THE FUNCTIONAL AND PHYLOGENETIC IMPLICATIONS OF NASOALVEOLAR CLIVUS LENGTH IN ANTHROPOID PRIMATES.

by

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ABSTRACT

The nasoalveolar clivus or subnasal clivus is the sagittally-located portion of the cranium that extends from the site of the anterior attachment of the nasal septum to the margin of the premaxillae at the osteometric point alveolar. In humans, the structure is the vertically-oriented area superior to the upper incisors and inferior to the nasal aperture, underlying the philtrum of the soft tissue. In the majority of primates the structure is formed by the premaxilla, which contain the roots of the upper incisors. Diversity in the relative length of the nasoalveolar clivus is evident among extant primates, with some taxa having a deep clivus and others a relatively short clivus. There is currently no comparative account of nasoalveolar clivus variation among primates. Reviewing the literature reveals that the feature is seldom referred to and little prior research has considered clivus depth as an informative variable in the phylogenetic analysis of the primate cranium. The aim of the present research is to investigate whether clivus depth is significantly different among anthropoid primates and to explore the possible structural and functional factors that influence clivus size. This research shows that the relationship between clivus size and body mass among anthropoid primates does not scale isometrically and that variations in clivus size relative to other traits appear to represent divergent specializations among anthropoids. Analyzing clivus depth measurements from 400 specimens representing 20 anthropoid taxa, the study examines clivus depth in relation to body mass and anterior tooth size, showing that functional constraints from masticatory stresses in the midface appear to influence clivus size. Further, the effects of allometric growth in clivus development and the influence of dietary adaptations are considered with regard to possible specializations in clivus size among Platyrrhini, Cercopithecidae, and Hominoidea. A better understanding of the relationship between these structural-functional variables will potentially have implications for interpreting

the evolutionary relationships and paleobiology of extant and fossil anthropoid primates, including early hominins.

INTRODUCTION

Much of the previous research related to the nasoalveolar clivus has focused more generally on the subnasal region, only considering the clivus among a suite of midfacial traits (Ward and Kimbel, 1983; Shea, 1985; McCollum et al., 1993; McCollum, 2007; Bastir and Rosas, 2004; Kaifu et al., 2011; Williams et al. 2012). Ward and Kimbel (1983) described the characteristics of the subnasal region (including the clivus) among extant hominoids. They noted differences in clivus shape while focusing on the phylogenetic significance of the African and Asian ape subnasal patterns. Ward and Kimbel also compared subnasal patterns of fossil hominins and discussed the potential utility of the morphology noted earlier by Robinson (1954a, b). Other researchers have studied the evolutionary significance of differences in midfacial forms between the African apes and *Pongo* (Ashley Montague, 1935; Gould, 1975; Jolly, 1970; Shea, 1985; Williams et al, 2012; Robinson, 1954a). Shea (1985) argued that, while differences in the nasal floor morphology in great apes may largely be due to differences in facial position, this explanation could be complicated by the possibility that enlarged incisors in orangutans directly influence the shape and orientation of the midfacial region, including the nasoalveolar clivus. Much of the past research on midfacial anatomy has linked variation in the region with that of the dentition, which is often considered in reference to dietary adaptations (Jolly, 1970; Hylander, 1975; Gould, 1975; Wolpoff et al., 1975; Smith, 1981; Gingerich, 1982; Eaglen, 1984; Wolpoff, 1985; Gingerich and Smith, 1985; Benefit and McCrossin, 1991; Anapol and Lee, 1994; Aiello and Wood, 1994; McCollum, 1997; Ungar, 1998; Godfrey et al., 2001; Weston et al., 2004; Strait et al., 2007; Strait et al., 2009; Deane, 2009; Godfrey et al., 2011; Kaifu et al., 2011; Deane 2012; Williams et al., 2012).

A decade after Ward and Kimbel described the shape of the subnasal region and the nasoalveolar clivus in hominoids, McCollum et al. (1993) compared the subnasal region of great apes and humans with those of *Australopithecus* and *Paranthropus*, but only presented clivus length as part of the qualitative description of the bony anatomy. This approach was similar to that of other researchers who compared clivus size and shape in fossil and extant taxa (Kaifu et al., 2011; Williams et al., 2012). McCollum and Ward (1997) also discussed clivus size when considering subnasal features, focusing on allometric and ontogenetic changes and sexual dimorphism. McCollum and Ward noted that the nasoalveolar clivus was significantly longer in males of *Pongo*, *Pan*, and *Gorilla* compared to females of the respective taxon. Additionally, they noted that body size, masticatory adaptations, and craniofacial orientation probably have varying influence on differing subnasal morphologies in hominoids. McCollum and Ward's focus on craniofacial form and orientation specifically refers to incisor size, following Shea's presumption that enlarged incisors in *Pongo* effect the shape and orientation of the midface, including the clivus. They comment only on the notably fast growth of the nasoalveolar clivus relative to the basicranium among nonhuman primates and the positive allometric scaling of clivus length with the basicranium in humans. While previous research has aimed to separate primitive and derived facial forms, variation in the nasoalveolar clivus apart from the general midfacial region has been overlooked. Further evaluation of the nasoalveolar clivus is warranted, as quantification of the feature may be of relevance beyond the scope of this study.

MATERIALS & METHODS

This research used data from 400 individual anthropoid primate crania across 20 genera to consider the influence of body mass and upper incisor size on clivus depth. Measurements of the nasoalveolar clivus were recorded from specimens in the Mammalogy collection of the Vertebrate Zoology Department at the Smithsonian Institution's National Museum of Natural History in Washington, D.C., and the Mammalogy Department of the American Museum of Natural History in New York, N.Y. Additional measurements of *Homo sapiens* were obtained from crania in the Anthropology collection at the American Museum of Natural History. Extant primate genera in this study included representatives from Platyrrhini, Cercopithecidae, and Hominoidea. The taxa were selected to sample the diversity of nasoalveolar clivus depth among extant anthropoid primates. Each genus was represented by one species and one subspecies where possible [Table 1]. The target sample for each species was 10 adult male and 10 adult female specimens. Adult status was determined by the full eruption of the upper and lower M3 (or M2 in taxa that typically lack M3) of each specimen. Sex determination relied upon the noted assignment of the collector. Specimens without specified sex or likely inaccurate assignments were excluded. Additionally, specimens were included only if they were free of pathological conditions or traumatic damage that may have affected the anatomy of the subnasal and alveolar regions.

Measurement of nasoalveolar clivus length was taken as a chord distance from the osteometric point alveolar (infradentale superius) to the point of greatest distance from alveolare along the sagittal plane at the anterior attachment site of the nasal septum. The latter point is typically identifiable as the osteometric point nasospinale (White, 2000). In some genera, for example those lacking a nasal spine or those displaying more pronounced midfacial prognathism, the superior demarcation of the clivus is less patent with greater retreat of the maxillae into the nasal cavity (McCollum et al., 1993). It is also necessary to note that definitions regarding the nasoalveolar clivus vary. Williams et al. (2012) reported using the chord length from infradentale superius to the anterior nasal spine, though they do not discuss the reduction of an anterior nasal spine among great apes. McCollum et al. (1993) refer to clivus length as the chord measurement from the anterior nasal attachment site to alveolare, clarifying that the anterior nasal attachment site is not developed as extensively in the great apes and most fossil hominins. In these latter cases, the presence of a small protuberance or tubercle on the clivus represents the most anterior attachment site of the nasal septum. McCollum and Ward (1997) define nasoalveolar clivus length simply as the chord measurement from nasospinale to prosthion (rather than alveolare). Kaifu et al. (2011) also referred to clivus length as the chord from nasospinale to prosthion. Prosthion is defined by White as "[T]he midline point at the most anterior point on the alveolar process of the maxillae." (White, 2000: p. 50). Thus, prosthion is an osteometric point defined by its maximum anterior position, not the more vertically-oriented, inferiormost position in relation to the nasal aperture that better captures the full length of the nasoalveolar clivus. In most cases, these points are synonymous, but in taxa with a vertically-oriented clivus, such as humans, the anteriormost and inferiormost points on the clivus are not necessarily the same. In this study, maximum clivus depth was measured to record greatest length. Therefore, clivus depth was recorded from the sagittal point at the anterior septal attachment site to alveolare, which White (2000) defines as "The midline point at the inferior tip of the bony septum between the upper central incisors." This replicates the method used by Williams et al. (2012) and McCollum et al. (1993).

