Nonsocial Influences on Canine Size in Anthropoid Primates

by

Jeremiah Ezekiel Scott

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

Approved November 2010 by the
Graduate Supervisory Committee:

William H. Kimbel, Chair
Gary T. Schwartz
Mark A. Spencer

ARIZONA STATE UNIVERSITY

December 2010

ABSTRACT

Early hominins present an unusual pattern of sexual dimorphism. On one hand, the canine teeth of these species are weakly size-dimorphic, vertically short, and nonhoning, suggesting a social system characterized by infrequent, low-intensity intermale competition and monogamous pair-bonding. On the other hand, marked size variation in skeletal remains attributed to species of *Australopithecus* is thought to reflect strong body-mass dimorphism, which is more consistent with intense intermale competition. Reconciling these conflicting signals and understanding their adaptive significance is a major goal of paleoanthropology. This dissertation research contributes to this objective by investigating factors that may constrain or reduce canine height in extant anthropoid primates.

Two hypotheses regarding the relationship between canine height and other elements of the masticatory system were tested using phylogenetic comparative methods. According to the first hypothesis, canine reduction is a pleiotropic by-product of changes in the sizes of other components of the dentition. With respect to canine height, the results of this study fail to support this idea. There is limited evidence for a relationship between basal canine crown dimensions and incisor and postcanine size, but significant interspecific correlations between these variables are not strong and are restricted primarily to the female maxillary dentition. These results indicate that if pleiotropy influences canine size, then its effects are weak.

The second hypothesis proposes that canine reduction is a consequence of selection for increased jaw-muscle leverage. This hypothesis receives some support: there is a clear inverse relationship between canine height and the leverage of the masseter muscle in male anthropoids. Females do not exhibit this association due to the fact that dimorphism in muscle leverage is weak or absent in most anthropoid species; in other words, female muscle leverage tracks male muscle leverage, which is linked to canine height. Leverage of the temporalis muscle is not correlated with canine height in either sex. Two specimens of the 3.0–3.7-million-year-old hominin *Australopithecus afarensis* fall at or beyond the upper end of the great ape range of variation in masseter leverage, which is consistent with the idea that hominin canine evolution was influenced by selection for increased jaw-muscle leverage.

To Charlie Lockwood (1970–2008)

ACKNOWLEDGMENTS

This dissertation could not have been completed without the support of numerous people. Foremost among them are the members of my committee: Bill Kimbel, Gary Schwartz, Mark Spencer, and, until his untimely death in 2008, Charlie Lockwood. Standing on the shoulders of these giants has been a humbling experience. I am particularly grateful to Bill for guiding me through this process; he is a great scientist, adviser, teacher, and friend. I am also indebted to Jay Kelley and Michael Plavcan for generously sharing their data with me, and to Bill Hylander, whose ideas about canine reduction in early hominins inspired a large portion of my dissertation research; I especially appreciate his willingness to discuss his work with me with such enthusiasm.

The friendship and encouragement of my family and friends were critical to my success. An entire dissertation could be written listing the various contributions made by my parents, Dianne and Sam Scott; without their love, support, and guidance, I probably would not have started this journey, and I definitely could not have completed it. For the last three and a half years, Thierra Nalley, my fellow traveler, has been there to cheer my victories—no matter how small—and lessen the agony of my defeats; she is a model of true strength and character and what they can accomplish. I am also grateful for the support of my sister and brother, Hannah and Jacob Scott, my uncle Mark Scott, and the many people that I have had the pleasure of getting to know during my time at ASU, especially Caley Orr, Laura Stroik, Matt Tocheri, Kristi Lewton, Stephanie Meredith, Terry Ritzman, and Kaye Reed. Special thanks to Alex Bjarnason,

Katharine Balolia, Fire Kovarovic, Nanneke Redclift, Brenda Bradley, Chris Dean, Louise Humphrey, Christophe Soligo, and Aalaa Al-Shamahi for making a difficult time in London more bearable. Kristopher Skelton deserves recognition for providing me with the perfect word when my brain stalled in the last throes of dissertating.

Funding for this project was generously provided by the Leakey Foundation, the Wenner-Gren Foundation, and the Graduate and Professional Student Association of Arizona State University. Additional support was provided by the Institute of Human Origins and the School of Human Evolution and Social Change. Thanks to the following people and institutions for granting access to specimens in their care and for their hospitality: Linda Gordon at the Smithsonian Institution; Darrin Lunde, Eileen Westwig, and Rob Vos at the American Museum of Natural History; Michi Schulenberg at the Field Museum; Judith Chupasko at the Harvard Museum of Comparative Zoology; Malcolm Harman and Julia Walton at the Powell-Cotton Museum; Paula Jenkins and Louise Tomsett at the Natural History Museum, London; Emmanuel Gilissen and Wim Wendelen at the Royal Museum of Central Africa; Marcia Ponce de Léon, Christoph Zollikofer, Renaud Lebrun, and Walther Fuchs at the University of Zurich Anthropological Institute and Museum; and Hein van Grouw at Naturalis.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

Figure Page

CHAPTER 1—INTRODUCTION

Most living primates possess large, daggerlike canines that function primarily as weapons in aggressive social encounters with conspecifics (Walker, 1984; Greenfield and Washburn, 1991; Greenfield, 1992c; Plavcan, 1993a, 2001; Plavcan et al., 1995; Leigh, 2008; Plavcan and Ruff, 2008). Among anthropoid primates, male canines are generally larger than those of females, reflecting the fact that males use these teeth to compete for access to mates, which has greater fitness consequences than interfemale competition for resources such as food (Leutenegger and Kelly, 1977; Harvey et al., 1978; Kay et al., 1988; Plavcan and van Schaik, 1992, 1994; Plavcan et al., 1995; Plavcan, 2001; Thorén et al., 2006). While it is well established that weaponized canines are primarily the product of sexual selection, the factors that limit canine size or favor canine reduction are not as well understood. This issue—the subject of this dissertation—is of particular interest to paleoanthropologists because, along with bipedality, canine reduction distinguishes the oldest-known hominin species from fossil and living apes (e.g., White et al., 1994, 2006, 2009; Haile-Selassie 2001; Senut et al., 2001; Ward et al., 2001; Brunet et al., 2002, 2005; Haile-Selassie et al., 2004, 2009; Semaw et al., 2005; Plavcan et al., 2009; Suwa et al., 2009b; Ward et al., 2010).

Early hominins present an unusual pattern. On one hand, variation in canine size is uniformly low in all hominin fossil samples, indicating that these teeth are only slightly sexually dimorphic in size (e.g., Leutenegger and Shell, 1987; Plavcan and van Schaik, 1997a; Plavcan et al., 2009; Suwa et al., 2009b). This reduced dimorphism is a consequence of the fact that male canines are vertically short: in absolute size, they are similar to or shorter than those of female *Pan troglodytes* (Fig. 1.1) (e.g., White, 1994; Haile-Selassie et al., 2004, 2009; Plavcan et al., 2009; Suwa et al., 2009b), and relative to estimates of body size, they are shorter than the canines of all ape species, except perhaps *Pan paniscus* (Plavcan and van Schaik, 1997a; Alba et al., 2001; Kelley, 2001; Suwa et al., 2009b). This pattern of canine size and dimorphism indicates low levels of intermale aggression, which has led some authors to argue that the earliest hominins were characterized by intragroup cooperation (Holloway, 1967) or monogamous pair-bonding (Lovejoy, 1981, 2009; Reno et al., 2003, 2005, 2010). On the other hand, skeletal remains of various Plio-Pleistocene hominin species suggest that many early hominins, particularly species of *Australopithecus*,[1] were moderately to highly dimorphic in body size, exceeding the dimorphism of modern humans and chimpanzees and perhaps approaching that of gorillas and orangutans (e.g., Johanson and White, 1979; McHenry, 1991, 1992, 1994; Richmond and Jungers, 1995; Lockwood et al., 1996, 2007; Plavcan and van Schaik, 1997a; Lockwood, 1999; Silverman, 2001; Ward et al., 2001; Harmon, 2006; Spoor et al., 2007; Gordon et al., 2008). Like canine size and dimorphism, body-size dimorphism is correlated with intensity of intermale competition in living anthropoids (Clutton-Brock et al., 1977; Ford, 1994; Mitani et al., 1996; Plavcan and van Schaik, 1997b; Lindenfors and Tullberg, 1998; Plavcan, 2004), and the levels of body-size dimorphism inferred for some early hominins are

---

[1] As used here, the genus *Australopithecus* includes species that are commonly assigned to *Paranthropus*.

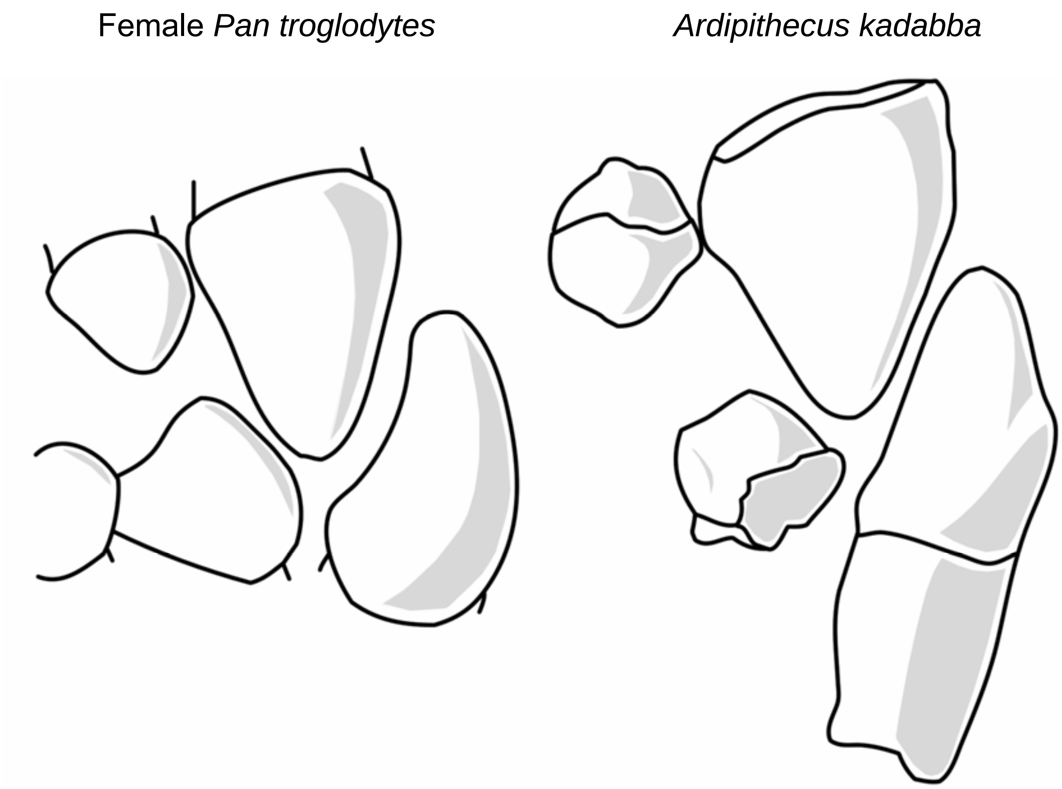


Fig. 1.1. Canines and anterior premolars of the late Miocene hominin *Ardipithecus kadabba* compared to those of a female *P. troglodytes* (redrawn from Haile-Selassie et al., 2004). Male *P. troglodytes* have maxillary canines that are approximately 50% taller than those of females (Kelley, 1995). The sex of the *Ar. kadabba* teeth is unknown, but they are the most apelike hominin specimens yet discovered. Canines from the geologically younger species *Ar. ramidus*, *Australopithecus anamensis*, and *Au. afarensis* are also similar in size to, or shorter than, those of female chimpanzees (White et al., 1994; Plavcan et al., 2009).

indicative of social systems in which males aggressively defend or compete for access to females, thus contradicting the sociobehavioral signal provided by the canines (e.g., Szalay, 1975; Leutenegger and Shell, 1987; Plavcan and van Schaik, 1997a).

The case for pronounced body-size dimorphism in early hominins is not without controversy. Reno et al. (2003, 2005, 2010; see also Lovejoy et al., 1989) presented evidence that sexual differences in skeletal size in *Australopithecus afarensis* were more moderate (i.e., humanlike) than other studies have concluded, raising the possibility that body-size dimorphism and canine size/dimorphism are not in conflict, at least for *Au. afarensis*. However, while there is evidence that early hominins were not uniform in the degree to which they were body-size-dimorphic—e.g., recent descriptions of fossil material attributed to *Ardipithecus ramidus* characterize this 4.4-million-year-old hominin as only slightly dimorphic or monomorphic in body size (Suwa et al., 2009b; White et al., 2009)—Reno et al.'s conclusions regarding *Au. afarensis* have been criticized on conceptual and methodological grounds (Plavcan et al., 2005; Scott and Stroik, 2006; Gordon et al., 2008), and other recent studies have provided support for the idea that this hominin combined short, minimally dimorphic canines with marked body-size dimorphism (Harmon, 2006; Gordon et al., 2008).

Another problem with characterizing body-size dimorphism in early hominins is that, although dimorphism in skeletal size is correlated with body-mass dimorphism, which is the presumptive target of sexual selection (e.g., Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Milton, 1985; Ford, 1994; Mitani et al., 1996; Plavcan and van Schaik, 1997b; Plavcan, 2001), they are not identical (e.g., Lague, 2003; Plavcan, 2003). Within the Hominoidea, for example, chimpanzees are more dimorphic in body mass than humans, but humans are more dimorphic in some measures of postcranial size (Richmond and Jungers, 1995; Lockwood et al., 1996; Reno et al., 2003, 2005, 2010; Plavcan et al., 2005; Gordon, 2008). Thus, it is possible that skeletal-size dimorphism in early hominins is a misleading indicator of body-size dimorphism. However, given the very high level of postcranial dimorphism suggested by most studies (e.g., Richmond and Jungers, 1995; Lockwood et al., 1996; Silverman et al., 2001; Harmon, 2006; Lockwood et al., 2007; Gordon et al., 2008), a low level of body-size dimorphism that is consistent with little or no intermale aggression is unlikely for at least some early hominins.

The combination of short, minimally dimorphic canines and pronounced body-size dimorphism documented in species of *Australopithecus* is unique among living anthropoids, making it unclear whether canine size and dimorphism or body-size dimorphism is the more reliable indicator of early hominin social behavior, thus obscuring the adaptive significance of canine size in the hominin clade. Some members of the extant Hominidae exhibit a similar pattern: *Gorilla* and *Pongo* are among the most body-size-dimorphic primates (males are over twice as large as females; Smith and Jungers, 1997) but the males of these taxa have canines that are among the shortest relative to body size in comparison to other Anthropoidea (Fig. 1.2) (Greenfield and Washburn, 1991; Plavcan, 1993a). Nevertheless, the canines of male gorillas and orangutans are still relatively much

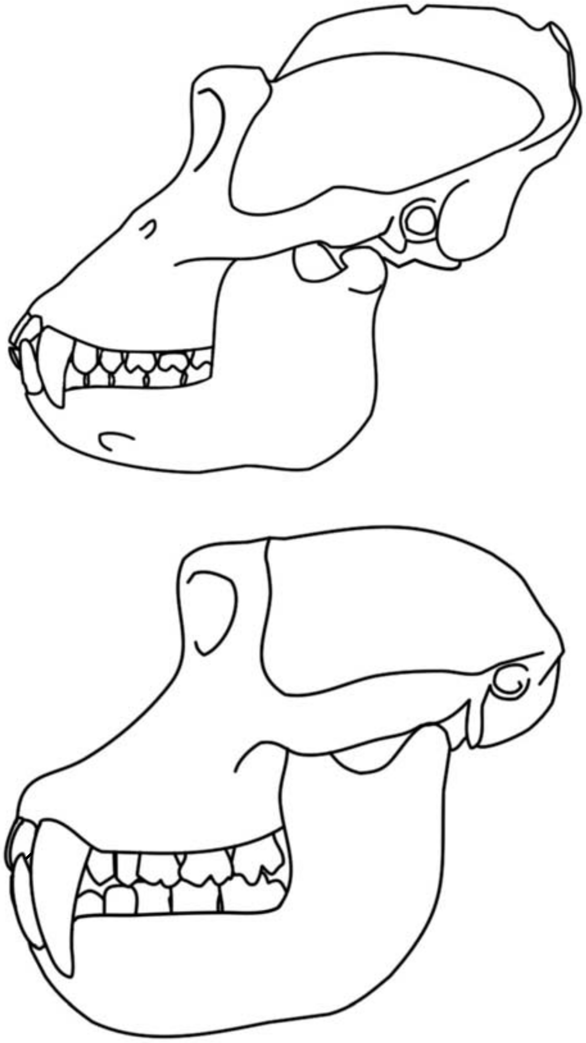


Fig. 1.2. Comparison of relative male canine size in *Gorilla gorilla* (top) and *Theropithecus gelada* (bottom). The skulls are scaled to roughly the same cranial length. These two species are usually classified as highly sexually selected (e.g., Plavcan and van Schaik, 1992; Mitani et al., 1996; Lindenfors and Tullberg, 1998), but they fall at the lower (*G. gorilla*) and upper (*T. gelada*) ends of the range of relative canine size for male anthropoid primates (Plavcan, 1993).

taller than those of early hominins (Plavcan and van Schaik, 1997a; Alba et al., 2001; Kelley, 2001), and canine size is strongly dimorphic in these two taxa (Kelley, 1995a). Notably, some extant primates exhibit the reverse of the hominin pattern. For example, most colobine monkeys possess large, highly dimorphic canines coupled with low body-size dimorphism (Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1997b; Plavcan, 2001). In these species, canine size and dimorphism appear to be more reflective of intensity of intermale competition than body-size dimorphism (Plavcan and van Schaik, 1997b).

Several authors have hypothesized that some of the variation in relative canine size and in the expression of sexual dimorphism observed in living anthropoids can be explained by the existence of factors that limit the evolution of male weaponry (e.g., Clutton-Brock et al., 1977; Clutton-Brock and Harvey, 1977; Leutenegger and Kelly, 1977; Milton, 1985; Plavcan and van Schaik, 1992, 1997b; Ford, 1994; Mitani et al., 1996; Plavcan, 2001). For example, arboreality and folivory have both been implicated as constraints on the evolution of sexual dimorphism. In the case of arboreality, body-size dimorphism may be limited because increasing male size compromises the ability of individuals to safely navigate and obtain food in small- and terminal-branch environments (Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Milton, 1985; Plavcan, 2001). With respect to folivory, Leutenegger and Kelly (1977) hypothesized that a low-quality diet limits male size in active arboreal species, and Milton (1985) argued that folivorous species may not engage in intense intermale competition because it is too energetically costly, which would eliminate selection for male weaponry (for competing predictions regarding diet and sexual dimorphism, see Ford, 1994; Mitani et al., 1996; Plavcan and van Schaik, 1997b; Plavcan, 2001).

Variation in relative canine height and in the expression of sexual dimorphism in living anthropoids also suggests that a weapon that is critical to male reproductive success in one species may not be as important for males of other species, even though the overall level of competitive intensity may be similar. Support for this idea comes from Plavcan's (2004, p. 247) observation that canine and body-size dimorphism each appear to be correlated with different measures of sexual selection (i.e., mating system, intensity of intermale competition, socionomic sex ratio, operational sex ratio), indicating complex associations among various aspects of social structure, mating system, and selection for male weaponry:

> canine and body-mass dimorphism are clearly under the influence of different selective pressures and constraints, even though there is overwhelming evidence that both are the product of sexual selection. This point is underscored by the simple observation that canine and body-mass data are only modestly correlated across species ($n = 79$, $r = 0.626$, $p < 0.001$). Rather than confounding analyses, this observation should actually provide further material for exploring hypotheses of the relationship between sexual selection and dimorphism in either trait. For example, why is the OSR [operational sex ratio] calculation strongly correlated with body-mass dimorphism, but not canine dimorphism, while the opposite is true for the SSR [socionomic sex ratio] data?

It is certainly true that male mammals compete in diverse ways using a wide variety of weapons (e.g., Darwin, 1871; Andersson 1994; Coltman et al., 2002; Kruuk et al., 2002; Robinson et al., 2006). Several authors have suggested that, within primates, strepsirrhines are not dimorphic in body or canine size because, in this group, the outcomes of intermale agonistic encounters, which can be as intense as those observed in dimorphic anthropoids, are decided by locomotor performance (e.g., speed, agility, leaping strength) rather canine and body size (Clutton-Brock and Harvey, 1977; Leutenegger and Kelly, 1977; Kappeler, 1990, 1991, 1996; Richard, 1992; Lindenfors, 2002). Lawler et al. (2005) provided support for this hypothesis, demonstrating that, in male *Propithecus verreauxi*, morphological traits associated with locomotor behavior covary with fertility, whereas body and canine size do not.

Variation in the importance of male weaponry among the Anthropoidea has not been investigated in this manner, but Plavcan (2001) speculated that one possible explanation for low body-size dimorphism in colobine monkeys is that body size does not determine the winner of intermale contests for access to mates. Similarly, the relatively short canines of *Gorilla* and *Pongo* in comparison to those of other catarrhines characterized by high-intensity intermale competition may indicate that, in the great apes, canine size is not as important as large body size for securing mating opportunities in comparison to species with relatively larger canines (e.g., *Mandrillus sphinx*; Leigh et al., 2008). In such cases, the relaxation—but not elimination—of sexual selection on a weapon would permit other selective pressures, particularly those that favor reducing the size of the weapon, to have greater influence.

With respect to early hominins, it is probably true that canine reduction occurred because the weapon function of these teeth was no longer a critical component of intrasexual competition (Plavcan and van Schaik, 1997a), but whether sexual selection on these teeth was relaxed because of decreased male aggression (Holloway, 1967; Lovejoy, 1981, 2009; Reno et al., 2003, 2005, 2010; Suwa et al., 2009b; White et al., 2009) or due to a shift in combat strategy that placed more emphasis on body size (Milton, 1985; Ward et al., 2001), thus allowing other selective regimes to reduce canine size, is difficult to resolve. The earliest hominin for which relative canine size, canine dimorphism, and body-size dimorphism can be estimated is *Ardipithecus ramidus*, which antedates the appearance of *Australopithecus* in the fossil record by 200,000 years (White et al., 2006). As noted above, this species has been characterized as only slightly dimorphic or monomorphic in body size by its describers (Suwa et al., 2009b; White et al., 2009). If this interpretation is correct, then canine reduction in the hominin lineage can be plausibly linked to a decrease in intermale competition (Suwa et al., 2009b; White et al., 2009). Under this scenario, the initial reduction of the canine would not be unusual—though it would still require a causal mechanism, given that reduced intraspecific competition does not by itself generate selection for short canines (e.g., Plavcan et al., 1995). The unusual phenomenon in this case would be the subsequent maintenance of short, minimally dimorphic canines in the more strongly body-size-dimorphic species of *Australopithecus*. However, this sequence of evolutionary events is contingent upon (1) the reliability of the estimate of body-size dimorphism for *Ar. ramidus*, which is based mainly on qualitative assessments of size variation in the sample of upper-limb bones (White et al., 2009), and (2) whether *Ar. ramidus* is representative of other pre-*Australopithecus* hominins (i.e., *Ar. kadabba*, *Orrorin* *tugenensis*, and *Sahelanthropus tchadensis*). Definitive demonstration that body-size monomorphism is primitive for the Hominini will require more fossil data.

In any event, most of the researchers who have discussed the pattern of dimorphism in *Australopithecus* have approached it from the perspective that it is the canine—not body-size dimorphism—that is sending the false sociobehavioral signal, and that canine reduction requires a nonsocial (i.e., unrelated to sexual selection) explanation (e.g., Darwin, 1871; Washburn, 1959, 1960; Brace, 1963, 1967; Jolly, 1970a; Szalay, 1975; Wolpoff, 1976; Jungers, 1978; Milton, 1985; Leutenegger and Shell, 1987; Greenfield, 1992b; Ward et al., 2001). While nonsocial factors almost certainly influence sexual differences in body size in primates (e.g., Leigh and Shea, 1995; Lindenfors, 2002; Gordon, 2006a,b), there are no plausible explanations that can account for the high levels of body-size dimorphism inferred for many Plio-Pleistocene hominins without appealing to sexual selection (Plavcan and van Schaik, 1997a; Plavcan, 2001).[2]

Notably, canine reduction is not limited to the hominin fossil record. Other extinct primates—Plio-Pleistocene *Theropithecus oswaldi* (Jolly, 1970a, 1972; Eck, 1993; Leakey, 1993; Frost and Delson, 2002; Frost and Alemseged, 2007; Frost, 2007), the Malagasy subfossil lemur *Hadropithecus stenognathus* (Jolly, 1970b; Jungers, 1978), the Eocene adapid *Adapis parisiensis* (Gingerich,

---

[2] As reviewed by Plavcan and van Schaik (1997a) and Plavcan (2001), hypotheses that account for high body-size dimorphism in early hominins by positing sexual niche differentiation or selection for reduced female body size do not receive comparative support among primates, and the idea that large male body size was maintained for predator defense rather than intermale competition does not address why large canines were not also maintained for this purpose.

1981; Greenfield, 1992b), and the late Miocene hominoid *Oreopithecus bambolii* (Alba et al., 2001)—possess canines that are unusually short in comparison to their close relatives. In the case of *T. oswaldi*, there is clear evidence of canine reduction through time during this species' approximately three-million-year duration (e.g., Frost and Delson, 2002). These species indicate that canine reduction in the human lineage was not a unique event in primate evolutionary history, suggesting that hominins are only an extreme example of the action of selective forces operating on all primates to some degree. This observation is significant because it implies that canine reduction can be studied as a primatewide phenomenon using the comparative method. In fact, while most of the hypotheses that have been proposed to explain canine reduction were developed in the context of the hominin fossil record, many of them have relied on observations from the fossil species discussed above, and others have used observations from living primates.

HYPOTHESES PROPOSED TO EXPLAIN CANINE REDUCTION

Functional replacement

Darwin (1871) was the first to offer an evolutionary explanation for the contrast between humans and other primates in canine size, arguing that hand-held weapons replaced the function of the canines, which subsequently became reduced through disuse (see also Bartholomew and Birdsell, 1953; Washburn, 1959, 1960; Washburn and Howell, 1960; Brace, 1963, 1967; DeVore, 1964; Wolpoff, 1976). Darwin (1859, 1871) observed that structures that are no longer functional tend to diminish in size, and he reasoned that such reductions might be due to a process he referred to as *economy of growth*, in which natural selection favors the diversion of metabolic resources away from vestigial structures in order to prevent energetic waste, thereby increasing an individual's fitness. Brace (1963, 1967) proposed that an alternative process, the *probable-mutation effect*, was responsible for dental reduction as hominins became more reliant on tool-use. According to this hypothesis, the elimination of selection for large teeth (including the canines) resulting from functional replacement by tools allowed for the accumulation of mutations, the inevitable consequence of which was size reduction (for critiques of the probable-mutation effect, see Prout, 1964; Bailit and Friedlaender, 1966; Holloway, 1966, 1968; Calcagno and Gibson, 1988).

Holloway (1967; see also Jolly, 1970a; Plavcan and van Schaik, 1997a) criticized the notion that tool-use by itself resulted in canine reduction in the earliest hominins, arguing that elimination of the selective value of projecting canines does not necessarily follow from the use of hand-held weapons, as daggerlike canines would still be useful in species characterized by intense agonistic interactions. The functional-replacement hypothesis may provide a plausible explanation for why sexual selection was relaxed on the canines, but it does not provide a mechanism that can account for their reduction (Greenfield, 1992b). A larger problem with this hypothesis is that it is inapplicable to other primates and therefore untestable using the comparative method (Plavcan and van Schaik, 1997a); other primates are known to use tools, but no nonhuman primate relies on them in the context of intermale competition.

Canine incisification

Szalay (1975) hypothesized that the canines of early hominins were under selection to become incorporated into the functional incisor row as an adaptation to carnivory. According to Szalay (1975), the morphological transformation of the canine into an incisorlike tooth was the primary evolutionary change, with reduction in size being a secondary outcome. Greenfield (1992b) agreed that hominin canine reduction could be explained as a consequence of selection for incisification and also emphasized the unusual form of the hominin canine rather than just its reduced projection (see also Greenfield, 1990a,c, 1992a, 1993), but he argued that Szalay's reliance on adaptation to a carnivorous diet as the cause of the change rendered the hypothesis untestable due to the absence of a suitable analogy among living primates.

In contrast, Greenfield (1992a,b, 1993) posited that most anthropoid primates experience selection for canine incisification but that this selective pressure is usually overwhelmed by sexual selection for weaponized canines. Greenfield (1992a,b, 1993) noted that, within a given anthropoid species, there usually exist three canine morphs—male, female, and deciduous—which form a gradient of increasing expression of incisorlike traits (e.g., reduced crown height, increased development of the mesial cristid). Greenfield argued that the reason for this gradient lies in the fact that individuals in a population experience different levels of selection for weaponized canines (i.e., male > female > juvenile), but selection for canine incisification operates with the same intensity on all individuals. Thus, deciduous and female canines more clearly reflect selection for incisiform canines because these individuals do not compete as intensely with conspecifics as do males, which possess canines that mainly reflect the effects of sexual selection. According to Greenfield's *dual-selection hypothesis*, once selection for weaponized canines in males is removed, selection for incisification will act quickly to transform the canine into an incisorlike tooth.

The dual-selection hypothesis relies heavily on the morphology of the mandibular canine and its occlusal relationship with the maxillary lateral incisor (Greenfield, 1992a,b, 1993, 1996, 1998). Specifically, in most anthropoids, the mesial margin of the mandibular canine (the mesial cristid) contacts the distal margin of I^2. Greenfield (1992a,b, 1993) argued that this contact is a fully functional component of the incisal edge in females and juveniles of most anthropoid species. In contrast, contact between the mandibular canine and I^2 in most male anthropoids is nonfunctional (Greenfield, 1992b, 1996). Plavcan and Kelley (1996) emphasized this point in their critique of the dual-selection hypothesis, noting that the fact that anthropoid males cannot use their mandibular canines as incisors precludes selection from altering them to do so (i.e., selection cannot modify the canine to function more effectively as an incisor if it is not already functioning as an incisor).

A larger issue with the dual-selection hypothesis concerns the maxillary canine (Plavcan and Kelley, 1996; Plavcan, 2001). In focusing on the mandibular canine and I^2, Greenfield's model fails to provide a satisfactory explanation for incisification of the maxillary canine (Plavcan and Kelly, 1996; Plavcan, 2001). Plavcan and Kelley (1996) showed that tip-to-tip contact between the maxillary and mandibular canines probably does not occur regularly in anthropoid primates, and thus there is no evidence that females or males use the maxillary tooth as an incisor. Moreover, these authors observed that there is evidence in primates that selection to incorporate the mandibular canine into the incisor row does not necessarily affect the maxillary canine—in strepsirrhines, the mandibular canine has been inarguably transformed into fully functional member of the incisor row (as part of the tooth comb), while the maxillary canine has been left unaltered (Plavcan and Kelley, 1996; Plavcan, 2001). Thus, it does not seem likely that selection for canine incisification can account for reduction in canine height.

On the other hand, Greenfield's work does highlight two important aspects of hominin canine evolution, namely that, in addition to a reduction in size, this tooth has been transformed morphologically (i.e., it is not merely a smaller version of ape canines; see also Szalay, 1975) and its functional role within the dentition, along with that of the honing mandibular premolar, has changed dramatically (e.g., Greenfield, 1990a,c; see also Morris, 1974). Plavcan and Kelley (1996) pointed out that, although the dual-selection hypothesis does not provide a satisfactory explanation for reduction in canine size, it could account for the changes in form and function that occurred subsequently. Thus, it may be that the hominin canine is the product of two selective regimes—the first reduced the canine, which allowed it to take on a new role (perhaps as a functional incisor; Greenfield, 1992b; but see Morris, 1974), and the second altered its form to better fit that new role (Ward et al., 2010).

Pleiotropy and development

The observation that many early hominins are characterized by relatively small incisors and relatively large postcanine teeth (e.g., McHenry, 1984; Kay, 1985; Ungar and Grine, 1991; Teaford and Ungar, 2000) has led a number of researchers to propose that canine reduction may be a by-product of selection operating on some other component of the dentition. Jolly (1970a) hypothesized that canine reduction might be the result of selection for small incisors. This hypothesis was presented as part of a larger model for the origin of the hominin lineage, in which Jolly (1970a) argued by analogy with extant and fossil *Theropithecus* that the fundamental hominin adaptation was to small-object feeding. Jolly observed that species that feed primarily on small objects requiring little incisal preparation tend to have smaller incisors than species with diets in which the incisors are used more intensively (see also Hylander, 1975a; Kay and Hylander, 1978; Eaglen, 1984; Ungar, 1996; for a contrary view, see Rosenberger, 1992; Anapol and Lee, 1994; McCollum, 2007), and he suggested two potential causes for this reduction: the *Oppenheimer effect* and the *somatic-budget effect*.

Oppenheimer (1964) argued that diminished use of the anterior teeth in early hominins (which he assumed had occurred because of reliance on tools) resulted in underdeveloped jaws, which led to crowding of these teeth. He reasoned that such crowding would have resulted in selection for smaller incisors and canines (Oppenheimer, 1964, 1966; see also Jolly, 1970a; Calcagno and Gibson, 1988; for critiques of this hypothesis, see Kustaloglu, 1966; Schultz, 1966). Thus, according to this idea, the canines of early hominins became reduced in size along with the incisors due to a lack of sufficient alveolar support at the anterior end of the dental arcade (Jolly, 1970a).

Jolly's (1970a) somatic-budget effect is similar to Darwin's (1859, 1871) economy of growth (see also Prout, 1964; Bailit and Friedlaender, 1966). Jolly (1970a) speculated that, as early hominins and fossil *Theropithecus* became adapted to a diet of small, hard objects, selection acted to reduce their incisors to a size more commensurate with their use in order to conserve metabolic resources, which had the pleiotropic effect of reducing the canines as well. Jolly further suggested that there might be a direct relationship between enlargement of the molars and premolars and reduction of the incisors and canines—i.e., selection might have favored reallocation of resources from the anterior teeth to the postcanine dentition. Jolly (1970b) made similar arguments regarding canine reduction in the subfossil lemur *Hadropithecus stenognathus*.

Other researchers have also posited a link between postcanine enlargement and canine reduction. Jungers (1978), building on a model of dental reduction developed by Sofaer et al. (1971; Sofaer, 1973), hypothesized that molarization of the premolars may have restricted the alveolar space available for the later-developing canine in early hominins and in *H. stenognathus*, which generated selection pressure to reduce the latter in order to maintain proper occlusion. Kieser et al. (1985, 1986) tested Sofaer et al.'s model in modern humans and found no support for the idea that early-developing teeth inhibit the development of those that develop later. However, in a later study, Kieser and Groeneveld

(1987a) found that, when the length of the dental arcade is held constant, there is an inverse relationship between the size of the anterior (incisors and canines) and posterior (molars and premolars) teeth,[3] which led them to hypothesized that the diminutive anterior teeth of *Au. boisei* and *Au. robustus* were a direct consequence of selection for enlarged postcanine teeth. More recently, McCollum and Sharpe (2001, p. 487) outlined a developmental-genetic model to account for the relationship between the postcanine megadontia and diminution of the incisors and canines within *Australopithecus*:

> The dentition of *A. boisei* suggests that expansion of the postcanine dentition may have been developmentally correlated with reduction of the canine. Such an effect might result if enlargement of the postcanine dentition was achieved by reproportioning the domains of the homeobox-containing genes expressed in the early initiation-stage oral mesenchyme. As these genes appear to partition what is essentially a spatially-restricted block of mesenchyme into smaller subunits (in a manner analogous to the partitioning of the vertebral region by *Hox* genes), it is conceivable that increasing the size of any one subunit may occur at the expense of others. In this respect, a simple "distalization" (anterior relocation) of the boundary between posterior and anterior tooth fields might result in the correlated development of large postcanine teeth and small canines and incisors.

Although these latter hypotheses do not directly address the question of why the earliest hominins had relatively smaller canines than living and fossil apes, they

---

[3] This result is at least partly related to Kieser and Groeneveld's analytical strategy, which involved computing partial correlations between mesiodistal diameters of each tooth while hold the length of the dental arcade, itself the sum of all mesiodistal diameters, constant. As pointed out by Van Valen (1962, p. 274), in this case, "a negative correlation is expected … because each measurement is included in the one being partialed out." While it is possible to identify partial correlations that are more negative than expected (Van Valen, 1962), Kieser and Groeneveld (1987) did not use this procedure, making their results difficult to interpret.

suggest that postcanine enlargement or incisor reduction played a role in canine reduction in later hominin species.

The idea that canine size is influenced by changes in other components of the dentition has been criticized. Greenfield (1992b, p. 154) rejected the hypothesis that canine reduction in early hominins was a side-effect of incisor reduction, citing the "large (not yet reduced) incisors" of *Au. afarensis*, the earliest known hominin at the time.[4] Greenfield (1992b) also took issue with the developmental-crowding hypothesis proposed by Jungers (1978), noting that the overall morphology and configuration of the antemolar teeth in *Au. afarensis* (e.g., presence of diastemata, unmolarized premolars) do not indicate that spatial constraints had an influence on canine size. This argument also applies to Jolly's (1970a) use of Oppenheimer's (1964) ideas to explain hominin canine reduction.

With respect to the hypothesis that there is a link between canine reduction and postcanine megadontia in the earliest hominins, Suwa et al.'s (2009b) recent analysis of the *Ar. ramidus* dental remains indicates that canine reduction occurred prior to the marked increase in relative postcanine size that characterizes species of *Australopithecus* (McHenry, 1984; Teaford and Ungar, 2000). Moreover, studies of intertooth correlations in humans (e.g., Moorrees and Reed,

---

[4] Greenfield (1992b) did not provide data to support this claim. Other studies that have estimated incisor size relative to body size in *Au. afarensis* indicate that the incisors of this early hominin were small in comparison to those of *Pan* and *Pongo*, but similar to those of *Gorilla* (e.g., Kay, 1985; Ungar and Grine, 1991; Teaford and Ungar, 2000). If *Pan* and *Pongo* represent the plesiomorphic condition for the Hominidae, then Greenfield's critique is invalid, though the combination of relatively small incisors and large canines in *Gorilla* presents a problem for the incisor pleiotropy hypothesis.

1964; Lombardi, 1975; Harris and Bailit, 1988; Kieser and Groeneveld, 1988) and other living hominoids (Mahler, 1973; Henderson and Greene, 1975; Wood, 1979a,b; Wood and Stack, 1980; Wolpoff, 1982) generally show that, contra Kieser and Groeneveld (1987a), canine size and postcanine size are positively correlated within species. However, while these results contradict the hypothesis that enlargement of the postcanine dentition leads to canine reduction, at least with respect to the Hominoidea, they are consistent with Alba et al.'s (2001) hypothesis that the relatively small canines of *Oreopithecus bambolii* and *Pan paniscus* are the result of an overall reduction of the dentition.

Although efforts to link the evolution of postcanine megadontia and incisor microdontia to canine reduction in the earliest hominins have been largely unsuccessful, the hypothesis that canine size is influenced by changes in other components of the dentition via pleiotropy in primates remains viable. For example, Alba et al.'s (2001) ideas are clearly inapplicable to hominins, but they may provide insight into the dental evolution of other primate lineages. Moreover, Greenfield's (1992b) critique of the hypothesis that incisor size and canine size are pleiotropically linked is specific to the initial episode of canine reduction in the hominin clade. It may apply to other primates, or to later hominin species (e.g., the robust australopiths).

Masticatory biomechanics

The idea that tall canines were selected against in early hominins because they interfered with mandibular movements during mastication (particularly lateral excursions) was suggested by Mills (1963), Brues (1966), and Jolly

(1970a). However, this hypothesis has not received support from comparative data (e.g., Kay, 1981b; Greenfield, 1990b) or experimental studies (Zanowiak, 1974; Gantt, 1979; Kay et al., 1986). More recently, Hylander and Vinyard (2006) argued that canine reduction might be explained as a consequence of selection for increasing the efficiency of bite-force production (see also Hylander, 1979).

Hylander and Vinyard's (2006; Hylander, 2009) hypothesis derives from their observation that catarrhine species with relatively tall canines are capable of wider gapes than those with relatively short canines. This relationship also holds at the intraspecific level, with sexual dimorphism in gape tracking sexual dimorphism in canine height (Hylander and Vinyard, 2006; Hylander, 2009). Hylander and Vinyard noted that changes to the configuration of the masticatory system that facilitate wide gapes have a negative effect on the efficiency of bite-force production: wider gapes can be achieved by (1) pushing the canines anteriorly, away from the temporomandibular joint (TMJ), which increases their vertical separation at a given degree of mandibular depression, and (2) moving the attachment sites for the masticatory muscles posteriorly, closer to the TMJ, thus reducing the extent to which the muscles must be stretched during jaw opening. However, in addition to increasing gape, these changes shorten the moment arms of the masticatory muscles relative to the bite-point moment arms, reducing their leverage (Hylander and Vinyard, 2006). Consequently, more effort is required to generate a given magnitude of bite force. On the other hand, moving the dentition posteriorly and/or positioning the masticatory muscles anteriorly increases muscle leverage—and the efficiency of bite-force production—but decreases gape potential. Thus, according to Hylander and Vinyard's (2006) hypothesis, when natural selection for increased masticatory efficiency is stronger than sexual selection for tall canines, gape potential will decrease, which will lead to a reduction in the height of the canines so that they can continue to function effectively as weapons (i.e., maintain adequate separation for display and biting).

Differences in skull form that have been linked to variation in requirements for masticatory-force production and gape have been studied in a wide variety of mammalian groups, including herbivores and carnivores (e.g., Arendsen de Wolff-Exalto, 1951a,b; Maynard Smith and Savage, 1959; Davis, 1964; Du Brul, 1974, 1977), suids and tayassuids (e.g., Herring, 1972), extant and saber-toothed carnivorans (e.g., Emerson and Radinsky, 1980; Bryant and Russell, 1995; Christiansen, 2006), and tree sloths (Naples, 1982). These studies generally show that there is a negative association between masticatory efficiency and canine height (or height of caninelike teeth in the case of the sloths). With respect to primates, the most comprehensive analysis of skull form, gape, and canine height is Smith's (1984a) study of female anthropoids. Although Smith (1984a) did not detect a relationship between the configuration of the masticatory system and canine height, other studies indicate that one exists.

Lucas (1981; Lucas et al., 1986) found that, among anthropoids, there is a relationship between mandibular shape and the angle of jaw opening at which the maxillary and mandibular canines clear each other (i.e., the canine-clearance angle). Specifically, taxa with high canine-clearance angles have condyles located close to the occlusal plane (i.e., short mandibular rami). This configuration is favorable for achieving wide gapes (e.g., Herring, 1972, 1975; Herring and Herring, 1974), but it can also reduce the mechanical advantage of the masticatory muscles (e.g., Maynard Smith and Savage, 1959; Du Brul, 1974, 1977; Spencer, 1995). In an analysis of the cercopithecoid face, Ravosa (1990) found that colobines have relatively shorter canines and greater muscle leverage than cercopithecines. Similarly, Spencer (1995) noted that the skull configurations of *Macaca*, *Theropithecus*, and *Papio* form a gradient in which muscle leverage decreases in conjunction with increased expression of features thought to facilitate wider gapes (see also Jablonski, 1993). Most recently, Vinyard et al. (2003) showed that the skull morphology of exudate-feeding callitrichines, cheirogaleids, and galagids that gouge trees with their mandibular incisors and canines to obtain gum and sap differs from that of closely related, non-tree-gouging species in ways that indicate the use of relatively wide gapes in the former.

The latter studies contradict Smith's (1984a) conclusions and suggest that selection pressure for increased gape (e.g., to accommodate increased canine height) results in predictable changes to the primate masticatory system that should have a negative impact of masticatory efficiency, as hypothesized by Hylander and Vinyard (2006). One reason for these conflicting results may be that Smith focused exclusively on female anthropoids, whereas the other studies included males. In fact, Lucas (1981; Lucas et al., 1986) noted that mandibular shape is not correlated with canine-clearance angle in females, as it is males. In any event, the hypothesis that canine reduction is related to selection for increased masticatory efficiency clearly warrants further consideration, especially given that the cranial and mandibular remains of early hominins, *Theropithecus oswaldi*, and *Hadropithecus stenognathus* suggest that these taxa possessed adaptations for processing mechanically demanding diets, including increased muscle leverage relative to closely related species (e.g., Jolly, 1970a,b; Du Brul, 1977; Rak, 1983, 1985; Jablonski, 1993; Kimbel et al., 2004).

RESEARCH OBJECTIVES

The goal of this dissertation research was to evaluate the pleiotropy and masticatory-efficiency hypotheses in living anthropoid primates. These hypotheses were tested using the comparative method, effectively treating the Anthropoidea as a natural experiment for examining the effects of different elements of the masticatory system—the incisors, postcanine teeth, and jaw adductors—on canine size. Despite the limitations of the comparative method for inferring the evolutionary mechanisms responsible for observed correlations between traits or between a trait and an environment (e.g., Cracraft, 1981; Lauder et al., 1993; Frumhoff and Reeve, 1994; Leroi et al., 1994), this approach still represents a powerful and necessary tool for evaluating evolutionary hypotheses (e.g., Kay and Cartmill, 1977; Harvey and Pagel, 1991; Doughty, 1996; Ross et al., 2002), particularly with respect to primates, which, for a variety of reasons, are not amenable to conventional experimental methods.

Although this study was primarily motivated by the problem of canine reduction in the hominin lineage, it is important to note that the focus of the research is on the nonsocial factors that influence canine size in the Anthropoidea generally. The main objective was to contribute to a more complete understanding of the factors that influence canine size and dimorphism in living primates. The results of this study are not intended to produce an explanation for canine reduction in the hominin clade; rather, they should be viewed as another piece in the puzzle. Ultimately, understanding why the weapon function of the canines of early hominins (and other fossil primates) was de-emphasized, permitting the reduction of these teeth, will rely on various lines of evidence, including detailed descriptions of intermale combat tactics in living primates, accurate reconstructions of the diets of fossil species, and a fossil record that is sufficiently complete to determine the timing of evolutionary changes in tooth size, skull form, and sexual dimorphism. In this context, what this study aims to provide is a mechanism (or mechanisms) for canine reduction that can be evaluated using fossil data. Importantly, the pleiotropy and masticatory-efficiency hypotheses both make predictions regarding fossilizable anatomy.

The pleiotropy hypothesis can be divided into three separate hypotheses. The *incisor pleiotropy hypothesis* (Jolly, 1970a) predicts a positive correlation between incisor size and canine size within species, and between relative canine size and relative incisor size among species. The *negative postcanine pleiotropy hypothesis*, the more commonly discussed version of the hypothesis linking canine size to postcanine size (e.g., Jolly, 1970a; Kieser and Groeneveld, 1987a; McCollum and Sharpe, 2001), predicts a negative correlation between canine size and postcanine size within species, and between relative canine size and relative postcanine size among species. The *positive postcanine pleiotropy hypothesis*, discussed by Alba et al. (2001) in the context of canine reduction in *Oreopithecus bambolii*, predicts a positive correlation between canine size and postcanine size within species, and between relative canine size and relative postcanine size among species.

With respect to the masticatory-efficiency hypothesis, the basic prediction is that there will be an inverse relationship between relative canine height and the leverage of the masticatory muscles across species (Hylander and Vinyard, 2006). This hypothesis further predicts that some species will possess relatively large masticatory muscles (i.e., greater physiological cross-sectional areas) in order to compensate for reduced muscle leverage associated with tall canines. Hylander and Vinyard (2006) also outlined predictions regarding internal muscle architecture, noting that gape can be increased by lengthening muscle fibers, whereas the potential for force production can be increased by shortening muscle fibers (see also Taylor and Vinyard, 2004, 2008, 2009; Eng et al., 2009 Taylor et al., 2009). Unfortunately, the broad comparative approach adopted for this dissertation renders an examination of muscle anatomy (other than estimates of overall size based on skeletal attachment sites) unfeasible. Moreover, such data will never be available for fossil taxa, and thus evaluating whether the masticatory-efficiency hypothesis is applicable to instances of canine reduction in the fossil record will necessarily rely on skeletal evidence.

CHAPTER 2—MATERIALS AND METHODS

There are two primary analytical components to this dissertation: the first tests the pleiotropy hypotheses and the second tests the masticatory-efficiency hypothesis. The goal of this chapter is to describe the samples and primary data, as well as the basic methods common to both analyses. Additional procedures specific to each analysis are discussed in subsequent chapters.

It is important to note that the two hypotheses are not mutually exclusive and both could receive support. Such an outcome would raise the possibility that the relationships among the explanatory variables (i.e., muscle leverage, incisor size, and postcanine size) could produce a spurious correlation between one of them and the dependent variable (i.e., canine size). For example, it may be that there is a causal connection between canine size and postcanine size, but selection for postcanine megadontia is associated with selection for increased jaw-muscle leverage, resulting in a noncausal (spurious) correlation between canine size and muscle leverage. If neither hypothesis is rejected, a third analytical component will be added to explore the intercorrelations among the independent variables and determine their effect on the results of the pleiotropy and masticatory-efficiency analyses.

SAMPLES AND TAXA

The thirty anthropoid species listed in Table 2.1 form the basis of this dissertation. The specimens representing these taxa are housed at the following museums in the United States and Europe: the Smithsonian Institution, Washington, D.C.; the American Museum of Natural History, New York, N.Y.;

TABLE 2.1. Species included in this study and sample sizes

		Skull morphometrics		Canine height[a]	
	Suprageneric taxonomy	M	F	M	F
PLATYRRHINI					
Alouatta seniculus	Atelidae, Alouattinae	15	15	17	15
Ateles geoffroyi	Atelidae, Atelinae	14	15	21	15
Cebus libidinosus	Cebidae, Cebinae	14	13	14	15
Cebus capucinus	Cebidae, Cebinae	14	13	17	15
Chiropotes satanas	Pitheciidae, Pitheciinae	14	10	13	9
Pithecia monachus	Pitheciidae, Pitheciinae	14	12	19	13
CATARRHINI					
Cercopithecus pogonias	Cercopithecinae, Cercopithecini	15	12	15	13
Cercopithecus wolfi	Cercopithecinae, Cercopithecini	15	15	24	17
Chlorocebus pygerythrus	Cercopithecinae, Cercopithecini	14	12	15	13
Erythrocebus patas	Cercopithecinae, Cercopithecini	18	12	14	13
Macaca mulatta	Cercopithecinae, Papionini	17	19	14	12
Macaca fascicularis	Cercopithecinae, Papionini	22	15	12	16
Theropithecus gelada	Cercopithecinae, Papionini	9	2	13	5
Mandrillus leucophaeus	Cercopithecinae, Papionini	17	15	18	11
Piliocolobus foai	Colobinae, Colobini	14	15	13	10
Procolobus verus	Colobinae, Colobini	15	15	16	14
Colobus satanas	Colobinae, Colobini	15	15	12	18
Colobus polykomos	Colobinae, Colobini	15	15	19	15
Presbytis chrysomelas	Colobinae, Presbytini	13	12	15	10
Presbytis potenziani	Colobinae, Presbytini	12	11	8	10
Trachypithecus obscurus	Colobinae, Presbytini	15	15	14	14
Trachypithecus shortridgei	Colobinae, Presbytini	16	8	15	6
Hylobates lar	Hylobatidae	15	16	14	14
Hylobates syndactylus	Hylobatidae	14	14	17	13
Gorilla beringei	Hominidae, Homininae	9	5	6	3
Gorilla gorilla	Hominidae, Homininae	15	12	19	13
Pan paniscus	Hominidae, Homininae	10	17	7	10
Pan troglodytes	Hominidae, Homininae	14	15	14	11
Pongo abelii	Hominidae, Ponginae	11	9	4	5
Pongo pygmaeus	Hominidae, Ponginae	16	15	18	23
Total		431	389	437	371

(continued)

TABLE 2.1. (Continued)

	Maxillary MD and LL/BL dimensions[b]					
	Incisors		Canine		Postcanine row	
	M	F	M	F	M	F
PLATYRRHINI						
Alouatta seniculus	16	18	20	18	20	13
Ateles geoffroyi	14	18	14	18	11	11
Cebus libidinosus	10	17	13	17	13	14
Cebus capucinus	23	22	23	23	23	23
Chiropotes satanas	11	17	11	17	11	15
Pithecia monachus	19	15	19	15	19	15
CATARRHINI						
Cercopithecus pogonias	15	16	19	16	19	16
Cercopithecus wolfi	16	11	19	14	19	14
Chlorocebus pygerythrus	7	10	7	13	7	13
Erythrocebus patas	23	8	23	8	22	5
Macaca mulatta	19	18	22	26	22	26
Macaca fascicularis	9	13	11	15	11	15
Theropithecus gelada	19	6	20	6	20	5
Mandrillus leucophaeus	16	14	21	16	21	16
Piliocolobus foai	20	18	20	18	19	12
Procolobus verus	23	22	24	22	24	20
Colobus satanas	19	22	19	23	19	23
Colobus polykomos	25	24	25	25	25	25
Presbytis chrysomelas	12	14	15	15	15	15
Presbytis potenziani	8	8	13	8	13	8
Trachypithecus obscurus	16	23	16	26	16	26
Trachypithecus shortridgei	6	6	7	6	7	6
Hylobates lar	19	16	19	18	18	18
Hylobates syndactylus	16	16	16	16	11	16
Gorilla beringei	10	4	11	5	11	5
Gorilla gorilla	11	11	13	19	13	19
Pan paniscus	10	8	14	11	14	11
Pan troglodytes	13	24	13	24	13	24
Pongo abelii	5	6	5	9	5	9
Pongo pygmaeus	17	19	19	19	19	18
Total	447	444	491	486	480	456

(continued)

TABLE 2.1. (Continued)

	Mandibular MD and LL/BL dimensions[b]					
	Incisors		Canine		Postcanine row	
	M	F	M	F	M	F
PLATYRRHINI						
Alouatta seniculus	15	16	21	16	21	13
Ateles geoffroyi	18	20	18	20	7	11
Cebus libidinosus	15	21	17	21	17	18
Cebus capucinus	25	21	25	21	24	21
Chiropotes satanas	12	17	12	17	11	16
Pithecia monachus	19	16	19	16	19	16
CATARRHINI						
Cercopithecus pogonias	18	16	19	16	19	16
Cercopithecus wolfi	14	12	19	14	19	14
Chlorocebus pygerythrus	8	11	8	13	8	13
Erythrocebus patas	24	8	24	8	18	7
Macaca mulatta	19	20	21	22	21	22
Macaca fascicularis	10	14	11	15	11	15
Theropithecus gelada	18	4	20	5	20	5
Mandrillus leucophaeus	17	17	20	17	20	15
Piliocolobus foai	22	18	23	18	23	18
Procolobus verus	21	20	22	21	22	21
Colobus satanas	20	21	20	22	20	22
Colobus polykomos	25	24	25	25	25	25
Presbytis chrysomelas	12	13	16	15	16	15
Presbytis potenziani	10	8	11	9	11	9
Trachypithecus obscurus	15	21	17	23	17	23
Trachypithecus shortridgei	7	6	7	6	7	6
Hylobates lar	19	18	19	18	17	15
Hylobates syndactylus	20	20	20	20	13	10
Gorilla beringei	8	3	9	6	9	6
Gorilla gorilla	12	14	14	19	14	19
Pan paniscus	8	10	12	10	12	8
Pan troglodytes	13	23	13	24	13	24
Pongo abelii	6	7	6	7	5	7
Pongo pygmaeus	17	20	18	20	18	20
Total	467	459	506	484	477	450

[a] Includes maxillary and mandibular canines for each individual. Data for great apes were provided by Jay Kelley (see Kelley, 1995a).

[b] Mesiodistal (MD), labiolingual (LL), and buccolingual (BL) dimensions for most species are from Plavcan (1990). The exceptions are *P. monachus*, *G. beringei*, and *P. abelii*.

the Field Museum, Chicago, Ill.; the Harvard Museum of Comparative Zoology, Cambridge, Mass.; the Powell-Cotton Museum, Birchington, United Kingdom; the Natural History Museum, London, United Kingdom; the Royal Museum of Central Africa, Tervuren, Belgium; the Anthropological Institute, Zurich, Switzerland; and Naturalis, Leiden, the Netherlands. Only fully adult skulls, as indicated by complete eruption of the canines and third molars, were measured. No zoo animals were included in this study.

The alpha taxonomy employed here follows that of Groves (2001), who elevated many taxa previously recognized as subspecies to the species level. Some of the more notable changes involving well-known species are listed here for clarity: *Cebus libidinosus*, formerly a subspecies of *Cebus apella*; *Chlorocebus pygerythrus*, formerly a subspecies of *Chlorocebus* (or *Cercopithecus*) *aethiops*; *Piliocolobus foai*, formerly a subspecies *Piliocolobus* (or *Procolobus*) *badius*; *Gorilla beringei*, formerly a subspecies of *Gorilla gorilla*; and *Pongo abelii*, formerly a subspecies of *Pongo pygmaeus*. Although some of these taxonomic assignments may be controversial, they were used to emphasize the fact that most of the samples come from geographically restricted ranges, thus mitigating the potentially confounding effects of mixing morphologically differentiated conspecific populations (e.g., Albrecht and Miller, 1993). However, in some cases (*Erythrocebus patas*, *Macaca mulatta*) this criterion could not be met due to the availability of specimens in museum collections. In these instances, it was decided that the benefit (increased sample size) of using specimens from disparate geographic regions or multiple subspecies outweighed the cost (mainly increasing size variation).

The decision to narrow the focus of this dissertation to these thirty species was made for two reasons. First, the phylogenetic comparative methods used here rely primarily on differences between mean values for closely related species; thus, obtaining accurate and precise estimates of these means was imperative (Purvis and Webster, 1999; Gordon, 2006b). This requirement made it necessary to sacrifice taxonomic sampling for data quality. In total, data were gathered for n = 808 to 990 specimens, depending on the variable (see Table 2.1), with mean sample sizes for the individual variables ranging from n = 14.4 to 16.9 for males and n = 12.4 to 16.2 for females. Eighty-four percent of the single-sex samples contained ten or more individuals, whereas only 4% of the samples contained five or fewer specimens (mainly female *Theropithecus gelada* and *Gorilla beringei*, and male and female *Pongo abelii*).

The second reason for focusing on these thirty species is that they broadly represent the range of variation in relative canine height among the Anthropoidea.[1] The only major anthropoid clade not included in the study is the Callitrichinae. Species of this subfamily present certain difficulties for this analysis. First, there appears to be very little variation in relative canine height

---

[1] Prior to conducting this study, estimates of relative canine height for 70 anthropoid species were computed using canine and mandibular measurements provided by J.M. Plavcan (see Plavcan, 1990, 2002, 2003). These data were used to select species.

within this clade.[2] Moreover, as noted in Chapter 1, recent studies suggest that tree-gouging callitrichines are capable of and regularly use wider gapes than callitrichines that do not gouge trees (Vinyard et al., 2001, 2003; Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009). These observations indicate that differences in relative canine size are not associated with differences in gape capability within this subfamily.

Nevertheless, the masticatory-efficiency hypothesis predicts that gougers should be relatively inefficient in terms of producing bite force because of their apparent emphasis on relatively wide gapes. With respect to muscle leverage, Vinyard et al.'s (2003) analysis of skull form in the marmoset *Callithrix jacchus* (a tree-gouger) and the tamarins *Leontopithecus rosalia* and *Saguinus fuscicollis* (nongougers) does not indicate a consistent difference between gougers and nongougers in this feature.[3] However, the masticatory muscles of marmosets are longer-fibered and have smaller physiological cross-sectional areas in comparison to those of tamarins (Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009). These architectural features permit wider gapes, but they reduce the

---

[2] Callitrichines are commonly divided into *short-tusked* (i.e., canines and incisors similar in height) and *long-tusked* (i.e., canines taller than incisors) species in the literature (e.g., Napier and Napier, 1967), but it is unclear whether this distinction represents differences in canine height, incisor height, or both (see Coimbra-Filho and Mittermeier, 1976, 1977; Rosenberger, 1977, 1978; Rosenberger et al., 1990). The data discussed in the previous footnote suggest that short-tusked and long-tusked species generally do not differ in relative canine height, but only five species were examined.

[3] Vinyard et al. (2003) did find that marmosets exhibit a number of skull features that reduce the extent to which their masseter muscle must be stretched at a given degree of mandibular depression (e.g., low mandibular condyles, anteroposteriorly long mandibles).

capacity for force production (e.g., Lieber, 2002). Thus, although the Callitrichinae may be uninformative with respect to the question of whether there is an association between canine size and masticatory efficiency in anthropoids, they do provide support for the idea that there is a trade-off between gape and bite-force generation, at least with respect to muscular anatomy (Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009).

Another problem with including callitrichines in this study is their unusual dental formula: all species, except *Callimico goeldii*, lack third molars, which confounds comparisons of relative postcanine size with other species. Differences in dental formula are also pertinent to the taxa included in this dissertation. Platyrrhines and catarrhines differ in premolar number, with the former possessing three and the latter possessing two. However, while the postcanine tooth rows of callitrichines are relatively short in comparison to all other anthropoids, noncallitrichine platyrrhines and catarrhines do not differ consistently from each in postcanine length, despite the difference in tooth number. In fact, some catarrhines have relatively longer postcanine rows than noncallitrichine platyrrhines (see Fig. 5:8 in Spencer, 1995, p. 290). This issue is discussed further in Chapter 3 with respect to size-adjustment and tooth-size scaling in the Anthropoidea.

MEASUREMENTS

The data used for this study include linear dimensions of the skull and teeth. These data derive from three sources: skull measurements for all species and the heights of the maxillary and mandibular canine crowns for platyrrhines, cercopithecoids, and hylobatids were collected for this study; canine heights for great apes were provided by J. Kelley (see Kelley, 1995a); and mesiodistal, labiolingual, and buccolingual dimensions of the maxillary and mandibular teeth for most of the species were taken from Plavcan (1990). In most cases, the data from the three sources were collected on specimens from the same museum collections; often, the same specimens were measured, depending on preservation. However, it is important to note that the cranial and dental data sets are not identical in terms of specimen composition, though they are identical in terms of the geographic origin.

Skull morphometrics

Skull data were collected primarily using an Immersion MicroScribe G2 three-dimensional digitizing system. Additional measurements used to estimate muscle "size" were taken with Mitutoyo Digimatic calipers. Skull digitization proceeded as follows. The cranium and mandible of each specimen were articulated (with maxillary and mandibular teeth in centric occlusion) and mounted on modeling clay. A set of 23 three-dimensional landmarks was then recorded using the MicroScribe and a laptop. The points are listed in Table 2.2 and illustrated in Figure 2.1. Several of these landmarks are standard craniometric points (e.g., White, 1991). Nonstandard points include the tips of the mesiobuccal cusps of each maxillary molar tooth (M^1, M^2, and M^3), the tip of the buccal cusp of the anteriormost maxillary premolar (P^2 in platyrrhines; P^3 in catarrhines), the tip of the maxillary canine, and the approximate centers of the superficial masseter's origin and insertion sites. Additionally, a midline point

TABLE 2.2. *List of skull landmarks*

Landmark[a]		Description[b]
1a,b	Bilateral	*Condylion laterale*—lateralmost point on the mandibular condyle
2a,b	Bilateral	*Auriculare*—point on the suprameatal crest of the temporal bone directly above the center of the external auditory meatus
3	Midline	*Opisthocranion*—posteriormost point on the midline of the neurocranium, instrumentally defined
4	Midline	Midline point on the frontal bone at the level of the superior orbital rim (interorbital superior)
5a,b	Bilateral	*Ectoconchion*—lateralmost point on the orbital rim
6	Unilateral	*Coronion*—tip of the coronoid process of the mandible
7	Unilateral	Approximate center of the superficial masseter's origin site on the zygomatic arch, typically half the distance from the masseteric tubercle to the posterior end of the zygomaticotemporal suture
8	Unilateral	Approximate center of the superficial masseter's insertion site, typically a third of the distance from the inferior margin of the mandible to the superior border of the ramus, centered between the posterior and anterior borders of the ramus; the ridge for the deep masseter tendon was used to define the superior border in species that possessed this feature (see Antón, 1996b, 1999)
9a,b	Bilateral	Maxillary M3 bite point, taken at the tip of the mesiobuccal cusp
10a,b	Bilateral	Maxillary M2 bite point, taken at the tip of the mesiobuccal cusp
11a,b	Bilateral	Maxillary M1 bite point, taken at the tip of the mesiobuccal cusp
12a,b	Bilateral	Anteriormost maxillary premolar bite point (P^3 in catarrhines, P^2 in platyrrhines), taken at the tip of the buccal cusp
13a,b	Bilateral	Canine bite point, taken at the tip of the cusp
14	Midline	*Prosthion*—anteroinferiormost point on the maxilla
15	Midline	*Infradentale*—tip of the septum separating the mandibular central incisors

[a] Landmark numbers refer to Figure 2.1. Bilateral points were taken on each side of the cranium (a = right side; b = left side); unilateral points were taken on left or right side, depending on specimen preservation.

[b] Craniometric points (in italics) follow the definitions given in White (1991).

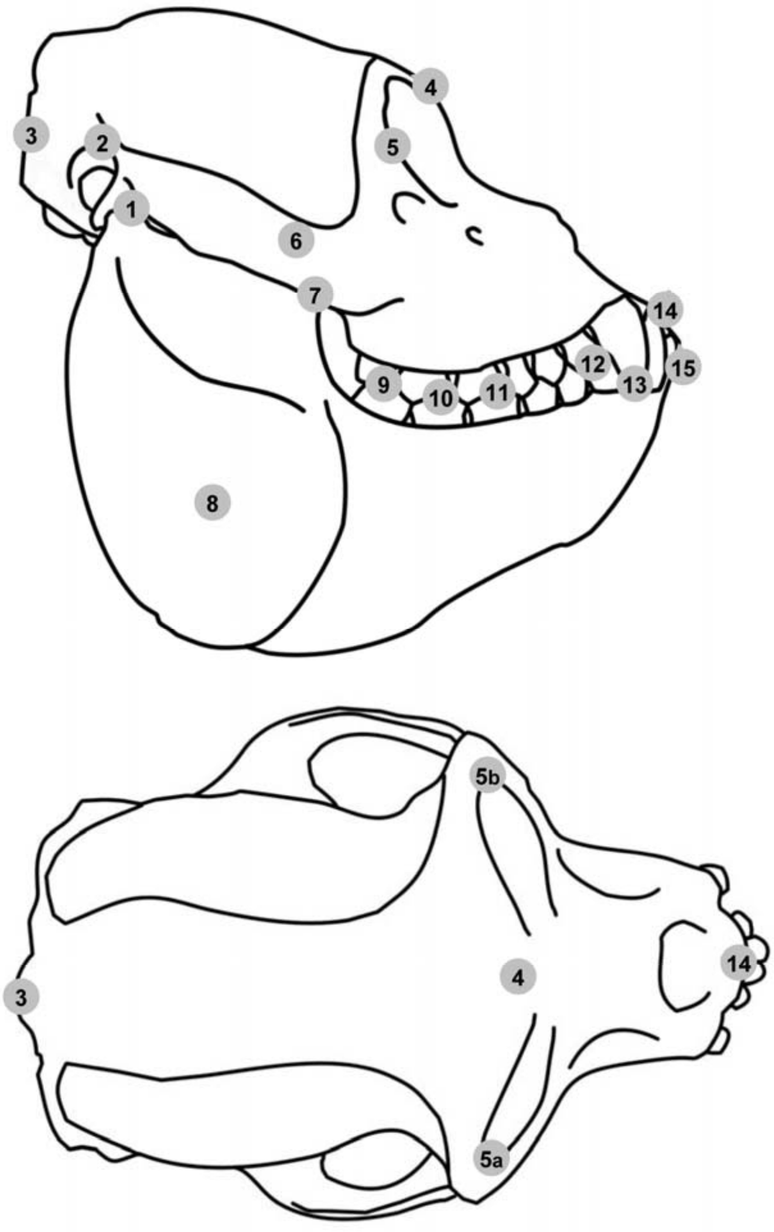


Fig. 2.1. Landmarks used in this study. The upper image shows the right-side and midline landmarks; landmark 6 is the tip of the mandibular coronoid process, which is hidden by the zygomatic arch. The lower image shows the midline landmarks and the bilateral landmarks that can be seen in dorsal view; landmarks 5a and 5b refer to right and left ectoconchion, respectively. See Table 2.2 for descriptions of landmarks.

located between the orbits at the level of the superior orbital rims was collected. This point, referred to as *interorbital superior*, was used in place of nasion (the point at which the two nasal bones and the frontal bone meet) to represent this region of the skull because the latter point is variable in position and often obliterated in adult specimens (Kimbel et al., 1984). Interorbital superior was preferred over glabella (anteriormost midline point on the frontal bone) and sellion (posteriormost point in the midline of the facial profile) because these latter points are difficult to define in airorhynch species (e.g., *Alouatta seniculus*; see Fig. 2.1).

Linear and angular measurements were derived from these landmark data using the MacMorph data-acquisition package (Spencer and Spencer, 1993). These measurements can be divided into three sets: muscle and bite-point moment-arm lengths, other features of the skull related to gape, and linear measurements used to compute a geometric mean for size-adjustment. These variables are discussed in greater detail below, followed by an analysis of measurement error.

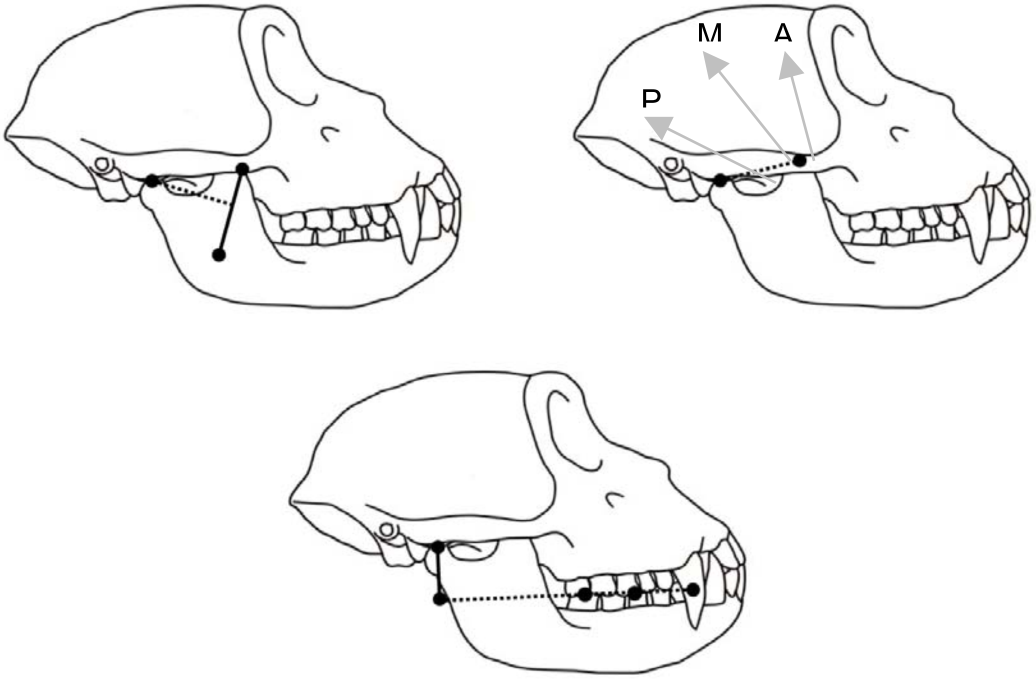
Moment-arm lengths

Estimates of moment-arm lengths for the superficial masseter, anterior temporalis, and three bite points—canine, M1, and M3—were used to quantify muscle leverage. The medial pterygoid was not examined because its origin and insertion sites were inaccessible when the articulated skulls were mounted for digitizing. Muscle leverage was computed as the ratio of muscle moment-arm length to bite-point moment-arm length. Species with higher ratios (i.e., relatively longer muscle moment arms) have greater muscle leverage and can therefore produce similar magnitudes of bite force with less effort in comparison to species with lower ratios, all other things being equal.

Different researchers have estimated masseter and temporalis moment-arm lengths using bony anatomy in a variety of ways (e.g., Carlson, 1977; Hylander, 1977; Demes and Creel, 1988; Ravosa, 1988, 1990, 1992, 1996; Dechow and Carlson, 1990; Cole, 1992; Jablonski, 1993; Spencer and Demes, 1993; Anapol and Lee, 1994; Spencer, 1995; Antón, 1996a; Taylor, 2002; Vinyard et al., 2003; O'Connor et al., 2005; Wright, 2005; Koyabu and Endo, 2009). With respect to the superficial masseter, perhaps the most common estimate of moment-arm length is the distance from a landmark representing the TMJ (the mandibular condyle, postglenoid process, or articular eminence) to one representing the anteriormost extent of this muscle's origin, usually the masseteric tubercle or the inferior border of the zygomaticomaxillary suture (e.g., Ravosa, 1988, 1990, 1992, 1996; Spencer and Demes, 1993; Antón, 1996a; Taylor, 2002; Wright, 2005; Koyabu and Endo, 2009). However, this measurement is problematic because it does not account for the fact that the superficial masseter's line of action runs anterosuperiorly from the muscle's insertion on the mandibular ramus to its origin on the zygomatic. Because of this configuration, the height of the ramus influences the length of the superficial masseter's moment arm such that, if all other factors are held constant, species with relatively tall rami will have longer superficial masseter moment arms than species with relatively short rami (e.g., Maynard Smith and Savage, 1959; Du Brul, 1974, 1977, Ward and Molnar, 1980; Rak and Hylander, 2008). In other words, identical values for the distance between the TMJ and the anterior origin of the superficial masseter do not necessarily reflect identical superficial masseter moment-arm lengths.

Another measurement that has been used to estimate the superficial masseter's moment-arm length is the orthogonal distance from the TMJ to a line connecting the centers of the muscle's origin and insertion sites, usually determined with the aid of the bony ridges and roughened areas left by the muscle's tendons (Carlson, 1977; Anapol and Lee, 1994; Spencer, 1995; O'Connor et al., 2005). This measurement probably represents the closest approximation to the true length of the superficial masseter's moment arm that can be obtained from bony anatomy, and thus it was used for this study. Nevertheless, given the complexity of internal muscle architecture and intramuscular recruitment patterns, this measurement should be regarded as a rough estimate (Spencer, 1995). The following procedure was used to derive the superficial masseter's moment-arm length from the landmark data using MacMorph: first, landmarks 1a (right condylion laterale), 7, and 8 (the superficial masseter's origin and insertion, respectively) were projected onto the sagittal plane, as defined by landmarks 3 (opisthocranion), 4 (interorbital superior), and 14 (prosthion); next, landmarks 7 and 8 were connected with a line; finally, the orthogonal distance from this line to landmark 1 was computed (Fig. 2.2, top left; refer to Table 2.2 and Fig. 2.1 for landmark definitions).

The temporalis is a fan-shaped muscle originating on the lateral wall of the neurocranium and converging onto the coronoid process of the mandible. This



2.2. Illustration of muscle and bite-point moment-arm lengths (black dotted lines). **Top row:** the superficial masseter's moment arm (left) is the orthogonal distance from the mandibular condyle to a line connecting the centers of the muscle's attachment sites; the anterior temporalis's moment arm (right) is the distance from the mandibular condyle to the coronoid process. The gray arrows indicate the approximate lines of action of the posterior (P), middle (M), and anterior (A) fibers of the temporalis. **Bottom row:** each bite-point moment arm (canine, M1, M3) is the distance from the bite point to the mandibular condyle, projected into the occlusal plane.

configuration results in marked variation in the orientation of its muscle fibers. The fibers directly posterior to the orbit are oriented approximately orthogonally to the occlusal plane and primarily have a vertical line of action. Moving posteriorly, the fibers become increasingly obliquely oriented (Fig. 2.2, top right). Thus, based on these distinctions in fiber orientation, the temporalis is frequently separated into two or three functional units for analysis—the anterior temporalis and the posterior temporalis, and in some cases, the middle temporalis (e.g., Cachel, 1979; Van Eijden, 1990; Van Eijden et al., 1990; Ross, 1995a; Spencer, 1995, 1998, 1999; Lieberman and Crompton, 2000; Ross and Hylander, 2000; Hylander et al., 2005; Vinyard et al., 2005; Taylor and Vinyard, 2008; Wall et al., 2008; Taylor et al., 2009).

Electromyographic studies confirm that the temporalis is functionally differentiated (Blanksma and Van Eijden, 1990; Van Eijden, 1990; Van Eijden et al., 1990; Ross and Hylander, 2000; Hylander et al., 2005; Wall et al., 2008). These studies show that the anterior temporalis is a major participant in the generation of bite forces oriented in most directions, but it is particularly active during the production of vertically directed forces. The latter direction is considered the most biomechanically relevant for analyses of the masticatory system because maximum bite forces are directed approximately perpendicularly relative to the occlusal plane (Van Eijden et al., 1988, 1990; Van Eijden, 1991; but see Hylander, 1978). In contrast, the posterior temporalis is mainly involved in generating posteriorly directed forces, though it is also active at other times (Van Eijden, 1990; Van Eijden et al., 1990). For these reasons, as well as the fact that it has the longest moment arm of any component of the temporalis, making it the most restrictive in terms of gape, only the anterior temporalis's moment arm was measured for this study.

Ideally, information regarding the origin of the anterior temporalis should be incorporated into a measure of this muscle's moment arm so that its line of action can be estimated. However, this is rarely done (e.g., Demes and Creel, 1988; Ravosa, 1988, 1990, 1992, 1996; Dechow and Carlson, 1990; Jablonski, 1993; Spencer and Demes, 1993; Anapol and Lee, 1994; Antón, 1996a; Taylor, 2002; Wright, 2005; Koyabu and Endo, 2009), mainly due to the difficulty in identifying a landmark to represent the origin of any part of the temporalis. A few studies have attempted to do so (e.g., Dechow and Carlson, 1990; Spencer, 1995; O'Connor et al., 2005; Ritzman and Spencer, 2009), but only Spencer (1995) developed criteria for locating the center of anterior temporalis. He used the coronal plane of narrowest postorbital constriction as the anteroposterior center of the anterior temporalis (with the dorsoventral position bounded by the temporal line and infratemporal crest), reasoning that this location "may lie close to the functional centroid [of the muscle] since the anterior temporalis is probably thickest over this landmark" (Spencer, 1995, p. 225). However, this landmark can be difficult to locate consistently, particularly on the crania of great apes, which often do not possess a single plane of narrowest postorbital position (i.e., there is a nontrivial anteroposterior dimension to this part of the neurocranium's contour), or on the crania of *Mandrillus*, the males of which possess temporal lines that take the form of a laterally projecting shelflike structure that hangs over (extensively in some cases) the origin of the anterior temporalis (Groves, 2001), rendering the topography of this taxon's anterior neurocranium unique among primates. Thus, for this study, condyle-to-coronoid-tip length (the distance between landmarks 1 and 6) was preferred as an estimate of anterior temporalis moment-arm length (Fig. 2.2, top right) because the landmarks for this measurement are easily identified (see also Ravosa, 1988, 1990, 1992, 1996; Dechow and Carlson, 1990; Jablonski, 1993; Antón, 1996a; Taylor, 2002; Koyabu and Endo, 2009).

Like the measurement used to estimate the superficial masseter's moment arm, this measurement of anterior temporalis moment-arm length should be regarded as coarse-grained. Given the variation in muscle-fiber orientation within the temporalis, condyle-to-coronoid-tip length probably represents the true moment arm of some portion of the temporalis muscle, most likely a combination of the anterior temporalis and the anteriormost middle temporalis (see Fig. 2.2). In this context, the height of the coronoid process is probably an important factor (Ritzman and Spencer, 2009). While raising the height of the coronoid process does not affect the moment arm of the portion of the muscle originating directly above this structure (mainly anterior temporalis), such a change will increase the moment arms of the portions that originate posteriorly to it (Ritzman and Spencer, 2009). Thus, in species with coronoid processes that are approximately the same height above the occlusal plane as the mandibular condyles, condyle-to-coronoid-tip length will more or less reflect the anterior temporalis's moment arm, whereas in species with relatively taller coronoid processes, condyle-to-coronoid-tip length will reflect the combined moment arm of the anterior temporalis and part of the middle temporalis.

With respect to the bite points, moment-arm lengths have been measured in two ways. The first involves measuring the orthogonal distance between a bite point and a line connecting the left and right TMJs, projected onto the occlusal plane. This method assumes that maximum bite forces are vertically directed (i.e., perpendicular to the occlusal plane) (e.g., Demes and Creel, 1988; Dechow and Carlson, 1990; Spencer and Demes, 1993; Spencer, 1995; Wright, 2005). The second method uses the raw distance (i.e., *not* projected onto the occlusal plane) from the TMJ to the bite point (e.g., Ravosa, 1988, 1990, 1992, 1996; Vinyard et al., 2003; Koyabu and Endo, 2009). This measurement assumes that maximum bite forces are directed anterosuperiorly (i.e., perpendicular to the line connecting the TMJ to each bite point).

As mentioned above, the few studies that have measured the direction of maximum bite forces indicate that they are oriented approximately vertically (within 10°) relative to the occlusal plane (Van Eijden et al., 1988, 1990; Van Eijden, 1991; but see Hylander, 1978). Thus, bite-point moment-arm lengths were measured assuming vertical bite forces using the following procedure in MacMorph: first, landmarks 1a and 1b (right and left condylion laterale) were connected with a line, the *intercondylar axis*; next, the intercondylar axis was projected onto the occlusal plane, defined by landmarks 9a, 9b (right and left M^3 bite points, respectively), and 12a (right anteriormost premolar bite point); finally, the orthogonal distance from the intercondylar axis to the bite points for right M^3

(landmark 9a), right M^1 (landmark 11a), and the right canine (landmark 13a) was computed (Fig. 2.2, bottom; refer to Table 2.2 and Fig. 2.1 for landmark definitions). If the right-side tooth was missing, its antimere was substituted.

