# DETERMINING THE RELATIONS BETWEEN CANINE CROWN HEIGHT, CROWN AND ROOT BASAL DIAMETERS AND ROOT LENGTH: IMPLICATIONS FOR THE HOMININ FOSSIL RECORD

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I dedicate this thesis and my Masters degree to

my wonderful, supportive and loving family

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ABSTRACT

Canine reduction is one of the original apomorphies to appear in hominin evolution. Canine crown size is sexually dimorphic in most primates, and sexual dimorphism is linked strongly to sexual selection; therefore quantification of canine crown size is necessary to reconstruct social behavior in primate fossil taxon. However, crowns are often broken or missing in fossil specimens. I investigate the validity of predicting maxillary canine crown height from root length and crown and root basal diameters in African hominoids, and examine the allometric relations of canine dimensions within and between species. Mesiodistal dimensions of the crown and root are the best predictors of crown height. Root length is a poor predictor. Crown height scales positively allometrically in gorillas relative to root length but isometrically in humans and chimpanzees. Chimpanzee canine crowns are taller and mesiodistally narrower than those of gorillas and shorter to those of humans relative to root length.

Humans have taller crowns relative to mesiodistal length than do chimpanzees and gorillas and shorter crowns relative to buccolingual breadth than do chimpanzees. My results demonstrate important inter-and intra-specific variation in canine form among hominoids

# Chapter 1 – Introduction and Background

## Introduction

Canine crown size reduction is one of the earliest apomorphies to appear in hominin evolution (Brace, 1972). Understanding the nature and timing of canine crown reduction is therefore critical for interpreting the pattern of natural selection that led to the earliest hominins, and operated to shape the earliest species of our lineage.

Canine crown size is sexually dimorphic in most anthropoids, and this variation is thought to be associated with sexual selection acting through the tooth's use as a weapon in intrasexual male-male competition. Canine crowns may also be affected by diet in pithecines, and perhaps other species that habitually use their canines to open hard objects. Canine dimorphism and canine size are associated with various behavioral measures – competition levels, mating system, socionomic sex ratio, and so can potentially offer important evidence of social behavior in extinct species.

The earliest part of the hominin fossil record is only sparsely known. Although canine size is reduced in *Australopithecus afarensis*, it is unclear to what degree canine reduction had occurred in the earlier species, *Australopithecus anamensis* (Ward et al., 2001). Out of the eight *A. anamensis* maxillary canine crowns known only one is unworn and undamaged (Ward et al., 2001). Crown size also appears to reduce before root size in early hominins such as in *A. anamensis* and *A. afarensis* (Demes and Creel, 1988; Plavcan and van Schaik, 1997a; Plavcan, 2001; Ward and Plavcan, 2004). Canine crown height, as opposed to occlusal diameters, is the strongest correlate of behavior in living species, which makes crown height the best measure for reconstructing behavior. We

would have a better understanding of canine size and canine dimorphism in the earliest definitive hominins *A. anamensis* and *A. afarensis* if it were possible to reconstruct crown height in these two taxa. Being able to accurately predict crown height would also be valuable information for inferring the morphology and social systems of early australopithecines. A better understanding of allometric relations among extant African hominoids will provide a basis for making more accurate conclusions about shapes and sizes of fossil hominin canines.

In this thesis, I explore maxillary canine proportions in extant African hominoids, which will provide a solid foundation for interpreting canine size, shape and facial structure in fossil hominins. This research has two components. First, I use least squares regression analysis to determine how successfully canine crown height can be predicted from root length and/or the basal diameters of the crown and root. Second, I explore allometric relations among canine dimensions in extant African hominoids and to assess scaling patterns within and among species.

## Background

### *Tooth development*

In tooth development there is an interaction between oral epithelial cells and mesenchymal cells (Avery, 1992). The enamel organ is derived from the oral epithelial cells from which enamel develops and the mesenchymal cells become the dental papilla which later results in dentin (Avery, 1992). The bud, cap, and bell stages are forms that a tooth takes during growth (Avery, 1992). In the bud stage the enamel organ grows to a bud shape. The cap stage is when the enamel organ and epithelial cells changes shape to be concave and the dental papilla forms. The bell stage begins after further growth of the

enamel organ and dental papilla. The enamel epithelial cells are then differentiated into layers which will outline the shape of the future tooth crown and become ameloblasts which form enamel. Odontoblast cells form from the peripheral dental papilla cells to make dentin (Avery, 1992). The dentin of the tooth crown is indistinct from the dentin of the tooth root; dentine formation is continuous (Aiello and Dean, 2002). Subsequently, the crowns and roots of the teeth begin to mineralize and the bone and cementum form (Avery, 1992). After the fully formed crown has erupted root formation continues until the supporting root and a complete tooth are fully formed (Avery, 1992).

The development of the canine root and crown occur at the same pace, the length of the root is at least partially dependent upon crown development (Avery, 1992). Canine crowns and roots are shown to be correlated by their rate of growth but we do not know what selection might be influencing the length of the canine root. It is suggested that root length must be to an extent dependent upon canine crown height. The root must be long/wide enough to support the crown. Since canine roots are not always finished forming when the crown has erupted enough to begin exhibiting wear and being used there can be an active influence on crown roots. Canine crowns are only affected by developmental selection which affects the crown by genetic controls. We need additional information on maxillary canine and facial growth in order to make conclusions about a known influencing selection on canine roots.

*Australopithecus africanus, A. afarensis* and *Homo habilis* have dental eruption patterns more similar to apes than to humans (Ramirez-Rozzi; 1993; Smith, 1994). *Homo erectus*, Neandertals and archaic *Homo sapiens* on the other hand, have a dental eruption pattern that is basically indistinguishable from anatomically modern humans

(Ramirez-Rozzi; 1993; Smith, 1994). Though eruption patterns in early hominins tend to be like those of apes, their reduced canine crown size prevents me from using great ape analogs exclusively in predicting canine crown height from basal dimensions and root length. Since there is no true analog for early hominins, we must use caution when making inferences about fossil specimens

Variation in canine proportions and patterns of eruption highlight the necessity of carefully evaluating canine proportions among taxa.

*Canine growth and structure*

Canine crown height sexual dimorphism occurs because there is variation in the rate and/or duration of growth between males and females of the same species (Masterson, 1997; Schwartz and Dean, 2001). Schwartz and Dean (2001) found that compared to females, male hominoid canine teeth take a longer form but then grow at a faster rate. Male capuchins also grow their canines at a faster rate than females (Masterson, 1997). Male gorillas can take up to 3-4 years longer to complete crown formation than females and chimpanzee males take 1.4 years longer than females. In both species the sexes grow their canines at different rates (Schwartz and Dean, 2001). Schwartz and Dean (2001) found that in chimpanzees there is overlap between the sexes in crown formation time as well as in canine height. Humans are also considered to have sexually dimorphic canines by Schwartz and Dean (2001, 2005). Growth patterns of fossil hominin canines are unknown, and would be difficult to predict given the observed interspecific variation among extant hominoids.

Plavcan (1993), Kay et al. (1988), and Plavcan and Van Schaik (1995) have shown that crown and root mesiodistal dimensions are more strongly correlated with

canine crown height than are buccolingual breadths. Mesiodistal dimensions along with crown height are also correlated with male-male competition (Plavcan, 1993). Plavcan, (1993) and Robinson agrees that canine crown height scales isometrically relative to mesiodistal and buccolingual diameters in hominoids (Plavcan, personal communication).

*Relations between canine size and facial proportions*

Canine structure may influence facial structure, or vice versa. In fossil hominins, canine roots vary in relation to the position of other structures. For example, *Australopithecus anamensis* canine roots contribute to the rounded lateral margin of the nasal aperture whereas those of other Australopithecus species do not. (Ward et al., 1999; 2001).

Kimbel et al. (2004) interprets the unique pattern of facial dimorphism in *A. afarensis* to the reduction of canine crowns. This is likely based on a presumed association between crown and root sizes although such an assumption has not been demonstrated. Wood (2002) suggests, however, that hominin roots are large relative to crown sizes, and if so might impact the influence of crown size on facial morphology.

McCollum (1994) found no evidence that patterns of masticatory stress result in common facial morphology of *Pan* and *Gorilla* suggesting that masticatory stress plays a very minor role in facial development (McCollum, 1994). Spencer (1999) disagrees arguing that facial form is influenced by changes in the masticatory system over time. Spencer (1999) found that diet, in relation to masticatory stress, influences the canine and premolar root and crown size of capuchin monkeys. In capuchins strain on the canine tooth from dietary pressures of eating hard seeds resulted in a stronger canine which was able to handle the strain (Spencer, 1999). More information is needed in regards to

canine root selective forces and development in order to resolve the issues brought up by McCollum (1994) and Spencer (1999).

*Canine size and diet*

Canine size and shape appears to be correlated with diet in hard-object feeding platyrrhines (Spencer, 2003). Spencer (2003) found canine root surface area, quantified by area of the root in standard radiographs, is significantly larger than crown surface area in platyrrhine species that eat resistant seeds compared to soft seed eating species. Specifically, male and female canine roots in the hard seed eating species *Cebus apella* and *Chiropotes satanas* are larger and more robust than the non-hard seed eating species *Cebus albifrons* and *Pithecia pithecia* (Spencer, 2003). In all of these species, differences in crown size are accompanied by differences in root size, although it is also possible that root and crown size could vary independently (Spencer, 2003). If hominins do have relatively large canine roots compared to their decreased crown heights, it would be evidence that crown height decreased independently of root length (Demes and Creel, 1988; Plavcan and van Schaik, 1997a; Plavcan, 2001; Wood, 2002; Ward and Plavcan, 2004).

Kay et al. (1988) found a strong relationship between variation in competition and canine size dimorphism, but noted that diet is also associated with variation in canine size among platyrrhines. Plavcan (1993) found no evidence that canine size/shape in male anthropoids is correlated with diet, however except for Pithecines which can be excluded because their canines are specialized for diet (Kinzey, 1971; Spencer, 2003). Taxa that have distinct differences in diet such as hard or soft seed eating platyrhines may have stronger selection in differing canine size than taxa who differ in frugivory and folivory.

*Canine dimorphism and social behavior*

Regardless of relations between diet and canine size in some taxa, diet has been suggested to have little to no influence on canine dimorphism in anthropoids (Plavcan and van Schaik, 1992; 1997a), although Kay et al. (1988) argue that it does in ceboid monkeys. When looking at how diet may affect canine size differing taxa seem to give differing results.

Canine crown size varies as a result of sexual selection (Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1997b). Male canines are used as weapons in aggressive or agonistic situations and possibly as a defense against predators (Harvey et al., 1978; Greenfield and Washburn, 1991; Plavcan and van Schaik, 1992; Plavcan et al., 1995). As such, sexual dimorphism is the only direct evidence for social behavior in the fossil record (Plavcan, 2001; 2003).

Canine size may also be affected to a lesser extent by other selective pressures (Harvey et al., 1978; Greenfield and Washburn, 1991; Plavcan and van Schaik, 1992; Plavcan et al., 1995). Kay et al. (1988) also asserts that competition and canine size are strongly correlated. Arboreal primates have less body mass dimorphism than do terrestrial ones, although there is no apparent effect on canine dimorphism (Leutenegger and Kelly, 1977; Harvey et al, 1978; Plavcan and van Schaik, 1997a).

Body size is also a determinant of canine dimorphism. Kay and colleagues (1988, p. 385) saw a following of Rensch's rule ("a tendency for body size dimorphism and canine dimorphism to increase with increased body size") in platyrrhines but also saw that mating systems were also size related. Larger bodied species of platyrrhines have higher levels of male-male competition in breeding than do smaller species, still

supporting the hypothesis that sexual selection in the form of male-male competition is responsible for large body and canine size dimorphism (Kay et al., 1988).

Female canine size is also associated with the amount of female-female agonistic competition in primates (Plavcan et al., 1995; Plavcan, 1998). Selection for larger female canine size is also influenced by, but not constrained by, correlated response from selection on male canines (Plavcan, 1988). Female canine size is significantly associated with estimates of the intensity and context (coalitionary or non-coalitionary) of agonistic female competition, but not with the potential frequency of female competition (Plavcan, 1998).

Still, the two variables most strongly correlated with canine size dimorphism are male-male competition levels (Leutenegger and Kelly, 1977; Kay et al., 1988; Greenfield, 1992; Plavcan et al, 1995; Plavcan, 1998) and mating systems (Smith, 1980; Greenfield, 1992; Plavcan and van Schaik, 1997ab; Plavcan, 2000; Plavcan, 2001; Schwartz and Dean, 2001). In mating systems, male-male competition levels and canine size dimorphism are all intertwined. Plavcan and van Schaik (1997b) explored the intensity and frequency of male-male competition and canine and body size dimorphism. Male-male competition consists of four levels: type 1 constitutes a low frequency and low intensity level of male-male competition; type 2 shows high frequency, low intensity competition; type 3 shows low frequency, high intensity competition and type 4 shows high frequency, high intensity male-male competition (Plavcan and van Schaik, 1992). A large amount of canine dimorphism is associated with a high level and frequency of male-male competition and polygyny (see also Leutenegger and Kelly, 1977; Harvey et al, 1978; Kay et al, 1988; Greenfield, 1992; Plavcan and van Schaik, 1992; Plavcan et al,

1995; Plavcan and van Schaik, 1997b; Plavcan, 2000; Plavcan, 2001; Plavcan, 2002). Less dimorphism is associated with monogamy or polyandry with competition levels 1 or 2, but is also found in some polygynous taxa, and so is uninformative about social system (Plavcan, 2000; 2001).

Among hominoids, relations between canine dimorphism is also related to mating system and competition levels. Gorillas have higher canine size dimorphism than do chimpanzees, and both are more dimorphic than humans (Table 1-1). Gorillas do not participate in coalitions and have high-intensity, low frequency male-male competition (Plavcan et al., 1995). Chimpanzees are polygynous in a multi-male society. They participate in coalitions and have high-intensity, low frequency male-male competition (Plavcan et al., 1995). Humans have a variety of mating systems throughout the world, but generally have strong pair bonds and low levels of male-male competition for mating.

These maxillary canine dimorphism indices are calculated by the male mean divided by the female mean of *Gorilla gorilla gorilla*, *Pan troglodytes schweinfurthi* and *Pan troglodytes troglodytes* (Plavcan, personal correspondence) (Table 1-1)

Table 1-1. Maxillary canine dimorphism indices calculated by the male mean divided by the female mean (Plavcan, personal correspondence)

| Species | Crown height | Crown mesiodistal | Crown buccolingual |
|---|---|---|---|
| *Gorilla gorilla gorilla* | 1.7302 | 1.5961 | 1.5045 |
| *Pan troglodytes schweinfurthi* | 1.4764 | 1.3621 | 1.2983 |
| *Pan troglodytes troglodytes* | 1.2668 | 1.4018 | 1.2537 |

*Fossil hominin canines*

Canine crown reduction is one of the first apparent apomorphies of the hominin lineage (Brace, 1972; Haile-Selassie, 2001, White et al., 2001; Brunet et al, 2002; Haile-Selassie et al., 2004; Ward and Plavcan, 2004). Another hallmark of hominin evolution is the lack of a C/P3 functional honing complex that is seen in great apes and most other anthropoids, which may be an accomplice to canine reduction (White, 1977; Greenfield, 1990; Wood, 2002).

Early hominins have reduced canine crowns, but it has been suggested that they retain large canine roots (Ward et al., 1999; Wood, 2002). If so, it is possible that though the crowns have been reduced, the roots have not yet followed suit. Early hominins also still had considerable dimorphism in basal dimensions even after their canine height was reduced; only later did basal diameters decrease as well (Ward and Plavcan, 2004). Canine reduction could occur very quickly if there was not any selection to maintain larger canines even if there was no particular selection for small canines due to selection for energetic savings during development (Plavcan et al., 1995).