Due to the possible structural-functional relationships between clivus depth, incisor size and body size noted by other researchers, data on body mass and incisor size for each taxon, presented in Table 2, were obtained from published (Swindler 2002) and unpublished sources (Bailey, personal communication). Incisor size was measured for each species following methods used by Eaglen (1984). Incisor size was recorded as the combined mesiodistal lengths of the upper central and lateral incisors from one side of the dental arcade. The right and left sides were measured and the mean was recorded when the sides differed [Table 3].

All data were analyzed and plotted using Microsoft Excel and Apple Numbers software. Data from males and females of each taxon were plotted separately. Measurements were transformed to base-10 logarithmic (log10) values for allometric analysis. Linear regression equations and R^2 values were calculated. The log10 values predicted by the plots for the dependent variables were then calculated for all data. The predicted log10 value of the dependent variable is found by multiplying the log10 value of the independent variable for each plot by the slope of the regression line then subtracting the y-intercept of the regression equation from the product [predicted log10 independent variable = (m x log10 independent variable) - b]. The predicted value of the independent variable was then used to calculate the statistical residual value, which measures the difference between the results obtained via observed measurement of the dependent variable and those predicted based on the overall sample body (Smith, 1981; Wolpoff, 1985; Aiello and Wood, 1994). Residual values are calculated by subtracting the predicted log10 value from the log10 value of the observed measurement, the difference from which is then divided by the same log10 value of the observed measurement and the quotient is then multiplied by 100. This formula [(observed measurement – predicted measurement) / predicted measurement x 100] provides a percentage deviation from the regression line, indicating the extent to which the variable deviates positively or negatively from the regression line [data listed in appendix].

RESULTS

Mean clivus length was plotted against mean body mass to examine the scaling effects of clivus size. The bivariate plot of the two variables is fit by a line with a coefficient of determination $R^2 = 0.8625$ and a slope of $m = 0.4447$, displaying a positive allometric relationship [Fig. 2]. General trends in the main taxonomic groups are apparent. The majority of platyrrhines have a relatively large clivus on average for their body size with a mean residual value of +5.036 [range: -16.345 to +29.897]. Notably, *Callithrix*, the smallest primate included in this study, has the largest residual value for clivus length relative to body mass. Conversely, cercopithecoids generally have a short clivus relative to their body size compared to other anthropoids with a mean residual value of -10.850 [range: -36.924 to +12.399]. Only *Macaca* and *Papio* females had positive residual values. The trend for a shortened clivus in cercopithecoids is particularly evident in the colobines, with *Nasalis* and *Presbytis* having the most negative residual values. Even when colobines are excluded, the mean cercopithecine residual value remains negative at -3.534. Hominoids have a mean residual value of +1.987 [range: -16.309 to +18.022]. It is noteworthy that hylobatids (which have a mean residual value of -10.116 and are more similar to the cercopithecids than to the great apes and humans) are the only hominoids with appreciably negative residual values. *Symphalangus* has the most negative residual, comparable to *Ateles* and *Nasalis* females. The mean residual value for the Hominidae is +8.039. Omitting *Homo*, which falls close to the regression line, increases the great ape residual value to +10.975. This highlights the specialized condition among the Hominidae, particularly *Pongo* and *Pan*.

Comparisons of mean body size to mean incisor size among the 14 taxa for which incisor data were available exhibit a distribution pattern similar to the comparisons of body mass and clivus length, suggesting a relationship between incisor size and clivus depth [Fig. 3]. Many genera fall close to the regression line ($R^2 = 0.796$, $m = 0.283$). There is a negative allometric relationship for mean incisor size and mean body mass, which is the converse of the positive allometric relationship of mean clivus size and mean body mass. Most of the great apes cluster above the regression line, while the hylobatids are located below the line and are clustered with the colobines, which have small incisors relative to body mass. The cercopithecines fall above the regression line with larger upper incisors than expected for their body sizes. *Homo* lies below the line with small teeth relative to body size. Although only three platyrrhine genera have published incisor width data, they all fall on the positive sides of the regression line as they did for mean clivus length plotted against mean body mass. The presence of *Homo* below the regression line brings the hominoid mean residual value to -0.189 with a standard deviation of 7.224 but the value rises to +2.652 when the hylobatids are excluded. This rises further to +6.159 with the exclusion of *Homo*. The mean residual value for cercopithecoids is in the positive range at +0.937, driven primarily by the cercopithecines with large incisors relative to their body masses, though their standard deviation is also the highest at 9.683. The platyrrhines have an average residual value of -3.947, but their standard deviation is also high at 9.307. Similar to the comparison of mean clivus size to mean body mass, the large-bodied hominoids appear to have a strong influence on the upper end of the regression line due to having both large incisors and large clivuses relative to body mass.

When mean clivus size is compared to mean upper incisor size all hominoids except *Gorilla* plot above the line of regression ($R^2 = 0.896$, $m = 1.687$) [Fig. 4]. The hominoids have a mean residual value of +3.756 [range: -3.148 to +11.277] and the smallest standard deviation (4.191). This value rises slightly to +3.843 with the exclusion of the hylobatids. *Homo* has the greatest residual values among all the hominoids reaching the positive tens range. All other hominoids are in the range of positive single digits for residual values (*Pan* females being the only other taxon above +5). The hylobatids are slightly above the line of regression and they cluster near the cercopithecoids due to their similar clivus sizes. The cercopithecoids again have mostly negative residual values and are below the line of regression with only the male macaques plotting slightly above (with a residual value of +2.289). Among the cercopithecoids, *Lophocebus* show the greatest negative values, reaching in to the -30s for both sexes. Even with the exclusion of *Lophocebus*, however, the cercopithecoids retain a negative mean residual value (-5.874, range: -13.210 to +2.289, SD = 12.783). This drops to -11.479 when *Lophocebus* is included. While the platyrrhines are variable, with a mean residual value of +6.355 (ranging from -5.544 to +20.743 with a standard deviation of 10.179), *Aotus* plots below the regression line with the other platyrrhines above it. *Alouatta* has the largest residual values with males reaching +20.734. Cercopithecoids have the greatest standard deviation but with the exclusion of *Lophocebus* this drops, leaving platyrrhines with the greatest standard deviation (which remains even when *Alouatta* is excluded). The R^2 value is stronger than for the other comparisons, implying that a significant relationship exists between clivus depth and incisor size.

