor modularity (Chapter 3), the estimated strength of r^2 among cercopithecids was shown to be variable and to be lower on average than for platyrrhines and hominoids (especially in MD lengths). Since r^2s capture information about the covariance structure among characters and $\mathbf{p}_{max}$ reflects both variance and covariance, it is not surprising that estimates of the cercopithecid incisor $\mathbf{p}_{max}$ are so variable among species. However, the extent to which this variation reflects biological reality is not clear; relative to the total sample size, there are fewer individuals for which all 8 incisor measurements could be recorded (Table 6.4), which means that the eigenvectors were estimated from a smaller sample than the estimates of r^2 for most incisor character pairs (Chapter 3). Undoubtedly, this introduces stochastic variation into the estimates of $\mathbf{p}_{max}$. In fact, other studies of variance-covariance have found that sampling errors scale inversely with sample size (Ackermann, 2010). Given the reduction

TABLE 6.5. $\boldsymbol{\Theta p_{max}\text{-}p_{max}}$ *and the angular correlation coefficient, in parentheses, for incisor breadths only. The comparisons that are significantly different from* $\boldsymbol{\Theta} = 0$ *are shaded grey.*

	Ateles geoffroyi	*Hylobates lar*	*Pan troglodytes*	*Gorilla gorilla*	*Colobus satanas*	*Macaca fascicularis*	*Cerco. cephus*	*Cerco. nictitans*	*Cerco. pogonias*
Cercopithecus nictitans	$\boldsymbol{\Theta} = 8.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0620$	$\boldsymbol{\Theta} = 9.4$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1440$	$\boldsymbol{\Theta} = 9.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0070$	$\boldsymbol{\Theta} = 6.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0860$	$\boldsymbol{\Theta} = 9.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.6170$	$\boldsymbol{\Theta} = 14.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p < 0.0001$	$\boldsymbol{\Theta} = 17.3$ $r_{\boldsymbol{\Theta}} = 0.95$ $p < 0.0001$	$\boldsymbol{\Theta} = 6.6$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.4360$	$\boldsymbol{\Theta} = 6.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0990$
Cercopithecus cephus		$\boldsymbol{\Theta} = 10.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1250$	$\boldsymbol{\Theta} = 3.2$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.3130$	$\boldsymbol{\Theta} = 12.3$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0140$	$\boldsymbol{\Theta} = 3.2$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.9860$	$\boldsymbol{\Theta} = 16.6$ $r_{\boldsymbol{\Theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\Theta} = 18.9$ $r_{\boldsymbol{\Theta}} = 0.95$ $p < 0.0001$	$\boldsymbol{\Theta} = 11.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0890$	$\boldsymbol{\Theta} = 12.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0150$
Macaca fascicularis			$\boldsymbol{\Theta} = 8.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1620$	$\boldsymbol{\Theta} = 15.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0370$	$\boldsymbol{\Theta} = 13.7$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2451$	$\boldsymbol{\Theta} = 7.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1400$	$\boldsymbol{\Theta} = 8.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1580$	$\boldsymbol{\Theta} = 7.0$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.4010$	$\boldsymbol{\Theta} = 9.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1500$
Colobus satanas				$\boldsymbol{\Theta} = 9.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.5426$	$\boldsymbol{\Theta} = 13.5$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2699$	$\boldsymbol{\Theta} = 14.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p < 0.0001$	$\boldsymbol{\Theta} = 16.4$ $r_{\boldsymbol{\Theta}} = 0.95$ $p < 0.0001$	$\boldsymbol{\Theta} = 11.3$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0630$	$\boldsymbol{\Theta} = 11.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0120$
Gorilla gorilla					$\boldsymbol{\Theta} = 14.5$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.3017$	$\boldsymbol{\Theta} = 20.7$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p < 0.0001$	$\boldsymbol{\Theta} = 9.5$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.2630$	$\boldsymbol{\Theta} = 13.3$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0180$
Colobus satanas						$\boldsymbol{\Theta} = 14.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2323$	$\boldsymbol{\Theta} = 16.4$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.1222$	$\boldsymbol{\Theta} = 11.3$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.7042$	$\boldsymbol{\Theta} = 11.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.5998$
Macaca fascicularis							$\boldsymbol{\Theta} = 5.7$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.1000$	$\boldsymbol{\Theta} = 13.6$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0140$	$\boldsymbol{\Theta} = 9.4$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0400$
Cerco. cephus								$\boldsymbol{\Theta} = 14.5$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0170$	$\boldsymbol{\Theta} = 14.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0140$
Cerco. nictitans									$\boldsymbol{\Theta} = 10.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1850$

in sample size associated with calculating incisor $\mathbf{p}_{max}$ using all eight measures of size, it is far more likely that the r^2 estimates reflect true population values than the $\mathbf{p}_{max}$ estimates do.

As incisors tend to be MD longest near their edges, even modest incisal wear results in a severe reduction in the number of individuals for which MD length can be measured (Table 6.4). In contrast, they tend to be LL broadest near their cervices and so breadths are for more numerous in the incisor data set. To determine if LL breadths share a common line of least evolutionary resistance, $\mathbf{p}_{max}$ was estimated using only LL breadths (Table 6.5). Sixteen out of 45 LL comparisons (36%) are significantly different from $\boldsymbol{\Theta} = 0°$, suggesting that results using the total data set were affected by stochastic variation associated with small sample sizes. As for the analysis that included all incisor measures, it is principally comparisons involving *Gorilla gorilla*, *Cercopithecus pogonias*, and *Macaca fascicularis* that are significantly different from $\boldsymbol{\Theta} = 0°$. Overall, the absolute values of $\boldsymbol{\Theta}$ tend to be quite low; in fact, only 2 comparisons (both involving *Gorilla gorilla*) are greater than $\boldsymbol{\Theta} = 20.0°$. The results of the two analyses of incisor size indicate that $\mathbf{p}_{max}$ is similar, but not identical, among anthropoid primates. The results do not suggest any obvious taxonomic division of patterns for $\mathbf{p}_{max}$. Instead, the hypothesis that the variation observed is stochastic (at least for the cercopithecids) deserves further evaluation.

The correspondence of $\boldsymbol{\Delta z}$ to an estimate of incisor size $\mathbf{p}_{max}$ for each species was investigated. The null hypothesis for the comparisons is $\boldsymbol{\Theta} = 0$ (i.e., that the vector describing the among species differences is in line with the maximum vector of phenotypic covariance); a rejection of the null hypothesis indicates that $\boldsymbol{\Delta z}$ is not aligned with $\mathbf{p}_{max}$. When all eight dimensions of incisor size are considered, 81 out of 90 comparisons are significantly different from zero (Table 6.6). In some cases, the $\boldsymbol{\Theta}$ values

TABLE 6.6. $\boldsymbol{\Theta p_{max}}$-$\boldsymbol{\Delta z}$ *for 8 incisor dimensions. Those comparisons that are significantly different from* $\boldsymbol{\Theta} = 0$ *are shaded grey.*

	$\mathbf{p_{max}}$ *Cercopithecus pogonias*	$\mathbf{p_{max}}$ *Cercopithecus nictitans*	$\mathbf{p_{max}}$ *Cercopithecus cephus*	$\mathbf{p_{max}}$ *Macaca fascicularis*	$\mathbf{p_{max}}$ *Colobus satanas*
Cercopithecus pogonias	—	$\boldsymbol{\Theta} = 37.1$ $r_{\boldsymbol{\Theta}} = 0.80$ $p < 0.0001$	$\boldsymbol{\Theta} = 62.9$ $r_{\boldsymbol{\Theta}} = 0.46$ $p = 0.0003$	$\boldsymbol{\Theta} = 18.5$ $r_{\boldsymbol{\Theta}} = 0.95$ $p < 0.0000$	$\boldsymbol{\Theta} = 45.3$ $r_{\boldsymbol{\Theta}} = 0.70$ $p = 0.0168$
Cercopithecus nictitans	$\boldsymbol{\Theta} = 32.7$ $r_{\boldsymbol{\Theta}} = 0.84$ $p = 0.0007$	—	$\boldsymbol{\Theta} = 45.7$ $r_{\boldsymbol{\Theta}} = 0.70$ $p < 0.0001$	$\boldsymbol{\Theta} = 15.4$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0047$	$\boldsymbol{\Theta} = 54.8$ $r_{\boldsymbol{\Theta}} = 0.58$ $p = 0.0041$
Cercopithecus cephus	$\boldsymbol{\Theta} = 60.2$ $r_{\boldsymbol{\Theta}} = 0.50$ $p = 0.0103$	$\boldsymbol{\Theta} = 36.7$ $r_{\boldsymbol{\Theta}} = 0.80$ $p < 0.0001$	—	$\boldsymbol{\Theta} = 15.6$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0009$	$\boldsymbol{\Theta} = 51.2$ $r_{\boldsymbol{\Theta}} = 0.63$ $p = 0.0070$
Macaca fascicularis	$\boldsymbol{\Theta} = 23.1$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.001$	$\boldsymbol{\Theta} = 31.9$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0003$	$\boldsymbol{\Theta} = 26.1$ $r_{\boldsymbol{\Theta}} = 0.90$ $p < 0.0001$	—	$\boldsymbol{\Theta} = 40.3$ $r_{\boldsymbol{\Theta}} = 0.76$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\Theta} = 40.3$ $r_{\boldsymbol{\Theta}} = 0.76$ $p < 0.0001$	$\boldsymbol{\Theta} = 44.9$ $r_{\boldsymbol{\Theta}} = 0.71$ $p < 0.0001$	$\boldsymbol{\Theta} = 47.4$ $r_{\boldsymbol{\Theta}} = 0.68$ $p < 0.0001$	$\boldsymbol{\Theta} = 44.6$ $r_{\boldsymbol{\Theta}} = 0.71$ $p < 0.0001$	—
Gorilla gorilla	$\boldsymbol{\Theta} = 14.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0147$	$\boldsymbol{\Theta} = 13.3$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0738$	$\boldsymbol{\Theta} = 16.7$ $r_{\boldsymbol{\Theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\Theta} = 38.9$ $r_{\boldsymbol{\Theta}} = 0.78$ $p < 0.0001$	$\boldsymbol{\Theta} = 32.8$ $r_{\boldsymbol{\Theta}} = 0.84$ $p < 0.0001$
Pan troglodytes	$\boldsymbol{\Theta} = 15.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0129$	$\boldsymbol{\Theta} = 12.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0595$	$\boldsymbol{\Theta} = 15.4$ $r_{\boldsymbol{\Theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\Theta} = 37.3$ $r_{\boldsymbol{\Theta}} = 0.80$ $p < 0.0001$	$\boldsymbol{\Theta} = 60.1$ $r_{\boldsymbol{\Theta}} = 0.50$ $p < 0.0001$
Hylobates lar	$\boldsymbol{\Theta} = 81.6$ $r_{\boldsymbol{\Theta}} = 0.15$ $p < 0.0001$	$\boldsymbol{\Theta} = 56.0$ $r_{\boldsymbol{\Theta}} = 0.56$ $p < 0.0001$	$\boldsymbol{\Theta} = 65.1$ $r_{\boldsymbol{\Theta}} = 0.42$ $p = 0.0002$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0002$	$\boldsymbol{\Theta} = 41.3$ $r_{\boldsymbol{\Theta}} = 0.75$ $p = 0.0095$
Ateles geoffroyi	$\boldsymbol{\Theta} = 88.1$ $r_{\boldsymbol{\Theta}} = 0.03$ $p < 0.0001$	$\boldsymbol{\Theta} = 67.2$ $r_{\boldsymbol{\Theta}} = 0.39$ $p < 0.0001$	$\boldsymbol{\Theta} = 75.0$ $r_{\boldsymbol{\Theta}} = 0.26$ $p < 0.0001$	$\boldsymbol{\Theta} = 32.4$ $r_{\boldsymbol{\Theta}} = 0.84$ $p < 0.0001$	$\boldsymbol{\Theta} = 34.6$ $r_{\boldsymbol{\Theta}} = 0.82$ $p = 0.0298$
Cebus libidinosus	$\boldsymbol{\Theta} = 74.6$ $r_{\boldsymbol{\Theta}} = 0.27$ $p < 0.0001$	$\boldsymbol{\Theta} = 57.6$ $r_{\boldsymbol{\Theta}} = 0.54$ $p < 0.0001$	$\boldsymbol{\Theta} = 60.9$ $r_{\boldsymbol{\Theta}} = 0.49$ $p < 0.0001$	$\boldsymbol{\Theta} = 32.6$ $r_{\boldsymbol{\Theta}} = 0.84$ $p < 0.0001$	$\boldsymbol{\Theta} = 34.2$ $r_{\boldsymbol{\Theta}} = 0.83$ $p = 0.0266$

(cont.)

TABLE 6.6. continued.

	$\mathbf{P}_{\mathbf{max}}$ *Gorilla gorilla*	$\mathbf{P}_{\mathbf{max}}$ *Pan troglodytes*	$\mathbf{P}_{\mathbf{max}}$ *Hylobates lar*	$\mathbf{P}_{\mathbf{max}}$ *Cebus libidinosus*	$\mathbf{P}_{\mathbf{max}}$ *Ateles geoffroyi*
Cerco. pogonias	$\boldsymbol{\Theta} = 15.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0281$	$\boldsymbol{\Theta} = 6.0$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.3091$	$\boldsymbol{\Theta} = 83.6$ $r_{\boldsymbol{\Theta}} = 0.11$ $p < 0.0001$	$\boldsymbol{\Theta} = 76.9$ $r_{\boldsymbol{\Theta}} = 0.23$ $p < 0.0001$	$\boldsymbol{\Theta} = 87.0$ $r_{\boldsymbol{\Theta}} = 0.05$ $p < 0.0001$
Cerco. nictitans	$\boldsymbol{\Theta} = 15.0$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0273$	$\boldsymbol{\Theta} = 5.3$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.3886$	$\boldsymbol{\Theta} = 65.1$ $r_{\boldsymbol{\Theta}} = 0.42$ $p = 0.0002$	$\boldsymbol{\Theta} = 63.5$ $r_{\boldsymbol{\Theta}} = 0.45$ $p < 0.0001$	$\boldsymbol{\Theta} = 70.7$ $r_{\boldsymbol{\Theta}} = 0.33$ $p < 0.0001$
Cerco. cephus	$\boldsymbol{\Theta} = 14.4$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0343$	$\boldsymbol{\Theta} = 5.2$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.3895$	$\boldsymbol{\Theta} = 80.4$ $r_{\boldsymbol{\Theta}} = 0.17$ $p < 0.0001$	$\boldsymbol{\Theta} = 75.0$ $r_{\boldsymbol{\Theta}} = 0.26$ $p < 0.0001$	$\boldsymbol{\Theta} = 86.2$ $r_{\boldsymbol{\Theta}} = 0.07$ $p < 0.0001$
Macaca fascicularis	$\boldsymbol{\Theta} = 17.3$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0192$	$\boldsymbol{\Theta} = 10.1$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0826$	$\boldsymbol{\Theta} = 37.5$ $r_{\boldsymbol{\Theta}} = 0.79$ $p = 0.0290$	$\boldsymbol{\Theta} = 37.3$ $r_{\boldsymbol{\Theta}} = 0.80$ $p < 0.0001$	$\boldsymbol{\Theta} = 40.4$ $r_{\boldsymbol{\Theta}} = 0.76$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\Theta} = 22.6$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0052$	$\boldsymbol{\Theta} = 19.7$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 11.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.4304$	$\boldsymbol{\Theta} = 16.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\Theta} = 20.4$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$
Gorilla gorilla	—	$\boldsymbol{\Theta} = 37.1$ $r_{\boldsymbol{\Theta}} = 0.80$ $p = 0.0002$	$\boldsymbol{\Theta} = 23.1$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.1389$	$\boldsymbol{\Theta} = 20.8$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 14.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0137$
Pan troglodytes	$\boldsymbol{\Theta} = 37.5$ $r_{\boldsymbol{\Theta}} = 0.79$ $p < 0.0001$	—	$\boldsymbol{\Theta} = 20.3$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 19.6$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 13.8$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0088$
Hylobates lar	$\boldsymbol{\Theta} = 17.8$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0142$	$\boldsymbol{\Theta} = 8.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1491$	—	$\boldsymbol{\Theta} = 81.6$ $r_{\boldsymbol{\Theta}} = 0.15$ $p < 0.0001$	$\boldsymbol{\Theta} = 70.0$ $r_{\boldsymbol{\Theta}} = 0.34$ $p < 0.0001$
Ateles geoffroyi	$\boldsymbol{\Theta} = 18.2$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0157$	$\boldsymbol{\Theta} = 9.2$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1179$	$\boldsymbol{\Theta} = 64.6$ $r_{\boldsymbol{\Theta}} = 0.43$ $p < 0.0001$	$\boldsymbol{\Theta} = 55.8$ $r_{\boldsymbol{\Theta}} = 0.56$ $p < 0.0001$	—
Cebus libidinosus	$\boldsymbol{\Theta} = 19.6$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0091$	$\boldsymbol{\Theta} = 10.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0684$	$\boldsymbol{\Theta} = 85.9$ $r_{\boldsymbol{\Theta}} = 0.07$ $p < 0.0001$	—	$\boldsymbol{\Theta} = 52.8$ $r_{\boldsymbol{\Theta}} = 0.60$ $p = 1.000$

TABLE 6.7. ***Θp_{max}-Δz*** *for incisor breadths. Those comparisons that are significantly different from* $\Theta = 0$ *are shaded grey.*

	$\mathbf{P_{max}}$ *Cercopithecus pogonias*	$\mathbf{P_{max}}$ *Cercopithecus nictitans*	$\mathbf{P_{max}}$ *Cercopithecus cephus*	$\mathbf{P_{max}}$ *Macaca fascicularis*	$\mathbf{P_{max}}$ *Colobus satanas*
Cercopithecus pogonias	—	$\Theta = 42.6$ $r_\Theta = 0.74$ $p = 0.0308$	$\Theta = 68.5$ $r_\Theta = 0.37$ $p < 0.0001$	$\Theta = 11.7$ $r_\Theta = 0.98$ $p < 0.0001$	$\Theta = 18.9$ $r_\Theta = 0.95$ $p = 0.1995$
Cercopithecus nictitans	$\Theta = 44.4$ $r_\Theta = 0.71$ $p = 0.0004$	—	$\Theta = 56.0$ $r_\Theta = 0.56$ $p < 0.0001$	$\Theta = 11.8$ $r_\Theta = 0.98$ $p < 0.0001$	$\Theta = 16.7$ $r_\Theta = 0.96$ $p = 0.2469$
Cercopithecus cephus	$\Theta = 59.2$ $r_\Theta = 0.51$ $p < 0.0001$	$\Theta = 42.9$ $r_\Theta = 0.73$ $p = 0.0001$	—	$\Theta = 12.1$ $r_\Theta = 0.98$ $p < 0.0001$	$\Theta = 20.8$ $r_\Theta = 0.94$ $p = 0.1403$
Macaca fascicularis	$\Theta = 10.5$ $r_\Theta = 0.98$ $p = 0.0266$	$\Theta = 23.6$ $r_\Theta = 0.92$ $p = 0.0004$	$\Theta = 17.7$ $r_\Theta = 0.95$ $p < 0.0001$	—	$\Theta = 62.4$ $r_\Theta = 0.46$ $p = 0.0001$
Colobus satanas	$\Theta = 22.3$ $r_\Theta = 0.93$ $p = 0.0004$	$\Theta = 15.4$ $r_\Theta = 0.96$ $p = 0.4932$	$\Theta = 33.1$ $r_\Theta = 0.84$ $p < 0.0001$	$\Theta = 80.3$ $r_\Theta = 0.17$ $p < 0.0001$	—
Gorilla gorilla	$\Theta = 11.7$ $r_\Theta = 0.98$ $p = 0.0087$	$\Theta = 8.6$ $r_\Theta = 0.99$ $p = 0.4439$	$\Theta = 17.9$ $r_\Theta = 0.95$ $p < 0.0001$	$\Theta = 19.2$ $r_\Theta = 0.94$ $p < 0.0001$	$\Theta = 12.9$ $r_\Theta = 0.97$ $p = 0.2752$
Pan troglodytes	$\Theta = 8.5$ $r_\Theta = 0.99$ $p = 0.0536$	$\Theta = 6.5$ $r_\Theta = 0.99$ $p = 0.7127$	$\Theta = 15.5$ $r_\Theta = 0.96$ $p < 0.0001$	$\Theta = 16.1$ $r_\Theta = 0.96$ $p < 0.0001$	$\Theta = 15.6$ $r_\Theta = 0.96$ $p = 0.1266$
Hylobates lar	$\Theta = 65.9$ $r_\Theta = 0.41$ $p < 0.0001$	$\Theta = 51.1$ $r_\Theta = 0.63$ $p < 0.0001$	$\Theta = 59.0$ $r_\Theta = 0.52$ $p < 0.0001$	$\Theta = 17.5$ $r_\Theta = 0.95$ $p < 0.0001$	$\Theta = 9.1$ $r_\Theta = 0.99$ $p = 0.4292$
Ateles geoffroyi	$\Theta = 81.1$ $r_\Theta = 0.15$ $p < 0.0001$	$\Theta = 86.0$ $r_\Theta = 0.07$ $p < 0.0001$	$\Theta = 88.0$ $r_\Theta = 0.03$ $p < 0.0001$	$\Theta = 22.1$ $r_\Theta = 0.93$ $p < 0.0001$	$\Theta = 13.5$ $r_\Theta = 0.97$ $p = 0.2350$
Cebus libidinosus	$\Theta = 84.5$ $r_\Theta = 0.10$ $p < 0.0001$	$\Theta = 701$ $r_\Theta = 0.34$ $p < 0.0001$	$\Theta = 75.6$ $r_\Theta = 0.25$ $p < 0.0001$	$\Theta = 21.2$ $r_\Theta = 0.93$ $p < 0.0001$	$\Theta = 11.4$ $r_\Theta = 0.98$ $p = 0.2414$

(cont.)