Other features related to gape

A number of other features have been examined by previous investigators interested in the relationship between gape capability and skull form (Herring, 1972, 1975; Herring and Herring, 1974; Emerson and Radinsky, 1980; Lucas, 1981; Smith, 1984a; Lucas et al., 1986; Ravosa, 1990; Wall, 1995; Vinyard et al., 2003; Christiansen, 2006). The foundation for this line of research is Herring's (1972) work on the differences in skull morphology between the Suidae and Tayassuidae (see also Herring and Herring, 1974; Herring, 1975). Herring noted that species with TMJs positioned close to the occlusal plane have greater effective gape than species with TMJs high above the occlusal plane because the former configuration increases the vertical separation between the maxillary and mandibular canines at a given degree of mandibular depression (Fig. 2.3). Moreover, a low TMJ decreases the posterior displacement of the mandibular canine relative to its maxillary counterpart (Fig. 2.3), maintaining these teeth in alignment for biting (Herring, 1972; see also Arendsen de Wolff-Exalto, 1951a,b; Lucas, 1981; Smith, 1984a).

The height of the TMJ above of the occlusal plane is related to estimates of muscle leverage, and therefore these variables are expected to covary. As noted above, the height of the TMJ influences the length of the superficial masseter's moment arm—species with high TMJs should have longer muscle

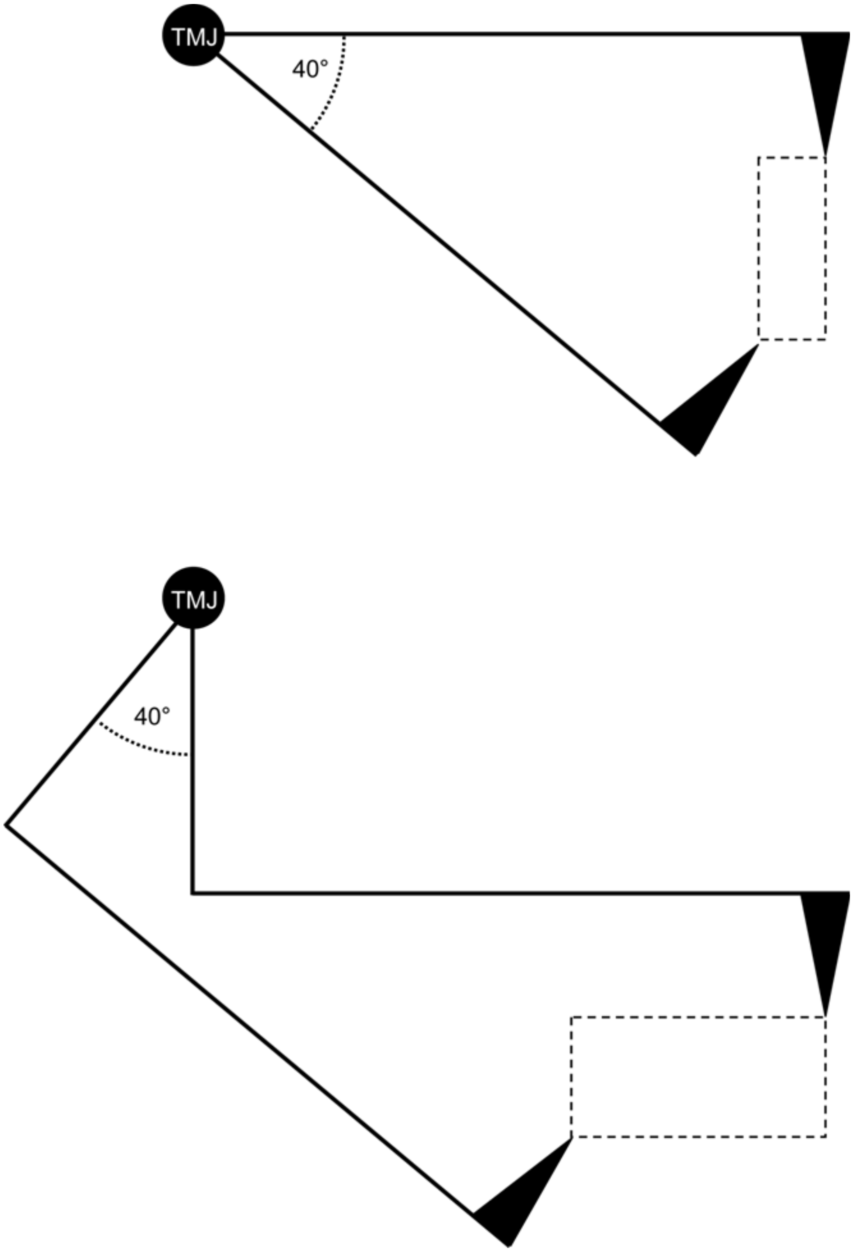


Fig. 2.3. The effect of raising the TMJ above the occlusal plane on gape (after Herring, 1972). Gape is the vertical distance between the canines. Species in which the TMJ is close to the occlusal plane (top) have greater vertical separation between the maxillary and mandibular canines—and less posterior displacement of the mandibular canine—at a given degree of mandibular depression than species in which the TMJ is positioned high above the occlusal plane (bottom).

moment arms, all other factors being equal. Furthermore, the *relative* height of the TMJ can be modified in two ways: (1) by raising or lowering the TMJ and (2) by shortening or lengthening the anteroposterior dimension of the mandible. Changing the length of the mandible alters the length of the bite-point moment arms. Thus, holding the absolute height of the TMJ constant, gape can be increased by lengthening the mandible (and bite-point moment arms), whereas muscle leverage can be increased by shortening the mandible (and bite-point moment arms).

Despite their expected relationship with muscle leverage, TMJ height and anteroposterior mandibular length were measured and examined separately and as the ratio of height to length, the *H/L ratio*, for this study. The height of the TMJ above the occlusal plane was obtained in MacMorph by calculating the orthogonal distance from landmark 1a (right condylion laterale) to the occlusal plane, defined by landmarks 9a, 9b (right and left M^3 bite points, respectively), and 12a (right anteriormost premolar bite point). Anteroposterior mandibular length was taken as the orthogonal distance from the intercondylar axis (i.e., a line connecting landmarks 1a and 1b) to landmark 15 (infradentale), projected onto the occlusal plane (as defined above; see also Table 2.3).

Another important component of Herring's work is the *stretch factor* (Herring and Herring, 1974; Herring, 1975), which is a measure of how far a muscle is stretched relative to its resting length at a given degree of mandibular depression. Herring and Herring (1974) constructed a geometric model for estimating stretch factor using four variables (Fig. 2.4): (1) line *a*, the distance

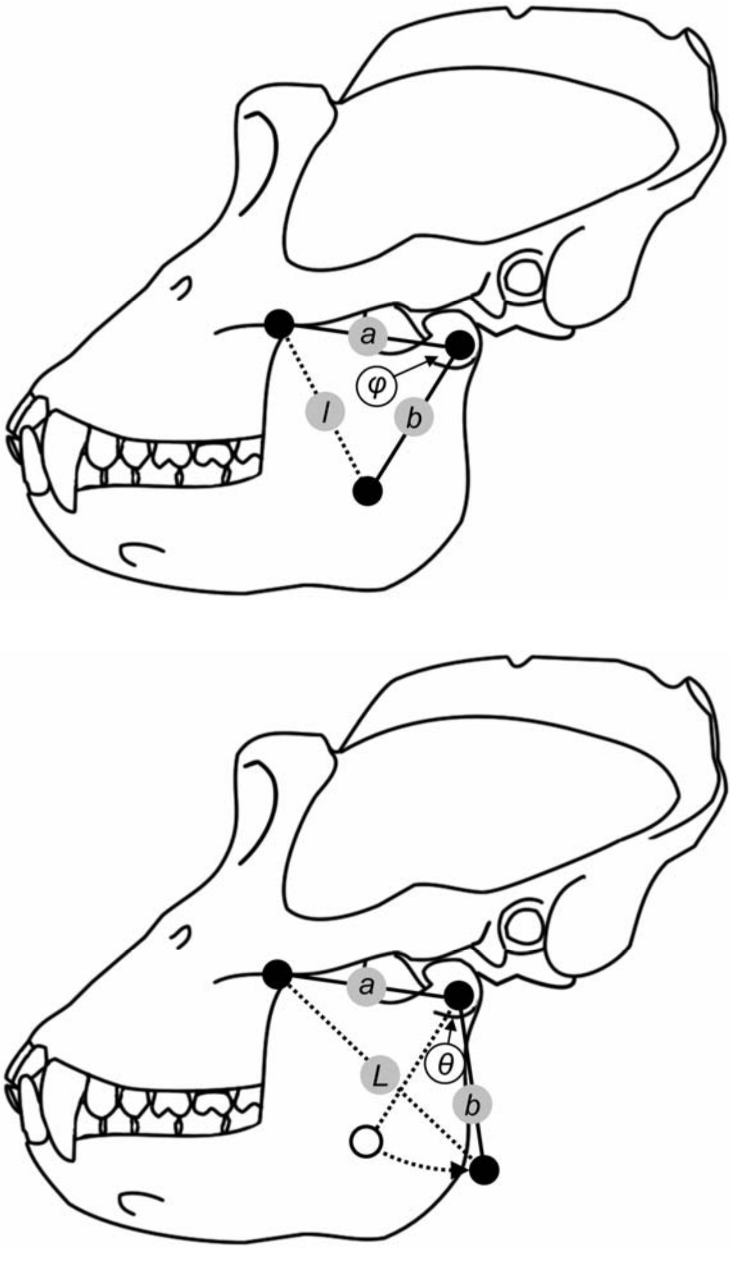


Fig. 2.4. The variables used to compute Herring and Herring's (1974) stretch factor for the superficial masseter. Lines *a* and *b* are the distances from the mandibular condyle to the superficial masseter's origin and insertion sites, respectively. Angle φ is the angle formed by lines *a* and *b*. Line *l* is the length of the superficial masseter when the teeth are in centric occlusion. Line *L* is the length of the masseter when the mandible is rotated open θ degrees. See text for discussion.

from the TMJ to the muscle's origin site (the *origin length*); (2) line b, the distance from the TMJ to the muscle's insertion site (the *insertion length*); (3) angle φ, the angle between lines a and b (the *origin-insertion angle*); and (4) angle θ, an arbitrarily chosen degree of mandibular rotation. These variables are entered into the following equation:

$$L/l = \left(\frac{a^2 + b^2 - 2ab \cos(\theta + \varphi)}{a^2 + b^2 - 2ab \cos \varphi} \right)^{1/2} \qquad \text{(Eq. 1)}$$

which solves for L/l, the stretch factor, where l is the resting length of the muscle and L is the length of the muscle when the mandible is rotated open θ degrees (Herring and Herring, 1974). Species with higher L/l values stretch their muscles more at a given degree of mandibular depression than species with lower stretch factors. Thus, species that require wide gapes are predicted to have low stretch factors.

Importantly, Herring and Herring's (1974) model shows that, in principle, the origin and insertion sites of the masticatory muscles can be repositioned to increase gape (by decreasing the stretch factor) without necessarily compromising muscle leverage. The variables that determine stretch factor can be expressed as the *origin-insertion ratio*, which is computed as origin length divided by insertion length (i.e., a/b), and the origin-insertion angle, which, as noted above, is simply angle φ (Herring and Herring, 1974). Origin-insertion angles that are favorable for gape have a negative impact on muscle moment-arm length—decreasing the angle increases stretch factor but decreases muscle moment-arm length (Herring and Herring, 1974). Thus, for this variable, the prediction that there is a trade-off between gape and masticatory efficiency holds. However, this pattern does not hold for the origin-insertion ratio. With respect to the latter variable, a value of one is the least favorable for gape. Shifts away from unity (i.e., $a/b \neq 1$) decrease stretch factor, thus increasing gape capability, and muscle moment-arm length is related to the origin-insertion ratio in the same way. In other words, holding other factors constant, changes in the origin-insertion ratio that increase gape should increase muscle leverage as well (Herring and Herring, 1974).

Most previous studies of the morphological correlates of gape in primates have examined the origin-insertion ratio and angle separately but have ignored the effect that their constituent variables have on overall stretch factor (Smith, 1984a; Ravosa, 1990; Vinyard et al., 2003). This approach is problematic because the ratio and angle are not necessarily correlated, and it may be that these variables will provide conflicting signals in some cases. For this reason, stretch factor was examined as a single variable in this study (see also Herring and Herring, 1974; Herring, 1975; Emerson and Radinsky, 1980; Wall, 1995). Given the problems associated with identifying a landmark to represent the temporalis's origin or the origins of its commonly recognized functional divisions (discussed above), only the superficial masseter's stretch factor was examined. The lengths of lines a, b, and l were each measured in the sagittal plane (defined using landmarks 3, 4, and 14, as above) as follows: origin length (a) was measured as the distance between landmarks 1a (right condylion laterale) and 7 (superficial masseter origin); insertion length (b) was measured as the distance between landmarks 1a and 8 (superficial masseter insertion); and line l was the distance between landmarks 7 and 8. The angle formed by lines *a* and *b* (i.e., angle φ) was derived using the law of cosines. Finally, angle θ was arbitrarily set at 40° for all species (identified as a commonly used angle of gape among anthropoids by Wall, 1995). Lengths *a* and *b* and angles φ and θ were then entered into equation 1 to obtain the stretch factor for each specimen.

It is important point out that the center of mandibular rotation is not located at the mandibular condyle in primates, as assumed here for the calculation of stretch factor. Rather, because the condyle translates anteriorly as it rotates during depression (e.g., Carlson, 1977; Hylander, 1978; Wall, 1995, 1999), the mandible moves about a mobile instantaneous center of rotation (ICR) located in the gonial region, near the insertion sites for the superficial masseter and the medial pterygoid (Grant, 1973; Gallo et al., 1997). One consequence of the ICR's proximity to these insertion sites is that the superficial masseter and medial pterygoid are stretched much less than would be the case if the condyle simply rotated (Carlson, 1977; Hylander, 1978; Wall, 1995). Wall (1995) compared stretch-factor values calculated using the condyle as the center of rotation and using a more inferior point to represent the ICR (half the distance between the condyle and the inferior border of the mandible) and found that, as predicted, shifting the center of rotation below the condyle decreases stretch factor for the superficial masseter and medial pterygoid.[4] Thus, using the condyle in

---

[4] Wall's (1995) data also show that inferior displacement of the mandible's axis of rotation reduces the stretch factor of the anterior temporalis. On the other hand, the middle and posterior components of the temporalis have greater stretch factors.

calculations of stretch factor will overestimate muscle stretch in the masseter, but this landmark was preferred here over the ICR due to the uncertainty in the latter's position.[5]

Finally, although not examined here, it is worth noting that the morphology of the bony TMJ has been examined for possible gape adaptations (Wall, 1995; Vinyard et al., 2003). Vinyard et al.'s (2003) analysis of tree-gouging callitrichines, cheirogaleids, and galagids (which, as noted, are inferred to use relatively wide gapes) demonstrated that, in these species, the anteroposterior dimensions of the mandibular condyle and temporal articular surface are relatively long in comparison to those of their closely related, nongouging sister taxa. According to Vinyard et al. (2003) these features increase gape by increasing both rotational excursion of the mandible (in the case of condyle length) and condylar translation (in the case of temporal articular surface).

Skull size

The final set of measurements derived from the landmark data consisted of seven linear dimensions of the skull. These measurements were combined into a geometric mean (GM) to represent skull size, which was used to size-adjust the variables for interspecific comparisons (discussed in greater detail below). The measurements are described in Table 2.3 and illustrated in Figure 2.5. Note that the three length measurements and the single height measurement were taken in

---

[5] As noted by Stern (1974) and Hylander (1975b), the variable position of the ICR does not affect estimates of muscle moment-arm lengths.

TABLE 2.3. Description of measurements used to compute the skull geometric mean

Landmarks	Description	
4, 14	Facial length	Distance from interorbital superior to prosthion
10a, 10b	Snout width	Distance between left M2 and right M2
1a, 1b, 15	Mandibular length	Orthogonal distance from the intercondylar axis to infradentale, projected onto the occlusal plane (defined by points 9a, 9b, and 12a)
4, 9a	Posterior facial height	Distance from M3 bite point to anterior frontal bone, projected onto the sagittal plane (defined by points 3, 4, 14)
5a, 5b	Biorbital width	Distance from left ectoconchion to right ectoconchion
2a, 4	Auriculo-orbital length	Distance from auriculare to interorbital superior, projected onto the sagittal plane (defined by points 3, 4, and 14)
2a, 2b	Neurocranial width	Distance from left auriculare to right auriculare

Landmark numbers refer to Figure 2.1.

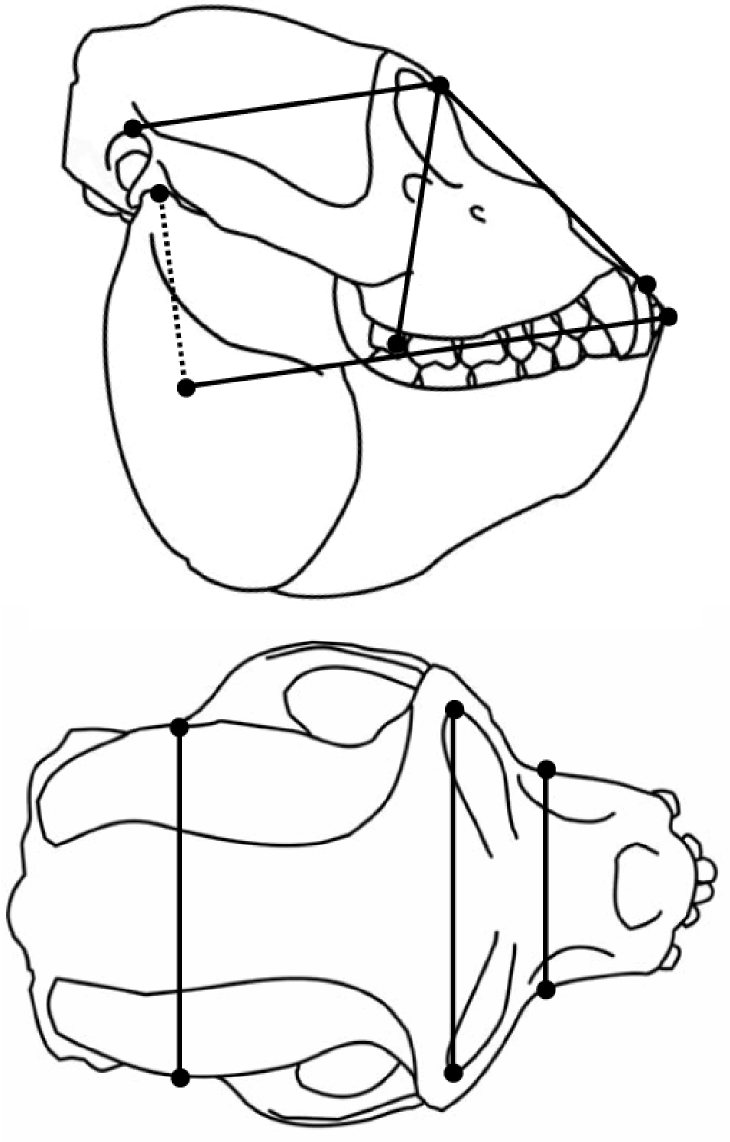


Fig 2.5. Illustration of the linear measurements used to calculate the skull geometric mean. All measurements shown in lateral view were taken in the sagittal plane. Mandibular length was measured as the orthogonal distance from the anterior tip of the mandible (infradentale) to the intercondylar axis, projected into the occlusal plane (indicated by the dotted line).

the sagittal plane. Five of the measurements are from the face (facial length, mandibular length, posterior facial height, biorbital width, and snout width) and two are from the neurocranium (auriculo-orbital length and neurocranial width).

Mean GMs for each species, divided by sex, are given in Table 2.4, along with body-mass data from Smith and Jungers (1997). Not surprisingly, the skull GM is highly correlated with body mass: using $\log_e$-transformed values, $r = 0.98$ and 0.97 for females and males, respectively. Scaling of the skull GM to body mass is discussed in Chapter 3. Also shown is the index of sexual dimorphism (ISD, male mean divided by female mean) for each species. For the skull GM, these values range from monomorphism (e.g., *Chiropotes satanas*, ISD = 1.01) to complete separation between the male and female distributions (e.g., *Mandrillus leucophaeus*, ISD = 1.31). Sexual dimorphism in skull size roughly parallels dimorphism in body mass ($r = 0.85$).[6]

Measurement error

Twelve specimens were redigitized 2–16 days after the initial digitization event in order to assess the repeatability of the measurements used in this study. These specimens range in size from a female specimen of *Cebus libidinosus* to a male specimen of *Erythrocebus patas* (see Table 2.4). For each variable,

---

[6] This correlation coefficient excludes the values for *Mandrillus leucophaeus*, which is an obvious outlier. Including this species results in a correlation of $r = 0.72$. The reliability of the *M. leucophaeus* body-mass values is questionable, as they are approximations based on ranges given by Haltenorth and Diller (1980; see Smith and Jungers, 1997). These values do not affect the correlations between skull size and body mass within each sex.

TABLE 2.4. Summary statistics for the skull GM

	Males			Females			ISD	
	Mean	SD	BM	Mean	SD	BM	GM	BM
Al. seniculus	52.14	2.27	6.7	46.18	1.18	5.2	1.13	1.28
At. geoffroyi	46.72	1.30	7.8	46.09	1.24	7.3	1.01	1.07
Ceb. libidinosus	42.12	1.23	3.7	39.08	0.71	2.5	1.08	1.45
Ceb. capucinus	44.91	1.45	3.7	41.48	1.01	2.5	1.08	1.45
Ch. satanas	38.31	1.14	2.9	38.09	0.68	2.6	1.01	1.12
Pith. monachus	36.17	1.37	2.6	35.90	0.64	2.1	1.01	1.24
Cer. pogonias	46.08	0.99	4.3	42.19	1.03	2.9	1.09	1.47
Cer. wolfi	45.04	1.02	3.9	41.85	0.99	2.9	1.08	1.36
Chl. pygerythrus	49.57	1.32	5.5	44.29	1.06	4.1	1.12	1.35
Er. patas	62.52	2.49	12.4	51.21	1.23	6.5	1.22	1.90
Mac. mulatta	55.19	2.17	7.7	49.35	2.07	5.4	1.12	1.44
Mac. fascicularis	52.29	1.64	5.4	45.88	1.32	3.6	1.14	1.49
Th. gelada	77.14	2.53	19.0	67.80	2.06	11.7	1.14	1.62
M. leucophaeus	82.54	2.30	17.5	62.96	2.05	12.5	1.31	1.40
Pil. foai	53.14	2.28	12.3	48.95	1.65	8.3	1.09	1.49
Pro. verus	42.97	1.18	4.7	41.59	1.20	4.2	1.03	1.12
Col. satanas	52.11	0.87	10.4	50.22	0.89	7.4	1.04	1.40
Col. polykomos	53.90	1.57	9.9	51.23	1.94	8.3	1.05	1.19
Pre. chrysomelas	44.05	0.93	6.6	43.60	0.89	6.5	1.01	1.02
Pre. potenziani	46.78	1.50	6.2	46.15	1.00	6.4	1.01	0.96
Tr. obscurus	48.22	1.37	7.9	45.45	1.29	6.3	1.06	1.26
Tr. shortridgei	53.70	1.41	12.0	49.79	1.75	9.9	1.08	1.22
Hy. lar	49.20	1.39	5.9	47.99	1.41	5.3	1.03	1.10
Hy. syndactylus	59.17	1.91	11.9	56.58	2.21	10.7	1.05	1.11
Go. beringei	124.01	3.80	162.5	105.28	1.88	97.5	1.18	1.67
Go. gorilla	118.67	4.82	170.4	102.38	2.59	71.5	1.16	2.38
Pan paniscus	78.31	1.78	45.0	77.43	1.99	33.2	1.01	1.36
Pan troglodytes	93.79	4.30	59.7	89.32	2.62	45.8	1.05	1.30
Po. abelii	101.76	6.19	77.9	86.28	3.51	35.6	1.18	2.19
Po. pygmaeus	104.38	3.73	78.5	88.49	3.96	35.8	1.18	2.19

Abbreviations are as follows: SD = standard deviation; CV = coefficient of variation; BM = body mass (from Smith and Jungers, 1997); ISD = index of sexual dimorphism.

measurement error was quantified using the following procedure described by White (1991, p. 292):

(1) The mean of trials 1 and 2 for a given specimen was computed.

(2) Next, the smaller of the values from trials 1 and 2 was subtracted from the mean obtained in step 1. Note that subtracting the higher of the two values from the mean would produce the same value but of opposite sign (i.e., negative instead of positive).

(3) Finally, the value obtained in step 2 (the absolute deviation from the mean) was divided by the mean obtained in step 1 and multiplied by 100.

The resulting value is the percent deviation of each trial from the mean of the two trials, referred as *percent measurement error*.

Table 2.5 presents the results of the error analysis. In the majority of cases, percent measurement error is below 2%—commonly considered an acceptable level—and appears to be unaffected by days between digitization (i.e., error is not greater for specimens redigitized after 16 days versus those redigitized after 2 days) and size (compare the values for female *Ceb. libidinosus* and male *Er. patas*). These results indicate that the landmark-based measurements devised for this study are as repeatable as traditional caliper-based measurements. A notable exception, however, is TMJ height. For this variable, percent measurement error is between 5% and 6% for the male specimens of *Er. patas* and *Chlorocebus pygerythrus* and for the female specimen of *Trachypithecus obscurus*. As a result, TMJ height is the only measurement for which mean error

TABLE 2.5. Results of measurement-error analysis

		Percent measurement error[a]			
Specimen	Days apart	Neurocranial width	Auriculo-orbital length	Posterior facial height	Biorbital width
Al. seniculus					
Male	16	<1.0%	<1.0%	1.6%	<1.0%
Female	16	<1.0%	<1.0%	1.4%	<1.0%
At. geoffroyi					
Male	14	<1.0%	<1.0%	<1.0%	1.3%
Female	14	<1.0%	<1.0%	<1.0%	<1.0%
Ceb. libidinosus					
Male	14	<1.0%	<1.0%	1.4%	<1.0%
Female	14	<1.0%	<1.0%	<1.0%	1.8%
Er. patas					
Male	5	<1.0%	<1.0%	<1.0%	<1.0%
Chl. pygerythrus					
Male	5	<1.0%	<1.0%	<1.0%	<1.0%
Tr. obscurus					
Male	3	<1.0%	<1.0%	<1.0%	1.2%
Female	3	<1.0%	<1.0%	<1.0%	1.7%
Pro. verus					
Male	2	<1.0%	<1.0%	<1.0%	1.4%
Female	2	<1.0%	<1.0%	<1.0%	<1.0%
Mean		<1.0%	<1.0%	<1.0%	<1.0%

(continued)

TABLE 2.5. (Continued)

Specimen	Days apart	Percent measurement error[a]			
		Facial length	Snout width	Jaw length	TMJ height
Al. seniculus					
Male	16	1.1%	1.0%	<1.0%	1.8%
Female	16	<1.0%	<1.0%	<1.0%	<1.0%
At. geoffroyi					
Male	14	1.3%	<1.0%	<1.0%	1.6%
Female	14	2.4%	<1.0%	<1.0%	<1.0%
Ceb. libidinosus					
Male	14	2.2%	<1.0%	<1.0%	1.7%
Female	14	<1.0%	<1.0%	<1.0%	<1.0%
Er. patas					
Male	5	<1.0%	<1.0%	<1.0%	5.3%
Chl. pygerythrus					
Male	5	<1.0%	<1.0%	<1.0%	5.2%
Tr. obscurus					
Male	3	<1.0%	2.3%	<1.0%	<1.0%
Female	3	<1.0%	1.9%	<1.0%	5.8%
Pro. verus					
Male	2	<1.0%	1.6%	<1.0%	1.4%
Female	2	<1.0%	<1.0%	<1.0%	2.0%
Mean		<1.0%	<1.0%	<1.0%	2.2%

(continued)

TABLE 2.5. (Continued)

Specimen	Days apart	Percent measurement error[a]			
		Masseter origin	Masseter insertion	Masseter moment arm	Temporalis moment arm
Al. seniculus					
Male	16	1.2%	1.4%	1.1%	2.7%
Female	16	<1.0%	<1.0%	<1.0%	<1.0%
At. geoffroyi					
Male	14	2.2%	1.5%	2.6%	3.9%
Female	14	1.5%	1.3%	1.6%	2.8%
Ceb. libidinosus					
Male	14	<1.0%	<1.0%	<1.0%	1.4%
Female	14	1.2%	3.3%	3.0%	2.4%
Er. patas					
Male	5	<1.0%	<1.0%	<1.0%	1.6%
Chl. pygerythrus					
Male	5	1.1%	<1.0%	<1.0%	<1.0%
Tr. obscurus					
Male	3	<1.0%	<1.0%	1.1%	<1.0%
Female	3	1.3%	<1.0%	1.1%	<1.0%
Pro. verus					
Male	2	<1.0%	1.3%	1.1%	1.0%
Female	2	<1.0%	<1.0%	<1.0%	1.1%
Mean		<1.0%	<1.0%	1.1%	1.5%

(continued)

TABLE 2.5. (Continued)

		Percent measurement error[a]			
Specimen	Days apart	M3 moment arm	M1 moment arm	Canine moment arm	Masseter φ
Al. seniculus					
Male	16	2.5%	1.6%	<1.0%	<1.0%
Female	16	<1.0%	<1.0%	<1.0%	<1.0%
At. geoffroyi					
Male	14	2.0%	<1.0%	<1.0%	3.5%
Female	14	<1.0%	<1.0%	<1.0%	1.5%
Ceb. libidinosus					
Male	14	<1.0%	<1.0%	<1.0%	1.1%
Female	14	<1.0%	<1.0%	<1.0%	1.6%
Er. patas					
Male	5	<1.0%	<1.0%	<1.0%	<1.0%
Chl. pygerythrus					
Male	5	<1.0%	<1.0%	—[b]	1.9%
Tr. obscurus					
Male	3	<1.0%	<1.0%	<1.0%	1.2%
Female	3	<1.0%	<1.0%	<1.0%	<1.0%
Pro. verus					
Male	2	1.5%	<1.0%	<1.0%	<1.0%
Female	2	<1.0%	<1.0%	<1.0%	1.2%
Mean		<1.0%	<1.0%	<1.0%	1.3%

[a] Computed following White (1991); see text for procedure.

[b] Specimen was missing right canine.

for all of the specimens exceeds 2%, though only slightly so (2.2%). The reason for such relatively high error in TMJ height probably lies in the fact that it was derived using four landmarks—right condylion laterale, the left and right M^3 bite points, and the bite point for the right anteriormost maxillary premolar—and thus there are four sources of error for this measurement.

Muscle "size"

As discussed briefly in Chapter 1, the masticatory-efficiency hypothesis predicts that, in certain cases, species will possess jaw adductors with relatively large physiological cross-sectional areas (PCSAs) to compensate for reduced jaw-muscle leverage associated with tall canines and wide gapes. Increased muscle "size" should occur in at least two situations. First, if two species differ in relative canine height but not in the mechanical demands of their respective diets, then the species with taller canines should have "larger" muscles (i.e., greater PCSA) to offset the decrease in muscle leverage—and concomitant decrease in bite force—predicted to be associated with taller canines. Second, if two species do not differ in relative canine height but do differ in diet, then the species with the more mechanically demanding diet should have larger muscles than the species with the less mechanically demanding diet. In this case, the two species should not differ in jaw-muscle leverage, and therefore the species with the harder/tougher diet will need larger muscles to produce higher-magnitude bite forces.

That the anatomy of the masticatory musculature is influenced by diet is generally assumed, but researchers have only recently begun to examine the details of this relationship in primates. Muscle adaptations for wide gapes in tree-gouging callitrichines have already been discussed (Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009), but in the context of the present discussion, a recent study of the genus *Cebus* is particularly relevant (Taylor and Vinyard, 2009). Taylor and Vinyard (2009) showed that the masticatory muscles of *C. apella* have relatively greater PCSAs than those of other species in the genus, reflecting the former species' well-known ability to process very hard objects using their incisors, canines, and anterior postcanine teeth (Moynihan, 1976; Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Izawa, 1979; Terborgh, 1983; Janson and Boinski, 1992; Wright, 2005; Wright et al., 2009). Notably, the greater PCSAs of *C. apella* are achieved by increasing muscle mass rather than by shortening muscle fibers and increasing fiber pinnation angle (Taylor and Vinyard, 2009). The significance of this distinction lies in the fact that larger muscles require more energy to use and maintain, whereas shortening fibers and increasing their pinnation is less costly but reduces muscle excursion and therefore gape potential (Taylor and Vinyard, 2009; see also Taylor and Vinyard, 2004, 2008; Taylor et al., 2009). Taylor and Vinyard (2009) speculated that the condition observed in *C. apella* allows individuals of this species to use wide gapes in conjunction with high-magnitude bite forces when processing relatively large, hard objects.[7]

---

[7] Another possible explanation is that *C. apella* males need to maintain wide gapes because their canines are relatively taller than or similar in size to those of males of other species of *Cebus* (Masterson, 2003). This explanation and the one proposed by Taylor and Vinyard (2009) are not mutually exclusive.

Species inferred to have gape-compromised masticatory systems should compensate for reduced muscle leverage by increasing PCSAs using the same pathway as *C. apella*. According to the masticatory-efficiency hypothesis, species that increase PCSA by decreasing fiber length and increasing pinnation angle should incur a decrease in gape and canine height. Thus, when sexual selection for tall canines is stronger than natural selection for efficient mastication, a species should respond to selection for high-magnitude bite-force production by increasing muscle mass.

Unfortunately, the specific predictions regarding the details of muscle anatomy cannot be evaluated using the data collected for this study, as differences among species in fiber length and pinnation angle cannot be inferred from bony anatomy (but see Smith, 1984a; Ravosa, 1990). However, it is possible to obtain rough estimates of differences in relative muscle size among closely related species using muscle attachment sites (e.g., Hylander, 1977; Rak, 1983; Shea, 1983a; Smith et al., 1983; Demes and Creel, 1988; Ravosa, 1990; Cole, 1992; Spencer, 1992, 1995; Taylor, 2002; O'Connor et al., 2005; but see Antón, 1999, 2000).

Following procedures outlined by Spencer (1995), linear dimensions describing various aspects of the attachment sites for the masseter and temporalis muscles were collected using digital calipers. For the masseter, muscle size is represented by the cross-sectional area of the zygomatic arch. This variable is thought to reflect the forces generated by the masseter (e.g., Hylander, 1977; Rak, 1983; Spencer, 1992, 1995), and thus it is a crude estimate of the size of this muscle. Arch area was calculated as the product of the height and width of the arch, each measured just anterior to the most anterosuperior extent of the zygomaticotemporal suture on the lateral surface.

With respect to the temporalis, two variables were used to estimate muscle size. It is important to note that these two variables are highly dependent on the size and shape of the neurocranium, and thus comparisons between species that differ in these parameters are unreliable (Spencer, 1995). The first variable is the distance between the left and right inferior temporal lines at the coronal suture, also referred to as the *intertemporalis distance*. This distance is an estimate of the area of attachment of the muscles—species with narrow intertemporalis distances are expected to have larger muscles than species with greater separation between the temporal lines (Spencer, 1995). Temporal-line form is extremely variable among and within primate species. In some individuals, the inferior and superior lines are separated by a distinct gap; in others, the lines are nearly coincident. In the most extreme cases, the left and right temporal lines merge at the midline to form a sagittal crest. In these cases, the width of the crest was measured. Among species that possess sagittal crests, crest width cannot be used to distinguish species that differ in temporalis size.

The second variable used to estimate temporalis size is the area of the temporal foramen. This variable is thought to reflect the PCSA of the temporalis (e.g., Hylander, 1977; Rak, 1983; Shea, 1983a; Demes and Creel, 1988; Cole, 1992), but its correspondence to the size of the muscle has not been demonstrated (Spencer, 1995). Foramen area was computed using the formula for the area of an ellipse: area = π × length/2 × width/2. Length was measured as the maximum distance from the anterior margin of the preglenoid plane to the posterior border of the postorbital septum, in approximately the same transverse plane. Width was derived from two measurements: (1) maximum cranial width, the distance between the most lateral points on the right and left zygomatic arches, and (2) minimum frontal width, taken in superior view. Foramen width was obtained by subtracting minimum frontal width from maximum cranial width and dividing the difference by two.

Dental data

Canine height

Canine crown height was defined following Plavcan (1990, 1993a; see also Plavcan et al., 2009) as the distance between the cusp apex and the basalmost extension of the cementoenamel junction's mesiobuccal segment (Fig. 2.6). Digital calipers were used to quantify this dimension. As noted above, the canine-height data for platyrrhines, cercopithecoids, and hylobatids were collected for this study, while the data for the Hominidae were provided by J. Kelley (see Kelley, 1995a). Only specimens preserving maxillary and mandibular canines were measured so that *combined canine height*, the sum of the heights of the maxillary and mandibular teeth, could be computed for each individual. This measurement was used to estimate gape requirements. Although combined canine height overestimates the arc length that the anterior end of the mandible must travel for the canines to clear each other, it has the advantage that it incorporates the heights of both teeth into a single metric.

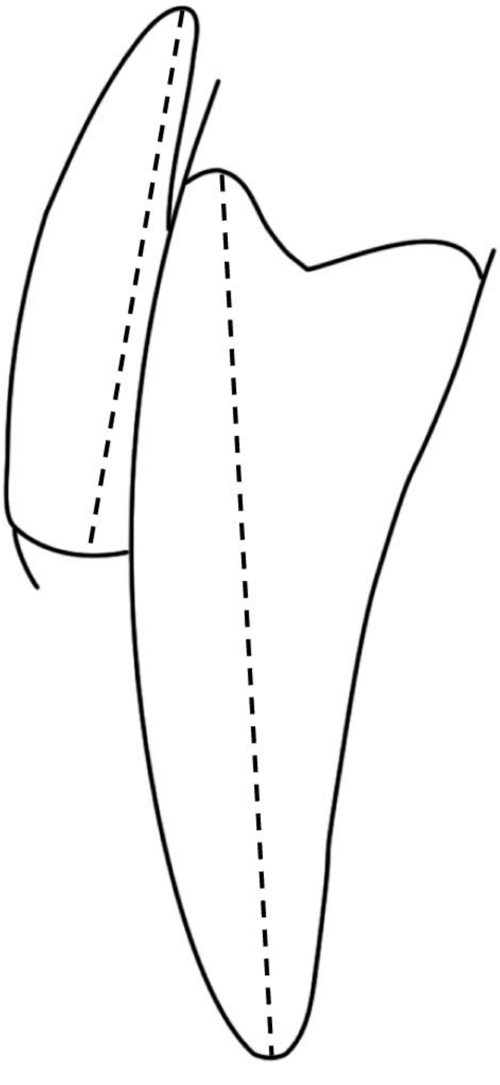


Fig. 2.6. Maxillary and mandibular canine heights. Each tooth was measured in lateral view from the apex of the cusp to the mesiobuccal segment of the cementoenamel junction (following Plavcan, 1990, 1993).

An alternative to canine height is Greenfield and Washburn's (1991) *canine projection*, which attempts to quantify the portion of the canine crown that projects beyond the occlusal plane of the postcanine teeth. In principle, this measurement will provide a more accurate estimate of the canine-clearance arc than raw crown heights, given that the basal portions of the maxillary and mandibular canine crowns lie above and below, respectively, the occlusal plane. However, canine crown height was preferred over projection because the latter measurement is sensitive to a variety of factors, including premolar number, differences in crown height among the postcanine teeth, and variation in the curvature of the occlusal plane (i.e., the curve of Spee) (Plavcan, 1993a). Moreover, canine projection cannot be accurately measured on specimens that are missing adjacent teeth or in cases where the canine is loose or not fully erupted (but still measurable; such teeth are desirable because they are minimally worn).

Ideally, only unworn teeth should be included in analyses of canine height. However, given the limited number of specimens available in museum collections and their condition, the exclusion of all worn teeth is impractical. In many species, particularly cercopithecines, the male maxillary canine begins to hone against the anteriormost mandibular premolar before it is fully erupted (Kay, 1981a; Plavcan and van Schaik, 1992; pers. obs.), and thus it may not be possible to obtain more than one or two unworn canines for some species.

Previous researchers have used measurements obtained from teeth with some degree of wear (Plavcan, 1990; Greenfield and Washburn, 1991; Plavcan and van Schaik, 1992; Kelley, 1995a,b; Plavcan et al., 2009), but because it is difficult to accurately estimate how much of the canine crown has been lost, the amount of wear tolerated by these researchers is usually described in imprecise, subjective terms. For example, Greenfield and Washburn (1991, p. 20) included "unworn (or only very slightly worn) specimens" and excluded those that were "more heavily worn." Plavcan and van Schaik (1992, p. 465) described the canines they rejected as showing "excessive wear in comparison to conspecifics," and Plavcan et al. (2009, p. 4) "included 'moderately' worn specimens … defined as those showing clear facets and/or exposure of dentine along the distal and mesial edges of the tooth, without excessive blunting of the apex" (see also Plavcan, 1990). Kelley's (1995a, p. 368) criteria for measuring the hominid canines included in this study are the most explicit:

> I used only specimens in which wear or breakage was judged to be minimal, with no more than approximately 2.5 mm (in most cases less) of the crown apex estimated to have been lost. Specimens were not used if mesial and distal wear facets met at the crown apex (in the case of upper canines) or if more than a very small dentine pit was exposed at the crown apex. Specimens were used if apical enamel was broken away but the underlying dentine apex was intact.

Moreover, in contrast to the other studies, Kelley reconstructed the heights of these worn specimens by comparing them to unworn teeth.

With respect to the data collected for this study (i.e., for platyrrhines, cercopithecoids, and hylobatids), canine wear was dealt with as follows. Each sample contained some unworn canines or canines that were determined to be only minimally worn based on comparisons with unworn teeth or the absence of apical dentine exposure and tip blunting. Using these teeth as standards, teeth with greater amounts of wear were measured. No attempt was made to reconstruct the original crown heights of these teeth, except in cases where a millimeter or less of the tip was missing due to breakage. Adding worn canines to a sample of unworn specimens will have two effects: the sample mean will decrease and sample variation will increase. The strategy adopted here was to reduce the influence of worn canines by minimizing sample variation. Each species was divided into male and female subsamples, and variation in combined canine height within these subsamples was quantified using the coefficient of variation (CV). An arbitrary threshold CV of 10.0 was used to identify samples that were "too variable." Samples with CVs below this threshold were left intact. Samples with CVs that exceeded the threshold were reduced by removing worn specimens, starting with the shortest, until the CV was at or below 10.0. The resulting samples were used for analysis. The samples sizes reported in Table 2.1 reflect these samples.

Table 2.6 presents the CVs for each sample, along with the means, standard deviations, and ISDs. The mean and median CVs for the male samples are 6.67 and 6.54, respectively. For females, these values are 6.81 and 7.00. Thus, many of the CVs fall well below the threshold value and are similar to those for molar dimensions (e.g., Plavcan, 1993b). An exception is the CV for the male *Pongo abelii* sample, which is 10.52, exceeding the threshold. However, canines were not discarded from this sample because it is small (*n* = 4). Moreover, Kelley's (1995a) criteria for including worn specimens were stringent, and, importantly, he estimated unworn crown height.

TABLE 2.6. Summary statistics for combined canine height

	Males			Females			
	Mean	SD	CV	Mean	SD	CV	ISD
Alouatta seniculus	25.31	2.38	9.40	18.95	1.36	7.17	1.34
Ateles geoffroyi	22.34	1.65	7.38	15.34	1.21	7.89	1.46
Cebus libidinosus	28.83	1.17	4.04	19.06	1.77	9.30	1.51
Cebus capucinus	28.58	2.01	7.04	17.86	1.18	6.59	1.60
Chiropotes satanas	22.46	1.27	5.65	21.39	1.67	7.80	1.05
Pithecia monachus	20.71	1.37	6.63	17.77	0.79	4.42	1.17
Cercopithecus pogonias	29.85	1.16	3.90	18.23	1.43	7.86	1.64
Cercopithecus wolfi	30.78	1.89	6.15	17.85	0.94	5.27	1.72
Chlorocebus pygerythrus	34.79	2.36	6.80	21.23	2.12	10.00	1.64
Erythrocebus patas	48.36	3.12	6.45	22.29	1.90	8.51	2.17
Macaca mulatta	35.80	2.30	6.42	17.83	1.52	8.51	2.01
Macaca fascicularis	40.94	3.75	9.15	20.55	1.03	5.00	1.99
Theropithecus gelada	66.76	3.21	4.81	26.03	1.74	6.69	2.56
Mandrillus leucophaeus	75.49	5.20	6.89	24.96	1.77	7.10	3.02
Piliocolobus foai	39.37	2.36	6.00	18.30	0.54	2.93	2.15
Procolobus verus	28.89	1.52	5.27	14.22	1.12	7.91	2.03
Colobus satanas	31.51	2.28	7.23	16.70	1.23	7.37	1.89
Colobus polykomos	35.74	2.18	6.09	20.70	1.43	6.90	1.73
Presbytis chrysomelas	24.70	1.38	5.58	15.12	0.58	3.85	1.63
Presbytis potenziani	25.93	2.31	8.91	17.77	0.95	5.37	1.46
Trachypithecus obscurus	30.23	1.76	5.81	17.30	1.15	6.66	1.75
Trachypithecus shortridgei	35.37	1.69	4.79	21.78	1.81	8.29	1.62
Hylobates lar	30.61	2.55	8.32	26.82	2.06	7.68	1.14
Hylobates syndactylus	35.16	2.84	8.07	30.77	2.03	6.61	1.14
Gorilla beringei	55.42	2.88	5.20	32.57	0.75	2.30	1.70
Gorilla gorilla	60.18	5.87	9.76	35.18	2.32	6.59	1.71
Pan paniscus	32.03	1.31	4.09	23.70	1.34	5.67	1.35
Pan troglodytes	44.71	3.07	6.86	29.90	2.84	9.49	1.50
Pongo abelii	52.55	5.53	10.52	30.30	2.00	6.61	1.73
Pongo pygmaeus	51.34	3.55	6.91	33.38	2.69	8.04	1.54
Mean CV			6.67			6.81	
Median CV			6.54			7.00	

Combined canine height is the sum of each individual's maxillary and mandibular canine heights (in millimeters). Data for great apes were provided by J. Kelley (see Kelley, 1995a). Abbreviations are as follows: SD = standard deviation; CV = coefficient of variation; ISD = index of sexual dimorphism.

Incisor, canine, and postcanine areas

Mesiodistal (MD), labiolingual (LL), and buccolingual (BL) dimensions of the incisors, canines, and postcanine teeth for nearly all of the taxa listed in Table 2.1 were taken from Plavcan (1990). The exceptions are *Pithecia monachus*, *Gorilla beringei*, and *Pongo abelii*, which were measured for this study using digital calipers. As noted, Plavcan's (1990) dental data derive from the same subspecies and in most cases are from the same museum collections as the skull and canine measurements collected for this study. These data were used to compute estimates of the overall size of different components of the dentition.

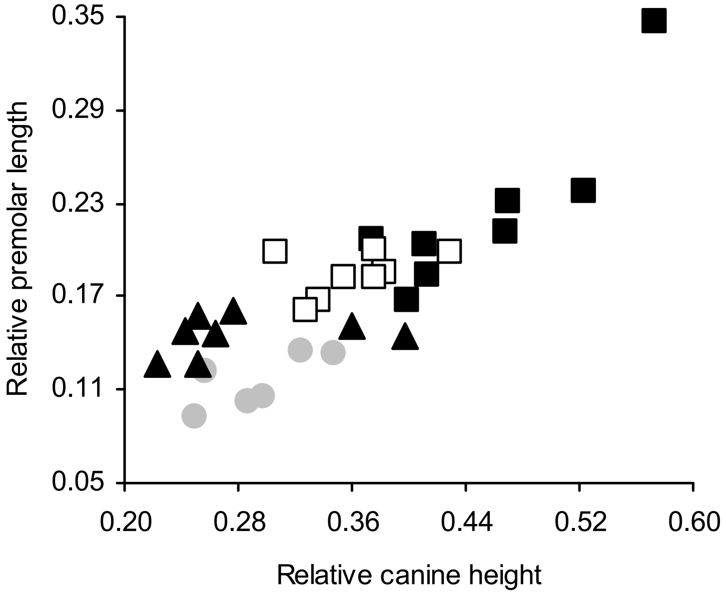
The primary variable used to represent dental size is area. Canine area is simply the product of the basal MD and LL dimensions. For the incisors and postcanine teeth, individual tooth areas (MD × LL for the incisors; MD × BL for the premolars and molars) were summed within each tooth class to produce estimates of the overall sizes of the incisor and postcanine rows. In the case of *Pithecia monachus*, MD dimensions for individual incisors and postcanine teeth were not collected; instead, because of the difficulty in obtaining repeatable MD measurements from the individual teeth of such a small species (the smallest included here; see Table 2.4) using standard digital calipers, only MD lengths of the entire incisor and postcanine rows were measured.[8] Therefore, this species could not be included in analyses conducted using incisor and postcanine areas. In order to examine the effect of excluding *P. monachus*, analyses were rerun

---

[8] Note that Plavcan (1990) used a microscope with a calibrated reticle to measure his specimens, which mitigates the effect of size on measurement error.

using total MD length for each component of the dentition. Results generated using this variable did not differ in their overall signal from those generated using areas, and thus only the results for the latter are reported.

The anteriormost mandibular premolar—P_2 in platyrrhines and P_3 in catarrhines—was excluded from the calculation of postcanine size variables because this tooth participates in the canine/premolar complex, providing a surface for the maxillary canine to hone against (Zingeser, 1969; Every, 1970; Kay, 1981a; Walker, 1984; Greenfield and Washburn, 1992; Plavcan, 2001). Given this functional relationship, the relative size of the anterior mandibular premolar, particularly its MD dimension, is expected to covary with the relative height of the maxillary canine in males (Plavcan, 1990; Greenfield, 1992b; Greenfield and Washburn, 1992), and Figure 2.7 shows that this is indeed the case. Given its functional role within the dentition, this tooth almost certainly varies independently of the remaining postcanine teeth to some degree. Moreover, the anterior mandibular premolar is the longest tooth in many anthropoid species, and in some male cercopithecines, it accounts for 30% or more of the length of the postcanine row. Thus, including this tooth in measures of postcanine size has the potential to confound tests of the postcanine pleiotropy hypotheses. The maxillary anterior premolar was also excluded from analysis to make the results for the maxillary and mandibular dentitions comparable.



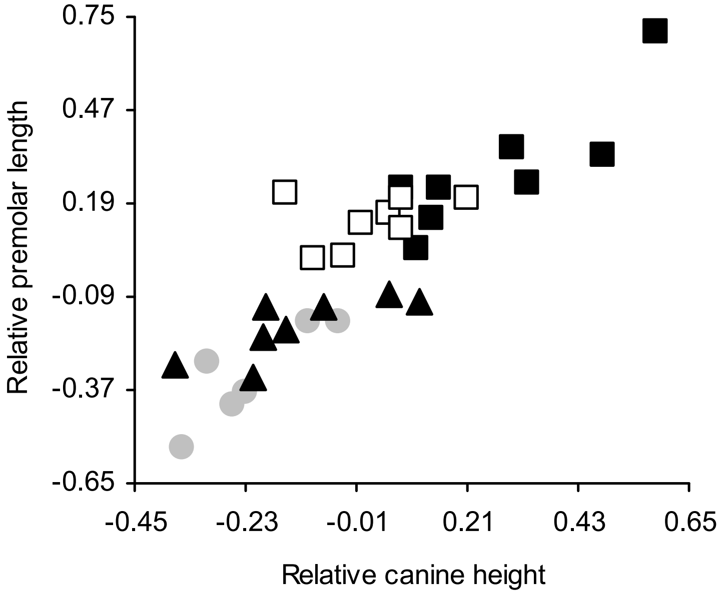


Fig. 2.7. The relationship between relative maxillary canine height and the relative length (MD) of the anterior mandibular premolar (P_2 in platyrrhines; P_3 in catarrhines) in male anthropoids. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines. Values in the upper plot were size-adjusted using shape ratios (i.e., variable divided by skull GM); values in the lower plot were size-adjusted using residuals from a least-squares regression line (dependent variables regressed on skull GM).

ANALYTICAL PROCEDURES

Phylogenetic comparative methods

It is now widely accepted that, because species are related through common descent, they cannot be treated as independent data points in comparative studies, and numerous analytical techniques have been developed to deal with this issue (e.g., Clutton-Brock and Harvey, 1977; Ridley, 1983; Stearns, 1983; Cheverud et al., 1985; Dunham and Miles, 1985; Felsenstein, 1985; Elgar and Harvey, 1987; Huey and Bennett, 1987; Bell, 1989; Grafen, 1989; Pagel and Harvey, 1989; Maddison, 1990, 2000; Harvey and Pagel, 1991; Martins and Garland, 1991; Garland et al., 1992, 1993, 1999; Møller and Birkhead, 1992; Smith, 1994; Díaz-Uriarte and Garland, 1996, 1998; Grafen and Ridley, 1996; Martins and Hansen, 1997; Purvis and Webster, 1999; Garland and Ives, 2000; Nunn and Barton, 2001; Rohlf, 2001, 2006; Ross et al., 2002; Smith and Cheverud, 2002; O'Neill and Dobson, 2008; Legendre and Desdevises, 2009). The consensus view that has emerged from discussions of this problem is that evolutionary events—represented by differences between sister taxa—are the proper units of analysis. The logic behind this approach is that, in contrast to trait values inherited from a common ancestor, differences that accrue in two lineages subsequent to cladogenesis are independent and can be treated as such in, for example, correlation and regression analyses (e.g., Felsenstein, 1985; Harvey and Pagel, 1991; Garland et al., 1999).

Two methods based on this logic are used here: phylogenetically independent contrasts and pairwise comparisons (Felsenstein, 1985; Møller and

Birkhead, 1992). Both of these methods rely on differences between closely related taxa, but they differ in the amount of information retained for analysis. This difference is illustrated in the cladogram presented in Figure 2.8. The pairwise-comparisons approach focuses only on differences between the tips of the cladogram and ignores differences between the internal nodes. In other words, differences between closely related species are retained for analysis while differences between higher taxa are discarded. Moreover, comparisons are further restricted to sister species, indicated by the solid arrows in Figure 2.8. The end result is that, given n species in a sample, there are $n/2$ independent evolutionary events that can be analyzed. On the other hand, the independent-contrasts approach uses differences between the tips and between the internal nodes (dashed arrows in Fig. 2.8), resulting in $n - 1$ independent evolutionary events.[9] Thus, while both methods reduce the original sample size, the reduction is much less severe when independent contrasts are used than when pairwise comparisons are used, making the former method statistically more powerful. Moreover, and more importantly, unlike pairwise comparisons, which do not make use of potentially informative differences among higher taxa, independent contrasts retain all of the information contained in the original sample (Felsenstein, 1985).

Why, then, might pairwise comparisons be preferred in some cases? Closely related species are generally similar in most aspects of their biology, and thus pairwise comparisons allow researchers to control for variables that are likely

---

[9] The value for each internal node is the weighted average of its two descendent nodes (e.g., node A’s value is the mean of nodes 1 and 2).

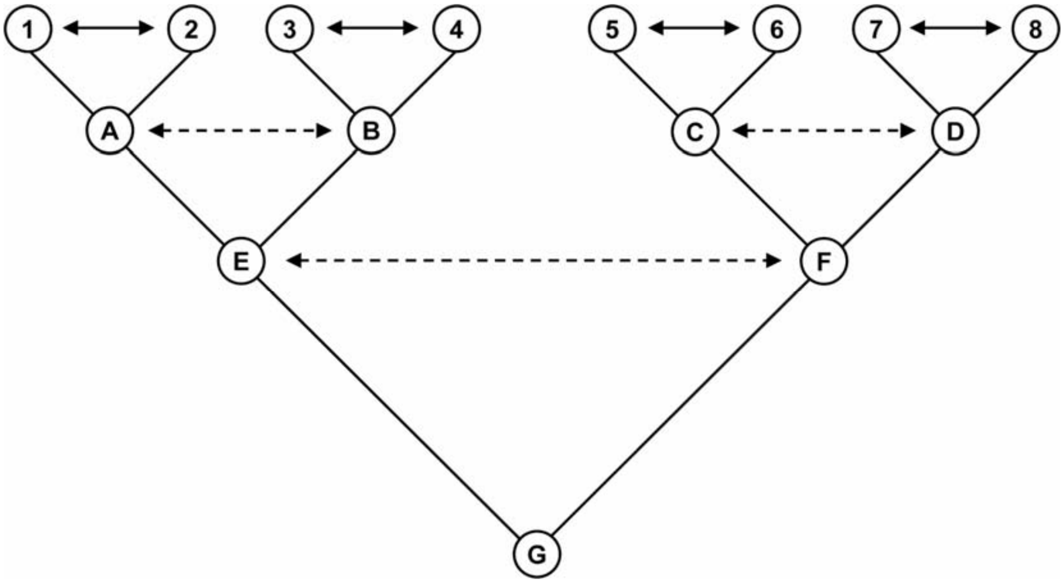


Fig. 2.8. Cladogram illustrating the difference between independent contrasts and pairwise comparisons. Nodes 1–8 are extant species; nodes A–G represent hypothetical ancestors. Both methods rely on differences between sister species (represented by solid arrows), but the independent-contrasts approach also incorporates differences between internal nodes (represented by dashed arrows). See text for further discussion.

to confound comparisons between taxa that are more distantly related (Fleagle, 1976, 1977; Fleagle and Meldrum, 1988; Møller and Birkhead, 1992; Spencer, 1995; Grafen and Ridley, 1996; Maddison, 2000; Vinyard et al., 2003). For example, as noted above, the measurements used to estimate temporalis size are dependent on the size and shape of the cranial vault, and because distantly related species are likely to differ in these variables, comparisons of temporalis size should be limited to closely related species (Spencer, 1995). Moreover, the measurements of muscle size used in this study assume that differences in PCSA resulting from variation in fiber length and pinnation angle are minor. While this assumption is unlikely to be true in many cases, closely related species are more likely to be similar in these parameters than species that are more distantly related (Spencer, 1995).

The procedures used to evaluate pairwise comparisons are described in the section on resampling methods at the end of this chapter, and further details are provided in subsequent chapters where relevant. The procedures used for obtaining and analyzing independent contrasts are outlined below. This discussion is based mainly on the summary of the method given by Smith and Cheverud (2002).

Independent contrasts were generated using the PDAP:PDTREE module (version 1.14) of Mesquite 2.6 (Midford et al., 2008; Maddison and Maddison, 2009). The phylogeny used to calculate contrasts is shown in Figure 2.9. Of the relationships depicted in this figure, only the branching order of the three platyrrhine families—Atelidae, Cebidae, and Pitheciidae—lacks consensus,

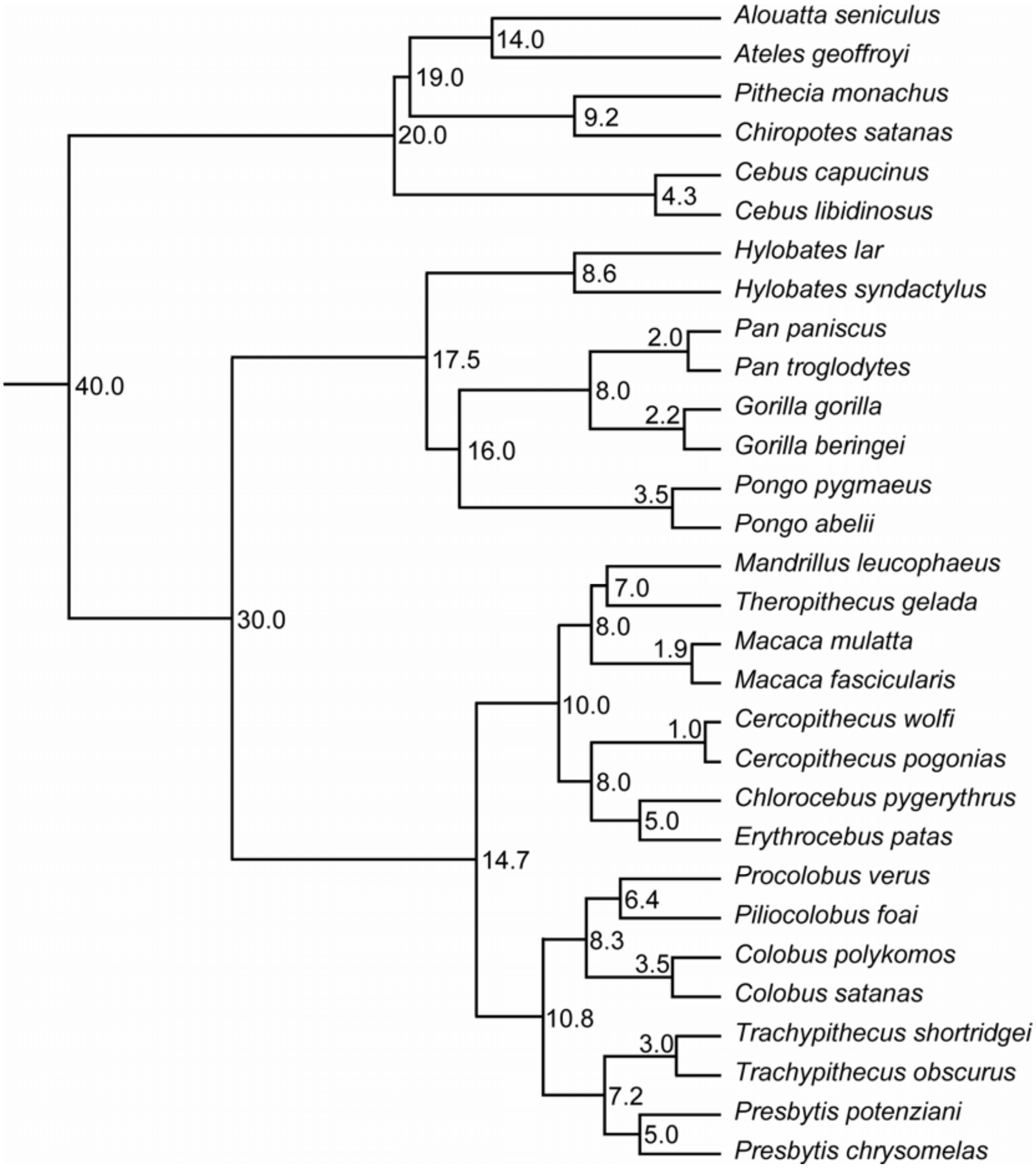


Fig. 2.9. Phylogeny and divergence dates (in millions of years) used to calculate independent contrasts.

probably reflecting the rapid radiation of these lineages from a common ancestor in the early Miocene (e.g., Schneider et al., 1993, 1996, 2001; Harada et al., 1995; Horovitz and Meyer, 1995; Porter et al., 1995, 1997, 1999; Barroso et al., 1997; Goodman et al., 1998; Horovitz et al., 1998; Canavez et al., 1999; von Dornum and Ruvolo, 1999; Steiper and Ruvolo, 2003; Prychitko et al., 2005; Ray et al., 2005; Opazo et al., 2006; Schrago, 2007; Hodgson et al., 2009; Osterholz et al., 2009; Wildman et al., 2009). This polytomy was arbitrarily resolved for analysis, with the Pitheciidae and Atelidae linked to the exclusion of Cebidae. The effect of this decision was evaluated by reanalyzing subsets of the data using alternative phylogenetic relationships, but the results differed only minimally and so are not reported.

Figure 2.9 also presents the divergence dates (in millions of years) for each clade, which were used to estimate branch lengths between nodes. Most of these dates are based on molecular data (Schneider et al., 1993; Hayasaka et al., 1996; Ruvolo, 1997; Page et al., 1999; Raaum et al., 2005; Chatterjee, 2006; Opazo et al., 2006; Steiper and Young, 2006; Sterner et al., 2006; Schrago, 2007; Ting, 2008; Wangchuk et al., 2008; Hodgson et al., 2009), but in cases where such information was unavailable, branch lengths were taken from Smith and Cheverud (2002). As discussed by Felsenstein (1985), the variance of each contrast is proportional to the sum of the contrast's branch lengths, and thus the standard deviation of each contrast can be estimated as the square root of the sum of its branch lengths. Independent contrasts are typically divided by their standard deviations in order to equalize their variances (Felsenstein, 1985). This standardization procedure is necessary because differences between two species (or nodes) separated by a long period of time are generally expected to be greater than those between species separated by a short period of time (Felsenstein, 1985; Garland et al., 1992). Thus, standardization prevents contrasts between distantly related taxa from having undue influence on correlation and regression statistics (Garland et al., 1992).

Standardization using raw branch lengths is not guaranteed to produce a set of contrasts with equal weights (Garland et al., 1992). One way to evaluate whether contrasts have been properly standardized is by plotting the absolute values of the standardized contrasts against their original (i.e., unstandardized) standard deviations (Garland et al., 1992; Díaz-Uriarte and Garland, 1996, 1998). The correlation between these two variables should be as close to zero as possible; a positive correlation indicates that the contrasts between distantly related nodes are understandardized (i.e., standardization has not removed the effects of branch length), whereas a negative correlation indicates that contrasts between distantly related nodes have been overstandardized, thus giving the contrasts between closely related species greater weight (Garland et al., 1992). In cases where standardized contrasts are correlated with their standard deviations, various branch-length transformations can be attempted to obtain proper standardization (Garland et al., 1992; Díaz-Uriarte and Garland, 1996, 1998). This procedure was followed here using the transformation options provided by the PDAP:PDTREE module. For most variables, branch-length transformations were necessary. Following the recommendations of Díaz-Uriarte and Garland

(1996, 1998), a degree of freedom was subtracted for each variable in an analysis that required branch-length transformation.

Independent contrasts were used to compute interspecific correlations. Unlike correlations and regressions derived from species means, contrast-based correlations and regressions must be forced through the origin (i.e., regression intercept must equal zero) because the sign of a contrast is arbitrary (Garland et al., 1992). For example, in Fig. 2.8, node 1 can be subtracted from node 2 or vice versa.[10] If correlations and regressions are not computed through the origin, then the correlation coefficient and slope of the regression will vary depending on the direction of subtraction (Legendre and Desdevises, 2009). Because the regression intercept is not estimated from the data, only a single degree of freedom is lost (Garland et al., 1992). Thus, if no branch-length transformations are required, the degrees of freedom for contrast-based correlations and regressions are the same as for correlations and regressions derived from species means (i.e., $n - 2$) (Garland et al., 1992).

Size-adjustment

Two species will differ in the size of a particular structure simply because they differ in body size. Because many biological questions, including the ones addressed in this dissertation, are concerned with differences in form (i.e., shape or relative size) rather than differences in absolute size, it is necessary when conducting interspecific comparisons to scale traits of interest using another

---

[10] Note that, although the direction of subtraction is arbitrary, it must be the same for all variables.

variable chosen to represent organismal size. For example, *Gorilla beringei* males have a mean combined canine height that is approximately 15% greater than that for *Erythrocebus patas* males (i.e., 55.42 mm versus 48.36 mm; Table 2.6). However, with respect to skull size (as represented by the skull GM; see Table 2.4), male mountain gorillas are nearly twice as large as male patas monkeys (i.e., 124.01 versus 62.52). Thus, relative to skull size, the canines of male patas monkeys are taller than those of male mountain gorillas. It is this relationship—relative size—that is the most relevant in terms of testing the interspecific predictions of the pleiotropy and masticatory-efficiency hypotheses.

There are several methods available for size-adjustment (reviewed by Jungers et al., 1995); the two most commonly used in the anthropological literature are shape ratios and residuals from a least-squares regression line. The distinction between these two methods can be summarized as *relative size* versus *controlling for size* (Smith, 2005). A shape ratio expresses relative size: the structure of interest (e.g., combined canine height) is divided by a size variable (e.g., skull GM), and the resulting quotient is the size of the structure relative to the size variable. Shape ratios do not eliminate size-correlated changes in shape (i.e., allometry) and are therefore not completely size-free (Corruccini, 1987, 1995; Albrecht et al., 1993, 1995; Jungers et al., 1995). In contrast, when residuals are used, size and size-correlated shape are statistically removed from the trait of interest (Corruccini 1987, 1995; Jungers et al., 1995). This approach uses the scaling relationship between two variables as a criterion of subtraction: the regression slope is interpreted as the line of functional equivalence, and species with similar residual values are thought to "represent the 'same' animal displayed over a wide range of body size" (Pilbeam and Gould, 1974, p. 898; see also Gould, 1975). When the relationship between the trait of interest and the size variable is isometric, residuals and shape ratios will produce identical results (Jungers et al., 1995). When the relationship is allometric, results will diverge.

Both methods of size-adjustment were used here, with the skull GM acting as the size variable. Skull size was used instead of body size for two reasons: first, body-mass data are not available for most of the museum specimens measured for this study, and it is not clear that the species means compiled by Smith and Jungers (1997; see Table 2.4) are reliable for every species included in this analysis; second, for some of the questions examined here, a local, functionally related size variable is more appropriate. For example, in terms of testing the predictions of the masticatory-efficiency hypothesis, the size of the canines relative to their functional environment (i.e., the skull) is more relevant than their size relative to body mass (Ravosa, 1990; see also Hylander, 1985; Vinyard et al., 2003).

Shape ratios were the preferred method of size-adjustment for pairwise comparisons because each comparison comprises closely related species of similar size, thus mitigating the effects of allometry. On the other hand, given the wide range of size represented by the species included in the study (see Table 2.4), allometric effects are a potentially confounding factor for interspecific correlations computed using independent contrasts. Because shape ratios do not control for size-correlated changes in shape, several researchers have recommended that residuals be used instead (e.g., Reist, 1985; Packard and Boardman, 1987, 1988; Albrecht et al., 1993, 1995). However, although residuals are size-free, they present a number of problems. Paramount among these is the fact that there is usually no basis for equating a scaling relationship with functional equivalence (Smith, 1980; Corruccini, 1987, 1995; Harvey and Pagel, 1991; Jungers et al., 1995). In many cases, an allometric relationship will reflect functional differentiation related to size, and thus the removal of size-correlated shape through the use of residuals has the potential to mask important functional information (Oxnard, 1978; Smith, 1980; Harvey and Pagel, 1991); as noted by Jungers et al. (1995, p. 153): "Residuals are by definition size-free, but they are also frequently shape-free, especially when allometry is present in the data set." Moreover, residuals, unlike shape ratios, have the undesirable property of not being intrinsic features of organisms; rather, because the relationship between two variables will vary depending on sample composition, residual values are sample-dependent (Corruccini, 1987, 1995; Jungers et al., 1995). In this study, both shape ratios and residuals were used to compute interspecific correlations unless (1) the relationship of each variable in the analysis to skull size was isometric or (2) the use of shape ratios could be justified using functional criteria.

Resampling methods

Resampling methods were used to evaluate differences between the two species in each pairwise comparison. Each sex was examined separately because most anthropoids are sexually dimorphic (see Tables 2.4 and 2.6). Two procedures were employed—permutation tests and the bootstrap (Efron and

Tibshirani, 1993; Manly, 1997). The use of two different procedures was necessary because the samples from which the dental and skull data derive are not identical in terms of specimen composition. Consequently, measurements from some individuals could not be directly size-adjusted (i.e., the dental measurements for some individuals do not have associated skull GMs), precluding the use of permutation tests. However, indirect size-adjustment for the purpose of significance testing was possible using the bootstrap. This procedure is described below using the comparison of relative combined canine height between males of *Macaca mulatta* and *Macaca fascicularis* as an example (see also Scott et al., 2009).

Step 1. Bootstrap (i.e., resample with replacement) the sample of combined canine heights for *M. mulatta* 2000 times, with each bootstrap sample being identical in size to the original sample (n = 14 in this case).[11]

Step 2. Compute the mean for each bootstrap sample.

Step 3. Perform steps 1 and 2 using the sample of skull GMs for *M. mulatta* (n = 17).

Step 4. Randomly pair the 2000 combined-canine-height means with the 2000 skull-GM means and divide the former by the latter. The

---

[11] Note that, because resampling was conducted with replacement, a specimen could be included in each bootstrap sample multiple times or not at all. When a sample of size n = 14 is resampled with replacement, the total number of unique combinations of specimens is over 20 million, and thus it is highly unlikely that any two iterations will produce samples with identical specimen compositions.

resulting quotients are shape ratios representing mean relative combined canine height.

Step 5. Repeat steps 1–4 using the *M. fascicularis* samples ($n = 12$ for combined canine height; $n = 22$ for skull GM).

Steps 1–5 produce two distributions of shape ratios, one for *M. mulatta* and one for *M. fascicularis*. The middle 95% of each distribution is equivalent to the 95% confidence interval for mean relative combined canine height for each species (Efron and Tibshirani, 1993; Manly, 1997). A crude estimate of the statistical significance for the comparison between the two macaque species can be obtained by comparing their 95% confidence intervals; if the two intervals do not overlap, then the two species can be said to differ at the $\alpha = 0.05$ level. A more precise *p*-value was obtained as follows:

Step 6. Randomly pair the 2000 shape ratios for *M. mulatta* with those for *M. fascicularis*.

Step 7. For each pairing, subtract the shape ratio for *M. mulatta* from the shape ratio for *M. fascicularis*. This step produces a distribution of pairwise differences in relative combined canine height.

Step 8. Recenter the distribution of pairwise differences on zero by subtracting the mean of the 2000 pairwise differences from each pairwise difference (Figure 2.10). This step is necessary because the distribution of pairwise differences will be centered on the observed difference between *M. mulatta* and *M. fascicularis*. In

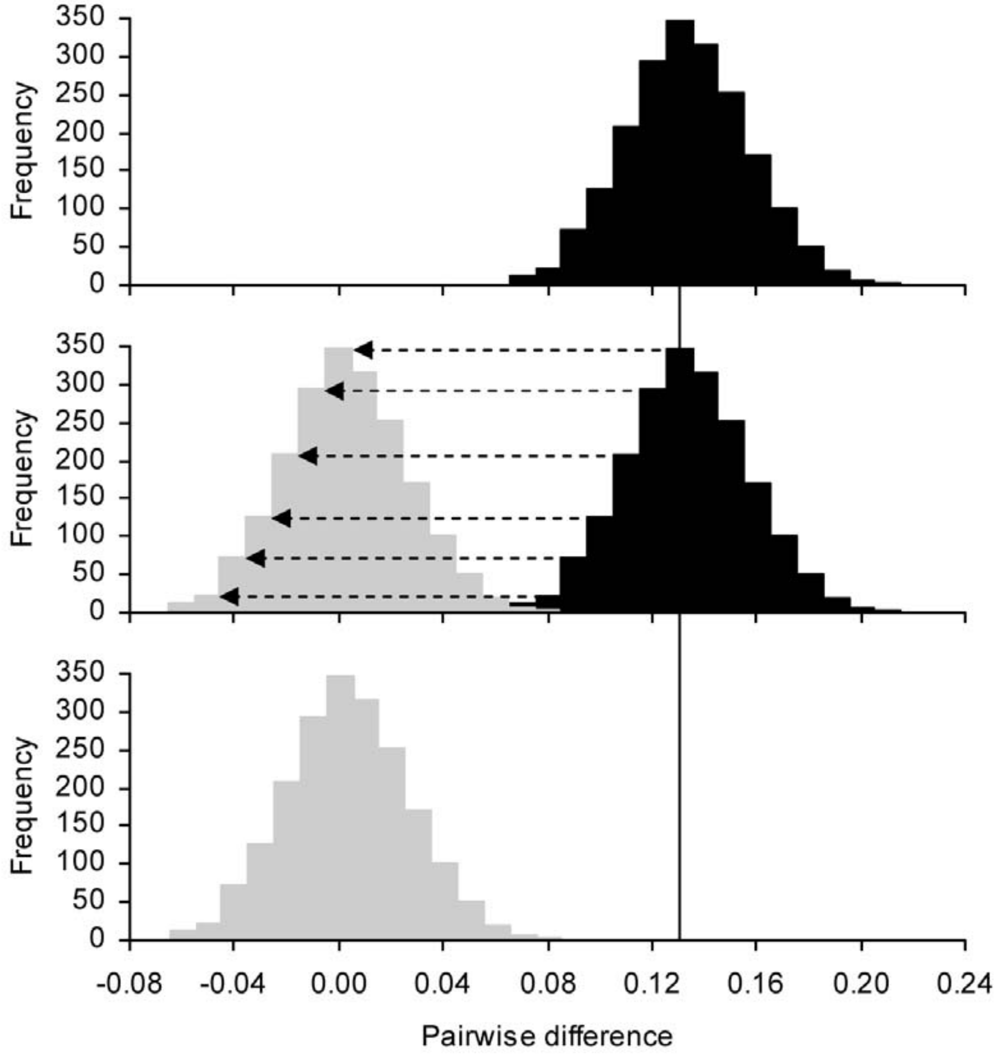


Fig. 2.10. Illustration of step 8 in the bootstrap procedure. Top: Bootstrap distribution of pairwise differences in relative combined canine height between males of *M. mulatta* and *M. fascicularis*. Middle: The distribution is recentered on zero. Bottom: The observed difference between the two species, represented by the solid vertical line, is evaluated using the zero-centered distribution. In this case, because the observed difference falls outside of the zero-centered distribution, *M. mulatta* and *M. fascicularis* are highly

order to derive a *p*-value for the observed difference between the two species, the distribution must be recentered on—i.e., the mean of the distribution must equal—zero. According to Manly (1997, p. 99), “the idea with this approach is to use bootstrapping to approximate the distribution of a suitable test statistic when the null hypothesis is true” (i.e., no difference between samples).

Step 9. Using the zero-centered distribution, count the number of values that are as extreme as or more extreme than the observed difference between *M. mulatta* and *M. fascicularis* (disregarding the sign of the difference).

Step 10. Use the following formula to obtain the *p*-value for the comparisons: $p = (M + 1)/(N + 1)$, where M is the number of bootstrap differences (absolute values) greater than or equal to the observed difference, N is the total number of bootstrap differences (i.e., 2000), and one is added to M and N to include the observed difference.

If each dental individual had an associated skull GM, then the shape ratios would be computed prior to using the bootstrap procedure, and steps 3 and 4 would be omitted. The difference between bootstrapping each variable within a species separately and then calculating shape ratios (i.e., *indirect size-adjustment*, as described above) versus bootstrapping a sample of shape ratios calculated for each individual specimen (i.e., *direct size-adjustment*) has to do with the correlation between the two variables. Indirect size-adjustment assumes a correlation of zero between the trait of interest (combined canine height) and the size variable (skull size). If the trait of interest and the size variable are not correlated, then bootstrapping the variables separately and creating shape ratios from the means of the bootstrap samples will produce results that are similar to those obtained using direct size-adjustment. On the other hand, covariation between the numerator and denominator of a ratio reduces the ratio's standard error (Smith, 1999). In other words, if there is a correlation between the trait of interest and the size variable, then using direct size-adjustment will produce a distribution of pairwise differences that is narrower than the one obtained using indirect size-adjustment, resulting in a lower p-value. In such cases, the bootstrap procedure described above will be a *conservative* test of the null hypothesis of no difference.

Given the large number of statistical tests performed in this study, the possibility that some of the significant results ($p < 0.05$) are type I errors (i.e., false rejections of the null hypothesis) is a concern. The normal way of dealing with this issue is to lower the level at which a test achieves statistical significance using Bonferroni adjustments so that the overall error rate for a study, or some component of the study, is maintained at $\alpha = 0.05$ (e.g., Holm, 1979; Rice, 1989; Sokal and Rohlf, 1995). This approach is not adopted here because it would reduce the power to detect significant differences to an unreasonably low level (Perneger, 1998; Moran, 2003; Nakagawa, 2004). Rather, following the arguments made by Moran (2003),[12] the overall *pattern* of significant differences is used to evaluate the pleiotropy and masticatory-efficiency hypotheses rather than the individual *p*-values for each statistical test.

---

[12] "For example, suppose a researcher has 10 individual tests in a table with five of them significant at p = 0.049. Using the sequential Bonferroni correction, the maximum p-value to reject the first null hypothesis is 0.005. None fall below that level, so the researcher is forced to fail to reject all null hypotheses. However, the probability of having five significant tests at a p-value of 0.049, and all of these results being due to random chance is very low" (Moran, 2003, p. 403).

CHAPTER 3—THE PLEIOTROPY HYPOTHESES

The predictions of the three pleiotropy hypotheses tested in this study are illustrated in Figure 3.1 using an idealized two-species model: the two species are sisters and do not differ in body size (obviating the need to size-adjust the data). One species represents the primitive conditions for canine and incisor or postcanine size (white circles); the other species represents the derived, reduced-canine condition (black circles). According to the incisor pleiotropy hypothesis (Fig. 3.1, upper plot; Jolly, 1970a), canine size and incisor size should be positively correlated within species (i.e., the intraspecific prediction) and between species (i.e., the interspecific prediction). With respect to the two versions of the postcanine pleiotropy hypothesis, the negative postcanine pleiotropy hypothesis (Fig. 3.1, lower left plot; Jolly, 1970a; Kieser and Groeneveld, 1987a; McCollum and Sharpe, 2001) predicts a negative correlation between canine size and postcanine size within and between species, whereas the positive postcanine pleiotropy hypothesis (Fig. 3.1, lower right plot; Alba et al., 2001) predicts a positive correlation between these two variables. Note that, in each plot, the interspecific relationship is an extension of the intraspecific relationship between canine size and incisor or postcanine size.