Plotting the residual values of clivus length with the residual values of incisor size (both calculated relative to mean body mass) removes the effects of allometry [Fig. 5]. The plot displays a relationship between clivus size and incisor size, showing that the majority of taxa fall into two quadrants: those with both a large clivus and large incisors relative to body mass, and those with both a small clivus and small incisors relative to body mass. The large-bodied hominoids fall into quadrant 1 (large-large), where *Aotus* females and the macaques are also found. That *Macaca* males cluster closer to *Pan* is perhaps unsurprising as *Macaca* males have larger clivuses relative to body mass than other cercopithecoids, as well as larger clivuses relative to mean incisor size and larger incisors relative to mean body mass. *Nasalis* and *Presbytis* are both in quadrant 3 (small-small). Notably, *Homo* and the hylobatids are also in quadrant 3 but *Homo* plots near the neutral line of the x-axis, showing that their clivus is close to nearly proportional relative to body mass compared to the other taxa, but with small incisors. Quadrants 2 and 4 show those taxa that have clivus sizes that are counter to the association with incisor size seen in most anthropoid primates.. *Cercopithecus* and *Lophocebus* of both sexes are in quadrant 4 with incisors that are large relative to body mass but a small clivus and *Alouatta* males is the only sample that falls in quadrant 2. This again displays the character of cercopithecines to have a shortened clivus while the colobines are similar to several of the platyrrhines. Additionally, the hylobatids again show dissimilarity to the other hominoids, being in quadrant 3, but further away from the x-axis than *Homo*. The expanded clivus of the large-bodied hominoids is also again displayed. This plot highlights the clustering of the taxa into specialized morphological groups, and that clivus size is strongly linked with upper incisor size.

DISCUSSION

The study documents the variation present in nasoalveolar clivus length in anthropoid primates. Relative to platyrrhines, cercopithecoids have reduced the length of the clivus with notable differences between the cercopithecines and the colobines, the latter having distinctly shortened clivuses relative to their body mass and incisor width. The presence of small incisors relative to body mass in platyrrhines has been discussed as a plausible primitive condition (Eaglen, 1984; Swindler, 2002). The hominoids exhibit clivus expansion, particularly among the hominids, although humans appear to have secondarily reduced the length of the clivus compared to the great apes in association with shortening of the lower face. The hylobatids are more similar to the cercopithecines, and the two groups arguably retain the ancestral catarrhine condition. The observed specializations in clivus length among anthropoid primates appear to be related, in part, to incisor size, though other structural-functional factors may contribute to variation in clivus length

The plot of mean clivus length to mean body mass in anthropoids exhibits a positive allometric relationship (m = 0.445). However, this relationship is largely determined by the very deep clivuses in the large-bodied great apes. When *Gorilla, Pan,* and *Pongo* are removed from the plot the slope is very close to isometry (m = 0.346). The plot of mean clivus size to mean incisor size also shows a positive allometric relationship (m = 1.687). When hominoids are excluded the slope value is m = 0.905. This value only rises to 0.930 when the hylobatids are included. The plot of mean incisor size to mean body mass is negatively allometric (m = 0.283). Additional analysis of the slope of mean clivus length to mean body mass for cercopithecoids and platyrrhines (excluding all hominoids) shows that many of the remaining taxa do not fall close to the regression line. These results confirm that clivus size variation in anthropoids is not simply proportionally scaled with body mass, but rather is influenced by adaptive specializations in certain clades.

While non-human hominoids have a specialized clivus that is expanded compared with the inferred primitive catarrhine condition, *Homo* is notably different. Comparing mean clivus depth to mean body mass, *Homo* is close to the regression line with residual values close to zero (+0.055 in males and -1.596 in females). The incisors of *Homo* have negative residual values relative to body mass, while mean clivus length in *Homo* has positive residual values relative to body mass. Thus, even though their teeth are relatively small, the clivus depth is neither notably large nor small relative to body size. Among hominids this is unusual, as *Pan* and *Pongo* both have large clivuses and large incisors relative to body mass. Residual values for clivus length relative to incisor size in *Pan* and *Pongo* are lower than *Homo,* though. *Gorilla* stands out among the great apes with a negative residual value for clivus size relative to incisor size. *Gorilla* males also have a residual value of only +1.235 for clivus size relative to body mass and a residual value of +0.584 for incisor size relative to body mass (*Gorilla* females have greater residual values than males for both these residual values, while female *Gorilla* have incisors and a clivus approximately the same size as males but a body mass that is less than half that of males). Like *Homo,* the hylobatids have a clivus that is large relative to incisors size, and incisors that are small relative to body mass. However, hylobatids have a clivus that is small relative to their body mass. This supports the inference that hominids evolved an enlarged clivus along with enlarged incisors relative to body size. The reduced incisor size in humans relative to body mass is documented by their positive residual values for clivus size relative to incisor size. Among hylobatids the clivus arguably may retain the ancestral condition, having incisors that are relatively small for their body mass. It is worth considering if the variations observed in the residual values among the great apes may be influenced by sexual dimorphism. While sexual dimorphism of subnasal form has only been noted in *Pongo* and *Gorilla,* overall dimorphism of tooth size relative to the face and body size are reported (McCollum and Ward, 1997; Weston et al., 2004). Males and females in Pan have relatively similar mean clivus lengths, while males are over 10 kg larger than females with a 2 mm difference in mean incisor size. *Pongo* males have a clivus which is on average 5 mm longer than females and mean incisor width 1 mm larger though they have nearly twice the body mass of females.

While the hominoids in general show expansion of the clivus, and many of the cercopithecoids show reduction, the platyrrhines are more diverse. All the platyrrhines included in this study have a clivus that is large relative to their body mass. If incisor size influences clivus size then it might be expected that the platyrrhines would have large incisors for their body mass as well. Incisor size data was only available for three of the platyrrhine taxa in this study. Among these, *Alouatta* and *Ateles* both have small incisors relative to their body mass as well as a generally small clivus size for their body mass (*Alouatta* males being an exception with a slightly larger clivus for their body mass). *Aotus* is the other platyrrhine with incisor width data available and they show incisors that are on average large relative to their body mass but a clivus that is small relative to their body mass as well as relative to incisor width. It has been inferred that platyrrhines may retain the ancestral anthropoid primate condition of generally small incisors relative to body size (Eaglen, 1984).

The relationship between clivus size and incisor size is more strongly correlation than the relationship between clivus size and body mass. This is particularly the case for cercopithecoids. For example, *Presbytis* is near the middle of the range for body mass among cercopithecoids but has the most negative residual values for clivus size relative to body mass. Their incisors are also small for their body mass, as is their mean incisor size relative to their mean clivus size, but each less markedly so than their mean clivus size relative to mean body mass. *Macaca*, the smallest cercopithecoid in this study, has the only positive residual values for clivus depth relative to incisor size among the males, whereas the similar-sized *Cercopithecus* has negative residual values. *Macaca* also has upper incisors that are large relative to their body mass and a clivus that is also large relative to their body mass, while *Cercopithecus* have lower residual values for incisors relative to body mass. The platyrrhines show some diversity in clivus size in relation to body mass. *Saguinus* is only slightly larger than *Callithrix*, yet *Saguinus* has residual values slightly above +0 and +1 (respective of sex) while *Callithrix* has residual values at approximately +25 to +30 for clivus size relative to body mass. Additionally, three-quarters of the platyrrhines with negative residual values are among the larger genera of New World monkeys. However, this is not a general predictor of relatively smaller clivus length relative to body mass among the platyrrhines. Male *Alouatta* and both sexes of *Cebus* and *Pithecia,* three of the largest platyrrhines, all remain in the positive residual value range. Meanwhile, *Ateles*, the largest platyrrhine in the study, has the most negative residual value among the New World monkeys. Of the smaller-bodied (less than 1 kg) platyrrhines all except *Aotus* have positive residual values. Thus, many of the platyrrhines have larger clivuses relative to their body mass, but the largest taxa tend to have a relatively small clivus. Apparent here is the association between small incisors and a small clivus in relation to body size, respectively. Concurrently, incisors and clivus are large in relation to each other, which some researchers have explained in reference to dietary differences (Anapol and Lee, 1994).