TABLE 6.7 continued

	$\mathbf{P}_{\mathbf{max}}$ *Gorilla gorilla*	$\mathbf{P}_{\mathbf{max}}$ *Pan troglodytes*	$\mathbf{P}_{\mathbf{max}}$ *Hylobates lar*	$\mathbf{P}_{\mathbf{max}}$ *Cebus libidinosus*	$\mathbf{P}_{\mathbf{max}}$ *Ateles geoffroyi*
Cerco. pogonias	$\boldsymbol{\Theta} = 11.0$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0031$	$\boldsymbol{\Theta} = 5.1$ $r_{\boldsymbol{\Theta}} = 1.0$ $p = 0.0556$	$\boldsymbol{\Theta} = 60.9$ $r_{\boldsymbol{\Theta}} = 0.49$ $p = 0.0006$	$\boldsymbol{\Theta} = 88.8$ $r_{\boldsymbol{\Theta}} = 0.02$ $p < 0.0001$	$\boldsymbol{\Theta} = 75.2$ $r_{\boldsymbol{\Theta}} = 0.26$ $p < 0.0001$
Cerco. nictitans	$\boldsymbol{\Theta} = 11.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0021$	$\boldsymbol{\Theta} = 5.2$ $r_{\boldsymbol{\Theta}} = 1.0$ $p = 0.0620$	$\boldsymbol{\Theta} = 45.0$ $r_{\boldsymbol{\Theta}} = 0.71$ $p = 0.0012$	$\boldsymbol{\Theta} = 74.0$ $r_{\boldsymbol{\Theta}} = 0.28$ $p < 0.0001$	$\boldsymbol{\Theta} = 87.4$ $r_{\boldsymbol{\Theta}} = 0.04$ $p < 0.0001$
Cerco. cephus	$\boldsymbol{\Theta} = 10.3$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0060$	$\boldsymbol{\Theta} = 5.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0284$	$\boldsymbol{\Theta} = 66.3$ $r_{\boldsymbol{\Theta}} = 0.40$ $p = 0.0001$	$\boldsymbol{\Theta} = 87.1$ $r_{\boldsymbol{\Theta}} = 0.05$ $p < 0.0001$	$\boldsymbol{\Theta} = 72.5$ $r_{\boldsymbol{\Theta}} = 0.30$ $p < 0.0001$
Macaca fascicularis	$\boldsymbol{\Theta} = 10.8$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0034$	$\boldsymbol{\Theta} = 7.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0022$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0117$	$\boldsymbol{\Theta} = 35.2$ $r_{\boldsymbol{\Theta}} = 0.82$ $p < 0.0001$	$\boldsymbol{\Theta} = 35.1$ $r_{\boldsymbol{\Theta}} = 0.82$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\Theta} = 16.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0004$	$\boldsymbol{\Theta} = 6.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0110$	$\boldsymbol{\Theta} = 5.2$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.4256$	$\boldsymbol{\Theta} = 11.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0010$	$\boldsymbol{\Theta} = 8.7$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0830$
Gorilla gorilla	—	$\boldsymbol{\Theta} = 30.8$ $r_{\boldsymbol{\Theta}} = 0.86$ $p < 0.0001$	$\boldsymbol{\Theta} = 6.3$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.3063$	$\boldsymbol{\Theta} = 10.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0035$	$\boldsymbol{\Theta} = 14.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p < 0.0001$
Pan troglodytes	$\boldsymbol{\Theta} = 35.6$ $r_{\boldsymbol{\Theta}} = 0.81$ $p < 0.0001$	—	$\boldsymbol{\Theta} = 3.2$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.6606$	$\boldsymbol{\Theta} = 10.0$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0024$	$\boldsymbol{\Theta} = 8.5$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0440$
Hylobates lar	$\boldsymbol{\Theta} = 15.3$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0004$	$\boldsymbol{\Theta} = 6.0$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0334$	—	$\boldsymbol{\Theta} = 40.7$ $r_{\boldsymbol{\Theta}} = 0.76$ $p < 0.0001$	$\boldsymbol{\Theta} = 27.8$ $r_{\boldsymbol{\Theta}} = 0.88$ $p < 0.0001$
Ateles geoffroyi	$\boldsymbol{\Theta} = 5.3$ $r_{\boldsymbol{\Theta}} = 1.00$ $p = 0.2043$	$\boldsymbol{\Theta} = 6.4$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0222$	$\boldsymbol{\Theta} = 27.1$ $r_{\boldsymbol{\Theta}} = 0.89$ $p = 0.0030$	$\boldsymbol{\Theta} = 60.4$ $r_{\boldsymbol{\Theta}} = 0.49$ $p < 0.0001$	—
Cebus libidinosus	$\boldsymbol{\Theta} = 15.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0231$	$\boldsymbol{\Theta} = 7.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0050$	$\boldsymbol{\Theta} = 43.5$ $r_{\boldsymbol{\Theta}} = 0.73$ $p = 0.0017$	—	$\boldsymbol{\Theta} = 60.1$ $r_{\boldsymbol{\Theta}} = 0.50$ $p < 0.0001$

*TABLE 6.8. Magnitude of difference for 8 dimensions of incisor size, calculated as the vector length of **Δz**.*

	Cerco. pogonias	*Cerco. nictitans*	*Cerco. cephus*	*Macaca fascicularis*	*Colobus satanas*
Cercopithecus nictitans	**Δz mag** = 0.75	—	—	—	—
Cercopithecus cephus	**Δz mag** = 0.41	**Δz mag** = 0.54	—	—	—
Macaca fascicularis	**Δz mag** = 2.66	**Δz mag** = 2.21	**Δz mag** = 2.58	—	—
Colobus satanas	**Δz mag** = 3.53	**Δz mag** = 3.14	**Δz mag** = 3.52	**Δz mag** = 2.26	—
Gorilla gorilla	**Δz mag** = 16.81	**Δz mag** = 16.14	**Δz mag** = 16.58	**Δz mag** = 14.46	**Δz mag** = 14.18
Pan troglodytes	**Δz mag** = 14.79	**Δz mag** = 14.15	**Δz mag** = 14.59	**Δz mag** = 12.41	**Δz mag** = 12.07
Hylobates lar	**Δz mag** = 1.52	**Δz mag** = 1.63	**Δz mag** = 1.60	**Δz mag** = 3.43	**Δz mag** = 3.43
Cebus libidinosus	**Δz mag** = 1.93	**Δz mag** = 2.23	**Δz mag** = 2.13	**Δz mag** = 3.74	**Δz mag** = 3.54
Ateles geoffroyi	**Δz mag** = 1.43	**Δz mag** = 1.62	**Δz mag** = 1.59	**Δz mag** = 3.16	**Δz mag** = 3.05

	Gorilla gorilla	*Pan troglodytes*	*Hylobates lar*	*Cebus libidinosus*
Pan troglodytes	**Δz mag** = 2.37	—	—	—
Hylobates lar	**Δz mag** = 17.01	**Δz mag** = 14.99	—	—
Cebus libidinosus	**Δz mag** = 17.45	**Δz mag** = 15.42	**Δz mag** = 1.08	—
Ateles geoffroyi	**Δz mag** = 16.86	**Δz mag** = 14.82	**Δz mag** = 0.86	**Δz mag** = 0.89

TABLE 6.9. Mean incisor size (mm) for Ateles geoffroyi and Cebus libidinosus. The taxon with the larger mean value is shaded in grey.

	I_1MD	I_1LL	I_2MD	I_2LL	I^1MD	I^1LL	I^2MD	I^2LL
Ateles geoffroyi	3.6	3.0	4.2	3.4	4.3	4.6	4.1	3.6
Cebus libidinosus	3.5	2.6	3.9	2.9	4.1	4.3	4.3	3.7
Difference	0.1	0.4	0.3	0.5	0.2	0.3	0.2	0.1

TABLE 6.10. Incisor $\boldsymbol{p_{max}}$ for 8 dimensions of Ateles geoffroyi and Cebus libidinosus.

	I_1MD	I_1LL	I_2MD	I_2LL	I^1MD	I^1LL	I^2MD	I^2LL
Ateles geoffroyi	0.261	0.267	0.349	0.326	0.482	0.379	0.416	0.290
Cebus libidinosus	0.415	0.205	0.435	0.252	0.387	0.350	0.467	0.212

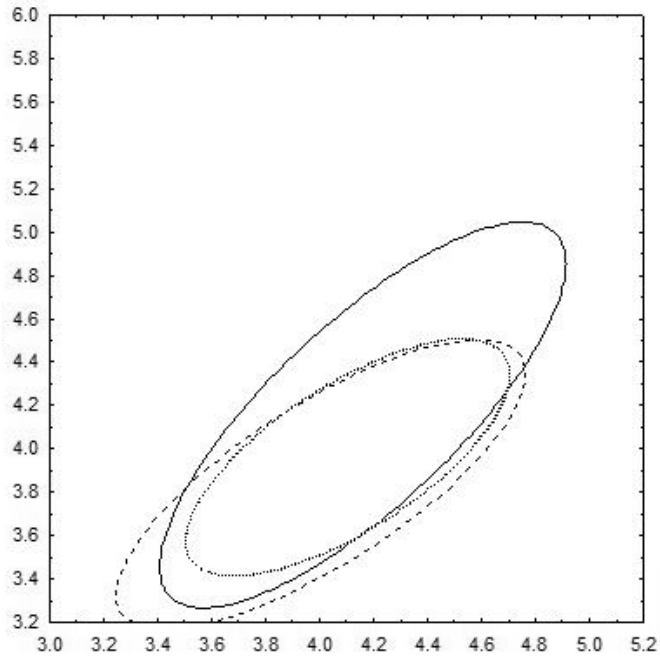

Fig. 6.1. 95% confidence ellipses for I_1LL (x-axis) and I_2LL (y-axis) for three guenon species. The three species are similar in their means and range of values but minimally different in incisor size.

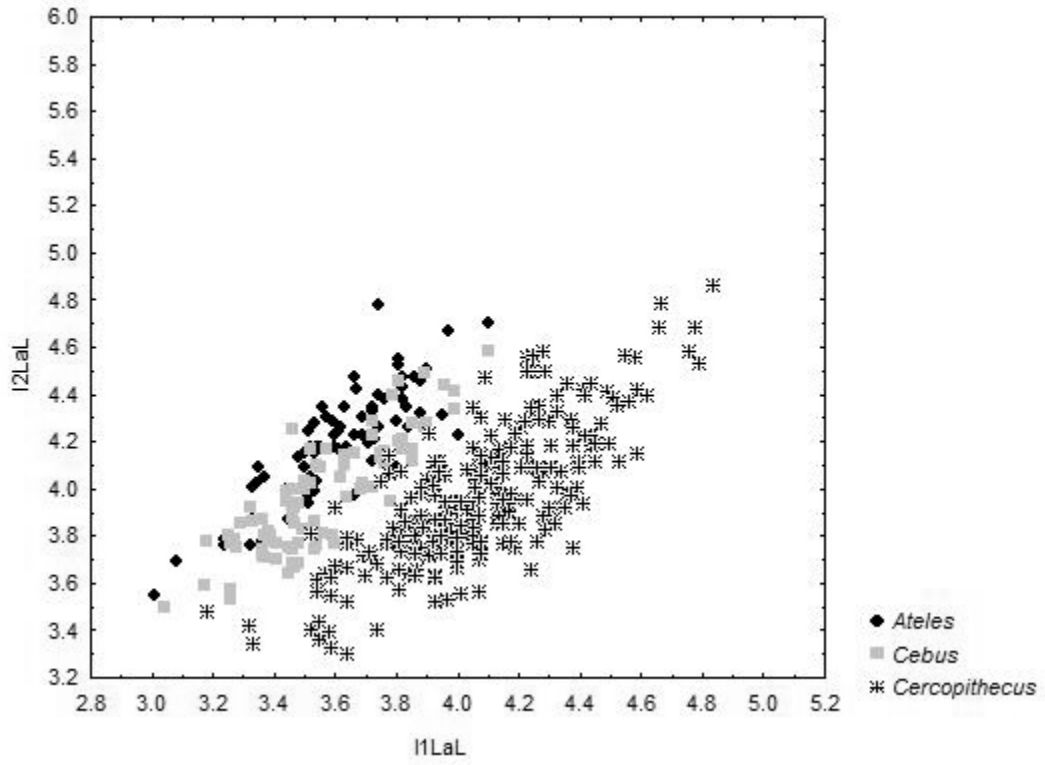

Fig. 6.2. I_1LL (x-axis) and I_2LL (y-axis) breadth in guenons and platyrrhines. The distributions for the platyrrhines and guenons do not overlap significantly and the difference between the clades could not have accumulated along the $\mathbf{p_{max}}$ associated with either extant platyrrhines or extant guenons.

TABLE 6.11. Mandibular incisor LL breadths (mm) for guenons and platyrrhines.

	I_1LL	I_2LL	I_1LL/I_2LL
Ateles geoffroyi	3.0	3.4	0.88
Cebus libidinosus	2.6	2.9	0.90
Cercopithecus cephus	4.0	3.9	1.03
Cercopithecus nictitans	4.0	4.0	1.00
Cercopithecus pogonias	4.1	3.9	1.05

are quite high (30 out of 90 estimates are greater than $\boldsymbol{\Theta} = 45°$). The highest $\boldsymbol{\Theta}$ values are observed between guenons, between guenons and platyrrhines, and between guenons and *Hylobates lar*. The reasons for the large $\boldsymbol{\Theta}$ values are explored below.

To determine if the more numerously represented incisor breadths evolve along a shared $\mathbf{p}_{\mathbf{max}}$, the correspondence of $\mathbf{p}_{\mathbf{max}}$ and $\boldsymbol{\Delta}\mathbf{z}$ was investigated for incisor LL breadths only (Table 6.7). For the incisor breadths, 71 out of 90 comparisons are significantly different from zero. Thus, the vast majority of comparisons for the both the complete incisor data set and for breadths only do not indicate a divergence along a shared $\mathbf{p}_{\mathbf{max}}$. The unavoidable conclusion of these analyses is that incisor change among species is frequently not aligned with $\mathbf{p}_{\mathbf{max}}$. Assuming that selection has driven the among species diversification in incisor size, then selection vectors have not frequently been aligned with $\mathbf{p}_{\mathbf{max}}$, which indicates that $\mathbf{p}_{\mathbf{max}}$ itself is not aligned with adaptive peaks of an adaptive landscape (e.g., Arnold, 2005).

Many of the large $\boldsymbol{\Theta}\mathbf{p}_{\mathbf{max}}$–$\boldsymbol{\Delta}\mathbf{z}$ values are observed between taxa that have incisors of similar size. For example, the $\boldsymbol{\Theta}\mathbf{p}_{\mathbf{max}}$–$\boldsymbol{\Delta}\mathbf{z}$ between *Cebus libidinosus* and *Ateles geoffroyi* is greater than 50° using either taxon's estimate of $\mathbf{p}_{\mathbf{max}}$ (Table 6.7). No difference between the incisor sizes of these taxa exceeds 0.5 mm (Tables 6.8 and 6.9). In six of eight dimensions, the *Ateles geoffroyi* mean is larger; however, for two of eight of dimensions the *Cebus libidinosus* mean is larger. As $\mathbf{p}_{\mathbf{max}}$ in both *Cebus libidinosus* and *Ateles geoffroyi* predicts positive divergence for all characters (Table 6.10), the difference between the two platyrrhine taxa is not consistent with divergence along $\mathbf{p}_{\mathbf{max}}$.

The lack of correspondence of incisor $\boldsymbol{\Delta}\mathbf{z}$ to $\mathbf{p}_{\mathbf{max}}$ in the guenons can be explained as the result of minimal divergence among the taxa. In Figure 6.1, the 95% confidence ellipses for *Cercopithecus cephus*, *Cercopithecus nictitans*, and *Cercopithecus pogonias* are plotted for I_1LL and I_2LL. It is evident that the means and ranges are nearly identical

in the three guenon species (Table 6.8 and 6.11). Though $\boldsymbol{\Theta p_{max}}$–$\boldsymbol{\Delta z}$ values indicate that differences between them have not accumulated as a result of change along $\mathbf{p_{max}}$, this is because the guenons are only minimally different (if at all) in size to begin with.

The difference between the two platyrrhine taxa and the guenons is not consistent with divergence along a shared $\mathbf{p_{max}}$. In Figure 6.2, the LL dimensions of the I_1 and I_2 are plotted for *Cebus libidinosus*, *Ateles geoffroyi*, *Cercopithecus cephus*, *Cercopithecus nictitans*, and *Cercopithecus pogonias*. The two dimensions are strongly correlated within all species, but, for a given I_1LL breadth, the guenons have a narrower I_2LL breadth (Table 6.11). As a result, the point clouds for the guenons and the platyrrhines minimally overlap. The differences between platyrrhines and guenons for these dimensions did not accumulate as a result of change along a $\mathbf{p_{max}}$ that characterizes either platyrrhines or guenons. It must be born in mind that catarrhines and platyrrhines diverged approximately 43 million years ago (Steiper and Young, 2006). As genetic constraints have been shown to be most powerful in the short term (e.g., Schluter, 1996), divergence between platyrrhines and catarrhines relative to an estimate of $\mathbf{p_{max}}$ derived from the opposite infraorder should be expected.

Postcanine $\mathbf{p_{max}}$ ***and*** $\boldsymbol{\Delta z}$***:*** For catarrhine primates, only four of 28 comparisons involving $\mathbf{p_{max}}$ are significantly different from $\boldsymbol{\Theta} = 0°$ (three of these involve *Gorilla gorilla*). Catarrhine primates, therefore, share a common $\mathbf{p_{max}}$ for postcanine size (Table 6.12). In contrast, 13 of 16 comparisons of $\mathbf{p_{max}}$ between platyrrhines and catarrhines are significantly different from $\boldsymbol{\Theta} = 0°$, indicating that the platyrrhines and catarrhines do not share the same $\mathbf{p_{max}}$ for postcanine dental size (Table 6.12).

TABLE 6.12. $\boldsymbol{\Theta p_{max}\text{-}p_{max}}$ and the angular correlation for the MD length and BL breadth of P4–M3. Those comparisons that are significantly different from $\boldsymbol{\Theta} = 0$ are shaded grey.

	Cercopithecus nictitans	*Cercopithecus cephus*	*Macaca fascicularis*	*Colobus satanas*	*Gorilla gorilla*	*Pan troglodytes*	*Hylobates lar*	*Ateles geoffroyi*	*Cebus libidinosus*
Cerco. pogonias	$\boldsymbol{\Theta} = 9.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.4620$	$\boldsymbol{\Theta} = 12.6$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1151$	$\boldsymbol{\Theta} = 10.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.2415$	$\boldsymbol{\Theta} = 15.5$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.2137$	$\boldsymbol{\Theta} = 13.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0640$	$\boldsymbol{\Theta} = 12.1$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1777$	$\boldsymbol{\Theta} = 15.3$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.1045$	$\boldsymbol{\Theta} = 25.3$ $r_{\boldsymbol{\Theta}} = 0.90$ $p = 0.0264$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0060$
Cerco. nictitans		$\boldsymbol{\Theta} = 8.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.3141$	$\boldsymbol{\Theta} = 9.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.3186$	$\boldsymbol{\Theta} = 19.9$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0360$	$\boldsymbol{\Theta} = 11.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.2323$	$\boldsymbol{\Theta} = 9.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1128$	$\boldsymbol{\Theta} = 15.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0549$	$\boldsymbol{\Theta} = 23.1$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0219$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0039$
Cerco. cephus			$\boldsymbol{\Theta} = 9.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0289$	$\boldsymbol{\Theta} = 16.8$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0478$	$\boldsymbol{\Theta} = 11.6$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0005$	$\boldsymbol{\Theta} = 8.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.1108$	$\boldsymbol{\Theta} = 7.7$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.3573$	$\boldsymbol{\Theta} = 21.0$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.0358$	$\boldsymbol{\Theta} = 19.5$ $r_{\boldsymbol{\Theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0039$
Macaca fascicularis				$\boldsymbol{\Theta} = 13.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.1261$	$\boldsymbol{\Theta} = 12.1$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0020$	$\boldsymbol{\Theta} = 9.1$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0928$	$\boldsymbol{\Theta} = 12.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.0694$	$\boldsymbol{\Theta} = 24.0$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0203$	$\boldsymbol{\Theta} = 22.3$ $r_{\boldsymbol{\Theta}} = 0.93$ $p < 0.0001$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0039$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0060$
Colobus satanas					$\boldsymbol{\Theta} = 13.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.1188$	$\boldsymbol{\Theta} = 15.5$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.1074$	$\boldsymbol{\Theta} = 17.2$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.0954$	$\boldsymbol{\Theta} = 22.8$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0115$	$\boldsymbol{\Theta} = 23.8$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0211$	$\boldsymbol{\Theta} = 19.9$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0095$	$\boldsymbol{\Theta} = 17.5$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.1788$	$\boldsymbol{\Theta} = 23.1$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0240$	$\boldsymbol{\Theta} = 19.6$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0722$
Gorilla gorilla						$\boldsymbol{\Theta} = 11.4$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0411$	$\boldsymbol{\Theta} = 9.3$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.2389$	$\boldsymbol{\Theta} = 17.5$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.1788$	$\boldsymbol{\Theta} = 19.0$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0095$	$\boldsymbol{\Theta} = 21.3$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.0014$				
Pan troglodytes							$\boldsymbol{\Theta} = 11.8$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1297$	$\boldsymbol{\Theta} = 23.1$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0240$	$\boldsymbol{\Theta} = 23.2$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0001$				
Hylobates lar								$\boldsymbol{\Theta} = 20.3$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0853$	$\boldsymbol{\Theta} = 19.6$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0722$				
Ateles geoffroyi													

TABLE 6.13. $\boldsymbol{\theta p_{max}}$-$\boldsymbol{\Delta z}$ and the angular correlation for the MD length and BL breadth of P4–M3. Those comparisons that are significantly different from $\boldsymbol{\theta} = 0$ are shaded grey.