The earliest well-known definitive hominin is *Australopithecus anamensis*, known as far back as 4.2 Ma (Leakey et al., 1998). There is no doubt that *A. anamensis* is a hominin, and unlike some of the earlier discoveries such as *Sahelanthropus tchadensis*, *A. anamensis* is no longer under contention for hominin status. It has been suggested that *A. anamensis* had slightly larger canines than did later hominins (Ward et al., 1999; 2001). *A. anamensis* also had larger basal dimensions than did *A. afarensis*. It was also suggested that *A. anamensis* may have had more canine dimorphism than did *A. afarensis* based on a large alveolus of the large presumed male *A. anamensis* mandible

KNM-KP 29287 (Ward et al., 2001). However, all but one of the *A. anamensis* maxillary canines are worn, so it is difficult to quantify actual height (Ward et al., 2001). There are some maxillary canine heights known for *A. afarensis*. The collection of canine crown heights in *A. afarensis* range from 9.2mm to 15.4mm (Ward, personal communication). (See Table 1-2). Some of these specimens have been corrected for wear to their crown height and mesiodistal surfaces. Some of these measurements are smaller than the original tooth would have been with no wear because they were not corrected (Ward, personal communication).

Table 1-2. *Australopithecus afarensis* crown height, root length and basal diameter measurements in mm.

| Specimen | Crown height | Crown Mesiodistal | Crown Buccolingual | Root Mesiodistal | Root Buccolingual |
|---|---|---|---|---|---|
| A.L. 199-1 | 9.2 | 8.9 | 9.3 | 8.1 | 6.2 |
| A.L. 200-1a | 12.7 | 9.5 | 10.9 | 10.4 | 6.8 |
| A.L. 333-2 | 10.2 | 9.8 | 10.9 | 10.5 | 7.3 |
| A.L. 333x-3 | 15.4 | 10.4 | 11.5 | 10.9 | 8.2 |
| A.L. 400-1b | 12.5 | 9.2 | 10.3 | 9.9 | 6.8 |
| L.H. 3 | 14.2 | 11.6 | 12.5 | N/A | N/A |
| L.H. 5 | 10.6 | 9.6 | 9.8 | 7.2 | 7.2 |
| L.H. 5 | 13.7 | 10.1 | 10.0 | N/A | N/A |

In addition, one partial and worn canine of *Sahelanthropus tchadensis* and one complete crown of *Orrorin tugenensis* are known (Wood, 2002; Haile-Selassie et al., 2004). An accurate reconstruction of crown sizes in these newer fossils is key to understanding canine evolution in early hominin evolution. *Ardipithecus kadabba* and *Ardipithecus ramidus* canines are a mixture of primitive and derived features and have

been used to make inferences about their phylogenetic relationships (Haile-Selassie, 2001; Haile-Selassie et al., 2004). An accurate reconstruction of crown size would aid in determining those relationships.

*Australopithecus* species have a modest to slight amount of canine dimorphism, which is greater than seen in humans but less than seen in extant apes (Brace, 1972; Plavcan, 2001). Plavcan (2003) and Plavcan and van Schaik (1997b) assert that though early hominins have very dimorphic faces they do not have as strong of a degree of postcranial dimorphism. This could lead to an underestimation of body mass dimorphism in hominoids because of differing signals (Plavcan, 1998; Lockwood, 1999; Plavcan, 2002; Plavcan, 2003). Humans and australopithecines both have greater levels of body mass dimorphism than canine dimorphism (Plavcan and van Schaik, 1997b). The dimensions of "overall skull and jaw proportions increas[e] broadly with increasing body mass dimorphism (Plavcan, 2002, p. 599).

Social systems in australopithecine species are difficult to classify because of their low degree of canine dimorphism and high level of body mass dimorphism; a unique combination among hominoids (Plavcan and van Schaik, 1997b). Using data combinations of body mass dimorphism, body weight dimorphism, diet, substrate and competition levels Plavcan and van Schaik (1997b) have made statements about affects of these variables on social systems in *Australopithecus*. Based on reduced canine dimorphim, Lovejoy (1981) inferred a monogamous mating system for *Australopithecus* species. However, *Australopithecus* species are characterized by fairly high degree of body weight dimorphism as by McHenry and Coffing (2000), but see Reno et al. (2003), which are more likely to reflect a polygynous mating system with intense male-male

competition (Plavcan and van Schaik, 1997b). Certainly, in these and earlier hominins, if it is impossible to accurately reconstruct canine size in fossil taxa, it is impossible to estimate dimorphism and interpret behavior.

Jolly (1970) hypothesizes that canine reduction may have resulted from a shift from fruit diet to one based on cereals and grains, for which large canines would not be needed.

In summary, being able to accurately reconstruct canine sizes in fossil taxa will provide important data for developing and testing hypotheses about social and dietary selection in hominin evolution. Furthermore, determining proportions among canine tooth dimensions will be important for examining the pattern of anatomic changes that canines underwent, further elucidating the pattern of selection in hominin origins and early evolution.

# Chapter 2 - Materials and Methods

## Materials

Canine crown and root data were collected for *Pan troglodytes, Gorilla gorilla* and *Homo sapiens* from the Hamann-Todd Osteological Collection at the Cleveland Museum of Natural History (Table 2-1).

Table 2-1: Sample sizes

| *Pan troglodytes* | *Gorilla gorilla* | *Homo sapiens* |
|---|---|---|
| 15 Males | 25 Males | 25 Males |
| 15 Females | 25 Females | 25 Females |

All *Pan* and *Gorilla* specimens were wild-shot. Specimens were included only if they had complete eruption of the permanent dentition and had only minimal attrition of the canine crown. Three of the *Gorilla* specimens had roots that were not fully closed but because they were not outliers from the rest of the *Gorilla* specimens in root length or any other dimensions they were not excluded. Canine roots are not always finished forming when the crown has erupted enough to begin exhibiting wear. Humans ranged from 25-48 years of age.

**Methods**

Canine crown height and crown and root basal dimensions were measured using sliding calipers and recorded to the nearest .01mm. Three crown and two root dimensions of the right maxillary canine were measured for each specimen (Fig. 2-1). Maxillary canine crown height (CH) was measured as the maximum distance from the tip of the canine to the labial surface of the cementoenamel junction (CEJ). Dimensions were not corrected for wear. In many species, tooth wear can begin before eruption is finished (Plavcan and van Schaik, 1992). Since canine wear is normal and not pathological, selection on canine height takes place on the existing crown dimensions, so it can be argued that actual, not corrected, crown height is the operative dimension (Plavcan and van Schaik, 1992). Still, specimens with minimal wear were included, while those with moderate to extreme wear were not used. Maximum crown mesiodistal length (CMD) was measured from the most mesial to the most distal crown bulge near the base of the crown. Maximum crown buccolingual breadth (CBL) was taken as a maximum breadth measured perpendicular to and at the same level as the mesiodistal (CMD) measurement (Fig. 2-1). Root mesiodistal (RMD) and buccolingual (RBL)

diameters were taken parallel to their corresponding crown dimensions at the widest point of the root near the CEJ (Fig. 2-1).

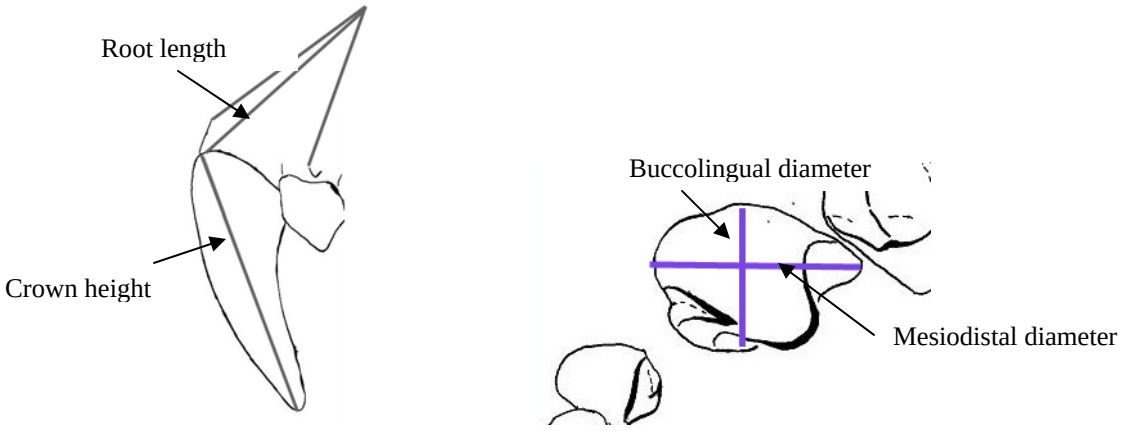


Figure 2-1. Measurements taken on the canine crown and root (drawings modified from those of J.M. Plavcan).

Except immediately adjacent to the crown, canine roots cannot be measured on osteological specimens because most do not have loose teeth that can be removed, so root length was measured from radiographs. Radiographs were taken by a Hewlett Packard Faxitron on Kodak Industrex Ready Pack film. Radiographs were taken by orienting the skull so that the root was parallel to the film. Enamel often thins when nearing the root, so the cementoenamel junction is not easily seen on a radiograph. To compensate, the cementoenamel junction was marked by attaching a length of radioopaque of wire directly at the cementoenamel junction. Unless subject-to-film and source-to-film distances are known, direct measurements cannot be taken accurately from radiographs, so a scale bar was positioned in a plane adjacent to the tooth root at the same height above the film at the root midline. Length of the root on the radiograph was measured

from the labial side of the CEJ to the apex of the root using sliding calipers. Actual root length was then calculated by calibrating this measurement using the scale bar.

**Statistical methods**

Data analysis proceeded in two steps. First, least squares regression was used to explore the validity of predicting crown height from basal root and crown diameters and root length. Linear regression is appropriate for predicting one dimension from another because the independent variable is assumed to have no error variance (Smith 1980; Hoffman, 1988; Greenfield and Washburn, 1991; Greenfield, 1992).

All data were Ln-transformed in order to examine allometric relations between variables and for prediction (Hoffman, 1988; Plavcan, 1993; Plavcan and Cope, 2001). When the original data were examined it appeared exponential in form so I transformed the data to logarithmic to obtain a more linear form (Hoffman, 1988). Each variable involved in the statistical manipulation was treated symmetrically, by being ln-transformed, by the slope so that there is a normal distribution of the data. Regressions were calculated for species individually, and for the comparative sample as a whole. Coefficients of determination between all variables and canine height were low within sexes (see Results), so they were not analyzed.

Canine crown height was first regressed on each individual variable. Regression equations were calculated within each sex for each species, for each species as a whole, and for the combined sample as a whole using Excel software. Pearson's product-moment correlation was used to assess the strength of the coefficient of determination of crown height on each variable (Zar, 1999). Percent standard errors of the estimate of the predicted y-value for each x-value were calculated using the STEYX function in Excel to

determine the error amount that can be expected when predicting crown height from the other variables.

Regression lines for each pair of species were tested to determine if they were statistically equivalent in slope (Zar, 1999). The residual sum of squares, degrees of freedom, and the sums of $x^2$, $y^2$ and xy were used to calculate a t-test calculated value to test for statistical equivalence in slope. Since none of the lines had statistically equivalent slopes no test for elevation was required. Confidence intervals of the slope were calculated using the SPSS statistical package for all linear regression lines. The confidence intervals of the slopes were calculated for each variable in the multiple regression lines rather than the entire line. This was not done for the line's predictive power, rather only for giving information regarding the dispersal around the individual slopes. Calculating the power of this statistical test is not possible because there is no other distribution with which to compare the distribution of this sample. The sample of gorillas, chimpanzees and humans used in this study could be part of a parent population that describes all apes, or they each could be part of different populations that are so close together in overlap that we cannot distinguish them. Further research with a larger sample could elucidate potential differences between each species.

Hierarchical multiple linear regression was used to incorporate multiple independent variables in predicting canine crown height in order to assess the strength of predictors when holding each of the other variables as constants. I used the SPSS statistical package to complete these tests. First, I used only root basal dimensions as the independent variables because of previous testing which indicated a high $r^2$. Second, all variables were used simultaneously as independent variables. The two results were then

statistically tested using the hierarchical multiple linear regression to see if all variables provided a better correlation with crown height than did just the root basal dimensions.

I also calculated multiple linear regression statistics using the SPSS statistical package to calculate predicted canine crown height from various sets of independent predictors for fossil specimens. The predicted crown height was then compared to the actual crown height of the specimen.

The second phase of analysis was to assess allometric relations among canine tooth dimensions, also using Ln-transformed data. Data were analyzed using reduced (standard) major axis (RMA) regression because both measurements in each comparison have different error variances, and it is considered most appropriate for analyzing allometric relations in biology (Clarke, 1980; Rayner, 1985; Hofman 1988; Plotnick, 1989; Greenfield and Washburn, 1991; Ward et al, 1995; Masterson 1997; Plavcan, 1998; Plavcan, 2000; Plavcan, 2003). With RMA, variables are independent of error correlation (Rayner, 1985). RMA regression minimizes the sum of the areas of triangle bounded by the line of best fit and lines drawn from it to the datapoints, parallel with the coordinate axes (Fig. 2-2) (Imbrie, 1956; Rayner, 1985; Hofman, 1988; Warton and Weber, 2002). Linear regressions are represented as follows: Y on X as $\triangle$ y, X on Y is $\triangle$ x, and principle major axis is $\triangle$ h (Fig. 2-2).

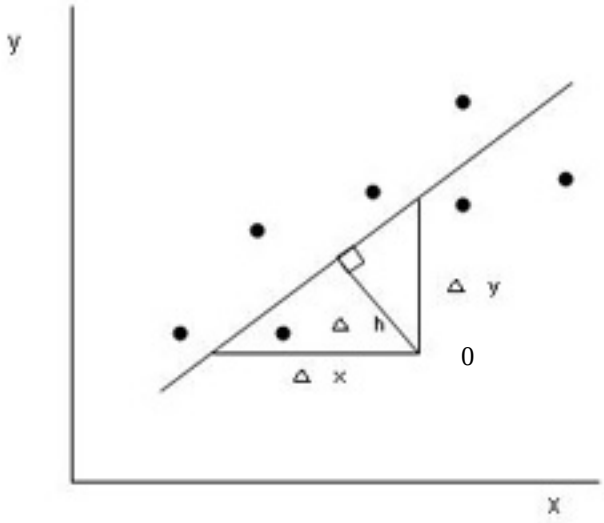


Figure 2-2. Figure redrawn from Hofman, 1988. Lines drawn from the point 0 show the distance minimized for the proposed regression models (Hofman, 1988).

The software package (S)MATR (Version 1, Falster DS, Warton DI and Wright IJ http://www.bio.mq.edu.au.ecology/SMATRT) was used to calculate bivariate relationships of RMA lines (which were produced by (S)MATR) to ln-transformed data. The (S)MATR program compares two or more groups and tests for the common slope using algorithms from Warton and Weber (2002) which are also shown in the (S)MATR manual by Falster (2003, pg. 14). If slopes of the two RMA lines are equivalent then standard ANOVA is used to determine directional shifts in elevation and along the common slope.

Differences in relations between variables among groups can be described as shifts (Fig. 2-3) (Falster, 2003). Shift A occurs when groups have a different slope. Shift B arises when groups have the same slope but differ in the y axis. Shift C occurs when groups have the same slope, a shift in the x axis and the same relations between variables

but one group is larger or smaller in size. Shift D is a combination B and C and occurs when groups have a common slope but differ in size and elevation. This shift happens when one group is larger/smaller in size as well as a shift in elevation with a change in the relationship between the two variables. When samples shared equivalent slopes and elevations, as in C, they were combined and an RMA line recalculated for the combined sample.