The three pleiotropy hypotheses are based primarily on patterns of morphological variation in tooth size observed among living and fossil primate species (e.g., the combination of diminutive anterior teeth and postcanine megadontia in *Au. boisei* and *Au. robustus*) rather than on data indicating that different components of the dentition are genetically correlated *within* species

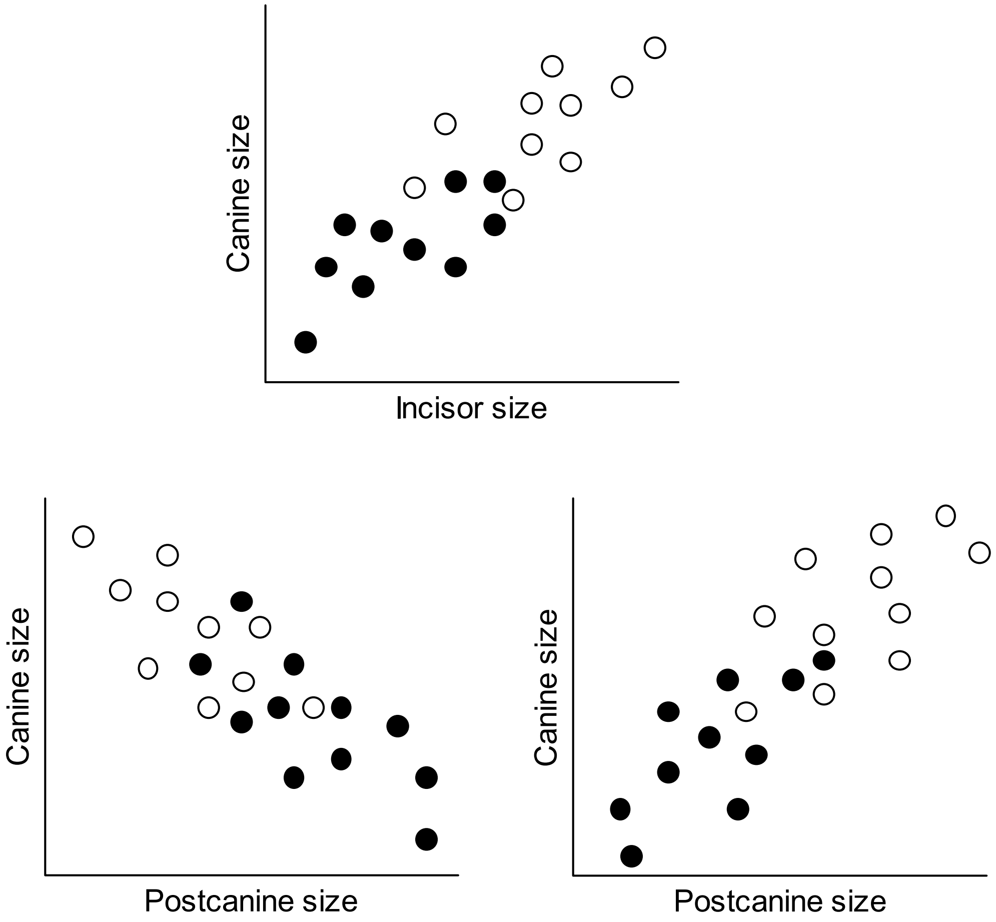


Fig. 3.1. Predictions made by the incisor (top) and postcanine (bottom) pleiotropy hypotheses. Each plot contains two closely related species, one represented by the white circles and the other by the black circles. See text for discussion.

(Jolly, 1970a; Alba et al., 2001; McCollum and Sharpe, 2001; but see Kieser and Groeneveld, 1987a). Such correlations provide evidence for pleiotropic links among structures, and thus demonstrating their existence is a necessary first step in testing any hypothesis linking macroevolutionary change to pleiotropy. Unfortunately, estimating genetic correlations requires very large samples of related individuals (Cheverud, 1988), which is problematic for broad-scale comparative studies such as this one.

An alternative is to rely on within-species phenotypic correlations. Several studies have shown that phenotypic correlations are similar in magnitude to reliably estimated genetic correlations (i.e., those estimated using a large effective sample size)[1] (Cheverud, 1988; Roff, 1995; Reusch and Blanckenhorn, 1998; Waitt and Levin, 1998; Réale and Festa-Bianchet, 2000; Åkesson et al., 2007; but see Willis et al., 1991), and some of the authors of these studies have argued that phenotypic correlations are preferable when effective sample size is too small to generate accurate estimates of genetic correlations. Several investigators have taken advantage of this correspondence to examine morphological integration (sensu Olson and Miller, 1958; Cheverud, 1982, 1996b)[2] in the anthropoid skull using only phenotypic data (e.g., Cheverud, 1989;

---

[1] Cheverud (1988) defined *effective sample size* as the heritability of a trait multiplied by the number of families used to estimate the genetic correlation. He further recommended using an effective sample size of $n \geq 40$ for generating accurate genetic correlations.

[2] Morphological integration is “the interdependency of morphological parts that, in combination, produce an organized, integrated, functional whole” (Cheverud, 1995, p. 63).

Ackermann and Cheverud, 2000; Marroig and Cheverud, 2001; Ackermann, 2002, 2005; González-José et al., 2004; Marroig et al., 2004; Polanski and Franciscus, 2006; Mitteroecker and Bookstein, 2008; Bandoni de Oliveira et al., 2009). The few studies of morphological integration that have included comparisons of phenotypic and genetic correlations and variance/covariance matrices generally support the legitimacy of this approach (Cheverud, 1982; Cheverud 1995, 1996a; Hlusko and Mahaney, 2009), and thus it is adopted here.

In order to maximize statistical power, intraspecific correlations between canine size and incisor and postcanine size were computed using combined-sex samples. In order to circumvent the confounding influence of sexual dimorphism (i.e., a spurious positive correlation driven solely by differences in male and female means; e.g., Siegel, 1978; Wood, 1979a,b; Siegel and Gest, 1980; Wood and Stack, 1980), male and female values were size-adjusted using sex-specific means (Plavcan and Daegling, 2006). In other words, the female mean was subtracted from each female value, the male mean was subtracted from each male value, and the resulting residuals were combined into a single sample. These data were used in the primary test of the intraspecific prediction of the pleiotropy hypotheses. Single-sex correlations were also computed for comparison, but note that the power to detect significant associations between variables is severely reduced in these samples.

Dental data were not size-adjusted in the conventional sense of the term prior to computing intraspecific correlations, mainly because the specimen compositions of the dental and skull samples used in this study are not identical.

However, size-adjustment is unnecessary in this portion of the analysis for two reasons. First, numerous studies have found that very little of the variance in tooth size within species is attributable to overall organismal size when sex is controlled (e.g., Garn et al., 1968; Anderson, 1975; Lauer, 1975; Swindler and Sirianni, 1975; Henderson and Corruccini, 1976; Anderson et al., 1977; Siegel, 1978; Wood, 1979a,b; Siegel and Gest, 1980; Wood and Stack, 1980; Kieser and Groeneveld, 1987b,c, 1988, 1990, 1991; Shea and Gomez, 1988; Hlusko et al., 2006); in fact, these studies show that tooth size is frequently uncorrelated with measures of skull or body size in adults, indicating that tooth size is largely independent of these variables at the intraspecific level.[3] Second, absolute size is of interest because canine reduction is not merely a relative-size phenomenon; for example, the canines of early hominins are not only relatively smaller than those of living and fossil apes—they are absolutely smaller. Moreover, within species, it is the absolute size of the canine that is relevant in terms of social behavior (Leigh et al., 2008). Thus, the intraspecific predictions of the pleiotropy hypotheses, particularly the negative postcanine pleiotropy hypothesis, should be tested using absolute size (adjusted for sexual differences).

Canine height was not included in the intraspecific portion of the analysis because this measurement is more affected by tooth wear than the other dimensions. As noted in Chapter 2, it is impossible in many cases to determine

---

[3] This is not to say that they are completely independent. Hlusko et al. (2006) suggested that the lack of a clear phenotypic relationship between tooth size and body size can be attributed to environmentally induced variation, the effect of which is amplified by the disparity in the ages at which dental and body growth cease.

how much of the original crown height is missing, even in teeth that are clearly only slightly worn. This unavoidable problem is exacerbated by the fact that within-species differences in canine height among individuals of the same sex are relatively slight. Thus, while the inclusion of slightly worn canines is unlikely to unduly affect the results of comparisons of crown height between sexes or between species (e.g., Plavcan, 1990; Greenfield and Washburn, 1991; Greenfield, 1992c; Plavcan and van Schaik, 1992; Plavcan, 1993; Plavcan et al., 1995, 2009; Thorén et al., 2006; Plavcan and Ruff, 2008), attempts to correlate canine height with postcanine or incisor size within species are probably unreliable. Thus, the relationships between basal canine area and other components of the dentition were used as a proxy for canine height. This procedure undoubtedly introduces error into the analysis, as canine height and basal crown area are unlikely to be perfectly correlated within species, but the lack of large samples of unworn canines renders it necessary.

Following the intraspecific analysis, two procedures were used to test the interspecific prediction of each pleiotropy hypothesis: the *strong interspecific test* and the *weak interspecific test*. The strong test used the pairwise-comparisons approach (i.e., comparisons of the sister species in the phylogeny presented in Fig. 2.9) and included only those comparisons in which both of the constituent species exhibited the predicted intraspecific correlations. Thus, with respect to the incisor pleiotropy hypothesis and positive postcanine pleiotropy hypothesis, the strong test required that each species in a comparison exhibit a significant positive intraspecific correlation; in the case of the negative postcanine pleiotropy hypothesis, each species in a comparison was required to exhibit a significant negative correlation. The idea behind the strong test is that a robust test of the pleiotropy hypothesis should include only those species that exhibit evidence of pleiotropy (i.e., the predicted intraspecific correlations). Moreover, because pleiotropic connections can be expected to evolve—weakening, strengthening, or dissolving based on changing developmental or functional relationships (e.g., Lande, 1979; Cheverud, 1996b)—it is desirable to compare closely related species in which the intraspecific correlations are in the same direction, as it is reasonable to infer that these relationships were inherited from a recent common ancestor. Predictions regarding difference in relative tooth size cannot be made for comparisons that do not meet these conditions, and thus they were removed from the strong test.

Differences in relative tooth size—including the heights of the maxillary and mandibular canines (but not combined canine height)—between sister species were analyzed using the bootstrap procedure described at the end of Chapter 2. Sexes were examined separately in this portion of the analysis. Shape ratios were used to estimate relative size, with the skull GM acting as the size variable. Given that most of the pairwise comparisons encompassed species that were very similar is size, the potentially confounding influence of allometry was not a concern, making the use of regression residuals to estimate relative size unnecessary.

With respect to the weak test, the interspecific predictions of the incisor and postcanine pleiotropy hypotheses were tested using interspecific correlations generated from the entire sample of species (except *Pithecia monachus*; see Chapter 2). The weak test, as its name implies, represents the opposite extreme of the strong test: it sacrifices the rigor of the strong test by including species regardless of whether or not they exhibit evidence of pleiotropy (i.e., a significant intraspecific correlation between canine size and incisor or postcanine size). However, in doing so, it maximizes statistical power by increasing sample size and incorporating information on the magnitude of interspecific differences. Thus, whereas the strong test is statistically conservative (i.e., less likely to reject the statistical null hypothesis of no effect) and can thus provide strong support for the pleiotropy hypothesis but only a weak rejection, the weak test is more powerful and therefore capable of detecting a weaker interspecific signal.[4] It is worth noting that the absence of a significant intraspecific correlation between canine size and another component of the dentition in some species may be the result of small sample size or sampling error. However, using such species reduces the level of confidence that can be placed in implicating pleiotropy as the cause of an interspecific correlation (see also discussion in Plavcan, 1998).

Despite the inclusion of species that do not exhibit the predicted intraspecific correlations, the use of this test is still contingent upon the results of the intraspecific analysis. The weak test is only justified if there is no variation in the direction of the statistically significant intraspecific canine-incisor and canine-postcanine correlations among species. If, for example, some of the species in the sample exhibit positive canine-postcanine correlations and some exhibit negative

---

[4] See discussion of phylogenetic comparative methods in Chapter 2.

canine-postcanine correlations (i.e., some species support the positive postcanine pleiotropy hypothesis and some support the negative postcanine pleiotropy hypothesis), then there is no reason to predict a samplewide correlation between relative canine and incisor size.

An important feature of the weak test is that it allows the incisor and postcanine pleiotropy hypotheses to be evaluated simultaneously. If canine size is correlated with both incisor and postcanine size within species, then these two components of the dentition may have antagonistic effects on canine size in some species, preventing the manifestation of a clear interspecific signal. This situation presents a problem for the strong test but not for the weak test: the interspecific correlations generated for the weak test can be used to compute partial correlations, which allow the effects of one variable to be statistically controlled while examining the association between two other variables (Sokal and Rohlf, 1995). Thus, for example, if the correlation between relative canine size and relative postcanine size obscures an association between relative canine size and relative incisor size (i.e., acting as a suppressor variable), then the partial correlation between the latter two variables holding relative postcanine size constant will reveal a statistically significant association.

RESULTS

Intraspecific test

Intraspecific canine-incisor correlations

The results of the intraspecific canine-incisor correlation analysis are summarized in Figure 3.2 and Table 3.1. For the combined-sex analysis, nineteen

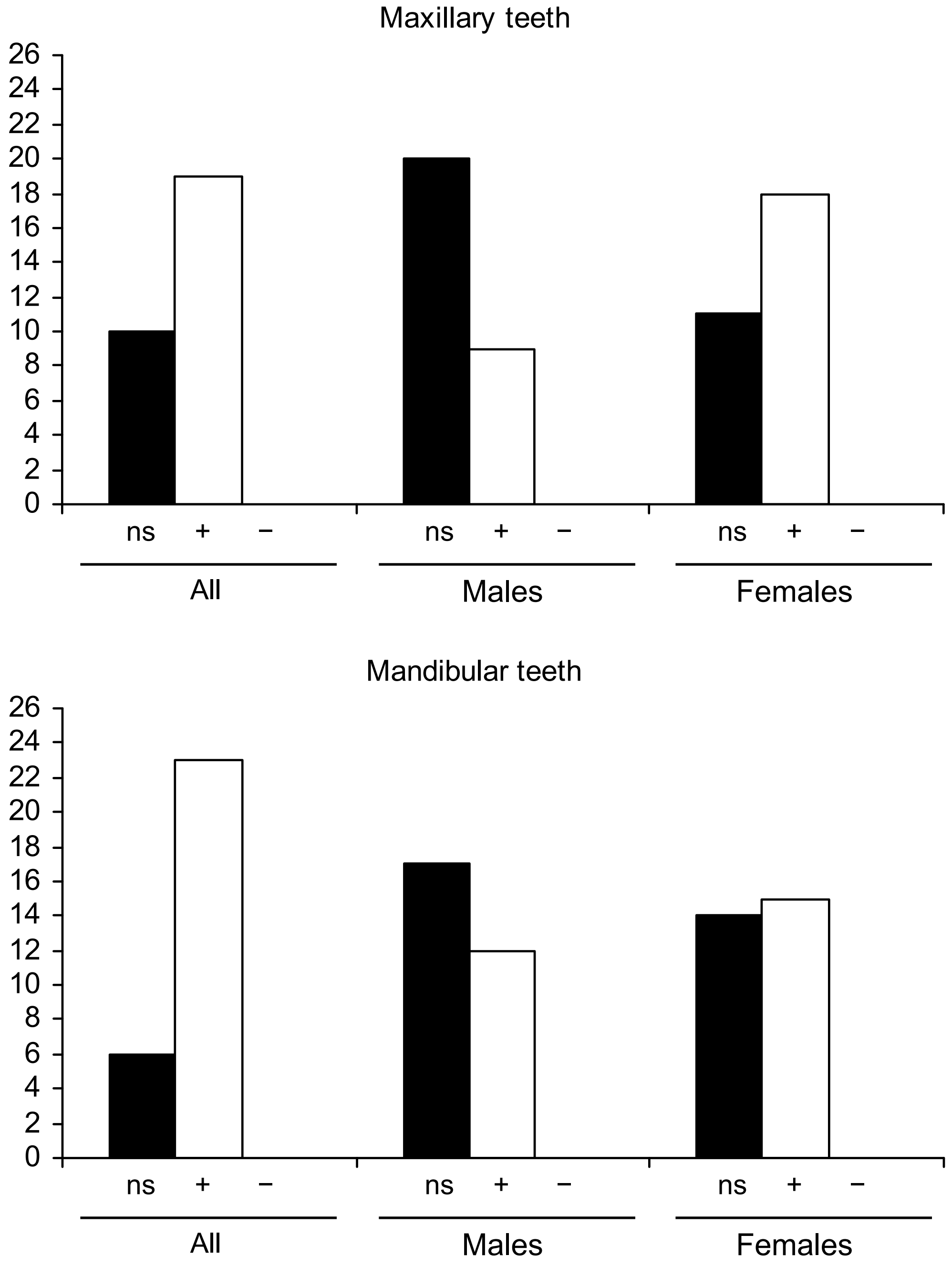


Fig. 3.2. Intraspecific canine-incisor correlations. Histograms show the number correlations that are nonsignificant (ns), positive (+), and negative (−).

TABLE 3.1. Intraspecific canine-incisor correlations

	Both sexes		Males		Females	
	Max	Mand	Max	Mand	Max	Mand
Al. seniculus	—	0.57	—	0.71	—	—
At. geoffroyi	0.67	0.37	0.60	—	0.82	0.47
Ceb. libidinosus	0.45	0.46	—	0.66	0.56	—
Ceb. capucinus	0.50	—	—	—	0.71	—
Ch. satanas	0.66	0.62	—	0.68	0.74	0.66
Cer. pogonias	0.42	—	0.69	0.55	—	—
Cer. wolfi	0.51	—	0.51	—	—	—
Chl. pygerythrus	—	0.81	—*	—*	0.66	0.90
Er. patas	—	0.66	—	0.67	0.76	—*
Mac. mulatta	0.47	0.57	0.66	0.52	0.62	0.69
Mac. fascicularis	0.50	0.44	—*	—	0.62	—
Th. gelada	0.64	0.85	0.61	0.84	0.96	0.97
M. leucophaeus	—	0.59	—	0.56	—	0.62
Pil. foai	0.46	0.49	—	0.50	0.63	0.52
Pro. verus	0.39	0.55	—	0.67	0.44	—
Col. satanas	0.49	0.37	0.56	—	—	0.61
Col. polykomos	0.59	0.50	—	—	0.75	0.66
Pre. chrysomelas	0.64	0.72	0.66	0.73	0.60	0.72
Pre. potenziani	—	0.57	—*	—	—*	—*
Tr. obscurus	0.36	0.53	—	—	0.57	0.66
Tr. shortridgei	—	0.73	—*	0.79	—*	—*
Hy. lar	—	—	—	—	—	—
Hy. syndactylus	0.66	0.42	0.65	—	0.72	0.67
Go. beringei	0.75	—	0.77	—*	—*	—*
Go. gorilla	—	0.44	—	—	0.77	0.57
Pan paniscus	—	—	—	—*	—*	—
Pan troglodytes	0.47	0.47	—	—	0.57	0.49
Po. abelii	—	0.56	—*	—*	—*	—*
Po. pygmaeus	0.47	0.48	—	—	0.54	0.57

A dash indicates that the correlation is nonsignificant; all other correlations are significant ($p < 0.05$). Samples comprising fewer than $n = 10$ individuals that exhibit nonsignificant correlations are marked with an asterisk (*).

of the twenty-nine species (65.5%) used to test the incisor pleiotropy hypothesis exhibit a significant positive association between maxillary basal canine area and incisor area, and twenty-three (79.3%) exhibit a significant positive association between these two components of the mandibular dentition. None of the correlations are negative. Thus, for species in which canine and incisor area are significantly correlated, the relationship is in the predicted direction.

Nonsignificant correlations (ten in the combined-sex maxillary analysis; six in the combined-sex mandibular analysis), which suggest a lack of pleiotropy in some species, are not patterned in any meaningful way. Sample size is a concern for some of the species; for example, the combined-sex *Pongo abelii* maxillary sample and the combined-sex *Gorilla beringei* mandibular sample, both of which fail to exhibit significant correlations, each contain only $n = 11$ individuals. However, nonsignificant correlations are also found among species represented by larger samples ($n > 30$), including one of the largest in the data set (the *Cebus capucinus* combined-sex mandibular sample, $n = 46$), indicating that sample size alone cannot explain the nonsignificant correlations. Additionally, nonsignificant correlations for the maxillary and mandibular teeth are randomly distributed with respect to each other; in only two species—*Pan paniscus* and *Hylobates lar*—are the correlations for both the maxillary and mandibular teeth nonsignificant. Nonsignificant correlations are also distributed randomly with respect to phylogeny. Only two pairs of sister species share nonsignificant correlations in the same dental arcade: *Erythrocebus patas* and *Chlorocebus pygerythrus* both lack a statistically significant association between incisor and canine area in the maxillary dentition, and *Cercopithecus wolfi* and *Cercopithecus pogonias* both lack a statistically significant association between incisor and canine area in the mandibular dentition. The fact that these pairs of sister species are sister clades (see Fig. 2.9) but exhibit the opposite pattern (i.e., nonsignificant maxillary association/significant mandibular association versus significant maxillary association/nonsignificant mandibular association) further underscores the lack of phylogenetic pattern.

The results of the single-sex analysis are broadly consistent with the combined-sex analysis in that all of the significant correlations are positive. The most notable difference between the single-sex and combined-sex results is the smaller number of significant correlations in the former, which, as discussed above, was expected based on the reduction in sample size. The male samples in particular show a dearth of significant correlations—only nine (31.0%) in the maxillary dentition and twelve (41.4%) in the mandibular dentition. In contrast, eighteen (62.1%) of the maxillary and fifteen (51.7%) of the mandibular female correlations are significant. This pattern is especially pronounced in the Hominoidea, in which only two male correlations out of sixteen (12.5%) are significant, whereas half of the female correlations achieve significance.[5] Given

---

[5] Note that the median sample size for male great apes is $n = 12$ (range: $n = 5–19$). Larger samples are available for *Gorilla gorilla* (Mahler, 1973; thirty-five sets of maxillary teeth and thirty-six sets mandibular teeth) and *Pan troglodytes* (Johanson, 1974; twenty-five sets of maxillary teeth and twenty-two set of mandibular teeth). In the case of *G. gorilla*, increasing the sample size does not result in significant correlations. On the other hand, canine area is significantly positively correlated with incisor area in both dental arcades in the expanded *P. troglodytes* sample.

the variation in sample size among the single-sex samples (e.g., n = 5–25 for the male maxillary data set; see Table 2.1), it is not possible to determine whether this difference among the sexes is biologically meaningful or the result of sampling error. However, it is notable that all five of the species in which males are represented by twenty or more maxillary dentitions do not exhibit significant male correlations (*Cebus capucinus*, *Erythrocebus patas*, *Piliocolobus foai*, *Procolobus verus*, and *Colobus polykomos*). In contrast, the correlations for the females of these species are significant. For the mandibular teeth, four of the seven species in which males are represented by twenty or more dentitions fail to exhibit significant male correlations (*Cebus capucinus*, *Colobus satanas*, *Colobus polykomos*, *Hylobates syndactylus*), whereas the female correlations for these species are significant, except in one case (*Ceb. capucinus*).

These results suggest that there may be sexual dimorphism in the effects of pleiotropy, with male canines being less influenced by changes in incisor size than those of females. Such a difference might be predicted based on the fact that the intensity of selection for weaponized canines differs between males and females. In other words, although pleiotropy may be present in both sexes, its effects may be obscured by sexual selection in males. Differences in the proportion of significant correlations exhibited by males and females were evaluated using McNemar's test for two related samples (Daniel, 1990). This test determines whether there is an association between a treatment (in this case, sex) and the presence/absence of a trait (in this case, a statistically significant correlation). The results for the mandibular teeth indicate that there is no difference between males and females ($p = 0.6056$) in the proportion of significant correlations; for the maxillary dentition, the p-value for the test is borderline significant ($p = 0.0523$).

Intraspecific canine-postcanine correlations

The results for the canine-postcanine correlation analysis are summarized in Figure 3.3 and Table 3.2. They are quite similar to the canine-incisor analysis and so are not discussed in the same level of detail. With respect the maxillary dentition, twenty-six of the twenty-nine (89.7%) combined-sex correlations are significant, and all are positive. There are fewer significant correlations—twenty-one (72.4%)—for the mandibular dentition, and these are positive as well. The negative postcanine pleiotropy hypothesis is therefore falsified: canine size does not decrease as postcanine size increases within any species examined.

The male-only and female-only analyses are consistent with the results of the combined-sex analysis—all significant correlations are positive. As in the canine-incisor analysis, the incidence of significant correlations is lower than in the combined-sex analysis, and there are once again fewer significant male-only correlations than female-only correlations, though the disparity is not as great as in the canine-incisor analysis: for males, fifteen maxillary (51.7%) and twelve mandibular (41.4%); for females: twenty maxillary (69.0%) and sixteen mandibular (55.2%). McNemar's test indicates that the proportion of significant correlations does not differ statistically between males and females (maxillary teeth, $p = 0.2673$; mandibular teeth: $p = 0.3865$).

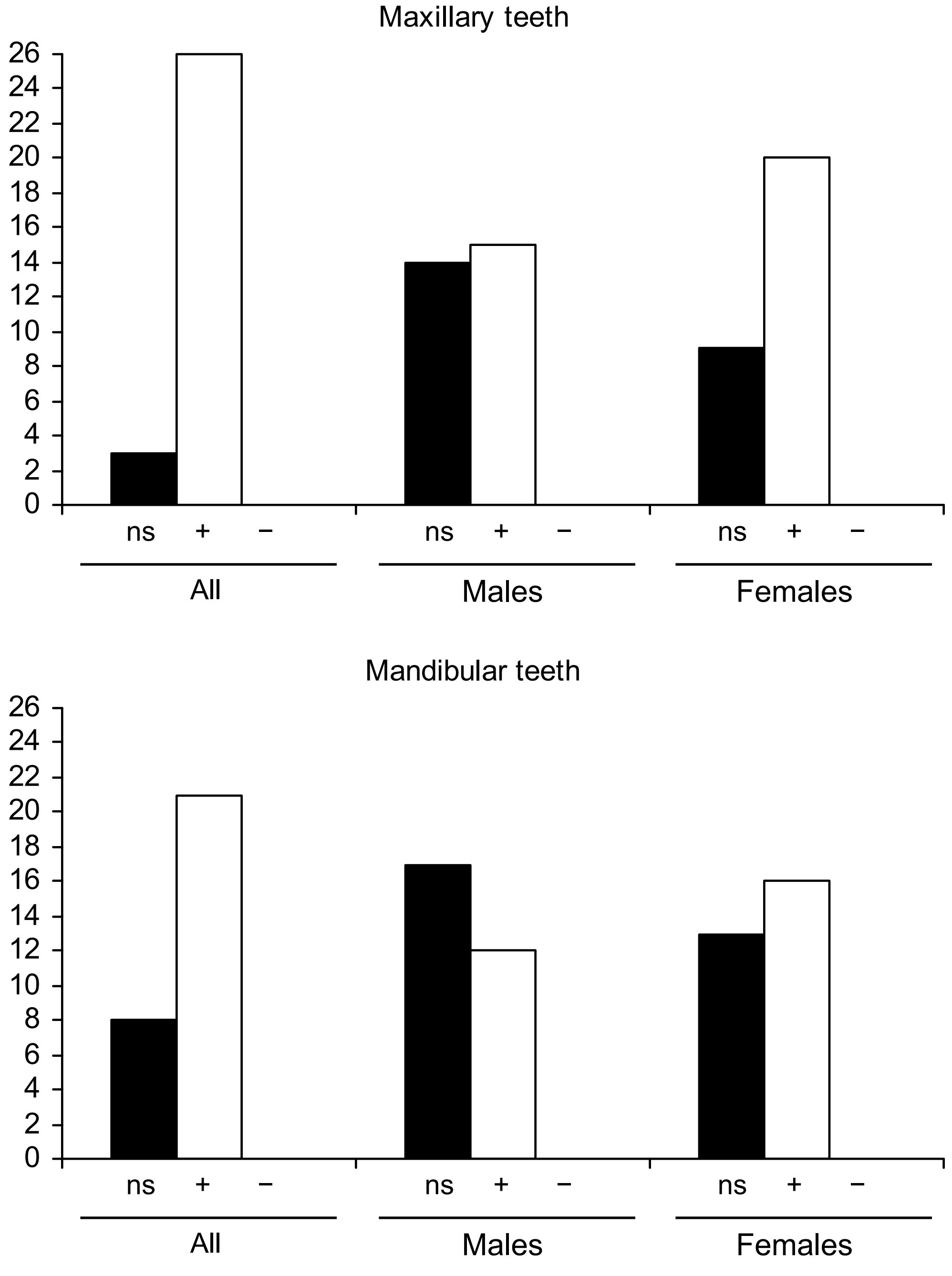


Fig. 3.3. Intraspecific canine-postcanine correlations. Histograms show the number correlations are nonsignificant (ns), positive (+), and negative (−).

TABLE 3.2. Intraspecific canine-postcanine correlations

	Both sexes		Males		Females	
	Max	Mand	Max	Mand	Max	Mand
Al. seniculus	0.35	0.61	—	0.59	0.59	0.71
At. geoffroyi	0.57	0.75	—	0.88	0.71	0.71
Ceb. libidinosus	0.51	—	—	0.49	0.77	—
Ceb. capucinus	0.45	0.41	0.45	—	0.46	0.59
Ch. satanas	0.81	0.73	0.77	0.73	0.84	0.73
Cer. pogonias	0.39	0.56	—	—	0.65	0.69
Cer. wolfi	0.79	0.49	0.86	0.46	0.54	0.66
Chl. pygerythrus	—	0.45	—*	—*	—	—
Er. patas	0.52	—	0.51	—	—*	—*
Mac. mulatta	0.66	0.79	0.61	0.86	0.79	0.85
Mac. fascicularis	—	0.50	—	—	—	—
Th. gelada	0.72	0.79	0.75	0.81	—*	—*
M. leucophaeus	0.48	0.45	0.48	—	0.51	—
Pil. foai	0.42	0.50	—	0.44	0.64	0.63
Pro. verus	0.50	0.49	0.41	—	0.59	0.64
Col. satanas	0.57	0.47	0.50	—	0.66	0.67
Col. polykomos	0.59	0.51	0.59	0.59	0.67	0.41
Pre. chrysomelas	0.69	0.68	0.72	0.65	0.68	0.76
Pre. potenziani	0.57	—	—	—	0.72	0.67
Tr. obscurus	0.48	0.61	—	—	0.55	0.75
Tr. shortridgei	0.60	0.72	—*	0.82	—*	—*
Hy. lar	—	0.47	—	—	—	0.64
Hy. syndactylus	0.64	0.61	0.75	0.67	0.59	—
Go. beringei	0.69	—	0.70	—*	—*	—*
Go. gorilla	0.39	—	—	—	—	—
Pan paniscus	0.56	—	0.59	—	0.71	—*
Pan troglodytes	0.36	0.48	0.60	—	—	0.47
Po. abelii	0.59	—	—*	—*	0.74	—*
Po. pygmaeus	0.45	—	—	—	0.50	—

A dash indicates that the correlation is nonsignificant; all other correlations are significant ($p < 0.05$). Samples comprising fewer than $n = 10$ individuals that exhibit nonsignificant correlations are marked with an asterisk (*).

Strong interspecific test

Tables 3.3 and 3.4 present the summary statistics for incisor area, postcanine area, basal canine area, and canine height for each species, separated by sex, and Table 3.5 lists the relative sizes of each component of the dentition, scaled against the skull GMs given in Table 2.4. The square roots of incisor area, canine area, and postcanine area were used to compute the shape ratios so that the numerator and denominator had the same dimensionality. Species included in the strong interspecific test are marked with asterisks in each of these tables. Note that the species included in the analysis of the maxillary dentition are not identical to those included in the analysis of the mandibular dentition, as species with significant canine-incisor or canine-postcanine correlations for one dental arcade did not necessarily have significant correlations for the other dental arcade.

Canine-incisor pairwise comparisons

The results of the canine-incisor pairwise comparisons are presented in Tables 3.6 (males) and 3.7 (females). For the maxillary teeth, there are five comparisons; for the mandibular teeth, there are nine. The incisor pleiotropy hypothesis predicts that the direction of difference between species should be the same for comparisons of relative basal canine area, relative canine height, and relative incisor area. Thus, the first comparison listed in Table 3.6, males of *Cebus libidinosus* versus males of *Cebus capucinus*, supports the hypothesis: *Ceb. libidinosus* has relatively larger canines and incisors than *Ceb. capucinus*, indicated by the greater-than symbols in each column of this row. In contrast, the comparison between males of *Colobus satanas* and males of *Colobus polykomos*

TABLE 3.3. Summary statistics for incisor and postcanine area

	Sex	Incisor area (mm^2) Mean	Incisor area (mm^2) SD	Postcanine area (mm^2) Mean	Postcanine area (mm^2) SD
MAXILLARY					
*Al. seniculus***	M	30.92	2.55	247.25	17.26
	F	25.62	2.77	205.20	13.74
*At. geoffroyi***	M	35.07	2.73	123.59	9.40
	F	33.49	4.56	123.31	11.06
*Ceb. libidinosus****	M	36.93	2.92	106.34	7.67
	F	34.69	2.61	104.30	4.23
*Ceb. capucinus****	M	37.08	3.07	109.00	6.50
	F	35.11	3.42	106.25	7.12
Ch. satanas	M	17.48	2.30	66.46	5.14
	F	18.04	2.32	65.71	5.85
*Cer. pogonias****	M	36.84	4.19	117.75	6.90
	F	35.16	4.41	110.83	8.33
*Cer. wolfi****	M	37.83	3.54	113.03	9.33
	F	34.47	2.85	102.74	5.11
Chl. pygerythrus	M	41.25	5.30	148.18	16.08
	F	38.15	3.21	135.31	11.67
Er. patas	M	52.34	5.20	190.42	15.83
	F	52.85	6.29	175.72	10.28
*Mac. mulatta**	M	52.24	6.77	213.30	18.37
	F	48.20	5.98	192.20	32.45
*Mac. fascicularis**	M	62.00	5.91	170.65	14.05
	F	54.41	6.00	153.75	14.57
*Th. gelada***	M	85.34	8.96	476.01	42.39
	F	77.66	13.41	384.14	20.25
*M. leucophaeus***	M	135.37	8.65	508.43	28.85
	F	98.99	7.61	412.19	35.78
*Pil. foai****	M	49.73	5.47	179.53	17.10
	F	50.12	5.34	181.77	15.21
*Pro. verus****	M	31.09	2.82	108.30	7.57
	F	31.09	3.10	110.92	8.46

(continued)

TABLE 3.3. *(Continued)*

		Incisor area (mm^2)		Postcanine area (mm^2)	
	Sex	Mean	SD	Mean	SD
MAXILLARY					
*Col. satanas****	M	58.04	4.88	183.66	7.92
	F	59.81	4.39	185.76	9.54
*Col. polykomos****	M	56.70	5.33	194.44	11.84
	F	56.22	5.18	186.24	13.19
*Pre. chrysomelas***	M	34.81	3.34	112.64	9.40
	F	36.76	2.27	118.36	8.85
*Pre. potenziani***	M	41.44	2.50	166.21	10.55
	F	39.75	3.40	165.76	9.21
*Tr. obscurus***	M	38.13	3.14	147.41	10.24
	F	35.96	3.35	139.48	11.34
*Tr. shortridgei***	M	51.91	4.92	190.53	17.53
	F	45.95	4.70	172.61	11.25
Hy. lar	M	36.85	3.41	144.51	12.02
	F	34.22	2.76	134.27	9.26
Hy. syndactylus	M	48.94	4.57	227.11	22.57
	F	44.30	5.39	208.97	28.55
*Go. beringei***	M	282.79	25.60	1059.69	115.08
	F	251.63	9.41	916.55	85.76
*Go. gorilla***	M	263.82	27.22	970.27	83.69
	F	225.46	25.93	812.44	65.02
*Pan paniscus***	M	153.10	21.01	339.80	30.88
	F	137.45	10.38	320.37	32.46
*Pan troglodytes***	M	195.95	17.40	460.74	43.07
	F	194.43	15.51	422.99	33.49
*Po. abelii***	M	260.68	16.61	694.37	37.14
	F	215.28	24.35	563.52	40.81
*Po. pygmaeus***	M	269.69	36.37	682.41	72.76
	F	219.05	22.13	569.15	44.61

(continued)

TABLE 3.3. (Continued)

		Incisor area (mm^2)		Postcanine area (mm^2)	
	Sex	Mean	SD	Mean	SD
MANDIBULAR					
*Al. seniculus****	M	24.58	2.27	216.43	15.89
	F	20.49	1.60	182.18	12.09
*At. geoffroyi****	M	26.96	2.36	113.60	6.42
	F	26.45	2.45	114.31	9.65
Ceb. libidinosus	M	22.63	1.78	97.46	8.58
	F	20.81	1.72	94.11	5.16
Ceb. capucinus	M	26.03	1.86	96.70	4.74
	F	25.53	2.38	96.32	6.69
Ch. satanas	M	11.79	1.80	62.00	4.45
	F	11.80	1.32	60.33	6.69
*Cer. pogonias***	M	30.17	3.71	100.71	6.86
	F	27.76	3.02	92.45	8.28
*Cer. wolfi***	M	29.56	2.43	98.23	9.50
	F	25.71	2.39	85.83	3.98
*Chl. pygerythrus**	M	31.06	3.59	135.64	18.18
	F	29.25	3.06	119.18	10.10
*Er. patas**	M	43.04	5.10	167.78	11.09
	F	42.75	5.06	148.03	10.60
*Mac. mulatta****	M	39.56	5.79	195.19	19.86
	F	35.78	6.18	178.67	27.58
*Mac. fascicularis****	M	47.44	5.29	155.86	14.45
	F	40.76	3.86	136.61	13.00
*Th. gelada****	M	64.91	5.68	434.98	37.10
	F	54.82	3.56	360.43	26.44
*M. leucophaeus****	M	106.48	9.32	484.75	28.66
	F	75.45	8.30	378.53	31.96
*Pil. foai****	M	41.25	3.55	168.74	15.89
	F	40.00	4.61	169.76	13.66
*Pro. verus****	M	26.47	2.32	97.28	6.85
	F	26.17	2.66	102.28	7.45

(continued)

TABLE 3.3. (Continued)

		Incisor area (mm^2)		Postcanine area (mm^2)	
	Sex	Mean	SD	Mean	SD
MANDIBULAR					
*Col. satanas****	M	45.39	2.82	168.51	6.42
	F	45.13	3.56	172.99	12.15
*Col. polykomos****	M	52.14	4.12	184.82	13.37
	F	50.61	4.71	176.59	11.93
*Pre. chrysomelas**	M	28.08	3.16	101.84	8.44
	F	29.74	1.97	107.72	7.15
*Pre. potenziani**	M	32.10	2.35	152.51	11.04
	F	32.66	3.62	153.79	9.54
*Tr. obscurus****	M	31.54	3.51	132.17	8.47
	F	29.40	3.48	129.30	10.53
*Tr. shortridgei****	M	35.58	3.51	168.14	18.73
	F	34.87	3.69	156.61	8.31
*Hy. lar***	M	25.75	3.10	137.56	14.63
	F	24.06	2.02	123.55	7.78
*Hy. syndactylus***	M	32.08	2.60	210.57	18.69
	F	30.05	3.23	202.88	19.01
Go. beringei	M	189.64	20.48	1062.96	112.33
	F	161.15	12.95	870.99	73.18
Go. gorilla	M	180.70	24.06	981.72	88.58
	F	149.90	14.27	809.47	76.35
Pan paniscus	M	114.81	14.35	326.06	27.98
	F	112.31	8.38	311.66	33.13
Pan troglodytes	M	158.07	13.38	443.64	38.00
	F	149.00	13.50	401.89	35.24
*Po. abelii**	M	185.39	17.27	697.53	31.05
	F	161.95	10.19	588.55	45.71
*Po. pygmaeus**	M	203.86	27.97	680.07	59.99
	F	167.74	22.01	570.84	47.45

Data are from Plavcan (1990), except in the case of *G. beringei* and *P. abelii*. Species marked with a single asterisk (*) were included only in the canine-incisor interspecific test; species marked with two asterisks (**) were included only in the canine-postcanine interspecific test; species marked with three asterisks (***) were included in both the canine-incisor and canine-postcanine interspecific tests.

TABLE 3.4. Summary statistics for canine basal crown area and height

	Sex	Canine basal crown area (mm^2)		Canine height (mm)	
		Mean	SD	Mean	SD
MAXILLARY					
*Al. seniculus***	M	56.84	4.69	13.42	1.51
	F	31.11	2.48	9.96	0.79
*At. geoffroyi***	M	33.46	6.56	11.68	1.09
	F	29.89	5.38	7.85	0.71
*Ceb. libidinosus****	M	51.10	5.10	14.63	0.83
	F	34.53	2.95	9.27	0.93
*Ceb. capucinus****	M	46.18	5.03	14.56	1.26
	F	34.18	3.68	8.70	0.62
Ch. satanas	M	36.99	4.26	10.99	0.74
	F	33.09	6.10	10.33	0.86
*Cer. pogonias****	M	32.73	4.92	18.40	0.93
	F	20.83	1.85	10.68	0.90
*Cer. wolfi****	M	36.30	6.05	18.61	1.10
	F	18.47	1.69	10.22	0.66
Chl. pygerythrus	M	44.84	5.14	20.40	1.64
	F	24.25	2.61	12.02	1.59
Er. patas	M	70.97	11.08	29.33	1.63
	F	32.53	3.11	11.94	1.13
*Mac. mulatta**	M	56.26	12.16	20.66	1.62
	F	27.22	4.77	9.29	0.92
*Mac. fascicularis**	M	62.98	11.92	24.62	2.57
	F	28.42	3.35	10.65	0.63
*Th. gelada***	M	139.70	18.71	40.43	2.08
	F	44.70	3.80	13.92	0.67
*M. leucophaeus***	M	193.37	17.76	47.25	3.93
	F	54.05	4.56	13.33	0.74
*Pil. foai****	M	74.90	12.78	22.77	1.38
	F	38.83	4.60	9.93	0.42
*Pro. verus****	M	40.20	4.88	16.44	0.88
	F	24.23	2.82	7.80	0.61

(continued)

TABLE 3.4. (Continued)

		Canine basal crown area (mm^2)		Canine height (mm)	
	Sex	Mean	SD	Mean	SD
MAXILLARY					
*Col. satanas****	M	48.79	4.70	17.55	1.31
	F	42.42	3.12	9.17	0.73
*Col. polykomos****	M	61.71	9.30	20.27	1.44
	F	49.85	4.83	11.13	0.90
*Pre. chrysomelas***	M	29.07	5.29	14.43	0.92
	F	28.75	3.28	8.45	0.38
*Pre. potenziani***	M	38.69	3.98	14.34	1.55
	F	38.10	4.59	10.15	0.64
*Tr. obscurus***	M	43.90	5.46	17.10	0.99
	F	33.05	3.39	9.22	0.87
*Tr. shortridgei***	M	60.55	6.55	20.21	0.90
	F	40.48	3.16	11.39	1.31
Hy. lar	M	42.27	5.52	19.54	1.97
	F	33.47	4.36	16.91	1.35
Hy. syndactylus	M	66.10	12.02	21.31	2.19
	F	48.95	7.60	18.61	1.36
*Go. beringei***	M	390.07	42.94	30.10	2.06
	F	182.75	21.39	16.63	0.51
*Go. gorilla***	M	397.43	85.19	32.82	3.55
	F	170.59	22.66	17.94	1.31
*Pan paniscus***	M	103.36	30.90	17.44	0.85
	F	63.37	7.26	12.06	0.66
*Pan troglodytes***	M	181.14	16.17	23.58	1.68
	F	113.60	10.21	15.23	1.52
*Po. abelii***	M	246.53	45.16	26.80	3.07
	F	130.48	9.33	14.96	0.92
*Po. pygmaeus***	M	248.83	37.50	26.31	2.02
	F	139.91	16.48	16.33	1.45

(continued)

TABLE 3.4. (Continued)

	Sex	Canine basal crown area (mm^2) Mean	SD	Canine height (mm) Mean	SD
MANDIBULAR					
*Al. seniculus****	M	45.02	5.43	11.89	1.08
	F	27.32	2.19	8.99	0.62
*At. geoffroyi****	M	29.12	3.78	10.66	0.66
	F	20.55	2.42	7.49	0.71
Ceb. libidinosus	M	48.44	4.69	14.19	0.65
	F	30.51	3.49	9.80	0.89
Ceb. capucinus	M	42.49	4.72	14.03	0.87
	F	31.14	2.37	9.16	0.63
Ch. satanas	M	32.71	3.39	11.46	0.59
	F	30.53	5.01	11.05	0.85
*Cer. pogonias***	M	22.32	2.49	11.45	0.77
	F	14.02	1.41	7.55	0.64
*Cer. wolfi***	M	24.94	3.44	12.17	1.02
	F	12.14	0.89	7.62	0.45
*Chl. pygerythrus**	M	33.70	3.72	14.39	1.10
	F	19.31	2.39	9.21	0.79
*Er. patas**	M	52.96	4.94	19.03	1.64
	F	25.64	3.29	10.34	0.94
*Mac. mulatta****	M	43.26	8.78	15.14	1.33
	F	20.88	2.78	8.54	0.68
*Mac. fascicularis****	M	46.41	7.23	16.32	1.41
	F	22.69	2.30	9.89	0.67
*Th. gelada****	M	88.31	15.22	26.33	1.63
	F	33.32	8.24	12.11	1.41
*M. leucophaeus****	M	121.64	8.94	28.24	1.71
	F	38.77	4.06	11.63	1.34
*Pil. foai****	M	59.99	9.89	16.60	1.21
	F	31.44	3.44	8.37	0.37
*Pro. verus****	M	31.26	3.66	12.46	0.92
	F	18.68	1.91	6.41	0.59

(continued)

TABLE 3.4. (Continued)

	Sex	Canine basal crown area (mm^2)		Canine height (mm)	
		Mean	SD	Mean	SD
MANDIBULAR					
*Col. satanas****	M	38.96	3.45	13.97	1.09
	F	32.04	3.17	7.53	0.57
*Col. polykomos****	M	46.23	5.08	15.48	0.94
	F	37.72	3.48	9.58	0.65
*Pre. chrysomelas**	M	22.54	2.53	10.27	0.62
	F	20.65	1.55	6.66	0.29
*Pre. potenziani**	M	26.68	2.57	11.59	0.90
	F	24.50	2.89	7.63	0.82
*Tr. obscurus****	M	30.15	3.03	13.13	0.90
	F	20.82	2.57	8.07	0.39
*Tr. shortridgei****	M	42.15	3.84	15.16	1.00
	F	31.93	3.61	10.39	0.59
*Hy. lar***	M	37.74	4.28	11.07	1.05
	F	30.86	4.15	9.91	0.91
*Hy. syndactylus***	M	55.92	10.06	13.85	0.76
	F	46.51	4.32	12.16	1.15
Go. beringei	M	302.56	30.48	25.32	1.36
	F	129.94	17.35	15.93	0.57
Go. gorilla	M	286.25	28.68	27.36	2.49
	F	145.23	18.80	17.24	1.16
Pan paniscus	M	79.92	14.44	14.59	0.50
	F	56.83	6.60	11.64	0.73
Pan troglodytes	M	164.47	20.88	21.14	1.60
	F	107.67	10.38	14.67	1.39
*Po. abelii**	M	230.20	58.87	25.75	2.66
	F	108.57	6.80	15.34	1.08
*Po. pygmaeus**	M	210.72	30.20	25.04	1.78
	F	109.45	17.90	17.05	1.36

Crown-area data are from Plavcan (1990), except in the case of *G. beringei* and *P. abelii*; height data for great apes were provided by J. Kelley (see Kelley, 1995a). Species marked with a single asterisk (*) were included only in the canine-incisor interspecific test; species marked with two asterisks (**) were included only in the canine-postcanine interspecific test; species marked with three asterisks (***) were included in both the canine-incisor and canine-postcanine interspecific tests.

TABLE 3.5. Relative tooth size

	Males				Females			
	I	PC	C_A	C_{HT}	I	PC	C_A	C_{HT}
MAXILLARY								
*Al. seniculus***	0.107	0.302	0.145	0.257	0.110	0.310	0.121	0.216
*At. geoffroyi***	0.127	0.238	0.124	0.250	0.126	0.241	0.119	0.170
*Ceb. libidinosus****	0.144	0.245	0.170	0.347	0.151	0.261	0.150	0.237
*Ceb. capucinus****	0.136	0.232	0.151	0.324	0.143	0.248	0.141	0.210
Ch. satanas	0.109	0.213	0.159	0.287	0.112	0.213	0.151	0.271
*Cer. pogonias****	0.132	0.236	0.124	0.399	0.141	0.250	0.108	0.253
*Cer. wolfi****	0.137	0.236	0.134	0.413	0.140	0.242	0.103	0.244
Chl. pygerythrus	0.130	0.246	0.135	0.411	0.139	0.263	0.111	0.271
Er. patas	0.116	0.221	0.135	0.469	0.142	0.259	0.111	0.233
*Mac. mulatta**	0.131	0.265	0.136	0.374	0.141	0.281	0.107	0.188
*Mac. fascicularis**	0.151	0.250	0.152	0.471	0.161	0.270	0.116	0.232
*Th. gelada***	0.120	0.283	0.153	0.524	0.130	0.289	0.099	0.205
*M. leucophaeus***	0.141	0.273	0.168	0.572	0.158	0.322	0.117	0.212
*Pil. foai****	0.133	0.252	0.163	0.428	0.145	0.275	0.127	0.203
*Pro. verus****	0.130	0.242	0.148	0.383	0.134	0.253	0.118	0.188
*Col. satanas****	0.146	0.260	0.134	0.337	0.154	0.271	0.130	0.183
*Col. polykomos****	0.140	0.259	0.146	0.376	0.146	0.266	0.138	0.217
*Pre. chrysomelas***	0.134	0.241	0.122	0.328	0.139	0.250	0.123	0.194
*Pre. potenziani***	0.138	0.276	0.133	0.307	0.137	0.279	0.134	0.220
*Tr. obscurus***	0.128	0.252	0.137	0.355	0.132	0.260	0.126	0.203
*Tr. shortridgei***	0.134	0.257	0.145	0.376	0.136	0.264	0.128	0.229
Hy. lar	0.123	0.244	0.132	0.397	0.122	0.241	0.121	0.352
Hy. syndactylus	0.118	0.255	0.137	0.360	0.118	0.255	0.124	0.329
*Go. beringei***	0.136	0.263	0.159	0.243	0.151	0.288	0.128	0.158
*Go. gorilla***	0.137	0.262	0.168	0.277	0.147	0.278	0.128	0.175
*Pan paniscus***	0.158	0.235	0.130	0.223	0.151	0.231	0.103	0.156
*Pan troglodytes***	0.149	0.229	0.143	0.251	0.156	0.230	0.119	0.170
*Po. abelii***	0.159	0.259	0.154	0.263	0.170	0.275	0.132	0.173
*Po. pygmaeus***	0.157	0.250	0.151	0.252	0.167	0.270	0.134	0.185

(continued)

TABLE 3.5. (Continued)

	Males				Females			
	I	PC	C_A	C_{HT}	I	PC	C_A	C_{HT}
MANDIBULAR								
*Al. seniculus******	0.095	0.282	0.129	0.228	0.098	0.292	0.113	0.195
*At. geoffroyi******	0.111	0.228	0.116	0.228	0.112	0.232	0.098	0.162
Ceb. libidinosus	0.113	0.234	0.165	0.337	0.117	0.248	0.141	0.251
Ceb. capucinus	0.114	0.219	0.145	0.312	0.122	0.237	0.135	0.221
Ch. satanas	0.090	0.206	0.149	0.299	0.090	0.204	0.145	0.290
*Cer. pogonias****	0.119	0.218	0.103	0.249	0.125	0.228	0.089	0.179
*Cer. wolfi****	0.121	0.220	0.111	0.270	0.121	0.221	0.083	0.182
*Chl. pygerythrus**	0.112	0.235	0.117	0.290	0.122	0.246	0.099	0.208
*Er. patas**	0.105	0.207	0.116	0.304	0.128	0.238	0.099	0.202
*Mac. mulatta******	0.114	0.253	0.119	0.274	0.121	0.271	0.093	0.173
*Mac. fascicularis******	0.132	0.239	0.130	0.312	0.139	0.255	0.104	0.216
*Th. gelada******	0.104	0.270	0.122	0.341	0.109	0.280	0.085	0.179
*M. leucophaeus******	0.125	0.267	0.134	0.342	0.138	0.309	0.099	0.185
*Pil. foai******	0.121	0.244	0.146	0.312	0.129	0.266	0.115	0.171
*Pro. verus******	0.120	0.230	0.130	0.290	0.123	0.243	0.104	0.154
*Col. satanas******	0.129	0.249	0.120	0.268	0.134	0.262	0.113	0.150
*Col. polykomos******	0.134	0.252	0.126	0.287	0.139	0.259	0.120	0.187
*Pre. chrysomelas**	0.120	0.229	0.108	0.233	0.125	0.238	0.104	0.153
*Pre. potenziani**	0.121	0.264	0.110	0.248	0.124	0.269	0.107	0.165
*Tr. obscurus******	0.116	0.238	0.114	0.272	0.119	0.250	0.100	0.178
*Tr. shortridgei******	0.111	0.241	0.121	0.282	0.119	0.251	0.113	0.209
*Hy. lar****	0.103	0.238	0.125	0.225	0.102	0.232	0.116	0.207
*Hy. syndactylus****	0.096	0.245	0.126	0.234	0.097	0.252	0.121	0.215
Go. beringei	0.113	0.267	0.142	0.207	0.121	0.280	0.108	0.151
Go. gorilla	0.113	0.264	0.143	0.231	0.120	0.278	0.118	0.168
Pan paniscus	0.137	0.231	0.114	0.186	0.137	0.228	0.097	0.150
Pan troglodytes	0.134	0.225	0.137	0.225	0.137	0.224	0.116	0.164
*Po. abelii**	0.134	0.260	0.149	0.253	0.147	0.281	0.121	0.178
*Po. pygmaeus**	0.137	0.250	0.139	0.240	0.146	0.270	0.118	0.193

Relative tooth size was calculated by dividing variables by the skull GM; areal measurements were raised to the 0.5 power before division. Abbreviations are as follows: I = relative incisor area; PC = relative postcanine area; C_A relative canine area; C_{HT} = relative canine height. Species marked with a single asterisk (*) were included only in the canine-incisor interspecific test; species marked with two asterisks (**) were included only in the canine-postcanine interspecific test; species marked with three asterisks (***) were included in both the canine-incisor and canine-postcanine interspecific tests.

TABLE 3.6. Pairwise comparisons of relative canine and incisor size in males

				Hypothesis supported?	
Comparison[a]	Canine area	Canine height	Incisor area	Canine area	Canine height
Maxillary results					
Ceb. libidinosus vs. *Ceb. capucinus*	>	>	>	Yes	Yes
Cer. pogonias vs. *Cer. wolfi*	<	=	=	No	—[b]
Mac. mulatta vs. *Mac. fascicularis*	<	<	<	Yes	Yes
Pil. foai vs. *Pro. verus*	>	>	=	No	No
Col. satanas vs. *Col. polykomos*	<	<	>	No	No
Mandibular results					
Al. seniculus vs. *At. geoffroyi*	=	<	<	No	Yes
Chl. pygerythrus vs. *Er. patas*	=	=	>	No	No
Mac. mulatta vs. *Mac. fascicularis*	<	<	<	Yes	Yes
Th. gelada vs. *M. leucophaeus*	<	=	<	Yes	No
Pil. foai vs. *Pro. verus*	>	>	=	No	No
Col. satanas vs. *Col. polykomos*	<	<	<	Yes	Yes
Pre. chrysomelas vs. *Pre. potenziani*	=	=	=	—	—
Tr. obscurus vs. *Tr. shortridgei*	<	=	=	No	—
Po. abelii vs. *Po. pygmaeus*	=	=	=	—	—

[a] For statistically significant comparisons, less-than and greater-than symbols indicate direction of difference (e.g., relative canine basal crown area is greater in *Ceb. libidinosus* than in *Ceb. capucinus*); equality sign indicates that difference is not statistically significant.

[b] Species do not differ in the two variables and thus cannot be used to evaluate the pleiotropy hypothesis (see text).

TABLE 3.7. Pairwise comparisons of relative canine and incisor size in females

				Hypothesis supported?	
Comparison[a]	Canine area	Canine height	Incisor area	Canine area	Canine height
Maxillary results					
Ceb. libidinosus vs. *Ceb. capucinus*	>	>	>	Yes	Yes
Cer. pogonias vs. *Cer. wolfi*	>	=	=	No	—[b]
Mac. mulatta vs. *Mac. fascicularis*	<	<	<	Yes	Yes
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	>	No	No
Mandibular results					
Al. seniculus vs. *At. geoffroyi*	>	>	<	No	No
Chl. pygerythrus vs. *Er. patas*	=	=	=	—	—
Mac. mulatta vs. *Mac. fascicularis*	<	<	<	Yes	Yes
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	<	Yes	Yes
Pre. chrysomelas vs. *Pre. potenziani*	=	<	=	—	No
Tr. obscurus vs. *Tr. shortridgei*	<	<	=	No	No
Po. abelii vs. *Po. pygmaeus*	=	=	=	—	—

[a] For statistically significant comparisons, less-than and greater-than symbols indicate direction of difference (e.g., relative canine basal crown area is greater in *Ceb. libidinosus* than in *Ceb. capucinus*); equality sign indicates that difference is not statistically significant. Note that one comparison (*Th. gelada* vs. *M. leucophaeus*) was excluded due to small sample size (i.e., some component of the shape ratios was less than $n = 5$).

[b] Species do not differ in the two variables and thus cannot be used to evaluate the pleiotropy hypothesis (see text).

(Table 3.6, maxillary results) is in the opposite of the predicted direction: *Col. satanas* has relatively larger maxillary canines than *Col. polykomos* (for both basal area and height), but *Col. polykomos* has relatively larger incisors. Note that species that do not differ from each other in relative canine and incisor size cannot be used to test the incisor pleiotropy hypothesis, though they are consistent with it.

Table 3.8 summarizes the results presented in Tables 3.6 and 3.7 in terms of the number of pairwise comparisons that are consistent/inconsistent with the incisor pleiotropy hypothesis. For males, the number of comparisons that are in the predicted direction is never greater than the number of comparisons that are not in the predicted direction, indicating that species with relatively large canines do not tend to have relatively large incisors. With respect to females, the number of comparisons that support the incisor pleiotropy hypothesis is greater than the number of comparisons that do not support for three of the four variables: maxillary and mandibular canine area and maxillary canine height. However, the total number of pairwise comparisons (four to six, depending on the variable) does not allow for a robust statistical test to establish that this pattern of results is biologically meaningful. In the case of canine area, the number of pairwise comparisons that are consistent with the incisor pleiotropy hypothesis is three and the number of comparisons that are inconsistent with it is two. Using a binomial test, the one-tailed probability of obtaining three or more comparisons out of five that support the incisor pleiotropy hypothesis by chance alone is $p = 0.5000$. In the case of maxillary canine height, in which three comparisons are in the

TABLE 3.8. Summary of results for canine-incisor pairwise comparisons

	Hypothesis supported?	
	Canine area	Canine height
Males		
Maxillary	2 yes, 3 no	2 yes, 2 no
Mandibular	3 yes, 4 no	3 yes, 3 no
Females		
Maxillary	3 yes, 2 no	3 yes, 1 no
Mandibular	3 yes, 2 no	3 yes, 3 no

predicted direction and one is not, the one-tailed probability is $p = 0.3125$. Thus, these results cannot be used to support the incisor pleiotropy hypothesis.

Canine-postcanine pairwise comparisons

The results of the canine-postcanine pairwise comparisons are presented in Tables 3.9 (males) and 3.10 (females), and are summarized in Table 3.11. Based on the results of the intraspecific analysis, species with relatively larger postcanine teeth in comparison to their sister species should also have relatively larger canines. For the maxillary teeth, there are eleven comparisons; for the mandibular teeth, there are eight. As shown in Table 3.11, the number of pairwise comparisons that are consistent with the positive postcanine pleiotropy hypothesis is less than the number of comparisons that are inconsistent with it for every variable except female maxillary canine area (four support, three do not support). Thus, there is no support for a positive relationship between relative canine and postcanine size. Note also that there is no evidence for an inverse relationship between relative canine size and relative postcanine size in the sample. There are only two pairwise comparisons in which the species with relatively smaller canines has relatively larger postcanine teeth: males and females of *Macaca mulatta* have relatively larger mandibular postcanine teeth and smaller mandibular canines (crown area and height) than males and females of *Macaca fascicularis*, respectively, and males of *Alouatta seniculus* have relatively larger mandibular postcanine teeth and smaller mandibular canines (crown height only) than males of *Ateles geoffroyi*.

TABLE 3.9. Pairwise comparisons of relative canine and postcanine size in males

				Hypothesis supported?	
Comparison[a]	Canine area	Canine height	Postcanine area	Canine area	Canine height
Maxillary results					
Al. seniculus vs. *At. geoffroyi*	>	=	>	Yes	No
Ceb. libidinosus vs. *Ceb. capucinus*	>	>	>	Yes	Yes
Cer. pogonias vs. *Cer. wolfi*	<	=	=	No	—[b]
Th. gelada vs. *M. leucophaeus*	<	<	=	No	No
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	=	No	No
Pre. chrysomelas vs. *Pre. potenziani*	<	=	<	Yes	No
Tr. obscurus vs. *Tr. shortridgei*	<	<	=	No	No
Go. beringei vs. *Go. gorilla*	=	<	=	—	No
Pan paniscus vs. *Pan troglodytes*	<	<	=	No	No
Po. abelii vs. *Po. pygmaeus*	=	=	=	—	—
Mandibular results					
Al. seniculus vs. *At. geoffroyi*	=	<	>	No	No
Cer. pogonias vs. *Cer. wolfi*	<	<	=	No	No
Mac. mulatta vs. *Mac. fascicularis*	<	<	>	No	No
Th. gelada vs. *M. leucophaeus*	<	=	=	No	—
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	=	No	No
Tr. obscurus vs. *Tr. shortridgei*	<	=	=	No	—
Hy. lar vs. *Hy. syndactylus*	=	=	<	No	No

[a] For statistically significant comparisons, less-than and greater-than symbols indicate direction of difference (e.g., relative canine basal crown area is greater in *Al. seniculus* than in *At. geoffroyi*); equality sign indicates that difference is not statistically significant.

[b] Species do not differ in the two variables and thus cannot be used to evaluate the pleiotropy hypothesis (see text).

TABLE 3.10. Pairwise comparisons of relative canine and postcanine size in females

				Hypothesis supported?	
Comparison[a]	Canine area	Canine height	Postcanine area	Canine area	Canine height
Maxillary results					
Al. seniculus vs. *At. geoffroyi*	=	>	>	No	Yes
Ceb. libidinosus vs. *Ceb. capucinus*	>	>	>	Yes	Yes
Cer. pogonias vs. *Cer. wolfi*	>	=	>	Yes	No
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	=	No	No
Pre. chrysomelas vs. *Pre. potenziani*	<	<	<	Yes	Yes
Tr. obscurus vs. *Tr. shortridgei*	=	<	=	—[b]	No
Pan paniscus vs. *Pan troglodytes*	<	<	=	No	No
Po. abelii vs. *Po. pygmaeus*	=	<	=	—	No
Mandibular results					
Al. seniculus vs. *At. geoffroyi*	>	>	>	Yes	Yes
Cer. pogonias vs. *Cer. wolfi*	=	=	=	—	—
Mac. mulatta vs. *Mac. fascicularis*	<	<	>	No	No
Pil. foai vs. *Pro. verus*	>	>	>	Yes	Yes
Col. satanas vs. *Col. polykomos*	<	<	=	No	No
Tr. obscurus vs. *Tr. shortridgei*	<	<	=	No	No
Hy. lar vs. *Hy. syndactylus*	=	=	<	No	No

[a] For statistically significant comparisons, less-than and greater-than symbols indicate direction of difference (e.g., relative canine height is greater in *Al. seniculus* than in *At. geoffroyi*); equality sign indicates that difference is not statistically significant. Note that two comparisons (*Th. gelada* vs. *M. leucophaeus* and *Go. beringei* vs. *Go. gorilla*) were excluded due to small sample size (i.e., some component of the shape ratios was less than $n = 5$).

[b] Species do not differ in the two variables and thus cannot be used to evaluate the pleiotropy hypothesis (see text).

TABLE 3.11. Summary of results for canine-postcanine pairwise comparisons

	Hypothesis supported?	
	Canine area	Canine height
Males		
Maxillary	4 yes, 5 no	2 yes, 7 no
Mandibular	1 yes, 7 no	1 yes, 5 no
Females		
Maxillary	4 yes, 3 no	4 yes, 5 no
Mandibular	2 yes, 4 no	2 yes, 4 no

Weak interspecific test

As noted at the beginning of this chapter, the weak interspecific test is only valid if there is no variation in the direction (positive or negative) of the significant intraspecific canine-incisor and canine-postcanine correlations. This condition is met: all of the significant intraspecific correlations are positive.

Allometry and size-adjustment

Prior to computing interspecific correlations and partial correlations, an interspecific allometric analysis was conducted in order to determine the most appropriate method of size-adjustment. The use of skull-GM-based shape ratios in the strong interspecific test was justified because the pairwise comparisons comprised species that were, in most cases, similar in size and design. However, the problem of allometry must be confronted in this section because (1) the species included in the analysis differ greatly in size,[6] and (2) the functional relationship between tooth size and organismal size is not well understood. A good illustration of the issues involved in deciding how to express relative tooth size is provided by the literature on the scaling of postcanine size with respect to body size in primates.

Several studies have produced conflicting conclusions regarding the scaling relationship between postcanine size and body size in primates, ranging from positive allometry (Pilbeam and Gould, 1974; Gould, 1975; Corruccini and Henderson, 1978; Goldstein et al., 1978) to isometry or slight negative allometry

---

[6] For example, among males, the species with the largest skull GM (*Gorilla beringei*) is 324% larger than the species with the smallest skull GM (*Chiropotes satanas*) (see Table 2.4).

(Kay, 1975a,b; Wood and Stack, 1980; Gingerich et al., 1982; Vinyard and Hanna, 2005). The disparity in these results can be attributed to a variety of factors, including differences in regression technique, sample composition, the measurement used to represent postcanine size, and the variable chosen to represent body size—typically body mass or skull dimensions (Smith, 1981b; Vinyard and Hanna, 2005; Copes and Schwartz, 2010). Of these factors, the last is the most important in the context of the present discussion. As demonstrated by Smith (1981b) and Vinyard and Hanna (2005), the scaling relationship between postcanine size and body mass is not identical to the scaling relationship between postcanine size and different skull dimensions. The former is isometric or negatively allometric, whereas the latter is positively allometric, a product of the fact that skull size tends to scale with negative allometry against body size (Vinyard and Hanna, 2005). Thus, the outcome of an interspecific analysis of relative tooth size is dependent on whether skull size or body mass is used to size-adjust the data (Smith, 1981b). The question is: Which variable is more relevant for defining relative tooth size?

Another issue concerns the interpretation of an allometric relationship between tooth size and the independent size variable. Pilbeam and Gould (1974; Gould, 1975) argued that the positive allometry exhibited by their primate samples represented a line of functional equivalence, possibly related to the scaling of basal metabolic rate to body mass. According to this view, relative postcanine size should be expressed using the regression slope as the criterion of subtraction; the relatively large teeth of large species are functionally equivalent to the relatively small teeth of small species, and thus the use of shape ratios will produce misleading results. However, Kay (1975a) found that the relationship between postcanine size and body size in primates is isometric when diet is controlled (i.e., when scaling is examined within dietary groupings; see also Corruccini and Henderson, 1978; Goldstein et al., 1978), and he suggested that Pilbeam and Gould's (1974) positively allometric slopes resulted from their failure to account for this factor:

> For example, for noncercopithecoid primates at a particular body size, frugivorous species have smaller teeth than do their insectivorous or folivorous relatives. Thus, for any group for which this holds, regression equations would appear to be positively allometric if the group's smallest member were frugivorous and its large members folivorous (Kay, 1975a, p. 63).

Based on Kay's (1975a) analysis, the allometric relationship observed by Pilbeam and Gould (1974; Gould, 1975) is adaptively meaningful. In this case, the use of shape ratios (or residuals from an isometric line) is warranted. Thus, the procedure used to size-adjust dental data has important consequences for an analysis of relative tooth size.

Tables 3.12 and 3.13 show how incisor area, postcanine area, canine area, and canine height scale against skull size and body mass (taken from Smith and Jungers, 1997; see Table 2.4) in the data set used for this dissertation. Males (Table 3.12) and females (Table 3.13) were examined separately to eliminate the effects of sexual dimorphism. All slopes were computed using independent contrasts (see Chapter 2). Slopes generated using reduced major axis (RMA) regression were preferred over those calculated using ordinary least squares

TABLE 3.12. Scaling of tooth size against skull size and body size in males

	Anthropoidea			Catarrhini		
	RMA slope	95% CI	r^2	RMA slope	95% CI	r^2
MAXILLARY						
Skull GM						
Incisor area	1.05	0.83–1.27	0.74	1.03	0.83–1.24	0.79
Postcanine area	1.29	1.09–1.49	0.85	1.13	0.98–1.29	0.91
Canine area	1.33	1.12–1.54	0.84	1.35	1.17–1.52	0.92
Canine height	1.34	1.04–1.63	0.69	1.38	1.05–1.71	0.71
Body mass$^{1/3}$						
Incisor area	0.93	0.71–1.15	0.65	0.91	0.67–1.15	0.65
Postcanine area	1.14	0.77–1.41	0.65	0.99	0.80–1.18	0.81
Canine area	1.17	0.88–1.46	0.62	1.19	0.93–1.45	0.75
Canine height	1.18	0.85–1.51	0.50	1.21	0.85–1.57	0.55
MANDIBULAR						
Skull GM						
Incisor area	1.13	0.96–1.30	0.86	1.03	0.81–1.25	0.77
Postcanine area	1.21	1.08–1.33	0.93	1.17	1.00–1.34	0.89
Canine area	1.23	1.06–1.40	0.88	1.33	1.15–1.52	0.90
Canine height	1.21	1.00–1.43	0.80	1.36	1.14–1.58	0.86
Body mass$^{1/3}$						
Incisor area	1.04	0.84–1.23	0.78	0.91	0.65–1.16	0.60
Postcanine area	1.10	0.92–1.28	0.83	1.02	0.82–1.23	0.79
Canine area	1.12	0.91–1.34	0.76	1.17	0.91–1.43	0.74
Canine height	1.11	0.84–1.38	0.62	1.19	0.90–1.48	0.70
Skull vs. body mass$^{1/3}$	0.88	0.75–1.01	0.85	0.88	0.76–1.00	0.90

TABLE 3.13. Scaling of tooth size against skull size and body size in females

	Anthropoidea			Catarrhini		
	RMA slope	95% CI	r^2	RMA slope	95% CI	r^2
MAXILLARY						
Skull GM						
Incisor area	1.26	1.08–1.44	0.87	1.23	1.06–1.41	0.89
Postcanine area	1.28	1.12–1.44	0.90	1.25	1.10–1.39	0.93
Canine area	1.11	0.92–1.29	0.82	1.16	0.97–1.36	0.86
Canine height	0.96	0.64–1.27	0.31	0.95	0.60–1.29	0.30
Body mass$^{1/3}$						
Incisor area	1.11	0.90–1.32	0.77	1.11	0.90–1.32	0.81
Postcanine area	1.13	0.94–1.32	0.82	1.12	0.93–1.31	0.86
Canine area	0.98	0.79–1.17	0.76	1.05	0.87–1.23	0.84
Canine height	0.85	0.55–1.15	0.21	0.85	0.52–1.18	0.21
MANDIBULAR						
Skull GM						
Incisor area	1.26	1.06–1.47	0.83	1.21	0.99–1.43	0.83
Postcanine area	1.33	1.17–1.49	0.90	1.31	1.15–1.47	0.92
Canine area	1.14	0.91–1.37	0.74	1.19	0.97–1.42	0.82
Canine height	1.09	0.80–1.38	0.55	1.12	0.84–1.40	0.67
Body mass$^{1/3}$						
Incisor area	1.11	0.89–1.33	0.75	1.09	0.85–1.33	0.76
Postcanine area	1.17	0.98–1.36	0.83	1.18	0.98–1.37	0.86
Canine area	1.00	0.77–1.23	0.67	1.07	0.86–1.29	0.80
Canine height	0.96	0.67–1.25	0.40	1.01	0.71–1.31	0.55
Skull vs. body mass$^{1/3}$	0.88	0.78–0.98	0.91	0.90	0.79–1.01	0.92

(OLS) because the former method is more appropriate for evaluating changes in shape that occur with changes in size (i.e., scaling), whereas the latter is more appropriate for prediction or if the goal is to obtain residuals for size-adjustment (e.g., Warton et al., 2006; Smith, 2009). Standard errors of OLS slopes were used to estimate each RMA slope's 95% confidence interval, using the procedure described by Sokal and Rohlf (1995). All data were log-transformed (base *e*) prior to analysis. For ease of interpretation, the square roots of areal measurements and the cube root of body mass were used to derive the RMA slopes. Thus, isometry is indicated by a slope of 1.00. Initially, anthropoids were examined as a group; platyrrhines were then removed from the analysis in order to evaluate the effect of the difference in premolar number between these species and catarrhines.

The scaling analysis indicates that dental variables tend to scale with positive allometry or isometry against skull size and with isometry against body mass. Skull size appears to be slightly negatively allometric with respect to body mass, but isometry can only be rejected at the $p < 0.05$ level in the case of female anthropoids. For a given dental variable, the slopes generated using skull size and body mass are similar to each other when differences are considered in relation to the widths of the 95% confidence intervals. For example, in anthropoid males, the scaling coefficient for maxillary canine area versus skull size is $b = 1.33$, whereas its body-mass counterpart is $b = 1.17$ (Table 3.12). The 95% confidence intervals for these two slopes are 1.12–1.54 and 0.88–1.46, respectively. Thus, although the former slope can be statistically distinguished from isometry (i.e., it is positively allometric) and the latter cannot, the two slopes are statistically indistinguishable from each other.

With respect to differences between platyrrhines and catarrhines in postcanine scaling, the RMA slope changes only slightly in most cases when the five species of New World monkey are removed from the analysis. The biggest difference is between the anthropoid and catarrhine slopes for male maxillary postcanine size (Table 3.12). When postcanine size is scaled against skull size, the anthropoid slope is $b = 1.29$ with a confidence interval that does not overlap isometry (1.09–1.49; indicating positive allometry), and the catarrhine slope is $b = 1.13$ with a confidence interval that just barely includes isometry (0.98–1.29). The two confidence intervals overlap extensively, however, indicating that the difference between the two slopes is not statistically significant. When postcanine size is scaled against body mass, the difference between the two slopes is similar ($b = 1.14$ versus $b = 0.99$), but the confidence intervals are even wider; in fact, the confidence interval for the anthropoid slope completely envelops the catarrhine confidence interval. These results indicate that the difference in premolar number between catarrhines and platyrrhines does not have a strong effect on the measure of postcanine size used in this analysis.

The coefficients of determination (r^2) presented in Tables 3.12 and 3.13 reveal that skull size accounts for more of the variance in tooth size than does body mass for all dental variables. The difference in the amount of variation explained ranges from two percentage points (maxillary and mandibular canine area in catarrhine females; Table 3.13) to twenty-two percentage points (maxillary canine area in anthropoid males; Table 3.12), with an average difference of eleven percentage points. The average disparity between r^2 values is nearly twice as great in males as it is in females (0.146 versus 0.078). Figure 3.4 shows log-log (base *e*) plots of maxillary postcanine size against body mass and skull size in male anthropoid primates, illustrating the difference in the dispersion of the data points (wider in the body-mass plot) about the RMA lines for the two independent variables; in this case, the difference in the amount of variance explained is twenty percentage points (skull size, $r^2 = 0.85$; body mass, $r^2 = 0.65$).

Some of the disparity in r^2 values may be due to unreliable estimates of body mass (e.g., the *Mandrillus leucophaeus* body-mass data discussed in Footnote 6 in Chapter 2). However, the difference in the positions of the Colobinae (white squares) and Cercopithecinae (black squares) in the two plots in Figure 3.4 suggests that the r^2 disparity is biologically real. When postcanine size is plotted against body mass, the Cercopithecinae generally fall above the anthropoid and catarrhine RMA lines and the line of isometry, whereas most of the Colobinae fall below or close to these lines, indicating that the Cercopithecinae as a group have relatively larger postcanine teeth than the Colobinae (see also Kay, 1978; Goldstein et al., 1978). However, when plotted against skull size, the difference between the two subfamilies largely disappears. The same is true for the incisors, and this pattern characterizes females as well. These data suggest that the Cercopithecinae have relatively larger skulls than the Colobinae. Figure 3.5, a log-log plot of skull size on body mass, confirms that this is true: the cercopithecines are transposed above the colobines and there is no

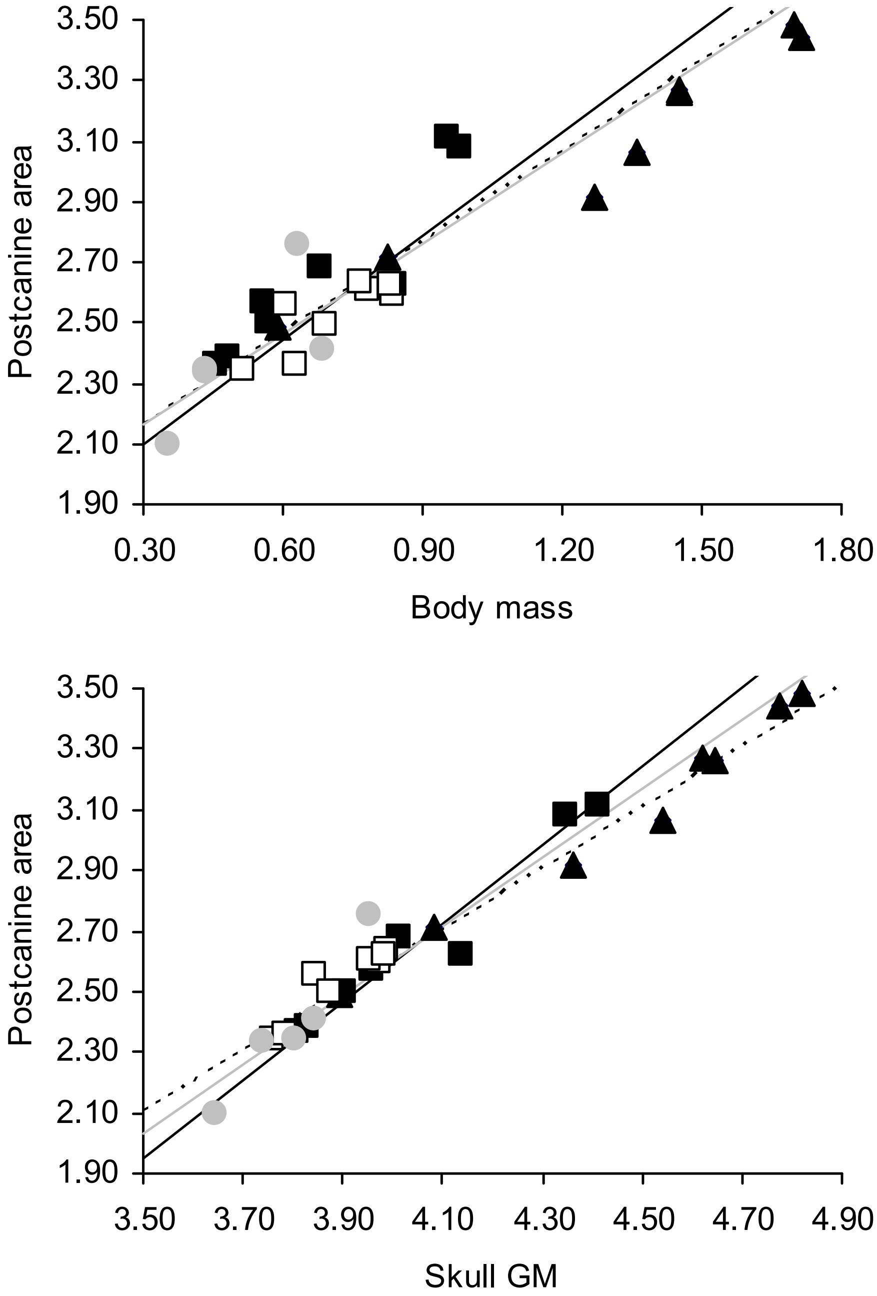


Fig. 3.4. Scaling of maxillary postcanine area in male anthropoids. Log postcanine area is plotted against log body mass (upper) and log skull geometric mean (lower). The solid black line is the RMA slope for all anthropoids; the line of isometry (dotted line) and the RMA slope for catarrhines only (gray line) are also shown for comparison. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

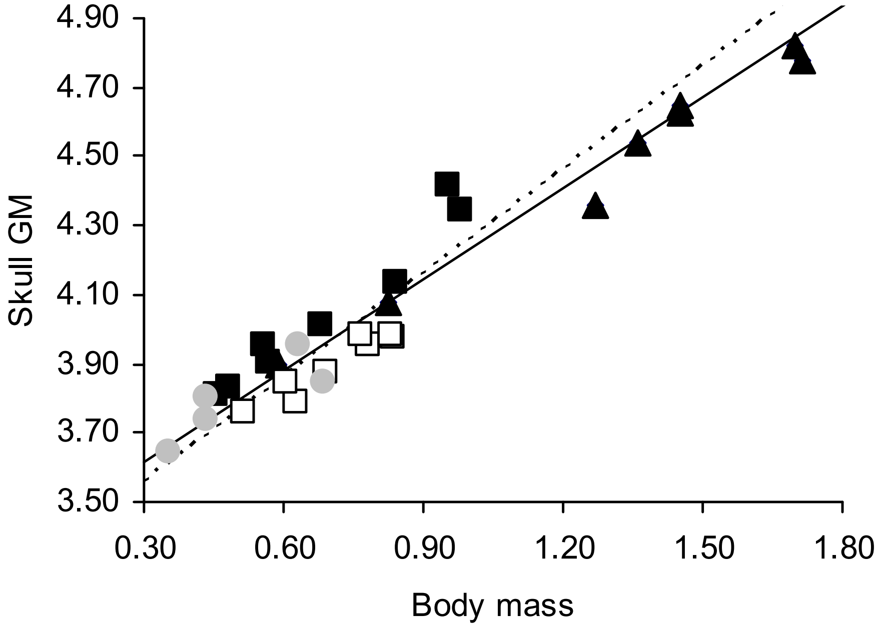


Fig. 3.5. Scaling of skull size in male anthropoids. Log skull geometric mean is plotted against log body mass. The solid black line represents the RMA slopes for all anthropoids and catarrhines only (i.e., the two slopes are nearly identical); the line of isometry (dotted line) is also shown for comparison. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

overlap between the two subfamilies. Cercopithecines are also transposed above the Hominoidea and, to a lesser extent, the Platyrrhini.