	$\mathbf{P_{max}}$ *Cercopithecus pogonias*	$\mathbf{P_{max}}$ *Cercopithecus nictitans*	$\mathbf{P_{max}}$ *Cercopithecus cephus*	$\mathbf{P_{max}}$ *Macaca fascicularis*	$\mathbf{P_{max}}$ *Colobus satanas*
Cerco. pogonias	—	$\boldsymbol{\theta} = 35.3$ $r_{\boldsymbol{\theta}} = 0.82$ $p < 0.0001$	$\boldsymbol{\theta} = 60.5$ $r_{\boldsymbol{\theta}} = 0.49$ $p < 0.0001$	$\boldsymbol{\theta} = 15.4$ $r_{\boldsymbol{\theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\theta} = 14.9$ $r_{\boldsymbol{\theta}} = 0.97$ $p = 0.0671$
Cerco. nictitans	$\boldsymbol{\theta} = 37.3$ $r_{\boldsymbol{\theta}} = 0.80$ $p = 0.0023$	—	$\boldsymbol{\theta} = 19.7$ $r_{\boldsymbol{\theta}} = 0.94$ $p < 0.0001$	$\boldsymbol{\theta} = 27.2$ $r_{\boldsymbol{\theta}} = 0.89$ $p < 0.0001$	$\boldsymbol{\theta} = 24.2$ $r_{\boldsymbol{\theta}} = 0.91$ $p = 0.0089$
Cerco. cephus	$\boldsymbol{\theta} = 53.9$ $r_{\boldsymbol{\theta}} = 0.39$ $p < 0.0001$	$\boldsymbol{\theta} = 15.1$ $r_{\boldsymbol{\theta}} = 0.97$ $p < 0.0001$	—	$\boldsymbol{\theta} = 17.1$ $r_{\boldsymbol{\theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\theta} = 17.7$ $r_{\boldsymbol{\theta}} = 0.95$ $p = 0.0341$
Macaca fascicularis	$\boldsymbol{\theta} = 23.1$ $r_{\boldsymbol{\theta}} = 0.92$ $p = 0.0019$	$\boldsymbol{\theta} = 28.4$ $r_{\boldsymbol{\theta}} = 0.88$ $p < 0.0001$	$\boldsymbol{\theta} = 16.2$ $r_{\boldsymbol{\theta}} = 0.96$ $p < 0.0001$	—	$\boldsymbol{\theta} = 31.4$ $r_{\boldsymbol{\theta}} = 0.85$ $p = 0.0036$
Colobus satanas	$\boldsymbol{\theta} = 22.7$ $r_{\boldsymbol{\theta}} = 0.92$ $p = 0.0008$	$\boldsymbol{\theta} = 26.6$ $r_{\boldsymbol{\theta}} = 0.89$ $p < 0.0001$	$\boldsymbol{\theta} = 15.8$ $r_{\boldsymbol{\theta}} = 0.96$ $p < 0.0001$	$\boldsymbol{\theta} = 37.7$ $r_{\boldsymbol{\theta}} = 0.79$ $p < 0.0001$	—
Gorilla gorilla	$\boldsymbol{\theta} = 16.4$ $r_{\boldsymbol{\theta}} = 0.96$ $p = 0.0193$	$\boldsymbol{\theta} = 15.6$ $r_{\boldsymbol{\theta}} = 0.96$ $p = 0.0485$	$\boldsymbol{\theta} = 11.2$ $r_{\boldsymbol{\theta}} = 0.98$ $p < 0.0001$	$\boldsymbol{\theta} = 16.2$ $r_{\boldsymbol{\theta}} = 0.96$ $p = 0.0002$	$\boldsymbol{\theta} = 14.9$ $r_{\boldsymbol{\theta}} = 0.97$ $p = 0.1002$
Pan troglodytes	$\boldsymbol{\theta} = 20.5$ $r_{\boldsymbol{\theta}} = 0.94$ $p = 0.0049$	$\boldsymbol{\theta} = 22.2$ $r_{\boldsymbol{\theta}} = 0.93$ $p = 0.0023$	$\boldsymbol{\theta} = 15.1$ $r_{\boldsymbol{\theta}} = 0.97$ $p < 0.0001$	$\boldsymbol{\theta} = 23.8$ $r_{\boldsymbol{\theta}} = 0.91$ $p < 0.0001$	$\boldsymbol{\theta} = 22.9$ $r_{\boldsymbol{\theta}} = 0.92$ $p = 0.0359$
Hylobates lar	$\boldsymbol{\theta} = 37.0$ $r_{\boldsymbol{\theta}} = 0.80$ $p = 0.0002$	$\boldsymbol{\theta} = 73.1$ $r_{\boldsymbol{\theta}} = 0.29$ $p < 0.0001$	$\boldsymbol{\theta} = 32.5$ $r_{\boldsymbol{\theta}} = 0.84$ $p < 0.0001$	$\boldsymbol{\theta} = 43.0$ $r_{\boldsymbol{\theta}} = 0.73$ $p < 0.0001$	$\boldsymbol{\theta} = 21.4$ $r_{\boldsymbol{\theta}} = 0.93$ $p = 0.0144$
Ateles geoffroyi	$\boldsymbol{\theta} = 75.8$ $r_{\boldsymbol{\theta}} = 0.25$ $p < 0.0001$	$\boldsymbol{\theta} = 58.4$ $r_{\boldsymbol{\theta}} = 0.52$ $p < 0.0001$	$\boldsymbol{\theta} = 85.5$ $r_{\boldsymbol{\theta}} = 0.08$ $p < 0.0001$	$\boldsymbol{\theta} = 33.1$ $r_{\boldsymbol{\theta}} = 0.84$ $p < 0.0001$	$\boldsymbol{\theta} = 24.2$ $r_{\boldsymbol{\theta}} = 0.91$ $p = 0.0135$
Cebus libidinosus	$\boldsymbol{\theta} = 53.8$ $r_{\boldsymbol{\theta}} = 0.59$ $p < 0.0001$	$\boldsymbol{\theta} = 44.6$ $r_{\boldsymbol{\theta}} = 0.71$ $p < 0.0001$	$\boldsymbol{\theta} = 58.4$ $r_{\boldsymbol{\theta}} = 0.52$ $p < 0.0001$	$\boldsymbol{\theta} = 32.2$ $r_{\boldsymbol{\theta}} = 0.85$ $p < 0.0001$	$\boldsymbol{\theta} = 28.8$ $r_{\boldsymbol{\theta}} = 0.88$ $p = 0.0067$

(cont.)

TABLE 6.13. continued

	$\mathbf{P_{max}}$ *Gorilla gorilla*	$\mathbf{P_{max}}$ *Pan troglodytes*	$\mathbf{P_{max}}$ *Hylobates lar*	$\mathbf{P_{max}}$ *Ateles geoffroyi*	$\mathbf{P_{max}}$ *Cebus libidinosus*
Cerco. pogonias	$\boldsymbol{\Theta} = 8.4$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0027$	$\boldsymbol{\Theta} = 19.0$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0002$	$\boldsymbol{\Theta} = 32.7$ $r_{\boldsymbol{\Theta}} = 0.84$ $p = 0.0019$	$\boldsymbol{\Theta} = 88.2$ $r_{\boldsymbol{\Theta}} = 0.03$ $p < 0.0001$	$\boldsymbol{\Theta} = 66.0$ $r_{\boldsymbol{\Theta}} = 0.41$ $p < 0.0001$
Cerco. nictitans	$\boldsymbol{\Theta} = 9.6$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0011$	$\boldsymbol{\Theta} = 22.2$ $r_{\boldsymbol{\Theta}} = 0.93$ $p < 0.0001$	$\boldsymbol{\Theta} = 68.3$ $r_{\boldsymbol{\Theta}} = 0.37$ $p < 0.0001$	$\boldsymbol{\Theta} = 71.2$ $r_{\boldsymbol{\Theta}} = 0.32$ $p < 0.0001$	$\boldsymbol{\Theta} = 60.4$ $r_{\boldsymbol{\Theta}} = 0.49$ $p < 0.0001$
Cerco. cephus	$\boldsymbol{\Theta} = 8.8$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0002$	$\boldsymbol{\Theta} = 19.6$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.0002$	$\boldsymbol{\Theta} = 33.0$ $r_{\boldsymbol{\Theta}} = 0.84$ $p = 0.0023$	$\boldsymbol{\Theta} = 86.0$ $r_{\boldsymbol{\Theta}} = 0.07$ $p < 0.0001$	$\boldsymbol{\Theta} = 70.4$ $r_{\boldsymbol{\Theta}} = 0.34$ $p < 0.0001$
Macaca fascicularis	$\boldsymbol{\Theta} = 9.5$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0002$	$\boldsymbol{\Theta} = 24.7$ $r_{\boldsymbol{\Theta}} = 0.91$ $p < 0.0001$	$\boldsymbol{\Theta} = 47.7$ $r_{\boldsymbol{\Theta}} = 0.67$ $p = 0.0009$	$\boldsymbol{\Theta} = 48.1$ $r_{\boldsymbol{\Theta}} = 0.67$ $p = 0.0019$	$\boldsymbol{\Theta} = 45.9$ $r_{\boldsymbol{\Theta}} = 0.70$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\Theta} = 8.2$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0057$	$\boldsymbol{\Theta} = 24.5$ $r_{\boldsymbol{\Theta}} = 0.91$ $p < 0.0001$	$\boldsymbol{\Theta} = 25.1$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0072$	$\boldsymbol{\Theta} = 33.9$ $r_{\boldsymbol{\Theta}} = 0.83$ $p = 0.0069$	$\boldsymbol{\Theta} = 35.6$ $r_{\boldsymbol{\Theta}} = 0.81$ $p < 0.0001$
Gorilla gorilla	—	$\boldsymbol{\Theta} = 9.4$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0548$	$\boldsymbol{\Theta} = 10.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.2400$	$\boldsymbol{\Theta} = 15.1$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2338$	$\boldsymbol{\Theta} = 17.4$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0001$
Pan troglodytes	$\boldsymbol{\Theta} = 5.9$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0378$	—	$\boldsymbol{\Theta} = 12.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.1577$	$\boldsymbol{\Theta} = 14.9$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.2953$	$\boldsymbol{\Theta} = 17.5$ $r_{\boldsymbol{\Theta}} = 0.95$ $p < 0.0001$
Hylobates lar	$\boldsymbol{\Theta} = 7.7$ $r_{\boldsymbol{\Theta}} = 9.9$ $p = 0.0066$	$\boldsymbol{\Theta} = 17.4$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.0008$	—	$\boldsymbol{\Theta} = 43.7$ $r_{\boldsymbol{\Theta}} = 0.72$ $p = 0.0031$	$\boldsymbol{\Theta} = 41.6$ $r_{\boldsymbol{\Theta}} = 0.75$ $p < 0.0001$
Ateles geoffroyi	$\boldsymbol{\Theta} = 6.7$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0182$	$\boldsymbol{\Theta} = 12.7$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0094$	$\boldsymbol{\Theta} = 31.5$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0053$	—	$\boldsymbol{\Theta} = 44.3$ $r_{\boldsymbol{\Theta}} = 0.72$ $p < 0.0001$
Cebus libidinosus	$\boldsymbol{\Theta} = 7.7$ $r_{\boldsymbol{\Theta}} = 0.99$ $p = 0.0045$	$\boldsymbol{\Theta} = 11.6$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.0097$	$\boldsymbol{\Theta} = 31.7$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0065$	$\boldsymbol{\Theta} = 47.6$ $r_{\boldsymbol{\Theta}} = 0.67$ $p = 0.0017$	—

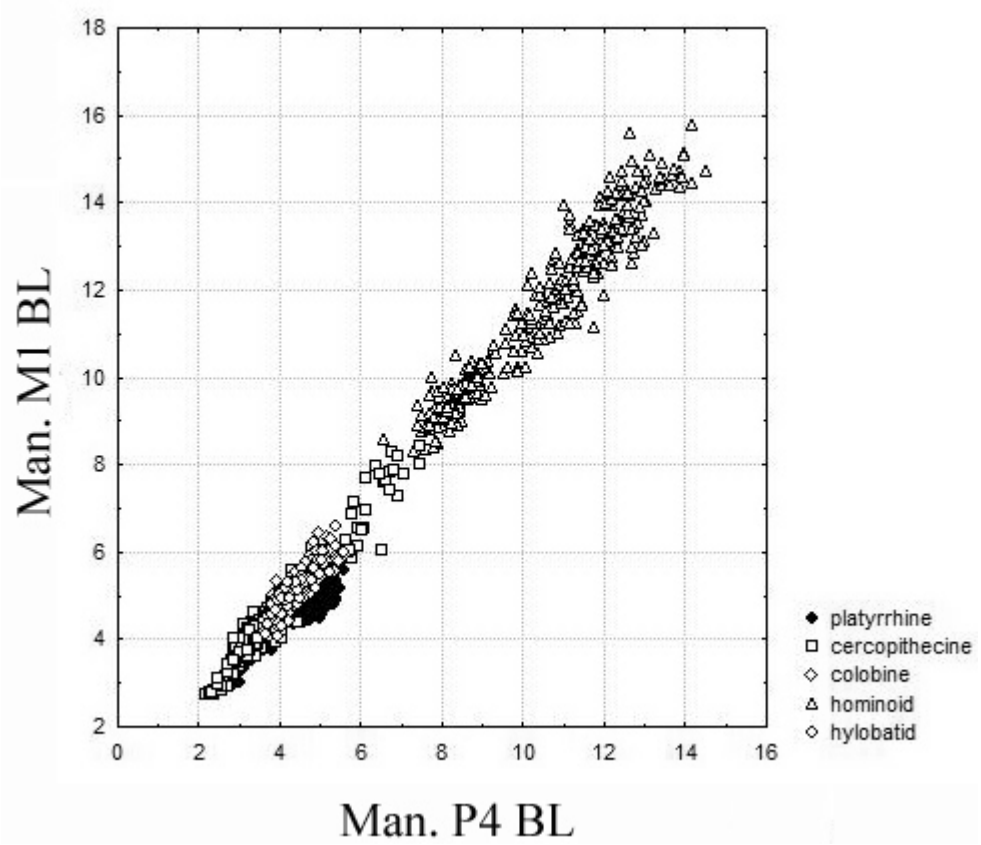

Fig. 6.3. Relationship between P_4BL and M_1BL in anthropoid primates. P_4 and M_1 breadth occupy a narrow range of morphospace, which explains why $\mathbf{p_{max}}$ and **Δz** are similarly oriented in anthropoids. This figure also shows why the $\mathbf{p_{max}}$ of catarrhines and platyrrhines are poor predictors of **Δz** between them for these two variables; the platyrrhines have wider P_4s for a given M_1 breadth than do the catarrhines. This figure was compiled using the following sample sizes: cercopithecine 441, colobine 165, hominid 307, hylobatid 97, platyrrhine 220, total 1230.

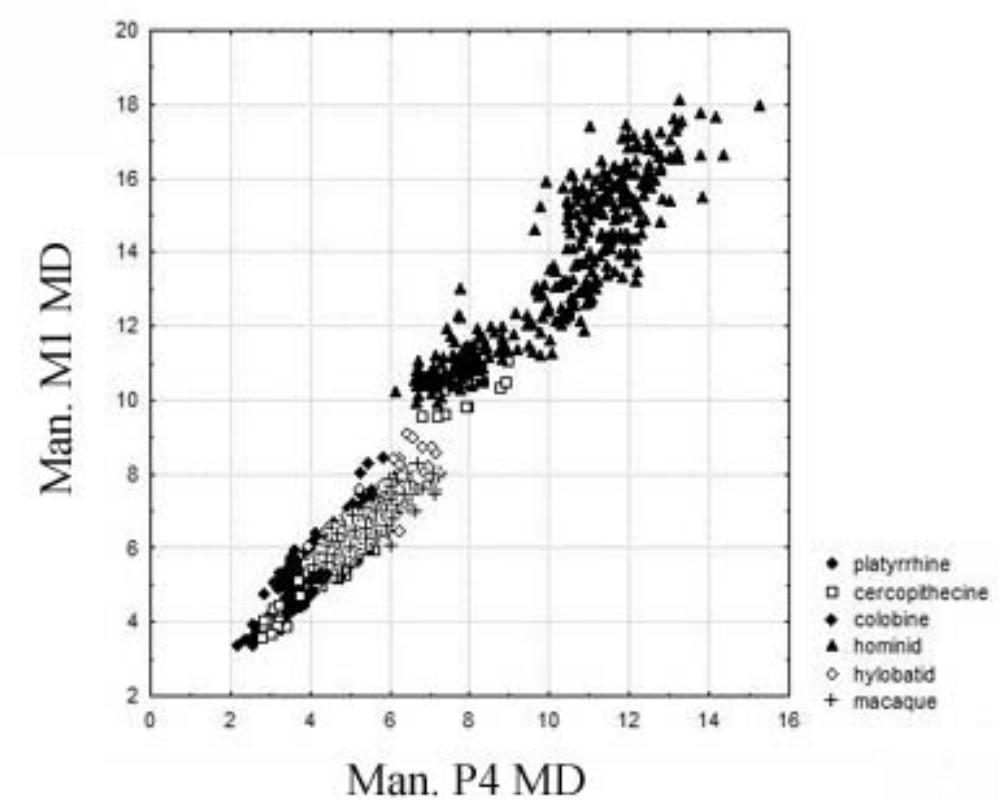

Fig. 6.4. Relationship between P_4 MD and M_1 MD in anthropoid primates. Like the breadths of the P_4 and M_1, P_4 and M_1 MD length occupy a narrow band of phenotypic space; however, there are clearly differences in the placement of taxa relative to one another. This explains why the angle between $\mathbf{p}_{max}$ and $\mathbf{\Delta z}$ is greater than $\mathbf{\Theta} = 0°$. This figure was compiled using the following sample sizes (cercopithecine 452, colobine 170, hominid 332, hylobatid 151, platyrrhine 252, total 1357).

Despite sharing a common $\mathbf{p}_{max}$, differences among catarrhine taxa have not accumulated along this $\mathbf{p}_{max}$, as almost all estimates of $\boldsymbol{\Theta}\mathbf{p}_{max}$–$\boldsymbol{\Delta}\mathbf{z}$ are significantly different from $\boldsymbol{\Theta} = 0°$ (Table 6.13). Only the comparisons between hominoid taxa indicate that divergence has accumulated along this axis. Because platyrrhines and catarrhines do not share a similar $\mathbf{p}_{max}$, the differences between them are not consistent with change along a shared $\mathbf{p}_{max}$. Explanations for the high $\boldsymbol{\Theta}\mathbf{p}_{max}$–$\boldsymbol{\Delta}\mathbf{z}$ values are explored below.

As for the incisors, the guenons exhibit high values for $\boldsymbol{\Theta}\mathbf{p}_{max}$–$\boldsymbol{\Delta}\mathbf{z}$ but minimal divergence in postcanine size; $\boldsymbol{\Delta}\mathbf{z}$ is essentially 0 among the guenons. Comparisons of platyrrhines to catarrhines show that primary differences are in the size of the premolars relative to the size of the molars. All catarrhine primates fall in a narrow band of phenotypic space for P_4BL and M_1BL breadth (Figure 6.3), but for a given molar breadth, the platyrrhine P_4 is broader. Another example of divergence is observed when P_4MD length is compared to M_1MD length (Figure 6.4). Here, the difference is not simply between catarrhines and platyrrhines; there are many gradistic shifts in premolar length, relative to molar length. The cercopithecids have relatively longer P_4s than do hominids, *Gorilla* has a relatively shorter P_4 than *Pan*, the *Cebus* P_4 is MD longer relative M_1MD length than is the *Ateles* P_4, and hylobatids have longer P_4s, relative to M_1 MD, than do hominids. Some of the highlighted contrasts in relative P_4 size capture potential differences in diet (e.g., *Cebus* vs. *Ateles*, *Gorilla* vs. *Pan*); however, without examining the functional morphology and diets for all of these contrasts, it cannot be determined with certainty that the departures represent adaptations to differing diets. If that is the case, then it makes a strong argument for selection driving postcanine $\boldsymbol{\Delta}\mathbf{z}$ into dimensions not aligned with $\mathbf{p}_{max}$. Though both examples (Figures 6.3 and 6.4) show that anthropoid postcanine size falls in a narrow band of phenotypic space, the highlighted contrasts

TABLE 6.13. ***Θp_{max}-p_{max}*** *and the vector correlation, in parentheses, for 7 dimensions of the canine honing complex in females. Those comparisons that are significantly different from zero are shaded grey.*

	Ateles geoffroyi	*Hylobates lar*	*Pan troglodytes*	*Gorilla gorilla*	*Colobus satanas*	*Macaca fascicularis*	*Cerco. cephus*	*Cerco. nictitans*	*Cerco. pogonias*
Cercopithecus nictitans									$\Theta = 16.4$ $r_\Theta = 0.96$ $p = 0.8146$
Cercopithecus cephus								$\Theta = 33.4$ $r_\Theta = 0.83$ $p = 0.0479$	$\Theta = 23.1$ $r_\Theta = 0.92$ $p = 0.1676$
Macaca fascicularis							$\Theta = 16.3$ $r_\Theta = 0.96$ $p = 0.5215$	$\Theta = 41.52$ $r_\Theta = 0.75$ $p = 0.1503$	$\Theta = 27.8$ $r_\Theta = 0.88$ $p = 0.2292$
Colobus satanas						$\Theta = 26.3$ $r_\Theta = 0.90$ $p = 0.2648$	$\Theta = 25.7$ $r_\Theta = 0.90$ $p = 0.0971$	$\Theta = 23.0$ $r_\Theta = 0.92$ $p = 0.1533$	$\Theta = 9.9$ $r_\Theta = 0.99$ $p = 0.7940$
Gorilla gorilla					$\Theta = 20.8$ $r_\Theta = 0.93$ $p = 0.0675$	$\Theta = 17.8$ $r_\Theta = 0.95$ $p = 0.4669$	$\Theta = 12.5$ $r_\Theta = 0.98$ $p = 0.3753$	$\Theta = 28.0$ $r_\Theta = 0.88$ $p = 0.0884$	$\Theta = 16.4$ $r_\Theta = 0.96$ $p = 0.2522$
Pan troglodytes				$\Theta = 21.9$ $r_\Theta = 0.93$ $p = 0.1548$	$\Theta = 26.8$ $r_\Theta = 0.89$ $p = 0.1210$	$\Theta = 19.6$ $r_\Theta = 0.94$ $p = 0.5509$	$\Theta = 16.6$ $r_\Theta = 0.96$ $p = 0.2964$	$\Theta = 38.8$ $r_\Theta = 0.78$ $p = 0.0220$	$\Theta = 27.8$ $r_\Theta = 0.88$ $p = 0.1135$
Hylobates lar			$\Theta = 31.6$ $r_\Theta = 0.85$ $p = 0.4195$	$\Theta = 18.9$ $r_\Theta = 0.95$ $p = 0.7754$	$\Theta = 23.3$ $r_\Theta = 0.92$ $p = 0.7671$	$\Theta = 32.9$ $r_\Theta = 0.84$ $p = 0.4824$	$\Theta = 22.1$ $r_\Theta = 0.93$ $p = 0.7879$	$\Theta = 20.5$ $r_\Theta = 0.94$ $p = 0.7542$	$\Theta = 18.7$ $r_\Theta = 0.95$ $p = 0.8887$
Ateles geoffroyi	$\Theta = 45.4$ $r_\Theta = 0.70$ $p = 0.3271$	$\Theta = 23.3$ $r_\Theta = 0.92$ $p = 0.8823$	$\Theta = 32.8$ $r_\Theta = 0.84$ $p = 0.7027$	$\Theta = 45.9$ $r_\Theta = 0.70$ $p = 0.3853$	$\Theta = 28.1$ $r_\Theta = 0.88$ $p = 0.7536$	$\Theta = 27.7$ $r_\Theta = 0.89$ $p = 0.8255$	$\Theta = 57.1$ $r_\Theta = 0.54$ $p = 0.1384$	$\Theta = 45.2$ $r_\Theta = 0.70$ $p = 0.1567$	
Cebus libidinosus	$\Theta = 39.7$ $r_\Theta = 0.77$ $p = 0.6825$	$\Theta = 11.6$ $r_\Theta = 0.98$ $p = 0.8655$	$\Theta = 25.0$ $r_\Theta = 0.91$ $p = 0.1055$	$\Theta = 21.0$ $r_\Theta = 0.93$ $p = 0.1199$	$\Theta = 24.8$ $r_\Theta = 0.91$ $p = 0.0713$	$\Theta = 33.1$ $r_\Theta = 0.84$ $p = 0.2532$	$\Theta = 21.3$ $r_\Theta = 0.93$ $p = 0.1480$	$\Theta = 24.9$ $r_\Theta = 0.91$ $p = 0.0699$	$\Theta = 21.9$ $r_\Theta = 0.93$ $p = 0.2320$

TABLE 6.14. ***Θp**$_{max}$-**p**$_{max}$ and the vector correlation, in parentheses, for 7 dimensions of the canine honing complex in males. Those comparisons that are significantly different from zero are shaded grey.*

	Cercopithecus cephus	*Gorilla gorilla*	*Pan troglodytes*
Gorilla gorilla	**Θ** = 22.3 r_{Θ} = 0.93 p = 0.1499	—	—
Pan troglodytes	**Θ** = 16.2 r_{Θ} = 0.96 p = 0.1737	**Θ** = 24.1 r_{Θ} = 0.91 p = 0.2105	—
Cebus libidinosus	**Θ** = 19.8 r_{Θ} = 0.94 p = 0.0412	**Θ** = 11.0 r_{Θ} = 0.98 p = 0.6646	**Θ** = 25.1 r_{Θ} = 0.91 p = 0.0618

provide morphological support for the observation that postcanine **Δz** between platyrrhines and catarrhines, and between many catarrhine taxa, did not accumulate as a result of change along a shared $\mathbf{p}_{max}$.