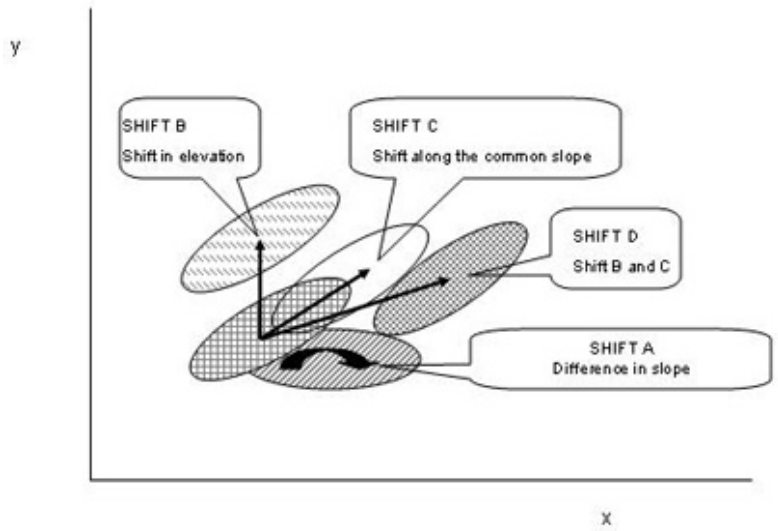


Figure 2-3. Description of shifts
Figure redrawn from Falster, 2003.

RMA lines were tested for potential deviations from isometry using algorithms and the Student's t-test from Hofman (1988).

# Chapter 3 – Results

## Least squares regression for prediction

Summary statistics for *Gorilla gorilla, Pan troglodytes* and *Homo sapiens* are included here for reference (Table 3-1).

Table 3-1. Summary statistics for extant ape sample

| ***PAN*** | | **Canine height** | **Crown buccolingual** | **Crown mesiodistal** | **Root buccolingual** | **Root mesiodistal** | **Root length** |
|---|---|---|---|---|---|---|---|
| FEMALES | MEAN | 14.72 | 9.31 | 11.07 | 9.05 | 9.78 | 27.69 |
| | STDEV | 2.48 | 1.14 | 1.17 | 1.34 | 1.31 | 3.57 |
| MALES | MEAN | 21.12 | 11.92 | 14.65 | 11.82 | 14.09 | 37.81 |
| | STDEV | 2.64 | 1.20 | 1.62 | 1.28 | 1.44 | 3.83 |
| TOTAL | MEAN | 17.45 | 10.62 | 12.86 | 10.44 | 11.94 | 32.75 |
| | STDEV | 4.12 | 1.75 | 2.29 | 1.91 | 2.58 | 6.30 |
| | MAX | 27.27 | | | | | |
| | MIN | 11.86 | | | | | |
| ***GORILLA*** | | | | | | | |
| FEMALES | MEAN | 15.85 | 11.48 | 14.28 | 10.82 | 12.55 | 34.87 |
| | STDEV | 1.61 | 0.95 | 1.08 | 0.89 | 1.09 | 3.69 |
| MALES | MEAN | 28.29 | 16.27 | 20.05 | 16.28 | 19.16 | 45.92 |
| | STDEV | 5.45 | 1.69 | 1.72 | 1.49 | 1.92 | 5.23 |
| TOTAL | MEAN | 22.07 | 13.88 | 17.17 | 13.55 | 15.86 | 40.39 |
| | STDEV | 7.44 | 2.77 | 3.24 | 3.01 | 3.68 | 7.16 |
| | MAX | 41.56 | | | | | |
| | MIN | 12.14 | | | | | |
| ***HOMO*** | | | | | | | |
| FEMALES | MEAN | 9.06 | 7.87 | 7.26 | 7.36 | 5.36 | 17.58 |
| | STDEV | 1.09 | 0.61 | 0.57 | 0.58 | 0.40 | 1.84 |
| MALES | MEAN | 9.49 | 8.60 | 7.65 | 8.30 | 6.07 | 18.77 |
| | STDEV | 1.34 | 0.61 | 0.51 | 0.60 | 0.46 | 2.36 |
| TOTAL | MEAN | 9.28 | 8.23 | 7.45 | 7.83 | 5.72 | 18.18 |
| | STDEV | 1.23 | 0.71 | 0.57 | 0.76 | 0.56 | 2.18 |
| | MAX | 12.26 | | | | | |
| | MIN | 6.48 | | | | | |

*Comparison 1 – root length to crown height (Fig. 3-1, Table 3-2)*

All correlations between root length and crown height were significant at the .05 level (Table 3-2). Even though all correlations are significant, there is a wide range of %SEE and $r^2$ values. *Pan* has the highest $r^2$, followed by *Gorilla* and *Homo*. The %SEE values also range from *Goriila* to *Pan* and *Homo.* Although the highest correlation is found for the sample as a whole, the combined sample also has a high standard error of the estimate at 17.9% (Table 3-2).

Table 3-2 Linear regression statistics for pooled-sex data

**Independent variable: Ln root length** **Dependent variable: Ln crown height**

| | **Slope +/- 95% CI** | **y-intercept** | **$r^2$** | **p** | **N** | **%SEE** | **Crown height Mean +- error** |
|---|---|---|---|---|---|---|---|
| *Pan* | .889 +- .28 | -.224 | .601 | .0001 | 30 | 14.7 | 17.45 + - 2.57 |
| *Gorilla* | 1.369 +- .346 | -2.002 | .569 | .0001 | 50 | 21.6 | 22.07 + - 4.77 |
| *Homo* | .407 +- .309 | 1.042 | .127 | .011 | 50 | 12.7 | 9.28 + - 1.18 |
| All combined | 1.045 +- .08 | -.797 | .839 | .0001 | 130 | 17.9 | 16.19 + - 2.9 |

**Independent variable: Ln root buccolingual** **Dependent variable: Ln crown height**

| | **Slope +/- 95% CI** | **y-intercept** | **$r^2$** | **p** | **N** | **%SEE** | **Crown height Mean +- error** |
|---|---|---|---|---|---|---|---|
| *Pan* | 1.041 +- .263 | .435 | .702 | .0001 | 30 | 12.7 | 17.45 + - 2.22 |
| *Gorilla* | 1.277 +- .208* | -.257 | .761 | .0001 | 50 | 16.1 | 22.07 + - 3.55 |
| *Homo* | .691 +- .346 | .801 | .251 | .0001 | 50 | 11.8 | 9.28 + - 1.1 |
| All combined | 1.415 +- .106* | -.599 | .845 | .0001 | 130 | 17.6 | 16.19 + - 2.85 |

**Independent variable: Ln crown buccolingual** **Dependent variable: Ln crown height**

| | **Slope +/- 95% CI** | **y-intercept** | **$r^2$** | **p** | **N** | **%SEE** | **Crown height Mean +- error** |
|---|---|---|---|---|---|---|---|
| *Pan* | 1.190 +- .285 | .064 | .724 | .0001 | 30 | 12.3 | 17.45 + - 2.15 |
| *Gorilla* | 1.452 +- .231 | -.750 | .768 | .0001 | 50 | 15.8 | 22.07 + - 3.49 |
| *Homo* | .795 +- .386 | .545 | .264 | .0001 | 50 | 11.7 | 9.28 + - 1.09 |
| All combined | 1.516 +- .114 | -.888 | .845 | .0001 | 130 | 17.7 | 16.19 + - 2.87 |

**Independent variable: Ln root mesiodistal** **Dependent variable: Ln crown height**

| | **Slope +/- 95% CI** | **y-intercept** | **$r^2$** | **p** | **N** | **%SEE** | **Crown height Mean +- error** |
|---|---|---|---|---|---|---|---|
| *Pan* | .929 +- .188* | .578 | .785*** | .0001 | 30 | 6.2***** | 17.45 + - 1.08 |
| *Gorilla* | 1.223 +- .198 | -.305 | .762 | .0001 | 50 | 16.1 | 22.07 + - 3.55 |
| *Homo* | .524 +- .36 | 1.308 | .152 | .005 | 50 | 12.5 | 9.28 + - 1.16 |
| All combined | .866 +- .053* | .701 | .891 | .0001 | 130 | 14.8 | 16.19 + - 2.4 |

**Independent variable: Ln crown mesiodistal** **Dependent variable: Ln crown height**

| | **Slope +/- 95% CI** | **y-intercept** | **$r^2$** | **p** | **N** | **%SEE** | **Crown height Mean +- error** |
|---|---|---|---|---|---|---|---|
| *Pan* | 1.140 +- .257 | -.035 | .748 | .0001 | 30 | 11.7 | 17.45 + - 2.04 |
| *Gorilla* | 1.515 +- .239 | -1.241 | .772*** | .0001 | 50 | 15.7 | 22.07 + - 3.46 |
| *Homo* | 1.026 +- .396* | .161 | .361*** | .0001 | 50 | 10.9 | 9.28 + - 1.01 |
| All combined | 1.069 +- .065* | .070 | .892** | .0001 | 130 | 14.7**** | 16.19 + - 2.38 |

NOTES:
* Lines were tested for difference between two population regression coefficients and found to be not statistically different. (Zar, 1999)
** highest $r^2$
*** highest $r^2$ for each species
**** when species are combined, lowest %SEE (standard error of the estimate) among all independent variables for predicting crown height
***** when species are separated, lowest %SEE among all independent variables for predicting crown height

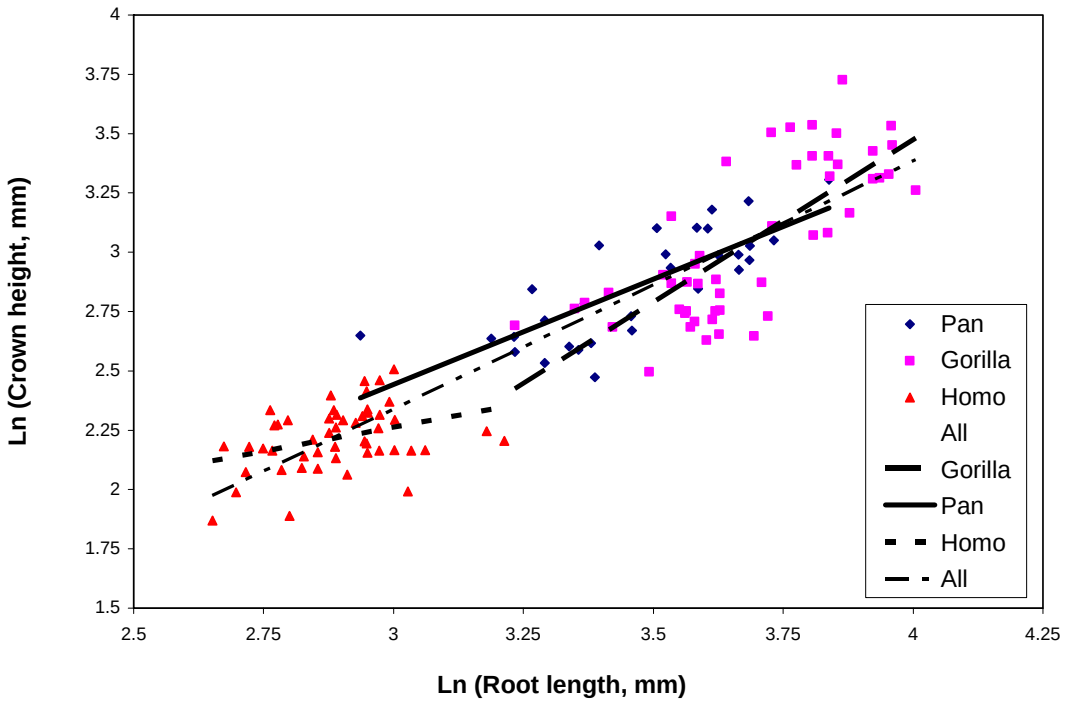


Figure 3-1. Bivariate plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to canine root lengths. Lines represent least-squares regressions for *Pan*, *Gorilla* and *Homo* data, separately as well as for the common sample.

*Comparison 2 – root and crown buccolingual breadth to crown height (Figs. 3-2, 3- 3, Table 3-2)*

Root and crown buccolingual breadths are slightly better predictors of crown height than is root length with higher $r^2$ and %SEE values (Table 3-2). Crown

buccolingual breadths are similar to root breadths (Table 3-2). For the root buccolingual diameter the regression lines for gorillas and for the combined sample are not statistically different (Table 3-2, Fig. 3-2).

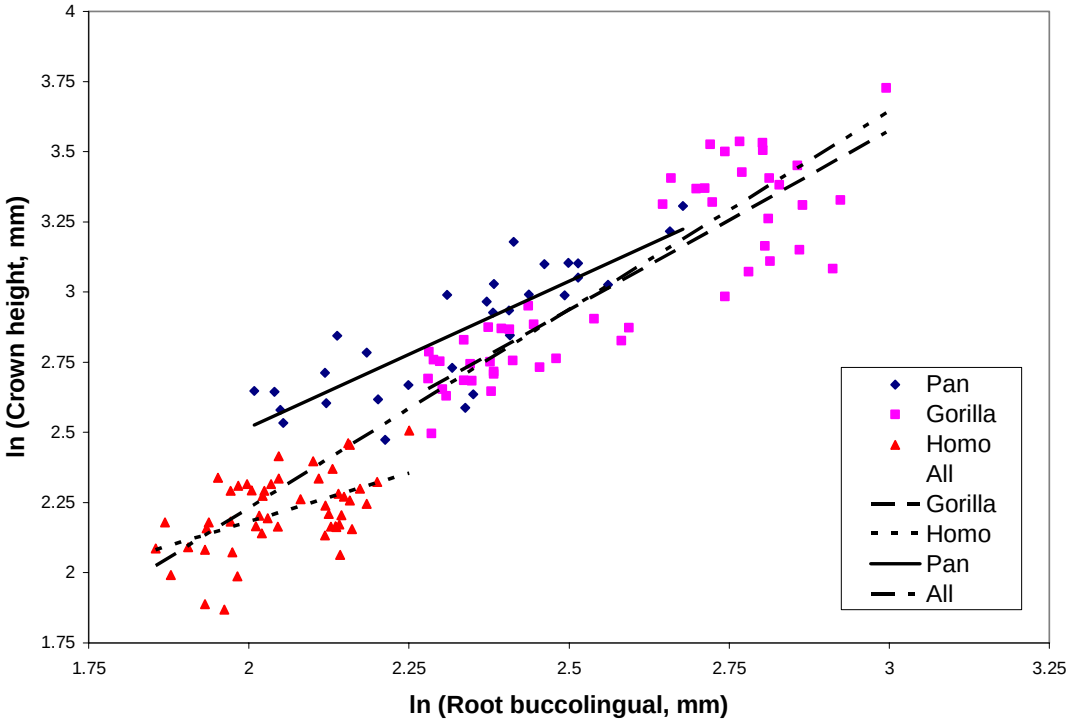


Figure 3-2. Bivariate plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to root buccolingual breadth. Lines represent least-squares regressions for *Pan*, *Gorilla* and *Homo* data, separately as well as for the common sample.