The nasoalveolar clivus accommodates the roots of the upper incisors. The incisor roots extend superiorly into the subnasal clivus region. In some taxa, such as *Saguinus* and *Ateles,* the nasal aperture descends inferiorly into the region medial to the upper central incisors. Strait et al. (2007) noted that the strains experienced during mastication are elevated in regions of the face other than just the palate and immediate dentition, implying a suite of facial features would likely develop together for adaptive resistance to masticatory stresses. Given the important role of incisors in food processing, it can be assumed that the anterior dentition will be influenced by selective pressures that arise from the functional mechanics of specific diets (Deane, 2009). Incisor root size, and the size of the incisors themselves, can be inferred to have a direct relationship on the development of the nasoalveolar clivus (Wolpoff, 1985). The effect which incisal preparation has on incisor size has received attention from numerous researchers for at least half a century (Robinson, 1954a; Jolly, 1970; Hylander, 1975; Eaglen, 1984; Gingerich, 1985; Anapol and Lee, 1994; Ungar, 1998; McCollum, 2007; Strait et al., 2009; Deane, 2009; Deane, 2012; Williams et al., 2012). Robinson (1954) and Jolly (1970) argued that small incisors relative to molars in fossil taxa could be indicative of a seed-eating diet. Deane (2009b) also contended that narrow incisors in Miocene catarrhines are indicative of greater folivory. Hylander (1975) noted a correlation between incisor size and incisal preparation, as increased preparation of food items would lead to greater tooth wear. Analyzing incisor size in relation to body mass and finding a near-isometric relationship, Hylander theorized that larger incisors are an adaptation to increased wear. Primates that eat food items, such as fruits, that require preparation prior to ingestion have larger incisors than those primates that eat leaves. Hylander also found a distinction between leaf-eating colobines and frugivorous cercopithecines, with smaller teeth relative to their body size in the former. Further, Hylander noted the division of hylobatids from other hominoids, and hypothesizes that the reduced dentition of *Homo* is a consequence of food preparation techniques. Eaglen (1984) found a negative allometric relationship between incisor size and body mass among the Platyrrhini. Noting that, regardless of diet, platyrrhines have smaller incisors relative to body mass compared to catarrhines. Eaglen argued that the smaller incisors of New World primates represent the primitive anthropoid condition. Further, Eaglen contends that increases in incisor size among other anthropoids are due to dietary shifts that require increased incisal preparation of food items. This supports the results of the present study regarding colobines and their similarity to platyrrhines in measures of incisor size relative to body mass. Goldstein et al. (1978) used a similar argument for cercopithecoids, noting that frugivorous and omnivorous taxa have notably wider incisors than folivorous colobines. Regarding the negative allometric relationship of incisor size relative to body mass, Eaglen noted that the largest platyrrhines are the most folivorous and those with the largest incisors relative to body mass are frugivorous. In general, these studies and the present study show that relative incisor size tends to decrease proportionally as body size increases among platyrrhines. Additionally, for species where the comparison is possible, platyrrhines are shown to have relatively smaller incisors than catarrhines when diets overlap (Eaglen, 1984; Deane, 2009). Anapol and Lee (1994) also analyzed platyrrhine diet and morphological adaptations, noting that broader incisors, such as those of *Ateles*, are a result of feeding primarily on fruit mesocarps. Relatively wider incisors are found in platyrrhines that consume fruits in addition to animal protein (*Cebus, Saimiri,* and *Saguinus)*, while narrower incisors are found in those where fruits are supplemented exclusively by non-animal foods (*Alouatta* and *Pithecia*). It has also been argued that small incisors may be the primitive condition for platyrrhines, while the opposite may be true for catarrhines (Eaglen, 1984). In this hypothesis, incisor reduction may be the evolutionary novelty with larger incisors being the primitive catarrhine condition. The reduced incisors of colobines is probably due to the demands of leaf-eating, associated with less extensive use of the incisors (Eaglen, 1984; Anapol and Lee, 1994; Ungar, 1998). The majority of small-bodied platyrrhines are frugivorous and insectivorous, while the larger platyrrhines combine folivory and frugivory. Among the hominoids, *Pan* and *Pongo* are both frugivorous while *Gorilla* and *Hylobates* have a mixed diet of fruits and leaves. *Pan* and *Pongo* differ though, since orangutans feed on hard objects while chimpanzees consume soft objects. Some research has found greater incisor size among hard object feeding hominoids than soft object feeders (Deane, 2009a, b, 2012). The seasonal folivore-frugivores are intermediate in incisor size to dedicated leaf or fruit eaters. *Pan*, *Pongo*, and *Gorilla* are the only hominoids with large incisors relative to their body size. In *Homo* the incisors are reduced relative to body size, while the hylobatids are more similar to cercopithecoids. Additionally, *Gorilla* is the most folivorous hominoid with incisors that are closest to the size expected for their body mass among the hominoids. Platyrrhines are not dissimilar to hominoids in this regard, which may be expected when considering their tendency for have a relatively deep clivus. These observations are correspond to those made when comparing mean clivus length to mean body mass [Table 2]. Previous research on platyrrhine incisor size and diet also corresponds with the data in the present study (Deane, 2012). *Aotus*, an omnivore, is the only platyrrhine with a positive residual value for mean incisor size compared to body mass, while *Ateles* (a frugivore) is located well below the regression line, along with *Alouatta* (a folivore). Likewise, *Aotus* is the only platyrrhine with a large clivus relative to body size. Among cercopithecoids, the diets of cercopithecines include leaves and fruits supplemented with animal protein, while the colobines rely primarily on leaves. In the present research, the colobines are the only cercopithecoids with small incisors relative to their body size and have extremely negative residual values among the cercopithecoids for mean clivus length relative to body mass. Other cercopithecoids, other than *Macaca*, also have small clivuses relative to body mass, but with less marked residual values. It should be noted, though, that some researchers have expressed concerns about how informative the relationship is between diet and dental size and morphology. Eaglen (1984) warned that distinctions between platyrrhines and catarrhines may be clouded by the overall body size differences between the two groups. Ungar (1998) also questioned whether diet and incisor size correlations are reliable across taxa, pointing to examples in which the frugivory/folivory distinction does not predict incisor size differences. For example, platyrrhines have relatively smaller incisors than cercopithecoids, but they are not necessarily more folivorous. This could complicate analyses of fossil taxa or make researchers wary of comparisons between taxa that are of unknown phyletic affinities. Godfrey et al. (2001) noted that consumption between different seasons or even forests may vary. They point out that among colobines, dedicated leaf consumption can vary from as little as 26% of total diet to as much as 94%, depending on season and geography. Additionally, seeds can make up anywhere from 0-50% of the same diets and frugivores at times may ingest large amounts of foliage (Godfrey et al., 2001). Using Hylander's (1975) study as a basis, McCollum (2007) sought to analyze African apes but found that incisor wear rates did not support the resistance hypothesis for development of broader incisor crowns. Ungar (1998) also found that incisors are used regularly by folivores during food preparation. However, Deane (2009a) points out that McCollum's analysis fails to distinguish the overlap in diets between the few taxa analyzed. More recent analyses have supported Hylander's original theory, that frugivores can be discriminated using incisor size as a guide (Deane, 2009a, 2012).