Canine honing complex $\mathbf{p}_{max}$ ***and Δz:*** In previous sections of this chapter, it was noted that the calculation of $\mathbf{p}_{max}$ for a suite of characters requires that all measurements be present in all individuals. As a result, the $\mathbf{p}_{max}$ estimates are based on fewer individuals than r^2 values for character pairs. This is especially problematic for the canine honing complex, where natural wear and post-mortem breakage significantly reduces the number of individuals for which canine heights can be estimated (Leigh et al., 2008; personal observation). Unlike the other dental elements, the honing complex is highly size dimorphic, making it difficult to justify pooling males and females in the analysis. Estimates of canine honing complex $\mathbf{p}_{max}$ and **Δz** are considered separately for males and females and are restricted to only those taxa in which canine heights are well represented. Canine height sample sizes are sufficient for all female samples to be analyzed, but only

TABLE 6.15. $\boldsymbol{\theta p_{max}\text{-}\Delta z}$ for female honing complex. Those comparisons that are significantly different from $\boldsymbol{\theta} = 0$ are shaded grey.

	$\mathbf{p}_{\mathbf{max}}$ *Cercopithecus pogonias*	$\mathbf{p}_{\mathbf{max}}$ *Cercopithecus nictitans*	$\mathbf{p}_{\mathbf{max}}$ *Cercopithecus cephus*	$\mathbf{p}_{\mathbf{max}}$ *Macaca fascicularis*	$\mathbf{p}_{\mathbf{max}}$ *Colobus satanas*
Cerco. pogonias	—	$\boldsymbol{\theta} = 31.3$ $r_{\boldsymbol{\theta}} = 0.85$ $p = 0.0359$	$\boldsymbol{\theta} = 40.8$ $r_{\boldsymbol{\theta}} = 0.76$ $p = 0.0644$	$\boldsymbol{\theta} = 37.6$ $r_{\boldsymbol{\theta}} = 0.79$ $p = 0.0201$	$\boldsymbol{\theta} = 70.7$ $r_{\boldsymbol{\theta}} = 0.33$ $p < 0.0001$
Cerco. nictitans	$\boldsymbol{\theta} = 15.4$ $r_{\boldsymbol{\theta}} = 0.96$ $p = 0.2047$	—	$\boldsymbol{\theta} = 29.5$ $r_{\boldsymbol{\theta}} = 0.87$ $p = 0.0469$	$\boldsymbol{\theta} = 81.1$ $r_{\boldsymbol{\theta}} = 0.15$ $p < 0.0001$	$\boldsymbol{\theta} = 82.4$ $r_{\boldsymbol{\theta}} = 0.13$ $p < 0.0001$
Cerco. cephus	$\boldsymbol{\theta} = 30.1$ $r_{\boldsymbol{\theta}} = 0.87$ $p = 0.3674$	$\boldsymbol{\theta} = 49.4$ $r_{\boldsymbol{\theta}} = 0.65$ $p = 0.0017$	—	$\boldsymbol{\theta} = 53.1$ $r_{\boldsymbol{\theta}} = 0.60$ $p = 0.0044$	$\boldsymbol{\theta} = 81.3$ $r_{\boldsymbol{\theta}} = 0.15$ $p < 0.0001$
Macaca fascicularis	$\boldsymbol{\theta} = 60.6$ $r_{\boldsymbol{\theta}} = 0.49$ $p = 0.0002$	$\boldsymbol{\theta} = 60.9$ $r_{\boldsymbol{\theta}} = 0.49$ $p = 0.0139$	$\boldsymbol{\theta} = 65.9$ $r_{\boldsymbol{\theta}} = 0.41$ $p < 0.0001$	—	$\boldsymbol{\theta} = 85.9$ $r_{\boldsymbol{\theta}} = 0.07$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\theta} = 74.1$ $r_{\boldsymbol{\theta}} = 0.27$ $p < 0.0001$	$\boldsymbol{\theta} = 65.5$ $r_{\boldsymbol{\theta}} = 0.42$ $p = 0.0132$	$\boldsymbol{\theta} = 68.4$ $r_{\boldsymbol{\theta}} = 0.39$ $p < 0.0001$	$\boldsymbol{\theta} = 80.6$ $r_{\boldsymbol{\theta}} = 0.16$ $p < 0.0001$	—
Gorilla gorilla	$\boldsymbol{\theta} = 42.1$ $r_{\boldsymbol{\theta}} = 0.74$ $p = 0.0034$	$\boldsymbol{\theta} = 57.5$ $r_{\boldsymbol{\theta}} = 0.54$ $p < 0.0001$	$\boldsymbol{\theta} = 27.8$ $r_{\boldsymbol{\theta}} = 0.88$ $p = 0.0164$	$\boldsymbol{\theta} = 22.9$ $r_{\boldsymbol{\theta}} = 0.92$ $p = 0.2121$	$\boldsymbol{\theta} = 35.0$ $r_{\boldsymbol{\theta}} = 0.82$ $p = 0.0040$
Pan troglodytes	$\boldsymbol{\theta} = 42.8$ $r_{\boldsymbol{\theta}} = 0.73$ $p = 0.0029$	$\boldsymbol{\theta} = 57.1$ $r_{\boldsymbol{\theta}} = 0.54$ $p < 0.0001$	$\boldsymbol{\theta} = 26.3$ $r_{\boldsymbol{\theta}} = 0.90$ $p = 0.0239$	$\boldsymbol{\theta} = 29.0$ $r_{\boldsymbol{\theta}} = 0.87$ $p = 0.1692$	$\boldsymbol{\theta} = 35.8$ $r_{\boldsymbol{\theta}} = 0.81$ $p = 0.0049$
Hylobates lar	$\boldsymbol{\theta} = 28.5$ $r_{\boldsymbol{\theta}} = 0.88$ $p = 0.1309$	$\boldsymbol{\theta} = 34.3$ $r_{\boldsymbol{\theta}} = 0.83$ $p = 0.0718$	$\boldsymbol{\theta} = 20.7$ $r_{\boldsymbol{\theta}} = 0.94$ $p = 0.1011$	$\boldsymbol{\theta} = 49.5$ $r_{\boldsymbol{\theta}} = 0.65$ $p = 0.1327$	$\boldsymbol{\theta} = 44.4$ $r_{\boldsymbol{\theta}} = 0.71$ $p = 0.0014$
Ateles geoffroyi	$\boldsymbol{\theta} = 83.1$ $r_{\boldsymbol{\theta}} = 0.12$ $p < 0.0001$	$\boldsymbol{\theta} = 45.8$ $r_{\boldsymbol{\theta}} = 0.70$ $p = 0.0236$	$\boldsymbol{\theta} = 86.9$ $r_{\boldsymbol{\theta}} = 0.05$ $p < 0.0001$	$\boldsymbol{\theta} = 55.7$ $r_{\boldsymbol{\theta}} = 0.56$ $p = 0.0029$	$\boldsymbol{\theta} = 57.8$ $r_{\boldsymbol{\theta}} = 0.53$ $p < 0.0001$
Cebus libidinosus	$\boldsymbol{\theta} = 74.9$ $r_{\boldsymbol{\theta}} = 0.26$ $p < 0.0001$	$\boldsymbol{\theta} = 85.8$ $r_{\boldsymbol{\theta}} = 0.07$ $p < 0.0001$	$\boldsymbol{\theta} = 64.9$ $r_{\boldsymbol{\theta}} = 0.42$ $p = 0.0004$	$\boldsymbol{\theta} = 89.3$ $r_{\boldsymbol{\theta}} = 0.01$ $p < 0.0001$	$\boldsymbol{\theta} = 89.4$ $r_{\boldsymbol{\theta}} = 0.01$ $p < 0.0001$

(cont.)

TABLE 6.15 continued

	$\mathbf{p}_{\mathbf{max}}$ *Gorilla gorilla*	$\mathbf{p}_{\mathbf{max}}$ *Pan troglodytes*	$\mathbf{p}_{\mathbf{max}}$ *Hylobates lar*	$\mathbf{p}_{\mathbf{max}}$ *Ateles geoffroyi*	$\mathbf{p}_{\mathbf{max}}$ *Cebus libidinosus*
Cerco. pogonias	$\boldsymbol{\Theta} = 32.1$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0037$	$\boldsymbol{\Theta} = 18.1$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.2607$	$\boldsymbol{\Theta} = 21.8$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.7574$	$\boldsymbol{\Theta} = 60.2$ $r_{\boldsymbol{\Theta}} = 0.50$ $p = 0.0009$	$\boldsymbol{\Theta} = 54.2$ $r_{\boldsymbol{\Theta}} = 0.59$ $p < 0.0001$
Cerco. nictitans	$\boldsymbol{\Theta} = 34.0$ $r_{\boldsymbol{\Theta}} = 0.83$ $p = 0.0029$	$\boldsymbol{\Theta} = 21.0$ $r_{\boldsymbol{\Theta}} = 0.93$ $p = 0.2116$	$\boldsymbol{\Theta} = 26.8$ $r_{\boldsymbol{\Theta}} = 0.89$ $p = 0.5767$	$\boldsymbol{\Theta} = 86.1$ $r_{\boldsymbol{\Theta}} = 0.07$ $p < 0.0001$	$\boldsymbol{\Theta} = 73.4$ $r_{\boldsymbol{\Theta}} = 0.29$ $p < 0.0001$
Cerco. cephus	$\boldsymbol{\Theta} = 33.2$ $r_{\boldsymbol{\Theta}} = 0.84$ $p = 0.0033$	$\boldsymbol{\Theta} = 19.5$ $r_{\boldsymbol{\Theta}} = 0.94$ $p = 0.2396$	$\boldsymbol{\Theta} = 25.2$ $r_{\boldsymbol{\Theta}} = 0.90$ $p = 0.5801$	$\boldsymbol{\Theta} = 71.9$ $r_{\boldsymbol{\Theta}} = 0.31$ $p < 0.0001$	$\boldsymbol{\Theta} = 62.3$ $r_{\boldsymbol{\Theta}} = 0.47$ $p < 0.0001$
Macaca fascicularis	$\boldsymbol{\Theta} = 30.4$ $r_{\boldsymbol{\Theta}} = 0.86$ $p = 0.0041$	$\boldsymbol{\Theta} = 18.5$ $r_{\boldsymbol{\Theta}} = 0.95$ $p = 0.2406$	$\boldsymbol{\Theta} = 28.6$ $r_{\boldsymbol{\Theta}} = 0.88$ $p = 0.5361$	$\boldsymbol{\Theta} = 76.8$ $r_{\boldsymbol{\Theta}} = 0.23$ $p < 0.0001$	$\boldsymbol{\Theta} = 68.3$ $r_{\boldsymbol{\Theta}} = 0.37$ $p < 0.0001$
Colobus satanas	$\boldsymbol{\Theta} = 26.5$ $r_{\boldsymbol{\Theta}} = 0.89$ $p = 0.0059$	$\boldsymbol{\Theta} = 13.2$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.3609$	$\boldsymbol{\Theta} = 29.4$ $r_{\boldsymbol{\Theta}} = 0.87$ $p = 0.5643$	$\boldsymbol{\Theta} = 48.5$ $r_{\boldsymbol{\Theta}} = 0.66$ $p = 0.0911$	$\boldsymbol{\Theta} = 68.9$ $r_{\boldsymbol{\Theta}} = 0.36$ $p < 0.0001$
Gorilla gorilla	—	$\boldsymbol{\Theta} = 34.5$ $r_{\boldsymbol{\Theta}} = 0.82$ $p = 0.0211$	$\boldsymbol{\Theta} = 63.1$ $r_{\boldsymbol{\Theta}} = 0.45$ $p < 0.0001$	$\boldsymbol{\Theta} = 15.3$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.9330$	$\boldsymbol{\Theta} = 43.4$ $r_{\boldsymbol{\Theta}} = 0.73$ $p = 0.0003$
Pan troglodytes	$\boldsymbol{\Theta} = 41.7$ $r_{\boldsymbol{\Theta}} = 0.75$ $p = 0.0007$	—	$\boldsymbol{\Theta} = 68.0$ $r_{\boldsymbol{\Theta}} = 0.37$ $p < 0.0001$	$\boldsymbol{\Theta} = 14.5$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.9759$	$\boldsymbol{\Theta} = 37.7$ $r_{\boldsymbol{\Theta}} = 0.79$ $p = 0.0029$
Hylobates lar	$\boldsymbol{\Theta} = 50.3$ $r_{\boldsymbol{\Theta}} = 0.64$ $p = 0.0003$	$\boldsymbol{\Theta} = 42.6$ $r_{\boldsymbol{\Theta}} = 0.74$ $p = 0.0265$	—	$\boldsymbol{\Theta} = 51.4$ $r_{\boldsymbol{\Theta}} = 0.62$ $p = 0.0213$	$\boldsymbol{\Theta} = 45.7$ $r_{\boldsymbol{\Theta}} = 0.70$ $p = 0.0003$
Ateles geoffroyi	$\boldsymbol{\Theta} = 28.8$ $r_{\boldsymbol{\Theta}} = 0.88$ $p = 0.0047$	$\boldsymbol{\Theta} = 11.2$ $r_{\boldsymbol{\Theta}} = 0.98$ $p = 0.4436$	$\boldsymbol{\Theta} = 25.4$ $r_{\boldsymbol{\Theta}} = 0.90$ $p = 0.7044$	—	$\boldsymbol{\Theta} = 53.7$ $r_{\boldsymbol{\Theta}} = 0.59$ $p < 0.0001$
Cebus libidinosus	$\boldsymbol{\Theta} = 32.3$ $r_{\boldsymbol{\Theta}} = 0.85$ $p = 0.0033$	$\boldsymbol{\Theta} = 14.8$ $r_{\boldsymbol{\Theta}} = 0.97$ $p = 0.3379$	$\boldsymbol{\Theta} = 39.1$ $r_{\boldsymbol{\Theta}} = 0.78$ $p = 0.204$	$\boldsymbol{\Theta} = 39.1$ $r_{\boldsymbol{\Theta}} = 0.78$ $p = 0.0005$	—

TABLE 6.16. $\boldsymbol{\Theta p_{max}}$-$\boldsymbol{\Delta z}$ for male honing complex. Those comparisons that are significantly different from $\boldsymbol{\Theta} = 0$ are shaded grey.

	$\mathbf{p_{max}}$ *Cercopithecus cephus*	$\mathbf{p_{max}}$ *Gorilla gorilla*	$\mathbf{p_{max}}$ *Pan troglodytes*	$\mathbf{p_{max}}$ *Cebus libidinosus*
Cercopithecus cephus	—	$\boldsymbol{\Theta} = 16.3$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.3145$	$\boldsymbol{\Theta} = 45.9$ $r_{\boldsymbol{\Theta}} = 0.70$ $p < 0.0001$	$\boldsymbol{\Theta} = 72.8$ $r_{\boldsymbol{\Theta}} = 0.30$ $p < 0.0001$
Gorilla gorilla	$\boldsymbol{\Theta} = 34.3$ $r_{\boldsymbol{\Theta}} = 0.83$ $p = 0.0069$	—	$\boldsymbol{\Theta} = 29.0$ $r_{\boldsymbol{\Theta}} = 0.87$ $p = 0.0231$	$\boldsymbol{\Theta} = 23.0$ $r_{\boldsymbol{\Theta}} = 0.92$ $p = 0.0362$
Pan troglodytes	$\boldsymbol{\Theta} = 44.5$ $r_{\boldsymbol{\Theta}} = 0.71$ $p < 0.0001$	$\boldsymbol{\Theta} = 17.1$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.3234$	—	$\boldsymbol{\Theta} = 25.1$ $r_{\boldsymbol{\Theta}} = 0.91$ $p = 0.0239$
Cebus libidinosus	$\boldsymbol{\Theta} = 89.4$ $r_{\boldsymbol{\Theta}} = 0.01$ $p < 0.0001$	$\boldsymbol{\Theta} = 16.9$ $r_{\boldsymbol{\Theta}} = 0.96$ $p = 0.3141$	$\boldsymbol{\Theta} = 36.0$ $r_{\boldsymbol{\Theta}} = 0.81$ $p = 0.0060$	—

4 male samples were included (*Cebus libidinosus*, *Gorilla gorilla*, *Pan troglodytes*, and *Cercopithecus cephus*).

For female anthropoids, only two out of 45 comparisons of $\boldsymbol{\Theta p_{max}}$-$\mathbf{p_{max}}$ for the honing complex are significantly different from $\boldsymbol{\Theta} = 0°$ (both involve *Cercopithecus nictitans)* (Table 6.13) and for the males, only one out of 6 comparisons is significantly different from $\boldsymbol{\Theta} = 0°$ (Table 6.14). In contrast to comparisons of $\mathbf{p_{max}}$ for the incisors and postcanine teeth discussed above, the $\boldsymbol{\Theta}$ values for comparisons of the honing complex are larger. The lack of statistical significance results from broader confidence intervals (i.e., less certainty in the estimate of $\boldsymbol{\Theta}$) in the analyses of the canine-honing complex, which is a reflection of the smaller sample sizes. Nevertheless, the hypothesis that anthropoid primates share a similar $\mathbf{p_{max}}$ for the dimensions of the honing complex cannot be rejected.

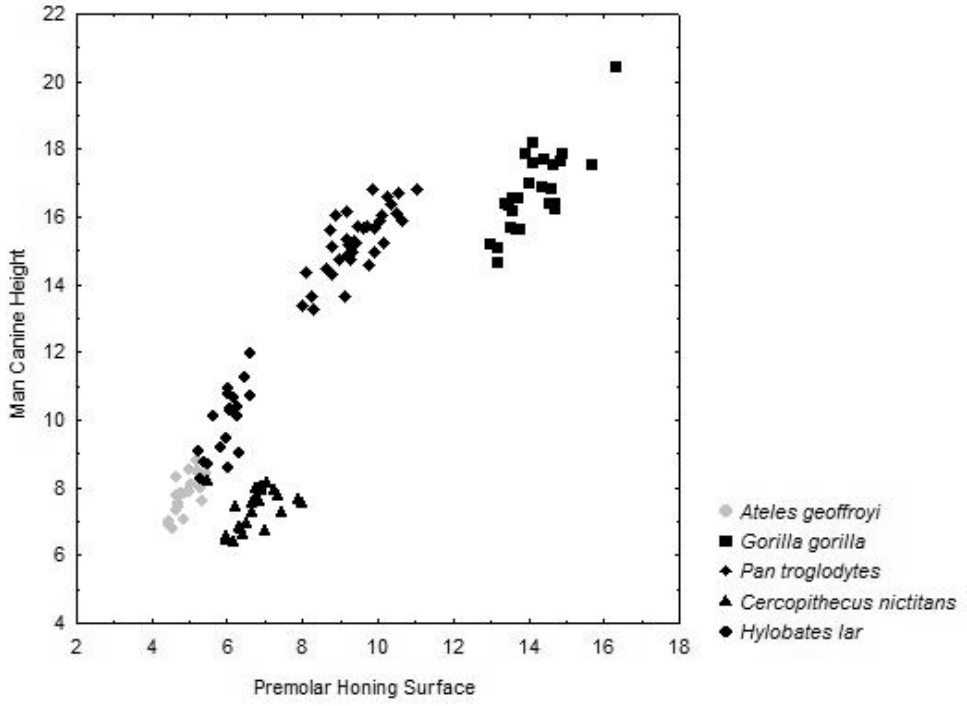

Fig. 6.5. For females of 5 species of anthropoid primates, premolar honing surface length (mm) and mandibular canine height (mm).

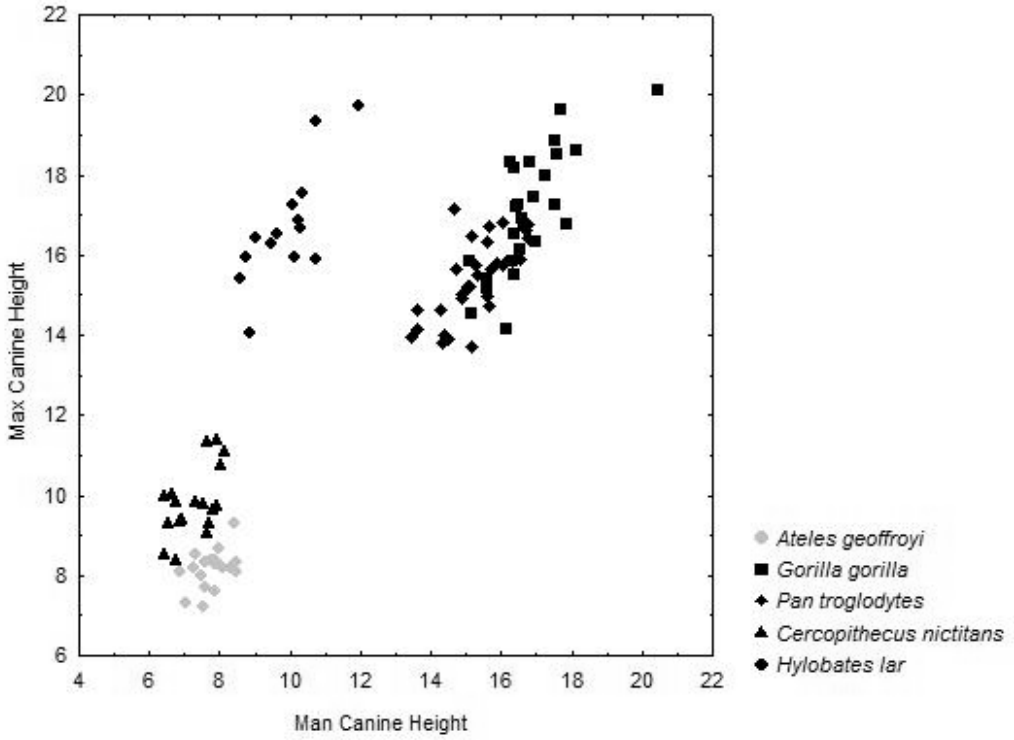

Fig. 6.6. For females of 5 species of anthropoid primates, mandibular canine height (mm) and maxillary canine height (mm).

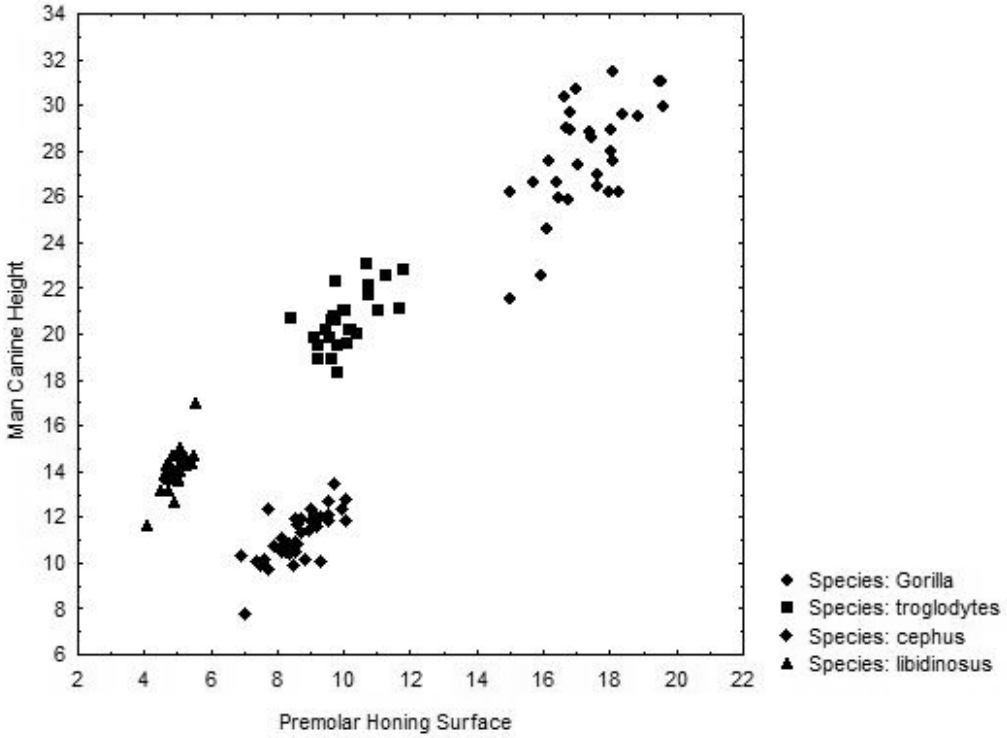

Fig. 6.7. For males of 4 species of anthropoid primates, premolar honing surface length (mm) and mandibular canine height (mm).