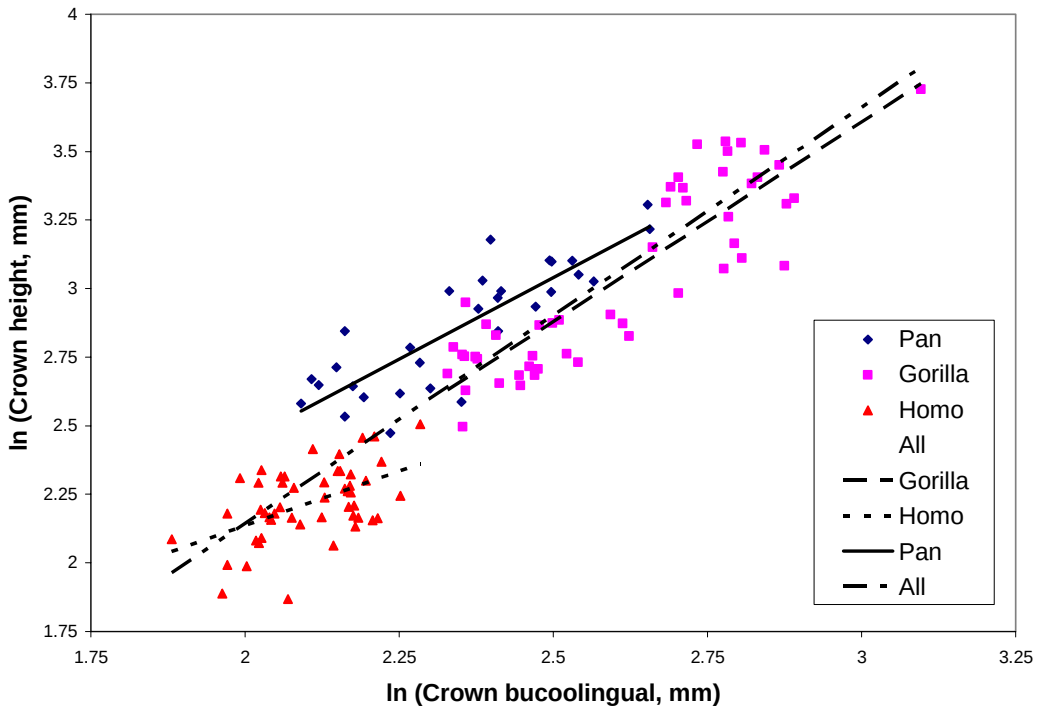


Figure 3-3. Bivariate plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to crown buccolingual breadth. Lines represent least-squares regressions for *Pan*, *Gorilla* and *Homo* data, separately as well as for the common sample.

*Comparison 3 – root and crown mesiodistal length to crown height (Figs. 3-4, 3- 5, Table 3-2)*

On the other hand, root and crown mesiodistal lengths have the highest correlations with crown height and the lowest %SEE values when compared with crown height. Chimpanzees have the highest correlation between crown height and root mesiodistal length ($r^2$=.891) and the lowest overall %SEE value (6.2%) of any other species or for the sample as a whole (Table 3-2). Crown mesiodistal length is the most tightly correlated variable with crown height in gorillas and humans and also yields the lowest %SEE values for each of those species. Within the sample as a whole the

mesiodistal diameter was also the best for predicting crown height (crown $r^2$=.892, %SEE 14.7% and root $r^2$=.891, %SEE 14.8%). (Table 3-2). For the root mesiodistal diameter the regression lines for chimpanzees and for the combined sample are not statistically different (Table 3-2, Fig. 3-4). For the crown mesiodistal diameter the regression lines for humans and for the combined sample are not statistically different (Table 3-2, Fig. 3-5).

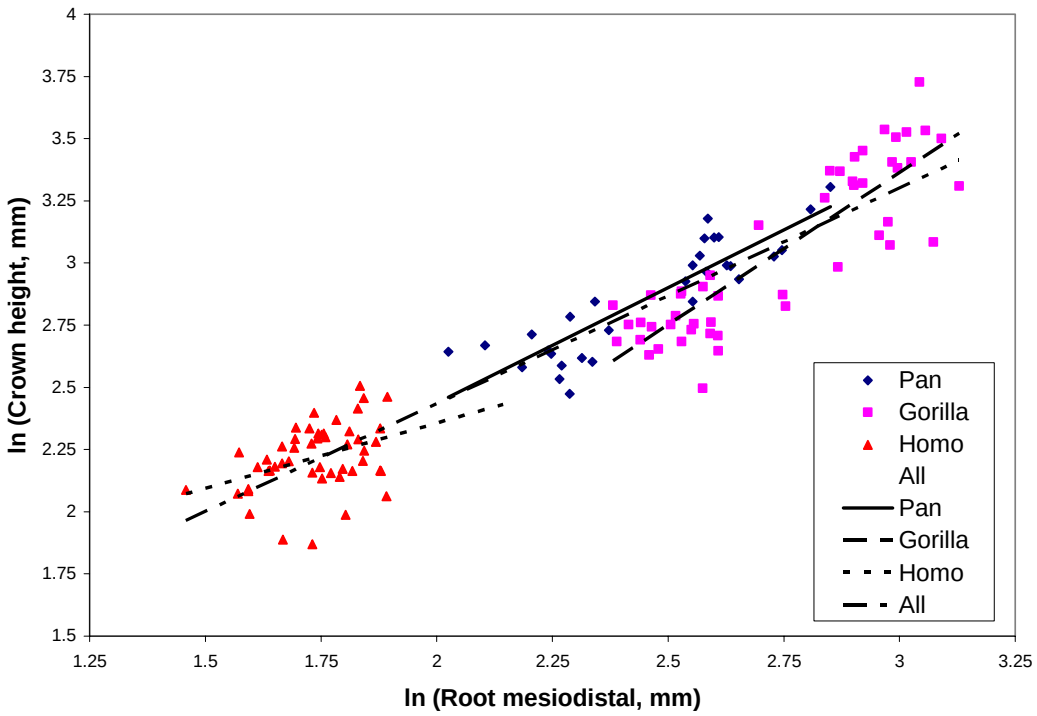


Figure 3-4. Bivariate plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to root mesiodistal length. Lines represent least-squares regressions for *Pan*, *Gorilla* and *Homo* data, separately as well as for the common sample.

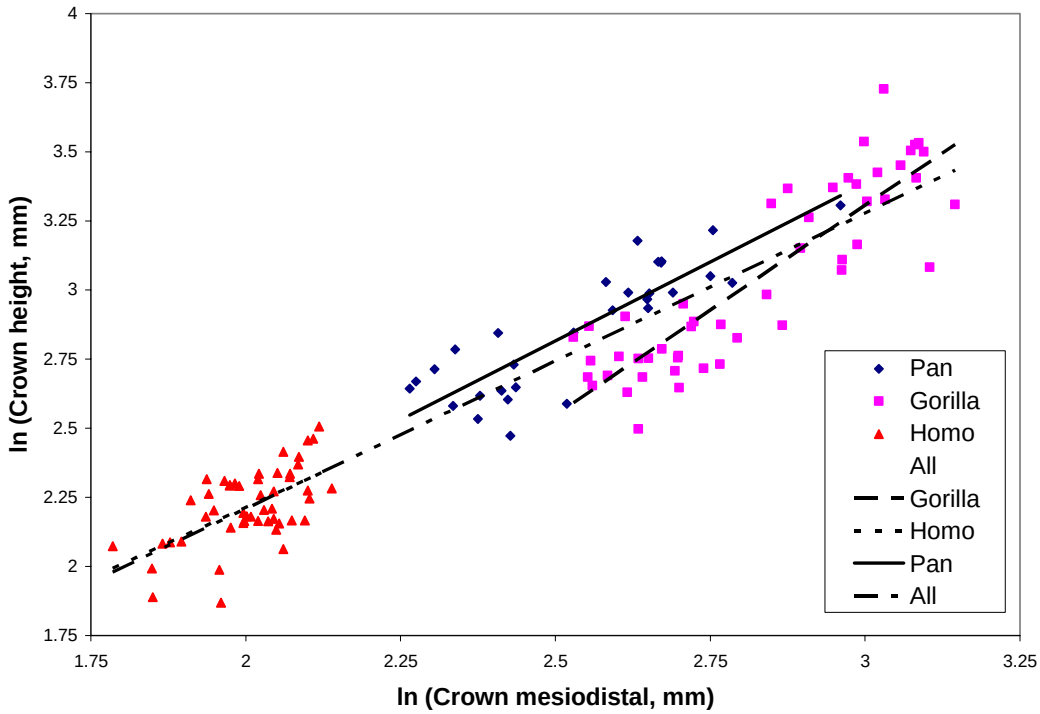


Figure 3-5. Bivariate plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to crown mesiodistal length. Lines represent least-squares regressions for *Pan*, *Gorilla* and *Homo* data, separately as well as for the common sample.

*Conclusions about predicting crown height from basal dimensions and root length*

Root length is the weakest predictor of crown height of all variables considered here, with a %SEE of 17.9% as well as low $r^2$ within each species (*Pan* $r^2$ =.601; *Gorilla* $r^2$ =.569; *Homo* $r^2$ =.127) (Table 3-2). Mesiodistal length is the best predictor having the highest $r^2$ values and the lowest %SEE values. Although there are significant correlations among dimensions, the observed variance, as measured by coefficient of determination and standard errors of the estimate, are large enough to suggest that there are other determinants of crown height not considered here.

Hierarchical multiple linear regression testing reveals that combining root length and crown basal dimensions with root basal dimensions does not improve the correlation of these variables with crown height. First, both root length and breadth were calculated as the independent variables because of previous testing which indicated a high $r^2$ of .904. Second, all variables were used simultaneously as independent variables which yielded an $r^2$ value of .906. The significance value of .361 indicates that there is not a statistically significant increased correlation with crown height even when using all variables instead of just the root basal dimensions. Thus when only using the root basal dimensions to predict crown height there is no need to include the other three variables.

There is also a decrease in $r^2$ and many correlations lose significance when males and females are considered separately for each of the three species (Table 3-3). Even within sex, however, highest $r^2$ and %SEE values are found for mesiodistal lengths to crown height.

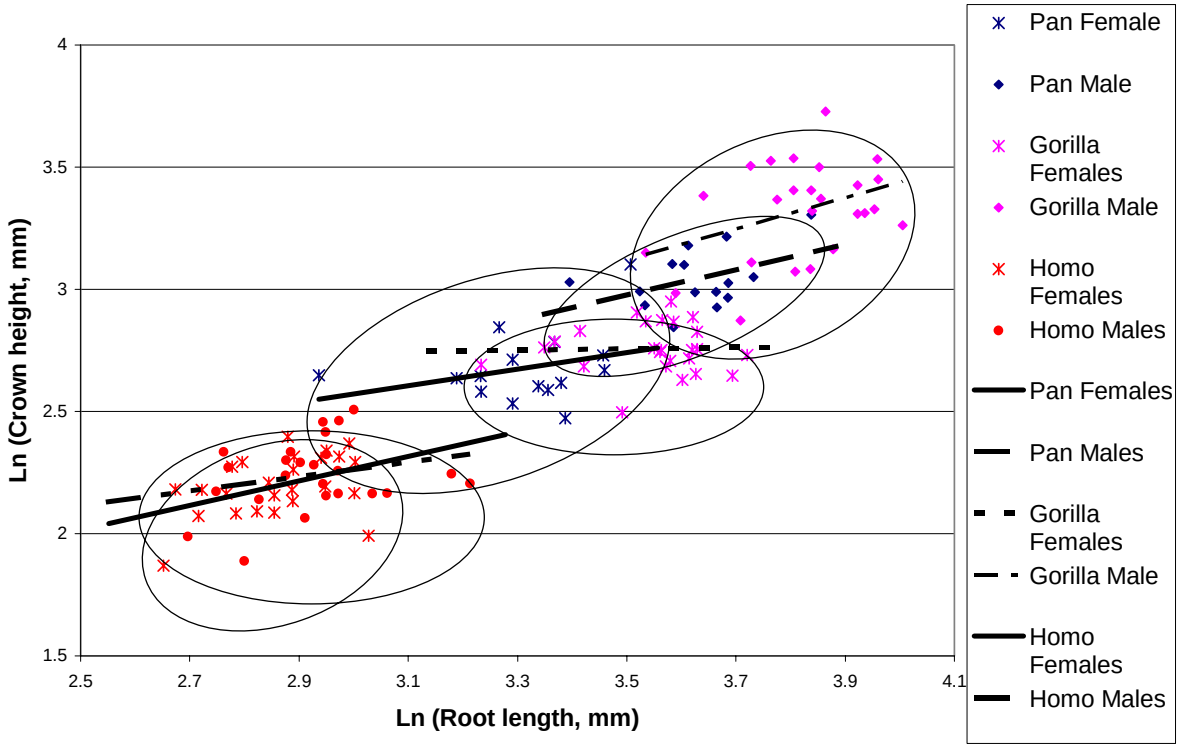


Figure 3-7
Bivariate plot of the ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown height to canine root lengths. Lines represent sex-distinct least-squares regressions for *Pan*, *Gorilla* and *Homo* separately. Ovals circumscribe the males/females for each species. *Homo* male and female data overlap throughout their range of x and y values, *Pan* females and *Gorilla* females overlap over their y values, *Gorilla* females and *Pan* males overlap over their x values and also partially overlap with the *Gorilla* males

Table 3-3. Linear regression statistics for sex-specific data

**Independent variable: Ln root length** **Dependent variable: Ln crown height**

| | | Slope | y-intercept | $r^2$ | p | N | %SEE |
|---|---|---|---|---|---|---|---|
| *Pan* | - M | .517 | 1.168 | .191 | .103 | 15 | N/A |
| | - F | .338 | 1.559 | .097 | .259 | 15 | N/A |
| *Gorilla* | - M | .634 | .903 | .142 | .063 | 25 | N/A |
| | - F | .027 | 2.663 | .001 | .890 | 25 | N/A |
| *Homo* | - M | .296 | 1.377 | .064 | .223 | 25 | N/A |
| | - F | .501 | .763 | .183 | **.033** | 25 | 11.5 |

**Independent variable: ln root buccolingual** **Dependent variable: Ln crown height**

| | | Slope | y-intercept | $r^2$ | p | N | %SEE |
|---|---|---|---|---|---|---|---|
| *Pan* | - M | .829 | 1.001 | .515 | **.003** | 15 | 8.7 |
| | - F | .556 | 1.459 | .273 | **.046** | 15 | 13.3 |
| *Gorilla* | - M | .557 | 1.771 | .065 | .219 | 25 | N/A |
| | - F | .709 | 1.073 | .302 | **.004** | 25 | 8.7 |
| *Homo* | - M | 1.041 | .039 | .296 | **.005** | 25 | 12.3 |
| | - F | .780 | .643 | .244 | **.012** | 25 | 11.0 |

**Independent variable: ln crown buccolingual** **Dependent variable: Ln crown height**

| | | Slope | y-intercept | $r^2$ | p | N | %SEE |
|---|---|---|---|---|---|---|---|
| *Pan* | - M | .812 | 1.034 | .436 | **.007** | 15 | 9.4 |
| | - F | .751 | 1.007 | .323 | **.027** | 15 | 12.8 |
| *Gorilla* | - M | 1.005 | .525 | .245 | **.012** | 25 | 17.7 |
| | - F | .414 | 1.750 | .107* | .110 | 25 | N/A |
| *Homo* | - M | 1.215 | -.371 | .381 | **.001** | 25 | 11.5 |
| | - F | .639 | .881 | .156 | .051 | 25 | N/A |

**Independent variable: ln root mesiodistal** **Dependent variable: Ln crown height**

| | | Slope | y-intercept | $r^2$ | p | N | %SEE |
|---|---|---|---|---|---|---|---|
| *Pan* | - M | .829 | 1.001 | .515 | **.003** | 15 | 9.4 |
| | - F | .718 | 1.046 | .377* | **.015** | 15 | 12.3 |
| *Gorilla* | - M | .906 | .652 | .209 | **.018** | 25 | 17.9 |
| | - F | .166 | 2.338 | .019 | .511 | 25 | N/A |
| *Homo* | - M | .452 | 1.427 | .063 | .225 | 25 | N/A |
| | - F | .824 | .8169 | .266 | **.008** | 25 | 10.8 |

**Independent variable: ln crown mesiodistal** **Dependent variable: Ln crown height**

| | | Slope | y-intercept | $r^2$ | p | N | %SEE |
|---|---|---|---|---|---|---|---|
| *Pan* | - M | .864 | .727 | .549* | **.002** | 15 | 8.4 |
| | - F | .732 | .920 | .238 | **.065** | 15 | N/A |
| *Gorilla* | - M | 1.189 | -.235 | .267* | **.008** | 25 | 17.4 |
| | - F | .322 | 1.904 | .056 | .253 | 25 | N/A |
| *Homo* | - M | 1.298 | -.397 | .385* | **.001** | 25 | 11.5 |
| | - F | .879 | .458 | .323* | **.003** | 25 | 10.4 |

NOTES:
* highest $r^2$ for each variable
Bolded values are significant
N/A: not applicable for %SEE values because the regression line is not significant

## Allometric comparisons

*Comparison 1 – root length and crown height (Fig. 3-8; Table 3-4, 3-5).*

*Homo* and *Pan* have statistically equivalent isometric relations between root length and crown height (Table 3-5, Fig. 3-8). Chimpanzees have larger canines overall than do humans, so there is a shift along the common slope. Gorillas on the other hand, have a positively allometric RMA slope.