The relatively large postcanine teeth of some cercopithecines have been linked to diet: Goldstein et al. (1978) divided the Cercopithecoidea into broad dietary categories (i.e., folivore, frugivore, and omnivore) and showed that their omnivore group—consisting of *Papio* baboons, geladas, and vervet monkeys—had relatively larger teeth than the frugivores and folivores. However, Goldstein et al. (1978, p. 524) were careful to note that their inference regarding diet and tooth size was not strongly supported because their omnivore group lacked taxonomic diversity:

> Four out of the five omnivores in our sample are long-faced, open country baboons, and are thus homogenous and distinct from members of the other diet classes. Hence the effect that we are attributing to diet here might just as well be interpreted as a phylogenetic or general ecological effect.

The allometric analysis presented above suggests another explanation—i.e., that the relatively large postcanine teeth of cercopithecines are a by-product of their relatively large skulls, particularly their anteroposteriorly long faces (see also Martin, 1993).

Among primates, the Cercopithecinae have the tallest canines relative to any measure of organismal size (e.g., Lucas, 1982; Plavcan, 1990, 1993a; Greenfield and Washburn, 1991; Plavcan et al., 1995), and their long faces have been functionally linked to the need to achieve wide gapes in order to use the canines in threat displays and as weapons when those displays escalate to physical violence (e.g., Hylander, 1979; Ravosa, 1990; see Chapter 1). Given that the teeth and facial skeleton share many of the same developmental pathways (reviewed by Vinyard and Hanna, 2005), it may be that selection for long faces in cercopithecines resulted in an increase in the size of the postcanine row. Thus, the large postcanine teeth of cercopithecines relative to body mass may be a nonadaptive developmental outcome of facial elongation.[7] On the other hand, the masticatory-efficiency hypothesis provides a possible adaptive explanation: elongation of the postcanine dentition in cercopithecines may be related to increasing the leverage of the masticatory muscles at the distal bite points. As cercopithecine canines increased in height and the facial skeleton elongated to accommodate them, the postcanine tooth rows would have migrated forward along with the canines, increasing bite-point moment arms and decreasing masticatory efficiency. Selection for elongated postcanine rows would have pushed the distal bite points posteriorly, thereby decreasing their moment arms and mitigating the negative impact that moving the dentition forward to increase gape has on the leverage of the masticatory muscles.

The point of the preceding discussion is not to say that cercopithecine tooth size is unrelated to diet; it is probably the case that, within the Cercopithecinae, differences in relative postcanine size can be linked to

---

[7] This hypothesis is at odds with the observation, discussed earlier in this chapter, that tooth size is frequently uncorrelated with skull size, including measurements of the facial skeleton, within primate species. This discrepancy was also noted by Vinyard and Hanna (2005, p. 261), who argued that “low correlations among adults do not necessarily preclude pleiotropic changes in form among modular features tied to shared pathways early in development.” As noted in Footnote 2, the lack of correlation between tooth size and skull or body size in adults may be the result of environmental variation (Hlusko, 2006).

differences in dietary demands (e.g., Spencer, 1995). Rather, the point is to highlight the fact that skull size appears to be more relevant than body mass in terms of expressing the relative size of the postcanine row in the Anthropoidea, at least in terms of evaluating the postcanine pleiotropy hypotheses. For example, a positive correlation between body-mass-adjusted canine size and body-mass-adjusted postcanine size is consistent with the positive postcanine pleiotropy hypothesis, but it is also consistent with the hypothesis that postcanine size responds to changes in skull size that are related to enlargement of the canines. In the latter case, the underlying arrow of causality is in the opposite of the direction specified by the positive postcanine pleiotropy hypothesis. By using the skull GM to size-adjust the data, this confounding factor is removed. Given that the r^2 disparity noted above is not restricted to the postcanine row, analogous arguments can probably be made with respect to the incisors and canines.

The conclusion that skull size is probably more appropriate than body mass for size-adjusting the dental variables receives further support from the results of a partial-correlation analysis of maxillary tooth size, skull size, and body mass, presented in Tables 3.14 and 3.15. Partial correlations between each dental variable and skull size, holding body mass constant, are moderate to strong in males (r = 0.51–0.87) and low to moderate in females (r = 0.43–0.71). However, when skull size is held constant, nearly all of the partial correlations between tooth size and body mass are nonsignificant, indicating that the correlation between tooth size and body mass is indirect. Thus, local factors (i.e.,

TABLE 3.14. Partial-correlation analysis of maxillary tooth size, skull size, and body mass in males

	Correlation with skull GM holding body mass constant	Correlation with body mass holding skull size constant
Anthropoidea		
Incisor area	0.51**	0.07
Postcanine area	0.78***	−0.29
Canine area	0.80***	−0.37
Canine height	0.65***	−0.27
Catarrhini		
Incisor area	0.66***	−0.26
Postcanine area	0.73***	−0.05
Canine area	0.87***	−0.49*
Canine height	0.66***	−0.34

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

TABLE 3.15. Partial-correlation analysis of maxillary tooth size, skull size, and body mass in females

	Correlation with skull GM holding body mass constant	Correlation with body mass holding skull size constant
Anthropoidea		
Incisor area	0.67***	−0.11
Postcanine area	0.67***	0.01
Canine area	0.50**	0.06
Canine height	0.45*	−0.29
Catarrhini		
Incisor area	0.65***	−0.05
Postcanine area	0.71***	0.03
Canine area	0.43*	0.26
Canine height	0.43*	−0.28

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

the facial skeleton) have a greater influence on tooth size than organism-wide factors (i.e., body mass) (see also Vinyard and Hanna, 2005).

With respect to the question of which method of size-adjustment to use—shape ratios or regression residuals—the answer is less clear. As noted, some of the dental variables are positively allometric when scaled to skull size and some are isometric. In most cases, the biological significance of the observed allometry is unclear. An exception is the positive allometry in male canine measurements, which can be plausibly linked to sexual selection—males of larger-bodied anthropoid species tend to have relatively large canines because there is a positive association between intensity of intermale competition and body size in the Anthropoidea (Plavcan and van Schaik, 1992, 1997b; Mitani et al., 1996; Plavcan, 2001). However, a good explanation for positive allometry in incisor and postcanine size is lacking (reviewed by Ungar, 1998). Thus, given the uncertainties regarding the potential adaptive meaning of allometry in tooth size, both methods of size-adjustment were used to compute interspecific correlations, and the results generated from each method were compared. Because residuals from an RMA line do not completely remove the effects of the independent size variable, residuals from a least-squares line were used, following the recommendations of Smith (2009).

Correlation analysis

Tables 3.16 and 3.17 present the correlations between relative canine size and relative incisor size. As discussed in Chapter 2, residuals do not technically express relative size; rather, they represent statistically size-controlled variables

TABLE 3.16. Correlations between relative incisor and canine size in males

	Shape ratios		Residuals	
Incisor area vs.:	r_{TIPS}	r_{IC}	r_{TIPS}	r_{IC}
Canine area				
Anthropoidea				
Maxillary	0.13	0.07	−0.05	0.14
Mandibular	−0.06	0.01	−0.18	−0.11
Catarrhini				
Maxillary	0.21	0.14	−0.08	0.16
Mandibular	0.18	0.13	0.08	0.14
Canine height				
Anthropoidea				
Maxillary	−0.23	−0.09	−0.11	−0.02
Mandibular	−0.10	−0.03	0.01	−0.11
Catarrhini				
Maxillary	−0.58**	−0.16	−0.47*	−0.17
Mandibular	−0.11	0.00	−0.06	−0.05

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at the $p < 0.05$ level.

** Significant at the $p < 0.01$ level.

TABLE 3.17. Correlations between relative incisor and canine size in females

	Shape ratios		Residuals	
Incisor area vs.:	r_{TIPS}	r_{IC}	r_{TIPS}	r_{IC}
Canine area				
Anthropoidea				
Maxillary	0.01	0.32†	0.05	0.32*
Mandibular	−0.18	0.04	−0.20	0.04
Catarrhini				
Maxillary	0.20	0.47*	0.12	0.42*
Mandibular	0.13	0.40*	0.05	0.30
Canine height				
Anthropoidea				
Maxillary	−0.52**	−0.34	−0.34	−0.27
Mandibular	−0.46**	−0.19	−0.36†	−0.17
Catarrhini				
Maxillary	−0.66***	−0.38	−0.53**	−0.31
Mandibular	−0.25	0.17	−0.21	0.05

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at the $p < 0.05$ level.

** Significant at the $p < 0.01$ level.

*** Significant at the $p < 0.001$ level.

† Borderline significant ($0.05 < p < 0.06$).

(see discussion in Jungers et al., 1995; Smith, 2005). However, for simplicity, the term *relative size* is used when discussing the results derived from both shape ratios and residuals for the remainder of this chapter. As in the analyses reported above, square roots of areal measurements were used for the shape-ratio and residual size-adjustment procedures. Correlations derived using species means (r_{TIPS}; referred to as *tip correlations* following Martins and Garland, 1991) are listed alongside correlations generated using independent contrasts (r_{IC}) for comparison. Species means were logged (base *e*) prior to computing independent contrasts and correlations.

In the analysis of species means, relative canine height and relative incisor area are significantly negatively correlated in male catarrhines (maxillary shape ratios and residuals), female anthropoids (maxillary and mandibular shape ratios), and female catarrhines (maxillary shape ratios and residuals). The direction of these correlations is the opposite of the direction predicted by the incisor pleiotropy hypothesis. Note, however, that the tip correlations are driven primarily by the combination of relatively short canines and large incisors in the Hominidae and, in females, the relatively tall canines and small incisors of the Hylobatidae (Fig. 3.6; hylobatid females are indicated by "Hy"). Removal of these species from the analysis reduces the magnitudes of these correlations and renders them nonsignificant, and in some cases, the sign of the correlation changes from negative to positive.

In the analysis of independent contrasts, relative canine height and relative incisor area are not significantly correlated, confirming that these two variables

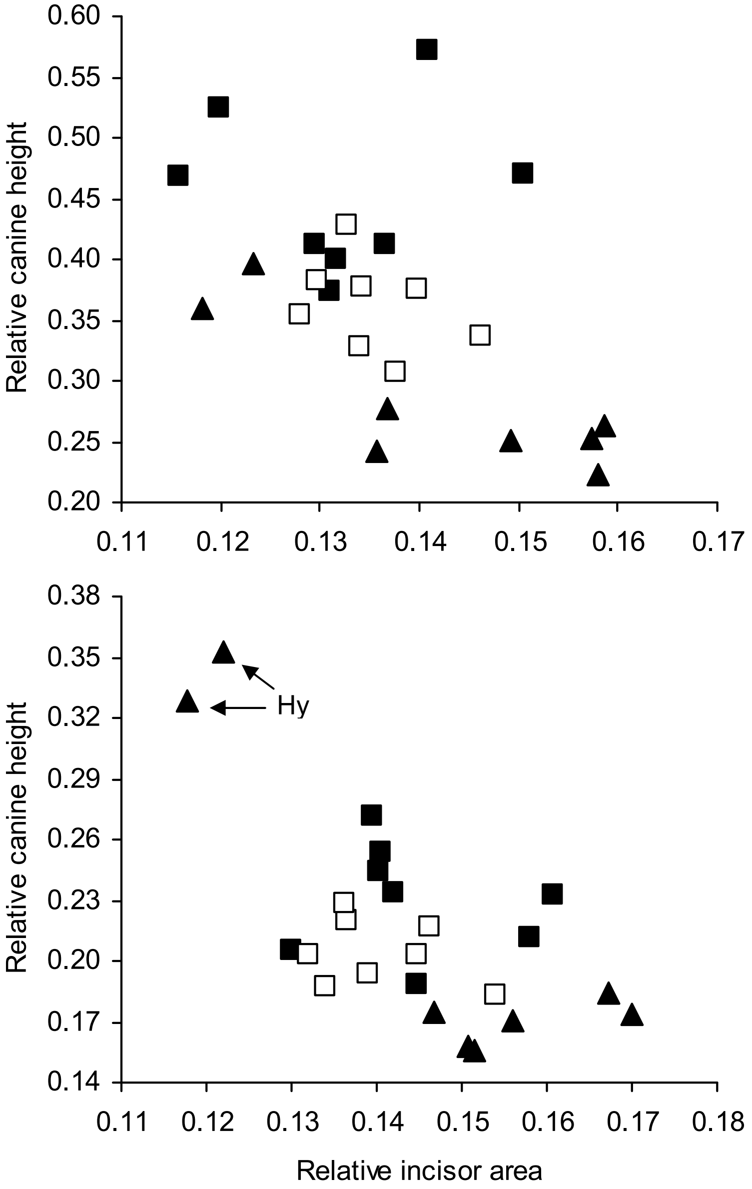


Fig. 3.6. Relative maxillary canine height in male (top) and female (bottom) catarrhines plotted against relative incisor area. Relative size is expressed using shape ratios. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Hy = *Hylobates*.

are not associated when phylogeny is controlled.[8] On the other hand, there is a significant positive association between relative canine area and relative incisor area in female anthropoids (maxillary residuals only, though the correlation for the maxillary shape ratios is borderline significant, $p = 0.0536$) and female catarrhines (maxillary shape ratios and residuals, mandibular shape ratios), as predicted by the incisor pleiotropy hypothesis. The female catarrhine correlations are higher in magnitude. The upper plot in Figure 3.7 illustrates why the tip correlations between these two variables are low and nonsignificant. First, note that female cercopithecines, as a group, do not differ from other taxa in relative incisor size but they have relatively smaller canine areas than most other anthropoids; thus, they are transposed below the other groups, increasing the dispersion of the data along the y-axis.[9] Second, *Chiropotes satanas* (indicated by "Ch" in the plot) is a distinct outlier; in comparison to the females of other species, *Chiropotes* has among the largest canine areas and smallest incisors relative to skull size, and thus it represents a strong violation of the interspecific

---

[8] When shape ratios are used, the independent-contrast correlations for relative maxillary canine height and relative maxillary incisor area in female anthropoids and female catarrhines are low in magnitude, $r = -0.34$ and -0.38, respectively, but they approach significance: $p = 0.0846$ for anthropoids and $p = 0.0775$ for catarrhines (p-values are two-tailed because the incisor pleiotropy hypothesis does not predict a negative association between canine size and incisor size). However, in these analyses, the hominid-hylobatid contrast is a clear outlier; excluding this point removes any suggestion of a relationship between relative canine height and relative incisor area.

[9] This distinction between female cercopithecines and the females of other anthropoid species does not extend to relative canine height. In fact, cercopithecine females have, on average, relatively taller maxillary and mandibular canines than female Colobinae and Hominidae (see Fig. 3.6).

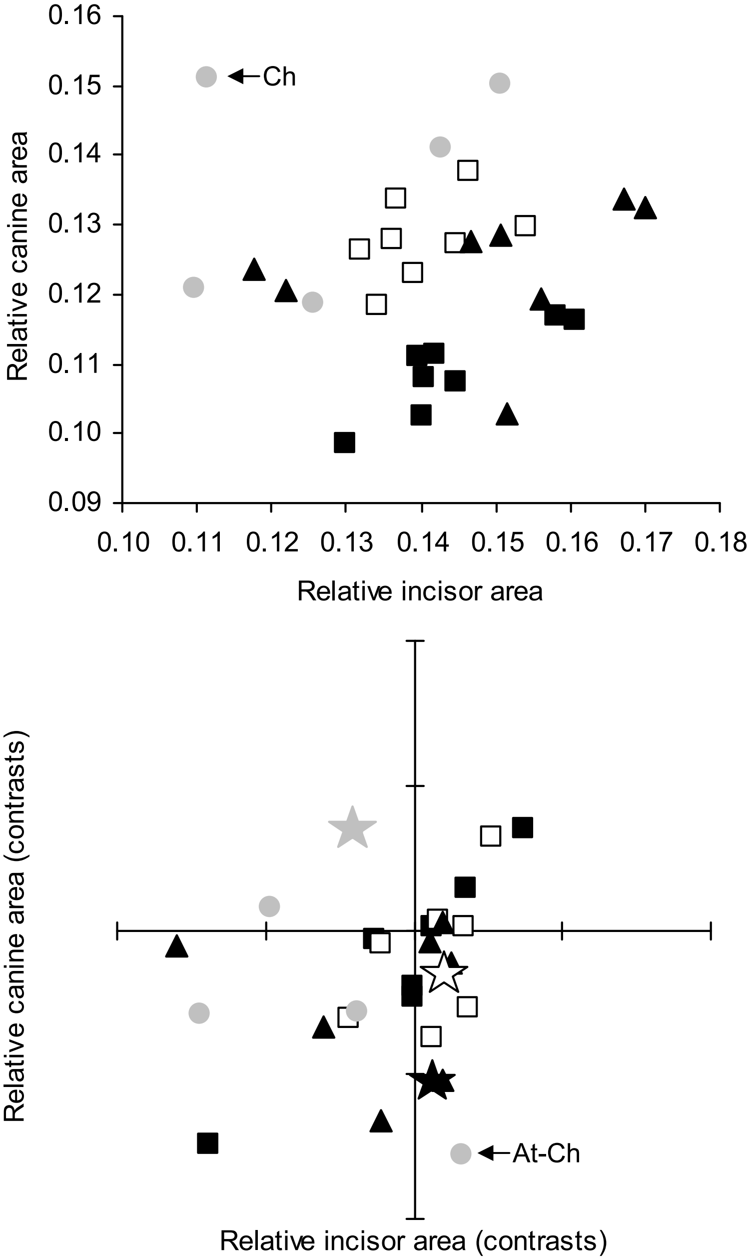


Fig. 3.7. Relative maxillary canine area in female anthropoids plotted against relative incisor area: top, species means; bottom, independent contrasts. Relative size is expressed using shape ratios. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Ch = *Chiropotes satanas*; At-Ch = Atelidae-*Chiropotes* contrast. The gray, white, and black stars represent the contrasts between the Platyrrhini and Catarrhini, Cercopithecoidea and Hominoidea, and Cercopithecinae and Colobinae, respectively.

prediction of the incisor pleiotropy hypothesis.[10] When independent contrasts are used (Fig. 3.7, lower plot), these effects are mitigated: the difference between cercopithecines and the other taxa is expressed primarily in only two data points—the cercopithecine-colobine contrast and cercopithecoid-hominoid contrast—rather than eight, and the contrast between *Chiropotes* and its sister taxon (the Atelidae; indicated by "At-Ch") is not an obvious outlier (though it is on the edge of the data scatter). When *Chiropotes* is removed from the analysis, the independent-contrast correlations between relative maxillary canine area and relative maxillary incisor area in female anthropoids increase to $r_{\mathrm{IC}} = 0.51$ ($p = 0.0042$) when shape ratios are used and $r_{\mathrm{IC}} = 0.48$ ($p = 0.0132$) when residuals are used.

Tables 3.18 and 3.19 present the correlations between relative canine size and relative postcanine size. There are fewer significant correlations than in the canine-incisor correlation analysis, and these are limited to catarrhines. In the analysis of species means, relative canine area is significantly positively correlated with relative postcanine size in catarrhine males (except in the mandibular dentition when residuals are used) but not in females. When independent contrasts are used, the pattern is reversed: the correlations for male catarrhines are no longer significant (though the maxillary shape-ratio correlation is borderline significant: $p = 0.0500225$), but the positive correlations between relative canine area and relative postcanine size in the maxillary dentition of

---

[10] Note, however, that *Chiropotes* conforms to the intraspecific prediction of the incisor pleiotropy hypothesis, both when males and females are combined for analysis and when females are considered separately (see Tables 3.1, 3.2).

TABLE 3.18. Correlations between relative postcanine and canine size in males

	Shape ratios		Residuals	
Postcanine area vs.:	r_{TIPS}	r_{IC}	r_{TIPS}	r_{IC}
Canine area				
Anthropoidea				
Maxillary	0.24	0.26	0.14	0.08
Mandibular	0.15	0.15	0.00	0.00
Catarrhini				
Maxillary	0.50**	$0.36^{\dagger}$	0.47*	0.22
Mandibular	0.49**	0.26	0.26	0.09
Canine height				
Anthropoidea				
Maxillary	0.08	−0.11	0.18	−0.15
Mandibular	−0.10	−0.03	0.08	−0.15
Catarrhini				
Maxillary	0.11	−0.05	0.27	−0.10
Mandibular	0.09	0.16	0.27	0.02

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at the $p < 0.05$ level.

** Significant at the $p < 0.01$ level.

† Borderline significant ($0.05 < p < 0.06$).

TABLE 3.19. Correlations between relative postcanine and canine size in females

	Shape ratios		Residuals	
Postcanine area vs.:	r_{TIPS}	r_{IC}	r_{TIPS}	r_{IC}
Canine area				
Anthropoidea				
Maxillary	−0.08	0.12	−0.06	0.12
Mandibular	−0.07	0.09	−0.08	0.08
Catarrhini				
Maxillary	0.22	0.52**	0.19	0.47*
Mandibular	0.21	0.21	0.08	0.21
Canine height				
Anthropoidea				
Maxillary	−0.19	−0.04	−0.06	0.12
Mandibular	−0.27	−0.11	−0.12	−0.02
Catarrhini				
Maxillary	−0.17	−0.13	−0.08	0.12
Mandibular	−0.04	−0.05	0.06	0.05

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at the $p < 0.05$ level.

** Significant at the $p < 0.01$ level.

female catarrhines are significant. As in the canine-incisor analysis, the lack of significant female tip correlations between relative canine area and relative postcanine size is due to the relatively small canine areas of female cercopithecines in comparison to other taxa (Fig. 3.8). The independent-contrast correlations for female catarrhines are consistent with the positive postcanine pleiotropy hypothesis, suggesting that maxillary postcanine size influences maxillary canine size in this group, but note that relative canine height is not correlated with relative postcanine area in female catarrhines or in any of the other groups (illustrated in Fig. 3.9). In fact, the average magnitude of the independent-contrast correlations (absolute values) involving relative canine height in Tables 3.18 and 3.19 is $r_{IC} = 0.09$.

Partial-correlation analysis

Simultaneous evaluation of the incisor and postcanine pleiotropy hypotheses using partial correlations does not alter the pattern of results obtained from testing each hypothesis separately. Tables 3.20 and 3.21 present the partial correlations computed using the independent-contrast correlations derived from shape ratios. Note that they differ only slightly from their counterparts in Tables 3.16–3.19. This similarity is due to the fact that the correlations between relative incisor and postcanine size for each subset of the data are low in magnitude, generally less than $r_{IC} = 0.20$ (absolute value), and nonsignificant (Table 3.22). These results are repeated when the independent-contrast correlations derived from residuals are used to compute partial correlations.

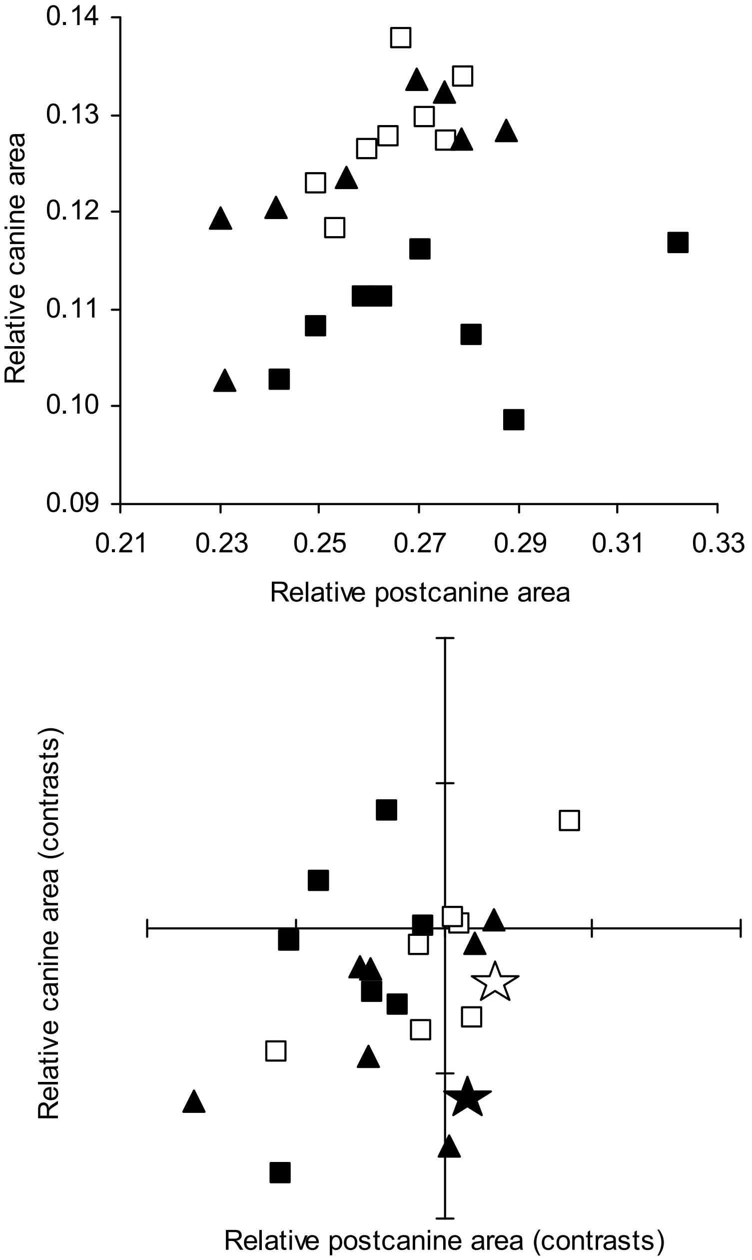


Fig. 3.8. Relative maxillary canine area in female catarrhines plotted against relative postcanine area: top, species means; bottom, independent contrasts. Relative size is expressed using shape ratios. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids. The white and black stars represent the contrasts between the Cercopithecoidea and Hominoidea and between the Cercopithecinae and Colobinae, respectively.

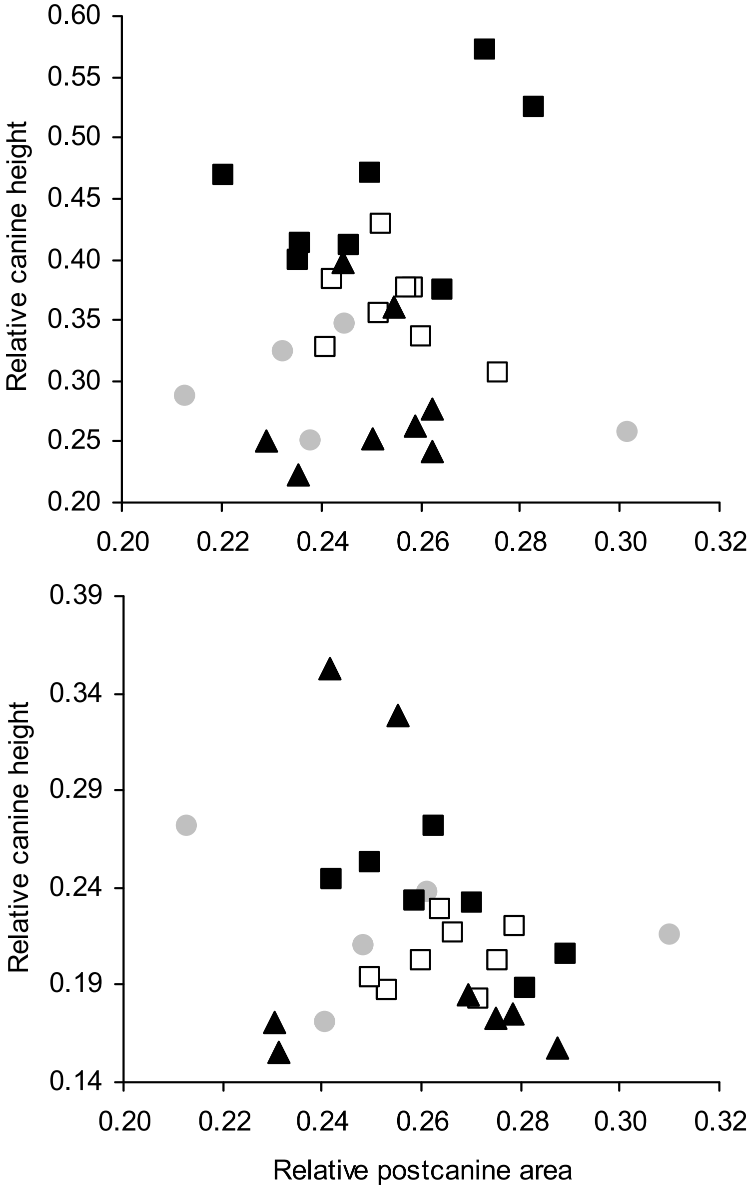


Fig. 3.9. Relative maxillary canine height in male (top) and female (bottom) anthropoids plotted against relative postcanine area. Relative size is expressed using shape ratios. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

TABLE 3.20. Partial-correlation analysis of relative male tooth size (shape ratios)

	Partial correlation with incisor size holding postcanine size constant		Partial correlation with postcanine size holding incisor size constant	
	Maxillary	Mandibular	Maxillary	Mandibular
Canine area				
Anthropoidea	0.10	0.04	0.26	0.15
Catarrhini	0.15	0.17	0.36†	0.28
Canine height				
Anthropoidea	−0.10	−0.03	−0.12	−0.03
Catarrhini	−0.16	0.03	−0.05	0.16

Partial correlations were computed using the independent-contrast correlations listed in Tables 3.22 and 3.24.

† Borderline significant ($0.05 < p < 0.06$).

TABLE 3.21. Partial-correlation analysis of relative female tooth size (shape ratios)

	Partial correlation with incisor size holding postcanine size constant		Partial correlation with postcanine size holding incisor size constant	
	Maxillary	Mandibular	Maxillary	Mandibular
Canine area				
Anthropoidea	0.31	0.03	0.08	0.08
Catarrhini	0.38†	0.41*	0.44*	0.25
Canine height				
Anthropoidea	−0.34	−0.19	0.01	−0.11
Catarrhini	−0.37	0.17	−0.01	−0.05

Partial correlations were computed using the independent-contrast correlations listed in Tables 3.23 and 3.25.

* Significant at $p < 0.05$.

† Borderline significant ($0.05 < p < 0.06$).

TABLE 3.22. Correlations between relative incisor and postcanine size (shape ratios)

	Maxillary	Mandibular
Males		
Anthropoidea	−0.11	−0.15
Catarrhini	<0.01	−0.13
Females		
Anthropoidea	0.14	0.14
Catarrhini	0.32	−0.03

All correlations were computed using independent contrasts.

DISCUSSION

Despite a vast literature documenting within-species correlations and associations among metric and nonmetric dental traits in humans and other primates (e.g., Dahlberg, 1945; Olson and Miller, 1958; Garn et al., 1961, 1963a,b, 1964, 1965; Moorrees and Reed, 1964; Morris, 1967; Turner, 1969; Suarez and Bernor, 1972; Suarez and Williams,1973; Swindler and Orlosky, 1974; Henderson and Greene, 1975; Lombardi, 1975; Corruccini, 1977; Scott, 1977; Wolpoff, 1978, 1982; Townsend and Brown, 1979; Wood, 1979a,b; Wood and Stack, 1980; Cochard, 1981; Kieser and Groeneveld, 1987a,b,c, 1988; Harris and Bailit, 1988; Line, 2001; Hlusko et al., 2004, 2007; Hlusko, 2006; Hlusko and Mahaney, 2009), the relationship between pleiotropy and interspecific differences in tooth size and form remain poorly understood. The idea that the mammalian dentition can be divided into a series of morphogenetic fields (Butler, 1939; Dahlberg, 1945), corresponding to the incisor row, canine, and postcanine row, has been particularly influential in this line of research, with many of the studies cited above concentrating on delineating fields within the dentition, identifying the centers of each field, or documenting areas of overlap and interaction between fields.[11] The focus of most of these studies has been primarily on single species, and thus the macroevolutionary consequences of the relationships they document

---

[11] According to Dahlberg (1945, p. 687) a morphogenetic field is “a field of influence governing size and form … in each tooth group.” In Butler’s (1939) original formulation of the field concept, he placed the different tooth classes in separate regions within a single morphogenetic field. Subsequent authors, including Dahlberg, have referred to these regions as separate fields.

remain largely unexplored. This study represents the first broad-scale attempt to link pleiotropy among different components of the dentition to interspecific differences in relative tooth size.

The results fail to support the hypothesis that canine height is influenced by changes in incisor and postcanine size via pleiotropy. The very low interspecific correlations between relative canine height and relative incisor and postcanine size obtained in the weak interspecific test are particularly definitive: canine height evolves independently of the other components of the dentition when differences in organismal size are controlled. Thus, changes in incisor and postcanine size can be rejected as explanations for the reduction in canine height observed in hominins and in other primate lineages.

On the other hand, the weak test does provide some evidence for a link between the basal dimensions of the canine crown and incisor and postcanine size among species. In female anthropoids, relative canine area is moderately positively correlated (i.e., $r_{\mathrm{IC}} \approx 0.50$) with relative incisor area when *Chiropotes satanas* (an obvious outlier) is excluded from the analysis. This relationship is mainly restricted to the maxillary dentition, but these two variables are significantly positively correlated in the mandibular dentition of catarrhine females when the data are size-adjusted using shape ratios (but not residuals). Catarrhine females also exhibit a moderate positive correlation between relative canine area and relative postcanine area in the maxillary dentition. These interspecific relationships are consistent with the results of the intraspecific test, which show that when canine area is correlated with postcanine or incisor area within species, the relationship is invariably positive. Thus, if only the basal dimensions of the canine are considered, then there is support for the incisor and positive postcanine pleiotropy hypotheses. However, this support must be considered limited for a number of reasons.

First, the strong test failed to detect the relationships documented by the weak test. The fact that the results of the two tests differ does not necessarily mean that they contradict each other. The strong test is not as statistically powerful as the weak test, and thus, given that the signals detected by the weak test are not particularly strong, it is not surprising that the strong test failed to detect them. However, as discussed at the beginning of this chapter, the weak test can only provide circumstantial support for the pleiotropy hypotheses because, unlike the strong test, it uses species that exhibit no evidence of pleiotropy to test interspecific predictions of each hypothesis. Moreover, whereas the strong test relies solely on differences between closely related, biologically similar species, the weak test incorporates information on differences among higher taxa, which are more likely than the latter types of comparisons to be influenced by the effects of factors such as adaptive differentiation and sexual selection. Thus, the possibility that the results of the weak test are driven by some other factor that produces interspecific patterns similar to those predicted by the pleiotropy hypotheses cannot be ruled out. One obvious alternative explanation is diet. However, while several studies have examined the relationship between canine size and diet in platyrrhines (e.g., Coimbra-Filho and Mittermeier, 1976, 1977; Greenfield, 1992c; Kinzey, 1992; Rosenberger, 1992; Anapol and Lee, 2004;

Spencer, 1995, 2003; Wright 2005; Plavcan and Ruff, 2008), none has produced evidence for a consistent relationship that can account for the results of the weak test.

Second, the relationships documented by the weak test are restricted to the females. A plausible explanation for the fact that males do not conform to the interspecific predictions of the pleiotropy hypotheses is that male anthropoids are a poor model for assessing the macroevolutionary effects of pleiotropy within the dentition because of sexual selection for weaponized canines. In other words, sexual selection may overwhelm the interspecific effects of pleiotropy in males. On the other hand, according to this argument, the macroevolutionary effects of pleiotropy may be more evident in females because females do not experience selection for canine weaponization as intensely as do males (Plavcan, 1990, 1998, 2001; Plavcan and van Schaik, 1992; Plavcan et al., 1995). It may be that the macroevolutionary effects of pleiotropy on canine size in males are only observable at the morphological level in clades of species in which sexual selection on males is relaxed. However, the fact that there is a dearth of such species in the Anthropoidea renders this hypothesis difficult to test. A further problem for this hypothesis is that sexual selection does not appear to obscure the morphological expression of pleiotropy in males within species. Although the results of the intraspecific test indicate that males tend to exhibit fewer significant intraspecific correlations between canine area and incisor or postcanine area than females, this pattern is not statistically significant.

Third, the signals detected by the weak test are further restricted, for the most part, to the female maxillary dentition. That the maxillary and mandibular dentitions exhibit different signals is not entirely unexpected, given that there is evidence that the two sets of teeth differ in their genetic architectures (e.g., Qiu et al., 1997; Thomas et al., 1997; Ferguson et al., 1998; Zhao et al., 2000; Mitsiadis and Drouin, 2008). However, the results of the intraspecific test do not indicate that pleiotropic links between the canine and other components of the dentition are stronger or more common in the maxillary dentition than in the mandibular dentition.

Finally, the fact that only a few of the many correlations generated for the weak test are statistically significant is a concern. As discussed in Chapter 2, evaluation of the overall pattern of results was preferred over adjusting significance levels for multiple tests in order to maximize statistical power and guard against false negative results. Nevertheless, the possibility that some of the results of the weak test are spurious must still be considered. Application of a procedure such as the sequential Bonferroni technique (e.g., Holm, 1979; Rice, 1989) would help identify such results and would certainly render some of the correlations nonsignificant, as most of the p-values for the significant results fall between $p = 0.05$ and $p = 0.01$. However, identifying which of these correlations would be affected is difficult to determine. The problem is that there are no objective criteria for deciding which tests should be included as part of a single multiple-test correction (e.g., Perneger, 1998). Should significance levels be adjusted for the total number of tests conducted in this chapter, or should each table receive its own correction? The answer to this question is unclear, but each of these options (or various others) is defensible. What is clear is that the results of the weak test are not statistically robust—they constitute, at most, only very weak confirmatory evidence that interspecific differences in the size of the basal canine crown are influenced by other components of the dentition. Thus, a conservative interpretation of the results of this study is that there is a link between canine size and incisor and postcanine size at the intraspecific level in many anthropoid species, but these relationships have very little, if any, impact on interspecific differences in canine size.

The finding that changes in canine size are largely independent of changes in incisor and postcanine size among species is consistent with the hypothesis that the anthropoid dentition is modularized (Hlusko and Mahaney, 2009). A module is a group of developmentally and/or functionally related traits that are (1) linked together by relatively strong pleiotropic effects (i.e., morphologically integrated) and (2) buffered from the pleiotropic effects of other such groups (i.e., parcellated) (Wagner, 1996; Wagner and Altenberg, 1996; see also Cheverud, 1996b; Cheverud et al., 1997; Beldade et al., 2002; Hallgrímsson et al., 2002; Klingenberg et al., 2003; West-Eberhard, 2003). Modularity is thought to facilitate adaptive evolution by permitting groups of functionally linked traits to change without causing potentially deleterious pleiotropy-induced changes in other, functionally distinct character complexes (Wagner, 1996; Wagner and Altenberg, 1996).

In their quantitative-genetic study of morphological integration in the maxillary dentition of a pedigreed population of captive baboons (*Papio hamadryas* sensu lato), Hlusko and Mahaney (2009) identified two primary modules that were almost completely genetically uncorrelated with each other—the incisor row and the postcanine teeth.[12] The lack of correlation between relative incisor area and relative postcanine area among the species included in this study (see Table 3.22) supports this distinction and suggests that Hlusko and Mahaney's results can be generalized to the Anthropoidea as a whole. Unfortunately, canine data were unavailable for the baboon population used by Hlusko and Mahaney (2009). The results obtained in this study suggest a pattern of partial pleiotropy with respect to the canine and other components of the dentition. The intraspecific results indicate that at least some aspects of the canine crown (i.e., the basal dimensions) are linked with incisor and postcanine size within species, whereas the interspecific results indicate that these pleiotropic effects have little or no influence on canine size. Thus, the canine teeth, along with the anteriormost mandibular premolar (Plavcan, 1990; Greenfield and Washburn, 1992; see also Chapter 2), constitute an independent or semi-independent module within the anthropoid dentition.

---

[12] Hlusko and Mahaney (2009) also found that the postcanine module could be further divided into two additional modules—comprising, respectively, the premolars and the molars—linked together by partial pleiotropy.

CHAPTER 4—THE MASTICATORY-EFFICIENCY HYPOTHESIS

PART I: CANINE HEIGHT AND MUSCLE LEVERAGE

The primary prediction of the masticatory-efficiency hypothesis—that there will be an inverse relationship between the leverage of the masticatory muscles and relative combined canine height among species—was tested using interspecific correlations. As in Chapter 3, correlations were computed using both species means (r_{TIPS}) and independent contrasts (r_{IC}), and all data were $\log_e$-transformed prior to analysis. Males and females were examined separately. The summary statistics for the muscle and bite-point moment-arm lengths for each species, separated by sex, are presented in Tables 4.1 and 4.2, respectively, and those for the leverage of the superficial masseter and anterior temporalis (i.e., muscle moment-arm length divided by bite-point moment-arm length) are given in Tables 4.3 and 4.4. Relative combined canine heights for each species are presented in Table 4.5 (see Tables 2.4 and 2.6 for the data used to generate these values).

Combined canine heights were size-adjusted using shape ratios, with the skull GM acting as the independent size variable. In the interspecific correlation analysis in the previous chapter (i.e., the weak interspecific test of the pleiotropy hypotheses), both shape ratios and regression residuals were used to size-adjust the dental data because, in that case, the biological significance of the positive allometry observed in some of the dental variables when scaled against skull size was unclear. However, with respect to size-adjusting combined canine height vis-à-vis testing the masticatory-efficiency hypothesis, relative size, in the strict meaning of the term, is the variable of interest. Recall that a distinction was made in Chapter 2 between relative size and controlling for size, following Smith (2005). Shape ratios represent the former, whereas regression residuals represent the latter. Because the masticatory-efficiency hypothesis posits a relationship between canine height and the configuration of the masticatory system, the most relevant variable for testing the hypothesis is the height of the canines *relative* to the size of the masticatory system. Given that canine height scales with positive allometry against skull size in anthropoid males (see Table 3.12), using regression residuals to size-adjust canine height would result in the removal of important size-correlated shape information.

The masticatory-efficiency hypothesis also predicts an intraspecific relationship between relative combined canine height and muscle leverage: in species characterized by sexual dimorphism in canine height, females will have greater muscle leverage than males due to the fact that they do not require nor do they use relatively wide gapes (Hylander and Vinyard, 2006; Hylander, 2009).[1] With respect to the species used for this study, males have relatively taller canines than conspecific females in every species with the exception of *Chiropotes satanas* (though the *p*-value for the comparison is low; $p = 0.0805$) (Table 4.5). Thus, differences between conspecific males and females were evaluated using Wilcoxon matched-pairs signed-ranks tests and permutation tests.

---

[1] In addition to this intersexual relationship, the masticatory-efficiency hypothesis predicts that canine height will be correlated with muscle leverage among conspecific individuals of the same sex. However, the fact that worn canines were included in this study renders attempts to test this prediction unreliable (see also Chapter 3, p. 92).

TABLE 4.1. Summary statistics for muscle moment-arm lengths

		Superficial masseter (mm)		Anterior temporalis (mm)	
	Sex	Mean	SD	Mean	SD
Al. seniculus	M	31.13	3.15	20.61	2.62
	F	26.46	2.67	16.55	1.02
At. geoffroyi	M	22.66	1.93	14.66	1.40
	F	22.50	1.82	14.22	1.20
Ceb. libidinosus	M	19.00	1.87	15.25	1.95
	F	15.74	1.21	12.34	1.17
Ceb. capucinus	M	19.19	1.39	15.49	1.40
	F	16.24	1.16	13.83	1.28
Ch. satanas	M	20.00	1.55	12.04	1.00
	F	19.39	0.92	11.88	0.42
Pith. monachus	M	18.38	1.50	13.08	1.17
	F	17.88	1.17	12.13	0.70
Cer. pogonias	M	20.47	1.23	15.36	0.88
	F	18.64	1.02	12.79	1.30
Cer. wolfi	M	18.71	1.50	15.35	1.26
	F	17.98	0.87	13.83	1.20
Chl. pygerythrus	M	21.58	1.16	17.51	1.23
	F	19.52	1.50	15.30	1.46
Er. patas	M	26.43	1.69	23.26	2.17
	F	20.19	1.16	17.35	1.36
Mac. mulatta	M	24.82	1.75	19.46	2.03
	F	22.67	1.18	16.79	1.67
Mac. fascicularis	M	22.88	1.94	19.17	1.50
	F	20.81	1.10	16.02	1.21
Th. gelada	M	33.82	2.01	28.91	1.60
	F	30.58	0.01	25.39	1.29
M. leucophaeus	M	35.86	3.51	27.26	3.04
	F	28.12	0.92	18.74	1.43
Pil. foai	M	25.56	2.12	20.64	1.48
	F	22.99	1.93	19.05	2.08

(continued)

TABLE 4.1. (Continued)

		Superficial masseter (mm)		Anterior temporalis (mm)	
	Sex	Mean	SD	Mean	SD
Pro. verus	M	17.10	1.01	15.23	1.29
	F	16.84	1.21	14.46	1.22
Col. satanas	M	24.40	1.08	18.89	1.12
	F	24.27	1.42	17.74	1.45
Col. polykomos	M	26.54	1.37	20.53	1.72
	F	25.06	1.67	18.96	1.12
Pre. chrysomelas	M	20.04	0.68	15.15	1.42
	F	19.55	1.17	14.93	1.22
Pre. potenziani	M	23.03	1.98	16.37	1.28
	F	21.87	1.17	16.28	1.42
Tr. obscurus	M	22.51	1.17	15.97	0.83
	F	22.02	1.31	15.23	1.28
Tr. shortridgei	M	23.77	1.36	16.51	1.25
	F	21.31	1.42	15.43	0.89
Hy. lar	M	20.13	1.97	16.63	1.20
	F	19.83	1.98	16.55	1.74
Hy. syndactylus	M	26.34	2.00	24.10	1.97
	F	25.10	2.27	22.70	1.78
Go. beringei	M	69.39	4.34	42.42	3.75
	F	56.66	1.74	33.83	1.72
Go. gorilla	M	58.53	3.90	41.18	4.89
	F	49.73	4.32	35.71	5.34
Pan paniscus	M	35.23	1.73	28.11	2.91
	F	33.83	1.99	28.27	1.75
Pan troglodytes	M	43.07	2.69	35.51	3.14
	F	41.60	3.34	34.65	2.84
Po. abelii	M	55.28	4.63	46.34	6.52
	F	43.84	3.34	36.57	3.71
Po. pygmaeus	M	60.02	4.62	46.18	4.90
	F	49.48	3.62	40.43	5.22

TABLE 4.2. Summary statistics for bite-point moment-arm lengths

		Canine (mm)		M1 (mm)		M3 (mm)	
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	69.23	4.02	49.74	3.49	34.65	3.38
	F	59.37	1.26	41.49	2.00	27.42	1.67
At. geoffroyi	M	55.13	2.45	40.45	2.18	30.74	2.21
	F	55.34	1.69	40.73	1.39	30.46	1.28
Ceb. libidinosus	M	49.78	2.74	33.44	2.76	24.97	2.41
	F	43.97	1.49	28.43	1.37	20.23	1.34
Ceb. capucinus	M	53.62	2.53	36.83	2.69	28.15	2.62
	F	48.09	1.22	31.97	1.33	23.35	1.44
Ch. satanas	M	43.18	1.52	29.23	1.34	22.56	1.45
	F	42.19	1.12	28.61	1.50	21.48	1.56
Pith. monachus	M	44.13	1.89	30.68	1.60	22.79	1.50
	F	43.25	1.32	30.51	1.13	22.69	1.10
Cer. pogonias	M	50.60	1.95	38.20	1.54	26.60	1.67
	F	45.25	1.75	33.26	1.77	21.60	1.85
Cer. wolfi	M	49.20	1.50	36.65	1.43	25.18	1.61
	F	45.36	1.75	33.50	1.52	22.44	1.57
Chl. pygerythrus	M	58.73	2.47	43.95	2.25	30.88	1.61
	F	50.44	1.87	37.21	1.78	24.12	1.97
Er. patas	M	78.91	5.42	60.68	3.60	45.32	3.50
	F	60.29	3.04	44.00	2.55	29.69	2.34
Mac. mulatta	M	65.45	3.96	48.73	3.04	32.81	2.98
	F	56.02	3.02	42.38	2.64	27.04	2.25
Mac. fascicularis	M	64.16	3.53	47.95	2.58	34.19	2.54
	F	53.76	2.73	39.98	2.03	26.38	1.88
Th. gelada	M	99.29	4.25	76.69	3.41	51.74	3.17
	F	87.57	0.86	69.11	1.20	45.54	0.28
M. leucophaeus	M	115.02	7.39	82.69	4.76	59.22	4.70
	F	81.35	3.31	59.88	3.35	38.13	3.42
Pil. foai	M	64.25	3.17	46.93	2.47	32.37	2.43
	F	57.23	3.25	41.24	2.64	26.56	2.71

(continued)

TABLE 4.2. (Continued)

		Canine (mm)		M1 (mm)		M3 (mm)	
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	45.92	1.92	33.21	1.83	22.32	1.76
	F	44.14	1.62	32.22	1.55	21.07	1.59
Col. satanas	M	60.57	1.61	44.13	1.40	30.28	1.35
	F	58.62	1.98	41.97	2.00	27.48	2.42
Col. polykomos	M	65.67	3.53	48.58	3.05	34.05	3.17
	F	62.01	3.13	45.37	2.60	31.36	2.72
Pre. chrysomelas	M	47.95	1.40	35.07	1.27	23.80	1.31
	F	48.28	1.56	35.32	1.24	23.86	1.09
Pre. potenziani	M	54.10	3.08	39.58	2.63	26.28	2.42
	F	54.09	2.04	39.08	1.69	25.58	1.98
Tr. obscurus	M	55.02	2.27	41.00	1.87	27.88	1.71
	F	52.22	2.36	38.23	2.36	25.71	2.40
Tr. shortridgei	M	59.44	2.40	44.54	1.89	30.59	2.19
	F	53.84	1.98	39.93	1.53	26.41	1.66
Hy. lar	M	55.65	2.33	42.80	2.16	30.17	2.02
	F	53.81	2.61	41.43	2.30	29.55	2.01
Hy. syndactylus	M	70.18	2.82	54.35	2.34	37.84	2.18
	F	67.83	3.32	51.21	2.04	34.79	2.49
Go. beringei	M	151.46	9.51	116.46	7.68	81.75	8.71
	F	122.78	5.07	90.28	4.31	58.41	5.60
Go. gorilla	M	137.95	8.20	104.10	5.91	73.14	5.60
	F	121.48	7.67	88.38	7.14	58.46	6.64
Pan paniscus	M	83.53	2.66	63.05	2.36	44.63	2.25
	F	82.85	4.00	62.95	3.70	44.58	3.87
Pan troglodytes	M	105.58	5.99	80.06	5.14	59.08	4.47
	F	100.06	3.82	76.24	3.76	55.15	3.90
Po. abelii	M	133.15	11.52	99.28	9.46	72.06	9.58
	F	106.97	7.09	77.67	6.22	54.32	5.96
Po. pygmaeus	M	131.05	6.48	98.40	5.24	72.78	5.97
	F	111.11	7.18	81.86	5.70	57.39	5.79

TABLE 4.3. Summary statistics for superficial masseter leverage

		Superficial masseter leverage at:					
		Canine		M1		M3	
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	0.449	0.029	0.625	0.034	0.899	0.046
	F	0.451	0.038	0.635	0.053	0.964	0.074
At. geoffroyi	M	0.411	0.027	0.560	0.034	0.738	0.046
	F	0.406	0.026	0.552	0.032	0.738	0.039
Ceb. libidinosus	M	0.378	0.023	0.568	0.022	0.761	0.025
	F	0.358	0.023	0.553	0.031	0.779	0.048
Ceb. capucinus	M	0.358	0.016	0.521	0.023	0.684	0.040
	F	0.338	0.022	0.508	0.027	0.696	0.035
Ch. satanas	M	0.463	0.032	0.684	0.039	0.887	0.047
	F	0.460	0.020	0.678	0.029	0.905	0.053
Pith. monachus	M	0.416	0.024	0.599	0.029	0.807	0.049
	F	0.413	0.018	0.586	0.022	0.788	0.043
Cer. pogonias	M	0.405	0.022	0.536	0.025	0.771	0.034
	F	0.412	0.023	0.561	0.026	0.867	0.057
Cer. wolfi	M	0.380	0.026	0.510	0.030	0.743	0.037
	F	0.396	0.017	0.537	0.024	0.803	0.046
Chl. pygerythrus	M	0.371	0.018	0.492	0.028	0.700	0.040
	F	0.387	0.027	0.525	0.035	0.812	0.059
Er. patas	M	0.335	0.023	0.436	0.025	0.585	0.042
	F	0.336	0.025	0.460	0.035	0.684	0.064
Mac. mulatta	M	0.380	0.022	0.510	0.026	0.759	0.044
	F	0.405	0.020	0.536	0.030	0.842	0.056
Mac. fascicularis	M	0.357	0.023	0.477	0.028	0.670	0.039
	F	0.388	0.020	0.521	0.026	0.791	0.042
Th. gelada	M	0.341	0.024	0.442	0.032	0.656	0.056
	F	0.349	0.003	0.442	0.008	0.671	0.004
M. leucophaeus	M	0.313	0.022	0.434	0.032	0.606	0.042
	F	0.346	0.018	0.471	0.028	0.743	0.065
Pil. foai	M	0.399	0.027	0.545	0.034	0.790	0.047
	F	0.402	0.027	0.558	0.036	0.870	0.071

(continued)

TABLE 4.3. (Continued)

		Superficial masseter leverage at:					
		Canine		M1		M3	
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	0.374	0.019	0.515	0.027	0.768	0.042
	F	0.381	0.020	0.523	0.029	0.801	0.054
Col. satanas	M	0.403	0.018	0.553	0.023	0.807	0.042
	F	0.414	0.019	0.578	0.025	0.887	0.060
Col. polykomos	M	0.404	0.019	0.547	0.026	0.783	0.056
	F	0.408	0.021	0.553	0.032	0.802	0.060
Pre. chrysomelas	M	0.418	0.012	0.572	0.016	0.844	0.037
	F	0.405	0.018	0.554	0.026	0.820	0.046
Pre. potenziani	M	0.426	0.035	0.583	0.047	0.880	0.074
	F	0.404	0.020	0.560	0.028	0.858	0.064
Tr. obscurus	M	0.409	0.018	0.549	0.024	0.809	0.049
	F	0.422	0.019	0.577	0.027	0.860	0.056
Tr. shortridgei	M	0.400	0.016	0.534	0.018	0.779	0.039
	F	0.396	0.016	0.533	0.021	0.807	0.034
Hy. lar	M	0.360	0.028	0.471	0.042	0.669	0.067
	F	0.375	0.019	0.478	0.033	0.671	0.048
Hy. syndactylus	M	0.375	0.022	0.485	0.030	0.697	0.052
	F	0.370	0.023	0.490	0.033	0.722	0.044
Go. beringei	M	0.459	0.025	0.597	0.027	0.854	0.063
	F	0.463	0.025	0.629	0.040	0.978	0.112
Go. gorilla	M	0.425	0.032	0.563	0.037	0.803	0.056
	F	0.413	0.024	0.563	0.031	0.856	0.076
Pan paniscus	M	0.422	0.014	0.559	0.020	0.790	0.032
	F	0.408	0.021	0.538	0.023	0.762	0.047
Pan troglodytes	M	0.412	0.030	0.539	0.031	0.731	0.047
	F	0.416	0.029	0.546	0.035	0.755	0.047
Po. abelii	M	0.413	0.030	0.559	0.041	0.775	0.079
	F	0.410	0.022	0.566	0.035	0.812	0.068
Po. pygmaeus	M	0.454	0.048	0.611	0.049	0.828	0.075
	F	0.445	0.021	0.605	0.025	0.865	0.044

TABLE 4.4. Summary statistics for anterior temporalis leverage

		Anterior temporalis leverage at:					
		Canine		M1		M3	
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	0.297	0.027	0.414	0.036	0.595	0.046
	F	0.282	0.011	0.397	0.019	0.604	0.032
At. geoffroyi	M	0.266	0.018	0.362	0.022	0.476	0.023
	F	0.257	0.021	0.349	0.027	0.467	0.036
Ceb. libidinosus	M	0.298	0.034	0.456	0.050	0.611	0.061
	F	0.281	0.024	0.434	0.038	0.611	0.052
Ceb. capucinus	M	0.289	0.020	0.421	0.032	0.552	0.041
	F	0.287	0.027	0.432	0.035	0.592	0.042
Ch. satanas	M	0.279	0.025	0.412	0.032	0.534	0.040
	F	0.280	0.007	0.416	0.013	0.555	0.028
Pith. monachus	M	0.296	0.020	0.426	0.028	0.574	0.037
	F	0.281	0.018	0.398	0.025	0.536	0.036
Cer. pogonias	M	0.304	0.017	0.402	0.023	0.579	0.037
	F	0.282	0.022	0.384	0.025	0.592	0.038
Cer. wolfi	M	0.312	0.023	0.419	0.032	0.611	0.054
	F	0.305	0.020	0.412	0.027	0.617	0.046
Chl. pygerythrus	M	0.300	0.022	0.399	0.033	0.568	0.048
	F	0.304	0.030	0.412	0.041	0.637	0.069
Er. patas	M	0.294	0.032	0.384	0.038	0.516	0.060
	F	0.289	0.027	0.396	0.038	0.588	0.069
Mac. mulatta	M	0.297	0.023	0.399	0.028	0.594	0.047
	F	0.300	0.026	0.396	0.035	0.623	0.059
Mac. fascicularis	M	0.299	0.022	0.400	0.029	0.562	0.044
	F	0.298	0.020	0.401	0.027	0.609	0.048
Th. gelada	M	0.291	0.011	0.377	0.015	0.560	0.039
	F	0.290	0.018	0.368	0.025	0.558	0.032
M. leucophaeus	M	0.239	0.024	0.329	0.030	0.461	0.041
	F	0.230	0.015	0.314	0.026	0.494	0.052
Pil. foai	M	0.321	0.024	0.440	0.033	0.640	0.061
	F	0.332	0.025	0.461	0.031	0.719	0.053

(continued)

TABLE 4.4. (Continued)

		Anterior temporalis leverage at:					
		Canine		M1		M3	
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	0.334	0.032	0.460	0.045	0.686	0.070
	F	0.327	0.022	0.449	0.031	0.688	0.050
Col. satanas	M	0.312	0.017	0.428	0.025	0.624	0.040
	F	0.303	0.020	0.423	0.027	0.648	0.052
Col. polykomos	M	0.313	0.019	0.423	0.026	0.605	0.046
	F	0.306	0.025	0.419	0.033	0.609	0.063
Pre. chrysomelas	M	0.316	0.027	0.432	0.034	0.637	0.048
	F	0.309	0.025	0.423	0.033	0.626	0.054
Pre. potenziani	M	0.303	0.026	0.415	0.036	0.627	0.064
	F	0.300	0.017	0.416	0.023	0.637	0.039
Tr. obscurus	M	0.290	0.014	0.390	0.017	0.574	0.027
	F	0.292	0.025	0.399	0.034	0.595	0.057
Tr. shortridgei	M	0.278	0.019	0.371	0.024	0.541	0.044
	F	0.287	0.018	0.387	0.026	0.586	0.046
Hy. lar	M	0.300	0.023	0.389	0.028	0.553	0.045
	F	0.311	0.022	0.399	0.027	0.560	0.039
Hy. syndactylus	M	0.343	0.025	0.443	0.027	0.637	0.041
	F	0.335	0.021	0.443	0.031	0.653	0.041
Go. beringei	M	0.280	0.016	0.364	0.020	0.521	0.037
	F	0.272	0.007	0.375	0.012	0.582	0.036
Go. gorilla	M	0.299	0.026	0.395	0.037	0.564	0.060
	F	0.292	0.040	0.404	0.048	0.612	0.076
Pan paniscus	M	0.336	0.029	0.446	0.043	0.631	0.067
	F	0.344	0.021	0.450	0.028	0.637	0.054
Pan troglodytes	M	0.341	0.031	0.444	0.038	0.603	0.054
	F	0.347	0.031	0.455	0.037	0.631	0.060
Po. abelii	M	0.352	0.052	0.468	0.059	0.650	0.098
	F	0.342	0.024	0.471	0.037	0.677	0.066
Po. pygmaeus	M	0.354	0.051	0.471	0.058	0.639	0.088
	F	0.363	0.035	0.493	0.044	0.704	0.055

TABLE 4.5. Mean relative combined canine height

	Male	Female		Male	Female
Alouatta seniculus	0.485	0.410	*Procolobus verus*	0.672	0.342
Ateles geoffroyi	0.478	0.333	*Colobus satanas*	0.605	0.333
Cebus libidinosus	0.684	0.488	*Colobus polykomos*	0.663	0.404
Cebus capucinus	0.636	0.431	*Presbytis chrysomelas*	0.561	0.347
Chiropotes satanas	0.586	0.561	*Presbytis potenziani*	0.554	0.385
Pithecia monachus	0.573	0.495	*Trachypithecus obscurus*	0.627	0.381
Cercopithecus pogonias	0.648	0.432	*Trachypithecus shortridgei*	0.659	0.437
Cercopithecus wolfi	0.683	0.426	*Hylobates lar*	0.622	0.559
Chlorocebus pygerythrus	0.702	0.479	*Hylobates syndactylus*	0.594	0.544
Erythrocebus patas	0.773	0.435	*Gorilla beringei*	0.447	0.309
Macaca mulatta	0.649	0.361	*Gorilla gorilla*	0.507	0.344
Macaca fascicularis	0.783	0.448	*Pan paniscus*	0.409	0.306
Theropithecus gelada	0.865	0.384	*Pan troglodytes*	0.477	0.335
Mandrillus leucophaeus	0.915	0.396	*Pongo abelii*	0.516	0.351
Piliocolobus foai	0.741	0.374	*Pongo pygmaeus*	0.492	0.377

Data on canine height for great apes were provided by Jay Kelley (see Kelley, 1995a). Conspecific males and females are significantly different from each other in relative combined canine height (males greater than females) in all cases except *Chiropotes satanas* (*p* = 0.0805). Statistical significance was determined using the bootstrap procedure described in Chapter 2.

Results

Interspecific analysis

The interspecific correlations between relative combined canine height and the leverage of the masticatory muscles at the canine, M1, and M3 in male anthropoids and male catarrhines are presented in Table 4.6. For the superficial masseter, the tip correlations and the independent-contrast correlations are moderately to strongly negative and all are highly significant ($p < 0.001$), consistent with the predictions of the masticatory-efficiency hypothesis. Not surprisingly, the magnitudes of the tip correlations are generally greater than the independent-contrast correlations, but in most cases, the difference is not marked, and the independent-contrast correlations for masseter leverage at M3 are actually slightly stronger than the corresponding tip correlations. Note also that when only catarrhines are considered, the correlations are stronger than when the Anthropoidea are examined as a whole, particularly in the case of leverage at M1. In contrast, although all of the correlations between anterior temporalis leverage and relative combined canine height are negative, they are much weaker and only a single independent-contrast correlation achieves significance, suggesting that the temporalis does not constrain gape to the same extent as does the masseter, if at all, or that such constraints are overcome primarily through alterations to muscle architecture (e.g., increases in fiber length and decreases in pinnation angle).

The difference between the two muscles is illustrated in Figures 4.1, 4.2, and 4.3. With respect to the anterior temporalis, only male cercopithecines

TABLE 4.6. Correlations between muscle leverage and relative canine height in males

	Superficial masseter leverage at:			Anterior temporalis leverage at:		
	Canine	M1	M3	Canine	M1	M3
Anthropoidea						
r_{TIPS}	−0.81***	−0.70***	−0.64***	−0.37*	−0.33*	−0.23
r_{IC}	−0.66***	−0.57***	−0.65***	−0.20	−0.18	−0.28
Catarrhini						
r_{TIPS}	−0.85***	−0.78***	−0.67***	−0.54**	−0.48**	−0.41*
r_{IC}	−0.77***	−0.75***	−0.75***	−0.29	−0.31	−0.44*

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

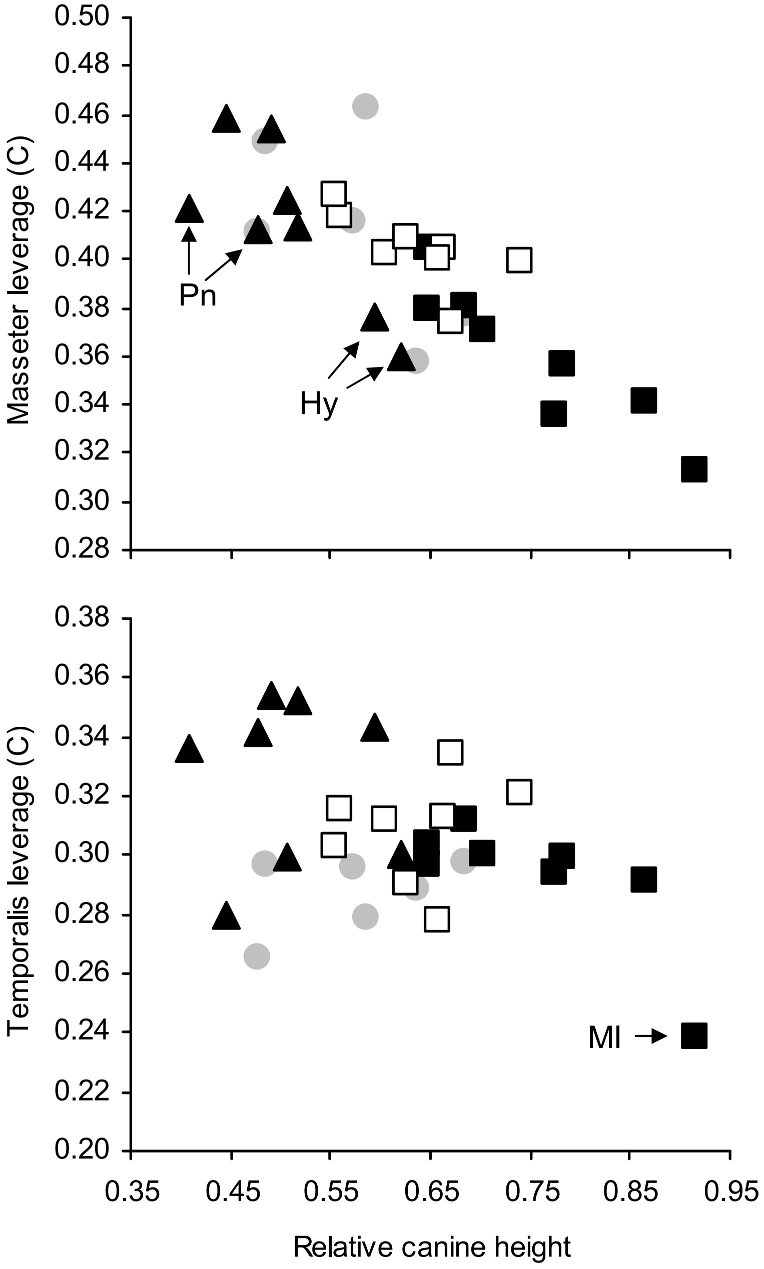


Fig. 4.1. Leverage of the superficial masseter and anterior temporalis at the canine in males plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Hy = *Hylobates*; Ml = *Mandrillus leucophaeus*; Pn = *Pan*.

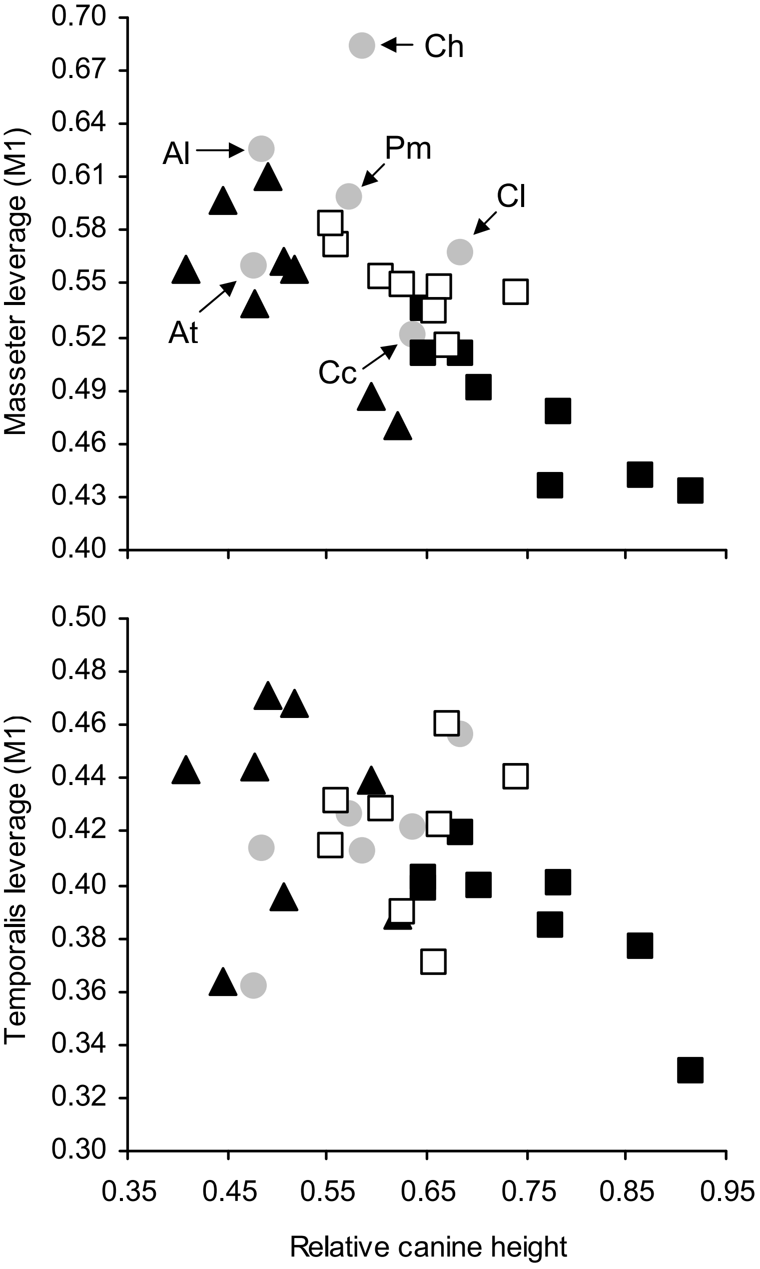


Fig. 4.2. Leverage of the superficial masseter and anterior temporalis at M1 in males plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Al = *Alouatta seniculus*; At = *Ateles geoffroyi*; Cc = *Cebus capucinus*; Cl = *Cebus libidinosus*; Ch = *Chiropotes satanas*; Pm = *Pithecia monachus*.

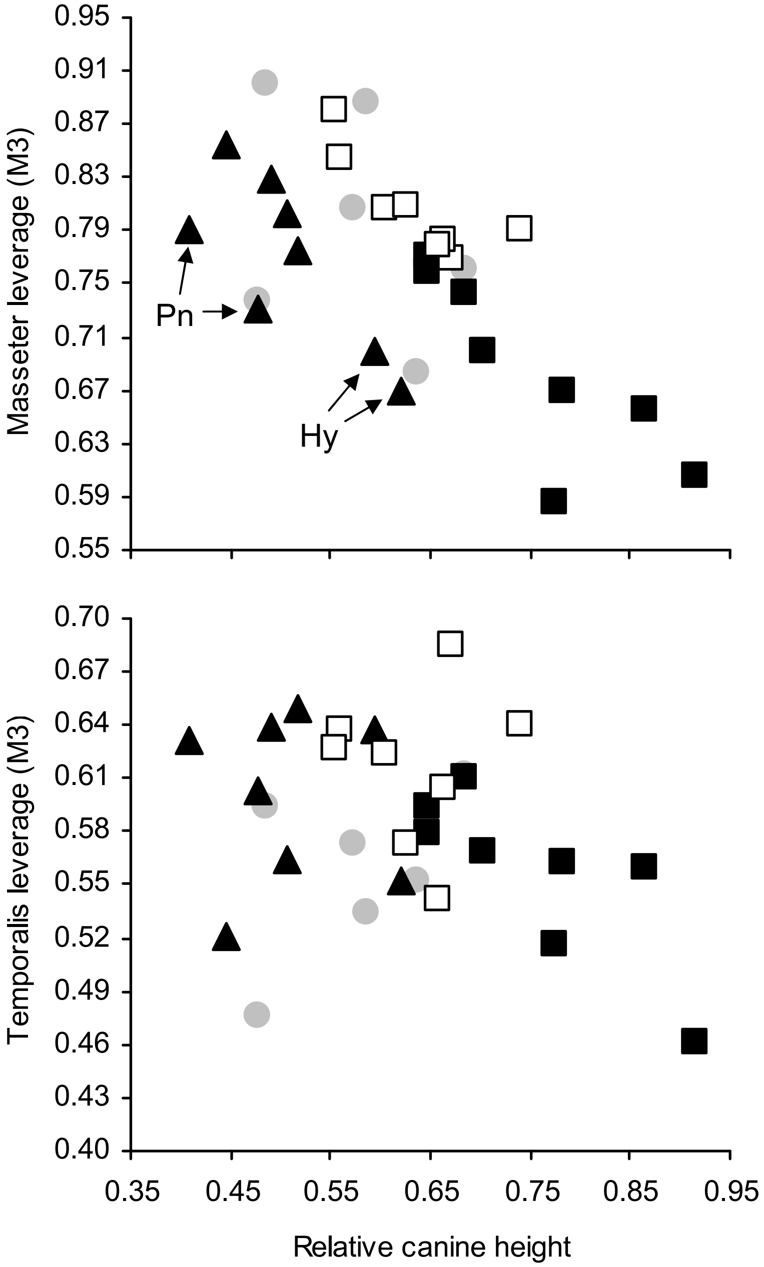


Fig. 4.3. Leverage of the superficial masseter and anterior temporalis at M3 in males plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Hy = *Hylobates*; Pn = *Pan*.

exhibit a consistent negative association between relative canine height and muscle leverage. Note that *Mandrillus leucophaeus* (indicated with an "Ml" in Fig. 4.1) is largely responsible for the significant tip correlations involving anterior temporalis leverage; when this species is removed from the analysis, only a single tip correlation remains significant—leverage at the canine versus relative combined canine height in catarrhines. Additionally, there appears to be a positive association between anterior temporalis leverage at M1 and relative canine height in male platyrrhines (Fig. 4.2). However, the small number of species in this group precludes meaningful statistical evaluation of this trend, and the other two bite points do not exhibit clear evidence of such a relationship.

The plots of masseter leverage versus relative canine height reveal the reason why the negative correlations between these two variables increase in magnitude when male platyrrhines are excluded from the analysis: none of the intrafamilial comparisons within this group are consistent with the predictions of the masticatory-efficiency hypothesis. The position of each platyrrhine species is indicated in Figure 4.2. Within the Atelidae and Pitheciidae comparisons, the species have similar values for relative combined canine height, but *Alouatta seniculus* and *Chiropotes satanas* have much greater muscle leverage than their sister taxa (*Ateles geoffroyi* and *Pithecia monachus*, respectively). Note that *Ch. satanas* in particular is an outlier in this figure (see also Fig. 4.1). In the case of the Cebidae, *Cebus libidinosus* has relatively taller canines and greater masseter leverage than *Cebus capucinus*.

On the other hand, within each of the male catarrhine groups, there is a clear negative association between muscle leverage and relative canine height. These trends are particularly evident in the Cercopithecinae and the Colobinae. With respect to the Hominoidea, the negative association between masseter leverage and relative canine height appears at first glance to be driven primarily by the difference between the Hominidae and the Hylobatidae (male hylobatids are indicated by "Hy" in Figs. 4.1 and 4.3), with the relationship breaking down within the Hominidae. However, closer inspection of the data shows that *Pan paniscus* and *Pan troglodytes* (indicated by "Pn" in Figs. 4.1 and 4.3) are transposed below *Gorilla* and *Pongo*, which gives the impression that masseter leverage in male hominids is distributed randomly with respect to relative canine height. When the two species of *Pan* are identified in the figures, there is a clear negative association between relative canine height and masseter leverage within genera.

The question of how increased masseter leverage is achieved in male anthropoids is explored in Figure 4.4. In this figure, the relative lengths of the canine and M1 moment arms are plotted against the relative length of the superficial masseter's moment arm.[2] Two trends are apparent in these plots. First, note that there is little variation in the relative length of the masseter's moment arm in male cercopithecines. In this subfamily, differences in muscle leverage are largely a function of variation in bite-point moment-arm lengths (see

---

[2] Relative moment-arm lengths were computed by dividing each moment arm by the skull GM.

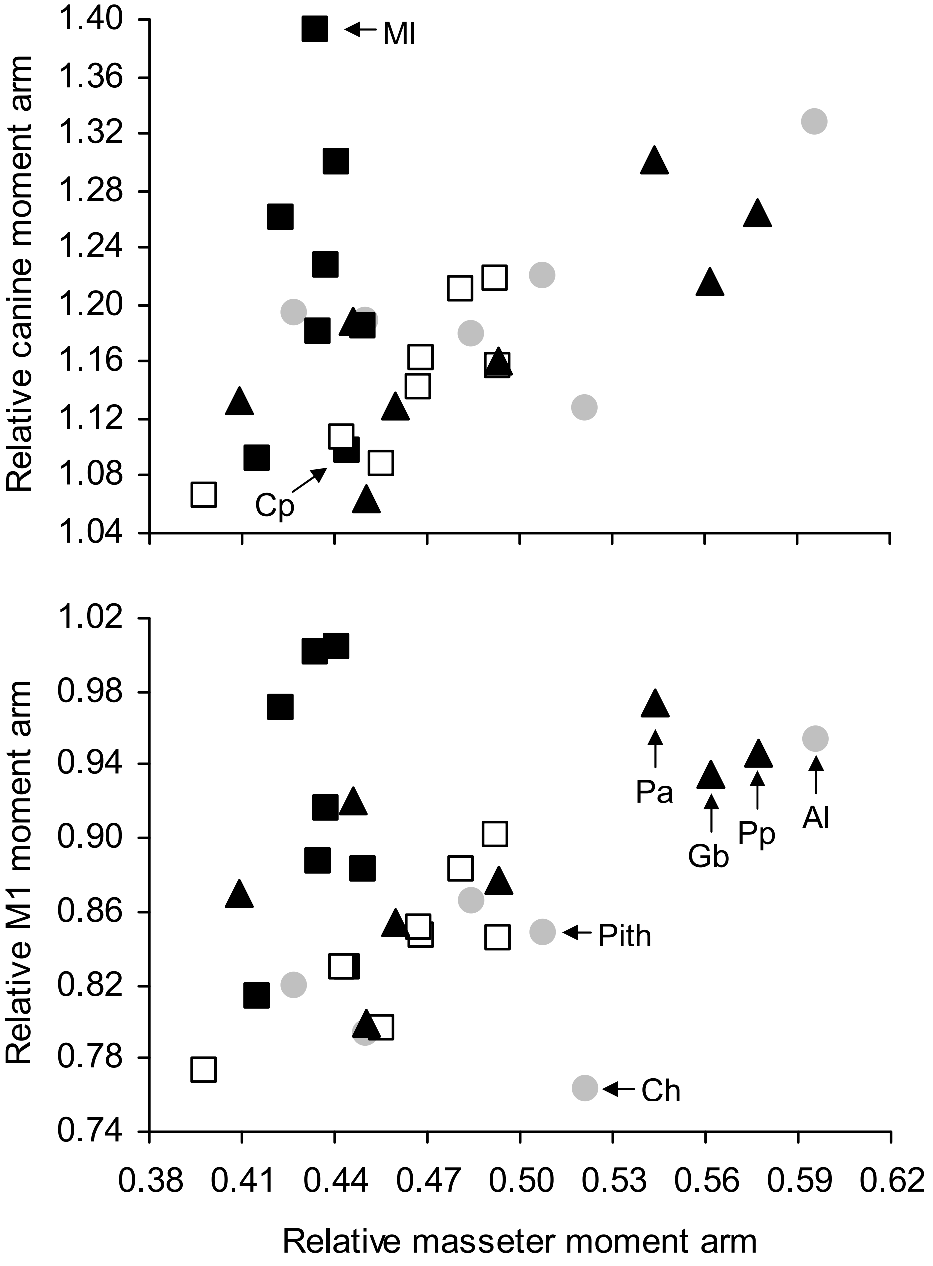


Fig. 4.4. Relative canine and M1 bite-point moment-arm lengths plotted against relative superficial masseter moment-arm length. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Al = *Alouatta seniculus*; Ch = *Chiropotes satanas*; Cp = *Cercopithecus pogonias*; Gb = *Gorilla beringei*; Ml = *Mandrillus leucophaeus*; Pith = *Pithecia monachus*; Pa = *Pongo abelii*; Pp = *Pongo pygmaeus*.

also Ravosa, 1990). For example, the relative length of the masseter's moment arm in *Cercopithecus pogonias* (indicated by "Cp" in Fig. 4.4) is similar to that in *Mandrillus leucophaeus* (indicated by "Ml" in Fig. 4.4), but these two species differ markedly in their relative bite-point moment-arm lengths, reflecting the fact that they represent the extremes of variation in relative canine height among cercopithecines (see Table 4.5).

The second trend is evident in the males of the remaining species, which exhibit positive correlations between relative bite-point moment-arm lengths and relative masseter moment-arm length (Table 4.7). Notably, species with canines that are among the shortest relative to skull size in the sample—*Alouatta seniculus*, *Gorilla beringei*, *Pongo abelii*, and *Pongo pygmaeus* (indicated by "Al," "Gb," "Pa," and "Pp" respectively, in Fig. 4.4)—have bite-point moment-arm lengths that are relatively long, falling within the range of cercopithecines. These species achieve high masseter-leverage values by having the longest masseter moment arms relative to skull size in the sample. These results indicate that, in noncercopithecine anthropoids, increased masseter leverage is achieved not by shortening the bite-point moment arms (as in male cercopithecines) or by lengthening the muscle's moment arm, but by lengthening both. One of the exceptions to the noncercopithecine trend is *Chiropotes satanas* (indicated by "Ch" in Fig. 4.4): note that the relative length of this species' M1 moment arm is unusually short in comparison to the relative length of its masseter moment arm, indicating that its position in Figure 4.2 (i.e., greatest masseter leverage at M1 in the sample) is largely a product of its retracted dentition, particularly in

TABLE 4.7. Correlations between relative superficial masseter moment-arm length and relative bite-point moment-arm lengths in males

	Relative superficial masseter moment arm vs.:		
	Relative canine moment arm	Relative M1 moment arm	Relative M3 moment arm
Anthropoidea			
r_{TIPS}	0.40*	0.29	$0.36^{\dagger}$
r_{IC}	0.57**	0.53**	0.41*
Cercopithecinae excluded			
r_{TIPS}	0.74***	0.63**	0.66***
r_{IC}	0.78***	0.71***	0.64***

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

† Borderline significant ($0.05 < p < 0.06$).

comparison to its sister taxon, *Pithecia monachus* (indicated by “Pith” in Fig. 4.4).