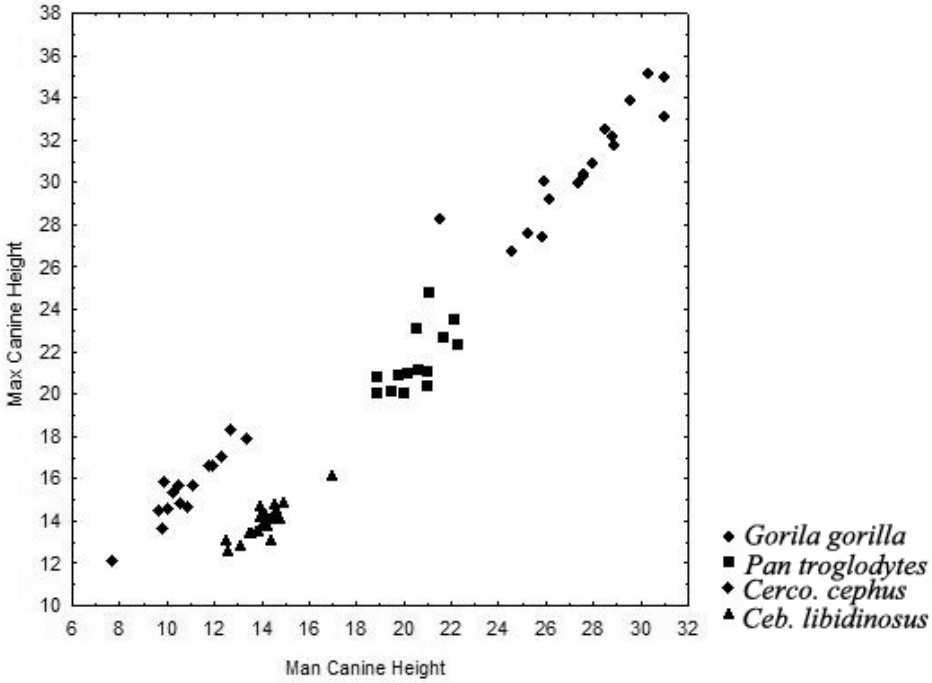

Fig. 6.8. For males of 4 species of anthropoid primates, mandibular canine height (mm) and maxillary canine height (mm).

The estimates of $\Theta \mathbf{p}_{max}$-$\Delta \mathbf{z}$ for both males and females (Tables 6.15 and 6.16) indicate little correspondence between the two vectors. For the females, 64 out of 90 estimates are significantly greater than $\Theta = 0°$; for the males, 8 out of 12 are significantly different from $\Theta = 0°$. Though many Θs are large in absolute value, comparisons of the platyrrhines to the cercopithecids are consistently among the largest Θs for both males and females; the morphological differences between them are not predicted by the pattern of $\mathbf{p}_{max}$ within either clade. Again, this result is consistent with others in this chapter; which showed that the most anciently diverged clades are the most divergent in covariance structure. As a result, the $\Delta \mathbf{z}$ between them could not have accumulated along a $\mathbf{p}_{max}$ estimated in the opposite infraorder.

In the analyses of independent contrasts among species in Chapter 5, several large contrasts were noted for both the male and female canine honing complexes. Given sample size constraints, the analyses of the honing complex in this chapter are confined to four male samples and ten female samples. Despite the limited taxonomic coverage, there are clear examples of species not diverging along a shared $\mathbf{p}_{max}$. For example, Figures 6.5 and 6.6 illustrate the lack of correspondence between $\mathbf{p}_{max}$ and $\Delta \mathbf{z}$ in female anthropoids for the length of the honing surface of the premolar and the heights of the maxillary and mandibular canines. Though some morphological divergence from estimates of $\mathbf{p}_{max}$ is expected between distantly related taxa, even comparisons of closely related species are seen to be divergent. Comparisons of female *Pan troglodytes* and *Gorilla gorilla*, which are closely related and numerically well represented, indicate that canine honing complex $\Delta \mathbf{z}$ between them did not accumulate along either taxon's $\mathbf{p}_{max}$ (the *Gorilla gorilla* mandibular canine is shorter than would be expected given the within-species relationship in *Pan troglodytes*) (Figures 6.5 and 6.6). Examination of the male samples also indicates that the $\Delta \mathbf{z}$ did not accumulate along a shared $\mathbf{p}_{max}$ (Figures

6.7 and 6.8). It is also evident by comparing the above examples in males and females that there are some cases where the two samples' $\mathbf{\Delta z}$ aligns closely with $\mathbf{p_{max}}$ in one sex but not the other. For example, in Figure 6.5 *Pan troglodytes* and *Gorilla gorilla* do not fall along a single line for the comparison of premolar honing surface length and mandibular canine height; however, in Figure 6.7 the male samples nearly fall along a single line. This suggests that selection is independently shifting changes in the sizes of the components of the complex in males and females, which is line with the model of sexual selection on canine size outlined in Chapter 1 (e.g., Plavcan, 1993; 2001).

Discussion and Summary

Whether tested as a pattern of correlation using a Mantel test, a pattern of variance-covariance using a random skewers test, or as bootstrap tests of lines of least evolutionary resistance for each functional module, the pattern of constraints among dental characters is similar among species. These patterns for dental size are remarkably similar despite shifts in morphology (e.g., reduction of M^3 size in platyrrhines, developmental of bilophodonty in cercopithecids, enhancement of mandibular premolar heteromorphy in catarrhines, enhancement of incisor heteromorphy in cercopithecids, loss of a mesial premolar in catarrhines, etc.). As patterns of variance-covariance can be shaped by evolutionary mechanisms (reviewed in Chapter 1), this finding suggests that selection has favored a consistent pattern of covariance among dental characters. That said, subtle differences in patterns of correlation and variance-covariance are apparent among taxa. Both the Mantel and random skewers tests indicated that catarrhines and platyrrhines are slightly divergent in correlation and variance-covariance structure. Some divergence in patterns of covariation between the infraorders is observed as relatively high $\mathbf{\Theta p_{max}\text{-}p_{max}}$ values in comparisons of the incisors and the postcanine dentition.

Based on genetic data, platyrrhines and catarrhines are estimated to have shared a most recent common ancestor more than 40 million years ago (Steiper and Young, 2006). If patterns of variance-covariance were only shaped by neutral evolutionary mechanisms (drift and mutation), then such stable patterns should not result. In a study of cranial size variance-covariance for 30 anthropoid taxa, comprising 29 catarrhine and one platyrrhine taxa, a "significant and positive correlation between the amount of divergence in correlation and covariance patterns…and their phylogenetic distances" was found (de Oliveira et al., 2009: 417). While that hypothesis was not tested in this study, it is consistent with the subtle divergence in patterns of covariation observed between platyrrhines and catarrhines. Whether selection or drift is responsible for the divergence is untested, but the minimal divergence in covariance and correlation structure implies that the developmental networks that underlie the pattern of variance-covariance have remained stable throughout anthropoid dental evolution (see also, Hlusko et al., 2010).

Though anthropoid dental morphology falls in a fairly restricted portion of phenotypic space, differentiation of species has, in general, not occurred along shared lines of maximum phenotypic variance. Though the bootstrapping procedure is powerful at detecting deviations of $\mathbf{\Delta z}$ from $\mathbf{p_{max}}$, the lack of correspondence between $\mathbf{\Delta z}$ and species' estimates is indicated by $\mathbf{\Theta p_{max} - \Delta z}$ values that are often quite high. Below, reasons for this divergence are explored using examples from each of the functional modules.

For the incisors, it was noted that taxa that are similar in size (e.g., comparisons of guenons, the comparison of *Ateles* and *Cebus*) or that are distantly related (e.g., the comparison of catarrhines to platyrrhines) showed little correspondence between $\mathbf{p_{max}}$ and $\mathbf{\Delta z}$. In the first case, the low correspondence should be dismissed because the taxa have not really diverged in size. In the second case, the lack of correspondence may reflect

minor deviations in $\mathbf{p}_{max}$ that have accumulated over 40+ million years, in which case it would be quite unlikely that $\mathbf{\Delta z}$ between platyrrhines and catarrhines would align with an estimate of $\mathbf{p}_{max}$ derived from a species in the opposite infraorder. In such a case, the lack of correspondence does not indicate that selection vectors are not generally aligned with $\mathbf{p}_{max}$, but that $\mathbf{p}_{max}$ itself has slightly diverged. Despite these limitations, which result from the initial choice of samples for intraspecific analysis, it is also obvious that there is generally a lack of correspondence between incisor $\mathbf{p}_{max}$ and $\mathbf{\Delta z}$. This is evident for both the whole incisor data set and for incisor breadths only. For example, *Pan troglodytes* and *Gorilla gorilla* are closely related, but the difference between them is not aligned with either sample's $\mathbf{p}_{max}$. For the African great apes, the lateral maxillary incisors are similar in MD length between *Pan* and *Gorilla*, but the central incisor is shorter MD in *Pan* (Kelley et al., 1996; Chapter 1); divergence along $\mathbf{p}_{max}$ would predict change in the same direction for both characters.

The selective argument for the existence of pleiotropy among functionally related characters is that it facilitates coevolution and allows character states to jointly change in response to changing environmental conditions; as stated in Chapter 1, "it makes adaptive phenotypes accessible" (Wagner et al., 2007: 926). If incisor sizes are responding to natural selection (a reasonable assumption), then it is clear that adaptive shifts are frequently into dimensions not aligned with $\mathbf{p}_{max}$. It must also be born in mind that the analyses in this chapter are confined to ten species. Broadening the analysis to include more species would only uncover more examples of divergence. Likely candidates for divergence were revealed in the analyses of independent contrasts. For example, in Figure 3.3, the large intrageneric contrast between mandibular incisor size in *Macaca fascicularis* and *Macaca mulatta* was noted. Divergence between the two macaques would not have accumulated along a shared $\mathbf{p}_{max}$. Similarly, as already noted in Chapter

1, maxillary incisor size in *Pongo* is more heteromorphic than in the African apes. For hominids, the among-species correlation indicates a negative relationship among maxillary incisor sizes (Kelley et al., 1996; Chapter 1), which is inconsistent with change along the vector predicted by genetic constraints in all taxa that were analyzed in this chapter. Also, the analyses in this chapter did not include taxa with highly derived incisor morphologies (e.g., pitheciines) (Kinzey, 1992; Rosenberger, 1992). Expanding the taxonomic coverage would only produce more examples of character change occurring in dimensions not aligned with that predicted by constraint. The frequent observation that among species differences do not align with any species' estimate of $\mathbf{p}_{max}$ indicates that selection vectors ($\boldsymbol{\beta}$) for incisor size have often been oriented in a direction that is not aligned with the vector of constraint.

The degree of independence that characters are expected to demonstrate among species is proportional to the strength of constraint among them (Marroig et al., 2009). As reported in Chapters 3–5, the magnitude of covariation is not high, or even moderate, among all character pairs within a module. For each module, the norm among nonhomologous dimensions is to exhibit only very low or low magnitude covariation (Figures 3.2, 4.2; Tables 5.4–5.11). It was shown that within some modules that there are teeth that consistently share the least covariation with other members of their functional module (e.g., I^2, M^3, and $P^{2,3}$). Given this relationship, it may be an exceptionally strict expectation that character change will consistently align itself with $\mathbf{p}_{max}$ for a functional module. While weakly covarying characters are expected to evolve with some independence among species, the lack of correspondence between $\mathbf{p}_{max}$ and $\boldsymbol{\Delta}\mathbf{z}$ cannot simply be attributed to the independence of these weakly covarying characters. For example, in Figure 6.4 and Figure 6.5 the sizes of the P_4 and M_1 are plotted for a diverse sample of anthropoids. Evident in the graph are gradistic shifts in the sizes of the teeth

relative to one another. Within species, these characters have an anthropoid average r^2 of about 0.40 for both MD length and BL breadths (Tables 4.8 and 4.9), yet they show independence among species. Given that more than half of the variation in each character is not shared, this implies that there is considerable independent variation for selection to act upon and to drive the characters into unique portions of phenotypic space. In general, the correspondence of $\mathbf{p}_{max}$ and $\mathbf{\Delta z}$ is not simply the effect of characters being so tightly constrained that they cannot evolve independently of another (clearly they can and have), but reflects the fact that $\mathbf{p}_{max}$ and selection vectors ($\boldsymbol{\beta}$) are often nearly aligned (e.g., Marroig and Cheverud, 2009).

The heights of the canines were shown to be among the most strongly covarying character pairs in the dentition (Table 5.3, average $r^2 = 0.56$). In Figure 6.7, it can clearly be seen that the female *Hylobates lar* distribution lies in a portion of phenotypic space that would not be predicted by the within species relationships of the great apes. The discrepancy occurs because the *Hylobates lar* females have a taller maxillary canine relative to mandibular canine height than observed in female great apes. In Figure 6.7, the height of the mandibular canine is plotted relative to the length of the P_3 honing surface length. For these characters the average r^2 among female hominoids is 0.59 (Table 5.12); however, for a given P_3 honing surface length, the *Gorilla gorilla* mandibular canine is shorter than would be expected given the relationship between the characters in *Pan troglodytes*. As stated previously, the flexibility of character pairs to evolve independently of one another is proportional to the magnitude of constraint between them (i.e., the magnitude of r^2). These shifts in canine size relative to one another suggest that selection must have been strong. Comparisons of honing complex $\mathbf{p}_{max}$ and $\mathbf{\Delta z}$ were restricted to a small sample of primates (especially so for the males). If more taxa were included in comparisons of $\mathbf{p}_{max}$ and $\mathbf{\Delta z}$, then more instances of discordance would likely

be uncovered. In Chapter 5, in the among-species analysis of male maxillary canine height and premolar honing surface length revealed a large residual for the contrast between pongines and hominines (Figure 5.2). Likely, the mean size of the elements of the *Pongo* honing complex would not lie on the $\mathbf{p}_{max}$ predicted by the hominines. It is a common assumption that such independent behavior for characters among species requires a change in the variance-covariance structure uniting them (see review in Lockwood, 2007; de Oliveira et al., 2009). Examples of divergence in the honing complex relative to $\mathbf{p}_{max}$ occurred without changing the underlying pattern of variance-covariance among the characters, as the hypothesis that $\mathbf{p}_{max}$ is the same could not be rejected for hominoids and there are no obvious differences in the strength of covariation among the characters of the honing complex (Table 5.12). The findings presented in this Chapter clearly indicate that considerable diversity in form among species can occur without altering the pattern of variance-covariance among the characters that are diverging. This was also the conclusion of a study of cranial size variance-covariance among anthropoids conducted by de Oliveira et al. (2009). If variation is present in any dimension, it is available for selection to act upon. The fact that highly covarying characters can behave with some independence among species should give caution to the development of constraint hypotheses to explain correlated changes in functionally unrelated dental characters, which share little variance.

Chapter 7

DISCUSSION

This study has attempted to determine if genetic constraints have strongly biased dental diversification, especially as it relates to derived hominin morphologies. In Chapters 3–6, the pattern and magnitude of phenotypic variance-covariance for tooth size and shape were thoroughly examined and used to test a variety of hypotheses, including 1) that functional modules are variational modules, 2) that patterns of variance-covariance are conserved among species, 3) that dental diversification occurred along lines of least evolutionary resistance (i.e., the vector predicted by genetic constraint), 4) that pleiotropy is negative between anterior (incisors and canines) and posterior teeth (premolars and molars), 5) that covariation is strong and positive between the incisors and canines, 6) that the honing complex coevolved in males but not in females, and 7) that the premolars and molars are quasi-independent subdivisions of a postcanine variational module. In addition, covariation within and among species was compared as an informal test of the hypothesis that magnitudes of constraint predict the relative independence (i.e., flexibility) of characters among species. Below, the evolution of anthropoid dental diversity is discussed in relation to these hypotheses.

Anthropoids Share a Common Pattern of Variational Modularity and Variance-Covariance: Evidence that patterns of variance-covariance for dental size are similar among species is provided by the results of three analyses. When all teeth are considered, the similarity in the magnitudes of correlation among characters is provided by the Mantel tests, which indicate statistical similarity in the 10 anthropoid taxa examined (Table 6.1). For all characters, the similarity of the pattern of variance-covariance is provided by the random skewers tests, which found that the **P**-matrix is similar for all 10

anthropoid taxa (Table 6.2). Both the Mantel and random skewers tests suggest some divergence between catarrhines and platyrrhines in variance-covariance/correlation structure, which is also reflected as divergence in $\mathbf{p}_{max}$ between catarrhines and platyrrhines for the postcanine teeth (Chapter 6). As stated in Chapter 6, given random change, some divergence in variance-covariance structure is expected over time (Roff, 2000). de Oliveira et al (2009) tested this hypothesis for cranial size variance-covariance in anthropoids and found a strong correlation between intertaxon $\mathbf{\Theta p}_{max}\text{-}\mathbf{p}_{max}$ values and their divergence dates. That dental variance-covariance structure is stable is remarkable, both because anthropoids are quite diverse in dental morphology and also because platyrrhines and catarrhines shared a most recent common ancestor more than 40 million years ago (Steiper and Young, 2006), implying the influence of stabilizing selection to maintain such a pattern (Arnold et al., 2008).

As reviewed in Chapter 1, the functional roles of the anthropoid dentition (food acquisition, social signaling and weapon use, food processing) are, in general, associated with specific classes of teeth (incisors, canines and honing premolar, and postcanine teeth, respectively). Thus, the dentition is organized into functional modules. Variational modularity is defined by the pattern and magnitude of covariation, so that covariation is strong in magnitude among characters within a module and only weak in magnitude between characters in different modules (Wagner et al., 2007). Variational modularity is hypothesized to characterize systems that have functional modularity because "sets of traits are more often selected together than others, [which] can lead to a reinforcement of pleiotropic effects among co-selected traits and suppression of pleiotropic effects that are not selected together" (Wagner et al., 2007: 928). The covariance structure of a suite of traits is shaped by "modular selection" to allow "adaptive evolution to proceed efficiently" (Dayan et al., 2002: 521).

Using dental shape and size data, the hypothesis that dental functional modules equate with variational modules is supported in all anthropoid taxa examined (Chapters 3–5). Within species, the highest magnitude of covariation is found within functional modules and only weak covariation exists between them (Figures 3.1, 3.2, 4.1, and 4.2; Tables 5.1–5.14).

Within a module, covariation is moderate to high (using the criteria outline in Table 2.3) between teeth in the same position in the opposite arch (Tables 3.3, 3.4, 4.4–4.7, 4.19, 4.22, and 5.3). For the postcanine teeth, the mesial portion of a maxillary tooth occludes with the distal portion of the mandibular tooth in the same position. As food processing is intimately tied to the proper occlusion of opposing teeth (Lucas, 2004), this produces a strong functional constraint on dental evolution (e.g., Renaud et al., 2009). Studies of dental covariation in carnivores (Szuma, 2000) and rodents (Renaud et al., 2009) have identified the same pattern, suggesting that it is a fundamental aspect of mammalian dental covariation that has been maintained by selection (see also Kurtén, 1953; Stock, 2001). Studies of odontogenesis have provided evidence that some genetic loci affect both mandibular and maxillary teeth (Stock, 2001; Wang et al., 2005; Charles et al., 2009; Renaud et al., 2009), which provides empirical support for the existence of shared genetic networks between the maxillary and mandibular teeth.

Covariation is also high between homologous measures of adjacent teeth within dental classes (e.g., breadths of adjacent molars). That adjacent teeth covary to a greater degree than nonadjacent teeth has been observed in other studies of the mammalian dentition (e.g., Kurtén, 1953). More recent studies of carnivores (Szuma, 2000; Dayan et al., 2002; Prevosti and Lamas, 2006) and murine rodents (Renaud et al., 2009) have also identified this pattern, which was referred to as the "neighborhood rule" or the "neighboring rule" (e.g., Renaud et al, 2009; the term itself is attributed to van Valen,

(1970)). The neighboring rule can be seen in several cases in the anthropoid dentition; for example, among platyrrhine premolars and anthropoid molars, where there are three elements in each dental class. For the platyrrhine premolars, the P4 covaries more strongly in size and shape with the P3 than it does with the P2 (Tables 4.5, 4.7, and 4.13). For the molars, it is the M1 and M3 that share least variance, while the M2 covaries strongly with both the M1 and M3 (Tables 4.17–4.22). There are, however, clear exceptions to the neighbor rule. The mesial mandibular premolar does not covary strongly with any other premolar and the I^2MD does not covary strongly with any other incisor dimension. For both of these exceptions, the neighboring rule is violated by teeth that are heteromorphic relative to their neighbor. Differences in the degree of heteromorphy among taxa are reflected in differences in the magnitude of covariation (e.g., greater incisor heteromorphy in cercopithecids than hominoids is associated with lower magnitude covariation among incisor dimensions in cercopithecids).

The perspective that functional modules are variational modules (e.g., Wagner, 1996; Wagner and Altenberg, 1996; Wagner and Zhang, 2001; Wagner et al., 2007; Wang et al., 2010) clearly predicts the low magnitude covariation between characters in different functional modules; however, viewing each functional module as a single variational module is a vast oversimplification of the pattern of covariation that is actually observed, as magnitudes of covariation are highly variable within each "variational" module. Though covariation is strong among homologous dimensions, between nonhomologous dimensions, the average magnitude of phenotypic covariation is typically low to very low ($0.00 \leq r^2 < 0.40$). Lumping such diverse magnitudes of covariation into a single unit makes it difficult to generalize expectations for evolutionary flexibility. For example, the expectation for the among-species behavior of I^2MD relative to other incisor dimensions is certainly not the same as for more highly covarying

character pairs. Should the low levels of covariation exhibited by I^2MD with other incisor dimensions exclude it from the incisor variational module? Are the mandibular incisors and maxillary incisors part of separate variational modules with overlapping pleiotropic effects? Are the LL breadths and the MD lengths of the mandibular incisors members of separate variational modules? If so, then dividing each "variational" module into finer and finer subdivisions so that only the most highly covarying character pairs remain would result in innumerable modules that have little relationship to shared function, which would render the concept of a variational module meaningless. The fact that most characters do not exhibit strong covariation indicates that there is ample genetic variance for selection to act upon to drive the independent evolution for most character pairs, even those within variational modules.