Although research on the nasoalvolar clivus in extant anthropoid primates has been sparse, some authors have considered the feature in the fossil record (McCollum et al., 1993; Deane, 2009b; Williams et al., 2012). Data on clivus length in fossil hominoids, while limited [Table 5], shows that the subnasal morphologies of extinct species are intermediate between those of extant great apes and humans (McCollum et al., 1993; Williams et a., 2012). The general subnasal morphology of *Homo erectus* is intermediate between African apes and modern humans. Measurements for *H. erectus* are close to *Gorilla* and *Pan* but smaller than

Paranthropus. In comparison, the clivus length of *A. afarensis* shows that the species had a clivus slightly larger than humans but smaller than in African apes. Also, *Australopithecus africanus* has a similar clivus length to *A. afarensis*. Additionally, the measurements for *Homo habilis* show a clivus that is of comparable in length or slightly larger than humans. This supports the notion that the clivus size reduction trend observed in modern humans may have begun in early hominins.

CONCLUSION

The differences observed in mean nasoalveolar clivus length among anthropoid primates can be interpreted in a phylogenetic context. Previous research has lacked substantial consideration or quantification of the variability seen in the nasoalveolar clivus of anthropoids. The results present study shows that functional constraints of the anthropoid face appear to dictate the relationship between clivus size and other anatomical factors. Specifically, a relationship likely exists between upper incisor size and clivus depth. The relationship between incisor size and clivus development may be a consequence of dietary adaptations to resist masticatory stresses in the midface.

The relationship between clivus size and body mass among anthropoid primates does not scale isometrically. There appears to be divergent specializations in relative clivus size and incisor size among anthropoid primates: those with large clivuses and large incisors relative to their body mass and those with small clivuses and small incisors. Great apes have a marked expansion of the nasoalveolar clivus relative to their body size, while a secondary reduction has occurred in *Homo*. Relative clivus size among fossil hominins shows that this secondary reduction may have begun among early hominins. Platyrrhines exhibit diversity in clivus length, but the taxa included in this study tend towards small incisors and a small clivus relative to body mass. The cercopithecines, being similar to platyrrhines, retain what can be inferred to be the ancestral anthropoid condition. In contrast, the colobines show a specialized condition with their clivus being small relative to their body size. The hylobatids share a similar condition to most cercopithecoids, and may be inferred to retain the primitive catarrhine condition. As described above, some of the specializations seen in extant anthropoids may be attributable to upper incisor size and its relationship to dietary adaptation. The variability in the size of the nasoalveolar clivus in anthropoids provides insight into the evolutionary pressures that may have shaped aspects of the lower face. Further exploration of the relationship between clivus depth and other cranio-dental variables may prove useful for interpreting primate phylogenetic relationships and adaptations.

Table 1. Taxa Included in this Study

Hominoidea	**Cercopithecidae**	**Platyrrhini**
Gorilla gorilla	*Cercopithecus mitis*	*Alouatta seniculus*
Homo sapiens	*Lophocebus johnstoni*	*Aotus trivirgatus*
Hoolock hoolock	*Macaca fascicularis*	*Ateles geoffroyi*
Pan troglodytes	*Nasalis larvatus*	*Callithrix argentata*
Pongo pygmaeus	*Papio anubis*	*Pithecia monachus*
Symphalangus syndactylus	*Presbytis melalophos*	*Saguinus nigricollis*
		Saimiri boliviensis
		Sapaju capucinus

Table 2. Mean Clivus Length & Mean Body Mass (Smith and Jungers, 1997)

	Taxon	Clivus (mm)	SD	Body Mass (g)	Residual
Hominoidea	*Gorilla gorilla* ♂	36.06	2.97	170400	1.014
	Gorilla gorilla ♀	30.79	2.50	71500	7.719
	Homo sapiens ♂	21.33	1.39	64240	-1.794
	Homo sapiens ♀	21.14	1.23	56170	-0.136
	Hoolock hoolock ♂	7.36	1.14	6870	-6.254
	Hoolock hoolock ♀	7.66	0.67	6880	-4.201
	Pan troglodytes ♂	31.08	2.60	59700	12.575
	Pan troglodytes ♀	34.27	2.45	45800	16.119
	Pongo pygmaeus ♂	37.76	1.83	78500	11.761
	Pongo pygmaeus ♀	32.25	2.35	35800	17.879
	Symphalangus syndactylus ♂	7.96	0.88	11900	-14.017
	Symphalangus syndactylus ♀	7.32	0.86	10700	-16.433
Cercopithecidae	*Cercopithecus mitis* ♂	6.49	0.94	5850	-14.277
	Cercopithecus mitis ♀	6.24	0.60	3930	-8.499
	Lophocebus johnstoni ♂	6.87	1.25	8250	-9.579
	Lophocebus johnstoni ♀	6.69	0.82	6020	-2.269
	Macaca fascicularis ♂	9.91	0.88	5360	12.339
	Macaca fascicularis ♀	7.29	1.61	3590	7.763
	Nasalis larvatus ♂	7.27	1.03	20400	-31.311
	Nasalis larvatus ♀	7.07	0.72	9820	-16.561
	Papio anubis ♂	13.88	2.65	25100	-2.534
	Papio anubis ♀	11.46	1.62	13300	0.992
	Presbytis melalophos ♂	5.05	0.90	6590	-30.467
	Presbytis melalophos ♀	4.61	0.60	6470	-37.036
Platyrrhini	*Alouatta seniculus* ♂	8.87	1.31	6690	3.371
	Alouatta seniculus ♀	6.14	1.24	5210	-10.088
	Aotus trivirgatus ♂	3.21	0.44	810	-0.335
	Aotus trivirgatus ♀	3.41	0.46	740	7.885
	Ateles geoffroyi ♂	6.48	1.21	7780	-16.455
	Ateles geoffroyi ♀	6.47	0.90	7290	-15.002
	Callithrix argentata ♂	3.02	0.45	330	30.255
	Callithrix argentata ♀	2.97	0.24	360	25.360
	Pithecia monachus ♂	5.56	0.48	2610	5.549
	Pithecia monachus ♀	4.96	1.08	2110	10.109
	Saguinus nigricollis ♂	2.94	0.36	470	1.462
	Saguinus nigricollis ♀	2.67	0.12	480	0.941
	Saimiri boliviensis ♂	3.99	0.50	910	13.935
	Saimiri boliviensis ♀	3.41	0.33	710	4.539
	Sapaju capucinus ♂	7.04	0.56	3680	11.696
	Sapaju capucinus ♀	6.47	0.81	2540	9.385

Table 3. Mean Clivus Length & Mean Incisor Width (Swindler, 2002; Bailey, 2013)

	Taxon	**Clivus Length (mm)**	**Incisor Width (mm)**	**Residual**
Hominoidea	*Gorilla gorilla* ♂	36.06	25.5	-1.652
	Gorilla gorilla ♀	30.79	23.9	-3.148
	Homo sapiens ♂	21.33	14.7	11.277
	Homo sapiens ♀	21.14	15.0	9.900
	Hoolock hoolock ♂	7.36	9.2	3.597
	Hoolock hoolock ♀	7.66	9.3	4.592
	Pan troglodytes ♂	31.08	22.7	2.201
	Pan troglodytes ♀	34.27	20.7	6.834
	Pongo pygmaeus ♂	37.76	23.5	3.432
	Pongo pygmaeus ♀	32.25	22.2	1.899
	Symphalangus syndactylus ♂	7.96	9.5	4.629
	Symphalangus syndactylus♀	7.32	9.4	1.509
Cercopithecidae	*Cercopithecus mitis* ♂	6.49	9.6	-6.727
	Cercopithecus mitis ♀	6.24	9.5	-8.052
	Lophocebus johnstoni ♂	6.87	14.1	-37.233
	Lophocebus johnstoni ♀	6.69	12.2	-30.562
	Macaca fascicularis ♂	9.91	11.1	2.289
	Macaca fascicularis ♀	7.29	10.9	-11.269
	Nasalis larvatus ♂	7.27	10.0	-4.093
	Nasalis larvatus ♀	7.07	9.5	-1.153
	Presbytis melalophos ♂	5.05	8.0	-4.779
	Presbytis melalophos ♀	4.61	8.2	-13.210
Platyrrhini	*Alouatta seniculus* ♂	8.87	8.2	20.734
	Alouatta seniculus ♀	6.14	7.5	12.964
	Aotus trivirgatus ♂	3.21	6.1	-5.544
	Aotus trivirgatus ♀	3.41	6.3	-4.781
	Ateles geoffroyi ♂	6.48	8.2	7.417
	Ateles geoffroyi ♀	6.47	8.2	7.341