In contrast to males, females exhibit very little evidence for a relationship between relative combined canine height and muscle leverage (Table 4.8; Figs. 4.5, 4.6, 4.7). Most of the correlations are negative, as predicted, but they are much weaker than those obtained in the analysis of males; only one of the independent-contrast correlations is significantly different from zero, and the absolute magnitudes of over half of the correlations (both r_{TIPS} and r_{IC}) between anterior temporalis leverage and relative canine height are less than or equal to $r = 0.10$. When only catarrhine females are considered, the tip correlations involving masseter leverage are moderate in magnitude, negative, and statistically significant. However, these correlations are driven by the difference between hylobatid females (indicated by “Hy” in Fig. 4.5) and hominid females, particularly *Gorilla beringei* (indicated by “Gb” in Fig. 4.5).

A few notable patterns are evident in Figures 4.5–4.7. First, *Chiropotes satanas* (indicated by “Ch” in Fig. 4.6) is once again an outlier. The females of this species have canines that are similar in relative height to those of hylobatid females, but their mean masseter leverage at each bite point is among the greatest in the sample. Second, in the plots of masseter leverage versus relative canine height, *Theropithecus gelada*, *Mandrillus leucophaeus*, and *Erythrocebus patas* (indicated by “Tg,” “Ml,” and “Ep,” respectively, in Fig. 4.6) are transposed below other female anthropoids, including other female cercopithecines. Note that the males of these three species occupy the upper extreme of the anthropoid

TABLE 4.8. Correlations between muscle leverage and relative canine height in females

	Superficial masseter leverage at:			Anterior temporalis leverage at:		
	Canine	M1	M3	Canine	M1	M3
Anthropoidea						
r_{TIPS}	−0.27	−0.14	−0.27	−0.16	−0.07	−0.20
r_{IC}	−0.17	−0.12	−0.18	0.02	−0.08	−0.01
Catarrhini						
r_{TIPS}	−0.51**	−0.53**	−0.51**	−0.10	−0.20	−0.24
r_{IC}	−0.25	−0.29	−0.36*	−0.12	−0.08	−0.01

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

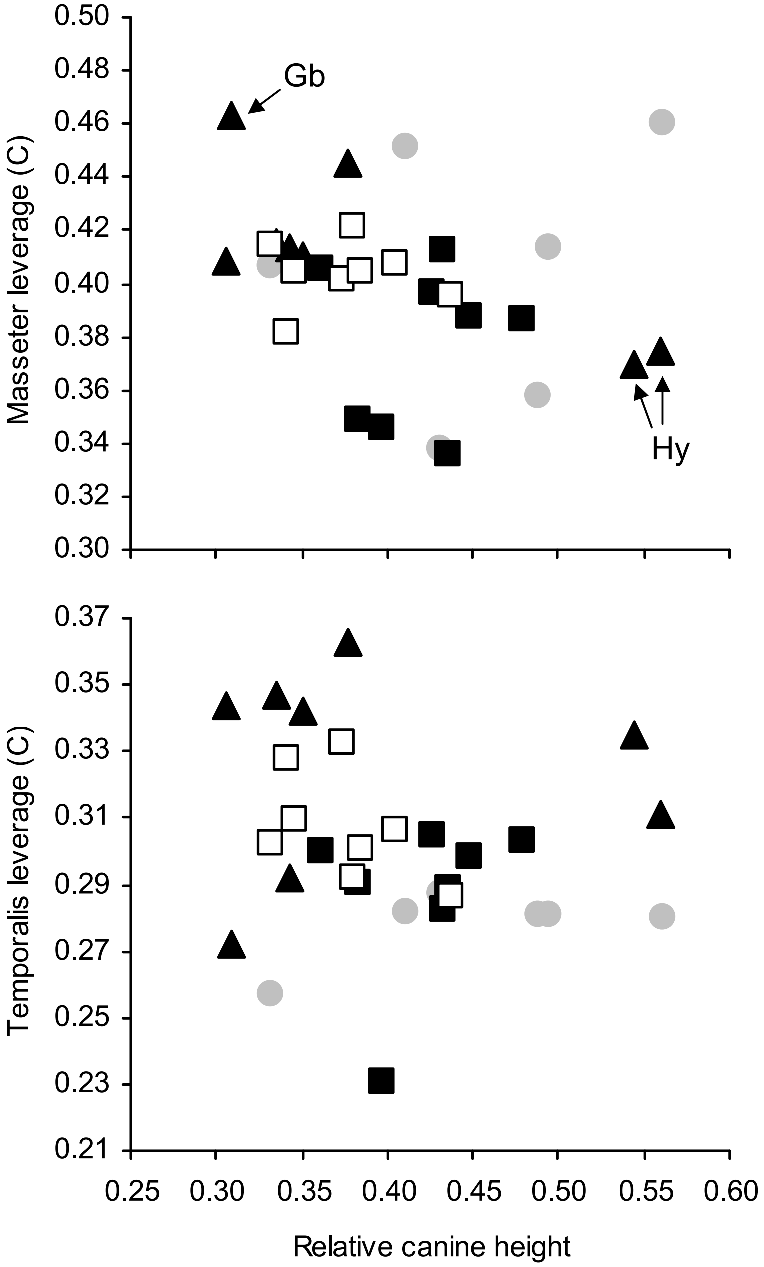


Fig. 4.5. Leverage of the superficial masseter and anterior temporalis at the canine in females plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Gb = *Gorilla beringei*; Hy = *Hylobates*.

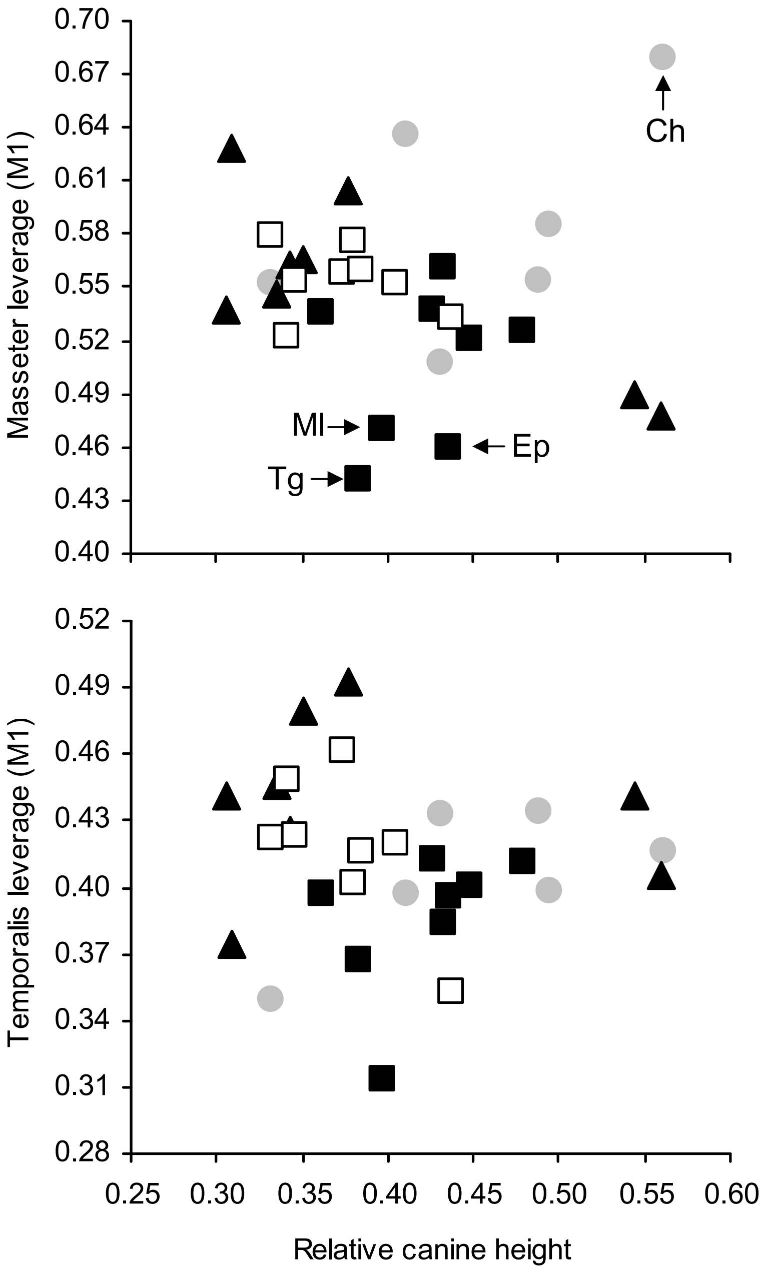


Fig. 4.6. Leverage of the superficial masseter and anterior temporalis at M1 in females plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Ch = *Chiropotes satanas*; Ep = *Erythrocebus patas*; Ml = *Mandrillus leucophaeus*; Tg = *Theropithecus gelada*.

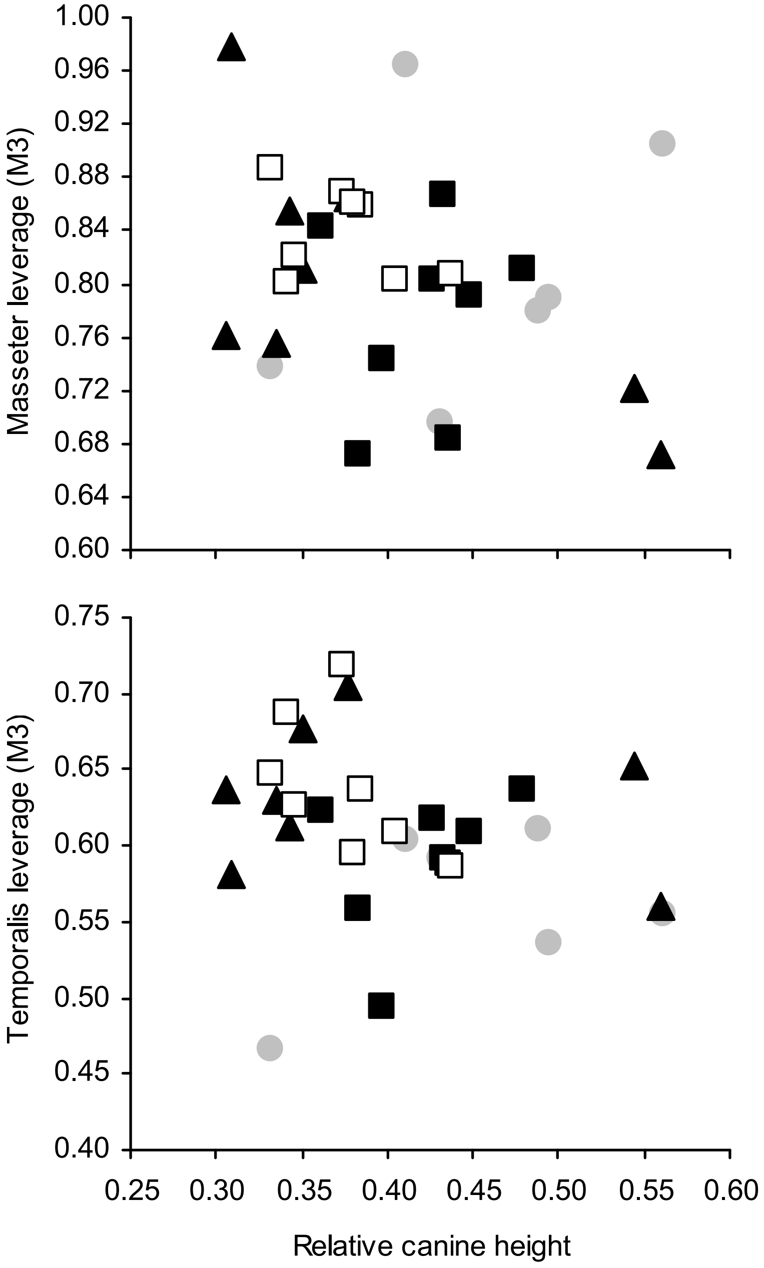


Fig. 4.7. Leverage of the superficial masseter and anterior temporalis at M3 in females plotted against relative canine height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

range of variation in relative combined canine height and the lower extreme of the anthropoid range of variation in masseter leverage (see Tables 4.3 and 4.5). These observations, combined with the fact that females of *Th. gelada*, *M. leucophaeus*, and *Er. patas* are unremarkable in comparison to other female anthropoids in relative canine height, suggest that in at least some species the configuration of the female masticatory apparatus tracks that of males, which in turn is influenced by canine height. This hypothesis is examined in the next section.

Intersexual analysis

Table 4.9 presents a summary of the intersexual comparisons. A Wilcoxon matched-pairs signed-ranks test was used to evaluate the overall pattern of differences at each bite point. This test ranks the absolute values of the female-male differences and then uses the sum of the ranks of the comparisons that are in the opposite of the predicted direction (i.e., males > females) as the test statistic, T_- (Daniel, 1990). Also shown in Table 4.9 is the number of intersexual comparisons in which the difference in muscle leverage is statistically significant. Significance was evaluated using permutation tests.

Initially, the prediction of the masticatory-efficiency hypothesis that females will have greater muscle leverage than males was tested using a one-tailed test. If the difference was found to be nonsignificant, the possibility that the difference was significant in the opposite of the predicted direction was evaluated using a two-tailed test. Graphic representations of these results are given in

TABLE 4.9. Sexual dimorphism in muscle leverage

		Significant comparisons[b]		Wilcoxon test	
	Females > males[a]	F > M	M > F	T_-	p
Superficial masseter					
Canine	17	6	3	201	0.2646
M1	20	10	2	130	0.0173
M3	26	16	0	39	<0.0001
Anterior temporalis					
Canine	10	0	2	323	0.9682
M1	15	0	2	243	0.5803
M3	25	10	1	43	<0.0001

[a] Number of comparisons (out of thirty) in which females have greater muscle leverage than males.

[b] Number of comparisons that are statistically significant ($p < 0.05$; using a permutation test).

Figures 4.8, 4.9, and 4.10, with the stars indicating the species in which males and females are significantly different at $p < 0.05$.

For the masseter, females tend to have greater muscle leverage than males at all bite points. However, the Wilcoxon test indicates that these tendencies are only significant at the two molar bite points—not at the canine. For the anterior temporalis, each bite point presents a different pattern: at the canine, males tend to have greater muscle leverage; at M1, the number of species in which females have greater muscle leverage than males is equal to the number of species in which males have greater muscle leverage than females; and at M3, females tend to have greater muscle leverage than males. For this muscle, only the pattern of differences at M3 is significant (but note that the pattern of muscle-leverage differences at the canine approaches significance; $p = 0.0636$ using a two-tailed test). Thus, in terms of statistical significance, the two muscles present a similar signal.

The permutation tests indicate that males and females are generally similar in terms of muscle leverage. Only fifty-two out of one hundred eighty intersexual comparisons (two muscles × three bite points × thirty species), or 28.9%, are significant. Of these fifty-two significant comparisons, forty-two are in the predicted direction. In the case of the masseter, the number of significant comparisons that are in the predicted direction increases from mesial to distal along the tooth row (from six to sixteen). Conversely, the number of significant comparisons that are in the opposite of the predicted direction decreases from

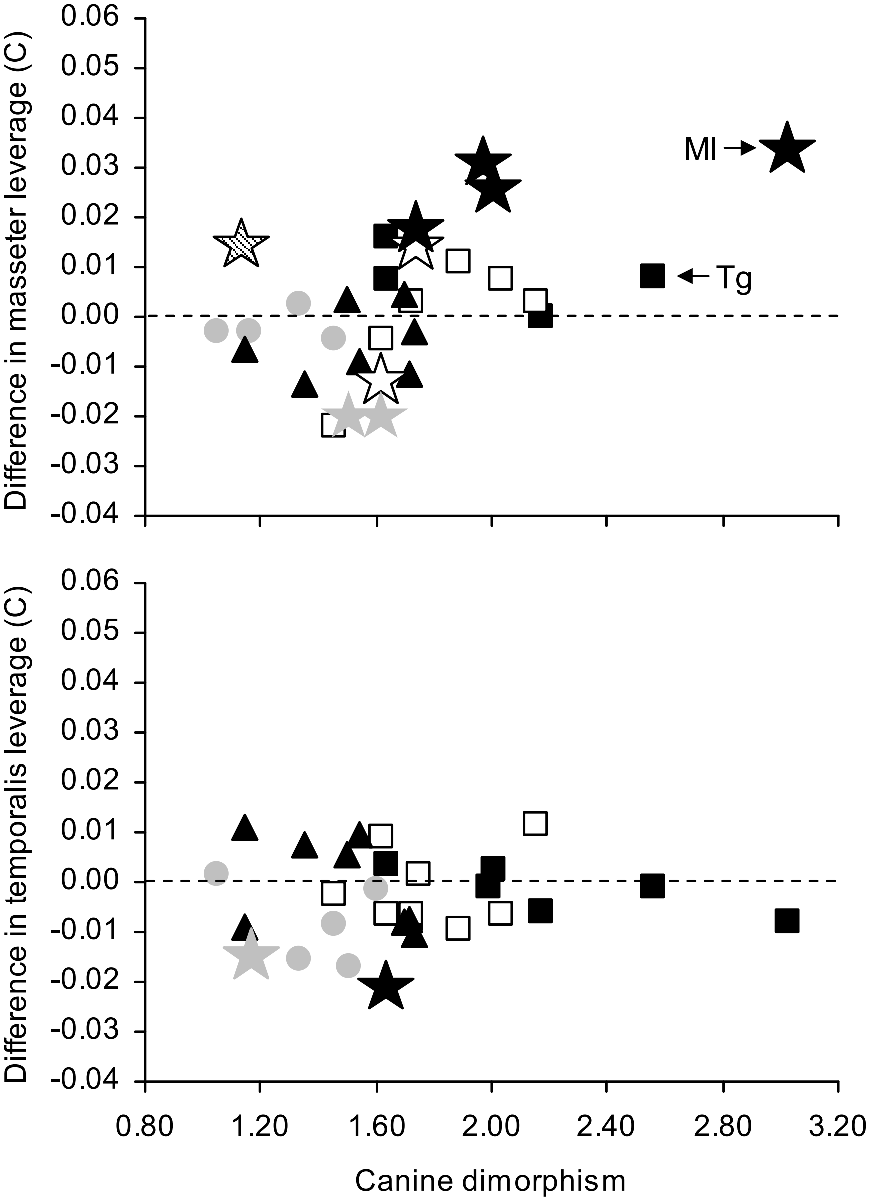


Fig. 4.8. Sexual dimorphism in muscle leverage (female mean minus male mean) at the canine plotted against sexual dimorphism in canine height (male mean divided by female mean). Points falling above the dashed line are species in which females have greater leverage than males. Stars indicate that the intersexual difference is significant. Symbols are as follows: black squares/stars = cercopithecines; white squares/stars = colobines; black triangles/hatched stars = hominoids; gray circles/stars = platyrrhines; Ml = *Mandrillus leucophaeus*; Tg = *Theropithecus gelada*.

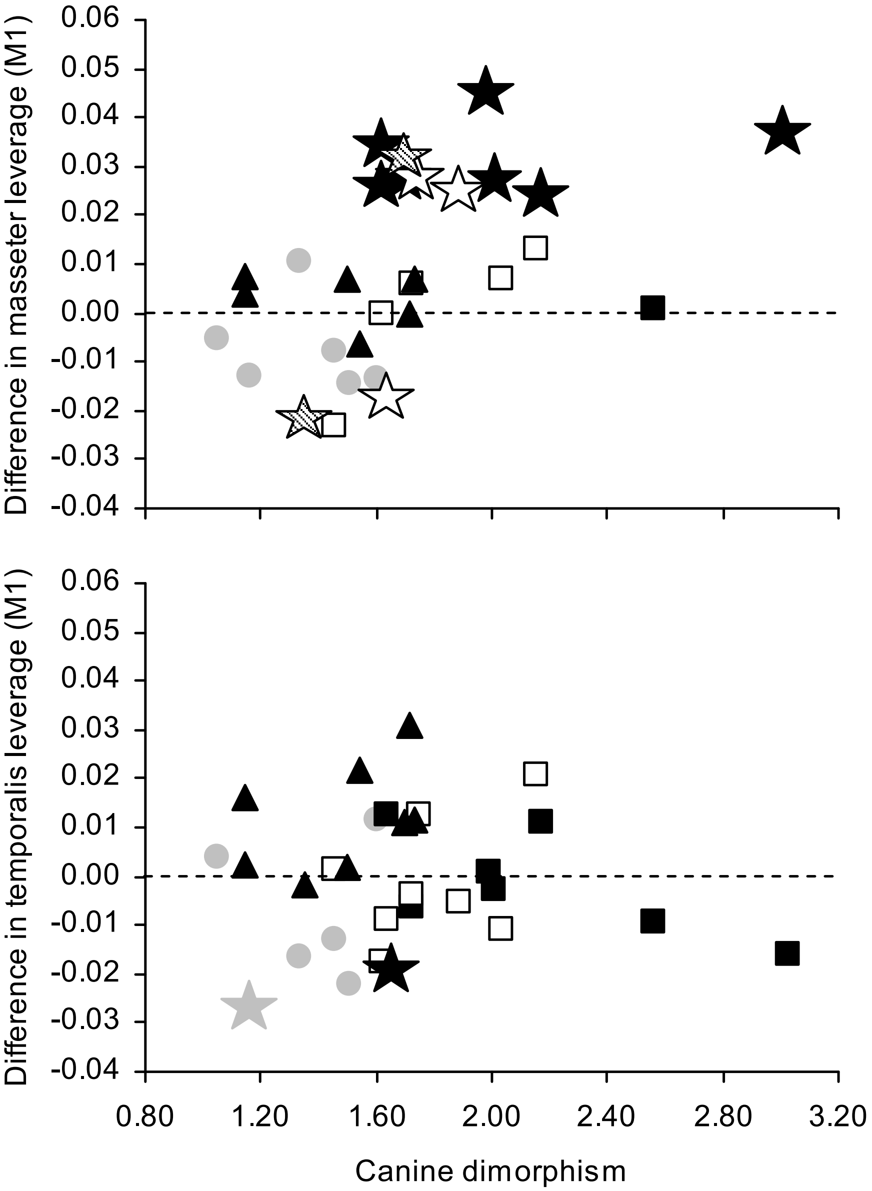


Fig. 4.9. Sexual dimorphism in muscle leverage (female mean minus male mean) at M1 plotted against sexual dimorphism in canine height (male mean divided by female mean). Points falling above the dashed line are species in which females have greater leverage than males. Stars indicate that the intersexual difference is significant. Symbols are as follows: black squares/stars = cercopithecines; white squares/stars = colobines; black triangles/hatched stars = hominoids; gray circles/stars = platyrrhines.

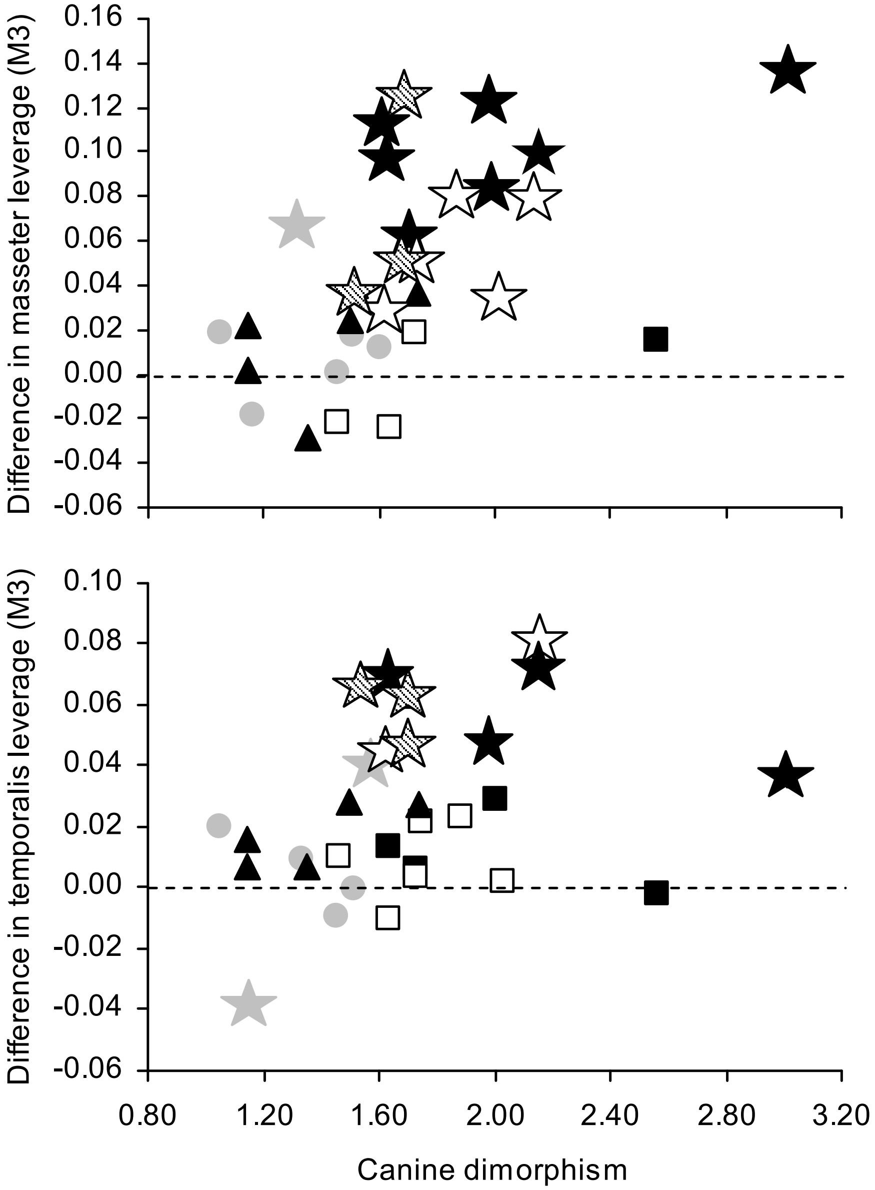


Fig. 4.10. Sexual dimorphism in muscle leverage (female mean minus male mean) at M3 plotted against sexual dimorphism in canine height (male mean divided by female mean). Points falling above the dashed line are species in which females have greater leverage than males. Stars indicate that the intersexual difference is significant. Symbols are as follows: black squares/stars = cercopithecines; white squares/stars = colobines; black triangles/hatched stars = hominoids; gray circles/stars = platyrrhines.

mesial to distal (from three to zero). A similar pattern is evident with regard to the anterior temporalis.

Inspection of Figures 4.8–4.10 reveals that most of the significant differences occur in cercopithecoids, particularly cercopithecines. Of the forty-two significant comparisons that are in the predicted direction, thirty-two (76.2%) are from the Cercopithecoidea, and of those thirty-two, twenty-two (68.8%; 52.4% of all significant comparisons) are from the Cercopithecinae. Moreover, note that there is little evidence for a relationship between sexual dimorphism in canine height and sexual dimorphism in muscle leverage in the Anthropoidea as a whole or within lower taxonomic groupings (all independent-contrast correlations are nonsignificant). The most canine-dimorphic species in the sample, *Mandrillus leucophaeus* (indicated by “Ml” in Fig. 4.8), gives the impression of a weak positive association between canine dimorphism and dimorphism in masseter leverage, but note that this species does not differ strongly from other cercopithecines with regard to the latter variable. Note also that, in *Theropithecus gelada* (indicated by “Tg” in Fig. 4.8), the second most canine-dimorphic species in the sample, males and females are very similar to each other in muscle leverage at each bite point.[3]

---

[3] Intersexual differences in this species could not be evaluated with permutation tests due to the fact that the female sample comprises only two individuals. However, the magnitudes of the intersexual differences in this species fall below those at which other anthropoids typically exhibit significant intersexual differences (e.g., compare the position of *Th. gelada* to the positions of the starred data points in Fig. 4.8).

These results present a puzzling pattern. On one hand, the overall pattern of intersexual differences in muscle leverage at the molar bite points, particularly M3, is generally in line with the predictions of the masticatory-efficiency hypothesis, though statistical support is weak when each species is examined individually, and there are a few comparisons in which males have significantly greater leverage than females. On the other hand, the lack of a statistically significant pattern of intersexual differences in muscle leverage at the canine, along with the low number of significant intersexual comparisons at this bite point, supports the hypothesis derived from the results of the interspecific analysis that, within species, the configuration of the female masticatory system tracks that of males, such that the positional relationships of the bite points and masticatory muscles do not vary by sex despite marked canine dimorphism. Strong positive correlations between male and female muscle leverage at all bite points provide further support for this hypothesis (Table 4.10; Fig. 4.11).

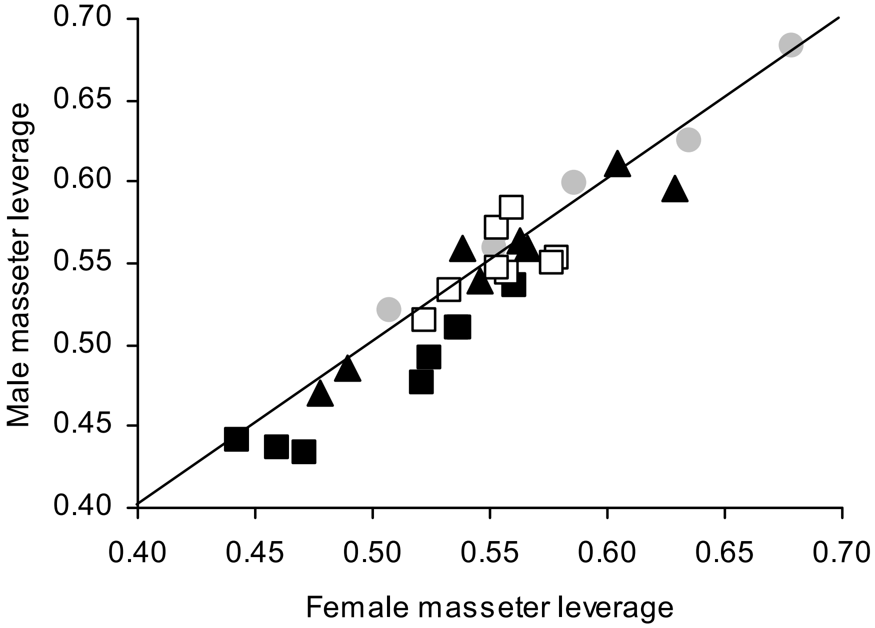
Sexual dimorphism in relative postcanine size provides a possible explanation for these seemingly contradictory results. Females tend to have relatively larger postcanine teeth than conspecific males (Kay, 1978), a consequence of the combination of moderate to high dimorphism in body (and skeletal) size and low dimorphism in molar size that is typical of most anthropoid species (Post, 1978; Cochard, 1985, 1987). Because the position of the canine appears to be comparatively stable vis-à-vis the positions of the masticatory muscles within species, the relatively larger—and longer—postcanine tooth rows of females should position the molar bite points more posteriorly in comparison to

TABLE 4.10. Correlations between male and female muscle leverage

	Superficial masseter leverage at:			Anterior temporalis leverage at:		
	Canine	M1	M3	Canine	M1	M3
r_{TIPS}	0.82***	0.94***	0.92***	0.87***	0.93***	0.95***
r_{IC}	0.84***	0.93***	0.82***	0.91***	0.89***	0.85***

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

*** Significant at $p < 0.001$.



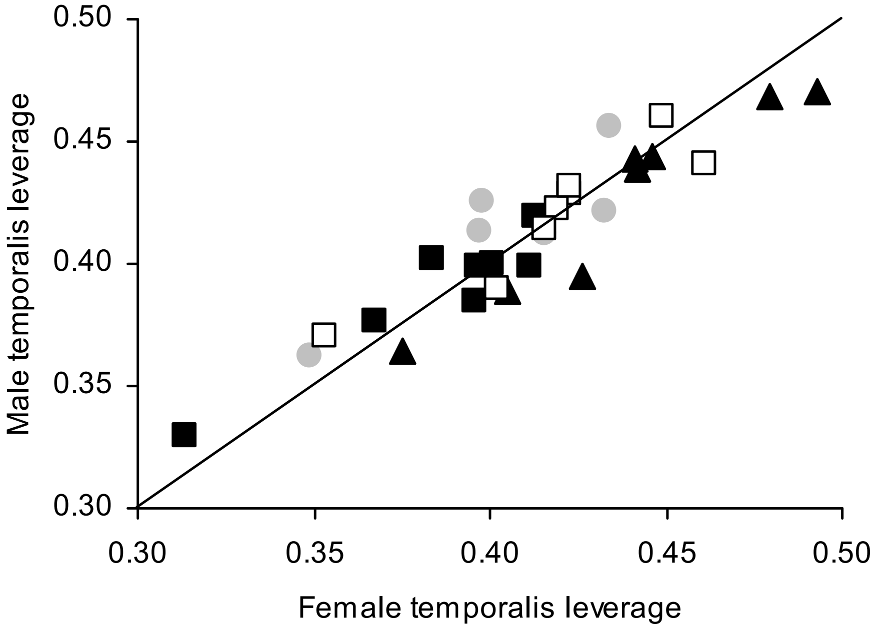


Fig. 4.11. Male muscle leverage at M1 plotted against female muscle leverage at M1. The solid line is the line of identity (male value = female value). Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

those of males, shortening their moment arms and producing a gradient in intersexual differences in muscle leverage along the tooth row. These relationships are illustrated in Figure 4.12, which shows a diagrammatic representation of the tooth rows (canine to M3) of a male and a female *Gorilla beringei* scaled to the same masseter moment-arm length. Note that the disparity between the bite-point positions increases progressively from mesial to distal. Thus, the female has greater muscle leverage at the distal bite points.

If the hypothesis outlined above is correct, then intersexual differences in muscle leverage at M3 should be positively correlated with intersexual differences in the relative length of the postcanine tooth row. Figure 4.13 presents bivariate plots of these variables. Intersexual differences in muscle leverage were computed as above (i.e., female mean minus male mean). Relative postcanine length was estimated by summing the mesiodistal lengths of each maxillary molar and premolar, including the anteriormost premolar, and dividing the result of the skull GM.[4] Dimorphism in relative postcanine length was quantified as the female mean minus the male mean. A clear positive trend is evident in both of the plots in Figure 4.13. The independent-contrast correlation for sexual dimorphism in masseter leverage versus dimorphism in relative postcanine length is fairly strong ($r_{\mathrm{IC}} = 0.70$) and highly significant ($p < 0.0001$). The independent-contrast correlation for dimorphism in anterior temporalis leverage versus dimorphism in relative postcanine length is weaker ($r_{\mathrm{IC}} = 0.56$) but still significant

---

[4] As discussed in Chapter 2, the mesiodistal diameters for most of the species used in this analysis were taken from Plavcan (1990). Those for *Pithecia monachus*, *Gorilla beringei*, and *Pongo abelii* were measured for this study.

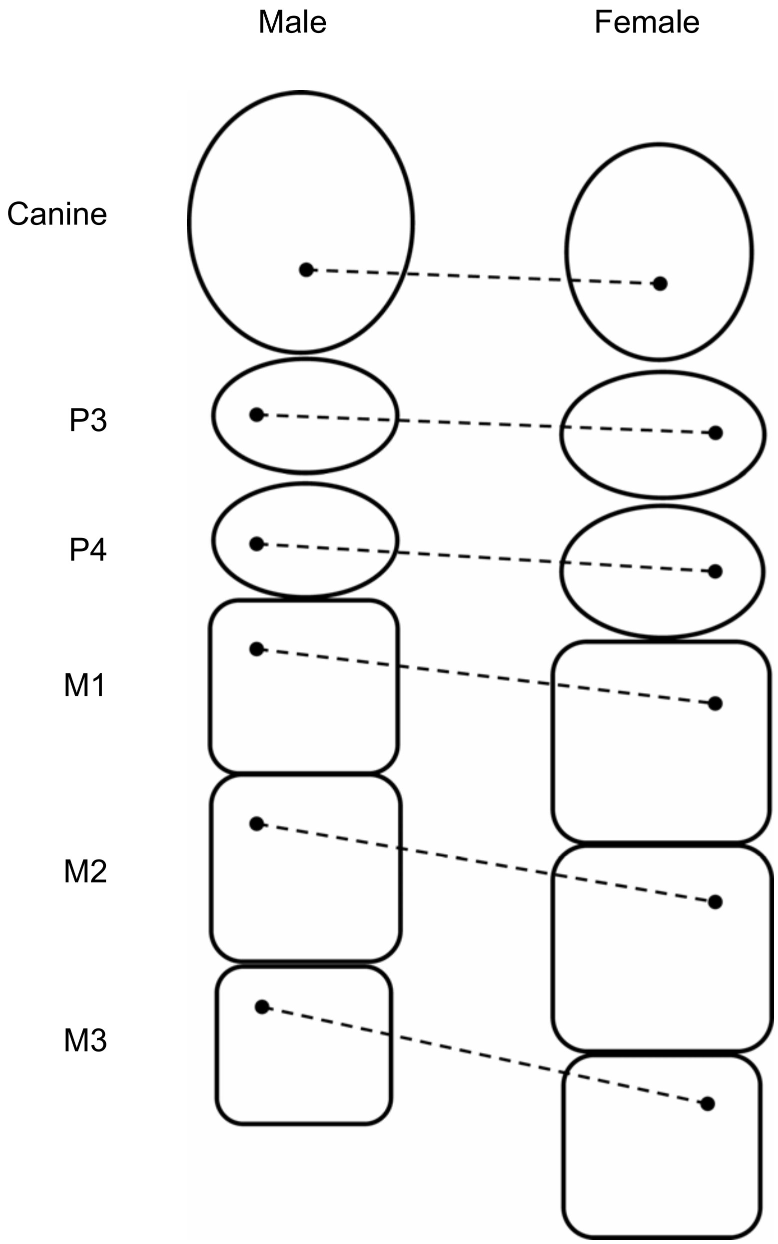


Fig. 4.12. Differences in relative bite-point positions in male and female *Gorilla beringei*. This image was produced by setting the female's masseter moment-arm length equal to that of the male, then increasing the female's bite-point moment-arm lengths and tooth sizes proportionately. Note that the female has relatively larger postcanine teeth. In both sexes, the canine is positioned similarly, whereas females have more posteriorly positioned distal teeth.

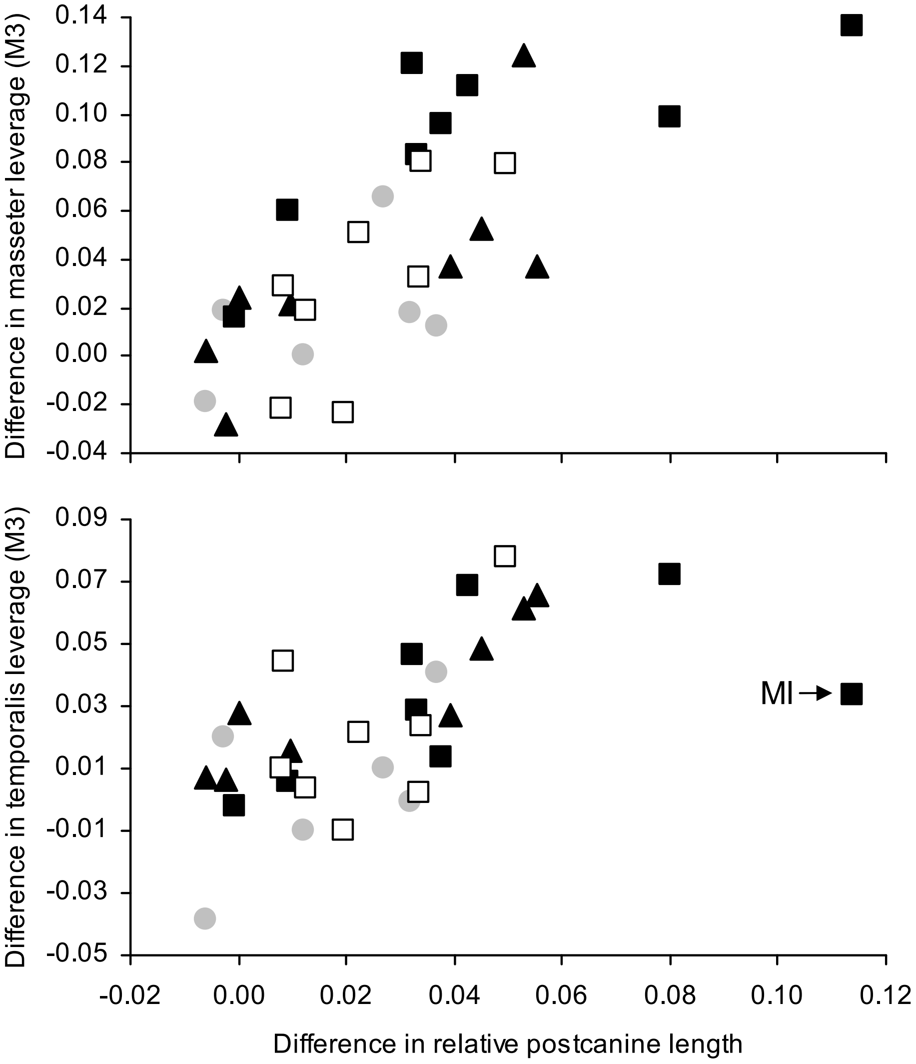


Fig. 4.13. Sexual dimorphism in masseter (top) and temporalis (bottom) leverage at M3 plotted against sexual dimorphism in relative maxillary postcanine length. For each variable, dimorphism was calculated as female mean minus male mean; postcanine length is the sum of the mesiodistal diameters of all maxillary postcanine teeth. The independent-contrast correlations for the upper and lower plots are $r_{IC} = 0.70$ ($p < 0.0001$) and $r_{IC} = 0.56$ ($p = 0.001$), respectively. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Ml = *Mandrillus leucophaeus*.

($p = 0.001$). Note that *Mandrillus leucophaeus* (indicated by “Ml” in Fig. 4.13) is an outlier with respect to intersexual differences in anterior temporalis leverage at M3.

These results indicate that the failure of females to meet the interspecific prediction of the masticatory-efficiency hypothesis is a consequence of the fact that the configuration of the bony masticatory system of anthropoid species is, generally speaking, monomorphic or, at most, only slightly dimorphic in shape. Thus, it appears that when selection produces changes in the positional relationships of the bite points and the attachment sites for the masticatory muscles in males related to canine height and gape requirements, females experience a correlated response (sensu Lande, 1980; see also Plavcan, 1998) regardless of the size of their canines. Nevertheless, despite a general lack of shape dimorphism in this aspect of the anthropoid masticatory system, males are still capable of producing relatively wider gapes than females in species that are canine-dimorphic (Hylander and Vinyard, 2006; Hylander, 2009).

PART II: OTHER FEATURES RELATED TO GAPE

In this section, the relationships between relative canine height and other aspects of skull form that have been linked to gape are examined. These features include relative anteroposterior mandibular length, relative height of the TMJ above the occlusal plane, the ratio of TMJ height to jaw length (H/L ratio), and masseter stretch factor (Herring, 1972; Herring and Herring, 1974). These data are presented in Table 4.11. Shape ratios were the preferred method of size-adjustment for mandibular length and TMJ height, but analyses of these variables

TABLE 4.11. Summary statistics for gape variables

		Mandibular length (mm)		TMJ height (mm)		H/L ratio	
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	78.10	4.09	31.05	3.70	0.397	0.036
	F	66.91	1.72	21.92	2.35	0.328	0.034
At. geoffroyi	M	62.42	2.60	8.06	2.11	0.129	0.034
	F	61.64	1.83	8.32	3.57	0.134	0.056
Ceb. libidinosus	M	55.12	2.57	6.70	2.28	0.121	0.039
	F	48.50	1.45	5.39	0.93	0.111	0.021
Ceb. capucinus	M	59.60	3.02	4.90	1.25	0.082	0.021
	F	52.98	1.27	2.50	1.62	0.047	0.030
Ch. satanas	M	50.24	2.01	6.23	2.05	0.123	0.039
	F	49.08	1.75	4.83	1.24	0.099	0.026
Pith. monachus	M	50.46	1.93	4.21	1.59	0.083	0.030
	F	49.28	1.27	4.51	1.74	0.091	0.035
Cer. pogonias	M	59.23	2.00	11.03	1.69	0.186	0.026
	F	51.93	1.91	8.69	1.52	0.167	0.030
Cer. wolfi	M	57.03	1.37	8.33	1.91	0.146	0.032
	F	51.17	1.78	8.07	1.46	0.158	0.030
Chl. pygerythrus	M	68.45	2.64	9.43	2.72	0.138	0.041
	F	58.79	2.09	6.84	1.27	0.116	0.021
Er. patas	M	92.81	5.35	10.32	2.02	0.112	0.025
	F	69.55	3.45	5.95	2.22	0.086	0.031
Mac. mulatta	M	74.75	3.75	15.91	3.03	0.213	0.039
	F	62.87	3.42	12.20	2.02	0.195	0.035
Mac. fascicularis	M	75.54	3.63	12.40	2.00	0.164	0.024
	F	61.29	2.36	9.89	1.59	0.161	0.024
Th. gelada	M	116.61	5.33	31.18	5.23	0.267	0.042
	F	96.15	1.41	23.53	0.57	0.245	0.002
M. leucophaeus	M	135.39	7.02	22.72	3.22	0.168	0.025
	F	90.70	3.76	17.12	3.37	0.189	0.036
Pil. foai	M	74.53	3.74	12.67	2.34	0.170	0.032
	F	65.85	3.29	10.06	1.81	0.152	0.024

(continued)

TABLE 4.11. (Continued)

		Mandibular length (mm)		TMJ height (mm)		H/L ratio	
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	52.30	2.39	9.07	1.99	0.173	0.035
	F	50.26	1.98	8.79	1.73	0.174	0.032
Col. satanas	M	70.39	1.68	11.05	1.53	0.157	0.022
	F	67.20	2.31	11.40	2.59	0.169	0.036
Col. polykomos	M	75.20	3.27	14.98	2.29	0.200	0.032
	F	71.09	3.26	13.96	2.03	0.196	0.026
Pre. chrysomelas	M	55.70	1.64	8.40	1.19	0.151	0.020
	F	54.99	1.93	7.72	1.41	0.140	0.025
Pre. potenziani	M	61.70	2.69	11.35	2.01	0.184	0.034
	F	60.74	1.71	11.82	1.42	0.195	0.024
Tr. obscurus	M	62.56	1.82	9.88	2.21	0.158	0.036
	F	58.99	2.33	9.81	1.57	0.166	0.025
Tr. shortridgei	M	68.64	2.23	11.39	1.90	0.166	0.027
	F	61.59	1.55	8.83	1.79	0.143	0.028
Hy. lar	M	64.46	2.88	10.78	2.29	0.167	0.034
	F	62.39	2.77	11.09	1.64	0.178	0.025
Hy. syndactylus	M	81.49	3.01	14.95	2.19	0.183	0.024
	F	77.73	3.59	12.60	2.66	0.162	0.032
Go. beringei	M	174.75	8.54	72.91	9.09	0.419	0.069
	F	139.63	5.26	63.85	4.68	0.457	0.024
Go. gorilla	M	158.31	7.60	63.05	7.42	0.399	0.051
	F	134.74	6.66	51.67	4.36	0.385	0.046
Pan paniscus	M	97.40	2.48	23.12	3.71	0.238	0.039
	F	95.70	4.50	21.09	3.81	0.221	0.042
Pan troglodytes	M	121.30	5.56	33.05	6.83	0.274	0.063
	F	115.39	3.83	31.09	6.14	0.270	0.054
Po. abelii	M	149.69	11.20	45.40	8.35	0.303	0.050
	F	119.24	7.33	41.03	3.24	0.345	0.036
Po. pygmaeus	M	150.28	6.74	50.17	8.22	0.335	0.062
	F	124.54	5.98	40.48	4.96	0.325	0.036

(continued)

TABLE 4.11. *(Continued)*

		Relative mandibular length		Relative TMJ height		Masseter stretch factor	
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	1.498	0.033	0.595	0.058	1.707	0.060
	F	1.449	0.028	0.474	0.044	1.713	0.056
At. geoffroyi	M	1.336	0.033	0.173	0.045	1.648	0.076
	F	1.337	0.024	0.179	0.073	1.678	0.064
Ceb. libidinosus	M	1.308	0.035	0.158	0.051	1.529	0.044
	F	1.241	0.026	0.138	0.024	1.533	0.061
Ceb. capucinus	M	1.326	0.034	0.109	0.026	1.628	0.056
	F	1.278	0.022	0.060	0.038	1.583	0.050
Ch. satanas	M	1.312	0.034	0.162	0.051	1.550	0.049
	F	1.288	0.039	0.127	0.034	1.531	0.046
Pith. monachus	M	1.395	0.036	0.116	0.041	1.603	0.069
	F	1.373	0.027	0.126	0.049	1.582	0.058
Cer. pogonias	M	1.285	0.032	0.239	0.035	1.546	0.064
	F	1.231	0.034	0.206	0.037	1.582	0.058
Cer. wolfi	M	1.266	0.024	0.185	0.040	1.525	0.041
	F	1.223	0.035	0.193	0.034	1.604	0.045
Chl. pygerythrus	M	1.381	0.034	0.191	0.056	1.656	0.064
	F	1.327	0.025	0.154	0.028	1.688	0.091
Er. patas	M	1.484	0.052	0.166	0.035	1.627	0.079
	F	1.358	0.057	0.116	0.044	1.625	0.055
Mac. mulatta	M	1.354	0.033	0.288	0.051	1.531	0.042
	F	1.274	0.038	0.247	0.040	1.583	0.057
Mac. fascicularis	M	1.444	0.042	0.237	0.035	1.544	0.054
	F	1.336	0.035	0.215	0.032	1.596	0.076
Th. gelada	M	1.527	0.023	0.407	0.071	1.392	0.029
	F	1.418	0.022	0.347	0.002	1.426	0.042
M. leucophaeus	M	1.640	0.051	0.275	0.040	1.478	0.054
	F	1.443	0.031	0.269	0.051	1.541	0.038
Pil. foai	M	1.403	0.040	0.238	0.043	1.483	0.052
	F	1.345	0.045	0.205	0.034	1.508	0.059

(continued)

TABLE 4.11. (Continued)

		Relative mandibular length		Relative TMJ height		Masseter stretch factor	
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	1.217	0.027	0.211	0.044	1.431	0.046
	F	1.208	0.024	0.211	0.039	1.464	0.042
Col. satanas	M	1.351	0.021	0.212	0.029	1.497	0.034
	F	1.338	0.036	0.227	0.051	1.530	0.035
Col. polykomos	M	1.395	0.039	0.278	0.043	1.487	0.043
	F	1.388	0.026	0.272	0.036	1.510	0.047
Pre. chrysomelas	M	1.264	0.024	0.191	0.027	1.620	0.068
	F	1.261	0.034	0.177	0.033	1.621	0.079
Pre. potenziani	M	1.319	0.039	0.243	0.043	1.568	0.052
	F	1.316	0.023	0.256	0.028	1.574	0.068
Tr. obscurus	M	1.298	0.037	0.205	0.045	1.509	0.039
	F	1.298	0.040	0.215	0.032	1.531	0.042
Tr. shortridgei	M	1.278	0.023	0.212	0.034	1.507	0.046
	F	1.238	0.022	0.177	0.033	1.510	0.047
Hy. lar	M	1.310	0.041	0.219	0.046	1.677	0.077
	F	1.300	0.030	0.231	0.033	1.756	0.097
Hy. syndactylus	M	1.380	0.036	0.253	0.034	1.585	0.070
	F	1.374	0.028	0.222	0.044	1.640	0.062
Go. beringei	M	1.411	0.056	0.591	0.088	1.539	0.033
	F	1.326	0.038	0.606	0.035	1.518	0.037
Go. gorilla	M	1.334	0.032	0.532	0.062	1.545	0.059
	F	1.315	0.064	0.509	0.044	1.515	0.055
Pan paniscus	M	1.243	0.031	0.297	0.051	1.502	0.043
	F	1.238	0.038	0.273	0.049	1.525	0.051
Pan troglodytes	M	1.294	0.039	0.354	0.077	1.528	0.052
	F	1.292	0.033	0.348	0.070	1.600	0.079
Po. abelii	M	1.470	0.035	0.445	0.073	1.521	0.060
	F	1.383	0.075	0.476	0.041	1.494	0.066
Po. pygmaeus	M	1.446	0.032	0.485	0.089	1.558	0.078
	F	1.408	0.043	0.457	0.046	1.567	0.034

were also run using residuals to evaluate the effect of allometry. As discussed in Chapter 2, species with relatively tall canines are predicted to have, in comparison to species with relatively short canines: (1) relatively anteroposteriorly long mandibles, (2) TMJs that are located close to the occlusal plane, (3) low H/L ratios (indicating either a relatively long mandible or a relatively low TMJ), and (4) low masseter stretch factors. As in Part I, this analysis is divided into interspecific and intersexual components, and the same analytical procedures are used to test the predictions outlined above (i.e., interspecific correlations using $\log_e$-transformed data, Wilcoxon matched-pairs signed-ranks tests, and permutation tests). Because the results obtained in Part I indicate that relative canine height and the shape of the masticatory system are uncorrelated in females, only males are examined in the interspecific analysis.

Results

Interspecific analysis

Relative mandibular length and TMJ height are plotted against relative canine height in Figure 4.14. The plot of the H/L ratio versus relative canine height is not shown, but it is virtually identical to the plot of relative TMJ height versus relative canine height. With respect to relative mandibular length, note that there is a strong positive relationship between this variable and relative canine height in the Cercopithecinae but not in any of the other anthropoid groups. In fact, within platyrrhines, *Alouatta seniculus* (indicated by “Al” in Fig. 4.14) has by far the longest mandible relative to skull size but its canines are among the shortest. The independent-contrast correlation between relative

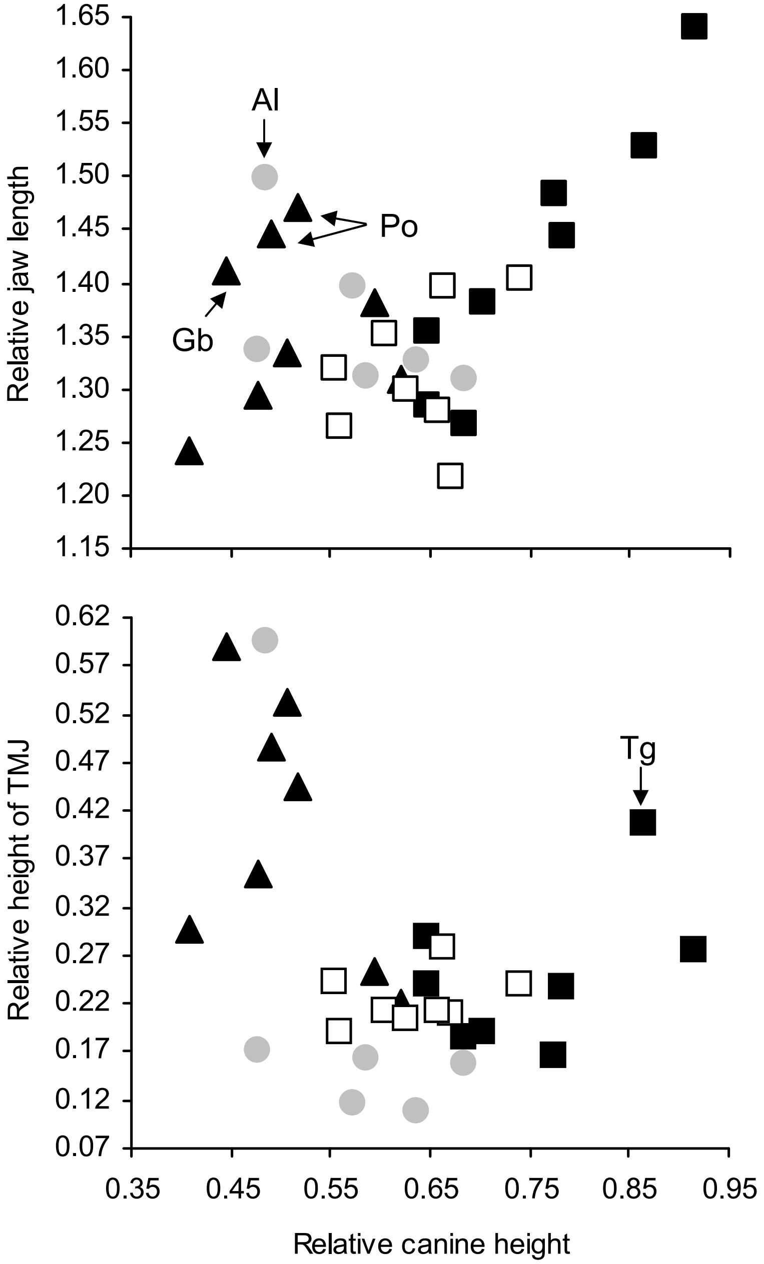


Fig. 4.14. Relative mandibular length (top) and TMJ height (bottom) plotted against relative canine height in anthropoid males. The independent-contrast correlation for the upper plot is $r_{IC} = 0.39$ ($p = 0.0147$); with cercopithecines removed, the correlation is $r_{IC} = 0.01$. Relative canine height is not significantly correlated with relative TMJ height. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Al = *Alouatta seniculus*; Gb = *Gorilla beringei*; Po = *Pongo*; Tg = *Theropithecus gelada*.

mandibular length and relative canine height for the sample as a whole is $r_{\mathrm{IC}} = 0.39$ ($p = 0.0147$); when cercopithecines are removed, the correlation approaches zero ($r_{\mathrm{IC}} = 0.01$), confirming the visual impression given by the plot. Thus, cercopithecines increase gape, in part, by lengthening their jaws, as noted by Ravosa (1990), but other anthropoids do not. This pattern of results reflects the dichotomy noted above between cercopithecines and other anthropoids regarding the relationship between the relative lengths of the masseter and bite-point moment arms. Recall that, in male cercopithecines, there is very little variation in the relative length of the masseter's moment arm, and that variation in masseter leverage is due almost entirely to variation in the relative lengths of the bite-point moment arms, whereas in other male anthropoids, variation in masseter leverage is a function of variation in the relative lengths of both the masseter and bite-point moment arms (see Fig. 4.4). In this latter group, relatively long mandibles are found in species with relatively short canines and increased masseter leverage (e.g., *Al. seniculus*, *Gorilla beringei*, and *Pongo*, indicated by "Al," "Gb," and "Po," respectively, in Fig. 4.14).

Relative canine height is not significantly correlated with relative TMJ height ($r_{\mathrm{IC}} = -0.15$, $p = 0.2071$; see Fig. 4.14) or the H/L ratio ($r_{\mathrm{IC}} = -0.23$, $p = 0.1069$). The Hominidae, *Al. seniculus*, and *Theropithecus gelada* (indicated by "Tg" in Fig. 4.14) are notable for having TMJs that are very high above the occlusal plane relative to skull size and mandibular length in comparison to other anthropoids. New World monkeys, excluding *Al. seniculus*, tend to have the lowest TMJs and H/L ratios, and hylobatids and cercopithecoids are intermediate.

When residuals from a least-squares regression slope (computed using independent contrasts) are used to size-adjust TMJ height, *Al. seniculus* remains distinctive, but the great apes and *Th. gelada* are no longer separated from other anthropoids (Fig. 4.15, top), but note that *Th. gelada* (indicated by "Tg" in Fig. 4.15) falls at the upper end of the range of the main data cluster. This difference between the two methods of size-adjustment is a product of the fact that the height of the TMJ above the occlusal plane is very strongly positively allometric with respect to skull size (Fig. 4.15, bottom); for the sample used in this study, the RMA slope is $b = 2.43$ with a 95% confidence interval of 1.88–2.99 (see also Spencer, 1995, 1999; Ravosa et al., 2000; Armfield and Vinyard, 2010). In contrast, mandibular length is only slightly positively allometric when scaled against skull size ($b = 1.25$, 95% confidence interval: 1.14–1.35), and thus, when residuals are used to size-adjust mandibular length, the results are similar to those derived from shape ratios.

These results indicate that relative TMJ height and the H/L ratio do not track gape among anthropoid primates. This lack of relationship is somewhat surprising, given that Lucas (1981) and Lucas et al. (1986) found a significant negative correlation between the H/L ratio and their estimate of gape, the canine-clearance angle (i.e., the angle of jaw opening at which the maxillary and mandibular canines clear each other) (see also Vinyard et al., 2003). Lucas et al.'s (1986) data for fifty-three anthropoid species are plotted in Figure 4.16. The negative association between the two variables is evident, but note that the three species with the lowest canine-clearance angles (*Aotus trivirgatus*, *Brachyteles*

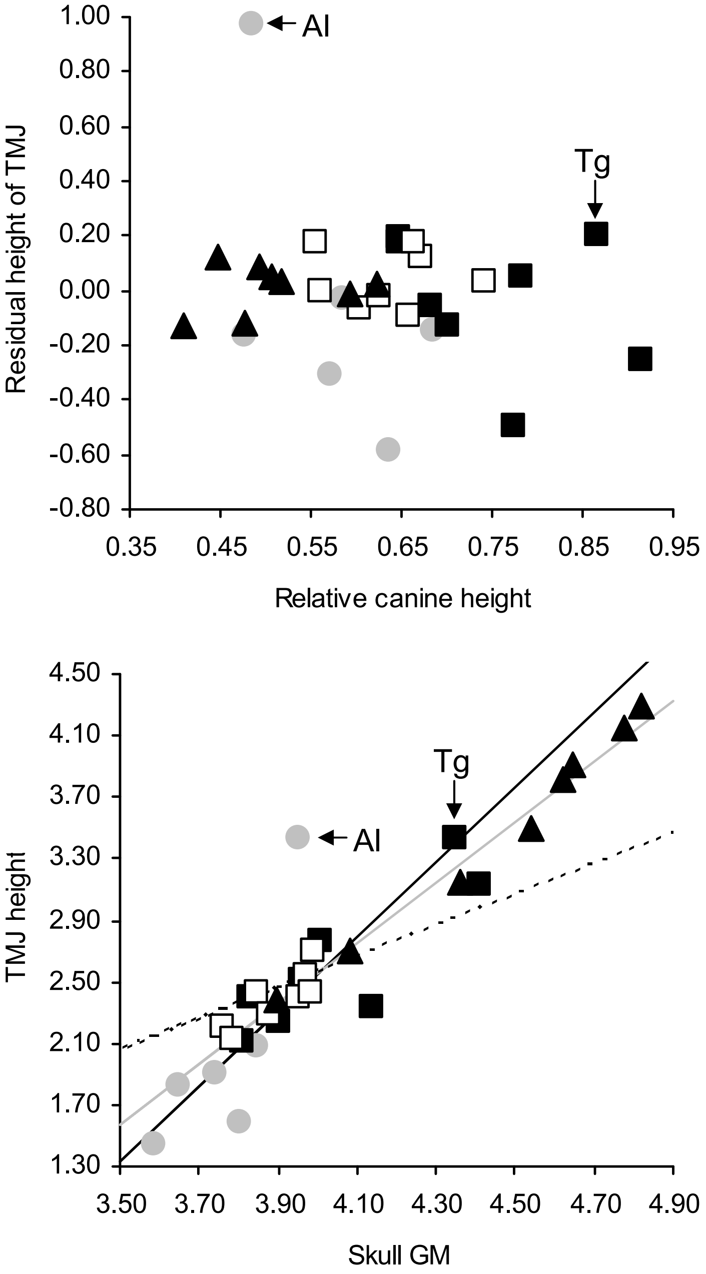


Fig. 4.15. Residual TMJ height plotted against relative canine height (top) and a log-log (base *e*) plot of TMJ height versus the skull GM (bottom). The solid black line is the RMA slope ($b = 2.43$) for all anthropoids; the line of isometry (dotted line) and the least-squares slope (gray line; $b = 1.97$) are also shown for comparison. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Al = *Alouatta seniculus*; Tg = *Theropithecus gelada*.

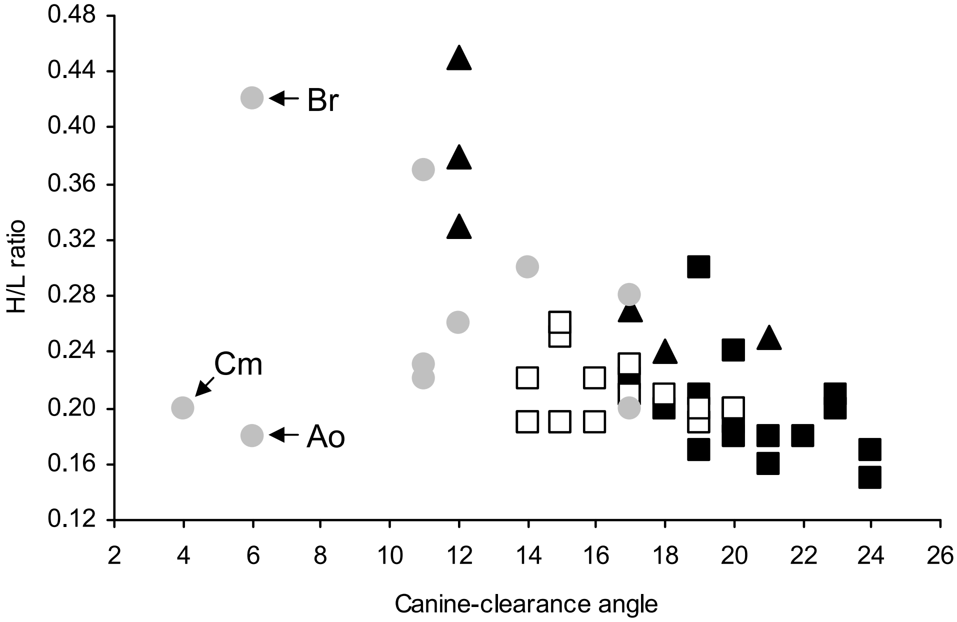


Fig. 4.16. Lucas et al.'s (1986) H/L ratio plotted against canine-clearance angle. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Ao = *Aotus trivirgatus*; Br = *Brachyteles arachnoides*; Cm = *Callicebus moloch*.

arachnoides, and *Callicebus moloch*, indicated by “Ao,” “Br,” and “Cm,” respectively, in Fig. 4.16) encompass nearly the entire range of variation in H/L ratio exhibited by the sample as a whole; only four species have an H/L ratio lower than that of *Ao. trivirgatus* and only one species has an H/L ratio greater than that of *Br. arachnoides*, but these two platyrrhines have identical canine-clearance angles.

Using independent contrasts, the correlation between Lucas et al.’s (1986) H/L ratio and the canine-clearance angle is weak ($r_{\mathrm{IC}} = -0.24$) but borderline significant (Table 4.12). However, the contrasts involving *Ao. trivirgatus* and *Cal. moloch* have a disproportionate influence on this correlation—excluding these two species more than doubles its magnitude ($r_{\mathrm{IC}} = -0.55$). *Brachyteles arachnoides* also has a strong effect on the correlation: removing this species along with *Ao. trivirgatus* and *Cal. moloch* results in an independent-contrast correlation of $r_{\mathrm{IC}} = -0.37$, which is similar to the correlation obtained when only catarrhines are considered ($r_{\mathrm{IC}} = -0.44$). These results indicate that, in contrast to the results obtained using relative canine height, the H/L ratio is related to gape in anthropoid primates, though the relationship does not appear to be very strong.

The reason for this disparity is not immediately obvious. A direct comparison of the relationships between the two gape estimates and all four of the gape-related features examined in this section is presented in Table 4.13. The independent-contrast correlations in this table were computed using the twenty species that are common to both Lucas et al.’s (1986) study and this one. As expected, the H/L ratio and relative TMJ height are more strongly correlated with

TABLE 4.12. Correlations between Lucas et al.'s (1986) H/L ratio and canine-clearance angle for various subsets of the data

	r_{TIPS}	r_{IC}
Anthropoidea	−0.41**	−0.24†
Excluding *Callicebus* and *Aotus*	−0.69***	−0.55***
Excluding *Callicebus*, *Aotus*, and *Brachyteles*	−0.63***	−0.37**
Catarrhini	−0.64***	−0.44**

Abbreviations are as follows: r_{TIPS} = correlation coefficient using species means; r_{IC} = correlation coefficient using independent contrasts.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

† Borderline significant ($0.05 < p < 0.06$).

TABLE 4.13. Correlations between gape estimates and gape-related features of the skull

	Relative canine height		Canine-clearance angle	
	r_{IC}	p	r_{IC}	p
H/L ratio	−0.39	0.0571	−0.62	0.0032
Relative TMJ height	−0.30	0.1114	−0.54	0.0097
Relative mandibular length	0.40	0.0503	0.23	0.1781
Masseter stretch factor	−0.32	0.0916	−0.03	0.4584

Correlations were computed using independent contrasts derived from the twenty species shared by Lucas et al.'s (1986) study and the sample used here.

canine-clearance angle than with relative canine height in these species. On the other hand, relative mandibular length and masseter stretch factor are more strongly correlated with relative canine height than with the canine-clearance angle. The latter correlations are not significant, but note that the correlation between relative mandibular length and relative canine height approaches significance and is similar in magnitude to the correlation between these two variables obtained using all thirty of the species examined for this study. Thus, although relative canine height and canine-clearance angle are highly correlated ($r_{\text{IC}} = 0.89$, $p < 0.0001$), they do not provide the same signal in terms of evaluating the relationship between gape and skull form.

The plot of masseter stretch factor versus relative canine height for the entire sample of anthropoids used in this study is shown in Figure 4.17. The independent-contrast correlation between these two variables is in the predicted direction but it is weak ($r_{\text{IC}} = -0.22$) and not significant ($p = 0.1228$), indicating that, as a group, anthropoids do not increase gape by decreasing muscle stretch. In fact, masseter stretch factor appears to be *positively* correlated with relative canine height in the hominoids—note that the great apes have lower stretch factors than hylobatids (indicated by “Hy” in Fig. 4.17). With these taxa removed from the analysis, the correlation strengthens to $r_{\text{IC}} = -0.37$ but it is only borderline significant ($p = 0.0506$). When only cercopithecoids are considered, the correlation drops to $r_{\text{IC}} = -0.20$ ($p = 0.2465$). These results hint at a possible relationship between relative canine height and masseter stretch factor among the

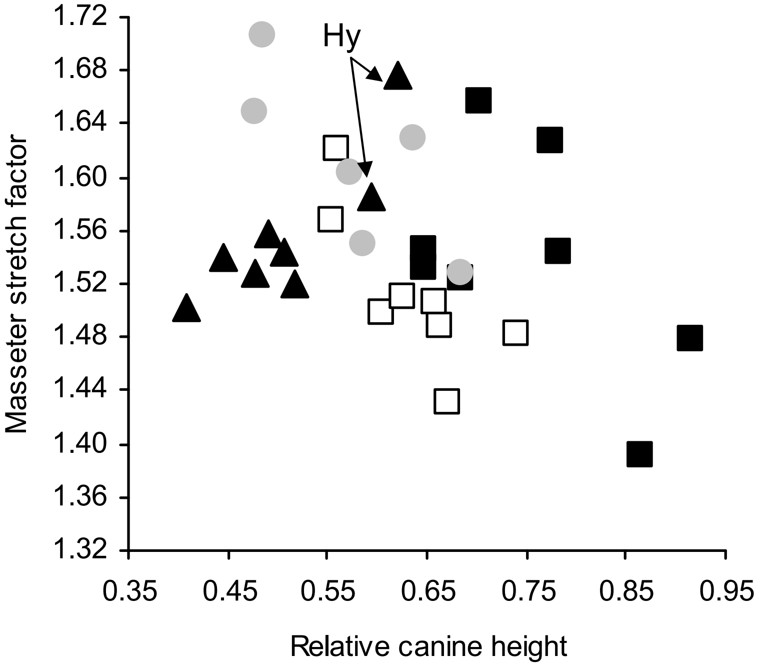


Fig. 4.17. Masseter stretch factor plotted against relative canine height in anthropoid males. Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines; Hy = hylobatids.

platyrrhines examined in this study, but the small number of species prevents statistical evaluation this hypothesis.[5]

Intersexual analysis

The results of the intersexual analysis are presented in Table 4.14 and Figures 4.18 and 4.19. As predicted, males have relatively longer mandibles than females in twenty-nine of the thirty species (*Ateles geoffroyi* is the exception), and sixteen of these male-female comparisons are significant. Moreover, as can be seen in Figure 4.18, relative mandibular length is positively correlated with dimorphism in canine height ($r_{\text{IC}} = 0.60$, $p = 0.0003$). However, given that intersexual differences in muscle leverage are generally small (indicating that males also tend to have relatively longer muscle moment arms), jaw length is unlikely to be the primary mechanism by which the males of most anthropoid species achieve their relatively wide gapes in comparison to females. Cercopithecines are probably an exception to this generalization, as they exhibit, on average, the highest degree of dimorphism in relative mandibular length and muscle leverage. Males also tend to have lower masseter stretch factors than females. Twenty-three of the thirty comparisons are in the predicted directions, but note that only nine of these comparisons are significant, and in one species, *Cebus capucinus*, the stretch factor of males is significantly greater than that of

---

[5] Four out of the five platyrrhine contrasts are in the predicted direction (sign test: $p = 0.1875$), and the independent-contrast correlation ranges from $r_{\text{IC}} = -0.65$ to $r_{\text{IC}} = -0.75$, depending on (1) how the branching order of the three platyrrhine families is resolved and (2) which branch-length transformations are used to standardize the contrasts (see Chapter 2).

TABLE 4.14. Sexual dimorphism in gape-related features

	Comparisons in predicted direction	Significant comparisons[a]		Wilcoxon test	
		F > M	M > F	T_-	p
Relative mandibular length	29	0	16*	2	<0.0001
Relative TMJ height	10	0*	10	375	0.9987
H/L ratio	11	2*	3	322	0.9667
Masseter stretch factor	23	9*	1	84	0.0008

[a] Number of comparisons that are statistically significant ($p < 0.05$; using a permutation test). Asterisks (*) indicate the predicted direction.

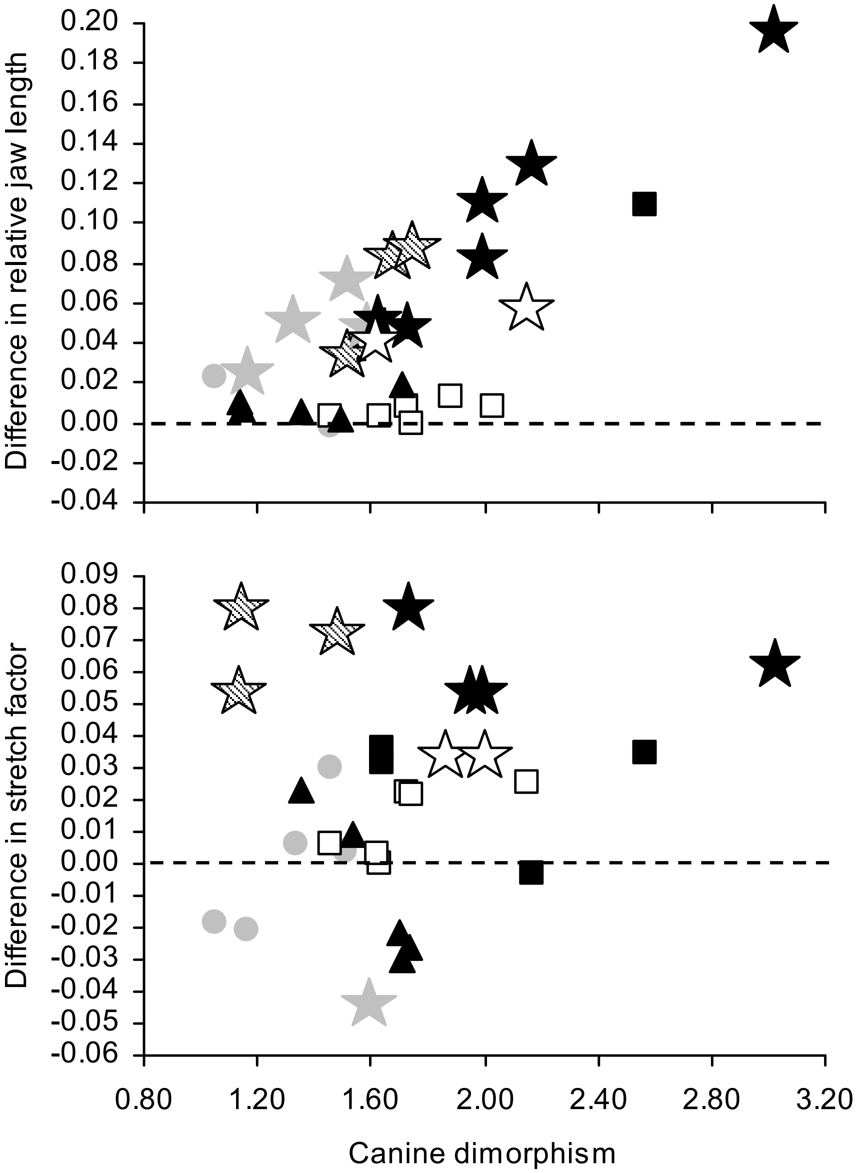


Fig. 4.18. Sexual dimorphism in relative mandibular length (top; male mean minus female mean) and masseter stretch factor (bottom; female mean minus male mean) plotted against sexual dimorphism in canine height (male mean divided by female mean). In the upper plot, points falling above the dashed line are species in which males have relatively longer jaws. In the lower plot, points falling above the dotted line are species in which females have greater masseter stretch factors. Stars indicate that the intersexual difference is significant. Symbols are as follows: black squares/ stars = cercopithecines; white squares/stars = colobines; black triangles/hatched stars = hominoids; gray circles/stars = platyrrhines.

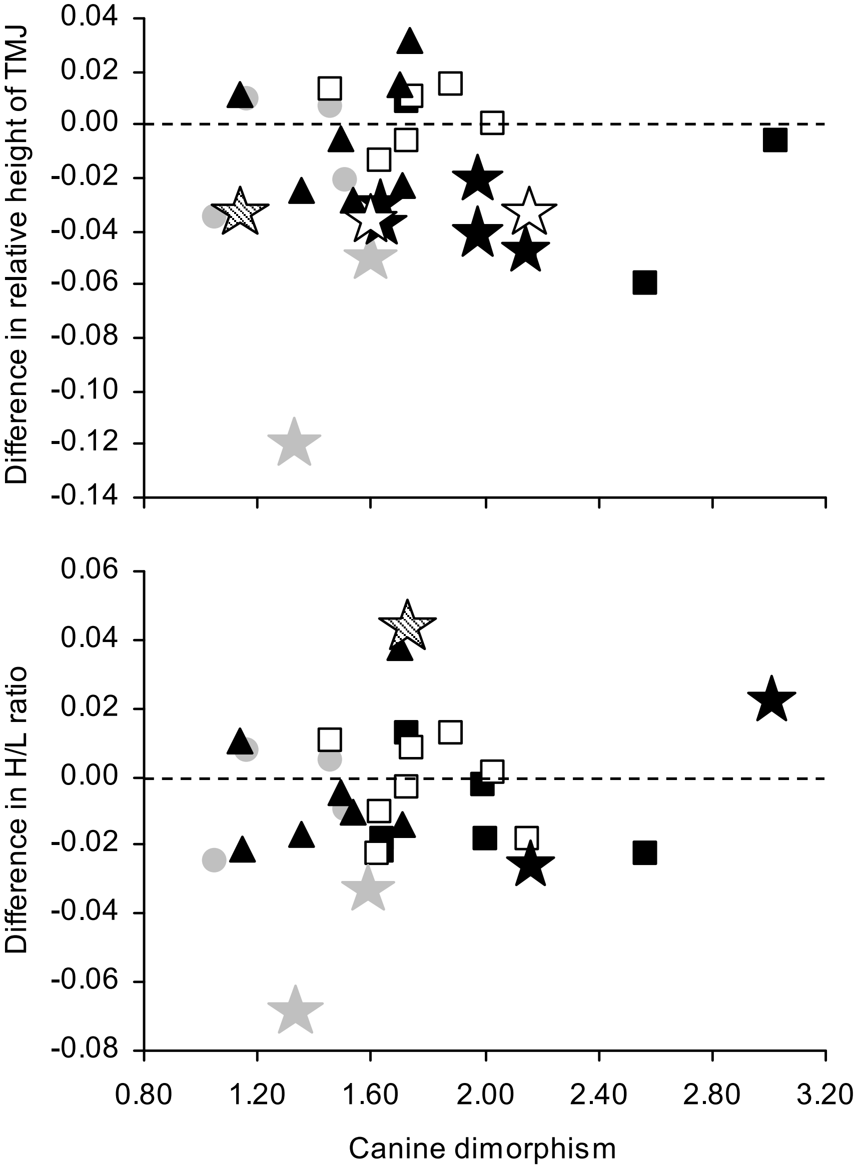


Fig. 4.19. Sexual dimorphism in relative TMJ height (top; female mean minus male mean) and H/L ratio (bottom; female mean minus male mean) plotted against sexual dimorphism in canine height (male mean divided by female mean). In both plots, points falling above the dashed line are species in which females have relatively higher TMJs or H/L ratios. Stars indicate that the intersexual difference is significant. Symbols are as follows: black squares/stars = cercopithecines; white squares/stars = colobines; black triangles/hatched stars = hominoids; gray circles/stars = platyrrhines.

females. Thus, there is some evidence that anthropoid males stretch their masseter muscles less at a given degree of mandibular depression than do females.

In contrast, relative TMJ height and the H/L ratio are not consistently lower in males within species. In fact, the results of the Wilcoxon test indicate that the tendency for males to have TMJs that are relatively *higher* above the occlusal plane than those of females (i.e., the opposite of the predicted direction) is significant ($p = 0.0026$; two-tailed test). Twenty of the intersexual comparisons are in this direction, and ten of these are significant. Similarly, with respect to the H/L ratio, nineteen of the intersexual comparisons are in the opposite of the predicted direction, though only three of these comparisons are significant, and the Wilcoxon test does not achieve significance ($p = 0.0666$; two-tailed test). These results are similar to those of Lucas (1981), who found that conspecific males and females generally exhibit similar H/L ratios, and that when the sexes were significantly different, males had larger ratios. Thus, TMJ height is unrelated to intersexual differences in gape among anthropoid primates.