Vestigial structures, which are under weak stabilizing selection, are more variable than other structures (e.g., Kurtén, 1953; Hoffmann and Merila, 1999; Dayan et al., 2002). While comparisons of levels of variation (quantified as the standard deviation or coefficient of variation) were not the object of this study, lower levels of covariation are observed for certain teeth within modules, such as heteromorphic teeth (e.g., I^2, $P_{2,3}$) or teeth that are small relative to the other teeth in the module. In this study, this is especially true for the *Ateles geoffroyi* and *Cebus libidinosus* M^3s, which are small relative to the size of the M^1 and M^2 and share less covariation with the other molars than in catarrhines (Tables 4.16, 4.19, 4.21, 4.22, and 4.34). If a moderately developed M3 is taken as a starting point, then reduction of M3 size in platyrrhines required some parcellation from the other molars (see Figure 1.1). As reviewed by Stock (2001: 1634), "in order for some members of these series to evolve independently of others, there must exist at least some developmental and genetic individualization within the series." The low magnitude of covariation expressed between the platyrrhine M^3 and other molar

dimensions, relative to levels of covariation in catarrhines, suggests that the platyrrhine M^3 acquired "individualism" from its neighbors.

The first step towards the evolutionary loss of a tooth may be to parcel out the tooth from the remainder of the teeth in its variational module. More interesting for hominin evolution would be to determine if the opposite process can occur. During hominin evolution, mandibular premolar heteromorphy was substantially decreased over time (Delezene and Kimbel, 2011) and the P_3 and P_4 show similar trajectories of talonid expansion (molarization) between species (Suwa, 1988). If sample sizes in the fossil record were adequate in size, then the hypothesis that the loss of premolar heteromorphy coincided with the "integration" of the two mandibular premolars genetically (Figure 1.1), which only weakly covary in size and shape in extant anthropoids (Chapter 4), could be tested. Given concerns about drift covariance between samples (Armbruster and Schwaegerle, 1996), then pooling samples from diverse localities would not be appropriate for testing such a hypothesis.

Lines of Least Evolutionary Resistance and Selection: Genetic constraints are predicted to channel phenotypic change along lines of least evolutionary resistance ($\mathbf{g}_{max}$), which, in *n*-dimensional space, is the vector that describes the dimension with the greatest genetic variance (Schluter, 1996). This study attempted to address several questions about lines of least evolutionary resistance; for example, were they stable during anthropoid evolution and did they exert a strong influence on diversification (e.g., Marroig and Cheverud, 2005). The stability of constraints was reviewed above, here the relationship between constraints and selection is reviewed.

Selection vectors aligned with $\mathbf{g}_{max}$ (estimated in this study as $\mathbf{p}_{max}$) are insufficient to explain the pattern of anthropoid dental diversification, as there are clear

examples of diversification of highly constrained characters occurring in dimensions not aligned with $\mathbf{p}_{max}$. Examples were illustrated for all functional modules in Chapter 6 (e.g., Figures 6.2–6.8; Tables 6.7, 6.13, 6.15, and 6.16). The formal test of this hypothesis was, however, limited to comparisons of 10 taxa, which represent a fraction of anthropoid dental diversity. Undoubtedly, including more species (especially those with highly derived morphologies) would only reveal more examples.

There is no evidence for complete pleiotropy between any dental dimensions; genetic constraints among dental size and shape are *relative*, not absolute (see Chapter 1). This finding, derived from estimates of phenotypic covariation, is at odds with the results of genetic correlations in SNPRC baboons published by Hlusko and Mahaney (2009; Hlusko et al., 2010), who found complete pleiotropy among 14 of 136 pairs of maxillary dental size. If the Hlusko and Mahaney (2009) findings are correct and generalizable across primates, then some character pairs would be absolutely constrained among species. While many within-species estimates of covariation are high and some are very high for homologous measures within modules, no evidence for complete pleiotropy was uncovered in this study. From a theoretical viewpoint, it is unexpected that dental traits would be absolutely constrained for, as Klingenberg (2010) reviews, absolute constraint indicates that all "dimensions are totally devoid of any genetic variation," which is unlikely for developmental systems, such as the dentition, that involve the participation of many genes (e.g., Stock, 2001; Workman et al., 2002; Shimuzo et al., 2004; Hlusko et al., 2010). It is possible that the Hlusko and Mahaney (2009) finding is correct for the SNRPC baboons and perhaps has resulted from a loss of genetic variation, due to genetic drift, in that laboratory population.

The flexibility of linked characters to evolve independently of one another is proportional to the strength of constraint between them (Marroig et al., 2009). The lower

the magnitude of constraint, the more flexible the characters are to evolve in an uncoordinated fashion. For reasons outlined below, the pattern of genetic constraint is insufficient to explain the pattern of diversification among species. First, there are many examples of low correspondence between $\mathbf{\Delta z}$ and $\mathbf{p_{max}}$ (even for highly covarying characters) (Figures 6.2–6.8; Tables 6.7, 6.13, 6.15, and 6.16) and, second, there are many cases of character pairs that covary weakly within species, but covary more strongly among species (e.g., incisor and postcanine size: Tables 3.7–3.10 and 3.12).

The fact that constraints alone are insufficient for understanding among-species diversification can be illustrated using incisor size as an example. Within anthropoid species, maxillary incisor MD lengths positively covary (about $r^2 = 0.20$; Table 3.5) and among all anthropoids they positively covary (about $r^2 = 0.45$; Table 3.11); however, among hominid species, there is a negative correlation (Chapter 1, see data in Kelley et al., 1996). These discordant patterns of correlation (positive among all anthropoids, negative within hominids) can be explained if we recall the multivariate selection model, $\mathbf{\Delta z = G\beta}$, which indicates that phenotypic change in a suite of characters is affected by both genetic variance-covariance and the strength and direction of selection. Simplifying this model to two characters, if both maxillary incisors experience selection that favors an increase in size, $\binom{+\text{I1MD}}{+\text{I2MD}}$, where the + indicates selection for an increase in size, then the characters will both become larger in the descendent population. For weakly covarying characters, in cases where selection does not favor change in the same direction, $\binom{+\text{I1MD}}{-\text{I2MD}}$, then the characters are mostly free to change in different directions. Figure 7.2 depicts a scenario where two characters are strongly correlated within species and $\mathbf{p_{max}}$ is oriented toward the white quadrants. Selection aligned with $\mathbf{p_{max}}$ will cause rapid phenotypic change (e.g., Marroig and Cheverud, 2010) and create positive

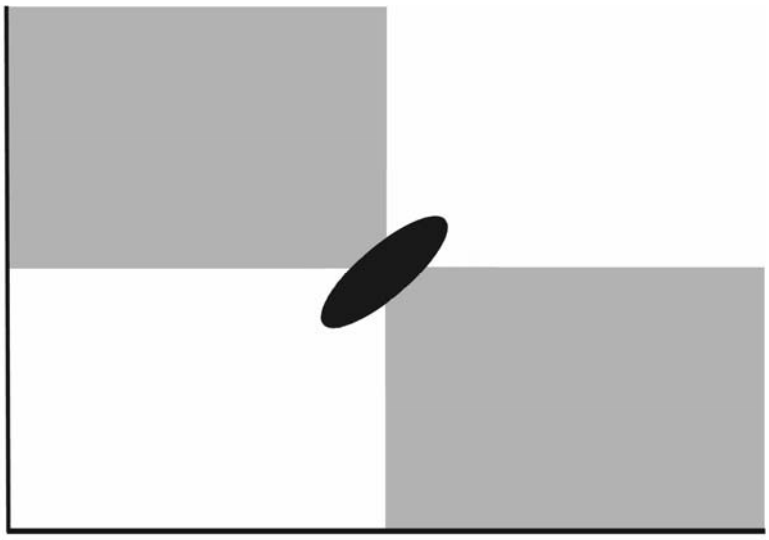

Fig. 7.2. In this hypothetical example, characters X and Y have a positive genetic correlation (represented by the black ellipse with an elongated major axis) and are relatively constrained. Selection vectors (**β**) aligned with $\mathbf{g}_{max}$ will cause **Δz** to shift into the white quadrants and produce a positive correlation among species.

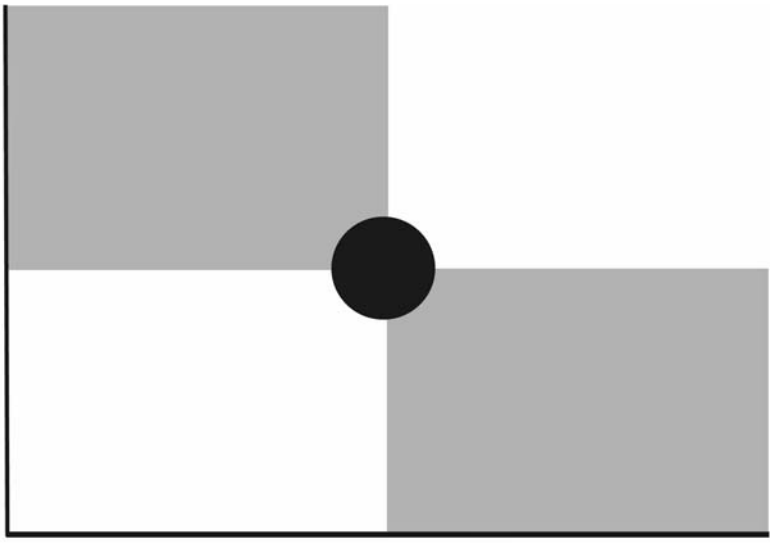

Fig. 7.3. In this hypothetical example, characters X and Y are not genetically correlated (represented by the black circle with equal major and minor axes) and are equally free to change in any dimension; however, selection vectors (**β**) oriented in the gray squares will produce a negative correlation among populations, while selection vectors oriented in the white squares will produce a positive correlation among species.

correlations among species. This is not the pattern observed for the maxillary incisors (or for most characters observed in this study). The scenario depicted in Figure 7.3 corresponds more closely to results for the maxillary incisor MD lengths. Covariation between maxillary incisor MD lengths is low and selection is mostly free to change characters in any direction among species. Within the extant hominids, selection vectors have been predominantly oriented toward the grey quadrants, producing a negative correlation; however, the more common pattern among anthropoids is for selection vectors to be oriented into the white quadrants. While incisors are used as an example, such flexibility exists for most character pairs.

The previous example using incisor size dealt with the ability of weakly covarying characters to evolve independently of one another. As the degree to which characters are expected to evolve independently of one another is a product of the strength of constraint between them (Marroig et al., 2009), then highly covarying characters are expected to evolve along $\mathbf{g}_{max}$ more frequently than do weakly covarying characters. However, selection can shift the phenotype into any dimension in which genetic variance is present (Klingenberg, 2010). What differs between weakly and strongly covarying character pairs is the amount of independent change that can be produced and the rate at which the means of the traits can be shifted. Selection aligned with $\mathbf{g}_{max}$ will produce rapid and significant change in the mean value of the characters; however, selection aligned with other dimensions of genetic variance produce smaller shifts in mean value over time (Schluter, 1996; Marroig and Cheverud, 2005; 2010). An artificial selection experiment on eyespot size in the butterfly *Bicyclus anynana* illustrates this principle (e.g., Beldade et al., 2002). *Bicyclus anynana* wings have two eyespots, one anterior and one posterior, and the size of these eyespots have a strong positive genetic correlation. The artificial selection experiment was designed to determine if selection

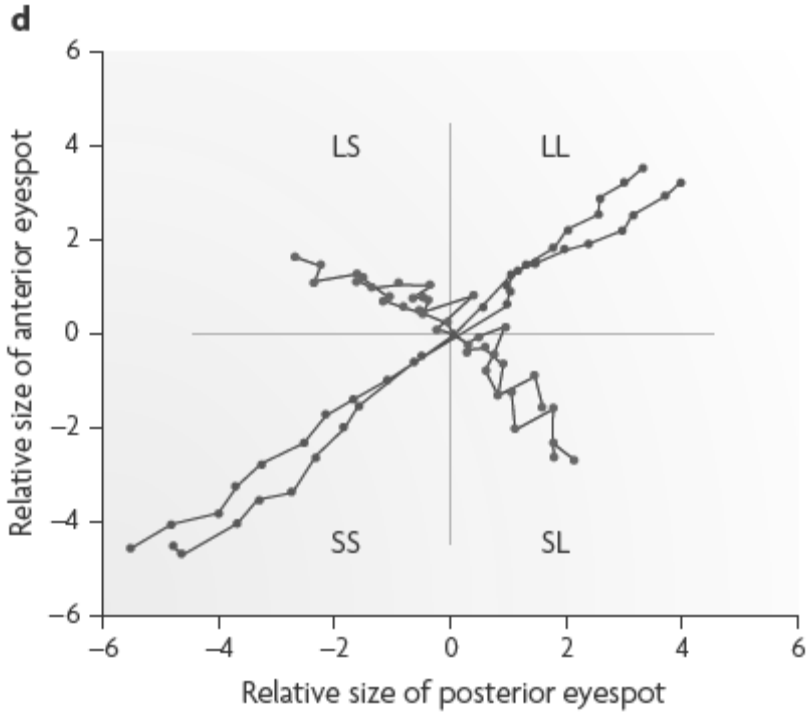

Fig. 7.1. The results of 20 generations of artificial selection on anterior and posterior eyespot size in the butterfly *Bicyclus anynana* (modified from Klingenberg, 2010). Selection for larger anterior and posterior eyespots (LL) and smaller anterior and posterior eyespots (SS), which are aligned with $\mathbf{g}_{max}$, produced larger divergences in mean eyespot size than did selection for "constrained" morphotypes that favored the decrease in one eyespot and increase in the other.

could generate "unconstrained" morphotypes (i.e, those that pair one small with one large eyespot). The results of 20 generations of artificial selection are illustrated in Figure 7.1. While change was possible in any dimension, it is clear that more change occurred when artificial selection pressures were oriented along the major axis of genetic covariation than when they were aligned perpendicular to the major axis.

As a result of the considerations outlined in this section, it is important to consider that relative constraints cannot prevent evolution in any direction. Continued selection vectors ($\boldsymbol{\beta}$) not aligned with $\mathbf{g}_{max}$ will produce "independent" evolutionary

change for pleiotropically-linked characters. When $\mathbf{g}_{max}$ and $\boldsymbol{\beta}$ are aligned, change is channeled along narrow dimensions of phenotypic space.

Tradeoff Hypothesis is Not Supported: The hypothesis that the anterior and posterior teeth negatively covary within species has a long history in paleoanthropogy. Over 40 years ago, Jolly (1970: 14–16) proposed a pleiotropy hypothesis to explain the convergent patterns of anterior dental reduction and posterior dental enlargement that were observed in the hominin *Paranthropus* and the extinct gelada *Theropithecus brumpti*. His hypothesis is printed below.

> To avoid the charge of Lamarckism, I should perhaps suggest some selectional mechanisms leading to incisal reduction in molar-dominant forms. . . In a monkey or hominoid adapting to a gelada-like diet, each unit of tooth-material allotted genetically to a molar will bring a greater return in food processed than a unit allotted to an incisor. Thus selection should favour the genotype which determines the incisors at the smallest size consistent with their residual function. This 'somatic budget effect' differs from Brace's (I963) 'random mutation effect' (criticised by Holloway (I966) among others) chiefly in that it proposes a positive advantage in reduction.
>
> A second mechanism is specific to teeth. While dental size is genetically (or at least antenatally) determined, the development of the alveolus depends partly upon the stresses placed upon it during its working life (Oppenheimer 1964). An under-exercised jaw may thus be too small to accommodate its dental series, which tends to become disadvantageously crowded and maloccluded. Natural selection will then favour the genotype which reduces the teeth to a size fitting the reduced alveolus. The 'Oppenheimer effect', originally proposed to explain the reduction of complete dentitions (as in the case of *Homo sapiens* after the introduction of cooking and food-preparation), could equally operate on particular dental regions, as in the case of *Theropithecus* and the early hominids, where the incisors were reduced but the molars were, if anything, larger than those of their forest- and woodland-dwelling relatives…Alternatively, the dependence might be at the genetic level, with canine reduction being a simple pleiotropic effect of a genotype which primarily determined incisal reduction. There is some evidence for a canine-incisal genetic 'field' in both Cercopithecoidea (Swindler et al. I967) and Hominoidea (Jolly & Chimene, unpublished data). It may well be that both selective factors are operative in canine reduction;

> adaptation to rotary chewing favouring crown height reduction, and effects stemming from incisal reduction acting upon crown-area dimensions. Since the genetic factors determining these two parameters of canine size are most unlikely to be independent of each other, the two processes would be mutually reinforcing."

McGollum and Sharpe (2001) revived Jolly's (1970) pleiotropy hypothesis by providing a developmental model that suggests that the boundary between "units" of developing teeth early in odontogenesis is under genetic control. In *Paranthropus* and *Theropithecus*, the boundary between the anterior and posterior teeth would have shifted mesially, relative to extant outgroups, so that the posterior teeth expanded in size and the anterior teeth reduced in size. There is no empirical evidence for the model produced by McCollum and Sharpe (2001); however, the study of genetic correlations in SNPRC baboons has provided limited support for the existence of negative correlations between anterior and posterior teeth.The notion that the anterior and posterior teeth share genetic covariation is not without basis. Studies of dental development indicate that, "from the genetic point of view, making teeth probably requires a set of similar genes whatever the tooth considered" (Renaud et al., 2009: 591). In various mammals, a variety of techniques has been used to identify genes that influence dental development. Some genes have phenotypic effects that cross functional modules, while others have more restricted effects (e.g., Stock, 2001; Renaud et al., 2009). As teeth share developmental networks, it should be expected that all variational modules share at least very low levels of size covariation between them (Figures 3.2, 4.1, 4.2, 5.4, 5.5, 5.6, 5.7–5.11, 5.13, and 5.14).

Though low levels of pleiotropy exist between modules, the pleiotropy/tradeoff hypotheses that predict strong negative within- and among-species covariation between the incisors and postcanine dentition are not supported by the analyses reported here. Within species, phenotypic covariation between incisor and postcanine size is *weak* and

positive in direction, contra McCollum and Sharpe (2001) and Hlusko et al. (2010) (Figure 4.2). Covariation between incisor and postcanine size is weaker than it is among most dimensions within either module (Figure 3.1, 3.2, and 4.1; Tables 3.7–3.10). Among species, covariation is also positive in direction (Table 3.12). The among-species pattern did not result from selection acting on a suite of strongly constrained characters, but, instead, reflects the outcome of common, long-term, selective pressures that often favored simultaneous increases or decreases in both incisor and postcanine size. The low levels of within-species covariation indicate that each module is fairly free to change independently of the other. In this sense, the pattern of evolutionary change is expected to be much like that of the maxillary incisor MD lengths, reviewed above. The average trend for selection vectors produced positive among-species covariation when anthropoids are considered broadly; however, there is no reason that selection could not independently shift the sizes of the anterior and posterior teeth to produce negative among-species covariation in some clades, as likely occurred for *Theropithecus* and *Paranthropus*. Interspecific correlations may be poor guides to the strength of covariation among characters within species. As anthropoid dental size spans a wide range (consider the comparison of *Gorilla* to *Callithrix*), among-species correlations reveal more about long term average selection than they do about the pattern of covariation within any species.

Even if the sign of within-species covariation between anterior and posterior teeth observed in this study is an error (which seems unlikely given that it was observed in 10 out 10 taxa), or if there is some unexplained contrast between the direction of covariation at the phenotypic and genetic level, it is clear that selection vectors have not been frequently aligned with the predicted negative genetic covariance (McCollum and Sharpe, 2001; Hlusko et al., 2010), as the general trend in primates is for larger incisors

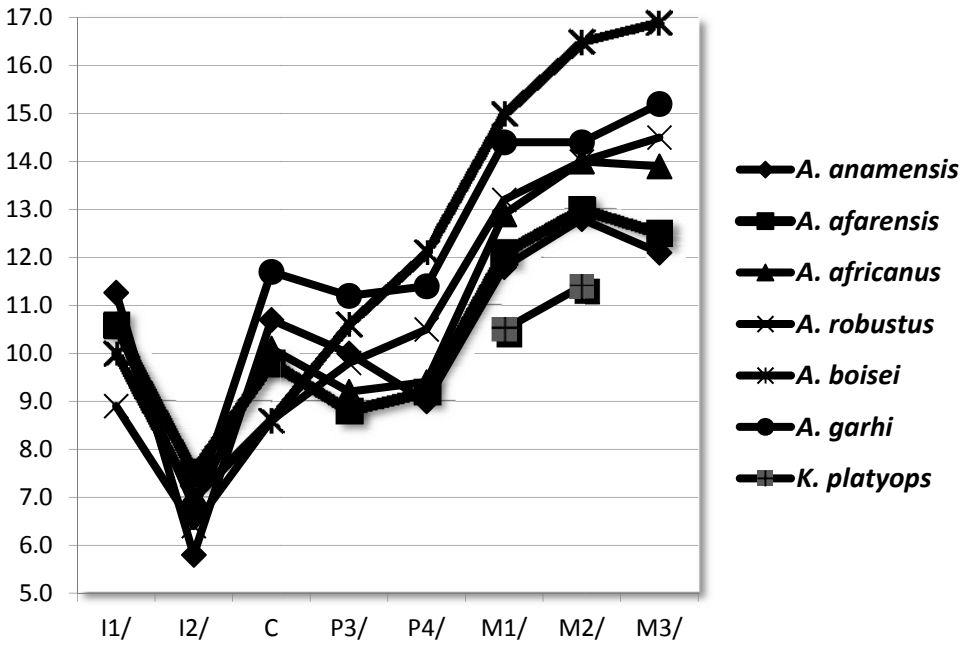

Fig. 7.2. Mean mesiodistal length (mm) for the maxillary dentition of seven hominin species (dated provided by W. Kimbel).

to be associated with larger postcanine teeth. A casual comparison of tooth size among primates is sufficient to see that this is true.

Fortunately, we do not have to rely only on the results of this study to reject the pleiotropy hypothesis. Fossil discoveries made in the 40 years subsequent to Jolly's proposal have provided a natural test case of the model and show that megadont postcanine teeth need not be paired with highly reduced anterior teeth. The 2.5-million-year-old hominin taxon *Australopithecus garhi* pairs molars and premolars of a size seen in *Paranthropus* with anterior teeth (incisors and canine) that are larger than seen on average in *Paranthropus* (Figure 7.2). If the geologically older hominin *Australopithecus afarensis* is used as a potential starting point, the relative sizes of the anterior and posterior teeth were changed in *Paranthropus*; however, in *Australopithecus garhi*, the size of all dental dimensions were enlarged without changing their relative proportions

(Asfaw et al., 1999). Thus, postcanine megadontia does not require reductions of the anterior dentition. As a result, anterior tooth size reduction and posterior tooth size enlargement should not be seen as "dependent" characters in phylogenetic reconstruction (contra the concerns expressed in McCollum and Sharpe (2001)). The hominin fossil record contains abundant examples of taxa that pair differing dental proportions with different masticatory configurations (e.g., review in Kimbel and Delezene, 2009), which removes support for the McCollum and Sharpe (2001) supposition that the masticatory complex is characterized by widespread genetic covariation. Even if the reduction of the anterior tooth size in *Paranthropus* represents a selective trade-off with posterior tooth size, this is not sufficient for considering them dependent characters (Lockwood, 2007).

***Pleiotropy and the Evolution of the Canine Honing Complex*:** A previous analysis of the coevolution of the canine honing complex concluded that maxillary canine projection and premolar honing surface length have coevolved in male but not in female anthropoids (Greenfield and Washburn, 1992; Greenfield, 1992). In Chapter 1, these results were discussed and several explanations for the pattern were offered: 1) that pleiotropy exists only in the male honing complex, 2) that pleiotropy is absent in both males and females and selective covariance drove the male pattern, or 3) that the pattern observed by Greenfield is an artifact of the metric used to quantify canine height. It is clear that Greenfield (1992: 168) did not envision a pleiotropic linkage between canine height and premolar honing surface length; for, he states "use of the canine as an incisor could be the behavior generating the selection that favors short canines and has no affect on the size of the occluding surface for the maxillary canines" (but see Plavcan and Kelley, 1996).