Table 4. Mean Incisor Width & Mean Body Mass (Smith and Jungers, 1997; Swindler, 2002; Bailey, 2013)				
	Taxon	**Mean Incisor Width (mm)**	**Mean Body Mass (g)**	**Residual**
Hominoidea	*Gorilla gorilla* ♂	25.5	170400	0.584
	Gorilla gorilla ♀	23.9	71500	6.756
	Homo sapiens ♂	14.7	64240	-8.977
	Homo sapiens ♀	15.0	56170	-6.761
	Hoolock hoolock ♂	9.2	6870	-3.483
	Hoolock hoolock ♀	9.3	6880	-3.000
	Pan troglodytes ♂	22.7	59700	6.853
	Pan troglodytes ♀	20.7	45800	6.493
	Pongo pygmaeus ♂	23.5	78500	5.421
	Pongo pygmaeus ♀	22.2	35800	10.852
	Symphalangus syndactylus ♂	9.5	11900	-8.914
	Symphalangus syndactylus♀	9.4	10700	-8.086
Cercopithecidae	*Cercopithecus mitis* ♂	9.6	5850	0.475
	Cercopithecus mitis ♀	9.5	3930	5.013
	Lophocebus Johnstoni ♂	14.1	8250	11.257
	Lophocebus Johnstoni ♀	12.2	6020	11.388
	Macaca fascicularis ♂	11.1	5360	7.507
	Macaca fascicularis ♀	10.9	3590	11.551
	Nasalis lavartus ♂	10.0	20400	-13.112
	Nasalis lavartus ♀	9.5	9820	-6.499
	Presbytis melalophos ♂	8.0	6590	-9.872
	Presbytis melalophos ♀	8.2	6470	-8.336
Platyrrhini	*Alouatta seniculus* ♂	8.2	6690	-8.785
	Alouatta seniculus ♀	7.5	5210	-10.091
	Aotus trivirgatus ♂	6.1	810	6.459
	Aotus trivirgatus ♀	6.3	740	9.489
	Ateles geoffroyi ♂	8.2	7780	-10.815
	Ateles geoffroyi ♀	8.2	7290	-9.941

Table 5. Mean Clivus Height Among Extant and Fossil Taxa Published Literature

		Taxon	**Mean Clivus Height (mm)**	**SD**	**EB Data**	**SD**
Williams et al. (2012)	**Extant**	*Gorilla gorilla*	33.2	6.15	33.4	2.74
		Homo sapiens	19.2	3.61	21.2	1.31
		Pan troglodytes	31.6	4.93	32.7	2.53
	Fossil	*Australopithecus africanus*	27.0	2.86	-	-
		Homo erectus	32.7	4.37	-	-
		Homo habilis	23.7	8.36	-	-
		Paranthropus aethiopicus	36.2	-	-	-
		Paranthropus boisei	36.6	5.15	-	-
		Paranthropus robustus	29.0	0.94	-	-
		StW 53	26.4	-	-	-
McCollum et al. (1993)	**Extant**	*Gorilla gorilla*	31.1	5.8	33.4	2.74
		Homo sapiens	19.3	2.5	21.2	1.31
		Pan troglodytes	32.1	4.5	32.7	2.53
		Pongo pygmaeus	29.9	4.4	35.0	2.09
	Fossil	*Australopithecus africanus*	25.2	4.2	-	-
		Australopithecus afarensis	24.3	1.5	-	-
		Paranthropus boisei	37.1	11.5	-	-
		Paranthropus robustus	29.0	3.0	-	-
		StW 53 (*Homo gautengensis*)	25.5	-	-	-
		KNM-WT 17000 (*Paranthropus aethiopicus*)	27.0			
		KNM-ER 1470 (*Homo rudolfensis*)	33.5	-	-	-
		KNM-ER 1805 (*Homo habilis*)	21.0	-	-	-
		KNM-ER 1813 (*Homo habilis*)	25.3	-	-	-
		OH 24 (*Homo habilis)*	25.7	-	-	-
		OH 62 (*Homo habilis*)	23.0	-	-	-
		KNM-ER 3733 (*Homo ergaster*)	31.00	-	-	-
		SK 847 (Early *Homo*)	32.00	-	-	-

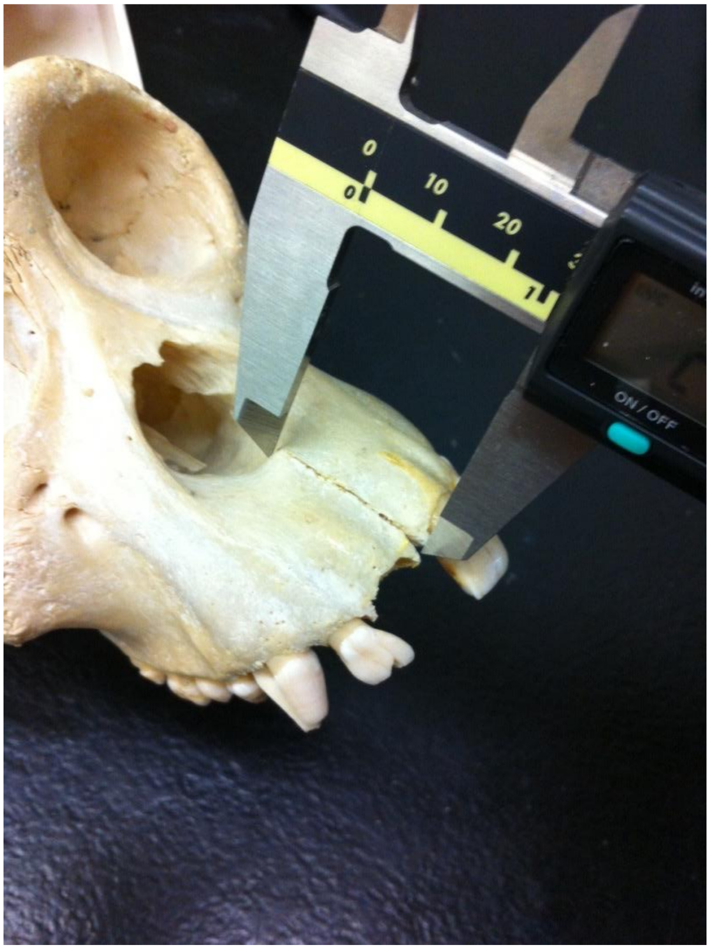
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Fig. 1: Measurement of maximum nasoalveolar clivus length in anthropoids. [Photo by author]