Taken as a whole, these results, in combination with those for the intersexual analysis of muscle leverage, indicate that differences between conspecific males and females in gape capability are not strongly associated with the configuration of the bony masticatory system. It follows that sexual dimorphism in gape is likely to be primarily a function of differences in muscle architecture (Hylander, 2009).

PART III: CANINE HEIGHT AND DIET

This section examines three questions. First, given that there is a negative relationship between canine height and masseter leverage among catarrhine primates, is there evidence that species with relatively tall canines compensate for decreased muscle leverage—and concomitant negative impact on bite-force magnitudes—by increasing the force-producing potential of their masticatory muscles? Second, is there evidence that selection for increased masticatory efficiency has constrained canine height or led to canine reduction among extant primates? Finally, given that some of the platyrrhines included in this study process hard objects using their canines, can the failure of these species to exhibit a relationship between relative canine height and muscle leverage be linked to diet? Each of these questions is addressed using pairwise comparisons of closely related species (sister taxa on the cladogram in Fig. 2.9) that can be characterized with respect to each other in terms of the mechanical demands of their diets. For the first two questions, only those comparisons for which clear predictions can be made are examined. Additionally, the comparison between *Pongo pygmaeus* and *Pongo abelii* was excluded from analysis because the small sample of *Po. abelii* combined canine heights ($n = 4$) does not permit reliable statistical testing of the difference in relative canine height between the two orangutan species.

As outlined in Chapter 2, rough estimates of muscle size are used to represent the force-producing potential of the masseter and temporalis. The dimensions used to estimate these parameters are, for the masseter, the cross-sectional area of the zygomatic arch anterior to the zygomaticotemporal suture and, for the temporalis, the area of the temporal foramen and the distance between the left and right temporal lines at the coronal suture (or intertemporalis distance). Table 4.15 presents the summary statistics for these variables. For each pairwise comparison, differences between sample means for these and other variables were evaluated using permutation tests and, in the case of relative canine height, the bootstrap. As in Part II of this chapter, only the results for males are reported because females do not exhibit a relationship between skull form and canine height.

Due to the dearth of data on the material properties (i.e., hardness and toughness) of the vast majority of food items consumed by primates, most of the species analyzed here were characterized with respect to the mechanical demands of their diets using coarse-grained qualitative estimates, though material-properties data were included where possible (mainly for the platyrrhines). The scheme used here follows that of Lucas and Luke (1984), Chivers et al. (1984), and Spencer (1995), and can be summarized as follows:

(1) *Hard-brittle* foods are those items that require high-magnitude bite forces of short to moderate duration to process. These foods are resistant to fracture initiation, but the fractures propagate relatively rapidly once initiated. Examples of hard-brittle foods include seeds and nuts.

(2) *Soft-tough* foods are less resistant to fracture initiation but are more resistant to fracture propagation. They therefore do not require bite forces that are as high in magnitude as those required to initiate

TABLE 4.15. Summary statistics for muscle-size variables

		Area (mm^2)				Intertemporalis distance[b] (mm)	
		Zygomatic arch		Temporal foramen			
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	32.21	8.03	394.41	79.55	17.69	4.89
	F	17.70	4.59	212.48	22.26	22.91	2.81
At. geoffroyi	M	7.01	2.03	180.65	21.32	43.83	2.85
	F	6.68	1.54	156.30	30.82	47.57	4.23
Ceb. libidinosus	M	9.63	2.24	282.02	69.18	9.65	8.64
	F	5.44	1.57	171.29	21.94	17.11	6.43
Ceb. capucinus	M	9.30	2.31	296.42	64.40	27.98	5.31
	F	5.89	1.25	189.98	19.65	33.25	3.88
Ch. satanas	M	3.30	0.98	167.95	24.46	7.55	5.59
	F	3.31	0.72	134.65	20.46	14.13	8.94
Pith. monachus	M	5.56	1.13	156.28	27.08	12.97	6.76
	F	4.86	0.90	137.42	19.34	17.27	6.18
Cer. pogonias	M	9.66	2.29	283.71	30.01	28.67	4.52
	F	7.12	1.14	184.18	18.26	30.84	3.90
Cer. wolfi	M	7.67	1.37	261.16	27.68	31.67	3.99
	F	6.42	1.93	185.77	24.82	34.43	3.60
Chl. pygerythrus	M	13.97	3.61	350.40	57.48	11.61	5.48
	F	9.72	1.94	200.54	29.71	25.89	4.24
Er. patas	M	29.54	5.96	534.47	60.80	15.83	7.08
	F	16.22	2.64	218.27	32.35	36.42	4.24
Mac. mulatta	M	17.63	3.08	473.23	70.04	20.04	5.17
	F	12.19	2.57	320.66	51.59	29.75	5.59
Mac. fascicularis	M	23.65	5.03	439.41	68.61	7.53	5.84
	F	11.32	2.66	256.12	40.92	22.91	5.64
Th. gelada	M	51.59	8.08	1105.71	90.51	2.26	0.82
	F	32.41	7.01	683.09	62.44	9.05	1.27
M. leucophaeus	M	84.35	23.19	1012.84	151.71	66.01	6.80
	F	26.57	6.84	403.81	47.77	57.42	2.23
Pil. foai	M	21.70	5.57	631.07	87.91	3.20	4.46
	F	11.76	2.40	401.83	54.96	18.03	4.78

(continued)

TABLE 4.15. (Continued)

		Area (mm^2)				Intertemporalis distance[b] (mm)	
		Zygomatic arch		Temporal foramen			
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	11.68	2.19	338.37	40.82	1.81	0.87
	F	7.11	1.28	268.02	29.19	7.54	5.09
Col. satanas	M	9.26	2.14	446.74	34.88	33.00	5.36
	F	10.49	2.17	374.80	32.69	35.06	3.54
Col. polykomos	M	16.56	4.24	532.14	41.64	21.13	5.07
	F	14.45	5.87	433.56	50.33	23.24	6.41
Pre. chrysomelas	M	7.11	2.80	246.21	20.59	31.21	3.46
	F	6.01	1.20	246.25	25.67	32.17	5.41
Pre. potenziani	M	15.10	2.20	416.63	48.30	18.96	4.13
	F	15.20	3.04	373.28	54.01	18.46	4.09
Tr. obscurus	M	12.82	2.58	371.82	32.97	16.99	6.22
	F	8.55	2.01	298.26	40.87	19.29	4.28
Tr. shortridgei	M	16.77	2.41	461.17	54.47	21.88	5.39
	F	11.48	2.13	326.83	53.72	30.29	5.42
Hy. lar	M	6.15	1.24	281.80	37.90	18.78	7.27
	F	5.91	1.35	246.18	35.77	19.68	4.09
Hy. syndactylus	M	10.67	2.61	579.93	89.50	26.66	5.73
	F	9.87	2.40	439.47	76.42	28.42	7.23
Go. beringei	M	90.33	28.28	3150.43	319.44	6.72	3.11
	F	67.49	7.43	1818.57	170.46	39.57	6.14
Go. gorilla	M	97.53	30.88	2360.77	240.52	4.98	1.91
	F	60.94	18.09	1395.51	181.78	19.83	10.71
Pan paniscus	M	22.21	4.65	815.46	100.27	57.06	8.25
	F	25.44	6.04	611.16	103.55	64.38	8.64
Pan troglodytes	M	40.27	8.72	1169.56	146.42	30.50	13.12
	F	37.06	13.27	837.91	75.19	55.29	10.72
Po. abelii	M	88.40	33.94	1834.68	409.23	24.91	19.82
	F	40.45	13.05	962.34	163.05	38.21	11.77
Po. pygmaeus	M	123.17	24.99	2013.31	267.31	18.70	12.68
	F	43.85	11.49	1188.82	175.14	36.74	12.44

(continued)

TABLE 4.15. (Continued)

		Relative area[a]				Relative intertemporalis distance[b]	
		Zygomatic arch		Temporal foramen			
	Sex	Mean	SD	Mean	SD	Mean	SD
Al. seniculus	M	0.108	0.013	0.379	0.028	0.343	0.107
	F	0.090	0.011	0.314	0.016	0.497	0.065
At. geoffroyi	M	0.056	0.008	0.287	0.017	0.939	0.072
	F	0.056	0.006	0.270	0.023	1.034	0.108
Ceb. libidinosus	M	0.073	0.008	0.395	0.041	0.234	0.215
	F	0.059	0.008	0.334	0.019	0.439	0.169
Ceb. capucinus	M	0.067	0.008	0.380	0.032	0.626	0.132
	F	0.058	0.006	0.332	0.016	0.803	0.101
Ch. satanas	M	0.047	0.007	0.337	0.018	0.199	0.150
	F	0.048	0.006	0.304	0.022	0.373	0.240
Pith. monachus	M	0.065	0.006	0.345	0.023	0.357	0.186
	F	0.061	0.005	0.326	0.025	0.481	0.173
Cer. pogonias	M	0.067	0.008	0.365	0.016	0.623	0.106
	F	0.063	0.005	0.321	0.014	0.732	0.096
Cer. wolfi	M	0.061	0.005	0.358	0.016	0.704	0.097
	F	0.059	0.008	0.321	0.017	0.836	0.100
Chl. pygerythrus	M	0.075	0.009	0.376	0.026	0.235	0.114
	F	0.070	0.007	0.319	0.018	0.586	0.105
Er. patas	M	0.087	0.008	0.369	0.014	0.254	0.115
	F	0.078	0.006	0.288	0.019	0.712	0.089
Mac. mulatta	M	0.076	0.005	0.393	0.021	0.364	0.096
	F	0.070	0.008	0.357	0.020	0.596	0.094
Mac. fascicularis	M	0.093	0.010	0.399	0.022	0.145	0.112
	F	0.073	0.008	0.347	0.019	0.500	0.127
Th. gelada	M	0.095	0.006	0.433	0.012	0.059	0.053
	F	0.084	0.007	0.385	0.006	0.133	0.015
M. leucophaeus	M	0.110	0.014	0.384	0.022	0.800	0.080
	F	0.081	0.010	0.318	0.015	0.908	0.042
Pil. foai	M	0.087	0.010	0.472	0.025	0.062	0.088
	F	0.070	0.007	0.408	0.021	0.369	0.096

(continued)

TABLE 4.15. (Continued)

		Relative area[a]				Relative intertemporalis distance[b]	
		Zygomatic arch		Temporal foramen			
	Sex	Mean	SD	Mean	SD	Mean	SD
Pro. verus	M	0.079	0.008	0.427	0.022	0.042	0.021
	F	0.064	0.006	0.393	0.014	0.184	0.126
Col. satanas	M	0.058	0.007	0.405	0.014	0.634	0.105
	F	0.064	0.006	0.385	0.014	0.699	0.079
Col. polykomos	M	0.075	0.009	0.428	0.013	0.392	0.095
	F	0.073	0.013	0.406	0.013	0.456	0.133
Pre. chrysomelas	M	0.059	0.011	0.356	0.015	0.709	0.085
	F	0.056	0.006	0.360	0.018	0.738	0.127
Pre. potenziani	M	0.083	0.007	0.436	0.020	0.406	0.091
	F	0.084	0.008	0.416	0.027	0.400	0.091
Tr. obscurus	M	0.074	0.007	0.400	0.016	0.352	0.128
	F	0.064	0.008	0.379	0.021	0.426	0.101
Tr. shortridgei	M	0.076	0.005	0.399	0.017	0.409	0.105
	F	0.068	0.007	0.362	0.023	0.610	0.116
Hy. lar	M	0.050	0.005	0.340	0.016	0.383	0.149
	F	0.050	0.006	0.325	0.022	0.409	0.087
Hy. syndactylus	M	0.055	0.007	0.405	0.028	0.448	0.093
	F	0.055	0.007	0.369	0.024	0.504	0.135
Go. beringei	M	0.076	0.011	0.455	0.030	0.054	0.024
	F	0.078	0.004	0.405	0.021	0.374	0.053
Go. gorilla	M	0.082	0.012	0.407	0.013	0.042	0.016
	F	0.076	0.011	0.365	0.023	0.195	0.106
Pan paniscus	M	0.061	0.006	0.363	0.025	0.720	0.100
	F	0.065	0.008	0.319	0.020	0.835	0.124
Pan troglodytes	M	0.067	0.007	0.364	0.017	0.328	0.149
	F	0.067	0.012	0.324	0.020	0.620	0.123
Po. abelii	M	0.091	0.013	0.417	0.033	0.254	0.214
	F	0.073	0.011	0.358	0.024	0.445	0.145
Po. pygmaeus	M	0.106	0.010	0.431	0.021	0.154	0.103
	F	0.074	0.008	0.388	0.017	0.417	0.144

[a] The square roots of the cross-sectional areas were used to compute relative size.

[b] Relative to skull size, smaller values for intertemporalis distance indicate relatively larger temporalis muscles.

fractures in hard-brittle foods, but the bite forces that are required must be sustained for a longer duration and produced at a higher frequency. Leaves are an example of soft-tough foods, with mature leaves being tougher (and less nutritious) than immature leaves.

(3) *Soft-brittle* foods require the lowest bite-force magnitudes to initiate fractures and the durations over which these forces must be sustained are short. Ripe fruits are an example of soft-brittle foods.

Thus, diets composed mainly of soft-brittle food items are less mechanically demanding than those that include higher proportions of hard-brittle and/or soft-tough items. Characterizing the differences in the mechanical demands of the diets that include higher proportions of hard-brittle items versus those that include higher proportions of soft-tough items (e.g., hard-object feeders versus folivores) is not possible using the categorical estimates of food material properties used here—although the former are expected to require higher-magnitude bite forces, the latter are expected to require moderate-magnitude bite forces that are sustained for longer durations and that are produced with greater frequency (e.g., Spencer, 1995).

Compensatory increases in muscle size

Tribe Cercopithecini

The tribe Cercopithecini comprises five extant cercopithecine genera, including *Allenopithecus*, *Cercopithecus*, *Chlorocebus*, *Erythrocebus*, and *Miopithecus*. The sample used for this study includes four species: two forest guenons (*Cercopithecus pogonias* and *Cer. wolfi*), the vervet (*Chlorocebus* *pygerythrus*), and the patas monkey (*Erythrocebus patas*). The forest guenons are primarily frugivorous, preferring ripe fruit when it is available, but they are also known to rely on substantial amounts of seeds and leaves (Guatier-Hion, 1980; Gautier-Hion et al., 1993; Tutin et al., 1997; Brugiere et al, 2002; Chapman et al., 2002). The diets of species of *Chlorocebus* are similar to those of the forest guenons, but these species are probably more omnivorous and gum is an important food source in some populations (Struhsaker, 1967; Galat and Galat-Luong, 1978; Wrangham and Waterman, 1981; Harrison, 1983, 1984; Nash, 1986; Butynski, 1988; Isbell et al., 1998; Pruetz and Isbell, 2000; Nakagawa, 2003). Patas monkeys eat many of the same food items used by vervets (Isbell et al., 1998; Nakagawa, 2003), but this species is notable for incorporating higher proportions of gum and insects in its diet in comparison to *Chlorocebus* (Olson and Chism, 1984; Olson, 1985; Nash, 1986; Chism and Wood, 1994; Isbell, 1998; Isbell et al., 1998; Nakagawa, 2003). Based on these descriptions, the diets of the four cercopithecins can be characterized as broadly similar to each other in terms of their mechanical properties, though there is some evidence that the diet of *Erythrocebus* is higher in quality (i.e., high protein-to-fiber ratio) and less demanding than that of *Chlorocebus* (Nakagawa, 2003); whether this distinction holds between *Erythrocebus* and the two forest guenons is not known.

With respect to canine height, *E. patas* has the tallest canines relative to skull size, followed by *Chl. pygerythrus* and *Cer. wolfi* (which cannot be statistically distinguished from each other), with *Cer. pogonias* having the relatively shortest canines in the group (Table 4.16). Differences in masseter leverage are in the direction predicted by the masticatory-efficiency hypothesis for each comparison (but note that *Cer. wolfi* has significantly greater masseter leverage at M3 than *Chl. pygerythrus*; Table 4.16). On the other hand, there are very few significant differences in anterior temporalis leverage; most of the comparisons that are significant involve *E. patas*, which has significantly less leverage than at least one of the other species for each bite point (Table 4.16). Thus, the masticatory-efficiency hypothesis predicts compensatory increases in the force-producing potential of the masseter as follows: *Erythrocebus* > *Chlorocebus*/*Cer. wolfi* > *Cer. pogonias*. With respect to the temporalis, the only clear prediction that can be made is that *E. patas* will exhibit increased force-producing potential relative to the other cercopithecins.

Prior to examining estimates of relative muscle size, it is important to note that the overall size of an organism is an important determinant of the force-producing potential of its masticatory muscles because larger animals have larger muscles. The patas monkey differs markedly in body size from the other cercopithecins; according to body-mass data compiled by Smith and Jungers (1997), males of *E. patas* weigh, on average, 12.4 kg, and are thus two to three times larger than males of *Chl. pygerythrus* (5.5 kg), *Cer. pogonias* (4.3 kg), and *Cer. wolfi* (3.9 kg).[6] The differences in body mass among these species are reflected in estimates of skull size (Table 4.16; see also Table 2.4). Thus, without

---

[6] The value for *Chlorocebus* used here is from the sample labeled "*Cercopithecus aethiops ngamiensis*, Botswana" by Smith and Jungers (1997), matching the taxonomic label and geographic origin provided by the museum records of the specimens measured for this study.

TABLE 4.16. Results of pairwise comparisons for the Cercopithecini

Variable	Direction of difference and statistical significance[a]						
Relative canine height	*C. pogonias*	<	*C. wolfi*	<	*Chlorocebus*	<	*Erythrocebus*
Masseter leverage:							
at canine	*C. pogonias*	>	*C. wolfi*	>	*Chlorocebus*	>	*Erythrocebus*
at M1	*C. pogonias*	>	*C. wolfi*	>	*Chlorocebus*	>	*Erythrocebus*
at M3	*C. pogonias*	>	*C. wolfi*	>	*Chlorocebus*	>	*Erythrocebus*
Temporalis leverage:							
at canine	*C. wolfi*	>	*C. pogonias*	>	*Chlorocebus*	>	*Erythrocebus*
at M1	*C. wolfi*	>	*C. pogonias*	>	*Chlorocebus*	>	*Erythrocebus*
at M3	*C. wolfi*	>	*C. pogonias*	>	*Chlorocebus*	>	*Erythrocebus*
Skull GM	*C. wolfi*	<	*C. pogonias*	<	*Chlorocebus*	<	*Erythrocebus*
Relative muscle size:							
Zygomatic arch	*C. wolfi*	<	*C. pogonias*	<	*Chlorocebus*	<	*Erythrocebus*
Intertemporalis[b]	*C. wolfi*	>	*C. pogonias*	>	*Erythrocebus*	>	*Chlorocebus*
Temporal foramen	*C. wolfi*	<	*C. pogonias*	<	*Erythrocebus*	<	*Chlorocebus*

---

[a] Species that are share the same underline are not significantly different from each other ($p > 0.05$).

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles. Thus, relative temporalis size increases from left to right.

even considering relative muscle size, it is reasonable to infer that the masticatory muscles of *E. patas* are more powerful than those of other cercopithecins—as predicted by the masticatory-efficiency hypothesis—by virtue of their greater absolute size. This is not meant to imply that *Erythrocebus* is larger than other cercopithecins in terms of body size in order to compensate for its decreased muscle leverage. Rather, given that the patas monkey is substantially larger and that it processes a diet that is similar in its mechanical demands to those of the other three species, if not less so (e.g., Isbell, 1998; Nakagawa, 2003), it may be that this species can afford to sacrifice muscle leverage without incurring a major selective cost. The same may also be true for *Chl. pygerythrus* in relation to the forest guenons, but note that the differences in body size among these species are not as great.

With respect to relative muscle size, the comparisons are generally in the predicted direction, but *Cer. wolfi* is an exception (Table 4.16). This species has relatively taller canines and reduced muscle leverage in comparison to *Cer. pogonias*, yet its masseter and temporalis are relatively smaller. The masticatory muscles of *Cer. wolfi* are also relatively smaller than those of *Chl. pygerythrus*, which is similar to *Cer. wolfi* in relative canine height and muscle leverage. These results suggest that the diets of *Cer. pogonias* and *Chl. pygerythrus* are more mechanically demanding than the diet of *Cer. wolfi*. This inference is plausible for *Chl. pygerythrus*, which inhabits dryer and more open environments than *Cer. wolfi*, and thus probably experiences more periods of resource scarcity in which it is forced to rely heavily on low-quality, hard-to-process fallback foods (e.g., Isbell, 1995), but currently available data do not provide the resolution necessary to test this hypothesis for either the vervet or *Cer. pogonias*. In any event, the other three species differ in the predicted direction with respect to each other for relative masseter size, and although the variables representing relative temporalis size do not consistently differentiate *Cer. pogonias*, *Chl. pygerythrus*, and *E. patas*, it appears that the latter two species have relatively larger temporalis muscles than *Cer. pogonias* based on relative intertemporalis distance (but not temporal-foramen area; Table 4.16).[7] These results suggest that relatively tall canines are associated with absolutely or relatively large muscles in cercopithecins, allowing these species to compensate for reductions in bite-force magnitudes that accompany reductions in muscle leverage.

Subtribe Papionina

The cercopithecine subtribe Papionina includes six African genera: *Cercocebus*, *Mandrillus*, *Lophocebus*, *Papio*, *Theropithecus*, and the recently identified *Rungwecebus* (Davenport et al., 2006). Two papioninans are represented here—the gelada (*Theropithecus gelada*) and the drill (*Mandrillus leucophaeus*). These two species are very different in terms of their diets. The gelada is a grazer, with grass parts accounting for 80% or more of its diet (Dunbar and Dunbar, 1974; Dunbar, 1977, 1984; Iwamoto, 1979, 1993; Iwamoto and Dunbar, 1983). The diet of the drill, on the other hand, is not as well known, but

---

[7] The fact that *Erythrocebus* and *Chlorocebus* do not differ in relative temporalis size should not be interpreted as evidence that *Erythrocebus* does not possess greater force-producing potential, given the differences in body size discussed above.

data presented by Astaras et al. (2008) indicate that this species is similar to the closely related *Mandrillus sphinx* and species of *Cercocebus* in relying mainly on fruits and, notably, hard nuts and seeds, as well as grasses and terrestrial herbaceous vegetation (Jones and Sabater Pi, 1968; Gautier-Hion, 1978; Homewood, 1978; Hoshino, 1985; Lahm, 1986; Harrison, 1988; Mitani, 1989; Caldecott et al., 1996; McGraw, 1996; Rogers et al., 1996; Tutin et al., 1997; Wahungu, 1998; Fleagle and McGraw, 2002; Shah, 2003). Thus, the drill probably has a fairly obdurate diet, though the mechanical properties of that diet are different from those of the gelada's diet: whereas geladas process large quantities of tough, low-quality grass, it is likely that drills regularly generate high-magnitude bite forces in order to crush hard objects.

Theropithecus gelada has relatively shorter canines than *M. leucophaeus* and, as predicted by the masticatory-efficiency hypothesis, greater masseter and anterior temporalis leverage (except for the masseter at M1; Table 4.17). Given this pattern of differences, the drill is predicted to exhibit compensatory increases in muscle size in order to generate high-magnitude bite forces. The skull GM of *M. leucophaeus* is significantly larger than that of *T. gelada*, suggesting that the former is larger in body size and may have absolutely larger muscles (Table 4.17). However, the data compiled by Smith and Jungers (1997) indicate that, if there is a difference in body size, male geladas (19.0 kg) may be slightly larger than male drills (approximately 17.5 kg), though the reliability of the drill data is questionable, as they derive from a source "with no citations or sample sizes" (i.e., Haltenorth and Diller, 1980) (Smith and Jungers, 1997, p. 535). Moreover,

TABLE 4.17. *Results of pairwise comparisons for the Papionina*

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Theropithecus gelada*	<	*Mandrillus leucophaeus*
Masseter leverage:			
at canine	*Theropithecus gelada*	>	*Mandrillus leucophaeus*
at M1	*Theropithecus gelada*	=	*Mandrillus leucophaeus*
at M3	*Theropithecus gelada*	>	*Mandrillus leucophaeus*
Temporalis leverage:			
at canine	*Theropithecus gelada*	>	*Mandrillus leucophaeus*
at M1	*Theropithecus gelada*	>	*Mandrillus leucophaeus*
at M3	*Theropithecus gelada*	>	*Mandrillus leucophaeus*
Skull GM	*Theropithecus gelada*	<	*Mandrillus leucophaeus*
Relative muscle size:			
Zygomatic arch	*Theropithecus gelada*	<	*Mandrillus leucophaeus*
Intertemporalis[b]	*Theropithecus gelada*	<	*Mandrillus leucophaeus*
Temporal foramen	*Theropithecus gelada*	>	*Mandrillus leucophaeus*

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

the fact that the drill has a larger skull is almost certainly related in part to its relatively larger canines. Recall that there is a strong relationship between relative canine height and relative jaw length in cercopithecines (e.g., Fig. 4.14); *T. gelada* and *M. leucophaeus* fit this pattern, with the drill having a relatively and absolutely longer facial skeleton than the gelada. Thus, no statement can be made regarding differences in absolute muscle size related to differences in body size.

With respect to relative muscle size, the cross-sectional area of the drill's zygomatic arch is relatively larger than that of the gelada, indicating greater force-producing potential in the former species (Table 4.17). This result is consistent with the prediction of the masticatory-efficiency hypothesis. On the other hand, both estimates of relative temporalis size indicate that the gelada has greater force-producing potential in this muscle. However, these two comparisons are confounded by differences in skull form between these two species. As discussed by Spencer (1995), differences in relative brain size and in the way in which the facial skeleton is hafted to the neurocranium influence the parameters used here to estimate temporalis size. For example, in comparison to species with relatively large brains, small-brained species will have temporal lines that are close together due to the fact that there is less area on the correspondingly small neurocranium for the attachment of the temporalis muscles (Riesenfeld, 1955). Previous researchers have noted that the brain of *T. gelada* is smaller in comparison to those of other papioninans (e.g., Dechow, 1980; Martin, 1993), probably including the drill, which renders intertemporalis distance an unreliable estimate of temporal size for this comparison.[8]

Another issue concerns the pathway and form of the temporal lines in the drill. As noted by Groves (2000), McGraw and Fleagle (2006), and Gilbert (2007), the temporal lines of male drills and mandrills follow a more-or-less straight path as they travel posteriorly from their anterior origin on the frontal and zygomatic bones, reaching their point of maximum convergence at a very posterior position on the neurocranium in comparison to other large-bodied papioninans. In males, the temporal lines typically unite into a short sagittal crest that quickly merges with the nuchal crest. Thus, the temporal lines are relatively far apart as they cross the coronal suture (where the intertemporalis distance was measured). This configuration produces a triangle that covers much of the neurocranium in superior view. In contrast, the temporal lines of male geladas take a strong medial course from their anterior origin before arcing posteriorly, and they frequently merge into a sagittal crest at or before crossing the coronal suture. If the disparity in brain size between geladas and drills is ignored, then this configurational difference suggests that *T. gelada* has a larger anterior temporalis than does *M. leucophaeus* and is thus able to generate higher-magnitude vertical bite forces using this muscle. However, the morphology of the

---

[8] Isler et al. (2008; see their supplementary information) provide data on endocranial volume for two male *M. leucophaeus* and eleven male *T. gelada*. The values for the two drills are 161.0 cm^3 and 198.0 cm^3; the mean value for gelada males is 142.1 cm^3 with a range of 128.0–153.2 cm^3. Thus, given that these two species appear to be similar in body size, the drill has a relatively larger brain than the gelada.

temporal lines of *M. leucophaeus* differs strikingly from that of *T. gelada* (and all other primates); in the drill, the temporal lines project markedly beyond the surrounding cranial vault, distorting the vault's shape along their path. In fact, the temporal lines are more accurately described as ridges or crests; Groves (2001) referred to them as shelflike. The significance of this morphology in terms of the size of the temporalis muscle is unclear.

The area of the temporal foramen is also problematic for this comparison due to the fact that the cranium of *T. gelada* is more airorhynch (i.e., the face is flexed dorsally with respect to the neurocranium) than that of *M. leucophaeus* (Dechow, 1980; Delson and Dean, 1993). Two of the consequences of airorhynchy are an increase in the anteroposterior dimension of the temporal foramen and a decrease in the width of the frontal bone posterior to the orbits (i.e., an increase in postorbital constriction) (Spencer, 1995). The effect of these modifications is to increase the size of the temporal foramen. Note that a small brain further reduces the width of the postorbital region. Thus, the relatively large temporal foramen of the gelada in comparison to that of the drill may be the result of these differences in skull form rather than muscle size. The morphology of the temporal lines in the drill also complicates the comparison of temporal-foramen area—their ridgelike structure distorts the shape of the postorbital region, making it difficult to obtain a measure of postorbital constriction that is analogous to that measured in *T. gelada*.

Given these caveats, it is not possible to link the differences in estimates of temporalis size between the gelada and drill to possible differences in force-producing potential in this muscle. On the other hand, the drill does appear to have a more powerful masseter muscle than the gelada: not only is the cross-sectional area of the zygomatic arch relatively larger in *M. leucophaeus*, it is markedly larger than that of *T. gelada* in terms of absolute size (84.35 mm^2 versus 51.59 mm^2; Table 4.15). Thus, there is some evidence that the drill exhibits compensatory increases in muscle size relative to the gelada.

Genus Trachypithecus

Two species of the genus *Trachypithecus* are represented here: *T. obscurus* and *T. shortridgei*. The latter species is a member of the *T. pileatus* species group (Groves, 2001), and records at the American Museum of Natural History and Natural History Museum (London) identify *T. shortridgei* as a subspecies of *T. pileatus*. Like all colobines, species of *Trachypithecus* are highly folivorous, with leaves accounting for approximately 60% of their diets (e.g., Bennett and Davies, 1994; Fashing, 2001). However, there is evidence suggesting that the diets of *T. obscurus* and *T. shortridgei* differ in their mechanical demands. Field studies of *T. obscurus* indicate that this species consumes more young leaves than mature leaves and feeds on a relatively high percentage of fruit (30%) (Curtin, 1976, 1980; Aldrich-Blake, 1978; Curtin and Chivers, 1978; MacKinnon and MacKinnon, 1978, 1980; Lambert, 1990). No direct dietary data are available for *T. shortridgei*, but studies of the closely related *T. pileatus* indicate that this species consumes higher percentages tough (mature foliage) and hard (seeds) food items than *T. obscurus* (Islam and Husain, 1982; Choudhury, 1989; Stanford, 1991a,b; Solanki et al., 2008). The extent to which this characterization can be extended to *T. shortridgei* is not clear, but it seems reasonable to infer that the diet of this species was at least as mechanically demanding as that of *T. obscurus*, if not tougher and harder. Thus, given that *T. obscurus* has relatively shorter canines and greater masseter and anterior temporalis leverage than *T. shortridgei* (except for the masseter at the canine; Table 4.18), the latter species is expected to exhibit more powerful masticatory muscles.

Contrary to the prediction of the masticatory-efficiency hypothesis, the two species do not differ in terms of relative muscle size (Table 4.18). On the other hand, in terms of absolute size, there is some support for the prediction: the skull GM of *T. shortridgei* is significantly larger than that of *T. obscurus* (Fig. 4.18). This difference in skull size probably reflects a difference in body size (and muscle mass), but the magnitude of this difference is not known, as body-mass data for *T. shortridgei* are not available. However, the absolute values for the variables used to estimate muscle size are greater in *T. shortridgei*: the area of temporal foramen and cross-sectional area of the zygomatic arch of the latter species are 24% and 31% larger, respectively, than those of *T. obscurus* (see Table 4.15; these differences are statistically significant). It is also worth noting that males of *T. pileatus* are approximately 50% larger than males of *T. obscurus* (12.0 kg versus 7.9 kg, respectively; see Smith and Jungers, 1997). Thus, *T. shortridgei* can be reasonably characterized as having more powerful masticatory muscles than *T. obscurus*.

TABLE 4.18. Results of pairwise comparisons for the genus Trachypithecus

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Trachypithecus obscurus*	<	*Trachypithecus shortridgei*
Masseter leverage:			
at canine	*Trachypithecus obscurus*	=	*Trachypithecus shortridgei*
at M1	*Trachypithecus obscurus*	>	*Trachypithecus shortridgei*
at M3	*Trachypithecus obscurus*	>	*Trachypithecus shortridgei*
Temporalis leverage:			
at canine	*Trachypithecus obscurus*	>	*Trachypithecus shortridgei*
at M1	*Trachypithecus obscurus*	>	*Trachypithecus shortridgei*
at M3	*Trachypithecus obscurus*	>	*Trachypithecus shortridgei*
Skull GM	*Trachypithecus obscurus*	<	*Trachypithecus shortridgei*
Relative muscle size:			
Zygomatic arch	*Trachypithecus obscurus*	=	*Trachypithecus shortridgei*
Intertemporalis[b]	*Trachypithecus obscurus*	=	*Trachypithecus shortridgei*
Temporal foramen	*Trachypithecus obscurus*	=	*Trachypithecus shortridgei*

---

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

Genus Pan

Pan troglodytes and *Pan paniscus* are both primarily frugivorous, but various field studies have noted that the bonobo appears to incorporate a higher percentage of terrestrial herbaceous vegetation (THV) into its diet than does the chimpanzee (van Lawick-Goodall, 1968; Wrangham 1977; Badrian et al., 1981; McGrew et al., 1981; Badrian and Malenky, 1984; Kano and Mulavwa, 1984; Tutin et al., 1984, 1991, 1997; Isabirye-Basuta, 1989; Uehara, 1990; Malenky and Stiles, 1991; Wrangham et al., 1991, 1996, 1998; Kano, 1992; Kuroda, 1992; Tutin and Fernandez, 1993; Malenky and Wrangham, 1994; Kuroda et al., 1996; Conklin-Brittain, 1998; Newton-Fisher, 1999). This distinction raises the possibility that the bonobo has a more mechanically demanding diet. However, available data suggest that the THV consumed by bonobos is higher in quality (i.e., high protein-to-cellulose ratio) and less mechanically resistant than that typically consumed by chimpanzees and gorillas (Malenky and Stiles, 1991; Wrangham et al., 1991, 1996). The results of Taylor's (2002; see also Taylor 2005, 2006) morphometric analysis of the African ape masticatory system suggest that any differences in the mechanical demands of the bonobo and chimpanzee diets that may exist are slight and have had very little influence on the skulls of these species. She concluded:

> Bonobos do not exhibit a clear pattern of differentiation from chimpanzees; nor are there systematic differences that could be linked specifically to repetitive loading of the jaws or resistance to larger internal forces … Rather than interpret the results as empirical evidence for rejecting a link between diet and morphology altogether, I would argue that the ecological data do not support a bonobo diet that requires unique mechanical solutions, particularly since the evidence for a diet specialized

> towards herbivory in bonobos is contradictory at best (Taylor, 2002, p. 151).

Thus, in the analysis that follows, *P. paniscus* and *P. troglodytes* are treated as similar in terms of the mechanical properties of their diets.

As is well known (e.g., Kelley, 1995a, 2001; Alba et al., 2001), *P. paniscus* has relatively shorter canines than *P. troglodytes* (Table 4.19). The configurations of the masticatory systems of these two species reflect this difference, but not to the degree that might be expected based on the magnitude of this difference: the bonobo has significantly greater masseter leverage at M1 and M3 than the chimpanzee, but the difference between the two species is not significant at the canine (Table 4.19). Moreover, there are no statistical differences between these two species in leverage of the anterior temporalis (Table 4.19), though this result is not surprising, given that this variable is generally not correlated with relative canine height across the Anthropoidea (see Part I). Thus, the chimpanzee is predicted to have greater force-producing potential in its masseter relative to the bonobo in order to compensate for its reduced leverage at the molar bite points.

Although there is a large amount of overlap in body size among the subspecies of *P. troglodytes* and *P. paniscus* (Smith and Jungers, 1997; Groves, 2001), the subspecies of chimpanzee included in this study, *P. t. troglodytes*, can be characterized as larger than the bonobo. According to the data summarized by Smith and Jungers (1997), males of *P. t. troglodytes* weigh, on average, approximately 60 kg, whereas the mean for *P. paniscus* males is 45 kg. Groves

TABLE 4.19. Results of pairwise comparisons for Pan

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Pan paniscus*	<	*Pan troglodytes*
Masseter leverage:			
at canine	*Pan paniscus*	=	*Pan troglodytes*
at M1	*Pan paniscus*	>	*Pan troglodytes*
at M3	*Pan paniscus*	>	*Pan troglodytes*
Temporalis leverage:			
at canine	*Pan paniscus*	=	*Pan troglodytes*
at M1	*Pan paniscus*	=	*Pan troglodytes*
at M3	*Pan paniscus*	=	*Pan troglodytes*
Skull GM	*Pan paniscus*	<	*Pan troglodytes*
Relative muscle size:			
Zygomatic arch	*Pan paniscus*	<	*Pan troglodytes*
Intertemporalis[b]	*Pan paniscus*	>	*Pan troglodytes*
Temporal foramen	*Pan paniscus*	=	*Pan troglodytes*

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

(2001) presented data suggesting a slightly lower mean body mass—52 kg—for *P. t. troglodytes*. This value comes from a larger sample of individuals (*n* = 18) than the one used to compute the mean reported by Smith and Jungers (1997; *n* = 5).[9] Whether or not the larger sample is more representative of body mass for this subspecies is not clear, but Smith and Jungers (1997) used data obtained from specimens that derive from the same geographical region as those that were measured for this study (various sites in Cameroon). The lower mean reported by Groves (2001) derives from chimpanzees housed at the Franceville Medical Research Centre in Gabon. Regardless of which value is more accurate, both give the same signal (i.e., *P. t. troglodytes* is larger than *P. paniscus*). This difference in body mass probably translates into a difference in muscle size, which is likely exaggerated by the fact that bonobos have smaller heads than chimpanzees (e.g., McHenry and Corruccini, 1981; Shea, 1983b; Table 4.19). Moreover, as shown in Table 4.19, *P. troglodytes* has relatively larger masseter and temporalis muscles (indicated by the intertemporalis distance but not temporal-foramen area) than *P. paniscus*. Thus, whether judged by estimates of absolute muscle size or relative muscle size, *P. troglodytes* appears to have greater force-producing potential than *P. paniscus*, as predicted.

Given the lack of differences in anterior temporalis leverage between these two species, these results suggest that *P. troglodytes* is capable of producing higher-magnitude bite forces than *P. paniscus*, which is not consistent with the

---

[9] Groves (2001) also discussed a subset of the data reported by Smith and Jungers (1997).

hypothesis that bonobos process a tougher diet than do chimpanzees. However, because bonobos have greater masseter leverage at the postcanine bite points, this species is slightly more efficient at converting muscle force into bite force than are chimpanzees. Selection is expected to favor increased leverage of the masticatory muscles in (at least) two different situations: (1) in species with diets that require high-magnitude bite forces, where increased leverage increases maximum bite force, and (2) in species with diets that require lower-magnitude bite forces to be sustained for long durations or produced at relatively high frequencies (Spencer, 1995). In the latter situation, the magnitude of the bite force is not the primary target of selection for configurational changes in the masticatory system. Given this distinction, it is tempting to argue that the relatively short canines of *P. paniscus* are related to selection for masticatory efficiency—but not high-magnitude bite-force production—due to this species' greater reliance on soft THV. Under this scenario, it is assumed that bonobos must process a greater volume of food items and thus must use a greater number of chewing cycles than chimpanzees because THV is not as energy-rich as the ripe fruit preferred by the latter species.[10] However, this argument is entirely speculative and cannot be tested using currently available data. Moreover, the difference between *P. paniscus* and *P. troglodytes* in the overall efficiency of the masticatory system is more plausibly explained by differences social structure, which suggest that the intensity of intermale competition is greater in

---

[10] In this context, the fact that the chimpanzees examined here have more powerful masticatory muscles than bonobos is almost certainly a consequence of differences in body and head size.

chimpanzees (e.g., Riss and Goodall, 1977; Goodall, 1986; Kano, 1992; Furuichi and Ihobe, 1994; Parish, 1994; McGrew, 1996; Furuichi, 1997; Stanford, 1998; Watts, 1998; Wrangham, 1999; Hohmann and Fruth, 2002, 2003; Paoli et al., 2006). Thus, in this case, the small size of the bonobo canines is probably not an example of natural selection for masticatory-efficiency overwhelming sexual selection for tall canines.

Dietary constraints on canine height

Two of the catarrhine genera included in this study offer potential examples of selection for increased muscle leverage constraining canine height or perhaps even leading to canine reduction in species that are highly sexually selected. However, prior to discussing these cases, it is important to note that a clear demonstration of the latter phenomena requires high-resolution estimates of sexual selection and the mechanical properties of diets, as well as a fossil record that is sufficiently complete to allow (1) the vector of evolutionary change to be established and (2) the timing of changes in canine height to be linked with changes in skull form. The cases examined here lack these data, but they are suggestive and are worth highlighting as potential models for instances of canine reduction in extinct species.

Genus Macaca

Macaca mulatta (rhesus monkey) and *M. fascicularis* (long-tailed or crab-eating macaque) are closely related members of the speciose genus *Macaca* and are frequently placed together in the *M. fascicularis* species group (e.g., Fooden, 1976, 1980; Delson, 1980; Richard et al., 1989; Hayasaka et al., 1996; Tosi et al., 2003; Li et al., 2009). These species diverged between two and three million years ago (Hayasaka et al., 1996; Li et al., 2009) but still hybridize where they come into contact on the Indochinese Peninsula (Fooden, 1997; Groves, 2001; Tosi et al., 2002; Kanthaswamy et al., 2008). From this region of parapatry, the rhesus monkey's range extends into China to just north of the Yellow River (approximately 35°N), and northwest into northern India, Nepal, Pakistan, and Afghanistan (Groves, 2001). The specimens measured for this study were collected from southern China, northern Vietnam, northern Thailand, northern and central Burma (Myanmar), southeastern Bangladesh, Nepal, and northwestern India.[11] The range of the long-tailed macaque covers the southern part of the Indochinese Peninsula, Sumatra, Borneo, the Philippines, and the Lesser Sunda Islands (Groves, 2001). The *M. fascicularis* sample used here derives mainly from northern Borneo, but specimens from Sumatra and some of the small islands between Sumatra and Borneo were also included.

Both species of macaque are typically described as frugivorous or omnivorous, but field observations suggest that the rhesus monkey relies heavily on resistant food items such as clover, grasses, leaves, seeds, and bark, particularly in the northern part of its range, whereas the long-tailed macaque appears to prefer and feed primarily on fleshy fruits, though it does broaden its diet during times of fruit scarcity (e.g., Lindburg, 1976, 1977; Roonwal and

---

[11] The inclusion of specimens from such a wide geographic range (covering approximately 3000 km) does not lead to an unusually high level of size variation in the *M. mulatta* sample in comparison to that observed in the other species in the data set.

Mohnot, 1977; MacKinnon and MacKinnon, 1978; Makwana, 1978; Rodman, 1978; Wheatley, 1980; Wada, 1983; van Schaik, 1985; Berenstain, 1986; Goldstein and Richards, 1989; Richard et al., 1989; Lucas and Corlett, 1991, 1998; Ungar, 1996; Yeager, 1996; Wich, 2002; Son, 2003; Lu et al., 2007). Both species live in multimale-multifemale groups in which males are highly aggressive toward one another and form clearly defined linear dominance hierarchies (Lindburg, 1969; Wilson and Boelkins, 1970; Bernstein et al., 1974a,b; Bernstein and Gordon, 1980; Shively et al., 1982; Wheatley, 1982; Chapais, 1983; van Noordwijk and van Schaik, 1985, 1988; Caldecott, 1986; de Ruiter et al., 1992, 1994; de Ruiter and van Hooff, 1993; Bercovitch, 1997; Berard, 1999; Engelhardt et al., 2006). The behavioral descriptions of these two species do not allow the males of one to be characterized as more sexually selected than males of the other; Plavcan (1990) classified intermale competition in both species as high-intensity, high-frequency (competition level 4; see also Plavcan and van Schaik, 1992). That these species do not differ markedly in the intensity of intermale competition is also suggested by the fact that they differ only slightly in sexual dimorphism in skull size (*M. fascicularis*, 1.14; *M. mulatta*, 1.12), body mass (1.49; 1.44), and canine height (1.99; 2.01) (see Tables 2.4 and 2.6).

Notably, despite the fact that *M. mulatta* and *M. fascicularis* exhibit nearly identical levels of sexual dimorphism in combined canine height, they differ in relative canine height, with males of the former species having relatively shorter canines than males of the latter (Table 4.20). In fact, *M. mulatta* males have the shortest canines relative to skull size of all cercopithecines included in this study except for males of *Cercopithecus pogonias* (Table 4.5). Moreover, even though male rhesus monkeys are larger than long-tailed macaques in body mass (7.71 kg versus 5.36 kg; Smith and Jungers, 1997) and skull size (Table 4.20), their canines are absolutely shorter (Table 2.6).[12] As predicted by the masticatory-efficiency hypothesis, this difference in relative canine height is accompanied by a difference in muscle leverage—*M. mulatta* has significantly greater masseter leverage at all bite points and significantly greater anterior temporalis leverage at M3 (Table 4.20). Importantly, this difference in muscle leverage can be linked directly with differences in gape: Hylander and Vinyard's (2006) data demonstrate that males of *M. fascicularis* have absolutely and relatively wider gapes than males of *M. mulatta.*

With respect to the force-producing potential of the masticatory muscles, *M. fascicularis* appears to have relatively larger muscles than *M. mulatta*: the cross-sectional area of the zygomatic arch is relatively larger in the long-tailed macaque and the distance between the temporal lines is relatively narrower (Table 4.20). However, the disparity in body mass noted above—*M. mulatta* males are approximately 40–50% larger than *M. fascicularis* males—almost certainly means that the rhesus monkey has absolutely larger masticatory muscles, and thus greater force-producing potential. This inference is supported by data on muscle size presented by Antón (1999, 2000) for the females of these two species, which

---

[12] Females of these two species are also characterized by this pattern of differences in absolute and relative combined canine height.

TABLE 4.20. Results of pairwise comparisons for Macaca

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Macaca mulatta*	<	*Macaca fascicularis*
Masseter leverage:			
at canine	*Macaca mulatta*	>	*Macaca fascicularis*
at M1	*Macaca mulatta*	>	*Macaca fascicularis*
at M3	*Macaca mulatta*	>	*Macaca fascicularis*
Temporalis leverage:			
at canine	*Macaca mulatta*	=	*Macaca fascicularis*
at M1	*Macaca mulatta*	=	*Macaca fascicularis*
at M3	*Macaca mulatta*	>	*Macaca fascicularis*
Skull GM	*Macaca mulatta*	>	*Macaca fascicularis*
Relative muscle size:			
Zygomatic arch	*Macaca mulatta*	<	*Macaca fascicularis*
Intertemporalis[b]	*Macaca mulatta*	>	*Macaca fascicularis*
Temporal foramen	*Macaca mulatta*	=	*Macaca fascicularis*

---

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

indicate that the masseter and medial pterygoid of female rhesus monkeys are more massive and have greater physiological cross-sectional areas than those of female long-tailed macaques. The difference in body mass between the females of these species is similar to that observed in the males. Data for the anterior temporalis are not available, but there is no reason to expect this muscle to deviate from the pattern exhibited by the other muscles.

The results of this pairwise comparison indicate that the masticatory system of *M. mulatta* is capable of generating higher-magnitude muscle forces and converting a greater percentage of those forces into bite force. This characterization is consistent with the differences in diet between these two species reported in the primatological literature. Given that these species exhibit qualitatively similar degrees of intermale competition (at least at the resolution provided by available observational data), it is reasonable to hypothesize that the difference in canine height (both relative and absolute) between these species is related to selection for improved muscle leverage. At least two scenarios are possible. The first assumes that *M. mulatta* males represent the primitive condition for the *M. fascicularis* species group. In this case, selection for greater muscle leverage would be constraining the height of the canines in male rhesus monkeys, whereas such selection would be relaxed in long-tailed macaques as a consequence of their more frugivorous diet, allowing the males of this species to evolve relatively (and absolutely) taller canines. The second scenario assumes that the short canines of male rhesus monkeys are derived within *Macaca*; in this case, reduction has occurred, even in the presence of intense intermale competition. Clearly these hypotheses are highly speculative, but they can be tested given (1) accurate and precise estimates sexual selection to confirm or refute the assumption that the two species of macaque do not differ significantly in the intensity of sexual selection and (2) a fossil record that allows the polarity of canine height within *Macaca* to be established.

Genus Gorilla

Gorillas are generally classified as folivores based on early descriptions of mountain gorillas (*Gorilla beringei*) as heavily reliant on terrestrial herbaceous vegetation (e.g., Schaller, 1963; Fossey and Harcourt, 1977; Watts, 1984; see also Elgart-Berry, 2004; Ganas et al., 2004; Rothman et al., 2007). However, various field studies conducted on the western lowland gorilla (*G. gorilla*) over the last three decades have revealed that this species prefers ripe, succulent fruits when they are available and consumes a relatively high percentage (30–40%) of them (Tutin and Fernandez, 1985, 1993; Rogers et al., 1990; Williamson et al., 1990; Nishihara, 1995; Doran and McNeilage, 1998; 2001; Rogers et al., 2004; Yamagiwa and Basabose, 2006; Harcourt and Stewart, 2007b; Doran-Sheehy et al., 2009; Masi et al., 2009). Recent reports (Ganas et al., 2004; Rothman et al., 2007) have noted that some populations of *G. beringei* eat more fruit than earlier studies indicated, but the sample used here is composed only of individuals from the population that inhabits the Virunga Mountains, where fruit is less abundant and therefore eaten only rarely. The diet of this population consists almost entirely (>90%) of tough leaves, stems, pith, shoots, and bark (Schaller, 1963; Fossey and Harcourt, 1977; Watts, 1984; Elgart-Berry, 2004). These mountain gorillas are thus thought to have a more mechanically demanding diet than other gorilla populations, particularly western lowland gorillas, and this distinction has been linked to variation in skull and tooth form within the genus (Groves, 1970; Taylor, 2002, 2005, 2006).

Gorillas typically organize themselves into one-male or multimale groups in which males attempt to monopolize sexual access to females (Sicotte, 1993; Tutin, 1996; Doran and McNeilage, 1998, 2000; Robbins, 1995, 1999, 2006; Watts, 2000; Doran-Sheehy et al., 2004; Bradley et al., 2004, 2005; Harcourt and Stewart, 2007a,b; Stoinski et al., 2009; Breuer et al., 2010). Multimale groups are far more common in mountain gorillas (Robbins, 1995; Bradley, 2004), but the reproductive skew is still marked in this species—Bradley et al. (2005) found that dominant males sired 85% of group offspring. There is some evidence that aggression and physical violence between resident males and lone males or males from other groups are more frequent in mountain gorillas than in western lowland gorillas (Sicotte, 1993; Doran-Sheehy et al., 2004), which may be related to the fact that male western lowland gorillas living in close proximity are often related to each other (Bradley et al., 2004).

Whether or not these distinctions indicate that the males of one species are more sexually selected than those of the other species is not clear. Estimates of body-mass dimorphism for these two species are quite different; according to published data (Smith and Jungers, 1997), male western lowland gorillas are nearly 2.4 times larger than conspecific females, whereas male mountain gorillas are only approximately 1.7 times larger than conspecific females, suggesting that males of the former species are more sexually selected. However, the reliability of the latter value is questionable, given that it was computed using only a single female mountain gorilla (the samples for male mountain gorillas and female western lowland gorillas are also small—$n = 5$ and 3, respectively). Moreover, as in the macaque species discussed above, *G. gorilla* and *G. beringei* are strikingly similar with respect to dimorphism in skull size (*G. beringei*, 1.18; *G. gorilla*, 1.16) and combined canine height (1.70; 1.71) (Tables 2.4 and 2.6). These data suggest a similar degree of sexual selection. Also as in the macaques, the nearly identical levels of canine dimorphism observed in the two species of gorilla are accompanied by a clear difference in canine height: male mountain gorillas have absolutely and relatively shorter canines than male western lowland gorillas (Table 4.21; see also Kelley, 1995a).

This difference in canine height is associated with a somewhat puzzling pattern of differences in muscle leverage. Mountain gorillas have greater masseter leverage than western lowland gorillas at all three bite points, as predicted by the masticatory-efficiency hypothesis, but the opposite is true for the anterior temporalis: western lowland gorillas have greater leverage at the canine and M1 (but not M3; Table 4.21). Based on these data, neither species of gorilla can be characterized as more efficient in terms of bite-force production. In principle, the leverage of the resultant force produced by these two muscles can be computed using estimates of muscle orientation and muscle force. However, the skeletal proxies used here to estimate the force-producing potential of the masseter and temporalis are far too crude to be used for this purpose. Moreover,

TABLE 4.21. Results of pairwise comparisons for Gorilla

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Gorilla beringei*	<	*Gorilla gorilla*
Masseter leverage:			
at canine	*Gorilla beringei*	>	*Gorilla gorilla*
at M1	*Gorilla beringei*	>	*Gorilla gorilla*
at M3	*Gorilla beringei*	>	*Gorilla gorilla*
Temporalis leverage:			
at canine	*Gorilla beringei*	<	*Gorilla gorilla*
at M1	*Gorilla beringei*	<	*Gorilla gorilla*
at M3	*Gorilla beringei*	=	*Gorilla gorilla*
Skull GM	*Gorilla beringei*	=	*Gorilla gorilla*
Relative muscle size:			
Zygomatic arch	*Gorilla beringei*	=	*Gorilla gorilla*
Intertemporalis[b]	*Gorilla beringei*	=	*Gorilla gorilla*
Temporal foramen	*Gorilla beringei*	>	*Gorilla gorilla*
Relative TMJ height	*Gorilla beringei*	>	*Gorilla gorilla*
Relative palate width[c]	*Gorilla beringei*	<	*Gorilla gorilla*

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

[c] Relative palate width was computed as the inter-M1 distance (landmarks 11a and 11b) divided by bicondylar width (landmarks 1a and 1b) (see Table 2.2 and Fig. 2.1).

while it is possible to estimate masseter orientation using the data collected for this study, the orientation of the anterior temporalis cannot be determined.

It could be inferred that the overall leverage of these two jaw adductors is greater in western lowland gorillas than in mountain gorillas based on the fact that, in primates, the temporalis is larger and generally has a greater physiological cross-sectional area (PCSA) than the masseter (Turnbull, 1970; Cachel, 1979; Bouvier and Tsang, 1990; Taylor et al., 2009; Taylor and Vinyard, 2009; Vinyard and Taylor, 2010). However, the anterior temporalis—the most relevant component of the temporalis in terms of generating high-magnitude, vertically oriented bite force—is not always larger than the masseter; Cachel (1979) presented data for a single adult male gorilla (geographical origin unknown) indicating that the masseter weighs approximately 10% more than the anterior temporalis. The extent to which this individual is representative of gorillas in general is unknown, and thus any inference regarding the leverage of the resultant force produced by the masseter and anterior temporalis derived from Cachel's (1979) data would be unreliable.

With respect to the variables used to estimate muscle size, the two species do not differ in the relative cross-sectional area of the zygomatic arch, but the mountain gorilla has a relatively (and absolutely) larger temporal foramen, suggesting that this species has a larger temporalis muscle, and thus greater force-producing potential, than the western lowland gorilla (Table 4.21). Note that *G. beringei* and *G. gorilla* do not differ in intertemporalis distance, a consequence of the fact that males of both species almost invariably possess sagittal crests. As discussed in Chapter 2, intertemporalis distance cannot be used to estimate interspecific differences in temporalis size in this situation. Published body-mass data indicate that the two species are similar in body size (*G. beringei* males, 162.5 kg; *G. gorilla* males, 170.4; Smith and Jungers, 1997), and this observation is supported by the fact that the skull GMs of the two species cannot be distinguished statistically (Table 4.21). Thus, given the difference in temporal-foramen size, the jaw musculature of the mountain gorilla appears to be more powerful than that of the western lowland gorilla.

This pattern of similarities and differences does not lend itself to a straightforward interpretation, but two lines of evidence, in addition to the difference in overall adductor mass, suggest that *G. beringei* can produce higher-magnitude bite forces than *G. gorilla*. First, the increased mechanical advantage of the masseter in *G. beringei* is associated with a TMJ that is positioned higher above the occlusal plane than is the case for *G. gorilla* (Tables 4.11 and 4.21; see also Taylor, 2002). The effect that this alteration has on bite-force magnitudes is complex (see discussion in Spencer, 1995), but when combined with an anterosuperiorly oriented muscle force, increasing the height of the TMJ above the occlusal plane will augment bite forces and produce a more even distribution of bite forces along the tooth row (see also Ward and Molnar, 1980).

The second line of evidence concerns the width of the palate relative to the distance between the mandibular condyles (bicondylar width). According to the constrained lever model of masticatory-force production (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1995, 1998, 1999), the resultant force produced by the jaw adductors must lie within a triangle of support formed by the left and right TMJs and the bite point; if the resultant force falls outside of this triangle, then the working-side TMJ will be subjected to potentially injurious tensile forces during biting. As the bite point moves posteriorly, the triangle of support decreases in size and the muscle resultant force must be shifted toward the working side in order to remain within the triangle of support. This shift is accomplished by decreasing balancing-side muscle activity (Spencer, 1995, 1998, 1999), which diminishes bite force. However, decreasing palate width relative to bicondylar width (or increasing the latter relative to the former) permits a less severe reduction in balancing-side muscle force:

> Such a configurational modification has the effect of changing the shape of the triangle of support so that the side between the bite point and the balancing side TMJ is closer to the midline muscle resultant force. As a consequence, the required suppression in balancing side muscle activity will be reduced (the muscle resultant must not move as far toward the working side). The maximum magnitudes of the muscle resultant force, and consequently the bite force, will therefore be increased (Spencer, 1995, p. 351).

Mountain gorillas have narrower palates relative to bicondylar width in comparison to western lowland gorillas (Table 4.21), and thus they are able to recruit their balancing-side muscles to a greater degree than their western counterparts during molar biting.

Incidentally, the constrained lever model provides an explanation for the relationship between the relative lengths of the bite-point moment arms and the masseter moment arm observed in Part I (see Fig. 4.4). Recall that there is a positive correlation between relative masseter moment-arm length and relative bite-point moment-arm length in noncercopithecine anthropoids, such that species with greater masseter leverage tend to have relatively longer masseter moment arms coupled with relatively longer bite-point moment arms than species with less masseter leverage. Because the resultant force generated by the jaw adductors must lie within the triangle of support, the degree to which muscle leverage at the molars can be increased by moving the tooth row posteriorly or by repositioning the muscle resultant force anteriorly is limited, as the muscle resultant force must lie posterior to the tooth row (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1995, 1998, 1999). The reason for this restriction is that moving the distal teeth closer to the muscle resultant force increases the likelihood that the resultant force will fall outside the triangle of support when loads are applied to these teeth, potentially resulting in the TMJ being pulled apart (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1995, 1998, 1999).

Muscle leverage at the molar bite points can be increased without compromising the TMJ by repositioning the dentition and the masticatory muscles anteriorly, which increases the ratio of muscle moment-arm length to bite-point moment-arm length without bringing the muscle resultant force closer to the teeth (Spencer and Demes, 1993; Spencer, 1995). However, moving the teeth forward is costly because it increases the magnitude of sagittal bending in the face. Within *Gorilla*, the relative lengths of the bite-point and masseter (but not anterior temporalis) moment arms of the mountain gorilla are significantly greater than those of the western lowland gorilla ($p < 0.05$), and thus *G. beringei* exhibits the configuration predicted by the constrained lever model. The association between greater muscle leverage and long bite-point and muscle moment arms also characterizes the *Trachypithecus* comparison, but not the *Pan* comparison or the cercopithecine comparisons. In the latter two cases, increases in muscle leverage are achieved mainly by decreasing bite-point moment-arm lengths. The restriction on increases in muscle leverage at the molars imposed by the constrained lever model is probably relaxed in cercopithecines due to the fact that they have, relative to skull size, the tallest canines among the Anthropoidea and therefore need the widest gapes. This requirement probably results in a greater separation between the distal molars and the muscle resultant force, and thus muscle leverage can be increased to a greater degree than in other anthropoids by retracting the dentition without compromising the TMJ. A similar situation may obtain for *Pan paniscus* and *Pan troglodytes*.

Returning to the *Gorilla* comparison, most of the ways in which *G. beringei* differs from *G. gorilla* noted above (i.e., increased masseter leverage, larger adductor mass, higher TMJ, narrower palate relative to bicondylar width) suggest that the former species is adapted to generating higher-magnitude bite forces than the latter in order to process its more mechanically demanding diet (see also Groves, 1970; Taylor, 2002, 2005, 2006), but the question of why the mountain gorilla has a relatively short anterior temporalis moment arm remains unanswered.[13] There are at least two possible explanations. First, there may be

---

[13] This characterization applies to the length of the anterior temporalis moment arm relative to the lengths of the bite-point moment arms. When skull size is used to size-adjust this variable, the two species of gorilla do not differ ($p = 0.7133$) (see also Taylor, 2002).

some factor—other than canine height—that limits the anterior placement of the temporalis but not the masseter. The existence of such a constraint would provide an explanation (at least a partial one) for why the moment arm of the anterior temporalis is not correlated with relative canine height in the Anthropoidea (see Part I). One hypothesis is that the position of the orbit and the postorbital septum, which form the anterior boundary of the temporalis muscle (e.g., Ross, 1995a), restrict the length of this muscle's moment arm. If this hypothesis is correct, then the relative anteroposterior distance between the TMJ and the orbit and postorbital septum should be positively correlated with the relative length the anterior temporalis moment arm. A direct test of this hypothesis cannot be made using the data collected for this study. Other constraints are possible but it is not immediately obvious what they may be.

The second possible explanation is that the masseter and anterior temporalis are functionally differentiated and are thus subject to different selection pressures. Very few investigations have addressed this issue. Some studies suggest that the masseter is particularly important for generating powerful bite forces on the anterior teeth (Hylander and Johnson, 1985; Ross and Hylander, 2000; but see Cachel, 1979). However, this explanation is unlikely to apply in the present case, as mountain gorillas are not known to process obdurate food items more frequently with their incisors than with their postcanine teeth. Moreover, the pattern variation in muscle leverage and size in *Gorilla* does not suggest functional differentiation within the genus—i.e., the increase in temporalis size in *G. beringei* is not consistent with the hypothesis that this muscle is de-emphasized in this species. This configuration indicates that functional differentiation is unlikely to explain the relatively low leverage of the anterior temporalis observed in the mountain gorilla.

In any case, increased masseter leverage is a key feature distinguishing mountain gorillas from western lowland gorillas, and as predicted by the masticatory-efficiency hypothesis, the relatively long masseter moment arm of mountain gorillas is associated with relatively (and absolutely) shorter canines. Given that the males of the two species of *Gorilla* are similarly sexually selected, it can be hypothesized that this difference in canine height is a result of changes in the masticatory system that produced an increase in masseter leverage in *G. beringei*. The specific target of selection in this case is unclear: either selection favored an increase in masseter leverage directly or it favored an increase in TMJ height, which led indirectly to an increase in masseter leverage. The latter explanation is suggested by the mountain gorilla's relatively low anterior temporalis leverage.

As in the case of *Macaca* discussed above, fossil evidence is needed to establish whether the canines of mountain gorillas are reduced (i.e., derived relative to the condition observed in western lowland gorillas) or have been constrained from increasing (i.e., primitive). Also as in *Macaca*, finer-grained estimates of the intensity of sexual selection acting on the males of these two species are needed to confirm that the difference in canine height cannot be attributed to subtle differences in intermale competition.

Canine height, diet, and muscle leverage in the Platyrrhini

Family Atelidae

As noted in Part I, *Alouatta seniculus* (red howler monkey) and *Ateles geoffroyi* (Geoffroy's, or Mexican, spider monkey) are similar in relative combined canine height—they cannot be distinguished statistically (p = 0.5972)—but the former species has greater masseter and anterior temporalis leverage than the latter (Table 4.22; for a more comprehensive analysis of the atelid masticatory system, see Spencer 1995). Notably, the greater muscle leverage in *Al. seniculus* is a product of relatively long muscle and bite-point moment arms, as in *Gorilla beringei* (see also Spencer, 1995). According to the masticatory-efficiency hypothesis, these species should not differ in muscle leverage. However, the stark contrast in skull form between *Alouatta* and *Ateles* raises the question of whether the skull GM is the most appropriate variable for size-adjusting canine height in this comparison.

Of all the closely related species compared up to this point, *Al. seniculus* and *At. geoffroyi* are by far the most morphologically distinct in terms of skull architecture (Fig. 4.20). This distinction is due primarily to the highly unusual skull of *Alouatta*, which has been modified from the presumed ancestral condition in a number of ways that have been linked to the enlarged vocal apparatus, particularly the hyoid, found in the species of this genus. These modifications include: (1) an elongated, massive, and dorsally flexed (airorhynch) facial skeleton; (2) a long, unflexed basicranium; (3) a flat, vertically oriented occipital squama; (4) a posteriorly oriented foramen magnum located on the posterior

TABLE 4.22. Results of pairwise comparisons for the Atelidae

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Alouatta seniculus*	=	*Ateles geoffroyi*
Masseter leverage:			
at canine	*Alouatta seniculus*	>	*Ateles geoffroyi*
at M1	*Alouatta seniculus*	>	*Ateles geoffroyi*
at M3	*Alouatta seniculus*	>	*Ateles geoffroyi*
Temporalis leverage:			
at canine	*Alouatta seniculus*	>	*Ateles geoffroyi*
at M1	*Alouatta seniculus*	>	*Ateles geoffroyi*
at M3	*Alouatta seniculus*	>	*Ateles geoffroyi*
Alternative canine size-adjustment:			
vs. face GM	*Alouatta seniculus*	<	*Ateles geoffroyi*
vs. mandibular length	*Alouatta seniculus*	<	*Ateles geoffroyi*

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

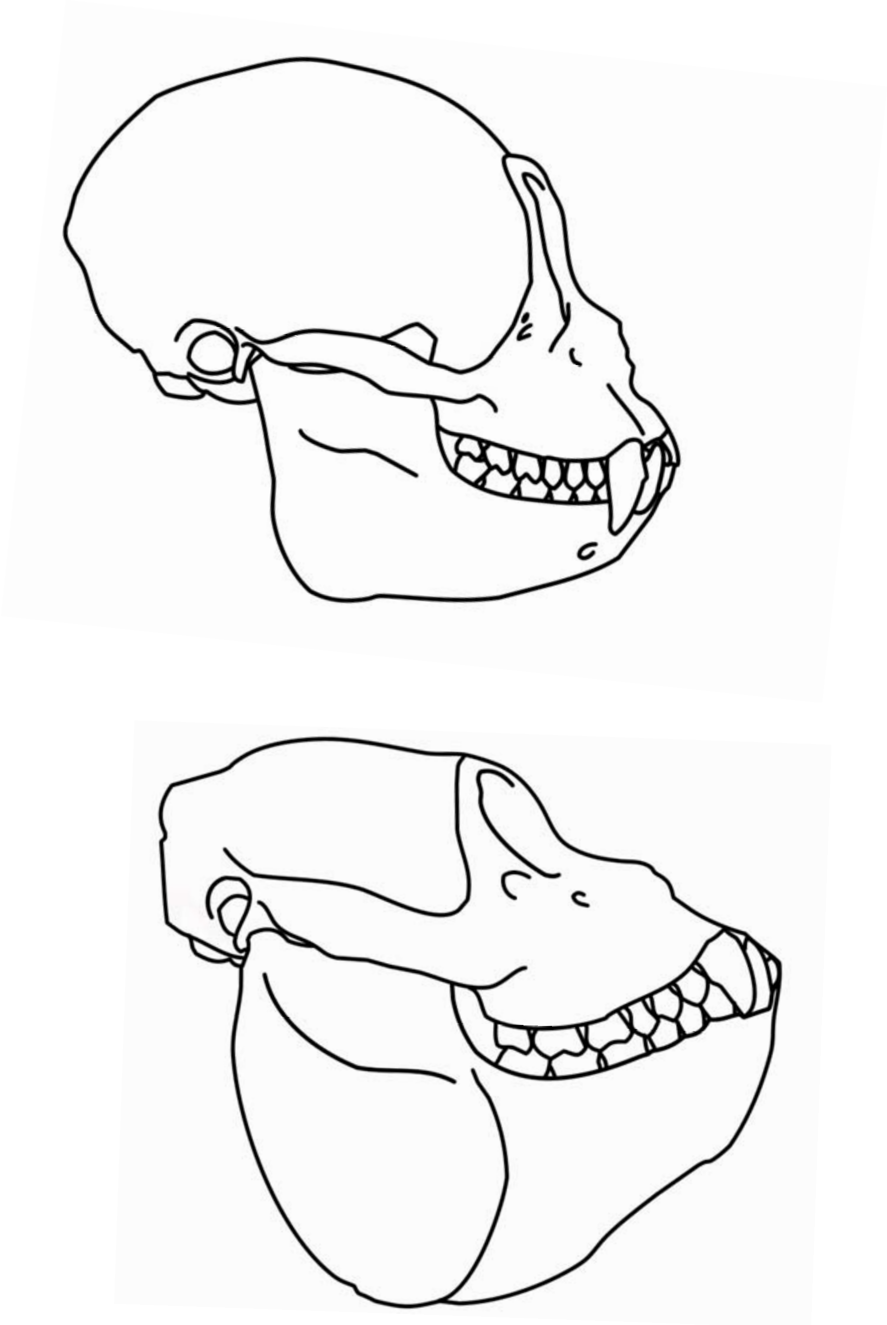


Fig. 4.20. The skulls of *Ateles geoffroyi* (top) and *Alouatta seniculus* (bottom). Both illustrations represent male specimens. The skulls are scaled to approximately the same maximum cranial length and are oriented in the Frankfurt horizontal plane.

aspect of the cranium; and (5) an expanded ascending ramus of the mandible (Biegert, 1963; Rosenberger and Strier, 1989; Fleagle et al., 2010). In addition to these differences, the size and shape of the neurocrania of these species are markedly dissimilar—in *Alouatta* the braincase is small, low, and cylindrical, whereas in *Ateles* it is large, high, and globular (Rosenberger and Strier, 1989; Fleagle et al., 2010).

The visual impression given by Fig. 4.20 is that the canines of the spider monkey are taller than those of the howler monkey relative to the size of the face, particularly with respect to its anteroposterior length. Moreover, given that the neurocranium of *At. geoffroyi* is much larger than that of *Al. seniculus*, especially when compared to the face, the inclusion of neurocranial measurements in the skull GM may confound the comparison of relative canine size in these taxa. Thus, combined canine height was size-adjusted using two additional variables: (1) a geometric mean composed of facial length, snout width, mandibular length, and posterior facial height (i.e., the face GM) and (2) mandibular length (see Table 2.3 and Fig. 2.5 for measurement definitions). When relative combined canine height is expressed as a shape ratio using either of the latter two variables as the denominator, the impression given by Figure 4.20 is confirmed: the howler monkey has relatively shorter canines than the spider monkey (Table 4.22). From this perspective, then, the *Alouatta-Ateles* comparison fits the prediction of the masticatory-efficiency hypothesis.

The greater muscle leverage in *Al. seniculus* compared to *At. geoffroyi* is congruent with the well-known difference in diet between the two genera—i.e., species of *Alouatta* are primarily folivorous while species of *Ateles* specialize on ripe fruits (Klein and Klein, 1975, 1977; Coelho et al., 1976; Glander, 1978; Milton, 1980; Mittermeier and van Roosmalen, 1981; Gaulin and Gaulin, 1982; Braza et al., 1983; Estrada, 1984; van Roosmalen, 1985; Chapman, 1987; Symington, 1988; van Roosmalen and Klein, 1988; Ungar, 1990; Julliot and Sabatier, 1993; Silver et al., 1998; Ramos-Fernández and Ayala-Orozco, 2003; Orihuela Lopez et al., 2005; González-Zamora et al., 2009). In contrast, the difference in relative canine height is at odds with behavioral descriptions of howler monkeys and spider monkeys. Species of *Alouatta* typically live in groups in which the alpha male attempts to prevent other resident males (if any) from mating with the group's females and must defend against aggressive invasions from outside males (Neville, 1972; Coelho et al., 1976; Rudran, 1979; Glander, 1980; Milton, 1980; Clarke, 1983; Thorington et al., 1984; Crockett and Eisenberg, 1987; Crockett and Pope, 1988; Pope, 1990, 1992; Clarke et al., 1994; DeGusta and Milton, 1998; Cristóbal-Azkarate et al., 2004). On the other hand, male *Ateles* are more affiliative and tolerant of each other, and competition for mates rarely results in aggressive confrontations (Klein and Klein, 1975; Fedigan and Baxter, 1984; van Roosmalen, 1985; White, 1986; van Roosmalen and Klein, 1988; Aureli et al., 2006; Aureli and Schaffner, 2007; Wallace, 2008; Slater et al., 2009; Gibson, 2010; but see Campbell, 2006; Valero, 2006).

These behavioral characterizations are supported by the fact that *Al. seniculus* is more dimorphic than *At. geoffroyi* in body mass (*Al. seniculus*, 1.28; *At. geoffroyi*, 1.07) and skull size (1.13; 1.01) (Table 2.4; see Smith and Jungers, 1997; see also Roseberger and Strier, 1989).[14] *Ateles geoffroyi* is significantly more dimorphic in canine height than *Al. seniculus* (1.46 versus 1.34; $p = 0.0265$), but this difference is largely a consequence of the fact that the females of the latter species have relatively taller canines than females of *At. geoffroyi* (see Table 4.5; $p < 0.001$, irrespective of the variable used to size-adjust canine height), which is consistent with reports that resident howler females aggressively exclude migrant females from joining their troop (Crockett, 1984; Crockett and Pope, 1988; Pope, 1992; Glander, 1992). In contrast, interfemale aggression appears to be rare and less intense in *At. geoffroyi* (Fedigan and Baxter, 1984; Symington, 1990; Slater et al., 2009). Thus, the lower level of canine dimorphism observed in *Al. seniculus* does not necessarily contradict the characterization of the males of this species as more sexually selected than the males of *At. geoffroyi*.

The pattern of differences in diet and social behavior in the two atelids, combined with the relatively short canines of male *Al. seniculus* (which is probably characteristic of the genus as a whole; Greenfield, 1992c), raises the possibility that the latter species (perhaps the entire genus) represents an example of natural selection for increased muscle leverage constraining or leading to a reduction in canine height despite the fact that the males of this species compete more intensely with each other than do male spider monkeys for access to mates. In some respects, the case is stronger for *Al. seniculus* than for *Macaca mulatta*

---

[14] The significance of the difference in body-mass dimorphism cannot be assessed, as Smith and Jungers (1997) presented only mean values for each sex. However, the difference in skull dimorphism is significant ($p < 0.001$; evaluated using the bootstrap).

and *Gorilla beringei* (discussed above) because intermale competition in this species can be characterized with a fair degree of confidence as more intense than that observed in *At. geoffroyi*, whereas the level of resolution provided by the primatological literature only allows the level of intermale competition within *Macaca* and within *Gorilla* to be described as similar. In the latter two cases, it is possible that differences in canine height may be influenced by subtle differences in sexual selection.

However, there is an alternative to the hypothesis that the canines of *Al. seniculus* are reduced or restricted from increasing in size because of selection for increased muscle leverage. Species of *Alouatta* have been described as “energy-minimizers” with respect to other atelids (Rosenberger and Strier, 1989; Rosenberger, 1992; Strier, 1992; see also Milton, 1980), meaning that, because howler monkeys subsist on a low-quality diet in comparison to *Ateles*, *Lagothrix*, and to a lesser extent *Brachyteles*, they limit their activities in order to conserve calories. For example, the primary mode of howler locomotion is slow, deliberate quadrupedalism, as opposed to the more active quadrupedalism and brachiation used by other atelids; howlers have smaller home ranges and shorter day ranges than other atelids; and a higher percentage of the howler daily activity budget is devoted to resting than is the case for other atelids (Milton, 1980; Rosenberger and Strier, 1989; Rosenberger, 1992; Strier, 1992). Using vocalizations as a means of defending resources (perhaps including access to mates; e.g., Sekulic, 1982b; Sekulic and Chivers, 1986; Chiarello, 1995; Kitchen, 2004; Delgado, 2006) rather than physical violence fits this adaptive profile. Thus, perhaps the enlarged vocal apparatus of *Alouatta* evolved as a way of minimizing energy output during agonistic encounters. The hypertrophy of the vocal apparatus, in turn, may have reduced gape, leading to a reduction in canine height and effectively "clearing the way" for selection for increased muscle leverage to modify the masticatory system for more efficient (i.e., energy-minimizing) bite-force production. Note that this hypothesis and the masticatory-efficiency hypothesis are not mutually exclusive—it may be that these two factors acted in concert. These hypotheses are testable given a fossil record that allows the timing of changes in the alouattine masticatory system and vocal apparatus to be established and linked with changes in canine height.

Genus Cebus *and subfamily Pitheciinae*

The two remaining platyrrhine comparisons do not fit the predictions of the masticatory-efficiency hypothesis: *Cebus libidinosus* has relatively taller canines and greater masseter and temporalis leverage than *Ceb. capucinus*, and *Chiropotes satanas* has greater masseter leverage than *Pithecia monachus*, despite the fact that these two species do not differ in relative canine height (Tables 4.23 and 4.24). Size-adjusting canine height using the face GM or mandibular length does not bring these comparisons in line with expectations.

Before speculating on why the inverse association between relative canine height and muscle leverage does not hold in these comparisons, it is important to note that the validity of the primary assumption of this analysis—that canine height is proportional to gape—has only been established for catarrhine primates (Hylander and Vinyard, 2006; Hylander, 2009). While there is no reason to

TABLE 4.23. Results of pairwise comparisons for Cebus

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Cebus capucinus*	<	*Cebus libidinosus*
Masseter leverage:			
at canine	*Cebus capucinus*	<	*Cebus libidinosus*
at M1	*Cebus capucinus*	<	*Cebus libidinosus*
at M3	*Cebus capucinus*	<	*Cebus libidinosus*
Temporalis leverage:			
at canine	*Cebus capucinus*	=	*Cebus libidinosus*
at M1	*Cebus capucinus*	<	*Cebus libidinosus*
at M3	*Cebus capucinus*	<	*Cebus libidinosus*
Relative TMJ height	*Cebus capucinus*	<	*Cebus libidinosus*
Masseter stretch factor	*Cebus capucinus*	>	*Cebus libidinosus*

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

TABLE 4.24. Results of pairwise comparisons for the Pitheciinae

Variable	Direction of difference and statistical significance[a]		
Relative canine height	*Pithecia monachus*	=	*Chiropotes satanas*
Masseter leverage:			
at canine	*Pithecia monachus*	<	*Chiropotes satanas*
at M1	*Pithecia monachus*	<	*Chiropotes satanas*
at M3	*Pithecia monachus*	<	*Chiropotes satanas*
Temporalis leverage:			
at canine	*Pithecia monachus*	=	*Chiropotes satanas*
at M1	*Pithecia monachus*	=	*Chiropotes satanas*
at M3	*Pithecia monachus*	>	*Chiropotes satanas*
Relative TMJ height	*Pithecia monachus*	<	*Chiropotes satanas*
Masseter stretch factor	*Pithecia monachus*	>	*Chiropotes satanas*

---

[a] Greater-than (>) and less-than (<) symbols indicate that comparison is statistically significant ($p < 0.05$) and the direction of the difference; equality symbol (=) indicates that species are not significantly different.

[b] Note that species with relatively small intertemporalis distances are inferred to have relatively large temporalis muscles.

expect platyrrhines as a group to deviate from this relationship, it is possible that the association is not as strong. For example, as discussed in Chapter 2, there appears to be little variation in relative canine height in the Callitrichinae, but tree-gouging species in this clade may use relatively wider gapes than those that do not gouge trees (Vinyard et al., 2001, 2003; Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009). In this case, no relationship between canine height and gape is expected. With respect to *Cebus* and the Pitheciinae, there are no observational data that would suggest a similar dissociation between canine height and gape, and thus in the discussion that follows, it is assumed that the relationship observed in catarrhines holds for these taxa as well.

As noted in Chapter 2 and Part II of this chapter, changing the positional relationships of the dentition and jaw adductors is not the only way to modify gape. There are three alternatives available to anthropoid primates, and *Ceb. libidinosus* and *Ch. satanas* may take advantage of one or more of these in order to achieve gapes that permit an adequate degree of canine clearance despite their increased muscle leverage. The first is to decrease the orthogonal distance between the TMJ and the occlusal plane, which will increase the vertical separation between the maxillary and mandibular canines at a given degree of mandibular depression (e.g., Herring, 1972; see Chapter 2, Fig. 2.3). However, neither *Ceb. libidinosus* nor *Ch. satanas* has a lower TMJ than its sister taxon; in fact, these two species have relatively *higher* TMJs than their sister taxa (Tables 4.23 and 4.24) and thus exhibit the gape-limiting condition.

The second way of increasing gape is to reposition the origin and insertion sites of the jaw adductors so as to reduce the extent to which the muscles are stretched at a given degree of mandibular depression—in other words, reduce the stretch factors of the masticatory muscles (Herring and Herring, 1974; Herring, 1975). This prediction is supported for the masseter: *Ceb. libidinosus* and *Ch. satanas* have significantly lower masseter stretch factors than *Ceb. capucinus* and *P. monachus*, respectively (Tables 4.23 and 4.24). These lower stretch factors will offset to some degree—and may completely negate—the gape-reducing effects of increased masseter leverage and relatively high TMJs in *Ceb. libidinosus* and *Ch. satanas*. Whether the stretch factor of the anterior temporalis exhibits a similar pattern of differences cannot be determined.