The results of this study indicate that the characters constituting the canine honing complex are linked by pleiotropy and have coevolved in both male and female

anthropoids (Tables 5.3, 5.12., and 5.16; Figures 5.1 and 5.2). As reviewed in Chapter 1, Greenfield measured only the maxillary canine's projection beyond the occlusal plane (Figure 1.13). Since, within species, female anthropoids typically have shorter canines than males, canine projection captures a smaller fraction of female canine height than male canine height. The contrast of the results from this study and those of Greenfield must be explained by his use of a different metric to capture canine "height." Greenfield (1992) interpreted the patterns he observed to reflect the selective unimportance of the honing complex in females. As the maxillary canine is honed in both males and females (personal observation), has been subjected to selection so that relative canine size covaries with levels of agonism and competition in both sexes (Plavcan, 1993; 2001), is used as weapon in both sexes (e.g., McGraw et al., 2002), and because it coevolves with the honing premolar in both sexes, the results of this study remove support for Greenfield's selective interpretation.

The finding that the height of the maxillary canine significantly covaries with the length of the honing surface on the mandibular premolar is surprising, as the functional relationship between the two dimensions is temporally quite fleeting. Especially in males with large projecting canines, the maxillary canines become heavily worn during an individual's lifetime and the tip is frequently broken, which results in the progressive reduction in canine height (e.g., Leigh et al., 2008). In taxa with large projecting canines, including most catarrhines, the maxillary canine begins to be honed before it is completely erupted (for example, the maxillary canine in Figure 1.11 is not completely erupted and already has visible evidence of having been honed). As a result, the maximum crown height of the maxillary canine exists for a very short period of time (Leigh et al., 2008). In contrast, the length of the premolar's honing surface does not change substantially, as its wear is mostly superficial. Therefore, the relative sizes of the

honing surfaces must change during an individual's lifetime. An explanation for the tight correlation between premolar honing surface length and the maximum height of the maxillary canine may be that the canine hypererupts (personal observation) after the crown begins to wear. As the crown height is reduced over time, the loss is offset by the continuing eruption of the canine, so that the apex of the canine remains at approximately the same height relative to the gum. Alternatively in males, the work of Leigh et al. (2008) indicates that the peak of reproductive success for male mandrills occurs when the maxillary canine is at or near its maximum crown height. If having a sharp canine enhances the reproductive success of males during this period, then the length of the premolar's honing surface may be selected to match that of the maximum canine height, after which time the lack of a tight correspondence in the relative sizes of the occluding surfaces does not influence fitness.

That pleiotropy is strong between canine heights and between canine heights and the length of the premolar's honing surface has important implications for the strength of selection that acted on the complex in early hominins. If selection vectors were oriented in line with $\mathbf{g}_{max}$, then a pattern of coordinated change in early hominins is expected. That is not the pattern that is observed in early *Australopithecus* or *Ardipithecus ramidus*, which provide the best evidence for the initial stages of hominin canine reduction (Suwa et al., 2009; Ward et al., 2010). Suwa et al. (2009) inferred that canine size dimorphism is minimal in *Ardipithecus ramidus* and resulted from the feminization of the male canine. In extant apes, the maxillary canine exceeds the mandibular canine in height by as much as 20%; however, in two associated *Ardipithecus ramidus* dentitions, the mandibular canine exceeds the maxillary canine in height by 10% (as it does in geologically younger hominins and humans), suggesting that the pace of canine height reduction was unequal for the mandibular and maxillary canines (Suwa et al., 2009). In addition, the heights and

the basal dimensions of early hominin canines changed independently of one another, as both *Ardipithecus ramidus* and *Australopithecus anamensis* have reduced canine heights paired with canine basal dimensions similar in size to that of *Pan* (Suwa et al., 2009; Ward et al., 2010). The pattern of character state change in early hominins suggests that the selection vector operating on canine size was not aligned with $\mathbf{g}_{max}$ as estimated by $\mathbf{p}_{max}$ in extant apes in this study. That canine bases would change independently of heights is not remarkable as they were shown in Chapter 5 to not covary strongly with one another within species (Tables 5.1 and 5.2); their flexibility among species was also demonstrated in the analyses of independent contrasts (Figures 5.3 and 5.4). The discordant reductions in canine heights are more remarkable, as canine heights are among the most tightly integrated characters in the anthropoid dentition (Table 5.3). While unexpected, there are other instances of canine size $\mathbf{\Delta z}$ not being aligned with $\mathbf{p}_{max}$ in hominoids; one need only look at the contrast between female *Hylobates lar* and the African apes in Figure 6.6. As Klingenberg (2010: 630) stated, relative constraints "cannot completely prevent evolution in any direction (although intense selection may be required)." The contrasts between *Hylobates lar* and the extant African apes and between *Ardipithecus ramidus* and the extant African apes are powerful illustrations of the ability of natural selection to shift linked characters in directions not aligned with $\mathbf{g}_{max}$.

As outlined in Marroig and Cheverud (2005) and discussed above for the butterfly eyespot experiment, the pace of evolutionary change is relatively slower when selection vectors are oriented in a dimension not aligned with $\mathbf{g}_{max}$ than it is when selection and $\mathbf{g}_{max}$ are aligned. If such a dichotomy exists for long enough, then the pattern of variance-covariance may itself be shaped by natural selection to match the orientation of the selection vector (e.g., Wagner et al., 2007). What remains to be determined for the hominins is if the pattern of uncoordinated change is coupled with a

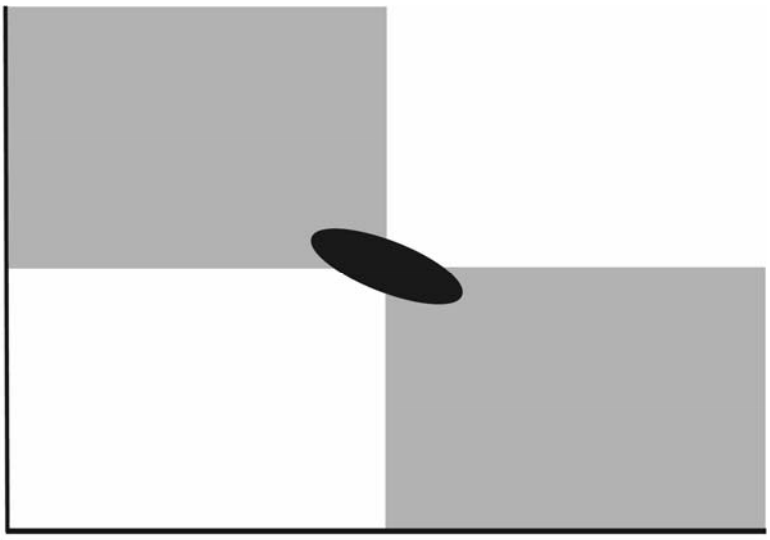

Fig. 7.4. In this hypothetical example, characters X and Y have a negative genetic correlation (represented by the black ellipse with an elongated major axis) and are relatively constrained. Selection vectors (**β**) oriented in the gray squares will generate rapid changes along $\mathbf{g}_{max}$ and produce negative correlations among species.

change in either the pattern or magnitude of covariance among the characters of the honing complex. If covariance itself evolved, then it would be predicted that the magnitude of covariation between canine heights was reduced, as was the magnitude of covariation between the maxillary canine height and the length of the P_3 honing surface.

Pleiotropy has been suggested to play an important role in the reduction of hominin canine size (see reprint of Jolly's (1970) pleiotropy hypothesis above). Specifically, the pleiotropy hypothesis predicts strong positive covariation between canines and incisors and strong negative covariation between canines and the postcanine teeth (e.g., Jolly, 1970; McCollum and Sharpe, 2001). These pleiotropy/trade-off hypotheses are not supported by the results of this study.

All within- and among-species covariation between canine and postcanine size and between canine size and incisor size is *weak* and *positive* in direction; there is no evidence for negative covariation among any dental dimensions (Chapter 5). Likewise, in

a large sample (n = 1453) of red fox, *Vulpes vulpes*, Szuma (2000) found no evidence for negative covariation between the size of the canines and the size of the postcanine dentition. That all size covariation is positive in direction does not imply that covariation is strong, as within species levels of covariation are quite weak between the honing complex and the incisor and postcanine variational modules (Tables 5.4–5.11). Figure 7.4 illustrates the negative covariance between canine and postcanine size as hypothesized by Jolly (1970) and McCollum and Sharpe (2001). In such an arrangement, selection vectors aligned with $\mathbf{g}_{max}$ will shift the population ellipse into the grey-shaded quadrants, producing a negative correlation among species. However, as Figure 7.3 shows, a shift into these quadrants can be produced if the traits are genetically uncorrelated (or at least minimally covarying) and selection favors a tradeoff in canine and postcanine size. The arrangement in Figure 7.3 represents the relationship between canine size and either incisor or postcanine size found in this study. As such, we might expect some pairwise comparisons of species means to indicate that negative tradeoffs occurred (as when *Theropithecus* and hominins are contrasted with their extant outgroups), but not in other cases where selection has favored the simultaneous increase or decrease of canine and postcanine size (i.e., selective covariance; Figure 1.7), as seems to be more common among extant anthropoids. While there may have been a selective tradeoff between anterior and posterior dental size in *Theropithecus* and *Australopithecus*/*Paranthropus* as argued by Jolly (1970), this tradeoff did not occur as a result of selection acting on pleiotropically linked traits.

The results of this study combined with the hindsight provided by the fossil record (i.e., *Ardipithecus* and *Australopithecus anamensis*) show conclusively that Jolly's pleiotropy hypothesis does not explain the initial reduction of hominin canine size. The McCollum and Sharpe (2010) and Jolly (1970) pleiotropy hypotheses and tests of their

predictions within species by Scott (2010), relate to canine basal areas. As stated, canine heights were substantially reduced before canine basal size (Suwa et al., 2009; Ward et al., 2010). Hypotheses that explain this initial reduction should explain not why bases were reduced, but why heights were reduced, and why the rate of reduction was different for the maxillary and mandibular canines (Suwa et al., 2009).

Implications for Cladistic Analyses: Dental characters are significantly represented in trait lists used in hominin cladistic analyses (e.g, Skelton and McHenry, 1992, 1998; Strait et al., 1997). Some have expressed concern that an overreliance on traits that are functionally (and presumably genetically) linked has biased hominin phylogenetic reconstructions in favor of certain scenarios (for example, in recognizing a monophyletic *Paranthropus* comprising *Paranthropus boisei*, *Paranthropus robustus*, and *Paranthropus aethiopicus*) (e.g., Skelton and McHenry, 1988; McCollum and Sharpe, 2001). Genetic linkage among the dental traits used for phylogenetic reconstructions has not been tested, but is presusumed to be common; as Strait and Grine (1998: 115) state "characters may be related for a variety of reasons other than function (e.g., developmental constraint, pleiotropy; see Gilbert et al., 1996), and those features, too, should not be considered independent." This current study was not designed to test for covariation for characters that have been used in particular cladistic analysis; however, the findings have implications.

The highest levels of character covariation are fairly predictable among characters; the highest magnitudes are among occluding teeth and neighbors in functional modules. Otherwise, phenotypic covariation within species is typically very low or low, which suggests that the concern about strong genetic constraints at a broad scale among dental characters is unwarranted. The independence of changes in the absolute and

relative sizes of the incisors, canines, and postcanine teeth were already discussed above. A few more examples are given below. Analyses of partial correlations for postcanine size indicated that premolars share a pool of genetic variance that is not accessible to molars (Tables 4.12 and 4.13). Covariation in premolar and molar shape is also very low or low (Tables 4.31 and 4.32). As a result, changes in the sizes of the premolars and molars are not completely dependent (Figure 7.2) and changes in premolar and molar shapes (e.g., the molarization of the premolars occurred as a result of the expansion of the distal part of the crown relative to the mesial) were likely not mediated by a pleiotropic connection. When considered at a detailed morphological level, the assumption of widespread pleiotropy among dental characters is biologically untenable. Take for example the transformation of the hominin P_3, which has been detailed elsewhere (Delezene and Kimbel, 2011). The morphological changes of the P_3, which resulted in a reduction of premolar heteromorphy, required a reduction of principal cusp height, development of an individualized secondary cusp, a shift in the orientation of the transverse crest, a shift in the principal cusp's location both mesiodistally and buccolingually, the elevation of both segments of the mesial marginal ridge, the fusion of the individual segments of the mesial marginal ridge, and a reduction in the obliquity of the crown's outline. The hominin *Australopithecus afarensis* presents a variety of combinations of apomorphic and plesiomorphic states for the features mentioned above; however, the derived states are nearly fixed in geologically younger hominins. As a result, what appears to be a stable complex of features in taxa arose through a series of independent changes. This is not to say that selection on pleiotropically linked traits has played no role in hominin dental evolution (principal cusp height reduction for P_3 and P^3 was hypothesized as an example in this study), only that a careful examination of dental morphology can produce a list of traits that probably share little genetic covariation.

Future Directions

Continued work on the evolution of the hominin honing complex will examine not just the functional (e.g., Zolnierz et al., 2011) and morphological transformation of the complex (e.g., Delezene and Kimbel, 2011), but also the role of pleiotropy in the transformation. Below, a few extensions of this research are outlined.

Honing removes enamel from the canines and the mesial premolar as wear progresses and generates sharp edges on the canines (Figure 1.10) (Ryan, 1979; Walker, 1984; Greenfield, 1990); however, the reciprocal honing surfaces of the premolar and maxillary canine are not necessarily equal in area (e.g., Greenfield, 1992). For example, in male *Papio cynocephalus* the honing surface on the maxillary canine is four times the area of the surface on the honing premolar (Walker, 1984). Walker hypothesized that the honing premolar should wear out faster than the maxillary canine unless there is a compensatory mechanism; he demonstrated that the enamel on the premolar's honing surface was absolutely thicker than that on the maxillary canine, which ensures its functional longevity. Such a relationship suggests that morphological adaptations for honing not only include the shapes and sizes of the occluding teeth but also the relative thickness of enamel on the reciprocal honing surfaces. The covariance among enamel thicknesses between occluding surfaces has not be investigated and neither has the transformation of enamel thickness on the canines and honing premolars.

Though the canine honing complex comprises the canines and mesial-most mandibular premolar, adjacent (nonhoning) teeth are also affected by this complex. During hominin evolution the specializations related to honing were lost in the P_3 (discussed in Chapter 1) and for the P^3 the paracone was reduced in height and area so that the paracone and protocone became similar in size. In Chapter 4, the weak

covariation of both mesial premolars with distal premolars was discussed and in Chapter 5, it was shown that the honing surface length of the P_3 and the mesial enamel extension of the P^3 expressed substantial covariation within species (Table 5.15) and it was suggested that this covariance likely reflects the fact that both features are related to having tall principal cusps. Therefore, in part, premolar heteromorphy is reduced for the P_3 and P^3 by shortening the height of the principal cusp. Future work will attempt to uncover the extent of the pleiotropic relationship between the P3s and will also attempt to determine if magnitudes of covariance increased between the P3s and P4s; that is, to determine if the P3s became integrated with the P4s (as in Figure 1.1).

Conclusion

The findings of this dissertation support the hypothesis that the functional modules of the dentition are also variational modules and that patterns of variance-covariance are conserved among species; though subtle differences exist between taxa when variational modules are examined in isolation. Despite these shared patterns of variance-covariance, dental diversification has frequently occurred along dimensions not aligned with the vector of genetic constraint. As there is no evidence for absolute constraints on dental morphology, it is important to consider both the history of selection and the pattern of constraint when studying the production of dental diversity. As regards the canine honing complex, there is no evidence for a difference in the pleiotropic organization or the coevolution of characters of the complex in males and females, which undermines arguments that the complex is selectively important only in males. For hominins, this indicates that selection must have been particularly strong in driving the divergent reductions in mandibular and maxillary canine height. The extent to which the elements of the complex were parceled out from one another remains to be determined.

Finally, there is no evidence for strong or negative pleiotropy between variational modules, which falsifies hypotheses that predict such relationships between incisors and postcanine teeth or between the canines and either the incisors or postcanine teeth.

LITERATURE CITED

Ackermann, R. R. (2005). Ontogenetic integration in the hominoid face. Journal of Human Evolution 48: 175-197.

Ackermann, R.R. (2009). Morphological integration and the interpretation of fossil hominin diversity. Evolutionary Biology 36: 149–156.

Agrawal, K. R., Ang, K., Sui, Z., Tan, H. T. W., and Lucas, P. W. (2008) Methods of Ingestion and Incisal Designs. In J. D. Irish and G. C. Nelson (eds), Technique and Application in Dental Anthropology (pp. 349–363). Cambridge: Carmbridge University Press.

Ang, K. Y., Lucas, P. W., and Tan, H. T. W. (2006) Incisal Orientation and Biting Efficiency. Journal of Human Evolution 50: 663–672.

Anapol, F., Lee, S. (1994). Morphological adaptation to diet in platyrrhine primates. American Journal of Physical Anthropology 94: 239–261.

Armbruster, W.S., Schwaegerle K.E. (1996). Causes of covariation of phenotypic traits among populations. Journal of Evolutionary Biology 9: 261–276.

Arnold, S. J. (2005). The ultimate causes of phenotypic integration: Lost in translation. Evolution 59: 2059-2061.

Arnold, S.J., Burger, R., Hohenlohe, P.A., Ajie, B.C., Jones, A.G., (2008). Understanding the evolution and stability of the G-matrix. Evolution 62: 2451–2461.

Arnold, S.J., Pfrender, M.E., Jones, A.G. (2001). The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetica 112: 9–32.

Arnold, C., Matthews, L. J. & Nunn, C. L. 2010. The 10kTrees Website: A New Online Resource for Primate Phylogeny. Evolutionary Anthropology 19: 114-118.

Barton, R.A. (2006). Primate brain evolution: Integrating comparative, neurophysiological, and ethological data. Evolutionary Anthropology 15: 224–236.

Beldade, P. and P. M. Brakefield (2002). The genetics and evo-devo of butterfly wing patterns. Genetics 3: 442-452.

Beldade, P., Brakefield, P.M. (2003). The difficulty of agreeing about constraints. Evolution and Development 5: 119–120.

Berner, D. (2009). Correction of a bootstrap approach to testing for evolution along lines of least resistance. Journal of Evolutionary Biology 22: 2563–2565.

Butler, P.M. (1939). Studies of the mammalian dentition, differentiation of the post-canine dentition. Proceedings of the Zoological Society of London 109: B1–B36.

Butler, P.M. (1967). Dental merism and tooth development. Journal of Dental Research 46: 845–850.

Caruso, C.M., Maherali, H., Mikulyuk, A., Carlson, K., Jackson, R.B. (2005). Genetic variance and covariance for physiological traits in *Lobelia*: Are there constraints on adaptive evolution. Evolution 59: 826–837.

Charles, C., Lazzari, V., Tafforeau, P., Schimmang, T., Tekin, M., Klein, O., Viriot, L. (2009). Modulation of Fgf3 dosage in mouse and men mirrors evolution of mammalian dentition. Proceedings of the National Academy of Sciences of the United States of America 106: 22364-22368.

Chernoff, B. and P. M. Magwene (1999). Afterword. Morphological integration: Forty years later. In *Morphological Integration* (E. C. Olson and R. L. Miller, eds), pp. 319-353. University of Chicago Press, Chicago.

Cheverud, J.M. (1982). Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36: 499–516.

Cheverud, J.M. (1988a). A comparison of genetic and phenotypic correlations. Evolution 42: 958–968.

Cheverud, J.M. (1988b). The evolution of genetic correlation and developmental constraints. In *Population Genetics and Evolution* (G. de Jong ed), pp. 94–101. Springer-Verlag, Berlin-Heidelberg.

Cheverud, J.M. (1989). The evolution of morphological integration. In *Trends in Vertebrate Morphology*: *Proceedings of the 2nd International Symposium on Vertebrate Morphology, Vienna, 1986* (H. Splechtna and H. Hilgers, eds), pp. 196–198. Stuttgart, New York.

Cheverud, J.M. (1995). Morphological integration in the saddle-backed tamarin, (*Saguinas fuscicollis*) cranium. American Naturalist 1: 63–89.

Cheverud, J.M. (1996). Developmental integration and the evolution of pleiotropy. American Zoologist 36: 44–50.

Cheverud, J.M. (2001). The genetic architecture of pleiotropic relations and differential epistasis. In *The Character Concept in Evolutionary Biology* (G. P. Wagner ed.), pp. 411–433. Academic Press, San Diego.

Cheverud, J.M., Marroig, G. Comparing covariance matrices: Random skewers method compared to the common principal components model. Genetics and Molecular Biology 30: 461–469.

Cheverud, J.M., Routman, E.J., Irschick, D.J. (1997). Pleiotropic effects of individual gene loci on mandibular morphology. Evolution 51: 2006–2016.

Cheverud, J.M., Ehrich, T.H., Vaughn, T.T., Koreishi, S.F., Linsey, R.B., Pletscher, L.S. (2004). Pleiotropic effects on mandibular morphology II: Differential epistasis

and genetic variation in morphological integration. Journal of Experimental Zoology (Mol Dev Evol) 302B: 424–435.

Cochard, L.R. (1981). Patterns of size variation and correlation in the dentition of the red colobus monkey (*Colobus badius*). American Journal of Physical Anthropology 54: 139–146.

Dahlberg, A. (1945). The changing dentition of man. Journal of the American Dental Association 32: 676–690.

Dayan, T., Wool, D., Simberloff, D. (2002). Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. Paleobiology 28: 508–526.

de Oliveira, F.B., Porto, A., Marroig, G. (2009). Covariance structure in the skull of Cattarhini: a case of pattern stasis and magnitude evolution. Journal of Human Evolution 56: 417–430.

Delezene, L.K., Kimbel, W.H. (2011). Evolution of the mandibular third premolar crown in early *Australopithecus*. Journal of Human Evolution 60: 711–730.

Dempsey, P.J., Townsend, G.C., Martin, N.G., Neale, M.C. (1995). Genetic covariance structure of incisor crown size in twins. J Dent Res 74: 1389–1398.

Devore, J.L., Farnum, N.R. (2005). Applied Statistics for Engineers and Scientists, 2nd Edition. Duxbury Press.

Eaglen, R.H. (1984). Incisor size and diet revisited: The view from a platyrrhine perspective. American Journal of Physical Anthropology 64: 263–275.

Edwards, E.J. (2006). Correlated evolution of stem and leaf hydraulic traits in *Pereskia* (Cactaceae). New Phytologist 172: 479–489.

Felsenstein, J. (1985). Phylogenies and the comparative method. The American Naturalist 125: 1–15.

Fink, W. L. and M. L. Zelditch (1996). Historical patterns of developmental integration in piranhas. American Zoologist 36: 61-69.

Fisher, R. A. (1930). The genetical theory of natural selection. Oxford Univ. Press, Oxford, U.K.

Garamszegi, L.Z., Møller, A.P., Erritzøe, J. (2002). Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proceedings: Biological Sciences 269: 961–967.

Garland, T. (1992). Rate tests for phenotypic evolution using phylogenetically independent contrasts. American Naturalist 140: 509–519.

Garland, T., Ives, A.R. (2000). Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155: 346–364.