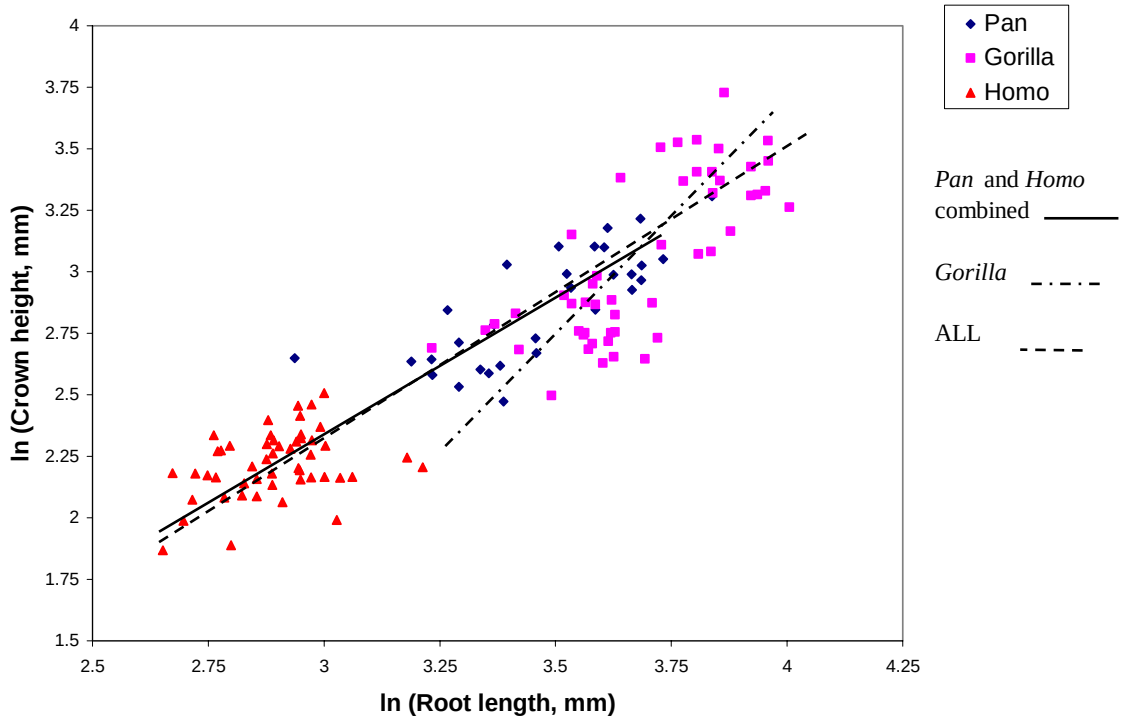


Figure 3-8. Reduced Major Axis plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary canine crown heights to ln-transformed *Pan*, *Gorilla* and *Homo* root lengths. RMA lines are shown for *Pan*, *Gorilla* and *Homo* separately and for the common sample. The *Pan* and *Homo* lines are not statistically different and isometric.

Table 3-4: RMA shift p-values for root length to canine height

| | Difference in slope (A) | Difference in elevation (B) | Difference along the common slope (C) | Difference in elevation and slope (D) |
|---|---|---|---|---|
| *Pan-Gorilla* | **p=.0002** | N/A | N/A | N/A |
| *Gorilla-Human* | **p=.011** | N/A | N/A | N/A |
| *Human-Pan* | p=.985 | p=.597 | **p<.0001** | N/A |

NOTE:
Bold indicates significance
ABCD refers to type of shift as illustrated in Faster (2003) and in Figure 2-3

Table 3-5. Reduced Major Axis table of the independent variable to the dependent variable of maxillary canine height

**Independent variable: Ln Root length** **Dependent variable: Ln Crown height**

| | **Slope** | **y-intercept** | **$r^2$** | **p** | **N** |
|---|---|---|---|---|---|
| *Pan* | 1.15* | -1.117 | .601 | p<.001 | 30 |
| *Gorilla* | 1.82 | -3.645 | .569 | p<.001 | 50 |
| Humans | 1.14* | -1.083 | .127 | p=.011 | 50 |
| All combined | 1.14 | -1.115 | .839 | p<.001 | 130 |

**Independent variable: Ln Root mesiodistal** **Dependent variable: Ln Crown height**

| | **Slope** | **y-intercept** | **$r^2$** | **p** | **N** |
|---|---|---|---|---|---|
| *Pan* | 1.05* | .285 | .785 | p<.001 | 30 |
| *Gorilla* | 1.40 | -.793 | .762 | p<.001 | 50 |
| Humans | 1.35 | -.120 | .152 | p=.005 | 50 |
| All combined | .918 | .584 | .891 | p<.001 | 130 |

**Independent variable: Ln Crown mesiodistal** **Dependent variable: Ln Crown height**

| | **Slope** | **y-intercept** | **$r^2$** | **p** | **N** |
|---|---|---|---|---|---|
| *Pan* | 1.32 | -.489 | .748 | p<.001 | 30 |
| *Gorilla* | 1.72 | -1.831 | .772 | p<.001 | 50 |
| Humans | 1.71 | -1.206 | .361 | p<.001 | 50 |
| All combined | 1.13 | -.084 | .892 | p<.001 | 130 |

**Independent variable: Ln Root buccolingual** **Dependent variable: Ln Crown height**

| | **Slope** | **y-intercept** | **$r^2$** | **p** | **N** |
|---|---|---|---|---|---|
| *Pan* | 1.24 | -.033 | .702 | p<.001 | 30 |
| *Gorilla* | 1.46 | -.739 | .761 | p<.001 | 50 |
| Humans | 1.38 | -.611 | .251 | p=.0002 | 50 |
| All combined | 1.54 | -.887 | .845 | p<.001 | 130 |

**Independent variable: Ln Crown buccolingual** **Dependent variable: Ln Crown height**

| | **Slope** | **y-intercept** | **$r^2$** | **p** | **N** |
|---|---|---|---|---|---|
| *Pan* | 1.4 | -.426 | .724 | p<.001 | 30 |
| *Gorilla* | 1.66 | -1.284 | .768 | p<.001 | 50 |
| Humans | 1.55 | -1.038 | .264 | p=.0001 | 50 |
| All combined | 1.65 | -1.203 | .845 | p<.001 | 130 |

NOTES:
*isometric lines

*Comparison 2 – root and crown mesiodistal length and crown height (Figs. 3-9, 3-10; Tables 3-5, 3-6, 3-7)*

Humans have shorter crowns and mesiodistally narrower roots and crowns than do chimpanzees and gorillas (Figs. 3-9, 3-10; Tables 3-5, 3-6, 3-7). All species show similar RMA slopes of crown height on root and crown mesiodistal length but with statistically different elevations (Figs. 3-9, 3-10; Tables 3-5, 3-6, 3-7). Human crowns are taller relative to mesiodistal length than are those of chimpanzees and gorillas. Chimpanzees have taller crowns relative to root and crown mesiodistal lengths. However, their range of crown heights partially overlaps that of gorillas. Gorillas and humans scale positively allometrically while chimpanzees are isometric.

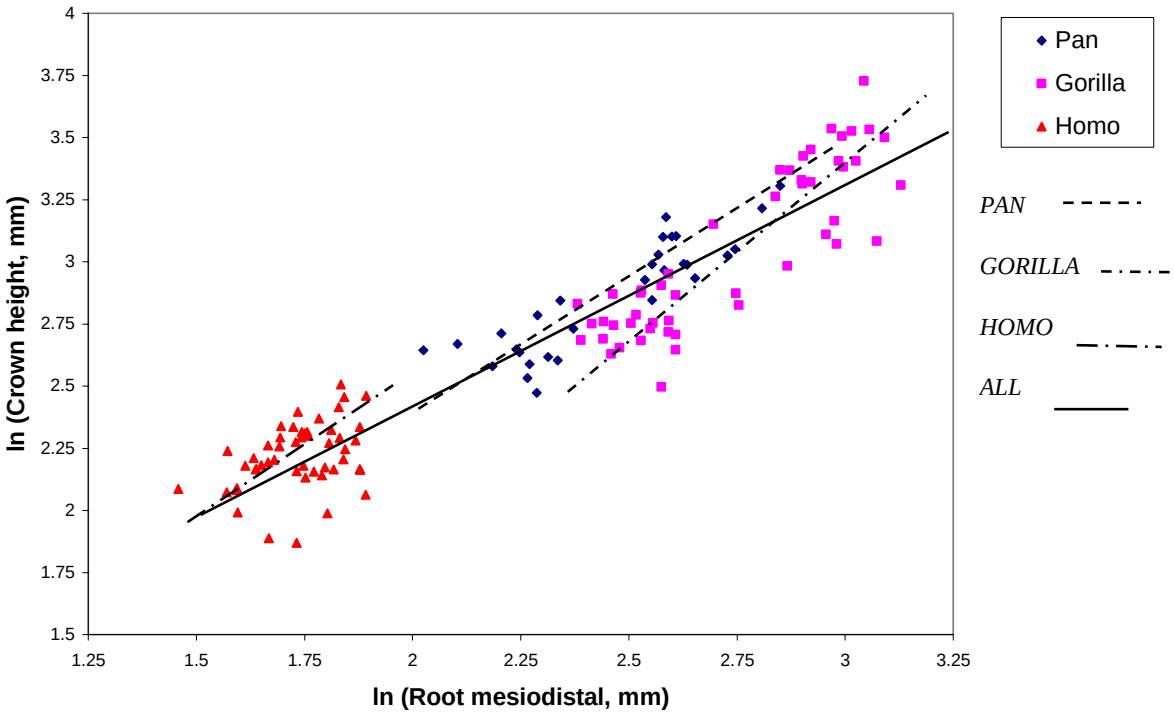


Figure 3-9. Reduced Major Axis plot of ln-transformed *Pan*, *Gorilla* and *Homo* maxillary crown heights to ln-transformed *Pan*, *Gorilla* and *Homo* root mesiodistal length. RMA lines are shown for *Pan*, *Gorilla* and *Homo* separately and for the common sample. There is a Shift D (shift in elevation and slope) between *Homo* and *Pan* and between *Homo* and *Gorilla*. *Pan* also scales isometrically while *Gorilla and Homo* scale positively allometric.

Table 3-6: RMA p-values for Root mesiodistal to canine height

| | Difference in slope (A) | Difference in elevation (B) | Difference along the common slope (C) | Difference in elevation and slope (D) |
|---|---|---|---|---|
| *Pan-Gorilla* | **p=.010** | N/A | N/A | N/A |
| *Gorilla-Human* | p=.787 | **p<.0001** | **p<.0001** | **YES** |
| *Human-Pan* | p=.131 | **p<.0001** | **p<.0001** | **YES** |

NOTE:
Bold indicates significance
ABCD refers to type of shift as illustrated in Faster (2003) and in Figure 2-3

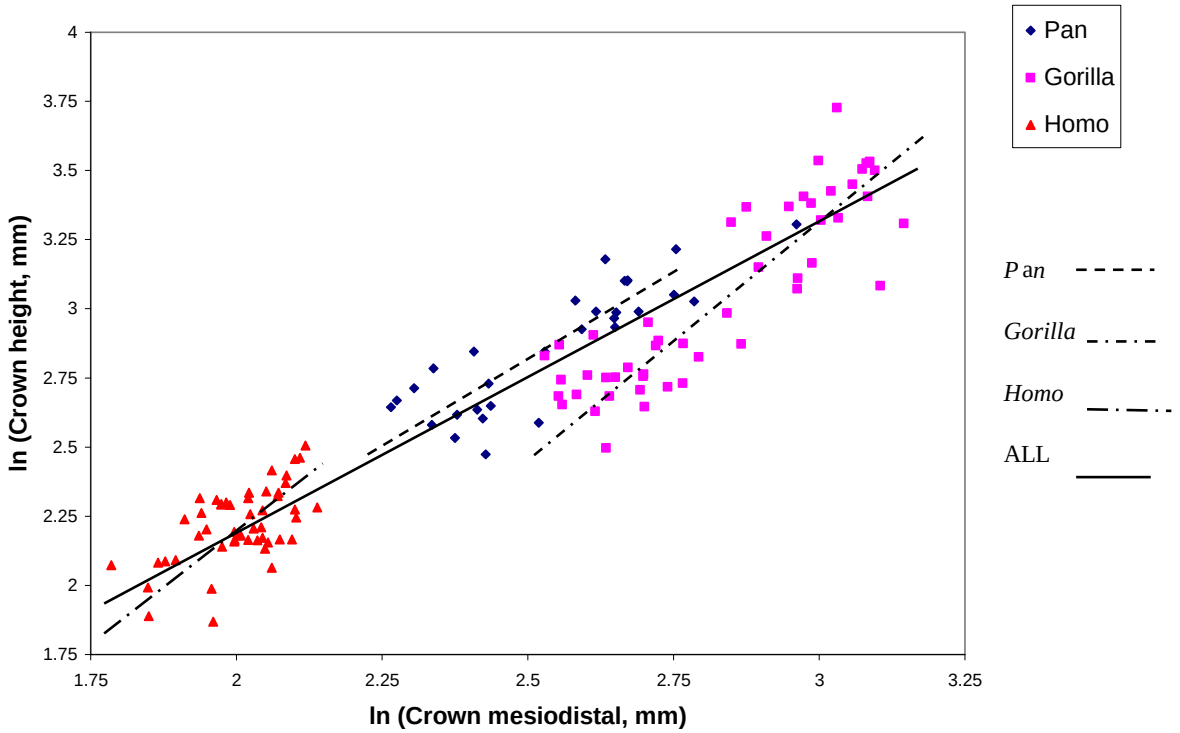


Figure 3-10. Reduced Major Axis plot of ln-transformed *Pan, Gorilla* and *Homo* maxillary crown heights to ln-transformed *Pan, Gorilla* and *Homo* crown mesiodistal lengths. RMA lines are shown for *Pan, Gorilla* and *Homo* separately and for the common sample. There is a Shift D (a shift in elevation and slope) between *Homo* and *Pan* and between *Homo* and *Gorilla*.

Table 3-7: RMA p-values for Crown mesiodistal to canine height

| | Difference in slope (A) | Difference in elevation (B) | Difference along the common slope (C) | Difference in elevation and slope (D) |
|---|---|---|---|---|
| *Pan-Gorilla* | **p=.037** | N/A | N/A | N/A |
| *Gorilla-Human* | p=.936 | **p<.001** | **p<.001** | **YES** |
| *Human-Pan* | p=.095 | **p<.001** | **p<.001** | **YES** |

NOTE:
Bold indicates significance
ABCD refers to type of shift as illustrated in Faster (2003) and in Figure 2-3

*Comparison 3 – root and crown bucco-lingual breadths and crown height (Figs. 3-11, 3-12; Tables 3-5, 3-8, 3-9).*

Humans and gorillas have shorter crowns relative to buccolingual breadth than do chimpanzees, with a statistically equivalent scaling relation differing only in the fact that gorillas are much larger overall (shift C). All species have the same RMA slope, but chimpanzees have significantly taller crowns *(Figs. 3-11, 3-12; Tables 3-5, 3-8, 3-9).* Chimpanzee canines are slightly smaller than are those of gorillas overall. All species scale positively allometrically.