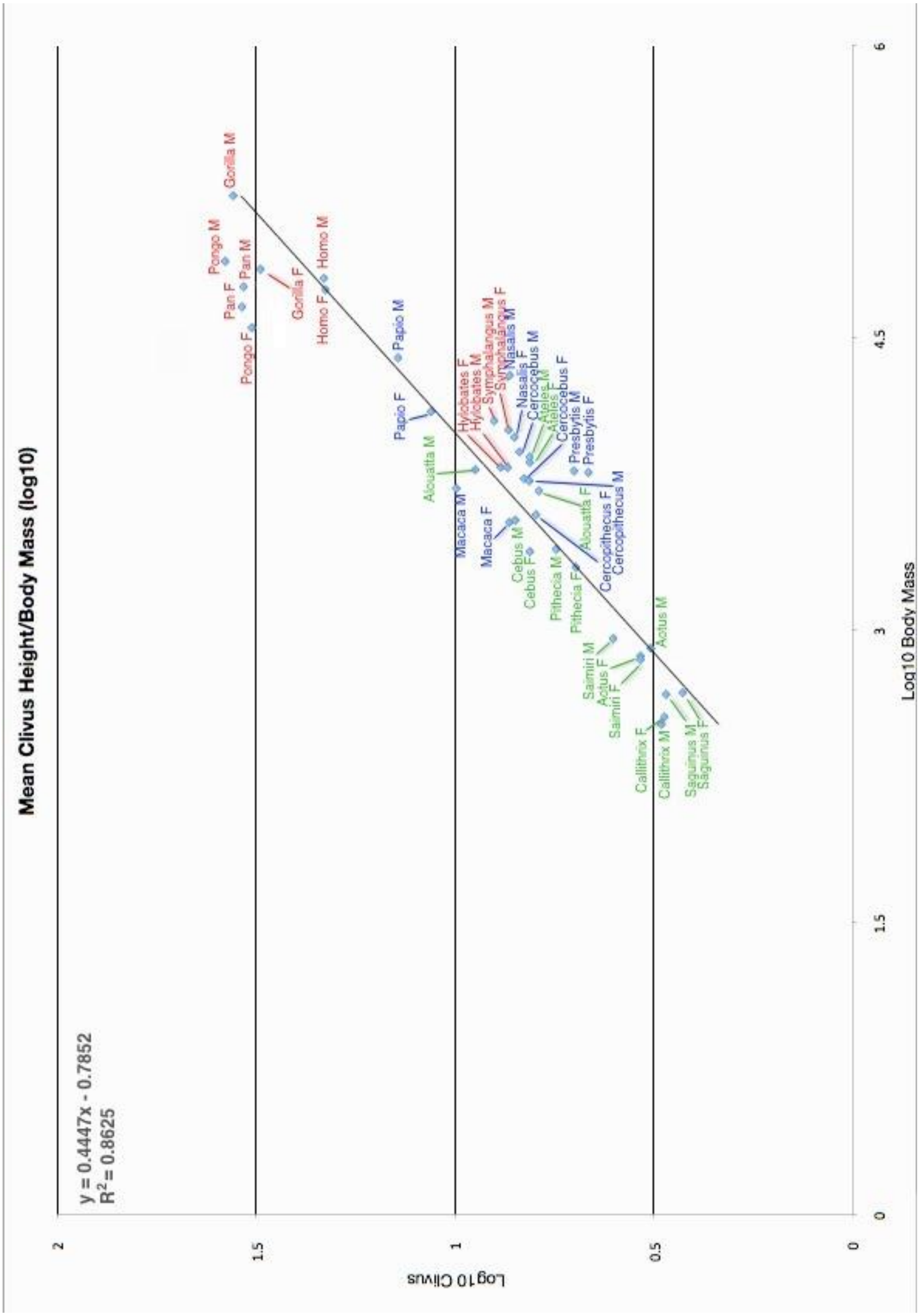

Figure 2. Log_{10} Mean Clivus Height and Log_{10} Mean Body Mass.

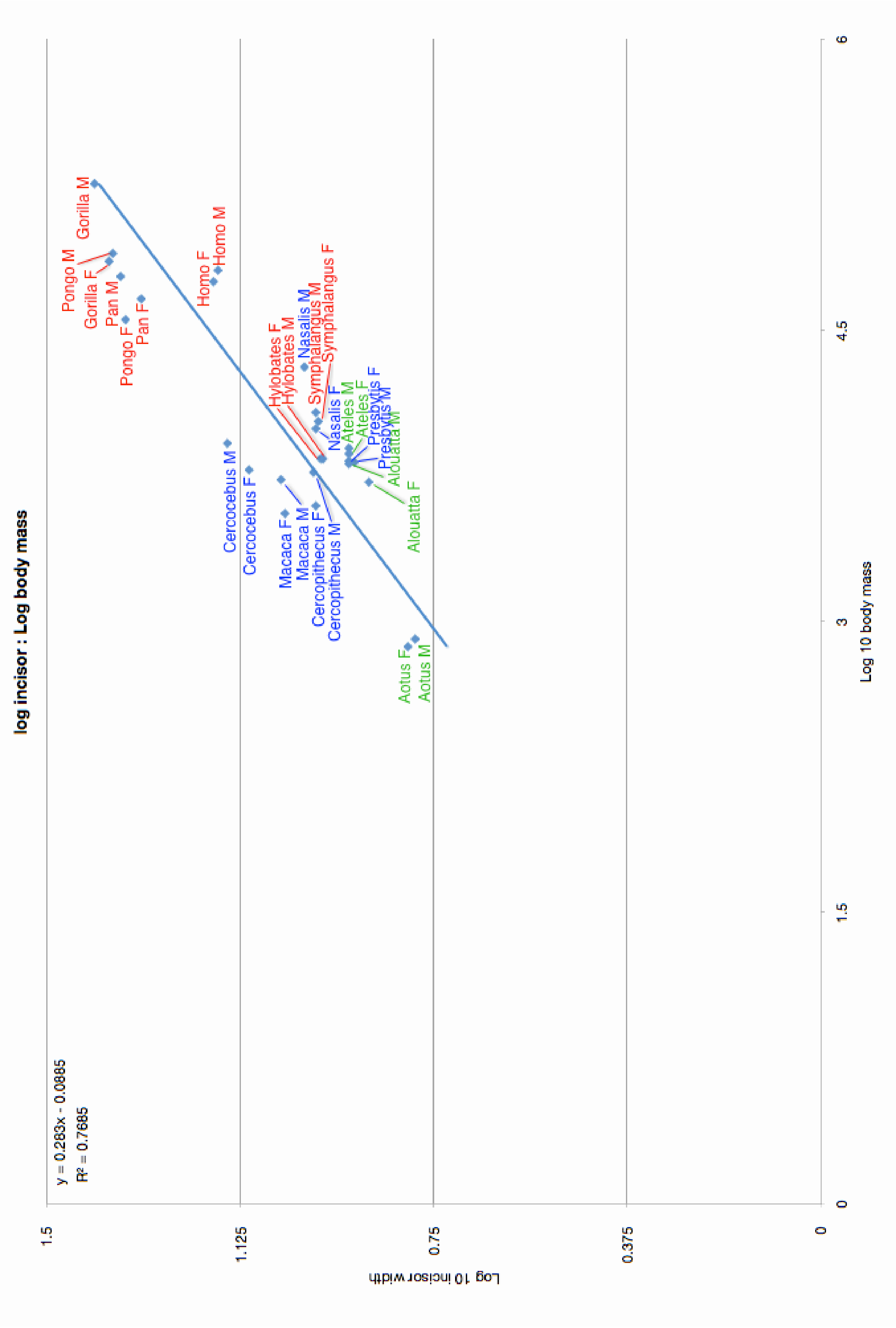

Figure 3. Log_{10} Mean Incisor Width and Log_{10} Mean Body Mass.