Garland, T., Harvey, P.H., Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41: 18–32.

Garland, T., Midford, P.E., Ives, A.R. (1999). An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39: 374–388.

Garn, S.M., Kerewsky, R.S., Swindler, D.R.. (1966). Canine "field" in sexual dimorphism in tooth size. Nature 212: 1501–1502.

Greenfield, L.O. (1990). Canine honing in *Australopithecus afarensis*. American Journal of Physical Anthropology 82: 135–143.

Greenfield, L.O. (1992). Origin of the human canine: A new solution to an old enigma. Yearbook of Physical Anthropology 35: 153–185.

Greenfield, L.O. (1993). Tooth at the border of two morphogenetic fields. Human Evolution 8: 187–204.

Greenfield, L.O. (1995). The anterior dentition of adapids and anthropoid origins. Folia Primatoligica 65: 59–84.

Greenfield, L.O., Washburn, A. (1991). Polymorphic aspects of male anthropoid canines. American Journal of Physical Anthropology 84: 17–34.

Greenfield, L.O., Washburn, A. (1992). Polymorphic aspects of male anthropoid honing premolars. American Journal of Physical Anthropology 87: 173–186.

Groves, C. (2003). Primate Taxonomy. Smithsonian Series in Comparative Evolutionary Biology. Smithsonian Institution Press, Washington, DC.

Gunnell, G.F., Miller, E.R. (2001). Origin of Anthropoidea: Dental evidence and recognition of early anthropoids in the fossil record, with comments on the Asian anthropoid radiation. American Journal of Physical Anthropology 114: 177–191.

Hallgrimsson, B., Jamniczky, H., Young, N.M., Rolian, C., Parsons, T.E., Boughner, J.C., Marcucio, R.S. (2009). Deciphering the palimpsest: Studying the relationship between morphological integration and phenotypic covariation. Evolutionary Biology 36: 355–376.

Hansen, T. F. (2003). Is modularity necessary for evolvability? Remarks on the relationship between pleiotropy and evolvability. BioSystems 69: 83–94.

Hlusko, L.J., Mahaney, M.C. (2003). Genetic contributions to expression of the baboon cingular remnant. Archives of Oral Biology 48: 663–672.

Hlusko, L.J., Mahaney, M.C. (2007a). A multivariate comparison of dental variation in wild and captive populations of baboons (Papio hamadryas). Archives of Oral Biology. 52: 195–200.

Hlusko, L.J., Do, N., Mahaney, M.C. (2007b). Genetic correlations between mandibular molar cusp areas in baboons. American Journal of Physical Anthropology 132: 445–454.

Hlusko, L.J., Mahaney, M.C. (2007c). Of mice and monkeys: Quantitative genetic analyses of size variation along the dental arcade. In *Dental Perspectives on Human Evolution: State-of-the-Art Research in Dental Paleoanthropology* (S. E. Bailey and J-J Hublin eds.), pp. 237–245.Springer.

Hlusko, L.J., Mahaney, M.C. (2009). Quantitative genetics, pleiotropy, and morphological integration in the dentition of *Papio hamadryas*. Evolutionary Biology 36: 5–18.

Hlusko, L.J., Maas, M-L., Mahaney, M.C. (2004a). Statistical genetics of molar cusp patterning in pedigreed baboons: Implications for primate dental development and evolution. Journal of Experimental Zooogy (Mol Dev Evol) 302B: 268–283.

Hlusko, L.J., Suwa, G., Kono, R.T., Mahaney, M.C. (2004b). Genetics and the evolution of primate enamel thickness: A baboon model. American Journal of Physical Anthropology 124: 223–233.

Hlusko, L.J., Lease, L.R., Mahaney, M.C. (2006). Evolution of genetically correlated traits: Tooth size and body size in baboons. American Journal of Physical Anthropology 131: 420–427.

Hlusko, L.J., Sage, R.D., Mahaney, M.C. (2010). Modularity in the mammalian dentition: Mice and monkeys share a common dental genetic architecture. Journal of Experimental Zoology: Molecular and Developmental Evolution 316: 21–49.

Hlusko, L.J., Weiss, K.M., Mahaney, M.C. (2002). Statistical genetic comparison of two techniques for assessing molar crown size in pedigreed baboons. American Journal of Physical Anthropology 117: 182–189.

Hodgkin, J. (1998). Seven types of pleiotropy. International Journal of Developmental Biology 42: 501-505.

Hoffmann, A.A., Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. Trends in Ecology and Evolution 14: 96–101.

Hughes, T.E., Bockmann, M.R., Seow, K., Gotjamanos, T., Gully, N., Richards, L.C., Townsend, G.C. (2007). Strong genetic control of emergence of human primary incisors. Journal of Dental Research 86: 1160–1165.

Hylander, W. L. (1975) Incisor Size and Diet in Anthropoids with Special Reference to Cercopithecidae. Science 189: 1095–1098.

Jernvall, J., Jung, H-S. (2000). Genotype, phenotype, and developmental biology of molar tooth characters. Yearbook of Physical Anthropology 48: 171-190.

Jolly, C.J. (1970). The seed-eaters: A new model of hominid differentiation based on a baboon analogy. Man 5: 5–26.

Juenger, T., Perez-Perez, J,M,, Bernal, S,, Micol, J.L. (2005). Quantitative trait loci mapping of floral and leaf morphology traits in *Arabidopsis thaliana*: Evidence for modular genetic architecture. Evolution and Development 7: 259–271.

Kangas, A.T., Evans, A.R., Thesleff, I., Jernvall, J. (2004). Nonindependence of mammalian dental characters. Nature 432: 211–214.

Kay, R. F., and Covert, H. H. (1984) Anatomy and Behavior of Extinct Primates. In D. J. Chivers, B. A. Wood, and A. Bilsborough (eds), *Food Acquisition and Processing in Primates* (pp. 467–508). New York: Plenum Press.

Kay, R. F. and W. L. Hylander. (1978). The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). Pages 173– 191 *in* G. G. Montgomery, ed. The Ecology of Arboreal Folivores. Smithsonian Institution Press, Washington, DC.

Kay, R.F., Plavcan, J.M., Glander, K.E., Wright, P.C. (1988). Sexual selection and canine dimorphism in New World monkeys. American Journal of Physical Anthropology 77: 385–397.

Kelley, J., Anwar, M., McCollum, M.A., Ward, S.C. (1995). The anterior dentition of *Sivapithecus parvada*, with comments on the phylogenetic significance of incisor heteromorphy in hominoidea. Journal of Human Evolution 28: 503–517.

Kimbel, W.H., Delezene, L.K. (2009). "Lucy" redux: A review of research on *Australopithecus afarensis*. Yearbook of Physical Anthropology 52: 2–48.

Kinzey, W.G. (1992). Dietary and dental adaptations in the Pitheciinae. American Journal of Physical Anthropology 88: 499–514.

Kinzey, W.G., Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. American Journal Physical Anthropology 81: 5–15.

Klingenberg, C. P. (2003). Developmental integration in a complex morphological structure: How distinct are the modules in the mouse mandible. Evolution and Development 5: 522-531.

Klingenberg, C. P. (2005). Developmental constraints, modules, and evolvability. In *Variation* (B. Hallgrímmson and B. K. Hall *ed*s), pp. 219-247. Academic Press, San Diego.

Klingenberg CP. (2008). Morphological integration and developmental modularity. Annual Review Ecological Systematics 39: 115–132.

Klingenberg, C.P. (2010). Evolution and development of shape: Integrating quantitative approaches. Nature Reviews Genetics 11: 623–635.

Klingenberg, C.P., Leamy, L.J., Cheverud, J.M. (2004). Integration and modularity of quantitative trait locus effects on geometric shape in the mouse mandible. Genetics 166: 1909–1921.

Koh, C., Bates, E., Broughton, E., Do, N.T., Fletcher, Z., Mahaney, M.C., Hlusko., L.J. (2010). Genetic integration of molar cusp size variation in baboons. American Journal of Physical Anthropology 142: 246–260.

Kurten, B. (1953). On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76:1-122.

Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. Evolution 33: 402–416.

Leamy, L.J., Routman, E.J., Cheverud, J.M. (1999). Quantitative trait loci for early- and late-developing skull characters in mice: A test of the genetic independence model of morphological integration
American Naturalist 153: 201–214.

Leigh, S.R., Setchell, J.M., Charpentier, M., Knapp, L.A., Wickings, E.J. (2008). Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). Journal of Human Evoluion 55: 75–85.

Li, J., Han, K., Xing, J.C., Kim, H.S., Rogers, J., Ryder, O.A., Disotell, T., Yue, B.S., Batzer, M.A. (2009). Phylogeny of the macaques (Cercopithecidae: Macaca) based on Alu elements. Gene 448: 242–249.

Lockwood, C.A. (2007). Adaptation and functional integration in primate phylogenetics. Journal of Human Evolution 52: 490–503.

Lombardi, A.V. (1978). A factor analysis of morphogenetic fields in the human dentition. American Journal of Physical Anthropology 42: 99–104.

Lucas, P.W. (2004). Dental functional morphology: How teeth work. Cambridge University Press, Cambridge.

Mackay, T.F.C. (2001). The genetic architecture of quantitative traits. Annual Review of Genetics 35: 303–339.

Magwene, P.M. (2006). Integration and modularity in biological systems: A review. Acta Zoologica Sinica. 52 (Supp. 1): 490–493.

Manly, B.F.J. (2001). Randomization, bootstrap, and Monte Carlo methods in Biology. Chapman and Hall, Boca Raton, Florida.

Marroig, G., Cheverud, J.M. (2005). Size as a line of least resistance. Diet and adaptive morphological radiation in new world monkeys. Evolution 59: 1128–1142.

Marroig, G., Cheverud, J.M. (2010). Size as a line of least resistance II: Direct selection on size or correlated response due to constraints. Evolution 64: 1470–1488.

Marroig, G., Shirai, L.T., Porto, A., de Oliveira, F.B., de Canto., V. (2009). The evolution of modularity in the mammalian skull II: Evolutionary consequences. Evolutionary Biology 36: 136–148.

Martínez-Abadías, N., Esparza, M., Sjovold, T., Gonzalez-Jose, R., Santos, M., Hernandez, M. (2009). Heritability of human cranial dimensions: Comparing the evolvability of different cranial regions. Journal of Anatomy 214: 19–35.

Matsudaira, K; Ishida, T (2010). Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. Molecular Phylogenetics and Evolution 55: 454–459.

Maynard Smith, J., Burian, J.R., Kaufman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D., Wolpert, L. (1985). Developmental constraints and evolution. Quarterly Review of Biology 60: 265–287.

McCollum, M.A., Sharpe, P.T. (2001). Developmental genetics and early hominid craniodental evolution. BioEssays 23: 481–493.

McGraw, W.S., Plavcan, J.M., Adachi-Kanazawa, K. (2002). Adult female *Cercopithecus diana* employ canine teeth to kill another adult female *C. diana*. International Journal of Primatology 23: 1301–1308.

Monteiro, L.R., Bonato, V., Dos Reis, S.F. (2005). Evolutionary integration and morphological diversification in complex morphological structures: mandible shape divergence in spiny rats (Rodentia, Echimyidae). Evol & Dev 7: 429–439.

Norconk, M.A. (2007). Sakis, uakaris, and titi monkeys: Behavioral diversity in a radiation of primate seed predators. In (C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger, S.K. Bearder eds) Primates in Perspective, pp. 123–138. New York: Oxford University Press.

Norconk, M.A., Wright, B.W., Conklin-Brittain, N.L., Vinyard, C.J. (2009). Mechanical and Nutritional Properties of foods as factors in Platyrrhine dietary adaptations. In (P.A. Garber, A. Estrada, J.C. Bicca-Marques, E.W. Heymann, K.B. Strier eds) South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation, pp. 279–319. Springer Science.

Nunn, C.L., Barton, R.A. (2000). Allometric slopes and independent contrasts: A comparative test of Kleiber's law in primate ranging patterns. American Naturalist 156: 519–533.

Olson, E.C., Miller, R.L. (1958). Morphological Integration. The University of Chicago Press, Chicago.

Opazo, J.C., Wildman, J.E., Prychitko, T., Johnson, R.M., Goodman, M. (2006). Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). Molecular Phylogenetics and Evolution 40: 274–280.

Pickford, M. (2005). Incisor-molar relationships in chimpanzees and other hominoids: Implications for diet and phylogeny. Primates 46: 21–32.

Pigliucci, M. (2003). Phenotypic integration: Studying the ecology and evolution of complex phenotypes. Ecology Letters 6: 265-272.

Pigliucci, M., Preston, K.A. (2004). Phenotypic Integration: Studying the ecology and evolution of complex phenotypes (Pigliucci, M., Preston, K.A., editors). Oxford University Press, New York, New York.

Plavcan, J.M. (1990). Sexual dimorphism in the dentition of extant Anthropoid primates. Dissertation: Department of Biological Anthropology and Anatomy, Duke University.

Plavcan, J.M. (1993). Canine size and shape in male anthropoid primates. American Journal of Physical Anthropology 92: 201–216.

Plavcan, J.M. (1998). Correlated response, competition, and female canine size in primates. American Journal of Physical Anthropology 107: 401–416.

Plavcan, J.M. (2001). Sexual dimorphism in primate evolution. Yearbook of Physical Anthropology 44: 35–53.

Plavcan, J.M., Daegling, D.J. (2006). Interspecific and intraspecific relationships between tooth size and jaw size in primates. Journal of Human Evolution 51: 171–184.

Plavcan, J.M., Kelley, J. (1996). Evaluating the "dual selection" hypothesis of canine reduction. American Journal of Physical Anthropology 99: 379–387.

Plavcan, J.M., Ruff, C. B. (2008). Canine size, shape, and bending strength in primates and carnivores. American Journal of Physical Anthropology 136: 65–84.

Plavcan, J.M., van Schaik, C.P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87: 461–477.

Plavcan, J.M., van Schaik, C.P. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. Journal of Human Evolution 32: 345–374.

Plavcan, J.M., van Schaik, C.P., Kappeler, P.M. (1995). Competition, coalitions and canine size in primates. Journal of Human Evolution 28: 245–276.

Purvis, A. (1995). A composite estimate of primate phylogeny. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 348: 405–421.

Prevosti, F.J., Lamas, L. (2006). Variation of cranial and dental measurements and dental correlations in the pampean fox (*Dusicyon gymnocercus*). Journal of Zoology 270: 636–649.

Renaud, S., Pantalacci, S., Quere, J.P., Laudet, V., Auffray, J.C. (2009). Developmental constraints revealed by co-variation within and among molar rows in two murine rodents. Evolution and Development 11: 590–602.

Reusch, T., Blanckenhorn, W.U. (1998). Quantitative genetics of the dung fly *Sepsis cynipsea*: Cheverud's conjecture revisited. Heredity 81: 111–119.

Roff, D.A. (1997). The evolution of genetic correlations: An analysis of patterns. Evolution 50: 1392–1403.

Roff, D.A. (2000). The evolution of the G matrix: selection or drift. Heredity 84: 135–142.

Rosenberger, A.L. (1992). Evolution of feeding niches in New World Primates. American Journal of Physical Anthropology 88: 525–562.

Rosenberger, A.L., Strier, K.B. (1989) Adaptive radiation of the ateline primates. Journal of Human Evolution 18: 717–750.

Ryan, A.S. (1979). Wear striation direction on primate teeth: A scanning electron microscope examination. American Journal of Physical Anthropology 50: 155–167.

Santos, J.C., Cannatella, D.C. (2011). Phenotypic integration emerges from aposematism and scale in poison frogs. Proceedings of the National Academy of Sciences of the United States of America 108: 6175–6180.

Schluter, D. (1996). Adaptive radiation along genetic lines of least resistance. Evolution 50: 1766–1774.

Scott, G.R., Turner, C.G. (1997). The anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press.

Scott, J.E. (2010). Nonsocial influences on canine size in anthropoid primates. Arizona State University.

Simons, E.L. (1989). Description of two genera and species of late Eocene Anthropoidea from Egypt. Proceedings of the National Academy of Science, USA 86: 9956–9960.

Simons, E.L. (1992). Diversity in the early Tertiary anthropoidean radiation in Africa. Proceedings of the National Academy of Sciences, USA 89: 10743–10747.

Skelton, R.R., McHenry, H. (1992). Evolutionary relationships among early hominids. Journal of Human Evolution 23: 309–349.

Skelton, R.R., McHenry, H. (1998). Trait list bias and a reappraisal of early hominid phylogeny. Journal of Human Evolution 34: 109–113.

Sokal, R.R., and Rohlf, F.J. (1995). Biometry: the principles and practice of statistics in biological research. 3rd edition W. H. Freeman and Co.: New York.

Steiper, M.E., Young, N.M. (2006). Primate molecular divergence dates. Molecular Phylogenetics and Evolution 41: 384–394.

Stefan, V.H. (2006). Brief Communication: Rotation of the maxillary premolars: Evidence in Support of Premolar morphogenetic field. Dental Anthropology 19: 70–73.

Stock, D.W. (2001). The genetic basis of modularity in the development and evolution of the vertebrate dentition. Philosophical Transactions of the Royal Society B: Biological Sciences 356: 1633-1653.

Strait, D.S. (2001). Integration, phylogeny, and the hominid cranial base. American Journal of Physical Anthropology 114: 273–297.

Strait, D.S., Grine, F.E. (1998). Trait list bias? A reply to Skelton and McHenry. Journal of Human Evolution 34: 115–118.

Strait, D.S., Grine, F.E., Moniz, M.A. (1997). A reappraisal of early hominid phylogeny. Journal of Human Evolution 32: 17–82.

Strait, S. G. 1993. Molar morphology and food texture among small bodied insectivorous mammals. Journal of Mammalogy 74: 391– 402.

Suarez, B. K., Williams, B.J. (1973). Dental growth fields and premolar morphology. Journal of Dental Research 52: 632.

Suwa, G. (1988). Evolution of the "robust" australopithecines in the Omo succession: Evidence from mandibular premolar morphology. In F.E. Grine (ed), Evolutionary History of the "Robust" Australopithecines. New York, Aldine de Gruyter, pp. 199–222.

Suwa, G. (1990). A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo valley, Ethiopia. Ann Arbor, UniversityMicrofilms.

Suwa, G., Kono, R.T., Simpson, S.W., Asfaw, B., Lovejoy, C.O., White, T.D. (2009). Paleobiological implications of the *Ardipithecus ramidus* dentition. Science 326: 94–99.

Szuma, E. (2000). Variation and correlation patterns in the dentition of the red fox from Poland. Annales Zoologici Fennici 2: 113-127.

Thinh, V.N., Rawson, B., Hallam, C., Kenyon, M., Nadler, T., Walter, L., Roos, C. (2010). Phylogeny and Distribution of Crested Gibbons (Genus Nomascus)

Based on Mitochondrial Cytochrome b Gene Sequence Data. American Journal of Primatology 72: 1047–1054.

Thoren, S., Lindenfors, P., Kappeler, P.M. (2006). Phylogenetic analyses of dimorphism in primates: Evidence for stronger selection on canine size than on body size. American Journal of Physical Anthropology 130: 50–59.

Ting, N. (2008). Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living colobus monkeys. Journal of Human Evolution 55: 312–325.

Tosi, A.J., Melnick, D.J., Disotell, T.R. (2004). Sex chromosome phylogenetics indicate a single transition to terrestriality in the guenons (tribe Cercopithecini). Journal of Human Evolution 46: 223-237.

Townsend, G.C., Brown, T. (1978). Heritability of permanent tooth size. American Journal of Physical Anthropology 49: 497–504.

Townsend, G.C., Brown T. (1981) Morphogenetic fields within the dentition. Australian Orthodontic Journal 7: 3–12.

Townsend, G., Richards, L., Messer, L.B., Hughes, T., Pinkerton, S., Seow, K., Gotjamanos, T., Gully, N., Bockmann, M. (2006). Genetic and environmental influences on dentofacial structures and oral health: Studies of Australian twins and their families. Twin Research and Human Genetics 9: 727–732.

Ungar, P.S (1998). Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evolutionary Anthropology 6: 205–217.

Ungar, P.S. (1994). Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. American Journal of Physical Anthropology 95: 197–219.

Ungar, P. S. (1996) Relationship of incisor size to diet and anterior tooth use in sympatric Sumatran Anthropoids. American Journal of Primatology 38: 145–15.

Ungar, P.S. (2010). Mammal teeth: Origin, evolution, and diversity. The Johns Hopkins University Press; Baltimore, Maryland.

Ungar, P.S., Lucas, P.W. (2010). Tooth form and function in biological anthropology. In *A Companion to Biological Anthropology (Larson, C.S., ed.):* pp. 516–529. Blackwell Publishing Limited.

Van Valen, L. (1970). An analysis of developmental fields. Developmental Biology 23: 456-477.

Wagner, G.P. (1996). Homologues, natural kinds and the evolution of modularity. American Naturalist 36: 36–43.

Wagner, G.P., Altenberg, L. (1996). Perspective: Complex adaptations and the evolution of evolvability. Evolution 50: 967–976.

Wagner, G.P., Pavlicev, M., Cheverud, J.M. (2007). The road to modularity. Nature Reviews Genetics 8: 921–931.

Wagner, G.P., Zhang, J.Z. (2011). The pleiotropic structure of the genotype-phenotype map; the evolvability of complex organisms. Nature Reviews Genetics 12: 204–213.

Waitt, D.E., Levin, D.A. (1998). Genetic and phenotypic correlations in plants: A botanical test of Cheverud's conjecture. Heredity 80: 310–319.

Walker, A. (1984). Mechanisms of honing in the male baboon canine. American Journal of Physical Anthropology 65: 47–60.

Wang, X.P., Aberg, T., James, M.J., Levanon, D., Groner, Y., Thesleff, I. (2005). Runx2 (Cbfa1) inhibits Shh signaling in the lower but not upper molars of mouse embryos and prevents the budding of putative successional teeth. Journal of Dental Research 84: 138–143.

Wang, Z., Liao, B.Y., Zhang, J.Z. (2010). Genomic patterns of pleiotropy and the evolution of complexity. Proceedings of the National Academy of Sciences of the United States of America 107: 18034–18039.

Ward, C.V., Plavcan, J.M., Manthi, F.K. (2010). Anterior dental evolution in the *Australopithecus anamensis-afarensis* lineage. Philosophical Transactions of the Royal Society B-Biological Sciences 365: 3333–3344.

Weigensberg, I., Roff, D.A. (1996). Natural heritabilities: Can they be reliably estimated in the laboratory. Evolution 50: 2149–2157.

Whittaker, D.J., Morales, J.C., Melnick, D.J. (2007). Resolution of the Hylobates phylogeny: Congruence of mitochondrial D-loop sequences with molecular, behavioral, and morphological data sets. Molecular Phylogenetics and Evolution 45: 620–628.

Wildman, D.E., Jameson, N.M., Opazo, J.C., Soojin, Y. (2009). A fully resolved genus level phylogeny of Neotropical primates (Platyrrhini). Molecular Phylogenetics and Evolution 53: 694–702.

Workman, M.S., Leamy, L.J., Routman, E.J., Cheverud, J.M. (2002). Analysis of quantitative trait locus effects on the size and shape of mandibular molars in mice. Genetics 160: 1573–1586.

Zeldtitch, M. L. and A. C. Carmichael (1989). Ontogenetic variation in patterns of developmental and functional integration in skulls of *Sigmodon fulviventer*. Evolution 43: 814-824.