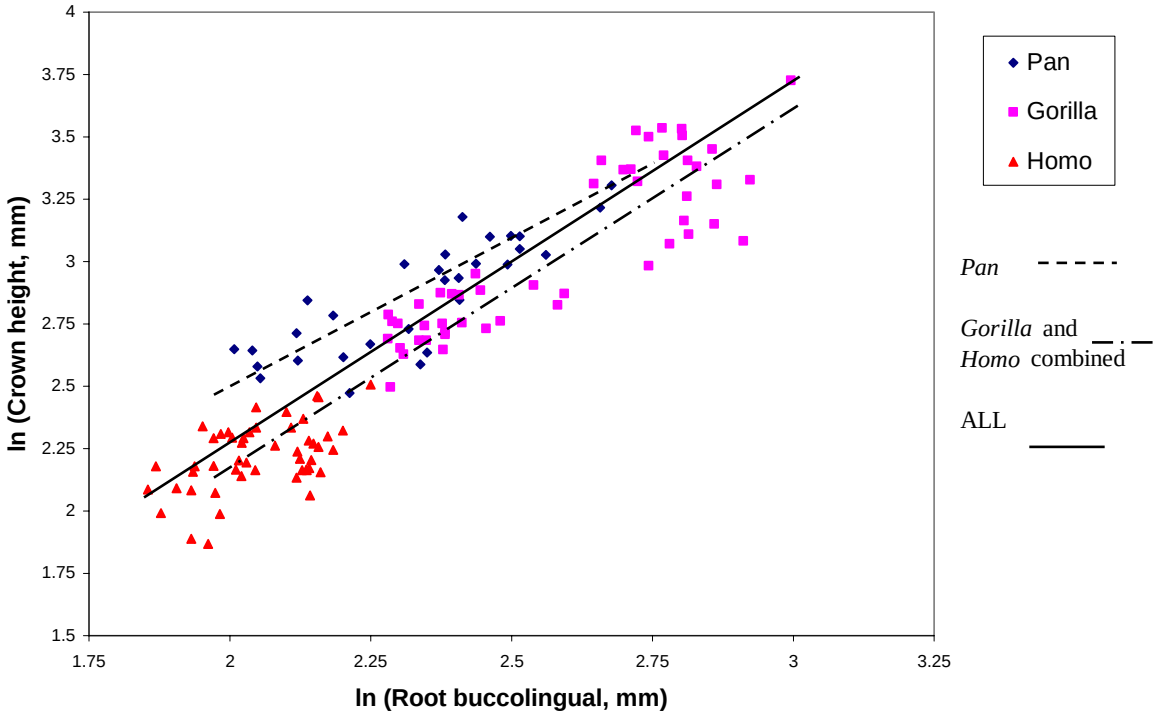


Figure 3-11. Reduced major axis plot of ln-transformed *Pan, Gorilla* and *Homo* maxillary crown heights to ln-transformed *Pan, Gorilla* and *Homo* root buccolingual breadths. RMA lines are shown for *Pan, Gorilla* and *Homo* separately and for the common sample. The *Gorilla* and *Homo* lines are not statistically different. Also note that there is a Shift D (shift in elevation and in slope) between *Homo* and *Pan* and between *Pan* and *Gorilla.* All lines scale positively allometric.

Table 3-8: RMA p-values for Root buccolingual to canine height

| | Difference in slope (A) | Difference in elevation (B) | Difference along the common slope (C) | Difference in elevation and slope (D) |
|---|---|---|---|---|
| *Pan-Gorilla* | p=.197 | **p<.0001** | **p<.0001** | **YES** |
| *Gorilla-Human* | p=.694 | P=.051 | **p<.0001** | N/A |
| *Human-Pan* | p=.550 | **p<.0001** | **p<.0001** | **YES** |

NOTE:
Bold indicates significance
ABCD refers to type of shift as illustrated in Faster (2003) and in Figure 2-3

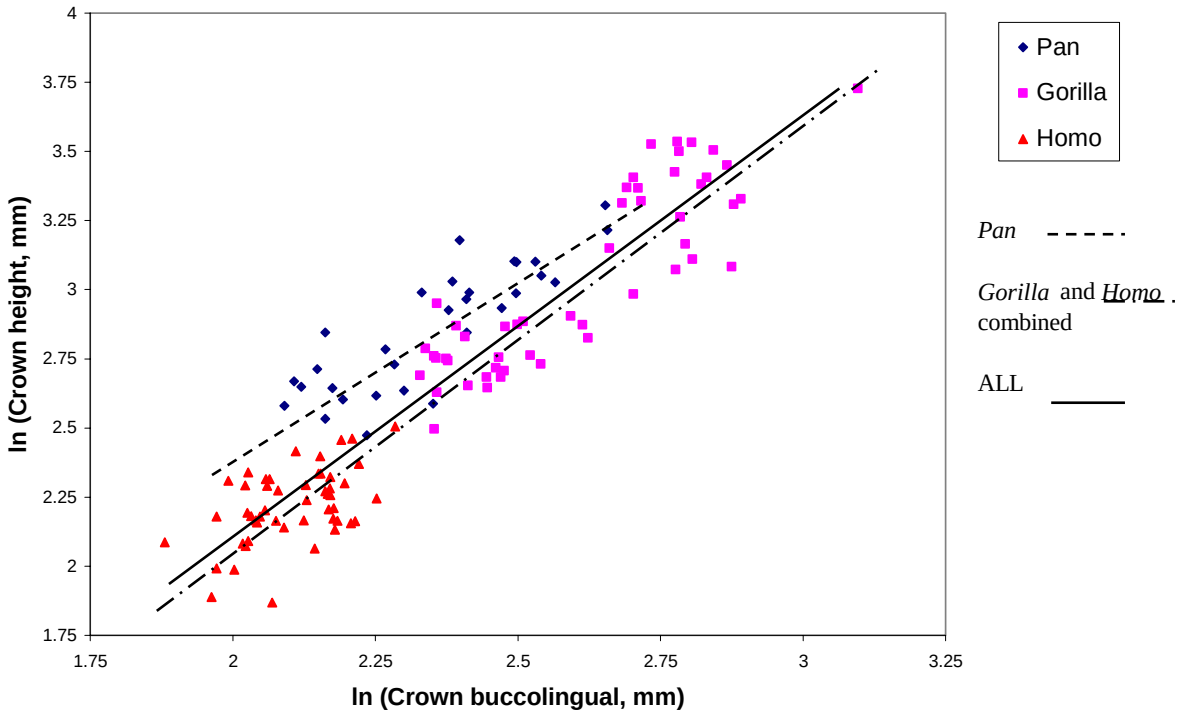


Figure 3-12. Reduced Major Axis plot of ln-transformed *Pan, Gorilla* and *Homo* maxillary canine crown heights to ln-transformed *Pan, Gorilla* and *Homo* crown buccolingual breadths. RMA lines are shown for *Pan, Gorilla* and *Homo* separately and for the common sample. The *Gorilla* and *Homo* lines are not statistically different. There is a Shift D (a shift in elevation and slope) between *Homo* and *Pan* and between *Pan* and *Gorilla.* All lines scale positively allometric.

Table 3-9: RMA p-values for Canine buccolingual to canine height

| | Difference in slope (A) | Difference in elevation (B) | Difference along the common slope (C) | Difference in elevation and slope (D) |
|---|---|---|---|---|
| *Pan-Gorilla* | p=.171 | **p<.0001** | **p<.0001** | **YES** |
| *Gorilla-Human* | p=.621 | p=.919 | **p<.0001** | N/A |
| *Human-Pan* | p=.521 | **p<.0001** | **p<.0001** | **YES** |

NOTE:
Bold indicates significance
ABCD refers to type of shift as illustrated in Faster (2003) and in Figure 2-3

# Chapter 4 – Discussion and Conclusions

## Discussion

Results of these analyses demonstrate that canine crown height can be predicted from other canine measurements, although with a 6-22% error. Of the variables considered here, crown and root mesiodistal lengths, which are the best predictors of canine crown height, still have a wide range of %SEE values. Kay et al. (1988), Plavcan (1993), and Plavcan and van Schaik (1995) have shown that crown and root mesiodistal dimensions are more strongly correlated with canine crown height than are buccolingual breadths and mesiodistal dimensions are also correlated with male-male competition (Plavcan, 1993). The results of this thesis agree with the findings of authors in that mesiodistal diameters are more strongly correlated with canine crown height than are buccolingual breadths.

Root length is also a poor predictor of canine crown height (SEE values: 12.7% to 21.6%), although is correlated both within and among species. This suggests that crown height does not strongly influence root length, or vice versa. Therefore, caution should be

exercised when attempting to predict canine crown size from worn crowns using only the root. It also means that conclusions about root size based on crown height, and the commensurate effect on facial structure, must be made cautiously as well (McCollum, 1994; Spencer, 2003). Simply observing crown size differences among taxa, or between sexes within taxa, is insufficient to accurately infer root size differences except at a very broad level.

The lack of a very high correlation between canine root and crown lengths is not surprising, as each is under different developmental control (Chapter 1; Avery, 1992). Even though some of the correlations for mesiodistal and buccolingual dimensions are high within taxa, the fact that there are high %SEE values and variation among taxa raises questions about the function and development of canine crowns and roots. Since maxillary canine crowns smoothly transitions to the root at the cementoenamel junction root and crown diameters should are necessarily tightly correlated. However, since the crown increases in height independently (in time and space) of the root there is no such restriction.

A high %SEE value indicates the wide variety and variation in canine dimensions. Together, a low $r^2$ and a high %SEE value indicate a low correlation and considerable variation in a sample. A limitation to concluding the determinants of variation among canine dimensions is the sample size of three species.

This observed variation among canine crown dimensions reflects different crown shapes, which in some, could be related to canine use. Seed predators have larger buccolingual and mesiodistal diameters relative to canine height than do soft fruit frugivores, for example (Spencer, 2003). This seems to be limited to pithecines that use

their canines for hard object feeding (Kinzey, 1971; Spencer, 2003). Among the African hominoids, chimpanzees have the thinnest canine crowns. The thicker crowns of gorillas are not simply allometrically scaled versions of chimpanzee canines, but instead reflect a different species-specific crown shape. It is unknown if this shape variation is associated with canine tooth function.

Gorillas, in all of the measurements, scale with greater positive allometry than any other species studied here, except in buccolingual breadth to crown height comparisons in which they scale the same as humans. In root length to crown height comparisons, however, chimps and humans do not significantly differ. This shows that gorillas are unique in their specific scaling patterns of the whole canine tooth. The reason for these different scaling relations is not clear. Gorillas, like chimpanzees, have dimorphic canines and the canines are used in male-male competition (Leutenegger and Kelly, 1977; Smith, 1980; Kay et al, 1988; Greenfield, 1992; Plavcan et al, 1995; Plavcan and van Schaik, 1997ab; Plavcan, 1998; Plavcan, 2000; Plavcan, 2001; Schwartz and Dean, 2001). The difference among species cannot easily be attributed to variation in any documented fighting strategy, nor diet. Chimpanzees and gorillas do not use their canines while eating nor do their diets differ enough to cause these differences.

Canine roots in gorillas are generally not as long as they would be for a chimpanzee with a similar sized canine crown. The relatively short roots of gorillas suggest that roots may be constrained by facial bone structure or other developmental or structural factors in some way. Dr. J. Michael Plavcan (personal communication) has suggested that when a certain amount of torque is acting upon the canine crown, a long root could have a “crowbar” affect, causing the root to exert pressure on the delicate

maxillary bone which could potentially damage the face. This hypothesis can be tested indirectly by looking for correlations between intensity of canine use during agonistic interactions and relative root length. No clear pattern is observable here, unless gorillas have disproportionately more torque applied to their canines. Gorillas also differ from chimpanzees in scaling patterns of crown height to basal dimensions. *Pan* canine crowns are tall relative to buccolingual breadth and mesiodistal length compared to *Gorilla*. *Pan* overlaps with *Gorilla* in the proportions of crown size relative to root length even though there are different allometric relations.

Results presented here do not support the hypothesis that humans have relatively long roots for their crowns (see Wood, 2002). Human crowns do not scale any differently than chimpanzees relative to root length, as these species share a common slope and elevation (Fig. 3-8; Table 3-4). However, humans do have taller crowns relative to mesiodistal crown diameter. This likely reflects a shorter crown mesiodistally, due to the lack of a honing complex in humans. If mesiodistal length decreased along with crown height the seemingly wide buccolingual breadth seen in humans compared with African apes is not really wide, but an illusion of such because the other two dimensions have decreased. This conclusion is supported by the observation that crown height scales equivalently relative to buccolingual breadth in both gorillas and humans.

Plavcan (1993) has shown that canine crown height scales isometrically relative to basal dimensions across anthropoids. Results of this study, on the other hand, only found isometric slopes among all relations examined for crown height to root length in chimps and humans and for crown height to root mesiodistal length in chimps (See Results; Table 3-5). Plavcan's results may be due to his large sample size of 79 primate

species, compared with the smaller sample considered here. It is common in scaling relations for smaller taxonomic units to have higher slopes than larger intertaxonomic comparisons (Pagel and Harvey, 1988).

The ability to make precise predictions of hominin canines from these data is limited. Relations identified in this study illustrate the difficulty in reconstructing maxillary canine crown height in fossil hominins. Radiographs of fossil hominins taken in standard anatomical planes cannot be used to accurately measure root length, because maxillary canine roots are oriented in an oblique plane, and so are distorted by parallax and foreshorted. However, the *Australopithecus anamensis* specimen KNM-KP 29283 has a very large exposed root but the crown has been destroyed by wear (Ward et al., 2001). This provides the opportunity to measure the length of its root, in addition to basal dimensions of the root, and mesiodistal diameter of its crown. The enamel is worn off of the lingual surface, so crown buccolingual breadth cannot be measured. This is not a significant shortcoming, because mesiodistal lengths are better predictors of crown height.

Using the regression line in which all three species (*Pan*, *Gorilla*, and *Homo sapiens*) were combined, I first predicted the crown height of KNM-KP 29283 for each available measurement (Table 4-1). I used the line for the combined sample because it is unknown what the allometric relations are like for early fossil hominins. I then used the *Pan* and *Gorilla* lines to see if the predicted values were similar. I did not use the *Homo* line for any test because the $r^2$ was under 0.5. Though it is more unlikely that early hominins have canines that are allometrically similar to gorillas it seems unwise to make that assumption and so I have included gorillas.

Table 4-1: *A. anamensis* KNM-KP 29283 range of predicted canine crown height measurements from root length, root buccolingual breadth and both mesiodistal lengths using the combined sample (For $r^2$ values and CI see Table 3-2)

| Variables | Actual measurements (mm) | Ln-transformed | Equation | lnY - arithmetic Y | %SEE | Range |
|---|---|---|---|---|---|---|
| Root length | 28.4 | 3.346 | Y=1.0451x -.7972 | 2.7 – 14.88 | 17.9% | 13.6 to 16.1 |
| Canine mesiodistal | 10.8 | 2.379 | Y=1.0691x +.0702 | 2.61 – 13.59 | 14.7% | 12.6 to 14.6 |
| Root mesiodistal | 10.8 | 2.379 | Y=.8662x +.7013 | 2.76 – 15.79 | 14.8% | 14.6 to 17.0 |
| Root buccolingual | 8.8 | 2.17 | Y=1.4146x -.5992 | 2.47 – 11.8 | 17.6% | 10.8 to 12.8 |

NOTE: %SEE values were calculated by taking the average of the %SEE values of the variables used

When using log-transformed data to predict other dimensions, detransforming log data back to arithmetic data can introduce systematic bias (Smith, 1980). Correcting for this bias can be complicated, and for the present purpose I have ignored this potential bias, and simply de-logged the data. This was deemed acceptable, because of the wide range of estimates obtained.