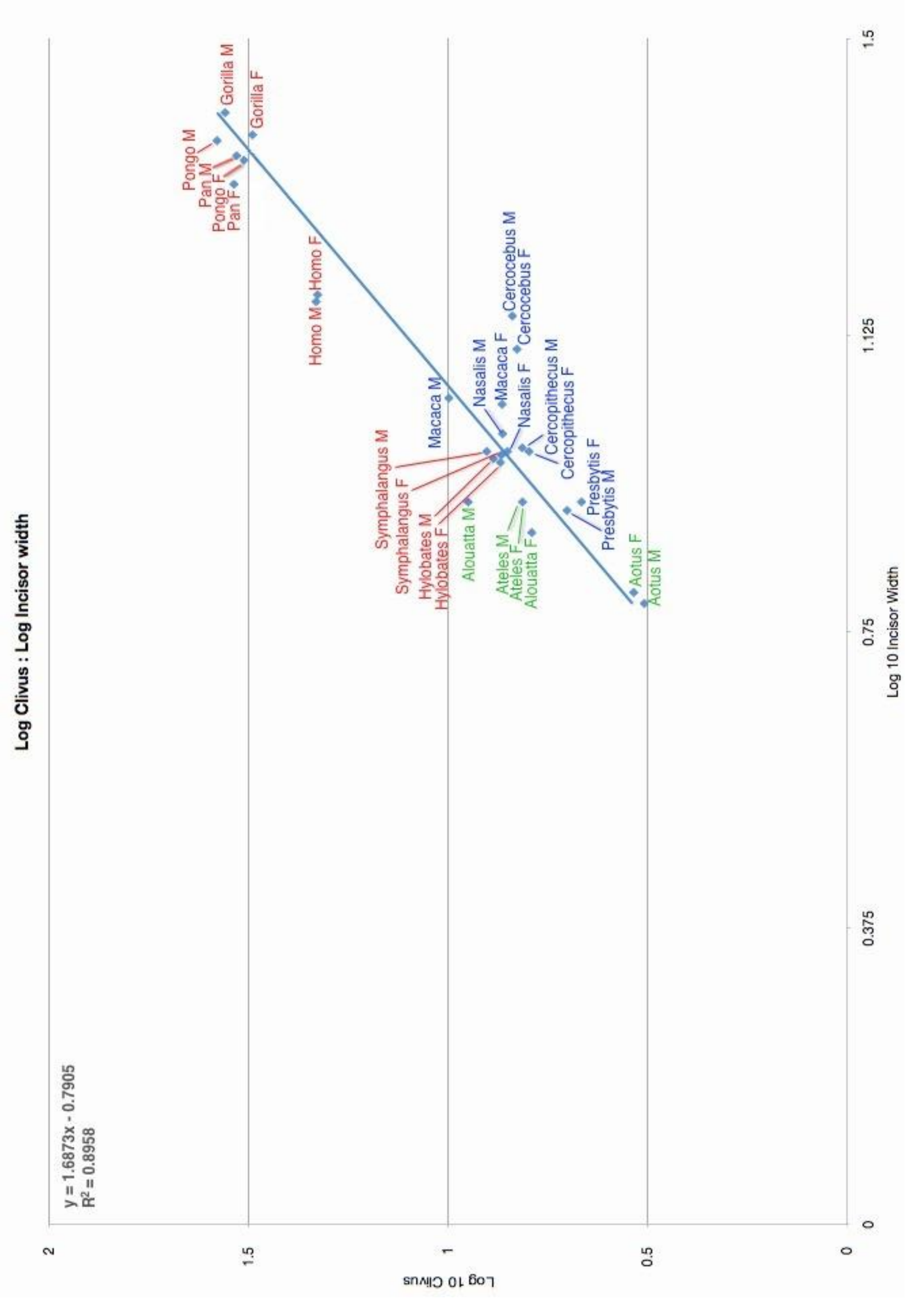

Figure 4. Log$_{10}$ Mean Clivus Length and Log$_{10}$ Mean Incisor Width

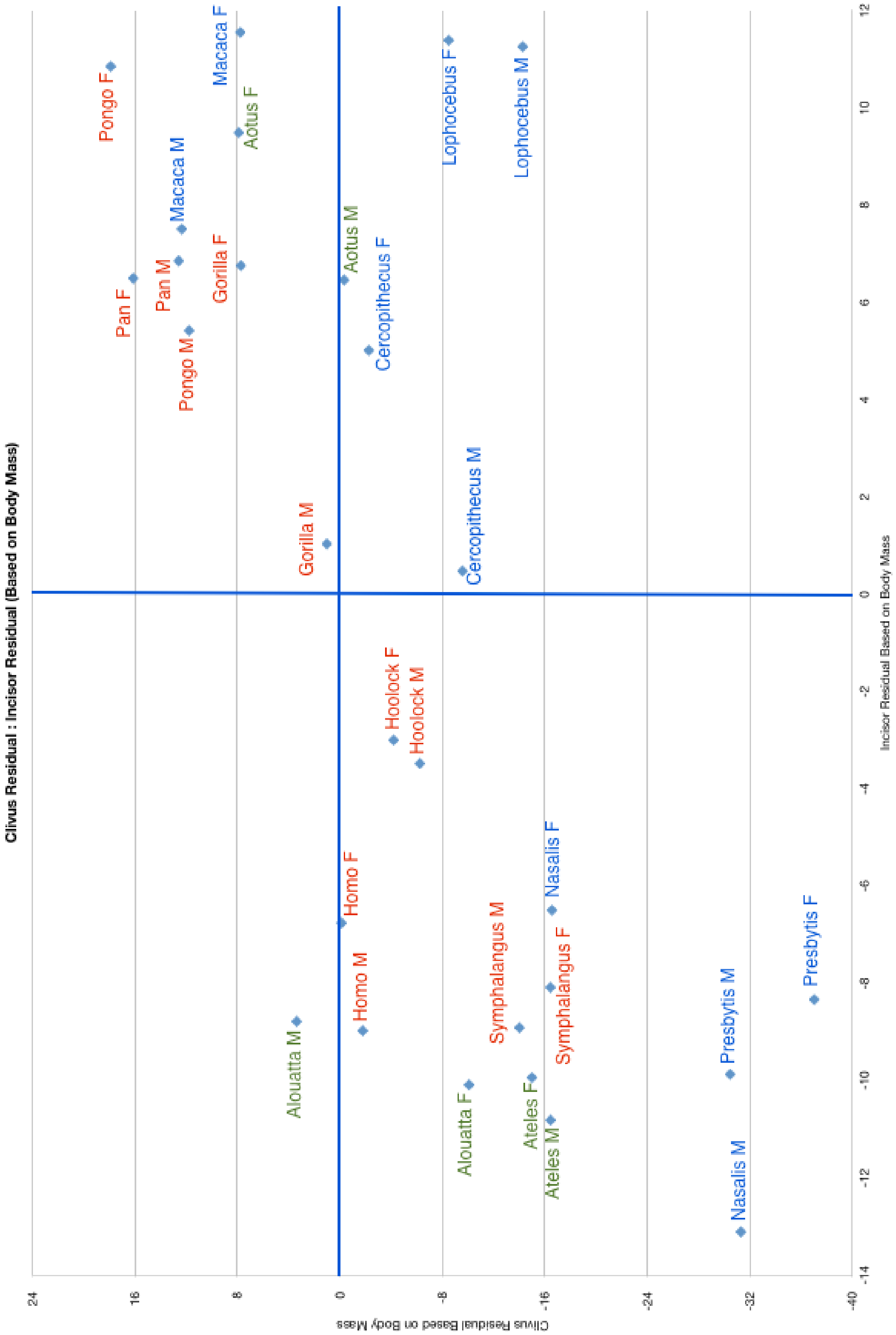

Figure 5. Clivus Residuals from Body Mass and Incisor Residuals from Body Mass.

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