The third way in which gape can be increased is to modify internal muscle architecture: increasing the length of muscle fibers and/or decreasing their angle of pinnation will allow the jaw adductors to stretch to a greater degree. Such alterations have been observed in tree-gouging callitrichines in comparison to nongouging callitrichines (Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009; see Chapter 2). Whether *Ceb. libidinosus* and *Ch. satanas* exhibit such modifications cannot be determined using the data collected for this study. However, Taylor and Vinyard (2009) found that there is little variation in fiber length and pinnation angle in *Ceb. apella*, *Ceb. albifrons*, and *Ceb. capucinus*. The extent to which these results can be applied to the present *Cebus* comparison is not known, but at least two of the specimens included in Taylor and Vinyard's *Ceb. apella* sample are probably more appropriately assigned to *Ceb.*

libidinosus: these two specimens derive from wild individuals collected in Paraguay, which, according to Groves (2001), is within the range of *Ceb. libidinosus* and outside that of *Ceb. apella* sensu stricto. The geographical origins of the rest of the individuals in the sample were not discussed, except to note that they were captive animals. These data are not definitive, but they suggest that differences in muscle architecture do not contribute to differences in gape capability in the two species of *Cebus* examined here. It is possible, then, that *Ceb. libidinosus* achieves a gape that is commensurate with the height of its canines solely through a reduction in muscle stretch factor, but clearly more data are needed to test this hypothesis. Comparable muscle-architectural data are not available for the pitheciines.

The fact that the *Ceb. libidinosus* and *Ch. satanas* are morphologically differentiated from their sister taxa in similar ways suggests that their deviation from the predictions of the masticatory-efficiency hypothesis may be related to another feature they share in common—intensive use of the anterior dentition. As noted in Chapter 2, members of the *Cebus apella* species group, which includes *Ceb. libidinosus*, use their incisors, canines, and anterior postcanine teeth to process food items that are more mechanically demanding than those consumed by other species of the genus (Moynihan, 1976; Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Izawa, 1979; Freese and Oppenheimer, 1981; Terborgh, 1983; Janson and Boinski, 1992; Wright, 2005; Wright et al., 2009). Similarly, although all pitheciines use their anterior teeth to harvest seeds from fruits with highly resistant pericarps, the fruits processed by *Chiropotes* are much more puncture-resistant than those processed by *Pithecia* (Kinzey and Norconk, 1990, 1993; Kinzey, 1992). In contrast, species of *Pithecia* frequently crush harder seeds using their postcanine teeth than does *Chiropotes*, and they include a higher percentage of leaves in their diets (Buchannon et al., 1981; Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1981, 1988; Happel, 1982; Soini, 1986; Ayres, 1989; Kinzey and Norconk, 1990, 1993; Kinzey, 1992; Peres, 1993; Cunningham and Janson, 2006). Thus, both pitheciines generate high-magnitude bite forces during food processing, but *Chiropotes* generates its highest-magnitude forces when using its incisors and canines, whereas *Pithecia* does so when using its molars.

Previous ecomorphological studies indicate that members of the *Ceb. apella* species group and *Ch. satanas* differ from closely related species in ways expected based on the differences in diet described above, suggesting that natural selection has modified their masticatory systems to cope with the extremely hard food items they process using their anterior teeth (e.g., Kinzey, 1974; 1992; Rosenberger and Kinzey, 1976; Bouvier, 1986; Cole, 1992; Daegling, 1992; Anapol and Lee, 1994; Spencer, 1995, 2003; Wright, 2005; Taylor and Vinyard, 2009; Wright et al., 2009). Tall, robust canines and increased muscle leverage are thought to be critical components of this adaptation; if this inference is correct, then *Ceb. libidinosus* and *Ch. satanas* require increased muscle leverage without compromising gape. As discussed above, these species appear to have accomplished this objective, at least in part, by decreasing the degree to which the masseter stretches during mandibular depression.

The fact that masseter leverage can be increased without a concomitant reduction in canine height raises the question of why catarrhines and atelids exhibit a clear inverse relationship between these variables. In other words, if the leverage-reducing effects of having tall canines can be avoided through decreases in muscle stretch factor, then why are masseter stretch factor and relative canine height uncorrelated across the Anthropoidea? The answer to this question is not clear. However, as outlined below, the increased muscle leverage of *Ceb. libidinosus* and *Ch. satanas* is associated with another cost that may constrain the response of the masticatory system to increases in canine height in species that are not specialized for forceful anterior biting.

In comparison to their sister taxa, *Ceb. libidinosus* and *Ch. satanas* each increase muscle leverage by decreasing the distance between their dentition and jaw adductors. As noted in Part I (see Fig. 4.4), the difference in masseter leverage observed in the two pitheciines is a product of the relatively short bite-point moment arms of *Ch. satanas* ($p < 0.001$ for each bite point). The relative length of the masseter moment arm of *Ch. satanas* is greater, but this difference is slight and nonsignificant ($p = 0.3227$).[15] In the case of *Cebus*, *Ceb. libidinosus* has a relatively longer masseter moment arm ($p = 0.0343$) and a relatively shorter M3 moment arm ($p = 0.0478$) than *Ceb. capucinus*; the moment arms of the anterior temporalis, canine, and M1 also follow this pattern, but the comparisons

---

[15] Note that the moment arm of the anterior temporalis of *Ch. satanas* is relatively shorter ($p < 0.001$), which is why (1) the two pitheciines have similar (i.e., not significantly different) temporalis leverage at the canine and M1 and (2) *P. monachus* has greater temporalis leverage at M3.

are not statistically significant ($p > 0.10$ in each case). Thus, assuming that the masticatory systems of *Ch. satanas* and *Ceb. libidinosus* are derived relative to those of their sister taxa (see Spencer, 1995; Wright, 2005), the greater masseter leverage of *Ch. satanas* results primarily from a retraction of the dentition, whereas in *Ceb. libidinosus*, greater muscle leverage is a product of the fact that the dentition is slightly retracted and the muscles are slightly more anteriorly positioned.

According to the constrained lever model of masticatory-force production (discussed above in the context of the *Gorilla* comparison; see Greaves, 1978; Spencer and Demes, 1993; Spencer, 1995, 1998, 1999), the configurations exhibited by *Ceb. libidinosus* and *Ch. satanas* increase the likelihood that the resultant force produced by the jaw adductors will fall outside of the triangle of support or close to its edge (i.e., within the buffer zone hypothesized to exist by Spencer [1995, 1999]) when biting on the distal molars, resulting in tensile stresses at the TMJ that have the potential to pull the joint apart. Spencer (1995) argued that, in this situation, teeth that are too close to the muscle resultant force will show evidence of impaired function in the form of a reduction in crown size, indicating that they are loaded less forcefully than the more mesial teeth in order to protect the TMJ.

This prediction is supported for the *Cebus* and pitheciine comparisons: although the maxillary M3 is smaller than M1 and M2 in all four species, the ratio of M3 width to M1 width for *Ceb. libidinosus* and *Ch. satanas* is significantly lower than for *Ceb. capucinus* and *P. monachus*, respectively (for *Cebus*: 0.69

versus 0.79, $p = 0.002$; for the pitheciines: 0.80 versus 0.90, $p < 0.001$). In other words, *Ceb. libidinosus* and *Ch. satanas* have disproportionately smaller M3s in comparison to their sister taxa, suggesting that they experience a more rapid decrease in occlusal loads from M1 to M3 due to the proximity of their molar rows to their jaw adductors (see also Spencer, 2003; Wright, 2005).

No other species included in this study exhibits a level of M3 reduction similar to that observed in *Cebus* and the Pitheciinae. Atelids and catarrhines have M3/M1 ratios greater than 0.90, and in eighteen of these twenty-six species, M3 width is equal to or greater than M1 width (range: 0.91–1.26; median: 1.03). The lack of marked M3 reduction in these species is probably related to how they increase muscle leverage. In noncercopithecine anthropoids, such increases are primarily the product of increases in both the relative length of the masseter's moment arm and the relative length of each bite point's moment arm (see Fig. 4.4 and Table 4.7; see also the *Gorilla* and atelid comparisons). The anterior temporalis is characterized by a similar pattern of relationships (results not shown). Thus, instead of reducing the distance between the dentition and jaw adductors—as in *Cebus* and the Pitheciinae—atelids, hominoids, and colobines tend to increase muscle leverage by moving the dentition and jaw adductors forward. This configuration will simultaneously protect the TMJ and preserve the functionality of the distal molars (Spencer and Demes, 1993; Spencer, 1995).

In cercopithecines, on the other hand, differences in muscle leverage are unrelated to the relative lengths of the muscle moment arms; rather, changes in muscle leverage are effected primarily through changes in the anteroposterior position of the dentition. Thus, cercopithecines with greater muscle leverage have more posteriorly positioned dentitions in comparison to those with lower muscle leverage. However, there is no evidence of compromised M3 function in these species; in fact, relative to M1 width, cercopithecines have the widest M3s in the data set (range: 0.99–1.26; median: 1.11). As argued above, the relatively tall canines of cercopithecines—and the wide gapes they presumably require—probably result in greater separation between the muscle resultant force and molars rows in these species, which means that they can increase muscle leverage by retracting the dentition to some degree without compromising the TMJ or M3 function. The prevalence of retraction within the Cercopithecinae is not known, but it is probably true that protraction is a more common occurrence. In other words, it is likely that, in many cercopithecine lineages, species with posteriorly positioned teeth and greater muscle leverage represent the plesiomorphic condition. However, retraction has probably occurred, and some of the species included in this analysis may represent instances of this phenomenon (e.g., *Macaca mulatta*, *Cercopithecus pogonias*).

Thus, increases in muscle leverage are associated with compromised M3 function in *Cebus* and the Pitheciinae but not in the other anthropoid clades examined in this study, suggesting that there is a cost to increasing leverage while simultaneously maintaining or increasing gape capability. Given that *Ceb. libidinosus* and *Ch. satanas* process very hard, tough objects using their anterior teeth, increasing muscle leverage by moving both the dentition and masticatory muscles anteriorly may not be an option due to the very high sagittal bending moments such a configurational change would engender. Thus, in these species, the ability to generate and resist high-magnitude forces at the anterior end of the dental arcade has been emphasized at the expense of M3 function.

With respect to other anthropoids, it should be possible, at least in principle, to increase muscle leverage by moving both the dentition and jaw adductors forward while decreasing stretch factor, thus maintaining or increasing gape without compromising the TMJ or M3 function. As discussed in Chapter 2, stretch factor can be broken down into two components—the origin-insertion ratio (OI ratio) and the origin-insertion angle (OI angle) (Herring and Herring, 1974). Recall that the OI ratio is the distance between the TMJ and the point that represents the muscle's origin site (the origin length) divided by the distance between the TMJ and the point that represents the muscle's insertion site (the insertion length) (see Fig. 2.4); the OI angle is simply the angle between the origin length and the insertion length. Stretch factor can be decreased in two ways. First, the disparity between the origin length and the insertion length can increased by lengthening one, shortening one, or lengthening one and shortening the other. Thus, a value of 1.0 (i.e., unity) is the least favorable OI ratio for gape, and increasing or decreasing the ratio will reduce muscle stretch. Importantly, if the OI ratio is moved further from unity by increasing one of the distances, the moment arm of the muscle will be increased (Herring and Herring, 1974). The other way to decrease stretch factor is to increase the OI angle. However, this modification will result in a decrease in the muscle's moment arm (Herring and Herring, 1974).

As shown in Figure 4.21, variation in masseter stretch factor among the Anthropoidea is driven almost entirely by variation in the OI angle; these two variables are nearly perfectly correlated and the correlation is negative ($r = -0.98$), as expected. In contrast, the OI ratio contributes little to decreases in masseter stretch factor; the correlation between these two variables is weak and nonsignificant ($r = 0.33$; note also that this correlation is in the opposite of the predicted direction).[16] Consequently, decreases in masseter stretch factor, in the absence of other changes, will tend to be associated with decreases in masseter leverage among anthropoid primates. Given this relationship, it may be that a simultaneous increase in masseter leverage and decrease in masseter stretch factor cannot be achieved without retracting the dentition and/or moving the muscle anteriorly, as in *Ceb. libidinosus* and *Ch. satanas*. If this hypothesis is correct, then none of the species included in this study should exhibit the following combination of features in comparison to its sister taxon: (1) decreased masseter stretch factor, (2) increased masseter leverage, (3) relatively long bite-point moment arms, and (4) relatively long masseter moment arm.

As shown in Table 4.25, this prediction is supported: greater masseter leverage in species with low masseter stretch factors is never associated with a more anteriorly positioned molar row or a relatively long masseter moment arm. Note also that in only four of the twelve catarrhine comparisons do the constituent

---

[16] Because masseter stretch factor should decrease as the ratio moves away from unity, the correlation coefficient was computed using the absolute deviation of each species' ratio from 1.0.

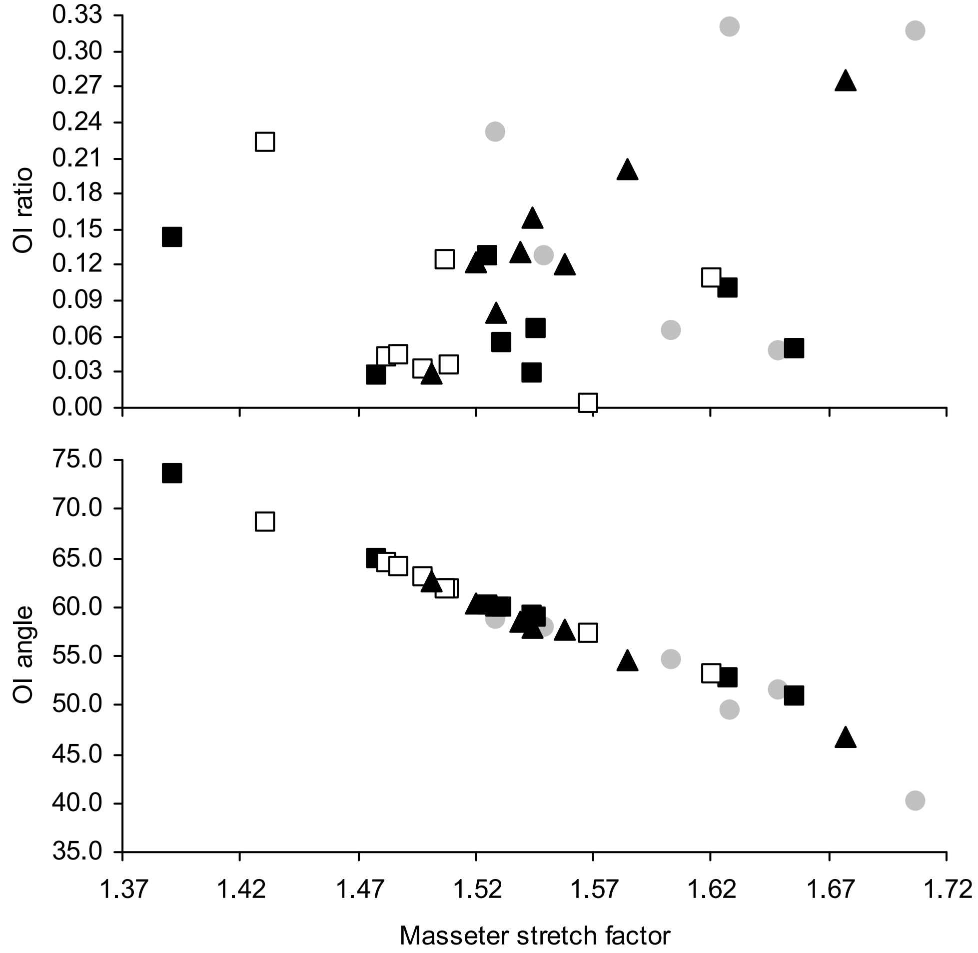


Fig. 4.21. Relationship between masseter stretch factor and the origin-insertion ratio (top) and origin-insertion angle (bottom). Each species' origin-insertion ratio is expressed as the absolute deviation of the ratio from 1.0, as masseter stretch factor is expected to decrease as the ratio moves away from unity in both directions (i.e., <1.0 and >1.0). Symbols are as follows: black squares = cercopithecines; white squares = colobines; black triangles = hominoids; gray circles = platyrrhines.

TABLE 4.25. Pattern of variation in masseter stretch factor, masseter leverage, and the relative lengths of the masseter and bite-point moment arms

	Species with lower masseter stretch factor has:		
Comparison	Greater leverage[a]	Anterior dentition[b]	Anterior masseter[c]
Atelidae	No	No	No
Cebus	Yes	No	Yes
Pitheciinae	Yes	No	No
Cercopithecus	—	—	—
Chlorocebus-Erythrocebus	—	—	—
Macaca	—	—	—
Theropithecus-Mandrillus	Yes	No	No
Piliocolobus-Procolobus	No	No	No
Colobus	—	—	—
Presbytis	No	Yes	Yes
Trachypithecus	—	—	—
Hylobates	No	Yes	Yes
Gorilla	—	—	—
Pan	—	—	—
Pongo	—	—	—

[a] "Yes" indicates that the species in the comparison with the lower masseter stretch factor has significantly ($p < 0.05$) greater masseter leverage than its sister taxon at two out of three bite points (minimally). "No" indicates that the latter criterion is not met. A dash indicates that the two species do not differ in masseter stretch factor ($p > 0.05$).

[b] "Yes" indicates that the relative lengths of at least two out of the three bite-point moment arms of the species in the comparison with the lower masseter stretch factor are significantly ($p < 0.05$) greater than those of its sister taxa (i.e., the former species' dentition is relatively more anteriorly positioned). "No" indicates that the latter criterion is not met. A dash indicates that the two species do not differ in masseter stretch factor ($p > 0.05$).

[c] "Yes" indicates that the relative length of the masseter moment arm of the species in the comparison with the lower masseter stretch factor is significantly ($p < 0.05$) greater than that of its sister taxa (i.e., the former species' masseter is more anteriorly positioned). "No" indicates that the latter criterion is not met. A dash indicates that the two species do not differ in masseter stretch factor ($p > 0.05$).

species differ from each other in masseter stretch factor. *Theropithecus gelada* is the only catarrhine in the sample with a lower masseter stretch factor and greater masseter leverage than its sister taxon (*Mandrillus leucophaeus*); the greater masseter leverage of this species is a product of its more posteriorly positioned dentition. In two of the other catarrhine comparisons (*Presbytis* and *Hylobates*), the species with the lower masseter stretch factor has a more anteriorly positioned dentition and a relatively longer masseter moment arm than its sister taxon, but these differences do not translate into increased masseter leverage. Moreover, in neither of the latter two comparisons do the constituent species differ in relative canine height.

Thus, the scenario outlined above suggests that, within the Anthropoidea, the bony masticatory system responds to increases in canine height in two distinct ways and that this distinction is related to diet. First, in species in which maintenance of M3 function is selectively important (e.g., species that rely on relatively large amounts of foliage), increases in canine height are associated with decreases in masseter leverage. The latter modification appears to render decreases in masseter stretch factor unnecessary for increasing gape. The second response is observed in species in which forceful anterior biting is adaptively important. These species increase masseter leverage by decreasing the distance between the jaw adductors and molar row, probably to reduce the magnitude of the sagittal bending moments in the face. However, this configuration impairs M3 function. In these species, wide gapes are achieved, at least in part, by decreases in masseter (and perhaps temporalis) stretch factor. It is important to emphasize that this scenario is highly speculative. The dearth of anthropoid species that specialize on processing hard objects using their anterior teeth makes the hypothesis difficult to test, but one option is to examine the durophagous mangabeys (*Cercocebus* and *Lophocebus*), which are thought to differ from each other in terms of which component of the dentition (i.e., anterior versus postcanine) is used more frequently when processing hard food items (e.g., Singleton, 2004; Daegling and McGraw, 2007).

DISCUSSION

Canine height and the configuration of the bony masticatory system

The results of this study provide some support for the hypothesis that there is a trade-off between canine height and the leverage of the jaw adductors in anthropoid primates (Hylander and Vinyard, 2006; Hylander, 2009). There is a clear inverse relationship between relative canine height and masseter leverage at all bite points in male anthropoids, and the association is particularly strong in male catarrhines. On the other hand, anterior temporalis leverage does not appear to be related to relative canine height in males, and neither muscle exhibits a particularly strong association with relative canine height in females: the correlations involving these variables are weak and for the most part nonsignificant when phylogeny is controlled, though they are in the predicted direction (i.e., negative).

The disparity between males and females in the masseter results can be attributed to a general lack of shape dimorphism in the configuration of the anthropoid masticatory system. Despite marked intersexual differences in canine height in most of the species included in this study, females do not consistently have significantly greater muscle leverage at the canine than males. These results indicate that female skull form tracks male skull form, which is linked to canine height. This relationship is best illustrated by the surprisingly low masseter leverage observed in the females of *Erythrocebus patas*, *Mandrillus leucophaeus*, and *Theropithecus gelada*. In these species, female relative canine height is unexceptional, but the canines of males are among the tallest relative to skull size in the data set. Thus, it appears that when male skull form responds to changes in canine height, female skull form experiences a correlated response (sensu Lande, 1980; see also Plavcan, 1998). The very strong intersexual genetic correlations ($\rho_G \approx 1.0$) in skull dimensions found in a captive population of *Papio* baboons support this idea (Willmore et al., 2009). The converse may also be true—i.e., intense selection on females to increase muscle leverage (due to reproductive costs) may influence canine height and skull form in males.

Females do tend to have greater muscle leverage than males at the more distal bite points, but this leverage dimorphism is, for the most part, slight (and in most cases nonsignificant) and appears to be related to the fact that females have relatively larger postcanine teeth, which "pushes" the molars more posteriorly in relation to the canines, shortening their moment arms (see Fig. 4.12). Intersexual differences in relative postcanine size are probably a by-product of the pattern of low dimorphism in postcanine size and moderate to high dimorphism in body mass and skull size observed in many anthropoids (Cochard, 1987). Thus, intersexual differences in muscle leverage at postcanine bite points can also be considered a by-product of the latter pattern of dimorphism rather than an adaptive response to a reduction in leverage induced by an increase in male canine height. If the relatively large postcanine teeth of females were a product of natural selection for increased muscle leverage, then males should also exhibit an increase in relative postcanine size to compensate for their decreased leverage.

The absence of significant correlations involving the anterior temporalis in males is difficult to explain. As suggested above, the anterior temporalis may not constrain gape to the same extent as does the masseter, or this muscle may adjust to gape requirements primarily through modifications in its internal architecture. The few studies that have examined muscle anatomy in primates indicate that the temporalis tends to have longer fibers than the masseter, particularly in species with relatively tall canines (Bouvier and Tsang, 1990; Eng et al., 2009; Taylor et al., 2009; Taylor and Vinyard, 2009; Vinyard and Taylor, 2010). For example, according to data presented by Vinyard and Taylor (2010), the masseter fibers of *Aotus*, *Cebus*, and *Macaca* are similar in length—11.08 mm, 11.56 mm, and 11.95 mm, respectively (see also Antón, 1999, 2000)—but the temporalis fibers increase in length markedly from *Aotus* (9.98 mm; 10% shorter than the masseter fibers) to *Cebus* (14.29 mm; 24% longer than the masseter fibers) to *Macaca* (17.36 mm; 45% longer than the masseter fibers), paralleling differences in relative canine height among these genera. For *Papio*, the males of which fall at the upper extreme of the anthropoid range of variation in absolute and relative canine height, the temporalis fibers are nearly 140% longer than the masseter fibers (45.64 mm versus 19.21 mm) (Vinyard and Taylor, 2010). These data are far from conclusive, but they suggest that the internal architecture of the masseter is less sensitive (but not insensitive; see Taylor and Vinyard, 2004; Taylor et al., 2009) to changes in canine height and gape than is the internal architecture of the temporalis. It is not clear why the masseter and temporalis respond differently to changes in canine height and gape.

There is also evidence that some factor other than canine height constrains the position of the anterior temporalis. The existence of such a constraint is suggested by the pattern of differences in muscle leverage observed in *Gorilla*; in this comparison, the species with shorter canines (*G. beringei*) has greater masseter leverage, as predicted by the masticatory-efficiency hypothesis, but the species with taller canines (*G. gorilla*) has greater anterior temporalis leverage. One obvious possibility, discussed above, is the position of the orbit, which bounds the origin of the temporalis anteriorly and probably limits the anterior migration of the mandibular coronoid process (the muscle's insertion site). The position of the orbit is subject to a variety of influences (e.g., Moss and Young, 1960; Shea, 1985; Ravosa, 1991; Ross and Ravosa, 1993; Ross, 1995b; Lieberman et al., 2000), and these may constrain the effects of selection for increased masticatory efficiency. The length of the masseter's moment arm, on the other hand, is probably less influenced by orbit position because this muscle's insertion site—the inferior portion of the mandible's ascending ramus—is structurally and spatially independent of the orbit; masseter leverage can be increased by extending the ramus inferiorly or by increasing the height of the TMJ above the occlusal plane. Moreover, although the masseter's origin site is connected to the bony orbit, this link does not appear to impose a rigid constraint on the anterior position of this muscle, as demonstrated by species such as *Australopithecus boisei* and *Theropithecus brumpti*, in which the infraorbital surface, along with the anteriormost attachment site for the masseter, slopes anteroinferiorly away from the orbital margin, creating a visorlike structure (Rak, 1983; Jablonski, 1993; Kimbel et al., 2004).

It is also possible that the pattern of results derived from the temporalis data are, to some degree, a methodological artifact of the measure of anterior temporalis moment-arm length used here. This measurement—the distance between the mandibular condyle and tip of the coronoid process—can only be considered a very rough estimate of moment-arm length, as it omits information regarding the muscle's line of action, which is difficult to determine due to the fact that the posterior border of the origin of the anterior temporalis cannot be distinguished from that of the more posterior components of the muscle using bony morphology (for more discussion, see Chapter 2 and Spencer, 1995). Addressing this issue, and those raised above, will require a detailed study of the anatomy of the anterior temporalis and its attachment sites in a broad sample of anthropoid species.

The other features that affect gape do not respond to changes in canine height in a consistent way across the Anthropoidea. Relative jaw length is positively correlated with relative canine height in male cercopithecines (see also Ravosa, 1990), but in other anthropoids, these variables do not covary; in fact, outside of cercopithecines, the species with the longest jaws relative to skull size fall at the lower end of the range of variation in relative male canine height (e.g., *Alouatta seniculus*, *Gorilla beringei*, and *Pongo pygmaeus*). The relative height of the TMJ above the occlusal plane and the H/L ratio are not correlated with relative canine height in any group of anthropoids, but these variables do exhibit an inverse relationship with Lucas's (1981) canine-clearance angle (males only; Lucas, 1981; Lucas et al., 1986). This pattern of results indicates that relative TMJ height and the H/L ratio are related to gape requirements in some way (cf. Vinyard et al., 2003), but raising the TMJ above the occlusal plane does not appear to necessitate a reduction in canine height. Masseter stretch factor is also uncorrelated with relative canine height (and canine-clearance angle), but it may play an important role in facilitating wide gapes in species that frequently use their anterior teeth to process hard, tough objects (e.g., *Cebus libidinosus* and *Chiropotes satanas*).

With respect to intersexual differences in gape-related features, the results are mixed. Males tend to have relatively longer mandibles and lower masseter stretch factors than females, as predicted, but these differences are not consistently statistically significant. Moreover, the lack of intersexual differences in muscle leverage indicates that increases in jaw length in males are accompanied by increases in muscle moment-arm lengths, which will offset increases in gape achieved by lengthening the jaws. Intersexual differences in relative TMJ height and the H/L ratio tend to be in the opposite of the predicted direction (i.e., males tend to have TMJs that are higher above the occlusal plane), but the number of species for which this characterization is statistically significant is low. This pattern of results and the overall lack of sexual dimorphism in muscle leverage indicate that, in general, the skull of male anthropoids is not configured to produce relatively wider gapes than that of female anthropoids, which implies that males achieve their wider gapes primarily through alterations in muscle anatomy (i.e., fiber length and pinnation; Hylander and Vinyard, 2006; Hylander, 2009).

The interplay between canine height and diet

The inverse relationship between canine height and masseter leverage documented in this study indicates that the anthropoid masticatory system partly reflects a compromise between the opposing influences of sexual selection for weaponized canines and selection pressures imposed by the mechanical properties of a species' diet. Thus, when sexual selection is sufficiently strong, it will interfere with a species' adaptive response to diet-related selection and obscure the relationship between skull form and diet. Conversely, when selection for increased bite force is stronger than sexual selection, it will constrain or reduce canine height. In extreme cases (perhaps early hominins; Hylander and Vinyard, 2006), selection for masticatory efficiency may be strong enough to overwhelm sexual selection even when intermale competition is moderate or high in intensity, resulting in species in which males have shorter canines than expected based on their social behavior.

The breakdown in the relationship between skull form and diet due to variation in canine height appears to characterize four of the pairwise comparisons discussed in Part III of this chapter: the Cercopithecini, the

Papionina, *Trachypithecus*, and *Pan*. The species within each of these comparisons are broadly similar in terms of the mechanical demands of their diets and thus are not expected, based on the latter criterion, to differ from each other with respect to the mechanical advantage of the masticatory muscles. However, masseter leverage and, to a lesser extent, temporalis leverage do vary within each comparison, and this variation tracks differences in relative canine height; regardless of diet, species with relatively short canines have greater muscle leverage.

Spencer (1995) obtained a similar pattern of results in his analysis of the papionin masticatory system. He initially hypothesized that the skulls of *Papio anubis* and *Theropithecus gelada* would exhibit modifications that increase the mechanical advantage of the jaw adductors in comparison to the skull of *Macaca fascicularis* due to the fact that the former two species include higher percentages of tough, fibrous foods in their diets than does the latter. Instead, the opposite pattern was observed: *M. fascicularis* consistently had greater muscle leverage than *P. anubis* and tended to have greater muscle leverage than *T. gelada*. Spencer (1995) linked these results to the tall canines of *P. anubis* and *T. gelada*, concluding that selection for wide gape had had a particularly strong influence on the evolutionary histories of the masticatory systems of these two species.

Because a reduction in muscle leverage will result in a decrease in maximum bite-force magnitude, species with relatively tall canines should exhibit compensatory increases in the force-producing potential of their jaw adductors, unless the increase in canine height is accompanied by a shift to a less mechanically demanding diet. This prediction is supported: the cercopithecin, papioninan, *Trachypithecus*, and *Pan* comparisons are each characterized by a positive association between relative canine height and the force-producing potential of the masticatory muscles. Notably, in three of these four comparisons, the species with the tallest canines relative to skull size is also the largest species in the comparison (i.e., *Erythrocebus patas* versus other cercopithecins, *Trachypithecus shortridgei* versus *T. obscurus*, and *Pan troglodytes* versus *P. paniscus*). Spencer (1995) similarly argued that *P. anubis* and *T. gelada* are able to process harder and tougher food items than *M. fascicularis* primarily by virtue of their much larger body size—and therefore larger masticatory musculature—in comparison to the latter species. These observations suggest that larger-bodied species may be able to "tolerate" the decreases in muscle leverage that accompany increases in canine height to a greater degree than smaller-bodied species because of their greater force-producing potential. The positive allometric relationship between canine height and skull size observed in male anthropoids (see Chapter 3, Table 3.12) is consistent with this hypothesis. It is important to note, however, that the validity of this argument rests upon the demonstration that increases in body size preceded increases in canine height. In any case, the positive association between relative canine height and the force-producing potential of the jaw adductors in these comparisons suggests that canine-related reductions in muscle leverage do have a selectively significant impact on the performance of the masticatory system and that the decreases in bite-force magnitudes that they engender must be counterbalanced by modifications to other components of the masticatory system.

The relative strengths of sexual selection for weaponized canines and natural selection for increased muscle leverage cannot be estimated for any of the species included in this study using currently available data, but it is probably true that sexual selection tends to be the more influential of two processes, particularly in species characterized by intense intermale competition. Identifying cases in which selection for increased muscle leverage has overwhelmed sexual selection, thus constraining canine height or leading to canine reduction in the face of strong sexual selection, as may have occurred in early hominins, is difficult, but three of the comparisons examined in Part III—*Macaca*, *Gorilla*, and the Atelidae—may represent examples of this phenomenon. It is important to emphasize, however, that more data are needed in order to corroborate some of the inferences made regarding these comparisons. First, and perhaps most importantly, accurate, high-resolution estimates of sexual selection are needed to verify that the species with relatively short canines in these comparisons are truly at least as sexually selected as their taller-canined sister taxa. Second, and relatedly, detailed analyses of male combat tactics are needed to determine whether (1) dietary demands have, in fact, overwhelmed sexual selection acting on canine height or (2) sexual selection on canine height has been relaxed due to a shift in how males compete with each other, allowing the effects of selection for increased muscle leverage to play a more prominent role in shaping the masticatory system. Third, data on the material properties of the foods these species consume are needed to bolster the characterization of dietary differences in each comparison. Finally, the polarity of canine height in each comparison needs to be established in order to determine the vector of evolutionary change; in other words, instances of canine reduction need to be distinguished from instances in which canine height has been constrained from increasing by selection for increased muscle leverage. This issue is particularly critical if the species in these comparisons are to be used as models for canine evolution in early hominins. A definitive determination of polarity for each clade will ultimately come from the fossil record, but in some of these cases it may be possible to make reliable inferences using character distributions in extant taxa.

It is important to note that not all anthropoids are subject to the trade-off between canine height and muscle leverage. Two of the pairwise comparisons examined in Part III—*Cebus* and the Pitheciinae—demonstrate that it is possible to increase leverage without a concomitant decrease in canine height. It was hypothesized above that the deviation of these two comparisons from the predictions of the masticatory-efficiency hypothesis is related to intensive use of the anterior dentition. This argument can be summarized as follows. Species that are specialized for processing hard, tough food items using their anterior teeth—such as *Cebus libidinosus* and *Chiropotes satanas*—have relatively tall canines and increased muscle leverage. These species overcome the gape-reducing effects of their increased muscle leverage, at least in part, by decreasing masseter stretch factor. Gape may be further enhanced through decreases in temporalis stretch factor and changes in internal muscle architecture, but the data collected for this study cannot confirm or refute these suggestions.

The morphological pattern described above is associated with disproportionately small M3s. According to Spencer and Demes (1993), Spencer (1995, 1999, 2003), and Wright (2005), marked M3 reduction is a response to the way in which these species increase muscle leverage—i.e., by decreasing the distance between the dentition and the jaw adductors. This configuration increases the likelihood that loads applied to the distal molar will produce injurious tensile stresses in the working-side TMJ (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1995, 1998, 1999, 2003; Wright, 2005). The TMJ can be protected by reducing M3 size, which limits the magnitude of the forces that can be applied to this tooth. Thus, in *Ceb. libidinosus* and *Ch. satanas*, the combination of relatively tall canines and increased muscle leverage is accompanied by a reduction in the functional area of the molar row. In other words, these species appear to trade one cost for another.

In contrast, the other species included in this study do not exhibit the marked degree of M3 reduction that characterizes *Ceb. libidinosus* and *Ch. satanas*. In these species, increases in muscle leverage are achieved while maintaining a safe distance between the TMJ and the molar row. For example, atelids, colobines, and hominoids tend to increase muscle leverage by moving both the dentition and the jaw adductors anteriorly. Thus, the TMJ is protected without compromising M3 function, which may have important fitness consequences in species that rely heavily on the molar teeth to process large quantities of tough, low-quality foods such as leaves (e.g., Logan and Sanson, 2002; King et al., 2005). As argued above, this option may not be available to species that frequently process hard objects using their anterior teeth because it would compromise the facial skeleton's ability to resist the high-magnitude bite forces that these species generate on their incisors and canines.

It was also argued that species that are not specialized for forceful anterior biting cannot increase masseter leverage and gape simultaneously by decreasing masseter stretch. Because the latter variable is decreased primarily by increasing the origin-insertion angle, which, in the absence of other changes, reduces the length of the masseter's moment arm, it appears that a concurrent increase in masseter leverage and decrease in masseter stretch factor requires that the dentition be retracted or that the jaw adductors be moved forward without an accompanying anterior repositioning of the dentition, which would compromise M3 function in some species. Moreover, the fact that variation in masseter stretch factor is driven by changes in the origin-insertion angle suggests that reductions in masseter leverage and decreases in masseter stretch factor are redundant in terms of increasing gape, which may explain why stretch factor is uncorrelated with relative canine height among the Anthropoidea.

A test of the masticatory-efficiency hypothesis using the hominin fossil record

As discussed in the introduction to this dissertation, the results of this study cannot answer the question of why early hominins have reduced canines. The fact that the masticatory-efficiency hypothesis receives support among living taxa means that it is a viable explanation for canine reduction in early hominins, but linking selection for increased muscle leverage to this hallmark feature of the hominin clade will require (1) a fossil record that allows the timing of changes in canine size, skull form, and sexual dimorphism in canine size and body size (as inferred from skeletal size) to be established, (2) accurate reconstructions of the evolution of early hominin feeding ecology, and (3) a better understanding of how primate males compete with each other for access to mates and the morphological consequences of such behaviors. However, the currently available fossil record has the potential to falsify the masticatory-efficiency hypothesis; specifically, rejection of the hypothesis would be warranted if it could be shown that masseter leverage in Miocene and Pliocene hominin specimens recovered to date was no greater than that in African apes. Note that no prediction regarding temporalis leverage can be made, given the lack of relationship between the latter variable and relative canine height in extant anthropoids.

One of the major impediments to testing the masticatory-efficiency hypothesis using fossil hominin material is the dearth of sufficiently complete skulls from which estimates of muscle and bite-point moment-arm lengths can be obtained. There are only two hominin specimens older than four million years whose preservation allows evaluation of the positional relationships of the dentition and jaw adductors. The first is the 6–7-million-year-old TM 266-01-60-1 partial cranium from Chad, assigned to *Sahelanthropus tchadensis* (Brunet et al., 2002; Guy et al., 2005; Zollikofer et al., 2005), and the second is the 4.4-million-year-old ARA-VP-6/500 partial skull from the Middle Awash, Ethiopia, assigned to *Ardipithecus ramidus* (Suwa et al., 2009a). However, reconstructions of these specimens are not yet widely available for study, and the *Sahelanthropus* specimen lacks a mandible, which precludes measurement of muscle moment-arm lengths (but not muscle positions).[17]

Two specimens that permit estimation of muscle and bite-point moment-arm lengths are the approximately three-million-year-old A.L. 444-2 and A.L. 822-1 partial skulls from Hadar, Ethiopia, assigned to *Australopithecus afarensis* (Kimbel et al., 1994, 2003, 2004; Kimbel and Rak, 2010). Of the two skulls, A.L. 822-1 is more complete in terms of the anatomy relevant to the present context: the origin and insertion sites of the masseter are preserved, and only the tip of the coronoid process (temporalis insertion) is missing; the latter element has been reconstructed (Kimbel and Rak, 2010). With respect to A.L. 444-2, the insertion site of the superficial masseter is very distinct in this specimen; Kimbel et al. (2004, p. 184) described it as "a well-defined platform" that is "set apart from the surrounding bone surface by a very prominent liplike rim." On the other hand, the ascending ramus of this specimen's mandible was not recovered, and therefore the insertion sites of the jaw adductors are not represented. However, the overall morphology of the ascending ramus is constrained somewhat by the surrounding anatomy (i.e., the mandibular corpus and temporal bone); Kimbel et al. (2004, p. 20) described the reconstruction of this element as follows:

---

[17] Note also that the hominin status of the species represented by these specimens has been questioned (Wolpoff et al., 2002, 2006; Sarmiento, 2010; for responses, see Brunet, 2002; White et al., 2010).

> The final stage of the reconstruction process entailed the mirror-image flipping of the … right mandible corpus to the left side through computerized tomography and stereolithography (Zollikofer et al., 1995). The left and right mandibular tooth rows were occluded with those of the deformed maxilla; in this orientation the mandible segments were joined … With the now bilaterally complete and occluded dental arches as a guide, ascending rami were carved of plaster following the contours of *A. afarensis* specimen A.L. 333-108 (White and Johanson, 1982; Kimbel et al., 1984).

Thus, masseter and temporalis moment-arm lengths can be estimated for A.L. 444-2, but these measurements are less reliable than those for A.L. 822-1.

Both of the reconstructed *Au. afarensis* skulls are characterized by some degree of distortion that precludes the use of the digitizing protocol for measuring moment-arm lengths described in Chapter 2. Recall that this procedure uses the sagittal and occlusal planes to derive the lengths of the muscle and bite-point moment arms, respectively; the deformation that is present in these reconstructions renders the delineation of these planes difficult.[18] Instead, an analogous two-dimensional procedure was used. Lateral digital photographs of the least distorted side of each reconstructed skull (right side in both cases; provided by W. Kimbel) were imported into the program ImageJ (Abramoff et al., 2004), and the same landmarks employed in the three-dimensional procedure were identified on these images with the aid of high-quality research casts (refer to Table 2.2 and Figs. 2.1): the lateralmost point on the mandibular condyle (landmark 1), the tip of the coronoid process (landmark 6), the approximate

---

[18] See Kimbel et al. (2004) for a detailed description of deformation in A.L. 444-2 and the steps taken to minimize its effect on the final reconstruction of this specimen. A preliminary account of deformation in A.L. 822-1 is provided by Kimbel and Rak (2010).

centers of the masseter's origin and insertion sites (landmarks 7 and 8, respectively), and the canine and M1 bite points (landmarks 11 and 13, respectively). In this procedure, the sagittal plane is simply the plane of the photograph, and the occlusal plane is represented by a straight line connecting the tip of the mesiobuccal cusp of maxillary M3 and the tip of the buccal cusp of maxillary P3 (or its approximate position in A.L. 444-2). Moment-arm lengths were measured as shown in Figure 2.2.

The leverage values for A.L. 444-2 and A.L. 822-1 are plotted along with those for the African apes and orangutans in Figures 4.22 and 4.23. Note that both *Au. afarensis* specimens fall at or beyond the upper end of the ape ranges of variation in masseter leverage at the canine and M1, which is consistent with the predictions of the masticatory-efficiency hypothesis. In contrast, the hominin values for temporalis leverage at the canine and M1 fall well within the ape ranges of variation, which is not surprising (see above). The most notable distinction evident in Figure 4.23 is between gorillas and all other hominids, with the former having lower temporalis leverage than the latter. The low temporalis leverage of *G. beringei* relative to *G. gorilla* has already been discussed; the data presented in Figure 4.23 suggest that *G. beringei* is an extreme expression of a trend that characterizes the genus as a whole (see also Taylor, 2002).

The extent to which A.L. 444-2 and A.L. 822-1 represent the central tendency of the population from which they derive is not clear, but the data presented above suggest that selection for increased masseter leverage had modified the early hominin masticatory system by at least 3.1 million years ago.

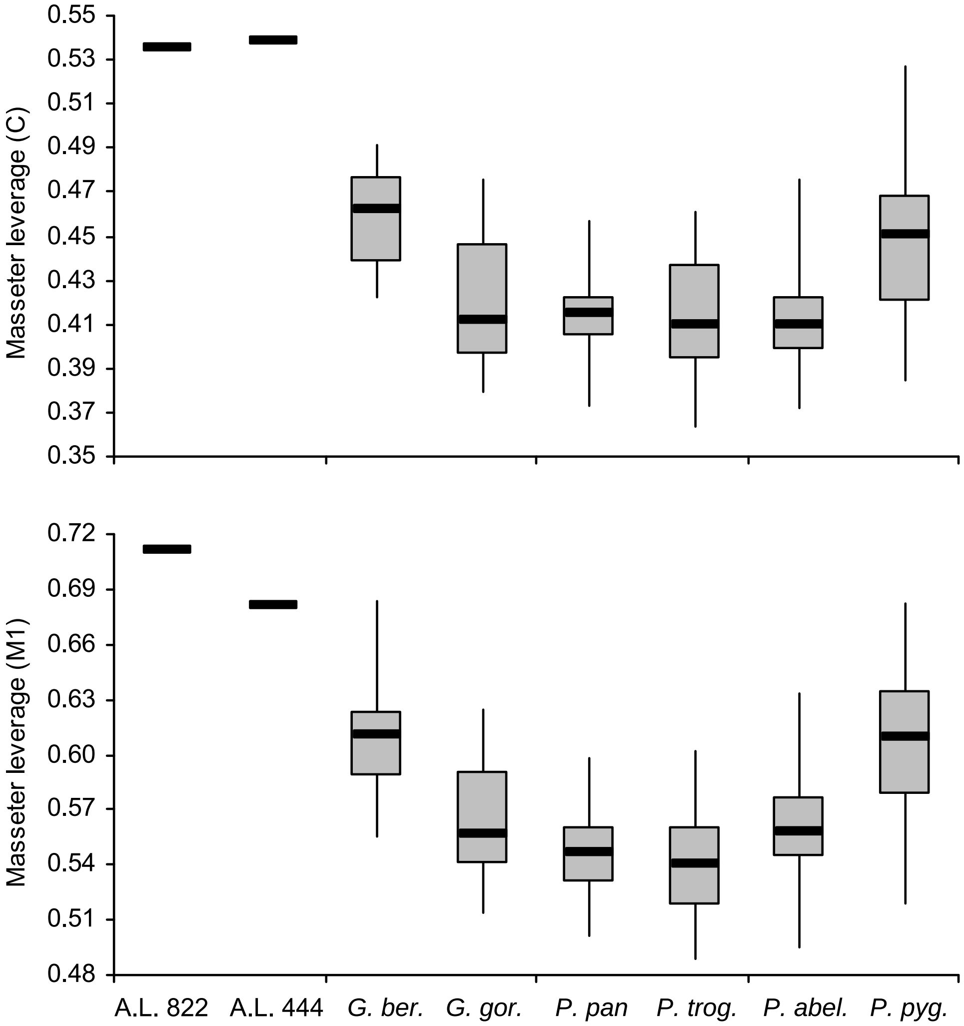


Fig. 4.22. Masseter leverage at the canine (top) and M1 (bottom) in great apes and two partial skulls of *Australopithecus afarensis* (A.L. 822-1 and A.L. 444-2). Abbreviations are as follows: *G. ber.* = *Gorilla beringei*; *G. gor.* = *Gorilla gorilla*; *P. pan.* = *Pan paniscus*; *P. trog.* = *Pan troglodytes*; *P. abel.* = *Pongo abelii*; *P. pyg.* = *Pongo pygmaeus*. For the great apes, the horizontal bars represent the sample medians, the gray boxes represent the interquartile ranges, and the vertical lines represent the sample ranges.

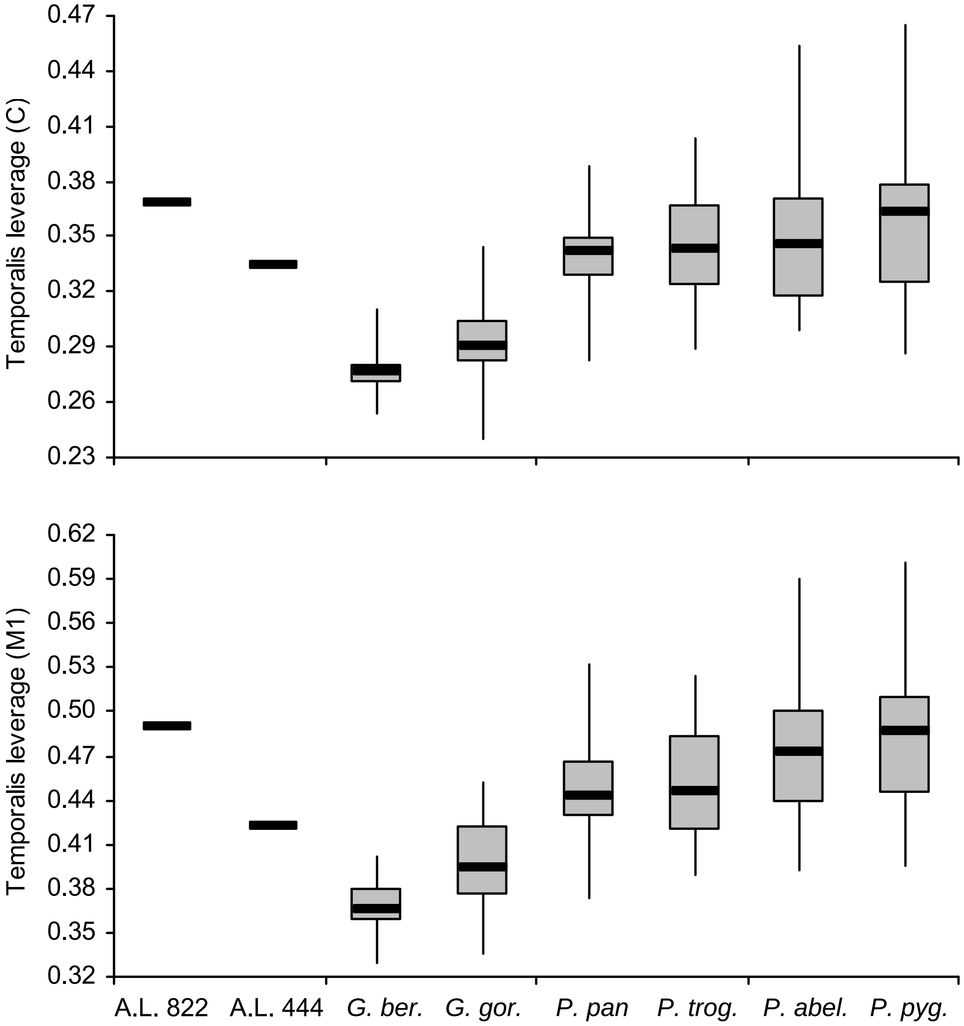


Fig. 4.23. Anterior temporalis leverage at the canine (top) and M1 (bottom) in great apes and two partial skulls of *Australopithecus afarensis* (A.L. 822-1 and A.L. 444-2). Abbreviations are as follows: *G. ber.* = *Gorilla beringei*; *G. gor.* = *Gorilla gorilla*; *P. pan.* = *Pan paniscus*; *P. trog.* = *Pan troglodytes*; *P. abel.* = *Pongo abelii*; *P. pyg.* = *Pongo pygmaeus*. For the great apes, the horizontal bars represent the sample medians, the gray boxes represent the interquartile ranges, and the vertical lines represent the sample ranges.

Whether or not this increase in leverage was coincident with, and causally related to, the initial episode of canine reduction in the hominin lineage remains to be determined, but the combination of reduced canines, increased muscle leverage, and moderate to strong skeletal-size dimorphism (Johanson and White, 1979; McHenry, 1991, 1992, 1994; Richmond and Jungers, 1995; Lockwood et al., 1996; Harmon, 2006; Gordon et al., 2008; but see Reno et al., 2003, 2005, 2010) in *Au. afarensis* is, at the very least, compatible with the hypothesis that selection for efficient bite-force production influenced canine evolution in hominins to some degree.

CHAPTER 5—SUMMARY AND CONCLUSIONS

Sexual dimorphism in canine size, particularly canine height, is an important morphological correlate of social behavior in anthropoid primates. It is well established that the canine teeth function as weapons in intraspecific combat and that canine dimorphism is a product of intense intermale competition for mating opportunities in species characterized by polygynous or multimale-multifemale social groups (Leutenegger and Kelly, 1977; Harvey et al., 1978; Kay et al., 1988; Greenfield and Washburn, 1991; Greenfield, 1992c; Plavcan and van Schaik, 1992, 1994; Plavcan, 1993a, 2001; Plavcan et al., 1995; Thorén et al., 2006; Leigh, 2008; Plavcan and Ruff, 2008). Because of this relationship, canine size and dimorphism are often used to infer aspects of social behavior in extinct primate species (e.g., Fleagle et al., 1980; Gingerich, 1981, 1995; Kay, 1982; Krishtalka et al., 1990; Simons et al., 1999; Plavcan and van Schaik, 1997a; Plavcan, 2000; Takai et al., 2009). Early hominins exhibit vertically short, weakly dimorphic canines (e.g., Leutenegger and Shell, 1987; White et al., 1994, 2006, 2009; Plavcan and van Schaik, 1997a; Haile-Selassie 2001; Senut et al., 2001; Ward et al., 2001; Brunet et al., 2002, 2005; Haile-Selassie et al., 2004, 2009; Semaw et al., 2005; Plavcan et al., 2009; Suwa et al., 2009b), suggesting that physically violent intermale competition was rare in these species (Holloway, 1967), perhaps due to the formation of long-term monogamous pair-bonds (Lovejoy, 1981; Reno et al., 2003, 2005, 2010). However, this sociobehavioral signal is contradicted by the moderate to high degree of body-mass dimorphism inferred from size variation in the skeletal remains of species of *Australopithecus* (e.g., Johanson and White, 1979; McHenry, 1991, 1992, 1994; Richmond and Jungers, 1995; Lockwood et al., 1996, 2007; Plavcan and van Schaik, 1997a; Lockwood, 1999; Silverman, 2001; Ward et al., 2001; Harmon, 2006; Gordon et al., 2008; but see Lovejoy et al., 1989; Reno et al., 2003, 2005), which is inconsistent with the canine-based behavioral inferences and suggests high-intensity intermale competition (Clutton-Brock et al., 1977; Ford, 1994; Mitani et al., 1996; Plavcan and van Schaik, 1997b; Lindenfors and Tullberg, 1998; Plavcan, 2004). Elucidating the adaptive significance of this unusual pattern of dimorphism is one of the major objectives of paleoanthropology.

While it is possible that the inferred level of body-size dimorphism in early hominins is a misleading indicator of social behavior (Plavcan and van Schaik, 1997a), it is more common in discussions of hominin sexual dimorphism to assume that the false signal comes from the canine (e.g., Darwin, 1871; Jolly, 1970a; Szalay, 1975; Wolpoff, 1976; Milton, 1985; Ward et al., 2001). Explanations for hominin canine reduction have a long history in evolutionary biology, beginning with Darwin's (1871) hypothesis that reduction occurred because the weapon function of these teeth was replaced by tools. From Darwin's perspective, canine reduction reflects a shift in how males competed with one another rather than a decrease in the intensity of such competition. This view is evident to varying degrees in many of the more recent treatments of this subject, which have focused on how dietary adaptation may influence canine size and morphology (e.g., Jolly, 1970a; Szalay, 1975; Jungers, 1978; Greenfield, 1992b; Hylander and Vinyard, 2006). The most recently proposed of these hypotheses—

Hylander and Vinyard's (2006; Hylander, 2009) masticatory-efficiency hypothesis—was the stimulus for this dissertation research, the goal of which was to identify factors operating in extant anthropoids that facilitate canine reduction, thus providing a comparative foundation for testing hypotheses regarding canine reduction in the hominin fossil record.

The first hypothesis examined in this dissertation—the pleiotropy hypothesis—links changes in canine height to changes in the size of other components of the dentition via pleiotropic interactions (Jolly, 1970a; Jungers, 1978; Kieser and Groeneveld, 1987a; Alba et al., 2001; McCollum and Sharpe, 2001). Such interactions are expected based simply on the common developmental origin of the dentition (reviewed by McCollum and Sharpe, 2001; Stock, 2001) and the fact that the incisors and postcanine teeth are spatially adjacent to the canines. The results of this study provide no comparative support for this hypothesis: relative canine height (size-adjusted using a geometric mean of linear skull dimensions) is not correlated with the relative size of the incisor row or postcanine teeth. The fact that males and females present an identical signal suggests that these results are not influenced by variation in the intensity of sexual selection. On the other hand, basal canine crown dimensions appear to be influenced to a limited degree by changes in incisor and postcanine size. In many of the species included in this study, basal canine crown size is positively correlated with incisor size and with postcanine size. However, statistically significant correlations between these variables at the interspecific level are restricted primarily to the female maxillary dentition and are low to moderate in magnitude. This pattern of results suggests that pleiotropy may influence some aspects of canine size, but its macroevolutionary effects are weak and easily obscured by other factors such as selection for weaponized canines. In any case, the results of this study are fairly conclusive in indicating that pleiotropy is unlikely to explain reductions in canine height in hominins or in other primate lineages.

The second hypothesis examined in this dissertation—the masticatory-efficiency hypothesis—links canine reduction to increases in the leverage of the jaw adductors (Hylander and Vinyard, 2006; Hylander, 2009). This hypothesis derives from two observations: (1) that canine height is correlated with gape among anthropoid primates and (2) that moving the masticatory muscles anteriorly in order to increase their mechanical advantage should, in the absence of other changes, reduce gape (Hylander and Vinyard, 2006). This study provides some support for this hypothesis: there is a clear inverse relationship between masseter leverage and relative canine height among male anthropoids. In contrast, the leverage of the anterior temporalis exhibits no relationship with relative canine height. The reason for this distinction between the two muscles is unclear, but it may be that the temporalis adjusts to gape requirements primarily through modifications in internal architecture, particularly increases in fiber length, or that there is some factor that inhibits this muscle from migrating anteriorly (e.g., orbit position).

Not all anthropoids exhibit a trade-off between muscle leverage and canine height. Among female anthropoids, there is no relationship between these variables. However, this violation of the masticatory-efficiency hypothesis can be attributed to the fact that there is little or no sexual dimorphism in the shape of the bony masticatory system in most anthropoid species. Thus, it was argued that female skull form is influenced by the association between canine height and masseter leverage in males via correlated response (i.e., the process by which selection on a trait in one sex affects the same trait in the other sex; Lande, 1980). A more serious challenge to the masticatory-efficiency hypothesis comes from New World monkeys that regularly process highly resistant food items using their anterior teeth. In these species, the primary skeletal adaptation to gape appears to be a repositioning of the masseter's origin and insertion sites that reduces the extent to which this muscle stretches at a given degree of mandibular depression, thus permitting an increase in masseter leverage without a concomitant decrease in canine height. However, it was hypothesized that this combination of features is uncommon in the other anthropoids examined in this study because it compromises the third molar's ability to resist occlusal loads. Thus, it appears that platyrrhine hard-object feeders trade one cost (i.e., reduced masseter leverage) for another (i.e., functional impairment of the distal molar row).

In any case, the strong negative association between canine height and masseter leverage in male anthropoid primates indicates that there is a selective advantage to having short canines. The masticatory-efficiency hypothesis thus emerges as the most promising explanation for the reduction in canine height observed in early hominins. Importantly, this hypothesis is potentially falsifiable given a sufficiently complete fossil record. Two partial skulls attributed to

Australopithecus afarensis—A.L. 444-2 and A.L. 822-1—fall at or beyond the upper end of the range of ape variation in masseter leverage, which is consistent with the idea that selection for increased muscle leverage played some role in early hominin canine evolution. The currently available fossil record suggests the following scenario.

The earliest hominin for which sexual dimorphism in canine and body size can be inferred is *Ardipithecus ramidus*; both aspects of dimorphism have been characterized as weak by the describers of this species (Suwa et al., 2009b; White et al., 2009). Therefore, the *Ar. ramidus* material suggests that, prior to 4.4 million years ago, there was a decrease in the intensity of sexual selection experienced by males, which would have allowed selection for increased masticatory efficiency to have a greater influence on hominin skull form.[1] Whether or not these morphological changes occurred in conjunction with a shift in diet cannot be determined based on current evidence, but it is clear that the masticatory system of *Ar. ramidus* lacks most of the specializations observed in the geologically younger australopiths, which are thought to have been adapted to a very mechanically demanding diet (e.g., Rak, 1983; Ryan and Johanson, 1989; Teaford and Ungar, 2000; White et al., 2000, 2006; Ward et al., 2001; Kimbel et al., 2004; Ungar, 2004; Laden and Wrangham, 2005; Grine et al., 2006; Dominy

---

[1] Given what is known about sexual dimorphism in canine and body size in fossil and extant apes, it is almost certainly true that the pattern of dimorphism exhibit by *Ar. ramidus* is apomorphic. Note, however, that Suwa et al. (2009b) argued that the pattern of dimorphism in *Ar. ramidus* (and the low level of intermale competition that it implies) represents the condition present in the last common ancestor of humans and African apes.

et al., 2008; Suwa et al., 2009a,b; Ungar et al., 2010). In any event, masseter leverage in *Ar. ramidus* should be greater than in African apes.

According to this scenario, the moderate to strong skeletal dimorphism evident in the australopiths (e.g., Johanson and White, 1979; McHenry, 1991, 1992, 1994; Richmond and Jungers, 1995; Lockwood et al., 1996, 2007; Plavcan and van Schaik, 1997a; Lockwood, 1999; Silverman, 2001; Ward et al., 2001; Reno et al., 2003, 2005, 2010; Harmon, 2006; Gordon et al., 2008) represents an increase in dimorphism, suggesting intensification of intermale competition without a concomitant increase in canine size and dimorphism. Given the current level of resolution afforded by the hominin fossil record, this increase in skeletal dimorphism—and, by inference, body-mass dimorphism—appears to have been broadly contemporaneous with the dietary shift indicated by the striking differences in craniodental anatomy between *Ar. ramidus* and the earliest species of *Australopithecus* (see references above). This association suggests that, despite an increase in the intensity of intermale competition, the canines of the australopiths remained short and only slightly dimorphic due to the strong selection to maintain efficient bite-force production engendered by the dietary shift.

The scenario described above assumes that the morphological pattern presented by *Ar. ramidus* represents the ancestral condition for the genus *Australopithecus*. However, this assumption may not be correct; the low level of skeletal dimorphism observed in *Ar. ramidus* may be an autapomorphic feature of a species that did not give rise to any of the taxa currently recognized in the hominin fossil record. In this case, two additional scenarios are possible:

Scenario 2—The strength of selection for weaponized canines in the earliest hominins was within the range of that experienced by the males of extant great apes. Selection for increased muscle leverage intensified due to a shift in diet and overwhelmed sexual selection, resulting in a decrease in canine height and dimorphism. This scenario is the simplest and most extreme version of the masticatory-efficiency hypothesis; it makes the following predictions regarding the fossil record: (1) the earliest hominins should have tall, strongly dimorphic canines (i.e., similar to those of *Pan troglodytes* or species of *Gorilla*) and (2) exhibit a level of body-mass dimorphism (as inferred from size variation in skeletal elements) similar to that inferred for species of *Australopithecus* (i.e., greater than in *Pan* and *Homo*; perhaps similar in some cases to *Gorilla* and *Pongo*); (3) in subsequent time periods, canine height and dimorphism should decrease in conjunction with craniodental indicators of a shift to a more mechanically demanding diet, which include—in addition to an increase in masseter leverage—an increase in the size of the postcanine dentition, a shift in patterns of tooth wear indicating more intensive postcanine processing, and increases in the robustness of the mandible and muscle attachment sites; (4) while these changes are taking place, body-mass dimorphism should remain pronounced.

Scenario 3—Intermale competition in the earliest hominins was intense, but the canine teeth became less critical (relative to the plesiomorphic condition, presumably represented by extant great apes) in determining the outcomes of such interactions; rather body size became the primary determinant of success in establishing mating priority (Milton, 1985; Ward et al., 2001). Thus, sexual selection on the canines was relaxed due to an emphasis on body size, allowing selection for efficient bite-force production to have a greater influence on skull form. These modifications may or may not have occurred concurrently with a shift to a more mechanically demanding diet. If a shift in diet did occur, then the predictions made by this scenario are similar to those made by Scenario 2, which will make it difficult to distinguish these scenarios from each other in the fossil record. However, it may be possible to do so if the shift in emphasis away from the canine to body size in intermale combat is associated with an increase in body-size dimorphism. On the other hand, if the reduction in canine size and dimorphism did not occur in conjunction with a shift in diet, then Scenario 3 predicts that the only change in the masticatory system that will be coincident with canine reduction is an increase in masseter leverage. The latter changes should be clearly separated in time from the appearance of other features (cited above) that signal a dietary shift.

It is important to note that these three scenarios are incomplete in that they do not address the marked difference between hominins and apes in canine shape. As has been noted by many researchers (e.g., Szalay, 1975; Greenfield, 1990a,c, 1992b, 1993; White et al., 1994; Haile-Selassie et al., 2004, 2009; Kimbel et al., 2006; Kimbel and Delezene, 2009; Suwa et al., 2009b; Ward et al., 2010), hominin canines are not simply smaller versions of ape canines; their morphology, typically described as incisiform, is highly unusual among anthropoid primates. While the masticatory-efficiency hypothesis may account for the height reduction observed in these teeth, it is silent with respect to changes in shape and the shift in function that they imply. Presumably, the reduction in height exposed the canines to novel selection pressures, and it is conceivable that such pressures may have constrained the canines from increasing in height after the initial episode of reduction. For example, in the first scenario outlined above, it was hypothesized that canine height and dimorphism did not increase along with body-size dimorphism in the transition from *Ardipithecus* to *Australopithecus* because the shift to a more mechanically demanding diet evident in the morphology of the species of the latter genus generated strong selection to preserve efficient bite-force production. However, it is also possible that short canines were maintained because their function had been altered to such a degree following the initial reduction in height that these teeth were buffered from the effects of sexual selection when it increased (as suggested by the increase in body-size dimorphism). Another possibility in this scenario is that short canines were maintained by a combination of both of these factors. It should be apparent from this discussion that the scenarios outlined above are merely a starting point in elucidating the adaptive meaning of the hominin canine. Testing the masticatory-efficiency hypothesis using the pre-*Au. afarensis* fossil record and clarifying the functional significance of changes in canine shape in early hominins are the next major steps in achieving this objective.

LITERATURE CITED

Abramoff MD, Magelhaes PJ, Ram SJ. 2004. Image processing with ImageJ. Biophotonics International 11:36–42.

Ackermann RR. 2002. Patterns of covariation in the hominoid craniofacial skeleton: implications for paleoanthropological models. J Hum Evol 42:167–187.

Ackermann RR. 2005. Ontogenetic integration of the hominoid face. J Hum Evol 48:175–197.

Ackermann RR, Cheverud JM. 2000. Phenotypic covariance structure in tamarins (genus *Saguinus*): a comparison of variation patterns using matrix correlation and common principal component analysis. Am J Phys Anthropol 111:489–501.

Åkesson M, Bensch S, Hasselquist D. 2007. Genetic and phenotypic associations in morphological traits: a long term study of great reed warblers *Acrocephalus arundinaceus*. J Avian Biol 38:58–72.

Alba DM, Moyà-Solà S, Köhler M. 2001. Canine reduction in the Miocene hominoid *Oreopithecus bambolii*: behavioural and evolutionary implications. J Hum Evol 40:1–16.

Albrecht GH., Miller JMA. 1993. Geographic variation in primates: a review with implications for interpreting fossils. In: Kimbel WH, Martin LB, editors. Species, species concepts, and primate evolution. New York: Plenum Press. p 123–161.

Albrecht GH, Gelvin BR, Hartman SE. 1993. Ratios as a size adjustment in morphometrics. Am J Phys Anthropol 91:441–468.

Albrecht GH, Gelvin BR, Hartman SE. 1995. Ratio adjustments in morphometrics: a reply to Dr. Corruccini. Am J Phys Anthropol 96:193–197.

Aldrich-Blake FPG. 1978. Dispersion and food availability in Malaysian forest primates. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, vol. 1. London: Academic Press. p 323–325.

Anapol F, Barry K. 1996. Fiber architecture of the extensors of the hindlimb in semiterrestrial and arboreal guenons. Am J Phys Anthropol 99:429–447.

Anapol F Gray JP. 2003. Fiber architecture of the intrinsic muscles of the shoulder and arm in semiterrestrial and arboreal guenons. Am J Phys Anthropol 122:51–65.

Anapol F, Lee S. 1994. Morphological adaptation to diet in platyrrhine primates. Am J Phys Anthropol 94:239–261.

Anderson DL, Thompson GW, Popovich F. 1977. Tooth, chin, bone and body size correlations. Am J Phys Anthropol 46:7–12.

Anderson DL, Thompson GW, Popovich F. 1975. Evolutionary dental changes. Am J Phys Anthropol 43:95–102.

Andersson MB. 1994. Sexual selection. Princeton: Princeton University Press.

Antón SC. 1996a. Cranial adaptation to a high attrition diet in Japanese macaques. Int J Primatol 17:401–427.

Antón SC. 1996b. Tendon-associated bone features of the masticatory system in Neandertals. J Hum Evol 31:391–408.

Antón SC. 1999. Macaque masseter muscle: internal architecture, fiber length and cross-sectional area. Int J Primatol 20:441–462.

Antón SC. 2000. Macaque pterygoid muscles: internal architecture, fiber length, and cross-sectional area. Int J Primatol 21:131–156.

Arendsen de Wolff-Exalto E. 1951a. On differences in the lower jaw of animalivorous and herbivorous mammals, I. Proc K Ned Akad Wet 54:237–246.

Arendsen de Wolff-Exalto E. 1951b. On differences in the lower jaw of animalivorous and herbivorous mammals, II. Proc K Ned Akad Wet 54:405–410.

Armfield BA, Vinyard CJ. 2010. An interspecific analysis of relative jaw-joint height in primates. Am J Phys Anthropol. 142:519–530.

Astaras C, Mühlenberg M, Waltert M. 2008. Note on drill (*Mandrillus leucophaeus*) ecology and conservation status in Korup National Park, southwest Cameroon. Am J Primatol 70:306–310.

Aureli F, Schaffner CM. 2007. Aggression and conflict management at fusion in spider monkeys. Biol Lett 3:147–149.

Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G. 2006. Raiding parties of male spider monkeys: insights into human warfare? Am J Phys Anthropol 131:486–497.

Ayres JM. 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. J Hum Evol 18:697–716.

Badrian N, Malenky R. 1984. Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman RL, editor. The Pygmy Chimpanzee: evolutionary biology and behavior. New York: Plenum Press. p 275–299.

Badrian N, Badrian A, Susman RL. 1981. Preliminary observations on the feeding behavior of *Pan paniscus* in the Lomako Forest of central Zaïre. Primates 22:173–181.

Bailit HL, Friedlaender JS. 1966. Tooth size reduction: a hominid trend. Am Anthropol 68:665–672.

Bandoni de Oliveira F, Porto A, Marroig G. 2009. Covariance structure in the skull of Catarrhini: a case of pattern stasis and magnitude evolution. J Hum Evol 56:417–430.

Barroso CML, Schneider H, Schneider MPC, Sampaio I, Harada ML, Czelusniak J, Goodman M. 1997. Update on the phylogenetic systematics of New World monkeys: further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the genus *Callithrix*. Int J Primatol 18:651–674.

Bartholomew GA Jr, Birdsell JB. 1953. Ecology and the protohominids. Am Anthropol 55:481–498.

Beldade P, Koops K, Brakefield PM. 2002. Modularity, individuality, and evo-devo in butterfly wings. Proc Natl Acad Sci 14262–14267.

Bell G. 1989. A comparative method. Am Nat 133:553–571.

Bennett EL, Davies AG. 1994. The ecology of Asian colobines. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. New York: Cambridge University Press. p 129–171.

Berard J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). Primates 40:159–175.

Bercovitch FB. 1997. Reproductive strategies of rhesus macaques. Primates 38:247–263.

Berenstain L. 1986. Responses of long-tailed macaques to drought and fire in eastern Borneo: a preliminary report. Biotropica 18:257–262.

Bernstein IS, Gordon TP. 1980. The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). Anim Behav 28:1033–1039.

Bernstein IS, Gordon TP, Rose RM. 1974a. Factors influencing the expression of aggression during introductions to rhesus monkey groups. In: Holloway RL, editor. Primate aggression, territoriality and xenophobia. New York: Academic Press. p 211–240.

Bernstein IS, Gordon TP, Rose RM. 1974b. Aggression and social controls in rhesus monkey (*Macaca mulatta*) groups revealed in group formation studies. Folia Primatol 21:81–107.

Biegert J. 1963. The evaluation of characteristics of the skull, hands, and feet for primate taxonomy. In: Washburn SL, editor. Classification and human evolution. Chicago: Aldine. p 116–145.

Blanksma NG, Van Eijden TMGJ. 1990. Electromyographic heterogeneity in the human temporalis muscle. J Dent Res 69:1686–1690.

Bouvier M. 1986. Biomechanical scaling of mandibular dimensions in New World monkeys. Int J Primatol 7:551–567.

Bouvier M, Tsang SM. 1990. Comparison of muscle weight and force ratios in New and Old World monkeys. Am J Phys Anthropol 82:509–515.

Brace CL. 1963. Structural reduction in evolution. Am Nat 97:39–49.

Brace CL, 1967. Environment, tooth form, and size in the Pleistocene. J Dent Res 46:809–816.

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L. 2004. Dispersed male networks in western gorillas. Curr Biol 14:510–513.

Bradley BJ, Robbins MM, Williamson EA, Steklis HD, Steklis NG, Eckhardt N, Boesch C, Vigilant L. 2005. Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. Proc Natl Acad Sci USA 102:9418–9423.

Braza F, Alvarez F, Azcarate T. 1983. Feeding habits of the red howler monkey (*Alouatta seniculus*) in the Llanos of Venezuela. Mammalia 47:205–214.

Breuer T, Robbins AM, Olejniczak C, Parnell RJ, Stokes EJ, Robbins MM. 2010. Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. Behav Ecol Sociobiol 64:515:528.

Brues AM. 1966. “Probable mutation effect” and the evolution of hominid teeth and jaws. Am J Phys Anthropol 25:169–170.

Brues AM. 1968. Mutation and selection—a quantitative evaluation. Am J Phys Anthropol 29:437–439.

Brugiere D, Gautier J-P, Moungazi A, Gautier-Hion A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. Int J Primatol 23:999–1024.

Brunet M. 2002. Reply to “*Sahelanthropus* or ‘*Sahelpithecus*’?” Nature 419:582.

Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie J-R, de Bonis L, Coppens Y, Dejax J, Denys C, Duringer P, Eisenmann V, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Campomanes PP, Ponce de León MS, Rage J-C, Sapanet M, Schuster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazzo A, Zollikofer C. 2002. A new hominid from the upper Miocene of Chad, central Africa. Nature 418:145–151.

Brunet M, Guy F, Pilbeam D, Lieberman DE, Likius A, Mackaye HT, Ponce de León MS, Zollikofer CPE, Vignaud P. 2005. New material of the earliest hominid from the upper Miocene of Chad. Nature 434:752–755.

Bryant HN, Russell AP. 1995. Carnassial functioning in nimravid and felid sabertooths: theoretical basis and robustness of inferences. In: Thomason JJ, editor: Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p 116–135.

Buchannon DB, Mittermeier RA, van Roosmalen MGM. 1981. The saki monkeys, genus *Pithecia*. In: Coimbra-Filho AF, Mittermeier RA, editors. Ecology and behavior of Neotropical primates. Rio de Janeiro: Academia Brasiliera de Ciencias. p 391–417.

Butler PM. 1939. Studies of the mammalian dentition.—Differentiation of the postcanine dentition. Proc Zool Soc Lond 109:B1–B36.

Butynski TM. 1988. Guenon birth seasons and correlates with rainfall and food. In: Gautier-Hion A, Bourliere F, Gautier J-P, Kingdon J, editors. A primate radiation: evolutionary biology of the African guenons. Cambridge: Cambridge University Press. p 284–322.

Cachel SM. 1979. A functional analysis of the primate masticatory system and the origin of the anthropoid post-orbital septum. Am J Phys Anthropol 50:1–17.

Calcagno JM, Gibson KR. 1988. Human dental reduction: Natural selection or the probable mutation effect. Am J Phys Anthropol 77:505–517.

Caldecott JO. 1986. Mating patterns, societies and ecogeography of macaques. Anim Behav 34:208–220.

Caldecott JO, Feistner ATC, Gadsby EL. 1996. A comparison of ecological strategies of pig-tailed macaques, mandrills and drills. In: Fa JE, Lindburg DG, editors. Evolution and ecology of macaque societies. Cambridge: Cambridge University Press. p 73–94.

Campbell CJ. 2006. Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). Am J Primatol 68:1197–1201.

Canavez FC, Moreira MAM, Ladasky JJ, Pissinatti A, Parham P, Seuánez HN. 1999. Molecular phylogeny of New World primates (Platyrrhini) based on β_2-microglobulin DNA sequences. Mol Phylogenet Evol 12:74–82.

Carlson DS. 1977. Condylar translation and the function of the superficial masseter muscle in the rhesus monkey (*M. mulatta*). Am J Phys Anthropol 47:53–63.

Chapais B. 1983. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. Behav Ecol Sociobiol 12:215–228.

Chapman C. 1987. Flexibility in the diets of three species of Costa Rican primates. Folia Primatol 49:90–105.

Chapman CA, Chapman LJ, Cords M, Gathua JM, Gautier-Hion A, Lambert JE, Rode K, Tutin CEG, White LJT. 2002. Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. In: Glenn ME, Cords M, editors. The guenons: diversity and adaptation in African monkeys. New York: Kluwer Academic/Plenum Publishers. p 325–350.

Chatterjee HJ. 2006. Phylogeny and biogeography of gibbons: a dispersal-vicariance analysis. Int J Primatol 27:699–712.

Cheverud JM. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36:499–516.

Cheverud JM. 1988. A comparison of genetic and phenotypic correlations. Evolution 42:958–968.

Cheverud JM. 1989. A comparative analysis of morphological variation patterns in the papionins. Evolution 43:1737–1747.

Cheverud, J.M. 1995. Morphological integration in the saddle-back tamarin (*Saguinus fuscicollis*) cranium. Am Nat 145:63–89.

Cheverud JM. 1996a. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*S. fuscicollis*) tamarins. J Evol Biol 9:5–42.

Cheverud JM. 1996b. Developmental integration and the evolution of pleiotropy. Am Zool 36:44–50.

Cheverud JM, Dow MM, Leutenegger W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. Evolution 39:1335–1352.

Cheverud JM, Routman EJ, Irschick DJ. 1997. Pleiotropic effects of individual gene loci on mandibular morphology. Evolution 51:2006–2016.

Chiarello AG. 1995. Role of loud calls in brown howlers, *Alouatta fusca*. Am J Primatol 36:213–222.

Chism J, Wood CS. 1994. Diet and feeding behavior of patas monkeys (*Erythrocebus patas*) in Kenya. Am J Phys Anthropol 18(Suppl):67.

Chivers DJ, Andrews P, Preuschoft H, Bilsborough A, Wood BA. 1984. Food acquisition and processing in primates: concluding discussion. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 545–556.

Choudhury A. 1989. Ecology of the capped langur (*Presbytis pileatus*) in Assam, India. Folia Primatol 52:88–92.

Christiansen P. 2006. Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). J Morphol 267:1186–1198.

Clarke MR. 1983. Infant-killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. Am J Primatol 5:241–247.

Clarke MR, Zucker EL, Glander KE. 1994. Group takeover by a natal male howling monkey (*Alouatta palliata*) and associated disappearance and injuries of immatures. Primates 35:435–442.

Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool Lond 183:1–39.

Clutton-Brock TH, Harvey PH, Rudder B. 1977. Sexual dimorphism, socionomic sex ratio and body weight dimorphism in primates. Nature 269:797–800.

Cochard LR. 1981. Patterns of size variation and correlation in the dentition of the red Colobus monkey (*Colobus badius*). Am J Phys Anthropol 54: 139–146.

Cochard LR. 1985. Ontogenetic allometry of the skull and dentition of the rhesus monkey (*Macaca mulatta*). In: Jungers WL, editor. Size and scaling in primate biology. New York: Plenum Press. p 231–255.

Cochard LR. 1987. Postcanine tooth size in female primates. Am J Phys Anthropol 74:47–54.

Coelho AM, Coelho LS, Bramblett CA, Bramblett SS, Quick LB. 1976. Ecology, population characteristics, and sympatric association in primates: a sociobioenergetic analysis of the energy budgets of howler and spider monkeys in Tikal, Guatemala. Yrbk Phys Anthropol 20:96–135.

Coimbra-Filho AF, Mittermeier RA. 1976. Exudate-eating and tree-gouging in marmosets. Nature 262:630.

Coimbra-Filho AF, Mittermeier RA. 1977. Tree-gouging, exudate-eating and the "short-tusked" condition in *Callithrix* and *Cebuella*. In: Kleiman DG, editor. The biology and conservation of the Callitrichidae. Washington: Smithsonian Institution Press. p 105–115.

Cole TM III. 1992. Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. J Hum Evol 23:253–282.

Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. Proc Biol Sci 269:165–172.

Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. Int J Primatol 19:971–998.

Copes LE, Schwartz GT. 2010. The scale of it all: postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law. Paleobiology 36:188–203.

Corruccini RS. 1977. Integration of occluding structures in hominoid molars. J Dent Res 56:190.

Corruccini RS. 1987. Shape in morphometrics: comparative analyses. Am J Phys Anthropol 73:289–303.

Corruccini RS. 1995. Of ratios and rationality. Am J Phys Anthropol 96:189–191.

Corruccini RS, Henderson AM. 1978. Multivariate dental allometry in primates. Am J Phys Anthropol 48:203–208.

Cracraft J. 1981. The use of functional and adaptive criteria in phylogenetic systematics. Am Zool 21:21–36.

Cristóbal-Azkarate J, Dias PAD, Veá JJ. 2004. Causes of intraspecific aggression in *Alouatta palliata mexicana*: evidence from injuries, demography, and habitat. Int J Primatol 25:939–953.

Crockett CM. 1984. Emigration by female red howler monkeys and the case for female competition. In: Small MF, editor. Female primates: studies by women primatologists. New York: Alan R. Liss. p 159–173.

Crockett CM, Eisenberg JF. 1987. Howlers: variations in groups size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 54–68.

Crockett CM, Pope T. 1988. Inferring patterns of aggression from red howler monkey injuries. Am J Primatol 15:289–308.

Cunningham EP, Janson CH. 2006. *Pithecia pithecia*'s behavioral response to decreasing fruit abundance. Am J Primatol 68:491–497.

Curtin SH. 1976. Niche separation in sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Yrbk Phys Anthropol 20:421–439.

Curtin SH. 1980. Dusky and banded leaf monkeys. In: Chivers DJ, editor. Malayan forest primates: ten years' study in tropical rain forest. New York: Plenum Press. p 105–145.

Curtin SH, Chivers DJ. 1978. Leaf-eating primates of peninsular Malaysia: the siamang and the dusky leaf-monkey. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington: Smithsonian Institution Press. p 441–464.

Daegling D. 1992. Mandibular morphology and diet in the genus *Cebus*. Int J Primatol 13:545–570.

Daegling DJ, McGraw WS. Functional morphology of the mangabey mandibular corpus: relationship to dental specializations and feeding behavior. Am J Phys Anthropol 134:50–62.

Dahlberg AA. 1945. The changing dentition of man. J Am Dent Assoc 32:676–690.

Daniel, WW. 1990. Applied nonparametric statistics, second edition. Pacific Grove, CA: Duxbury.

Darwin C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: John Murray.

Darwin C. 1871. The descent of man, and selection in relation to sex. London: John Murray.