When canine crown height is predicted from each of these variables for the combined sample, the range of estimates was from 10.8 to 17.0 mm (Table 4-1). The only unworn *A. anamensis* maxillary right canine KNM-KP 35839 has a measured canine height of 14.6mm (Ward et al., 2002). This fits in the larger end of some of the ranges provided for the combined sample. However, this table shows a large range and shows minimal utility for predicting crown height.

I also used multiple linear regression to predict canine crown height for KNM-KP 29283 using all four available measurements for *Pan, Gorilla,* and the combined sample (Table 4-2). The resulting range of canine crown height estimates for the combined

sample was from 12.8 to 15.1 mm. This range includes the measured canine height of KNM-KP 35839. The range of canine crown height when using only the *Pan* line was 14.4 to 16.9 mm which also includes the measured crown height of KNM-KP 35839. The *Gorilla* line range was from 10.6 to 12.5 which falls far below the measured crown height of KNM-KP 35839. In summary, the actual crown height of the KNM-KP 29283 canine could be anything from 10.6 to 16.9 based on its preserved dimensions. This range of estimates is too large to be useful for reconstructing crown height.

Table 4-2: *A. anamensis* KNM-KP 29283 range of predicted canine crown height using multiple regression using the combined variables of root length, root buccolingual breadth and both mesiodistal lengths

| Line | $r^2$ | Equation | CI | Ln Y – arithmetic Y | %SEE | Range |
|---|---|---|---|---|---|---|
| Combined sample | .906 | Y=-0.095+(0.241*CMD)+(0.338*RMD)+(0.42*RBL)+(0.132*RL) | RL +- .216<br>RBL +- .241<br>RMD +- .352<br>CMD +- .45 | 2.636 – 13.95 | 16.2% | 12.8 to 15.1 |
| *Pan* | .798 | Y= .279+(.068*RL)+(.239*RBL)+ (.613*RMD) +(.112*CMD) | RL +- .42<br>RBL +- .584<br>RMD +- .745<br>CMD +- .915 | 2.75 – 15.642 | 16.2% | 14.4 to 16.9 |
| *Gorilla* | .805 | Y= -1.114+(.5*CMD)+(.186*RL)+(.254*RMD)+(.527*RBL) | RL +- .407<br>RBL +- .526<br>RMD +- .737<br>CMD +- .937 | 2.446 – 11.539 | 16.2% | 10.6 to 12.5 |

NOTE: %SEE values were calculated by taking the average of the %SEE values of the variables used

To investigate the ability of the data from this study to predict crown heights in Australopithecus, I also predicted the crown height of eight *A. afarensis* specimens using the linear regression line in which all three species (*Pan*, *Gorilla*, and *Homo sapiens*) were combined for crown mesiodistal and buccolingual diameters (Table 4-3).

Table 4-3. *Australopithecus afarensis* actual and predicted crown height measurements predicted from crown mesiodistal and buccolingual diameters by linear regression using the combined sample

| Specimen | Actual Crown height | Crown Mesiodistal Range of Estimated Crown Height ($r^2$=.892) | | Crown Buccolingual Range of Estimated Crown Height ($r^2$=.845) | |
|---|---|---|---|---|---|
| | | Lower | Upper | Lower | Upper |
| A.L. 199-1 | 9.2 | 10.29 | 11.9 | 11.0 | 13.2 |
| A.L. 200-1a | 12.7 | 11.0 | 12.8 | 14.0 | 16.7 |
| A.L. 333-2 | 10.2 | 11.4 | 13.2 | 14.0 | 16.7 |
| A.L. 333x-3 | 15.4 | 12.2 | 14.1 | 15.2 | 18.2 |
| A.L. 400-1b | 12.5 | 10.7 | 12.4 | 12.9 | 15.4 |
| L.H. 3 | 14.2 | 13.7 | 15.8 | 17.3 | 20.6 |
| L.H. 5 | 10.6 | 11.2 | 12.9 | 11.9 | 14.2 |
| L.H. 5 | 13.7 | 11.8 | 13.6 | 12.3 | 14.7 |

Buccolingual dimensions give higher values of estimated crown height while the mesiodistal diameter predictions resulted in much closer values to the actual measured crown heights. It is important to note that some these measurements are small because of wear on the tooth. Though mesiodistal dimensions are shown again to be better predictors of canine crown height than buccolingual dimensions; because of high %SEE values and unknown qualifications to the relationships between dimensions no variable is a precise tool to predicting crown height.

I also used multiple linear regression using both crown buccolingual and mesiodistal diameters to predict the canine height of the eight *A. afarensis* specimens for *Pan*, *Gorilla*, and for the combined sample (Table 4-4). For the combined sample, half of the measured crown heights fell below the predicted range. This could be due to wear. However, one specimen fell above the predicted range. Using only data from *Pan*, the majority of *Australopithecus* specimens fell above the estimated crown heights while two

fell within the given range. The *Gorilla* line resulted in a more equal distribution with specimens falling below, above and within the given range. I also computed the confidence intervals (CI) of the individual variable slopes.

Table 4-4. *Australopithecus afarensis* actual and predicted crown height measurements predicted from multiple regression using the combined variables of crown mesiodistal and buccolingual diameters

| Specimen | Actual Crown height | **Lower range** | | | **Upper range** | | |
|---|---|---|---|---|---|---|---|
| Line | | Combined sample | *Pan* | *Gorilla* | Combined sample | *Pan* | *Gorilla* |
| $r^2$ value | | .898 | .764 | .803 | .898 | .764 | .803 |
| A.L. 199-1 | 9.2 | 10.4 | 11.8 | 8.7 | 12.2 | 13.9 | 10.2 |
| A.L. 200-1a | 12.7 | 11.6 | 13.3 | 10.3 | 13.7 | 15.7 | 12.1 |
| A.L. 333-2 | 10.2 | 11.9 | 13.6 | 10.5 | 14.0 | 16.0 | 12.4 |
| A.L. 333x-3 | 15.4 | 12.8 | 14.6 | 11.5 | 15.1 | 17.2 | 13.5 |
| A.L. 400-1b | 12.5 | 11.1 | 12.7 | 9.6 | 13.0 | 14.9 | 11.3 |
| L.H. 3 | 14.2 | 14.5 | 16.4 | 13.3 | 17.0 | 19.3 | 15.7 |
| L.H. 5 | 10.6 | 11.2 | 12.8 | 9.6 | 13.2 | 15.0 | 11.3 |
| L.H. 5 | 13.7 | 11.8 | 13.4 | 10.1 | 13.9 | 15.7 | 11.9 |

Ward and colleagues (1999; 2001) inferred the possibility of larger canines and greater canine dimorphism in *Australopithecus anamensis* relative to *A. afarensis* and later hominins on the basis of a large mandibular canine alveolus in KNM-KP 29287. While the present study did not explore mandibular canine structure, these results certainly cast into doubt the ability to make such statements about crown height, the aspect of canine structure affected most strongly by sexual selection, based on an alveolus. There are other worn canines with large roots and alveoli in the *A. anamensis* sample, however, which do indicate the larger crown size of this species relative to *A.*

*afarensis* (Ward et al., 1999; 2001). *Australopithecus anamensis* canine crowns are presumed to be larger than *A. afarensis* because even though worn, the crowns still appear to be larger.

This research has made several important and useful observations, which raise numerous questions about crown and root dimension scaling in hominoids. A larger sample of hominoids, particularly including orangutans and hylobatids, would be useful to explore potential functional relations between diet and crown shape, and would provide a further consideration of sexual dimorphism. A broader sample of anthropoids would allow me to explore the effects of diet and sexual selection on canine dimensions, and the relations of these dimensions to facial proportion. It will also allow the opportunity to explore to what extent scaling patterns observed within hominoids extend across anthropoids. A sample of only three species is a limitation to concluding the determinants of variation among canine dimensions.

A potential source of error, besides measurement or transcription errors, was the fact that root dimensions were taken from two dimensional radiographs. While the tooth roots were placed as parallel as possible to the x-ray film to prevent distortion, there is also the possibility that they were not perfectly parallel. Root closure was not always perfectly visible, although none of the questionable specimens fell at any margin of the observed distribution of root lengths. The scale bar was placed a close as possible to the actual height of the canine root above the film but slight misplacement could introduce bias. Collecting data from three dimensional images such as reconstructed CT or microCT scans would provide a more accurate method with which to collect these data.

Even with the potential sources of error, however, it is unlikely that the general conclusions made here would have been considerably different.

**Conclusions**

This thesis has investigated the potential for predicting maxillary canine crown height from root length and crown and root basal dimensions. Mesiodistal dimensions of the crown and root were the best predictors of crown height because they have the lowest percent standard error of the estimate and the highest correlations. However, in hominins, dimorphism of the occlusal dimensions is much stronger than of the crown height (Plavcan personal correspondence). This could potentially overestimate crown height dimorphism proportional to the occlusal dimensions (Plavcan personal correspondence). Root length is a very poor predictor of crown height. Estimates of crown height were predicted for *A. anamensis* specimen KNM-KP 29283 and each variable showed a wide range of potential crown heights. This study has demonstrated the inability of basal dimensions and root lengths to accurately reconstruct crown height, and so questions the validity of the conclusions made by Ward et al. (1999; 2001) that *A. anamensis* had more dimorphic canine crowns than did later hominins (contra Ward et al., 1999; 2001).

Crown height scales more positively allometrically in gorillas than in chimps or humans relative to root length, although the functional significance of this variation is unclear. Chimpanzee canine crowns are taller and mesiodistally thinner relative to basal dimensions compared to those of gorillas. Humans and chimpanzees have similar crown heights relative to root length, which fails to support the hypothesis that humans have

relatively longer canine roots than do apes, unless chimpanzees are also relatively long. Including more taxa would provide a test of this hypothesis.

This study highlights the relative independence of maxillary canine crown height, basal dimensions, and root lengths in African hominoids. Selection and/or developmental constraints appear to act at least somewhat independently on these three aspects of canine form. While selective pressures acting on crown height have been well-studied, those affecting basal dimensions have been less thoroughly explored, and those acting on roots are relatively unknown. Because of the intimate relations of canine root structure and facial form and canine dimorphism in hominins and other anthropoids, elucidating the nature and extent of the variation in root form stands to make a significant contribution to reconstructing the biology of fossil anthropoids.

# Appendix

Data were collected for this study from the Cleveland Museum of Natural History.

Crown height, crown and root buccolingual, and crown and root mesiodistal measurements are described in the Results section of this thesis (see Fig. 2-1). Root length measured from film in the measurement of the root length taken directly off of the radiograph. Actual root length is the real root length of the specimen calculated by using the scale bar. All measurements were measured in mm. The species listed here are abbreviated from *Pan troglodytes*, *Gorilla gorilla* and *Homo sapiens*.

# Appendix

| Specimen # | Species | Sex | Age | Crown height | Crown buccolingual | Crown mesiodistal | Root buccolingual | Root mesiodistal | Root length measured from film | Actual root length |
|---|---|---|---|---|---|---|---|---|---|---|
| HTB 1173 | Pan | F | Adult | 14.13 | 8.33 | 11.43 | 7.45 | 9.40 | 21.60 | 18.84 |
| HTB 1426 | Pan | F | Adult | 14.07 | 8.80 | 9.63 | 7.69 | 7.58 | 29.04 | 25.33 |
| HTB 1701 | Pan | F | Adult | 13.95 | 9.98 | 11.17 | 10.49 | 9.46 | 27.80 | 24.25 |
| HTB 1703 | Pan | F | Adult | 14.43 | 8.23 | 9.73 | 9.48 | 8.20 | 36.43 | 31.78 |
| HTB 1706 | Pan | F | Adult | 15.33 | 9.81 | 11.39 | 10.15 | 10.72 | 34.71 | 31.72 |
| HTB 1707 | Pan | F | Adult | 13.51 | 8.96 | 11.28 | 8.34 | 10.34 | 30.82 | 28.17 |
| HTB 1713 | Pan | F | Adult | 15.07 | 8.57 | 10.02 | 8.32 | 9.07 | 29.41 | 26.88 |
| HTB 1721 | Pan | F | Adult | 16.19 | 9.66 | 10.36 | 8.88 | 9.86 | 29.9 | 29.00 |
| HTB 1724 | Pan | F | Adult | 13.70 | 9.50 | 10.79 | 9.04 | 10.11 | 30.29 | 29.38 |
| HTB 1735 | Pan | F | Adult | 22.24 | 12.56 | 14.38 | 12.36 | 13.46 | 36.48 | 33.34 |
| HTB 1769 | Pan | F | Adult | 17.20 | 8.69 | 11.11 | 8.48 | 10.40 | 26.47 | 26.22 |
| HTB 1880 | Pan | F | Adult | 13.30 | 10.50 | 12.41 | 10.36 | 9.68 | 28.94 | 28.67 |
| HTB 1884 | Pan | F | Adult | 12.59 | 8.69 | 10.75 | 7.80 | 9.64 | 27.12 | 26.87 |
| HTB 1890 | Pan | F | Adult | 13.20 | 8.09 | 10.33 | 7.76 | 8.89 | 25.61 | 25.37 |
| HTB 1903 | Pan | F | Adult | 11.86 | 9.35 | 11.33 | 9.14 | 9.85 | 29.78 | 29.60 |
| HTB 1172 | Pan | M | Adult | 21.13 | 12.69 | 15.65 | 12.36 | 15.58 | 42.27 | 41.77 |
| HTB 1882 | Pan | M | Adult | 22.18 | 12.15 | 14.45 | 11.72 | 13.18 | 37.22 | 36.78 |
| HTB 1056 | Pan | M | Adult | 18.66 | 10.79 | 13.36 | 10.82 | 12.65 | 39.52 | 39.06 |
| HTB 1195 | Pan | M | Adult | 19.41 | 11.13 | 14.13 | 10.71 | 13.23 | 40.32 | 39.85 |
| HTB 1433 | Pan | M | Adult | 19.84 | 12.14 | 14.18 | 12.10 | 13.94 | 39.09 | 37.52 |
| HTB 1708 | Pan | M | Adult | 17.21 | 11.14 | 12.54 | 11.11 | 12.85 | 37.60 | 36.09 |
| HTB 1718 | Pan | M | Adult | 19.90 | 11.19 | 14.73 | 11.44 | 13.83 | 35.33 | 33.91 |
| HTB 1739 | Pan | M | Adult | 20.62 | 13.01 | 16.21 | 12.95 | 15.31 | 41.54 | 39.87 |
| HTB 1745 | Pan | M | Adult | 24.93 | 14.25 | 15.71 | 14.26 | 16.57 | 43.52 | 39.77 |
| HTB 1768 | Pan | M | Adult | 20.68 | 10.86 | 13.22 | 10.83 | 13.05 | 32.64 | 29.83 |
| HTB 1882 | Pan | M | Adult | 22.27 | 12.11 | 14.46 | 12.17 | 13.59 | 36.23 | 36.01 |
| HTB 1888 | Pan | M | Adult | 27.27 | 14.2 | 19.31 | 14.55 | 17.29 | 46.72 | 46.43 |
| HTB 2027 | Pan | M | Adult | 24.02 | 11.00 | 13.91 | 11.17 | 13.27 | 37.29 | 37.06 |
| HTB 2033 | Pan | M | Adult | 19.89 | 10.29 | 13.70 | 10.07 | 12.85 | 40.87 | 39.02 |