Davenport TRB, Stanley WT, Sargis EJ, De Luca DW, Mpunga NE, Machaga SJ, Olson LE. 2006. A new genus of African monkey, *Rungwecebus*: morphology, ecology, and molecular phylogenetics. Science 312:1378–1381.

Davis DD. 1964. The giant panda: a morphological study of evolutionary mechanisms. Chicago: Chicago Museum of Natural History.

Dechow PC. 1980. Functional morphology of the craniofacial skeleton of baboons. PhD dissertation, University of Chicago.

Dechow PC, Carlson DS. 1990. Occlusal force and craniofacial biomechanics during growth in rhesus monkeys. Am J Phys Anthropol 83:219–237.

DeGusta D, Milton K. 1998. Skeletal pathologies in a population of *Alouatta palliata*: behavioral, ecological, and evolutionary implications. Int J Primatol 19:615–650.

Delgado RA. 2006. Sexual selection in loud calls of male primates: signal content and function. Int J Primatol 27:5–25.

Delson E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: Lindburg DG, editor. The macaques: studies in ecology, behavior, and evolution. New York: Van Nostrand Reinhold. p 10–30.

Delson E, Dean D. 1993. Are *Papio baringensis* R. Leakey, 1969, and *P. quadratirostris* Iwamoto, 1982, species of *Papio* or *Theropithecus*? In: Jablonski N, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 125–156.

Demes B, Creel N. 1988. Bite force, diet, and cranial morphology of fossil hominids. J Hum Evol 17:657–670.

de Ruiter JR, van Hooff JARAM. 1993. Male dominance rank and reproductive success in primate groups. Primates 34:513–523.

de Ruiter JR, Scheffrahn W, Trommelen GJJM, Uiterlinden AG, Martin RD, van Hooff JARAM. 1992. Male social rank and reproductive success in wild long-tailed macaques. In: Martin RD, Dixson AF, Wickings EJ, editors. Paternity in primates: genetic tests and theories. Basel: Karger. p 175–191.

de Ruiter JR, van Hooff JARAM, Scheffrahn W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). Behaviour 129:203–224.

DeVore I. 1964. The evolution of social life. In: Tax S, editor. Horizons in anthropology. Chicago: Aldine Publishing Co. p 25–36.

Díaz-Uriarte R, Garland T Jr. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. Syst Biol 45:27–47.

Díaz-Uriarte R, Garland T Jr. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Syst Biol 47:654–672.

Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. Evol Biol 35:159–175.

Doran DM, McNeilage A. 1998. Gorilla ecology and behavior. Evol Anthropol 6:120–131.

Doran DM, McNeilage A. 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Robbins MM, Sicotte P, Stewart KJ, editors. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 123–149.

Doran-Sheehy DM, Greer D, Mongo P, Schwindt D. 2004. Impact of ecological and social factors on ranging in western gorillas. Am J Primatol 64:207–222.

Doran-Sheehy D, Mongo P, Lodwick J, Conklin-Brittain NL. 2009. Male and female western gorilla deit: preferred foods, use of fallback resources, and implications for ape versus Old World monkey foraging strategies. Am J Phys Anthropol 140:727–738.

Doughty P. 1996. Statistical analysis of natural experiments in evolutionary biology: comments on recent criticisms of the use of comparative methods to study adaptation. Am Nat 148:943–956.

Du Brul EL. 1974. Origin and evolution of the oral apparatus. In: Kawamura Y, editor. Frontiers of oral biology, vol. 1: physiology of mastication. Basel: S. Karger. p 1–30.

Du Brul EL. 1977. Early hominid feeding mechanisms. Am J Phys Anthropol 47:305–320.

Dunbar RIM, 1977. Feeding ecology of gelada baboons: a preliminary report. In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p 251–273.

Dunbar RIM, 1984. Theropithecines and hominids: contrasting solutions to the same ecological problem. J Hum Evol 12:647–658.

Dunbar RIM, Dunbar P. 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. Folia Primatol 21:36–60.

Dunham AE, Miles DB. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. Am Nat 126:231–257.

Eaglen RH. 1984. Incisor size and diet revisited: the view from a platyrrhine perspective. Am J Phys Anthropol 64:263–275.

Eck GG. 1993. *Theropithecus darti* from the Hadar Formation, Ethiopia. In: Jablonski NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 15–83.

Efron B, Tibshirani RJ. 1993. An introduction to the bootstrap. Boca Raton, FL: CRC Press, LLC.

Ellefson JO. 1974. A natural history of the white-handed gibbons in the Malayan Peninsula. In: Rumbaugh DM, editor. Gibbon and siamang: natural history, social behavior, reproduction, vocalizations, prehension. Basel: Karger. p 1–136.

Elgar MA, Harvey PH. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. Funct Ecol 1:25–36.

Elgart-Berry A. 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. Am J Primatol 62:275–285.

Emerson SB, Radinsky L. 1980. Functional analysis of sabertooth cranial morphology. Paleobiology 6:295–312.

Eng CM, Ward SR, Vinyard CJ, Taylor AB. 2009. The morphology of the masticatory apparatus facilitates muscle force production at wide jaw gapes in tree-gouging common marmosets (*Callithrix jacchus*). J Exp Biol 212:4040–4055.

Engelhardt A, Heistermann M, Hodges JK, Nürnberg P, Niemitz C. 2006. Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*)—male monopolisation, female mate choice or post-copulatory mechanisms? Behav Ecol Sociobiol 59:740–752.

Estrada A. 1984. Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. Int J Primatol 5:105–131.

Every R. 1970. Sharpness of teeth in man and other primates. Postilla 143:1–30.

Fashing PJ. 2001. Feeding ecology of guerezas in Kakamega forest, Kenya: the importance of Moraceae fruit in their diets. Int J Primatol 22:579–609.

Fedigan LM, Baxter MJ. 1984. Sex differences and social organization in free-ranging spider monkeys, *Ateles geoffroyi*. Primates 25:279–294.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Ferguson CA, Tucker AS, Christensen L, Lau AL, Matzuk MM, Sharpe PT. 1998. Activin is an essential early mesenchymal signal in tooth development that is required for patterning of the murine dentition. Genes Dev 12:2636–2649.

Fleagle JG. 1976. Locomotor behavior and skeletal anatomy of sympatric leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Yrbk Phys Anthropol 20:440–453.

Fleagle JG. 1977. Locomotor behavior and muscular anatomy of sympatric leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*. Am J Phys Anthropol 46:297–307.

Fleagle JG, Meldrum DJ. 1988. Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. Am J Primatol 16:227–249.

Fleagle JG, McGraw WS. 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. J Hum Evol 42:267–292.

Fleagle JG, Kay RF, Simons EL. 1980. Sexual dimorphism in early anthropoids. Nature 287:328–330.

Fleagle JG, Gilbert CC, Baden AL. 2010. Primate cranial diversity. Am J Phys Anthropol. 142:565–578.

Fooden J. 1976. Provisional classifications and key to living species of macaques (Primates: *Macaca*). Folia Primatol 25:225–236.

Fooden J. 1980. Classification and distribution of living macaques. In Lindburg, DG, editor. The macaques: studies in ecology, behavior, and evolution. New York: Van Nostrand Reinhold. p 1–9.

Fooden J. 1997. Tail length variation in *Macaca fascicularis* and *M. mulatta*. Primates 38:221–231.

Ford SM. 1994. Evolution of sexual dimorphism in body weight in platyrrhines. Am J Primatol 34:221–244.

Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorillas (*Gorilla gorilla beringei*). In Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. London: Academic Press. p 415–447.

Freese C, Oppenheimer JR. 1981. The capuchin monkeys, genus *Cebus*. In: Coimbra-Filho AF, Mittermeier RA, editors. Ecology and behavior of Neotropical primates. Rio de Janeiro: Academia Brasiliera de Ciencias. p 331–390.

Frost SR. 2007. Fossil Cercopithecidae from the middle Pleistocene Dawaitoli Formation, Middle Awash Valley, Afar Region, Ethiopia. Am J Phys Anthropol 460–471.

Frost SR, Alemseged Z. 2007. Middle Pleistocene fossil Cercopithecidae from Asbole, Afar Region, Ethiopia. J Hum Evol 53:227–259.

Frost SR, Delson E. 2002. Fossil Cercopithecidae from the Hadar Formation and surrounding areas of the Afar Depression, Ethiopia. J Hum Evol 43:687–748.

Frumhoff PC, Reeve HK. 1994. Using phylogenies to test hypotheses of adaptation: a critique of some current proposals. Evolution 48:172–180.

Furuichi T. 1997. Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol 18:855–875.

Furuichi T, Ihobe H. 1994. Variation in male relationships in bonobos and chimpanzees. Behaviour 130:211–228.

Galat G, Galat-Luong A. 1978. Diet of green monkeys in Senegal. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, vol. 1. London: Academic Press. p 257–258.

Gallo LM, Airoldi GB, Airoldi RL, Palla S. 1997. Description of mandibular finite helical axis pathways in asymptomatic subjects. J Dent Res 76:704–713.

Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 25:1043–1072.

Gantt DG. 1979. Patterns of dental wear and the role of the canine in Cercopithecinae. Am J Phys Anthropol 51:353–360.

Garland T Jr, Ives AR. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346–364.

Garland T Jr, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41:18–32.

Garland T Jr, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292.

Garland T Jr, Midford PE, Ives AR. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. Am Zool 39:374–388.

Garn SM, Lewis AB, Bonné B. 1961. Third molar polymorphism and the timing of tooth formation. Nature 192:989.

Garn SM, Lewis AB, Kerewsky RS. 1963a. Third molar agenesis and size reduction of the remaining teeth. Nature 200:488–489.

Garn SM, Lewis AB, Vicinus JH. 1963b. Third molar polymorphism and its significance to dental genetics. J Dent Res 42:1344–1363.

Garn SM, Lewis AB, Kerewsky RS. 1964. Third molar agenesis and variation in size of the remaining teeth. Nature 201:839.

Garn SM, Lewis AB, Kerewsky RS. 1965. Size interrelationships of the mesial and distal teeth. J Dent Res 44:350–354.

Garn SM, Lewis AB, Swindler DR. 1966. Canine “field” in sexual dimorphism of tooth size. Nature 212:1501–1502.

Garn SM, Lewis AB, Kerewsky RS. 1968. The magnitude and implications of the relationship between tooth size and body size. Arch Oral Biol 13:129–131.

Gaulin SJC, Gaulin CK. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. Int J Primatol 3:1–32.

Gautier-Hion A. 1978. Food niches and coexistence in sympatric primates in Gabon. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, vol. 2. London: Academic Press. p 270–286.

Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. J Anim Ecol 49:237–269.

Gautier-Hion A, Gautier J-P, Maisels F. 1993. Seed dispersal versus seed predation: an inter-site comparison of two related African monkeys. Vegetatio 107/108:237–244.

Gibson KN. 2010. Male mating tactics in spider monkeys: sneaking to compete. Am J Primatol.

Gilbert CC. 2007. Craniomandibular morphology supporting the diphyletic origin of mangabeys and a new genus of the *Cercocebus*/*Mandrillus* clade, *Procercocebus*. J Hum Evol 53:69–102.

Gingerich PD. 1981. Cranial morphology and adaptation in Eocene Adapidae. I. Sexual dimorphism in *Adapis magnus* and *Adapis parisiensis*. Am J Phys Anthropol 56:217–234.

Gingerich PD. 1995. Sexual dimorphism in earliest Eocene *Cantius torresi* (Mammalia, Primates, Adapoidea). Contrib Mus Paleontol Univ Mich 29:185–199.

Gingerich PD, Smith BH, Rosenberg K. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. Am J Phys Anthropol 58:81–100.

Glander KE. 1978. Howling monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington: Smithsonian Institution Press. p 561–574.

Glander KE. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. Am J Phys Anthropol 53:25–36.

Glander KE. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. Int J Primatol 13:415–436.

Goldstein SJ, Richard AF. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. Int J Primatol 10:531–567.

Goldstein S, Post D, Melnick D. 1978. An analysis of cercopithecoid odontometrics: I. The scaling of the maxillary dentition. Am J Phys Anthropol 49:517–532.

González-José R, Van der Molen S, González-Pérez E, Hernández M. 2004. Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. Am J Phys Anthropol 123:69–77.

González-Zamora A, Arroyo-Rodríguez V, Chaves ÓM, Sánchez-López S, Stoner KE, Riba-Hernández P. 2009. Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. Am J Primatol 71:8–20.

Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP. 1998. Toward a phylogenetic classification of Primates based on DNA evidence complemented by fossil evidence. Mol Phylogenet Evol 9:585–598.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge: Harvard University Press.

Gordon AD. 2006a. Scaling of size and dimorphism in primates I: microevolution. In J Primatol 27:27–61.

Gordon AD. 2006b. Scaling of size and dimorphism in primates II: macroevolution. Int J Primatol 27:63–105.

Gordon AD, Green DJ, Richmond BG. 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. Am J Phys Anthropol 135:311–328.

Gould SJ. 1975. On the scaling of tooth size in mammals. Am Zool 15:351–362.

Grafen A. 1989. The phylogenetic regression. Phil Trans Roy Soc Lond 326:119–156.

Grafen A, Ridley M. 1996. Statistical tests for discrete cross-species data. J Theor Biol 183:255–267.

Grant PG. 1973. Biomechanical significance of the instantaneous center of rotation: the human temporomandibular joint. J Biomech 6:109–113.

Greaves WS. 1978. The jaw lever system in ungulates: a new model. J Zool Lond 184:271–285.

Greenfield LO. 1990a. Canine "honing" in *Australopithecus afarensis*. Am J Phys Anthropol 82:135–143.

Greenfield LO. 1990b. Canine reduction in early man: a critique of three mechanical models. Hum Evol 5:213–226.

Greenfield LO. 1990c. Unicausal theories of human canine evolution: are they sufficient? Z Morph Anthropol 78:155–168.

Greenfield LO. 1992a. Incisification of anthropoid deciduous mandibular canines. Z Morph Anthropol 79:103–120.

Greenfield LO. 1992b. Origin of the human canine: a new solution to an old enigma. Yrbk Phys Anthropol 35:153–185.

Greenfield LO. 1992c. Relative canine size, behavior and diet in male ceboids. J Hum Evol 23:469–480.

Greenfield LO. 1993. A tooth at the border of two morphogenetic fields. Hum Evol 8:187–204.

Greenfield LO. 1996. Correlated response of homologous characteristics in the anthropoid anterior dentition. J Hum Evol 31:1–19.

Greenfield LO. 1998. Canine tip wear in male and female anthropoids. Am J Phys Anthropol 107:87–96.

Greenfield LO, Washburn A. 1991. Polymorphic aspects of male anthropoid canines. Am J Phys Anthropol 84:17–34.

Greenfield LO, Washburn, A. 1992. Polymorphic aspects of male anthropoid honing premolars. Am J Phys Anthropol 87:173–186.

Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297–319.

Groves CP. 1970. *Gigantopithecus* and the mountain gorilla. Nature 226:973–974.

Groves CP. 2000. The phylogeny of the Cercopithecoidea. In: Whitehead PF, Jolly CJ, editors. Cambridge: Cambridge University Press. p 180–213.

Groves C. 2001. Primate taxonomy. Washington: Smithsonian Institution Press.

Guy F, Lieberman DE, Pilbeam D, Ponce de León M, Likius A, Mackaey HT, Vignaud P, Zollikofer C, Brunet M. 2005. Morphological affinities of the *Sahelanthropus tchadensis* (late Miocene hominid from Chad) cranium. Proc Natl Acad Sci 102:18836–18841.

Haile-Selassie Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412:178–181.

Haile-Selassie Y, Suwa G, White TD. 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. Science 303:1503–1505.

Haile-Selassie Y, Suwa G, White T. 2009. Hominidae. In: Haile-Selassie Y, WoldeGabriel G, editors. *Ardipithecus kadabba*: late Miocene evidence from the Middle Awash, Ethiopia. Berkeley: University of California Press. p 159–236.

Hallgrímsson B, Willmore K, Hall BK. 2002. Canalization, developmental stability, and morphological integration in primate limbs. Yrbk Phys Anthropol 45:131–158.

Haltenorth T, Diller H. 1980. A field guide to the mammals of Africa. London: Collins.

Happel RE. 1982. Ecology of *Pithecia hirsuta* in Peru. J Hum Evol 11:581–590.

Harada ML, Schneider H, Schneider MPC, Sampaio I, Czelusniak J, Goodman M. 1995. DNA evidence on the phylogenetic systematics of New World monkeys: support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. Mol Phylogenet Evol 4:331–349.

Harcourt AH, Stewart KJ. 2007a. Gorilla society: conflict, compromise and cooperation between the sexes. Chicago: University of Chicago Press.

Harcourt AH, Stewart KJ. 2007b. Gorilla society: what we know and don't know. Evol Anthropol 16:147–158.

Harmon EH. 2006. Size and shape variation in *Australopithecus afarensis* proximal femora. J Hum Evol 51:217–227.

Harris EF, Bailit HL. 1988. A principal components analysis of human odontometrics. Am J Phys Anthropol 75:87–99.

Harrison MJS. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Anim Behav 31:969–977.

Harrison MJS. 1984. Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. Int J Primatol 5:435–471.

Harrison MJS. 1988. The mandrill in Gabon's rain forest—ecology, distribution and status. Oryx 22:218–228.

Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Harvey PH, Kavanagh M, Clutton-Brock TH. 1978. Sexual dimorphism in primate teeth. J Zool Lond 186:475–485.

Hayasaka K, Fujii K, Horai S. 1996. Molecular phylogeny of macaques: implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. Mol Biol Evol 13:1044–1053.

Henderson AM, Corruccini RS. 1976. Relationships between tooth size and body size in American blacks. J Dent Res 55:94.

Henderson AM, Greene DL. 1975. Dental field theory: an application to primate evolution. J Dent Res 54:344–350.

Herring SW. 1972. The role of canine morphology in the evolutionary divergence of pigs and peccaries. J Mammal 53:500–512.

Herring SW. 1975. Adaptations for gape in the hippopotamus and its relatives. Forma et Functio 8:85–100.

Herring SW, Herring SE. 1974. The superficial masseter and gape in mammals. Am Nat 108:561–576.

Hlusko LJ. 2006. Evolution of genetically correlated traits: tooth size and body size in baboons. Am J Phys Anthropol 131:420–427.

Hlusko LJ, Mahaney MC. 2009. Quantitative genetics, pleiotropy, and morphological integration in the dentition of *Papio hamadryas*. Evol Biol 36:5–18.

Hlusko LJ, Maas M-L, Mahaney MC. 2004. Statistical genetics of molar cusp patterning in pedigreed baboons: implications for primate dental development and evolution. J Exp Biol (Mol Dev Evol) 302B:268–283.

Hlusko LJ, Do N, Mahaney MC. 2007. Genetic correlations between mandibular molar cusp areas in baboons. Am J Phys Anthropol 132:445–454.

Hodgson JA, Sterner KN, Matthews LJ, Burrell AS, Jani RA, Raaum R, Stewart C-B, Disotell TR. 2009. Successive radiations, not stasis, in the South American primate fauna. Proc Natl Acad Sci USA 106:5534–5539.

Hohmann G, Fruth B. 2002. Dynamics in social organization of bonobos (*Pan paniscus*). In: Boesch C, Hohmann G, Marchant LF, editors. Behavioral diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press. p 138–150.

Hohmann G, Fruth B. 2003. Intra- and inter-sexual aggression by bonobos in the context of mating. Behaviour 140:1389–1413.

Holloway RL Jr. 1966. Structural reduction through the “probable mutation effect”: a critique with questions regarding human evolution. Am J Phys Anthropol 25:7–11.

Holloway RL Jr. 1967. Tools and teeth: some speculations regarding canine reduction. Am Anthropol 69:63–67.

Holm S. 1979. A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70.

Homewood KM. 1978. Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates). J Zool Lond 186:375–391.

Horovitz I, Meyer A. 1995. Systematics of New World monkeys (Platyrrhini, Primates) based on 16S mitochondrial DNA sequences: a comparative analysis of different weighting methods in cladistic analysis. Mol Phylogenet Evol 4:448–456.

Horovitz I, Zardoya R, Meyer A. 1998. Platyrrhine systematics: a simultaneous analysis of molecular and morphological data. Am J Phys Anthropol 106:261–281.

Hoshino J. 1985. Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. Primates 26:248–273.

Huey RB, Bennett AF. 1987. Phylogenetic studies of co-adaptation: preferred temperatures versus optimal performance temperatures of lizards. Evolution 41:1098–1115.

Hylander WL. 1975a. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science 189:1095–1098.

Hylander WL. 1975b. The human mandible: lever or link? Am J Phys Anthropol 43:227–242.

Hylander WL. 1977. The adaptive significance of Eskimo craniofacial morphology. In: Dahlberg AA, Graber TM, editors. Orofacial growth and development. The Hague: Mouton Publishers. p 129–169.

Hylander WL. 1978. Incisal bite force direction in humans and the functional significance of mammalian mandibular translation. Am J Phys Anthropol 48:1–7.

Hylander WL. 1979. The functional significance of primate mandibular form. J Morphol 160:223–239.

Hylander WL. 1985. Mandibular function and biomechanical stress and scaling. Am Zool 25:315–330.

Hylander WL. 2009. The functional significance of canine height reduction in early hominins. Am J. Phys Anthropol 48(Suppl):154.

Hylander WL, Johnson KR. 1985. Temporalis and masseter muscle function during incision in macaques and humans. Int J Primatol 6:289–322.

Hylander WL, Vinyard CJ. 2006. The evolutionary significance of canine reduction in hominins: functional links between jaw mechanics and canine size. Am J Phys Anthropol 42(Suppl):107.

Hylander WL, Wall CE, Vinyard CJ, Ross C, Ravosa MR, Williams SH, Johnson KR. 2005. Temporalis function in anthropoids and strepsirrhines: an EMG study. Am J Phys Anthropol 128:35–56.

Isabirye-Basuta G. 1989. Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In: Heltne P, Marquardt LA, editors. Understanding chimpanzees. Cambridge: Harvard University Press. p 116–127.

Isler K, Kirk EC, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. 2008. Endocranial volumes of primate species: scaling analysis using a comprehensive and reliable data set. J Hum Evol 55:967–978.

Isbell LA. 1995. Seasonal and social correlates of changes in hair, skin, and scrotal condition in vervet monkeys (*Cercopithecus aethiops*) of Amboseli National Park, Kenya. Am J Primatol 36:61–70.

Isbell LA. 1998. Diet for a small primate: insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). Am J Primatol 45:381–398.

Isbell LA, Pruetz JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behav Ecol Sociobiol 42:123–133.

Islam MA, Husain KZ. 1982. A preliminary study on the ecology of the capped langur. Folia Primatol 39:145–159.

Iwamoto T. 1979. Feeding ecology. In: Kawai M, editor. Ecological and sociological studies on gelada baboons. Tokyo: Kodansha. p 279–330.

Iwamoto T. 1993. The ecology of *Theropithecus gelada*. In Jablonski N, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 441–452.

Iwamoto T, Dunbar RIM. 1983. Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. J Anim Ecol 52:357–366.

Izawa K. 1979. Foods and feeding behavior of wild black-capped capuchins (*Cebus apella*). Primates 20:57–76.

Izawa K, Mizuno A. 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates 18:773–792.

Jablonski NG. 1993. Evolution of the masticatory apparatus in *Theropithecus*. In: Jablonksi NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 299–329.

Janson CH, Boinski S. 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. Am J Phys Anthropol 88:483–498.

Johanson, DC. 1974. An odontological study of the chimpanzee with some implications for hominoid evolution. PhD dissertation, University of Chicago, Chicago

Johanson DC, White TD. 1979. A systematic assessment of early African hominids. Science 203:321–330.

Jolly CJ. 1970a. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5:5–26.

Jolly CJ. 1970b. *Hadropithecus*: a lemuroid small-object feeder. Man 5:619–626.

Jolly CJ. 1972a. The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916), baboons of the African Plio-Pleistocene. Bull Br Mus Nat Hist (Geol) 22:1–123.

Jones C, Sabater Pi J. 1968. Comparative ecology of *Cercocebus albigena* (gray) and *Cercocebus torquatus* (Kerr) in Rio Muni, West Africa. Folia Primatol 9:99–113.

Julliot C, Sabatier D. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. Int J Primatol 14:527–550.

Jungers WL. 1978. On canine reduction in early hominids. Curr Anthropol 19:155–156.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 21:137–161.

Kano T. 1992. The last ape: pygmy chimpanzee behavior and ecology. Stanford: Stanford University Press.

Kano T, Mulavwa M. 1984. Feeding ecology of *Pan paniscus* at Wamba. In: Susman RL, editor. The pygmy chimpanzee: evolutionary biology and behavior. New York: Plenum Press. p 233–274.

Kanthaswamy S, Satkoski J, George D, Kou A, Erickson BJ-A, Smith DG. 2008. Hybridization and stratification of nuclear genetic variation in *Macaca mulatta* and *M. fascicularis*. Int J Primatol 29:1295–1311.

Kappeler PM. 1990. The evolution of sexual size dimorphism in prosimian primates. Am J Primatol 21:201–214.

Kappeler PM. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. Folia Primatol (Basel) 57:132–146.

Kappeler PM. 1996. Intrasexual selection and phylogenetic constraints in the evolution of sexual canine dimorphism in strepsirhine primates. J Evol Biol 9:43–65.

Kay CN, Scapino RP, Kay ED. 1986. A cinephotographic study of the role of the canine in limiting lateral jaw movement in *Macaca fascicularis*. J Dent Res 65:1300–1302.

Kay RF. 1975a. Allometry and early hominids. Science 189:63.

Kay RF. 1975b. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195–216.

Kay RF. 1978. Molar structure and diet in extant Cercopithecoidea. In: Butler PM, Joysey K, editors. Development, function, and evolution of teeth. New York: Academic Press. p 309–339.

Kay RF. 1981a. The ontogeny of premolar dental wear in *Cercocebus albigena* (Cercopithecidae). Am J Phys Anthropol 54:153–155.

Kay RF. 1981b. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141–151.

Kay RF. 1982. Sexual dimorphism in Ramapithecinae. Proc Natl Acad Sci USA 79:209–212.

Kay RF. 1985. Dental evidence for the diet of *Australopithecus*. Annu Rev Anthropol 14:315–341.

Kay RF, Cartmill M. 1977. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ? Primates), with a description of a new genus and species. J Hum Evol 6:19–53.

Kay RF, Hylander WL. 1978. The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In: Montgomery GG, editor. The ecology of arboreal folivores. Washington: Smithsonian Institution Press. p 173–191.

Kay RF, Plavcan JM, Glander KE, Wright PC. 1988. Sexual selection and canine dimorphism in New World monkeys. Am J Phys Anthropol 77:385–397.

Kelley J. 1995a. Sexual dimorphism in canine shape among extant great apes. Am J Phys Anthropol 96:365–389.

Kelley J. 1995b. Sex determination in Miocene catarrhine primates. Am J Phys Anthropol 96:391–417.

Kelley J. 2001. Phylogeny and sexually dimorphic characters: canine reduction in *Ouranopithecus*. In: de Bonis L, Koufos GD, Andrews P, editors. Hominoid evolution and climatic change in Europe: phylogeny of the Neogene hominoid primates of Eurasia. Cambridge: Cambridge University Press. p 269–283.

Kieser JA, Groeneveld HT. 1987a. Tooth size and arcadal length correlates in man. Int J Anthropol 2:37–46.

Kieser JA, Groeneveld HT. 1987b. Static intraspecific allometry of the jaws and teeth in *Cercopithecus aethiops*. J Zool Lond 212:499–510.

Kieser JA, Groeneveld HT. 1987c. Static intraspecific maxillofacial allometry in the chacma baboon. Folia Primatol 48:151–163.

Kieser JA, Groeneveld HT. 1988. Allometric relations of teeth and jaws in man. Am J Phys Anthropol 77:57–67.

Kieser JA, Groeneveld HT. 1990. Static intraspecific allometry of the dentition in *Otolemur crassicaudatus*. Zool J Linn Soc 98:295–306.

Kieser JA, Groeneveld HT. 1991. An allometric perspective on primate postcanine tooth size. Folia Primatol 56:33–38.

Kieser JA, Groeneveld HT, Preston CB. 1985. Compensatory tooth size interaction in a preliterate population. J Hum Evol 14:739–745.

Kieser JA, Groeneveld HT, Preston CB. 1986. On the non-existence of compensatory tooth size interactions in a contemporary Caucasoid population. J Dent Res 65:1105–1107.

Kimbel WH, Delezene LK. 2009. "Lucy" redux: a review of research on *Australopithecus afarensis*. Yrbk Phys Anthropol 52:2–48.

Kimbel WH, Rak Y. 2010. The cranial base of *Australopithecus afarensis*: new insights from the female skull. Phil Trans R Soc B 365:3365–3376.

Kimbel WH, White TD, Johanson DC. 1984. Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. Am J Phys Anthropol 64:337–388.

Kimbel W, Rak Y, Johanson D. 2003. A new hominin skull from Hadar: implications for cranial sexual dimorphism in *Australopithecus afarensis*. Am J Phys Anthropol 36(Suppl):129.

Kimbel WH, Rak Y, Johanson DC. 2004. The skull of *Australopithecus afarensis*. New York: Oxford University Press.

Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC. 2006. Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagensis in the hominin fossil record. J Hum Evol 51:134–152.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci 102:16579–16583.

Kinzey WG. 1974. Ceboid models for the evolution of the hominoid dentition. J Hum Evol 3:193–203.

Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. Am J Phys Anthropol 88:499–514.

Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. Am J Phys Anthropol 81:5–15.

Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int J Primatol 14:207–228.

Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Anim Behav 67:125–139.

Klein LL, Klein DJ. 1975. Social and ecological contrasts between four taxa of Neotropical primates. In: Tuttle RH, editor. Socioecology and psychology of primates. The Hague: Mouton. p 59–85.

Klein LL, Klein DJ. 1977. Feeding behavior of the Colombian spider monkey. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. London: Academic Press. p 154–181.

Klingenberg CP, Mebus K, Auffray J-C. 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? Evol Dev 5:522–531.

Koyabu DB, Endo H. 2009. Craniofacial variation and dietary adaptation of African colobines. J Hum Evol 56:525–536.

Kustaloglu ÖA. 1966. On tool-use and crowded teeth. Curr Anthropol 7:355–356.

Krishtalka L, Stucky RK, Beard KC. 1990. The earliest fossil evidence for sexual dimorphism in primates. Proc Natl Acad Sci USA 87:5223–5226.

Kruuk EB, Slate J, Pemberton JM, Brotherstone S, Guinness F, Clutton-Brock T. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution 56:1683–1695.

Kuroda S. 1992. Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabale Reserve, northern Congo. In: Itoigawa N, Sugiyama Y, Sackett GP, Thompson RKR, editors. Topics in primatology, vol. 2: behavior, ecology and conservation. Tokyo: University of Tokyo Press. p 385–394.

Kuroda S, Nishihara T, Suzuki S, Oko RA. 1996. Sympatric chimpanzees and gorillas in Ndoki Forest, Congo. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p 71–81.

Laden G, Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. J Hum Evol 49:482–498.

Lague MR. 2003. Patterns of joint size dimorphism in the elbow and knee of catarrhine primates. Am J Phys Anthropol 120:278–297.

Lahm S. 1986. Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications for foraging strategy. Am J Primatol 11:9–26.

Lambert F. 1990. Some notes on fig-eating by arboreal mammals in Malaysia. Primates 31:453–458.

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

Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

Lauder GV, Leroi AM, Rose MR. 1993. Adaptations and history. Trends Ecol Evol 8:294–297.

Lauer C. 1975. The relationship of tooth size to body size in a population of rhesus monkeys (*Macaca mulatta*). Am J Phys Anthropol 43:333–339.

Lawler RR, Richard AF, Riley MA. 2005. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). J Hum Evol 48:259–277.

Leakey MG. 1993. Evolution of *Theropithecus* in the Turkana Basin. In: Jablonski NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 85–123.

Legendre P, Desdevises Y. 2009. Independent contrasts and regression through the origin. J Theor Biol 259:727–743.

Leigh SR, Shea BT. 1995. Ontogeny and evolution of adult body size dimorphism in apes. Am J Primatol 36:37–60.

Leigh SR, Setchell JM, Charpentier M, Knapp LA, Wickings EJ. 2008. Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). J Hum Evol 55:75–85.

Leroi AM, Rose MR, Lauder GV. 1994. What does the comparative method reveal about adaptation? Am Nat 143:381–402.

Leutenegger W, Kelly JT. 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioral and ecological correlates in anthropoid primates. Primates 18:117–136.

Leutenegger W, Shell B. 1987. Variability and sexual dimorphism in canine size of *Australopithecus afarensis* and extant hominoids. J Hum Evol 16:359–367.

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

Lieber RL. 2002. Skeletal muscle structure, function, and plasticity. Baltimore: Lippincott Williams and Wilkins.

Lieberman DE, Crompton AW. 2000. Why fuse the mandibular symphysis? A comparative analysis. Am J Phys Anthropol 112:517–540.

Lieberman DE, Ross CF, Ravosa MJ. 2000. The primate cranial base: ontogeny, function, and integration. Yrbk Phys Anthropol 43:117–169.

Lindburg DG. 1969. Rhesus monkeys: mating season mobility of adult males. Science 166:1176–1178.

Lindburg DG. 1976. Dietary habits of rhesus monkeys (*Macaca mulatta* Zimmerman) in Indian forests. J Bombay Nat Hist Soc 73:261–269.

Lindburg DG. 1977. Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in north India. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. London: Academic Press. p 223–249.

Lindenfors P. 2002. Sexually antagonistic selection in primates. J Evol Biol 15:595–607.

Lindenfors P, Tullberg BS. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. Biol J Linn Soc 64:413–447.

Line SRP. 2001. Molecular morphogenetic fields in the development of human dentition. J Theor Biol 211:67–75.

Lockwood CA. 1999. Sexual dimorphism in the face of *Australopithecus afarensis*. Am J Phys Anthropol 108:97–127.

Lockwood CA, Richmond BG, Jungers WL, Kimbel WH. 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. J Hum Evol 31:537–548.

Lockwood CA, Menter CG, Moggi-Cecchi J, Keyser AW. 2007. Extended male growth in a fossil hominin species. Science 318:1443–1446.

Logan M, Sanson GD. 2002. The association of tooth wear with sociality of free-ranging male koalas (*Phascolarctos cinereus* Goldfuss). Austral J Zool 50:621–626.

Lombardi AV. A factor analysis of morphogenetic fields in the human dentition. Am J Phys Anthropol 42:99–104.

Lovejoy CO. 1981. The origin of man. Science 211:341–350.

Lovejoy CO. 2009. Reexamining human origins in light of *Ardipithecus ramidus*. Science 326:74e1–74e8.

Lovejoy CO, Kern KF, Simpson SW, Meindl RS. 1989. A new method for estimation of skeletal dimorphism in fossil samples with an application to *Australopithecus afarensis*. In: Giacobini G, editor. Hominidae. Milano: Jaca Book. p 103–108.

Lu J-Q, Hou J-H, Wang H-F, Ou W-Y. 2007. Current status of *Macaca mulatta* in Taihangshan Mountains area, Jiyuan, Henan, China. Int J Primatol 28:1085–1091.

Lucas PW. 1981. An analysis of canine size and jaw shape in some Old and New World non-human primates. J Zool Lond 195:437–448.

Lucas PW. 1982. An analysis of the canine tooth size of Old World higher primates in relation to mandibular length and body weight. Arch Oral Biol 27:493–496.

Lucas PW, Corlett RT. 1998. Seed dispersal by long-tailed macaques. Am J Primatol 45:29–44.

Lucas PW, Corlett RT, Luke DA. 1986. Sexual dimorphism of tooth size in anthropoids. Hum. Evol. 1:23–39.

Lucas PW, Luke DA. 1984. Chewing it over: basic principles of food breakdown. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 283–330.

MacKinnon JR, MacKinnon KS. 1978. Comparative feeding ecology of six sympatric primates in west Malaysia. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, vol. 1. London: Academic Press. p 305–321.

MacKinnon JR, MacKinnon KS. 1980. Niche differentiation in a primate community. In: Chivers DJ, editor. Malayan forest primates: ten years' study in tropical rain forest. New York: Plenum Press. p 167–190.

Maddison WP. 1990. A method for testing the correlation evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44: 539–557.

Maddison WP. 2000. Testing character correlation using pairwise comparisons on a phylogeny. J Theor Biol 202:195–204.

Maddison WP, Maddison DR. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.6. Available online at http://mesquiteproject.org.

Mahler PE. 1973. Metric variation in the pongid dentition. PhD dissertation, University of Michigan.

Makwana SC. 1978. Field ecology and behaviour of the rhesus monkey (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. Primates 19:483–492.

Malenky RK, Stiles EW. 1991. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. Am J Primatol 23:153–169.

Malenky RK, Wrangham RW. 1994. A quantitative comparison of terrestrial herbaceous food consumption in *Pan paniscus* in Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. Am J Primatol 32:1–12.

Manly BFJ. 1997. Randomization, bootstrap and Monte Carlo methods in evolutionary biology, second edition. London: Chapman & Hall.

Marriog G, Cheverud JM. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of the New World monkeys. Evolution 55:2576–2600.

Marroig G, Vivo M, Cheverud JM. 2004. Cranial evolution in sakis (*Pithecia*, Platyrrhini) II: evolutionary processes and morphological integration. J Evol Biol 17:144–155.

Martin RD. 1993. Allometric aspects of skull morphology in *Theropithecus*. In: Jablonski NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 273–298.

Martins EP, Garland T Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646–667.

Masi S, Cipolletta C, Robbins MM. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. Am J Primatol 71:91–100.

Masterson TJ. 2003. Canine dimorphism and interspecific canine form in *Cebus*. Int J Primatol 24:159–178.

Maynard Smith J, Savage RJG. 1959. The mechanics of mammalian jaws. School Sci. Rev. 141:289–301.

McCollum MA. 1999. The robust australopithecine face: a morphogenetic perspective. Science 284:301–305.

McCollum MA, Sharpe PT. 2001. Developmental genetics and early hominid craniodental evolution. Bioessays 23:481–493.

McCollum MA. 2007. Rethinking incisor size and diet in anthropoids: diet, incisor wear and incisor breadth in the African apes. Am J Phys Anthropol 133:986–993.

McGraw WS. 1996. The positional behavior and habitat use of six sympatric monkeys in the Tai Forest, Ivory Coast. PhD dissertation. State University of New York at Stony Brook.

McGraw WS, Fleagle JG. 2006. Biogeography and evolution of the *Cercocebus-Mandrillus* clade: evidence from the face. In: Lehman SM, Fleagle JG, editors. Primate biogeography: progress and prospects. New York: Springer. p 201–224.

McGrew WC. 1996. Dominance status, food sharing, and reproductive success in chimpanzees. In: Wiessner P, Schiefenhövel W, editors. Food and the status quest: an interdisciplinary perspective. Oxford: Berghahn Books. p 39–45.

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry, and open habitat: Mt. Assirik, Senegal, west Africa. J Hum Evol 10:227–244.

McHenry HM. 1984. Relative cheek-tooth size in *Australopithecus*. Am J Phys Anthropol 64:297–306.

McHenry HM. 1991. Sexual dimorphism in *Australopithecus afarensis*. J Hum Evol 20:21–32.

McHenry HM. 1992. Body size and proportions in early hominids. Am J Phys Anthropol 87:407–431.

McHenry HM. 1994. Behavioral ecological implications of early hominid body size. J Hum Evol 27:77–87.

McHenry HM, Corruccini RS. 1981. *Pan paniscus* and human evolution. Am J Phys Anthropol 54:355–367.

Midford PE, Garland T Jr, Maddison WP. 2008. PDAP package of Mesquite. Version 1.14. Available online at http://mesquiteproject.org.

Mills JRE. 1963. Occlusion and malocclusion of the teeth of primates. In: Brothwell DR, editor. Dental anthropology. Oxford: Pergamon Press. p 29–51.

Milton K. 1980. The foraging strategy of howler monkeys. New York: Columbia University Press.

Milton K. 1985. Multimale mating and the absence of canine tooth dimorphism in woolly spider monkeys (*Brachyteles arachnoides*). Am J Phys Anthropol 68:519–523.

Mitani M. 1989. *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. Primates 30:307–323.

Mitani JC, Gros-Louis J, Richards AF. 1996. Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. Am Nat 147:966–980.

Mitsiadis TA, Drouin J. 2008. Deletion of the Pitx1 genomic locus affects mandibular tooth morphogenesis and expression of the *Barx1* and *Tbx1* genes. Dev Biol 313:887–896.

Mittermeier RA, van Roosmalen MGM. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia Primatol 36:1–39.

Mitteroecker P, Bookstein F. 2008. The evolutionary role of modularity and integration in the hominoid cranium. Evolution 62:943–958.

Møller AP, Birkhead TR. 1992. A pairwise comparison method as illustrated by copulation frequency in birds. Am Nat 139:644–656.

Moorrees CFA, Reed RB. 1964. Correlation among crown diameters of human teeth. Arch Oral Biol 9:685–697.

Moran MD. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405.

Morris DH. 1967. Maxillary premolar variation among the Papago Indians. J Dent Res 46:736–738.

Morris DH. 1974. Hominid canine tooth semantics. Man 9:585–590.

Moss ML, Young RW. 1960. A functional approach to craniology. Am J Phys Anthropol 18:281–292.

Moynihan M. 1976. The New World primates. Princeton: Princeton University Press.

Nakagawa N. 2003. Difference in food selection between patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) in Kala Maloue National Park, Cameroon, in relation to nutrient content. Primates 44:3–11.

Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol 15:1044–1045.

Napier JR, Napier PH. A handbook of living primates. New York: Academic Press.

Naples VL. 1982. Cranial osteology and function in the tree sloths, *Bradypus*, and *Choloepus*. Am Mus Nov 2739:1–41.

Nash LT. 1986. Dietary, behavioral, and morphological aspects of gummivory in primates. Yrbk Phys Anthropol 29:113–137.

Neville MK. 1972. Social relations within troops of red howler monkeys (*Alouatta seniculus*). Folia Primatol 18:47–77.

Newton-Fisher NE. 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. Afr J Ecol 37:344–354.

Nishihara T. 1995. Feeding ecology of western lowland gorillas in the Nouabalé-Ndoki National Park, northern Congo. Primates 35:151–168.

Nunn CL, Barton RA. 2001. Comparative methods for studying primate adaptation and allometry. Evol Anthropol 10:81–98.

O'Connor CF, Franciscus RG, Holton NE. 2005. Bite force production capability and efficiency in Neandertals and modern humans. Am J Phys Anthropol 127:129–151.

Olson DK. 1985. Gum exudates as a dietary staple of patas monkeys. Am J Phys Anthropol 66:210–211.

Olson DK, Chism J. 1984. Gum feeding as a dietary adaptation of wild patas monkeys (*Erythrocebus patas*) in Kenya. Int J Primatol 5:370.

Olson EC, Miller RA. 1958. Morphological integration. Chicago: University of Chicago Press.

O'Neill MC, Dobson SD. 2008. The degree and pattern of phylogenetic signal in primate long-bone structure. J Hum Evol 54:309–322.

Opazo JC, Wildman DE, Prychitko T, Johnson RM, Goodman M. 2006. Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). Mol Phylogenet Evol 40:274–280.

Oppenheimer A. 1964. Tool use and crowded teeth in Australopithecinae. Curr Anthropol 5:419–421.

Oppenheimer A. 1966. On tool-use and crowded teeth. Curr Anthropol 7:357–359.

Orihuela Lopez G, Terborgh J, Ceballos N. 2005. Food selection by a hyperdense population of red howler monkeys (*Alouatta seniculus*). J Trop Ecol 21:445–450.

Osterholz M, Walter L, Roos C. 2009. Retropositional events consolidate the branching order among New World monkey genera. Mol Phylogenet Evol 50:507–513.

Oxnard CE. 1978. One biologist's view of morphometrics. Ann Rev Ecol Syst 9:219–241.

Packard GC, Boardman TJ. 1987. The misuse of ratios to scale physiological data that vary allometrically with body size. In: Feder ME, Bennett AF, Burggren WW, Huey RB, editors. New directions in ecological physiology. Cambridge: Cambridge University Press. p 216–239.

Packard GC, Boardman TJ. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. Physiol Zool 61:1–9.

Page SL, Chiu C-h, Goodman M. 1999. Molecular phylogeny of Old World monkeys (Cercopithecidae) as inferred from γ-globin DNA sequences. Mol Phylogenet Evol 13:348–359.

Pagel MD, Harvey PH. 1989. Comparative methods for examining adaptation depend on evolutionary models. Folia Primatol 53:203–220.

Paoli T, Palagi E, Borgognini Tarli SM. 2006. Reevaluation of the dominance hierarchy in bonobos (*Pan paniscus*). Am J Phys Anthropol 130:116–122.

Parish AR. 1994. Female relationships in bonobos (*Pan paniscus*): evidence for bonding, cooperation, and female dominance in a male-philopatric species. Hum Nat 7:61–96.

Peres CA. 1993. Notes on the ecology of buffy saki monkeys (*Pithecia alibcans*, Gray 1860): a canopy seed-predator. Am J Primatol 31:129–140.

Perneger TV. 1998. What's wrong with Bonferroni adjustments. Brit Med J 316:1236–1238.

Pilbeam D, Gould SJ. 1974. Size and scaling in human evolution. Science 186:892–901.

Plavcan JM. 1990. Sexual dimorphism in the dentition of extant anthropoid primates. PhD dissertation, Duke University.

Plavcan JM. 1993a. Canine size and shape in male anthropoid primates. Am J Phys Anthropol 92:201–216.

Plavcan JM. 1993b. Catarrhine dental variability and species recognition in the fossil record. In Kimbel WH, Martin LB, editors. Species, species concepts, and primate evolution. New York: Plenum Press. p 239–263.

Plavcan JM. 1998. Correlated response, competition, and female canine size in primates. Am J Phys Anthropol 107:401–416.

Plavcan JM. 2000. Inferring social behavior from sexual dimorphism in the fossil record. J Hum Evol 39:327–344.

Plavcan JM. 2001. Sexual dimorphism in primate evolution. Yrbk Phys Anthropol 44:25–58.

Plavcan JM. 2002. Taxonomic variation in the patterns of craniofacial dimorphism in primates. J Hum Evol 42:579–608.

Plavcan JM. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: implications for the fossil record. Am J Phys Anthropol 120:38–60.

Plavcan JM. 2004. Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In: Kappeler PM, van Schaik CP, editors. Sexual selection in primates: new and comparative perspectives. Cambridge: Cambridge University Press. p 230–252.

Plavcan JM, Daegling DJ. 2006. Interspecific and intraspecific relationships between tooth size and jaw size in primates. J Hum Evol 51:171–184.

Plavcan JM, Kelley J. 1996. Evaluating the "dual selection" hypothesis of canine reduction. Am J Phys Anthropol 99:379–387.

Plavcan JM, Ruff CB. 2008. Canine size, shape, and bending strength in primates and carnivores. Am J Phys Anthropol 136:65–84.

Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. Am J Phys Anthropol 87:461–477.

Plavcan JM, van Schaik CP. 1994. Canine dimorphism. Evol Anthropol 2:208–214.

Plavcan JM, van Schaik CP. 1997a. Interpreting hominid behavior on the basis of sexual dimorphism. J Hum Evol 32:345–374.

Plavcan JM, van Schaik CP. 1997b. Intrasexual competition and body weight dimorphism in anthropoid primates. Am J Phys Anthropol 103:37–68.

Plavcan JM, van Schaik CP, Kappeler PM. 1995. Competition, coalitions and canine size in primates. J Hum Evol 28:245–276.

Plavcan JM, Lockwood CA, Kimbel WH, Lague MR, Harmon EH. 2005. Sexual dimorphism in *Australopithecus afarensis* revisited: how stron is the case for a human-like pattern of dimorphism? J Hum Evol 48:313–320.

Plavcan JM, Ward CV, Paulus FL. 2009. Estimating canine tooth crown height in early *Australopithecus*. J Hum Evol. 57, 2–10.

Polanski JM, Franciscus RG. 2006. Patterns of craniofacial integration in extant *Homo*, *Pan*, and *Gorilla*. Am J Phys Anthropol 131:38–49.

Pope TR. 2002. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. Behav Ecol Sociobiol 27:439–446.

Pope TR. 1992. The influence of dispersal patterns and mating systems on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evolution 46:1112–1128.

Porter CA, Sampaio I, Schneider H, Schneider MP, Czelusniak J, Goodman M. 1995. Evidence on primate phylogeny from ε-globin gene sequences and flanking regions. J Mol Evol 40:30–55.

Porter CA, Czelusniak J, Schneider H, Schneider MP, Sampaio I, Goodman M. 1997. Sequences of the primate ε-globin gene: implications for systematics of the marmosets and other New World primates. Gene 205:59–71.

Porter CA, Sampaio I, Schneider H, Schneider MP, Czelusniak J, Goodman M. 1999. Sequence from the 5′ flanking region of the ε-globin gene support the relationship of *Callicebus* with the pitheciins. Am J Primatol 48:69–75.

Post D, Goldstein S, Melnick D. 1978. An analysis of cercopithecoid odontometrics: II. Relations between dental dimorphism, body size dimorphism and diet. Am J Phys Anthropol 49:533–544.

Prout T. 1964. Observations on structural reduction in evolution. Am Nat 98:239–249.

Pruetz JD, Isbell LA. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. Behav Ecol Sociobiol 49:38–47.

Prychitko T, Johnson RM, Wildman DE, Gumucio D, Goodman M. 2005. The phylogenetic history of New World monkey β globin reveals a platyrrhine β to δ gene conversion in the atelid ancestry. Mol Phylogenet Evol 35:225–234.

Purvis A, Webster AJ. 1999. Phylogenetically independent comparisons and primate phylogeny. In: Lee PC, editor. Comparative primate socioecology. Cambridge: Cambridge University Press. p 44–68.

Qiu M, Bulfone A, Ghattas I, Meneses JJ, Christensen L, Sharpe PT, Presley R, Pedersen RA, Rubenstein JLR. 1997. Role of the Dlx homeobox genes in the proximodistal patterning of the branchial arches: mutations of Dlx-1, Dlx-2, and Dlx-1 and -2 alter morphogenesis of proximal skeletal and soft tissue structures derived from the first and second arches. Dev Biol 185:165–184.

Raaum RL, Sterner KN, Noviello CM, Stewart C-B, Disotell TR. 2005. Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. J Hum Evol 48:237–257.

Rak Y. 1983. The australopithecine face. New York: Academic Press.

Rak Y. 1985. Australopithecine taxonomy and phylogeny in light of facial morphology. Am J Phys Anthropol 66:281–287.

Rak Y, Hylander WL. 2008. What else is the tall mandibular ramus of the robust australopiths good for? In: Vinyard CJ, Ravosa MJ, Wall CE, editors. Primate craniofacial function and biology. New York: Springer. p 431–442.

Ramos-Fernández G, Ayala-Orozco B. 2003. Population size and habitat use of spider monkeys in Punta Laguna, Mexico. In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer/Plenum Press. p 191–209.

Ravosa MJ. 1988. Browridge development in Cercopithecidae: a test of two models. Am J Phys Anthropol 76:535–555.

Ravosa MJ. 1990. Functional assessment of subfamily variation in maxillomandibular morphology among Old World monkeys. Am J Phys Anthropol 82:199–212.

Ravosa MJ. 1991. Interspecific perspective on mechanical and nonmechanical models of primate circumorbital morphology. Am J Phys Anthropol 86:369–396.

Ravosa MJ. 1992. Allometry and heterochrony in extant and extinct Malagasy primates. J Hum Evol 23:197–217.

Ravosa MJ 1996. Jaw morphology and function in living and fossil Old World monkeys. Int J Primatol 17:909–932.

Ravosa MJ, Vinyard CJ, Gagnon M, Islam SA. 2000. Evolution of anthropoid jaw loading and kinematic patterns. Am J Phys Anthropol 112:493–516.

Ray DA, Xing J, Hedges DJ, Hall MA, Laborde ME, Anders BA, White BR, Stoilova N, Fowlkes JD, Landry KE, Chemnick LG, Ryder OA, Batzer MA. 2005. *Alu* insertion loci and platyrrhine primate phylogeny. Mol Phylogenet Evol 35:117–126.

Réale D, Festa-Bianchet M. 2000. Quantitative genetics of life-history traits in a long-lived wild mammal. Heredity 85:593–603.

Reist JD. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Can J Zool 63:1429–1439.

Reno PL, Meindl RS, McCollum MA, Lovejoy CO. 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. Proc Natl Acad Sci USA 100:9404–9409.

Reno PL, Meindl RS, McCollum MA, Lovejoy CO. 2005. The case is unchanged and remains robust: *Australopithecus afarensis* exhibits only moderate skeletal dimorphism. A reply to Plavcan et al. (2005). J Hum Evol 49:279–288.

Reno PL, McCollum MA, Meindl RS, Lovejoy CO. 2010. An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. Phil Trans R Soc B 365:3355–3363.

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

Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Richard AF. 1992. Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. J Hum Evol 22:395–406.

Richard AF, Goldstein SJ, Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. Int J Primatol 10:569–594.

Richmond BG, Jungers WL. 1995. Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. J Hum Evol 29:229–245.

Ridley M. 1983. The explanation for organic diversity: the comparative method and adaptations for mating. Oxford: Oxford University Press.

Riesenfeld A. 1955. The variability of the temporal lines, its causes and effects. Am J Phys Anthropol 13:599–620.

Riss DC, Goodall J. 1977. The recent rise to the alpha-rank in a population of free-living chimpanzees. Folia Primatol 27:134–151.

Ritzman TB, Spencer MA. 2009. Coronoid process morphology and function in anthropoid primates. Am J Phys Anthropol 48(Suppl.):221.

Robbins MM. 1995. A demographic analysis of male life history and social structure of mountain gorillas. Behaviour 132:21–47.

Robbins MM. 1999. Male mating patterns in wild multimale mountain gorilla groups. Anim Behav 57:1013–1020.

Robbins MM. 2006. Gorillas: diversity in ecology and behavior. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York: Oxford University Press. p 305–320.

Robinson MR, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk LEB. 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60:2168–2181.

Rodman PS. 1978. Diets, densities and distributions of Bornean primates. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington: Smithsonian Institution Press. p 465–478.

Roff DA. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. Heredity 74:481–490.

Rogers ME, Maisels F, Williamson EA, Fernandez M, Tutin CEG. 1990. Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. Oecologia 84:326–339.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG. 1996. Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. Am J Primatol 40:297–313.

Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis MJ, Tutin CEG. 2004. Western gorilla diet: a synthesis from six sites. Am J Primatol 64:173–192.

Rohlf FJ. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. Evolution 51:2143–2160.

Rohlf FJ. 2006. A comment on phylogenetic correction. Evolution 60:1509–1515.

Roonwal ML, Mohnot SM. 1977. Primates of south Asia: ecology, sociobiology, and behavior. Cambridge: Harvard University Press.

Rosenberger AL. 1977. *Xenothrix* and cebid phylogeny. J Hum Evol 6:461–481.

Rosenberger AL. 1978. Loss of incisor enamel in marmosets. J Mammal 59:207–208.

Rosenberger AL. 1992. Evolution of feeding niches in New World monkeys. Am J Phys Anthropol 88:525–562.

Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45:281–298.

Rosenberger AL, Strier KB. 1989. Adaptive radiation of the ateline primates. J Hum Evol 18:717–750.

Rosenberger AL, Setoguchi T, Shigehara N. 1990. The fossil record of callitrichine primates. J Hum Evol 19:202–236.

Ross C. 1995a. Muscular and osseous anatomy of the primate anterior temporal fossa and the functions of the postorbital septum. Am J Phys Anthropol 98:275–306.

Ross CF. 1995b. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. J Hum Evol 29:201–227.

Ross CF, Hylander WL. 2000. Electromyography of the anterior temporalis and masseter muscles of owl monkeys (*Aotus trivirgatus*) and the function of the postorbital septum. Am J Phys Anthropol 112:455–468.

Ross CF, Ravosa MJ. 1993. Basicranial flexion, relative brain size, and facial kyphosis in nonhuman primates. Am J Phys Anthropol 91:305–324.

Ross CF, Lockwood CA, Fleagle JG, Jungers WL. 2002. Adaptation and behavior in the primate fossil record. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP, editors. Reconstruction behavior in the primate fossil record. New York: Kluwer Academic / Plenum Publishers. p 1–41.

Rothman JM, Plumptre AJ, Dierenfeld ES, Pell AN. 2007. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habits. J Trop Ecol 23:673–682.

Rudran R. 1979. The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In: Eisenberg JF, editor. Vertebrate ecology in the northern Neotropics. Washington: Smithsonian Institution Press. p 107–126.

Ruvolo M. 1997. Genetic diversity in hominoid primates. Annu Rev Anthropol 26:515–540.

Ryan AS. 1979. Tooth sharpening in primates. Curr Anthropol 20:121–122.

Ryan AS, Johanson DC. 1989. Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and nonhuman primates. J Hum Evol 18:235–268.

Sarmiento EE. 2010. Comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328:1105-b.

Schaller GB. 1963. The mountain gorilla: ecology and behavior. Chicago: University of Chicago Press.

Schneider H, Schneider MPC, Sampaio I, Harada ML, Stanhope M, Czelusniak J, Goodman M. 1993. Mol Phylogenet Evol 2:225–242.

Schneider H, Sampaio I, Harada ML, Barroso CML, Schneider MPC, Czelusniak J, Goodman M. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and ε-globin sequences. Am J Phys Anthropol 100:153–179.

Schneider H, Canavez FC, Sampaio I, Moreira MAM, Tagliaro CH, Seuánez HN. 2001. Can molecular data place each Neotropical monkey in its own branch? Chromosoma 109:515–523.

Schrago CG. 2007. On the time scale of New World primate diversification. Am J Phys Anthropol 132:344–354.

Schultz AH. 1966. On tool-use and crowded teeth. Curr Anthropol 7:356–357.

Scott GR. 1977. Lingual tubercles and the maxillary incisor-canine field. J Dent Res 56:1192.

Scott JE, Stroik LK. 2006. Bootstrap tests of significance and the case for humanlike skeletal-size dimorphism in *Australopithecus afarensis*. J Hum Evol 51:422–428.

Scott JE, Schrein CM, Kelley J. 2009. Beyond *Gorilla* and *Pongo*: alternative models for evaluating variation and sexual dimorphism in fossil hominoid samples. Am J Phys Anthropol 140:253–264.

Sekulic R. 1982a. Behavior and ranging patterns of a solitary female red howler (*Alouatta seniculus*). Folia Primatol 38:217–232.

Sekulic R. 1982b. The function of howling in red howler monkeys (*Alouatta seniculus*). Behaviour 81:38–54.

Sekulic R, Chivers DJ. 1986. The significance of call duration in howler monkeys. Int J Primatol 7:183–190.

Semaw S, Rogers MJ, Quade J, Renne PR, Butler RF, Dominguez-Rodrigo M, Stout D, Hart WS, Pickering T, Simpson SW. 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. J Hum Evol 45:169–177.

Semaw S, Simpson SW, Quade J, Renne PR, Butler RF, McIntosh WC, Levin N, Dominguez-Rodrigo M, Rogers MJ. 2005. Early Pliocene hominid from Gona, Ethiopia. Nature 433:301–305.

Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). C R Acad Sci Ser IIA 332, 137–144.

Shah N. 2003. Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). PhD dissertation. State University of New York at Stony Brook.

Shea BT. 1983a. Size and diet in the evolution of African ape craniodental form. Folia Primatol 40:32–68.

Shea BT. 1983b. Paedomorphosis and neoteny in the pygmy chimpanzee. Science 222:521–522.

Shea BT. 1985. On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. Am J Phys Anthropol 68:329–342.

Shea BT, Gomez AM. 1988. Tooth scaling and evolutionary dwarfism: an investigation of allometry in human pygmies. Am J Phys Anthropol 77:117–132.

Shively C, Clarke S, King N, Schapiro S, Mitchell G. 1982. Patterns of sexual behavior in male macaques. Am J Primatol 2:373–384.

Sicotte P. 1993. Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. Am J Primatol 30:21–36.

Siegel MI. 1978. Dentofacial relationships in sexually dimorphic populations. In: Chivers DJ, Joysey KA, editors. Recent advances in primatology, vol. 3. London: Academic Press. p 73–75.

Siegel MI, Gest T. 1980. The relationship between body weight, facial, and dental dimensions in a population of olive baboons (*Papio cynocephalus anubis*). Arch Oral Biol 25:601–602.

Silver SC, Ostro LET, Yeager CP, Horwich R. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. Am J Primatol 45:263–279.

Silverman N, Richmond B, Wood B. 2001. Testing the taxonomic integrity of *Paranthropus boisei sensu stricto*. Am J Phys Anthropol 115:167–178.

Simons EL, Plavcan JM, Fleagle JG. 1999. Canine sexual dimorphism in Egyptian Eocene anthropoid primates: *Catopithecus* and *Proteopithecus*. Proc Natl Acad Sci USA 96:2559–2562.

Singleton M. 2004. Geometric morphometric analysis of functional divergence in mangabey facial form. J Anthropol Sci 82:27–44.

Slater KY, Schaffner CM, Aureli F. 2009. Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). Am J Primatol 71:21–29.

Smith RJ. 1980. Rethinking allometry. J Theor Biol 87:97–111.

Smith RJ. 1981a. Interspecific scaling of maxillary canine size and shape in female primates: relationships to social structure and diet. J Hum Evol 10:165–173.

Smith RJ. 1981b. On the definition of variables in studies of primate dental allometry. Am J Phys Anthropol 55:323–329.

Smith RJ. 1984a. Comparative functional morphology of maximum mandibular opening (gape) in primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 231–255.

Smith RJ. 1984b. Determination of relative size: the “criterion of subtraction” problem in allometry. J Theor Biol 108:131–142.

Smith RJ. 1994. Degrees of freedom in interspecific allometry: an adjustment for the effects of phylogenetic constraint. Am J Phys Anthropol 93:95–107.

Smith RJ. 1999. Statistics of sexual size dimorphism. J Hum Evol 36:423–459.

Smith RJ. 2005. Relative size versus controlling for size: interpretation of ratios in research on sexual dimorphism in the human corpus callosum. Curr Anthropol 46:249–273.

Smith RJ. 2009. Use and misuse of the reduced major axis for line-fitting. Am J Phys Anthropol 140:476–486.

Smith RJ, Cheverud JM. 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch’s rule in primates. Int J Primatol 23:1095–1135.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–559.

Smith RJ, Petersen CE, Gipe DP. 1983. Size and shape of the mandibular condyle in primates. J Morphol 177:59–68.

Sofaer JA. 1973. A model relating tooth development interaction and differential evolutionary reduction of tooth size. Evolution 27:427–434.

Sofaer JA, Bailit HL, MacLean CJ. 1971. A developmental basis for differential tooth reduction during hominid evolution. Evolution 25:509–517.

Soini P. 1986. A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. Prim Conserv 7:63–71.

Sokal RR, Rohlf FJ. 1995. Biometry, third edition. New York: W. H. Freeman and Company.

Solanki GS, Kumar A, Sharma BK. 2008. Feeding ecology of *Trachypithecus pileatus* in India. Int J Primatol 29:173–182.

Son VD. 2003. Diet of *Macaca fascicularis* in a mangrove forest. Vietnam Lab Prim News 42:1–5.

Spencer MA. 1992. Zygomatic arch form and masticatory muscle development in primates. Am J Phys Anthropol 14(Suppl):153–154.

Spencer MA. 1995. Masticatory system configuration and diet in anthropoid primates. PhD dissertation, State University of New York at Stony Brook.

Spencer MA. 1998. Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. J Hum Evol 25–54.

Spencer MA. 1999. Constraints on masticatory system evolution in anthropoid primates. Am J Phys Anthropol 108:483–506.

Spencer MA. 2003. Tooth-root form and function in platyrrhine seed-eaters. Am J Phys Anthropol 122:325–335.

Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. Am J Phys Anthropol 91:1–20.

Spencer MA, Spencer GS. 1993. MacMorph data acquisition package. Stony Brook: State University of New York.

Spoor F, Leakey MG, Gathogo PN, Brown FH, Antón SC, McDougall I, Kiarie C, Manthi FK, Leakey LN. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. Nature 448:688–691.

Stanford CB. 1991a. The capped langur in Bangladesh: behavioral ecology and reproductive tactics. Basel: Karger.

Stanford CB. 1991b. The diet of the capped langur (*Presbytis pileata*) in a moist deciduous forest in Bangladesh. Int J Primatol 12:199–216.

Stanford CB. 1998. The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. Curr Anthropol 39:399–420.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. Oikos 41:173–187.

Steiper ME, Ruvolo M. 2003. New World monkey phylogeny based on X-linked G6PD DNA sequences. Mol Phylogenet Evol 27:121–130.

Steiper ME, Young NM. 2006. Primate molecular divergence dates. Mol Phylogenet Evol 41:384–394.

Stern JT Jr. 1974. Biomechanical significance of the instantaneous center of rotation: the human temporomandibular joint. J Biomech 7, 109.

Sterner KN, Raaum RL, Zhang Y-P, Stewart C-B, Disotell TR. 2006. Mitochondrial data support an odd-nosed colobine clade. Mol Phylogenet Evol 40:1–7.

Stock DW. 2001. The genetic basis of modularity in the development and evolution of the vertebrate dentition. Phil Trans R Soc Lond B 356:1633–1653.

Stoinski TS, Rosenbaum S, Ngaboyamahina T, Vecellio V, Ndagijimana F, Fawcett K. 2009. Patterns of male reproductive behaviour in multi-male groups of mountain gorillas: examining theories of reproductive skew. Behaviour 146:1193–1215.

Strier KB. 1992. Atelinae adaptations: behavioral strategies and ecological constraints. Am J Phys Anthropol 88:515–524.

Struhsaker TT. 1967. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. Ecology 48:892–904.

Struhsaker TT, Leland L. 1977. Palm-nut smashing by *Cebus apella* in Colombia. Biotropica 9:124–126.

Suarez BK, Bernor R. 1972. Growth fields in the dentition of the gorilla. Folia Primatol 18:356–367.

Suarez BK, Williams BJ. 1973. Dental growth fields and premolar morphology. J Dent Res 52:632.

Suwa G, Asfaw B, Kono RT, Kubo D, Lovejoy CO, White TD. 2009a. The *Ardipithecus ramidus* skull and its implications for hominid origins. Science 326:68e1–68e7.

Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO, White TD. 2009b. Paleobiological implications of the *Ardipithecus ramidus* dentition. Science 326:94–99.

Swindler DR, Orlosky FJ. 1974. Metric and morphological variability in the dentition of colobine monkeys. J Hum Evol 3:135–160.

Swindler DR, Sirianni JE, 1975. Tooth and body size correlations in *Macaca nemestrina*. J Dent Res 54:695.

Symington MM. 1988. Food composition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behavior 105:117–134.

Symington MM. 1990. Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol 11:47–61.

Szalay FS. 1975. Hunting-scavenging protohominids: a model for hominid origins. Man 10:420–429.

Takai M, Nishimura T, Shigehara N, Setoguchi T. 2009. Meaning of canine sexual dimorphism in fossil owl monkey, *Aotus dindensis* from middle Miocene of La Venta, Colombia. In: Koppe T, Meyer G, Alt KW, editors. Comparative dental morphology. Basel: Karger. p 55–59.

Taylor AB. 2002. Masticatory form and function in African apes. Am J Phys Anthropol 117:133–156.

Taylor AB. 2005. A comparative analysis of temporomandibular joint morphology in African apes. J Hum Evol 48:555–574.

Taylor AB. 2006. Diet and mandibular morphology in African apes. Int J Primatol 27: 181–201.

Taylor AB, Vinyard CJ. 2004. Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. J. Morphol. 261:276–285.

Taylor AB, Vinyard CJ. 2008. The relationship between jaw-muscle architecture and feeding behavior in primates: tree-gouging and nongouging gummivorous callitrichids as a natural experiment. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. Primate craniofacial function and biology. New York: Springer. p 241–262.

Taylor AB, Vinyard CJ. 2009. Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. J Hum Evol 57:710–720.

Taylor AB, Eng CM, Anapol FC, Vinyard CJ. 2009. The functional correlates of jaw-muscle fiber architecture in tree-gouging and nongouging callitrichid monkeys. Am J Phys Anthropol. 139:353–367.

Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. Proc Natl Acad Sci USA 97:13506–13511.

Terborgh J. 1983. Five New World primates: a study in comparative ecology. Princeton: Princeton University Press.

Thomas BL, Tucker AS, Qiu M, Ferguson CA, Hardcastle Z, Rubenstein JLR, Sharpe PT. 1997. Role of *Dlx-1* and *Dlx-2* genes in patterning of the murine dentition. Development 124:4811–4818.

Thorén S, Lindenfors P, Kappeler PM. 2006. Phylogenetic analyses of dimorphism in primates: evidence for stronger selection on canine size than on body size. Am J Phys Anthropol 130:50–59.

Thorington RW, Ruiz JC, Eisenberg JF. 1984. A study of a black howling monkey (*Alouatta caraya*) population in northern Argentina. Am J Primatol 6:357–360.

Ting N. 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living Colobus monkeys. J Hum Evol 55:312–325.

Tosi AJ, Morales JC, Melnick DJ. 2002. Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. Int J Primatol 23:161–178.

Tosi AJ, Morales JC, Melnick DJ. 2003. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. Evolution 57:1419–1435.

Townsend GC, Brown T. 1979. Family studies of tooth size factors in the permanent dentition. Am J Phys Anthropol 50:183–190.

Turnbull WD. 1970. Mammalian masticatory apparatus. Fieldiana Geol 18:147–356.

Turner CG. 1969. Directionality in the canine field model. J Dent Res 48:1310.

Tutin CEG. 1996. Ranging and social structure of lowland gorillas in the Lope´ Reserve, Gabon. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p 58–70.

Tutin CEG, Fernandez M. 1985. Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. Int J Primatol 6:27–43.

Tutin CEG, Fernandez M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. Am J Primatol 30:195–211.

Tutin CEG, Fernandez M, Pierce AH, Williamson EA. 1984. Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon. Int J Primatol 6:27–43.

Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. Phil Trans R Soc Lond 334B:179–186.

Tutin CEG, Ham RM, White LJT, Harrison MJS. 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. Am J Primatol 42:1–42.

Uehara S. 1990. Utilization patterns of a marsh grassland within the tropical rain forest by the bonobos (*Pan paniscus*) of Yalosidi, Republics of Zaire. Primates 31:311–322.

Ungar PS. 1990. Incisor use and microwear in *Cebus olivaceus* and *Alouatta seniculus*. Am J Primatol 20:43–50.

Ungar PS. 1996. Relationship of incisor size to diet and anterior tooth use in sympatric Sumatran anthropoids. Am J Primatol 38:145–156.

Ungar P. 1998. Dental allometry morphology, and wear as evidence for diet in fossil primates. Evol Anthropol 6:205–217.

Ungar, PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J Hum Evol 46:605–622.

Ungar PS, Grine FE. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. J Hum Evol 20:313–340.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Phil Trans R Soc B 365:3345–3354.

Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G. 2006. Intragroup lethal aggression in wild spider monkeys. Am J Primatol 68:732–737.

Van Eijden TMGJ. 1990. Jaw muscle activity in relation to the direction and point of application of bite force. J Dent Res 69:901–905.

Van Eijden TMGJ. 1991. Three-dimensional analyses of human bite-force magnitude and moment. Arch Oral Biol 36:535–539.

Van Eijden TMGJ, Koolstra JH, Brugman P, Weijs WA. 1988. A feedback method to determine the three-dimensional bite-force capabilities of the human masticatory system. J Dent Res 67:450–454.

Van Eijden TMGJ, Brugman P, Weijs WA, Oosting J. 1990. Coactivation of jaw muscles: recruitment order and level as a function of bite force direction and magnitude. J Biomech 23:475–485.

van Noordwijk MA, van Schaik CP. 1985. Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim Behav 33:849–861.

van Noordwijk MA, van Schaik CP. 1988. Male careers in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour 107:24–43.

van Lawick-Goodall J. 1968. The behaviour of free-living chimpanzees in Gombe Stream Reserve. Anim Behav Monogr 1:161–311.

van Roosmalen MGM. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus*, Linnaeus 1785) in Surinam. Acta Amazonica 15:1–238.

van Roosmalen MGM, Klein LL. 1988. The spider monkeys, genus *Ateles*. In: Mittermeier RA, Rylands AB, Coimbra-Filho A, Fonseca GAB, editors. Ecology and behavior of Neotropical primates, vol. 2. Washington: World Wildlife Fund. p 455–538.

van Roosmalen MGM, Mittermeier RA, Milton K. 1981. The bearded sakis, genus Chiropotes. In: Coimbra-Filho AF, Mittermeier RA, editors. Ecology and behavior of Neotropical primates. Rio de Janeiro: Academia Brasiliera de Ciencias. p 419–441.

van Roosmalen MGM, Mittermeier RA, Fleagle JG. 1988. Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): a Neotropical seed predator. Am J Primatol 14:11–35.

van Schaik CP. 1985. Socio-ecology of long-tailed macaques. PhD dissertation, University of Utrecht.

Van Valen L. 1962. Growth fields in the dentition of *Peromyscus*. Evolution 16:272–277.

Vinyard CJ, Hanna J. 2005. Molar scaling in strepsirrhine primates. J Hum Evol 49:241–269.

Vinyard CJ, Taylor AB. 2010. A preliminary analysis of the relationship between jaw-muscle architecture and jaw-muscle electromyography during chewing across primates. Anat Rec 293:572–582.

Vinyard CJ, Wall CE, Williams SH, Schmitt D, Hylander WL. 2001. A preliminary report on the jaw mechanics during tree gouging in common marmosets (*Callithrix jacchus*). In: Brooks A, editor. Dental morphology 2001: proceedings of the 12th international symposium on dental morphology. Sheffield: Sheffield Academic Press. p 283–297.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. Am J Phys Anthropol 120:153–170.

Vinyard CJ, Williams SH, Wall CE, Johnson KR, Hylander WL. 2005. Jaw-muscle electromyography during chewing in Belanger's treeshrews (*Tupaia belangeri*). Am J Phys Anthropol 127:26–45.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2008. Patters of variation across primates in jaw-muscle electromyography during mastication. Integr Comp Biol 48:294–311.

von Dornum M, Ruvolo M. 1999. Phylogenetic relationships of the New World monkeys (Primates, Platyrrhini) based on nuclear G6PD DNA sequences. Mol Phylogenet Evol 11:459–476.

Wada K. 1983. Ecological adaptation in rhesus monkeys at the Kumaon Himalaya. J Bombay Nat Hist Soc 80:469–498.

Wagner GP. 1996. Natural kinds and the evolution of modularity. Am Zool 36:36–43.

Wagner GP, Altenberg L. 1996. Complex adaptations and the evolution of evolvability. Evolution 50:967–976.

Waitt DE, Levin DA. 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. Am J Phys Anthropol 65:47–60.

Wall CE. 1995. Form and function of the temporomandibular joint in anthropoid primates. PhD dissertation, State University of New York at Stony Brook.

Wall CE. 1999. A model of temporomandibular joint function in anthropoid primates based on condylar movements during mastication. Am J Phys Anthropol 109:67–88.

Wall CE, Perry JGM, Briggs M, Schachat F. 2007. Mechanical correlates of sexual dimorphism in the jaw muscles and bones of baboons. Am J Phys Anthropol 44(Suppl):242.

Wall CE, Vinyard CJ, Williams SH, Johnson KR, Hylander WL. 2008. Specialization of the superficial anterior temporalis in baboons for mastication of hard foods. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. Primate craniofacial function and biology. New York: Springer. p 113–124.

Wallace RB. 2008. Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission-fusion societies. Am J Primatol 70:271–281.

Wangchuck T, Inouye DW, Hare MP. 2008. The emergence of an endangered species: evolution and phylogeny of the *Trachypithecus geei* of Bhutan. Int J Primatol 29:565–582.

Ward SC, Molnar S. 1980. Experimental stress analysis of topographic diversity in early hominid gnathic morphology. Am J Phys Anthropol 53:383–395.

Ward CV, Leakey MG, Walker A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J Hum Evol 41:255–368.

Ward CV, Plavcan JM, Manthi FK. 2010. Anterior dental evolution in the *Australopithecus anamensis–afarensis* lineage. Phil Trans R Soc B 365:3333–3344.

Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. Biol Rev 81:259–291.

Washburn SL. 1959. Speculations on the interrelations of the history of tools and biological evolution. Hum Biol 31:21–31.

Washburn SL. 1960. Tools and human evolution. Sci Am 253:62–75.

Washburn SL, Howell FC. 1960. Human evolution and culture. In: Tax S, editor. Evolution after Darwin, vol. 2. Chicago: University of Chicago Press. p 33–56.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7:323–356.

Watts DP. 1998. Coalitionary mate guarding by males chimpanzees at Ngogo, Kibale National Park, Uganda. Behav Ecol Sociobiol 44:43–55.

Watts DP. 2000. Causes and consequences of variation in male mountain gorilla life histories and group membership. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p 169–179.

West-Eberhard MJ. 2003. Developmental plasticity and evolution. New York: Oxford University Press.

Wheatley BP. 1980. Feeding and ranging of east Bornean *Macaca fascicularis*. In: Lindburg DG, editor. The macaques: studies in ecology, behavior, and evolution. New York: Van Nostrand Reinhold. p 215–246.

Wheatley BP. 1982. Adult male replacement in *Macaca fascicularis* of East Kalimantan, Indonesia. Int J Primatol 3:203–219.

White F. 1986. Census and preliminary observations on the ecology of the black-faced black spider monkey (*Ateles paniscus chamek*) in Manu National Park, Peru. Am J Primatol 11:125–132.

White TD. 1991. Human osteology. San Diego: Academic Press.

White TD, Johanson DC. 1982. Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974–1977 collections. Am J Phys Anthropol 57:501–544.

White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 371:306–312.

White TD, Suwa G, Simpson S, Asfaw B. 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. Am J Phys Anthropol 111:45–68.

White TD, WoldeGabriel G, Asfaw B, Ambrose S, Beyene Y, Bernor RL, Boisserie J-R, Currie B, Gilbert H, Haile-Selassie Y, Hart WK, Hlusko LJ, Howell FC, Kono RT, Lehmann T, Louchart A, Lovejoy CO, Renne PR, Saegusa H, Vrba ES, Wesselman H, Suwa G. 2006. Asa Issie, Aramis and the origin of *Australopithecus*. Nature 440:883–889.

White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G. 2009. *Ardipithecus ramidus* and the Paleobiology of early hominids. Science 326:75–86.

White TD, Suwa G, Lovejoy CO. 2010. Response to comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328:1105-c.

Wich SA, Fredriksson G, Sterck EHM. 2002. Measuring fruit patch size for three sympatric Indonesian primate species. Primates 43:19–27.

Wildman DE, Jameson NM, Opazo JC. 2009. A fully resolved genus level phylogeny of neotropical primates (Platyrrhini). Mol Phylogenet Evol 53:694–702.

Williamson EA, Tutin CEG, Rogers ME, Fernandez M. 1990. Composition of the diet of the lowland gorillas at Lopé in Gabon. Am J Primatol 21:265–277.

Willis JH, Coyne JA, Kirkpatrick M. 1991. Can one predict the evolution of quantitative characters without genetics? Evolution 45:441–444.

Willmore KE, Roseman CC, Rogers J, Richtsmeier JT, Cheverud JM. 2009. Genetic variation in baboon craniofacial sexual dimorphism. Evolution 63:799–806.

Wilson AP, Boelkins RC. 1970. Evidence for seasonal variation in aggressive behaviour by *Macaca mulatta*. Anim Behav 18:719–724.

Wolpoff MH. 1976. Some aspects of the evolution of early hominid sexual dimorphism. Curr Anthropol 17:579–606.

Wolpoff MH. 1978. Some aspects of canine size in the australopithecines. J Hum Evol 7:115–126.

Wolpoff MH. 1982. Relative canine size. J Hum Evol 11:151–158.

Wolpoff MH, Senut B, Pickford M, Hawks J. 2002. *Sahelanthropus* or '*Sahelpithecus*'? Nature 419:581–582.

Wolpoff MH, Hawks J, Senut B, Pickford M, Ahern J. 2006. An ape or *the* ape: is the Toumaï cranium TM 266 a hominid? PaleoAnthropology 2006:36–50.

Wood BA. 1979a. An analysis of tooth and body size relationships in five primate taxa. Folia Primatol 31:187–211.

Wood BA. 1979b. Models for assessing relative canine size in fossil hominids. J Hum Evol 8:493–502.

Wood BA, Stack CG. 1980. Does allometry explain the differences between "gracile" and "robust" australopithecines? Am J Phys Anthropol 52:55–62.

Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. London: Academic Press. p 503–538.

Wrangham RW. 1999. The evolution of coalitionary killing: the imbalance-of-power hypothesis. Yrbk Phys Anthropol 42:1–30.

Wrangham RW, Waterman PG. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. J Anim Ecol 50:715–731.

Wrangham RW, Conklin NL, Chapman CA, Hunt KD. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. Phil Trans R Soc Lond 334B:171–178.

Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p 45–57.

Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. Int J Primatol 19:949–970.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473–492.

Wright BW, Wright KA, Chalk J, Verderane MP, Fragaszy D, Visalberghi E, Izar P, Ottoni EB, Constantino P, Vinyard C. 2009. Fallback foraging as a way of life: using dietary toughness to compare fallback signal among capuchins and implications for interpreting morphological variation. Am J Phys Anthropol 140:687–699.

Yamagiwa J, Basabose AK. 2006. Diet and seasonal changes in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park. Primates 47:74–90.

Yeager CP. 1996. Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. Int J Primatol 17:51–62.

Zanowiak PP. 1974. Dynamics of dental occlusion in baboons. J Dent Res 53:1208–1214.

Zhao Z, Stock DW, Buchanan AV, Weiss KM. 2000. Expression of *Dlx* genes during the development of the murine dentition. Dev Genes Evol 210:270–275.

Zingeser MR. 1969. Cercopithecoid canine tooth mechanisms. Am J Phys Anthropol 31:205–214.

Zollikofer CPE, Ponce de León MS, Martin RD, Stucki P. 1995. Neanderthal computer skulls. Nature 375:283–285.

Zollikofer CPE, Ponce de León MS, Lieberman DE, Guy F, Pilbeam D, Likius A, Mackaye HT, Vignaud P, Brunet M. 2005. Virtual reconstruction of *Sahelanthropus tchadensis*. Nature 434:755–759.