| Specimen # | Species | Sex | Age | Crown height | Crown buccolingual | Crown mesiodistal | Root buccolingual | Root mesiodistal | Root length measured from film | Actual root length |
|---|---|---|---|---|---|---|---|---|---|---|
| HTB 2804 | Pan | M | Adult | 18.81 | 11.84 | 14.15 | 11.09 | 14.20 | 35.87 | 34.24 |
| HTB 1402 | Gorilla | M | Adult | 23.35 | 14.31 | 18.10 | 17.46 | 14.82 | 39.31 | 34.29 |
| HTB 1401 | Gorilla | M | Adult | 19.76 | 14.92 | 17.14 | 15.54 | 17.58 | 41.51 | 36.21 |
| HTB 1196 | Gorilla | M | Adult | 27.46 | 14.63 | 17.27 | 14.10 | 18.20 | 54.94 | 51.20 |
| HTB 1182 | Gorilla | M | Adult | 23.68 | 16.34 | 19.84 | 16.55 | 19.60 | 51.84 | 48.32 |
| HTB 1181 | Gorilla | M | Adult | 21.58 | 16.06 | 19.35 | 16.13 | 19.69 | 47.82 | 45.09 |
| HTB 1076 | Gorilla | M | Adult | 34.33 | 16.11 | 20.05 | 15.91 | 19.46 | 47.67 | 44.94 |
| HTB 1075 | Gorilla | M | Adult | 33.13 | 16.16 | 22.09 | 15.54 | 22.00 | 55.30 | 47.11 |
| HTB 1057 | Gorilla | M | Adult | 29.43 | 16.81 | 19.81 | 16.92 | 20.00 | 44.73 | 38.11 |
| HTB 1020 | Gorilla | M | Adult | 33.97 | 15.39 | 21.78 | 15.19 | 20.39 | 49.76 | 43.12 |
| HTB 650 | Gorilla | M | Adult | 30.12 | 14.92 | 19.56 | 14.29 | 19.78 | 51.87 | 44.94 |
| HTB 1795 | Gorilla | M | Adult | 29.02 | 15.04 | 17.73 | 14.86 | 17.67 | 45.04 | 43.63 |
| HTB 1790 | Gorilla | M | Adult | 27.89 | 18.01 | 20.75 | 18.61 | 18.16 | 54.51 | 52.10 |
| HTB 1754 | Gorilla | M | Adult | 27.36 | 17.79 | 23.23 | 17.54 | 22.85 | 52.87 | 50.53 |
| HTB 1746 | Gorilla | M | Adult | 33.29 | 17.17 | 21.62 | 16.49 | 19.94 | 42.46 | 41.56 |
| HTB 1736 | Gorilla | M | Adult | 26.10 | 16.19 | 18.35 | 16.63 | 17.10 | 56.06 | 54.87 |
| HTB 1909 | Gorilla | M | Adult | 41.56 | 22.12 | 20.70 | 20.00 | 20.97 | 49.12 | 47.66 |
| HTB 1910 | Gorilla | M | Adult | 17.68 | 13.64 | 17.57 | 13.38 | 15.61 | 42.46 | 40.79 |
| HTB 1919 | Gorilla | M | Adult | 21.82 | 17.72 | 22.30 | 18.39 | 21.62 | 48.24 | 46.34 |
| HTB 1966 | Gorilla | M | Adult | 29.08 | 14.74 | 19.07 | 15.06 | 17.28 | 48.15 | 47.24 |
| HTB 1987 | Gorilla | M | Adult | 27.67 | 15.12 | 20.15 | 15.24 | 18.55 | 47.40 | 46.50 |
| HTB 1995 | Gorilla | M | Adult | 30.13 | 16.97 | 21.82 | 16.65 | 20.60 | 47.42 | 46.41 |
| HTB 2741 | Gorilla | M | Adult | 22.43 | 16.54 | 19.36 | 16.68 | 19.22 | 42.54 | 41.62 |
| HTB 2767 | Gorilla | M | Adult | 31.52 | 17.58 | 21.27 | 17.40 | 18.56 | 53.00 | 52.46 |
| HTB 2794 | Gorilla | M | Adult | 34.20 | 16.52 | 21.91 | 16.48 | 21.24 | 52.92 | 52.38 |
| HTB 2795 | Gorilla | M | Adult | 30.75 | 16.04 | 20.49 | 15.96 | 18.23 | 52.59 | 50.52 |
| HTB 405 | Gorilla | F | Adult | 14.74 | 10.26 | 13.25 | 9.78 | 11.48 | 29.96 | 25.37 |
| HTB 842 | Gorilla | F | Adult | 15.66 | 10.74 | 13.93 | 10.77 | 11.19 | 41.68 | 35.29 |
| HTB 1398 | Gorilla | F | Adult | 15.79 | 10.51 | 13.50 | 9.86 | 11.49 | 41.13 | 34.82 |
| HTB 1399 | Gorilla | F | Adult | 16.94 | 11.10 | 12.54 | 10.34 | 10.82 | 35.90 | 30.39 |
| HTB 1400 | Gorilla | F | Adult | 16.23 | 10.36 | 14.47 | 9.79 | 12.39 | 33.04 | 29.03 |
| HTB 1412 | Gorilla | F | Adult | 14.65 | 11.82 | 12.84 | 10.34 | 10.90 | 40.48 | 35.57 |

| Specimen # | Species | Sex | Age | Crown height | Crown buccolingual | Crown mesiodistal | Root buccolingual | Root mesiodistal | Root length measured from film | Actual root length |
|---|---|---|---|---|---|---|---|---|---|---|
| HTB 1422 | Gorilla | F | Adult | 19.11 | 10.57 | 14.98 | 11.43 | 13.35 | 40.86 | 35.90 |
| HTB 1690 | Gorilla | F | Adult | 15.13 | 11.72 | 15.48 | 10.83 | 13.35 | 42.36 | 37.11 |
| HTB 1710 | Gorilla | F | Adult | 14.21 | 11.16 | 12.93 | 10.00 | 11.93 | 42.89 | 37.58 |
| HTB 1725 | Gorilla | F | Adult | 14.99 | 11.89 | 14.78 | 10.83 | 13.57 | 40.93 | 35.86 |
| HTB 1756 | Gorilla | F | Adult | 13.86 | 10.57 | 13.68 | 10.06 | 11.70 | 37.61 | 36.68 |
| HTB 1794 | Gorilla | F | Adult | 17.63 | 10.93 | 12.86 | 10.96 | 11.74 | 35.17 | 34.30 |
| HTB 1798 | Gorilla | F | Adult | 15.54 | 10.77 | 12.90 | 10.44 | 11.76 | 36.09 | 35.20 |
| HTB 1897 | Gorilla | F | Adult | 14.64 | 11.53 | 14.02 | 10.47 | 12.54 | 32.90 | 30.62 |
| HTB 1907 | Gorilla | F | Adult | 18.26 | 13.37 | 13.64 | 12.67 | 13.14 | 36.26 | 33.74 |
| HTB 1912 | Gorilla | F | Adult | 15.72 | 11.78 | 14.85 | 11.16 | 12.88 | 38.82 | 37.66 |
| HTB 1913 | Gorilla | F | Adult | 16.88 | 13.78 | 16.34 | 13.22 | 15.71 | 38.82 | 37.66 |
| HTB 1914 | Gorilla | F | Adult | 15.84 | 12.45 | 14.86 | 11.94 | 13.37 | 28.66 | 28.47 |
| HTB 1945 | Gorilla | F | Adult | 15.35 | 12.68 | 15.89 | 11.64 | 12.81 | 41.57 | 41.30 |
| HTB 1950 | Gorilla | F | Adult | 15.68 | 10.55 | 14.16 | 9.96 | 12.25 | 37.56 | 37.32 |
| HTB 1992 | Gorilla | F | Adult | 17.91 | 12.30 | 15.24 | 11.53 | 12.55 | 38.91 | 37.38 |
| HTB 1996 | Gorilla | F | Adult | 17.72 | 12.17 | 15.91 | 10.74 | 12.52 | 36.79 | 35.34 |
| HTB 1997 | Gorilla | F | Adult | 12.14 | 10.52 | 13.93 | 9.83 | 13.13 | 34.50 | 32.84 |
| HTB 1999 | Gorilla | F | Adult | 17.58 | 11.91 | 15.17 | 11.10 | 13.58 | 37.91 | 36.09 |
| HB 2774 | Gorilla | F | Adult | 14.10 | 11.55 | 14.88 | 10.79 | 13.58 | 42.22 | 40.19 |
| HTH 24 | Human | M | 35 | 9.07 | 8.74 | 7.61 | 8.54 | 6.30 | 25.70 | 24.86 |
| HTH 104 | Human | M | 35 | 6.61 | 7.12 | 6.36 | 6.90 | 5.30 | 16.99 | 16.44 |
| HTH 130 | Human | M | 39 | 10.21 | 8.77 | 7.93 | 9.03 | 6.12 | 19.76 | 19.12 |
| HTH 155 | Human | M | 46 | 8.63 | 9.09 | 7.80 | 8.68 | 5.88 | 19.74 | 19.10 |
| HTH 181 | Human | M | 37 | 8.70 | 9.16 | 7.66 | 8.47 | 6.55 | 22.18 | 20.79 |
| HTH 587 | Human | M | 40 | 8.50 | 8.08 | 7.21 | 7.54 | 5.99 | 17.37 | 16.90 |
| HTH 581 | Human | M | 38 | 7.87 | 8.53 | 7.85 | 8.52 | 6.63 | 18.88 | 18.37 |
| HTH 578 | Human | M | 35 | 9.69 | 8.69 | 7.73 | 8.57 | 6.09 | 16.41 | 15.97 |
| HTH 575 | Human | M | 25 | 9.05 | 7.82 | 7.02 | 7.51 | 5.37 | 19.53 | 19.00 |
| HTH 570 | Human | M | 47 | 7.30 | 7.41 | 7.08 | 7.26 | 6.07 | 15.03 | 14.83 |
| HTH 592 | Human | M | 35 | 8.78 | 8.81 | 7.73 | 8.51 | 6.03 | 15.51 | 15.62 |
| HTH 623 | Human | M | 30 | 9.79 | 8.76 | 8.49 | 8.50 | 6.48 | 18.55 | 18.68 |
| HTH 635 | Human | M | 32 | 8.72 | 8.37 | 8.13 | 8.46 | 6.54 | 21.20 | 21.35 |

| Specimen # | Species | Sex | Age | Crown height | Crown buccolingual | Crown mesiodistal | Root buccolingual | Root mesiodistal | Root length measured from film | Actual root length |
|---|---|---|---|---|---|---|---|---|---|---|
| HTH 32 | Human | M | 40 | 8.71 | 8.88 | 7.54 | 8.40 | 6.16 | 20.84 | 19.53 |
| HTH 515 | Human | M | 40 | 11.19 | 8.25 | 7.85 | 7.74 | 6.23 | 20.35 | 19.08 |
| HTH 402 | Human | M | 29 | 10.33 | 8.59 | 7.94 | 8.24 | 6.54 | 18.60 | 17.90 |
| HTH 350 | Human | M | 36 | 12.26 | 9.82 | 8.32 | 9.49 | 6.26 | 20.88 | 20.10 |
| HTH 638 | Human | M | 33 | 9.89 | 7.85 | 7.31 | 7.57 | 6.24 | 18.83 | 18.22 |
| HTH 620 | Human | M | 26 | 9.56 | 8.77 | 7.57 | 8.65 | 5.43 | 20.16 | 19.51 |
| HTH 598 | Human | M | 29 | 9.97 | 8.99 | 7.26 | 8.79 | 5.81 | 18.34 | 17.75 |
| HTH 596 | Human | M | 33 | 9.38 | 8.41 | 6.76 | 8.33 | 4.82 | 18.33 | 17.74 |
| HTH 594 | Human | M | 35 | 10.33 | 8.62 | 7.55 | 7.74 | 5.61 | 16.05 | 15.84 |
| HTH 699 | Human | M | 48 | 11.72 | 9.11 | 8.24 | 8.63 | 6.64 | 20.58 | 19.55 |
| HTH 658 | Human | M | 28 | 11.66 | 8.94 | 8.17 | 8.65 | 6.31 | 18.86 | 18.99 |
| HTH 306 | Human | F | 34 | 10.13 | 7.83 | 7.54 | 7.65 | 5.79 | 20.39 | 19.56 |
| HTH 339 | Human | F | 38 | 8.71 | 7.97 | 7.37 | 7.73 | 5.14 | 16.58 | 15.91 |
| HTH 514 | Human | F | 30 | 8.44 | 8.84 | 7.76 | 8.32 | 5.77 | 19.12 | 17.97 |
| HTH 690 | Human | F | 32 | 7.33 | 7.18 | 6.35 | 6.54 | 4.93 | 21.97 | 20.65 |
| HTH 886 | Human | F | 35 | 8.72 | 7.69 | 7.96 | 7.47 | 5.15 | 21.40 | 20.11 |
| HTH 1350 | Human | F | 28 | 8.06 | 6.56 | 6.54 | 6.39 | 4.30 | 17.84 | 17.36 |
| HTH 1273 | Human | F | 36 | 8.65 | 7.71 | 7.36 | 6.92 | 5.65 | 17.84 | 17.36 |
| HTH 1162 | Human | F | 28 | 8.09 | 7.59 | 6.66 | 6.72 | 4.92 | 17.29 | 16.83 |
| HTH 1157 | Human | F | 25 | 8.97 | 7.58 | 7.36 | 7.61 | 5.29 | 19.59 | 19.07 |
| HTH 1059 | Human | F | 28 | 10.99 | 8.61 | 8.05 | 8.17 | 5.67 | 18.05 | 17.81 |
| HTH 1759 | Human | F | 34 | 9.90 | 7.55 | 7.20 | 7.18 | 5.44 | 16.84 | 16.38 |
| HTH 1975 | Human | F | 48 | 8.86 | 7.63 | 7.40 | 7.18 | 5.21 | 14.89 | 14.49 |
| HTH 1976 | Human | F | 47 | 7.95 | 7.56 | 5.96 | 7.20 | 4.81 | 15.54 | 15.12 |
| HTH 128 | Human | F | 35 | 9.11 | 8.82 | 7.71 | 8.37 | 5.12 | 17.92 | 17.19 |
| HTH 461 | Human | F | 30 | 10.13 | 7.88 | 6.94 | 7.37 | 5.72 | 19.10 | 18.01 |
| HTH 520 | Human | F | 45 | 10.37 | 7.59 | 7.78 | 7.04 | 5.45 | 20.27 | 19.11 |
| HTH 529 | Human | F | 34 | 8.84 | 7.18 | 6.93 | 6.48 | 5.02 | 19.03 | 17.94 |
| HTH 589 | Human | F | 30 | 9.60 | 8.73 | 6.96 | 8.01 | 5.29 | 18.68 | 17.98 |
| HTH 1213 | Human | F | 32 | 8.02 | 7.52 | 6.46 | 6.90 | 4.92 | 16.51 | 16.20 |
| HTH 1105 | Human | F | 39 | 10.69 | 9.22 | 8.04 | 8.42 | 5.95 | 20.30 | 19.92 |
| HTH 931 | Human | F | 34 | 9.91 | 8.40 | 7.20 | 7.42 | 5.71 | 20.52 | 20.14 |

| Specimen # | Species | Sex | Age | Crown height | Crown buccolingual | Crown mesiodistal | Root buccolingual | Root mesiodistal | Root length measured from film | Actual root length |
|---|---|---|---|---|---|---|---|---|---|---|
| HTH 685 | Human | F | 45 | 6.48 | 7.92 | 7.10 | 7.11 | 5.65 | 14.37 | 14.18 |
| HTH 1277 | Human | F | 28 | 10.07 | 7.33 | 7.14 | 7.27 | 5.76 | 19.91 | 18.92 |

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