

Craniometric Variation in a Population of Mantled Howler Monkeys (*Alouatta palliata*): Evidence of Size Selection in Females and Growth in Dentally Mature Males

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ABSTRACT A large body of work on monkey cranial metrics (involving conclusions about interspecific variation, sexual dimorphism, and ontogeny) depends on the assumptions that growth effectively ceases with dental maturity and that intraspecific variation is negligible. We test these assumptions by examining variation in 39 measurements of 166 dentally mature *Alouatta palliata* skulls from animals found dead on Barro Colorado Island (BCI), Panama. We also investigate whether this population is under size-based selection, since our found-dead sample reflects the natural mortality in this population. The sample was divided into three age stages by occlusal wear (A–C, least to most wear). Female stage A means are significantly smaller than female stage B means for three cranial measures. Female stage B means are significantly smaller than female stage C means for five cranial measures. Male stage A means are significantly smaller than male stage B means for 21 cranial measures. Multivariate analyses confirm this trend of expansion between adult age stages. The dental metric and suture closure data suggest that the cranial expansion in females is due to size-based selection, while the cranial expansion in males is due to significant growth after dental maturity. Sexual dimorphism ratios are highly variable across different samples of *A. palliata*, indicating that dimorphism varies between populations of this species. These results provide insight into the selective forces operating on the BCI howlers and challenge the validity of the many studies which pool subspecies and assume growth ceases with maturity. *Am J Phys Anthropol* 113:411–434, 2000. © 2000 Wiley-Liss, Inc.

Numerous studies have examined variation in the cranial metrics of nonhuman primates to elucidate patterns of ontogeny, sexual dimorphism, and phylogeny. Most such investigations use museum collections of wild-shot primates from scattered localities to investigate this variation at the species level. In doing so,

several assumptions are usually made (often implicitly) regarding the uniformity of

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variation within a species and the nature of skeletal growth.

By pooling individuals from different geographic localities and subspecies into a single sample, studies that examine sexual dimorphism and ontogeny at the species level implicitly assume that these patterns do not differ significantly between populations of the same species (Shea, 1981, 1992; Ravosa, 1992; Miller, 1997; Masterson and Hartwig, 1998). If sexual dimorphism or ontogeny do vary within a species, then the geographic, populational, and/or subspecies composition of the samples used could significantly distort the results. This is true both for comparisons between species as well as for intraspecific studies of ontogeny (if different populations contribute different proportions of the various age stages) and sexual dimorphism (if different populations contribute different proportions of males and females). However, given the paucity of studies at the population level, it is not clear whether sexual dimorphism and ontogeny do vary significantly within some, or indeed any, nonhuman primate species.

Most studies of nonhuman primate cranial metrics also implicitly assume that significant cranial growth ceases with dental maturity by lumping all dentally mature individuals into the single category of "adult" (Ravosa, 1992, 1998; Shea, 1992; Ravosa and Ross, 1994; Masterson and Hartwig, 1998). If cranial growth continues beyond dental maturity, however, then the age composition of the various adult samples examined could significantly distort the results. Two ontogenetic samples from the same population would yield different growth curves if one sample had more younger adults than the other. Two populations that do not differ metrically would appear to do so if the sample from one had more younger adults than the other. But whether cranial growth does, in fact, continue beyond dental maturity in nonhuman primates is unclear, though this has been suggested for several primate taxa (Schultz, 1956; Fooden and Izor, 1983; Glassman, 1983; Watts, 1985; Godfrey et al., 1997). Others have considered the possibility of adult cranial remodeling due to alterations of muscle activity (Herring, 1974; DeGusta

and Milton, 1998), but we use "growth" here in the traditional sense of referring to linear increase of cranial dimensions.

The samples used in studies of ontogeny and sexual dimorphism are indeed quite likely to differ in the age composition of the "adult" category and to represent different populations, since they are usually drawn from mixed museum collections derived from hunting or trapping (e.g., Shea, 1981, 1992; Ravosa, 1992; Masterson and Hartwig, 1998). Therefore, it is important to test the assumptions that cranial growth does not continue after dental maturity and that sexual dimorphism is uniform within a species. To do so, however, requires large samples from single populations. We report here on a test of these assumptions in such a sample of *Alouatta palliata*.

Questions regarding cranial growth and dental maturity in *A. palliata*

This study characterizes the cranial metric variation present in a single population of the mantled howler monkey (*Alouatta palliata*) from Barro Colorado Island (BCI), Panama. All individuals in the sample were found dead of natural causes on BCI. We only used dentally mature individuals in our analysis, since it was not possible to determine the sex of immature individuals. We divided the dentally mature individuals into three age categories, based on occlusal wear. Some comparisons with *A. palliata* from other areas were possible, since howler monkeys are one of the few nonhuman primate species with published cranial metric data by geographic region (Schultz, 1960, though Schultz considered all but one of his regional samples to represent multiple populations).

The analysis of the cranial metric data from the BCI howlers, and the comparison of the BCI data with other *Alouatta* groups, allowed us to investigate three questions.

1. Is the level of cranial sexual dimorphism uniform within *A. palliata*? If it is, then the craniometric sexual dimorphism in the BCI howlers should not differ significantly from the different regional groups of *A. palliata* measured by Schultz (1960) or from composite *A. palliata* samples

- drawn from different populations (Ravosa and Ross, 1994; Miller, 1997; Masterson and Hartwig, 1998).
2. Does cranial growth continue past dental maturity in *A. palliata* in either sex? If there are no significant increases in the various cranial measures between the three dentally mature age stages, then it does not. However, significant increases in cranial measures between the age stages in this sample are not necessarily due to growth—they may indicate size-based selection instead (see below). If some measures increase while others decrease, then this may indicate shape remodeling rather than linear growth per se.
 3. Are adult BCI *A. palliata* of either sex under selection for increased size? This is not a question that can be addressed with skeletal samples derived from wild-shot individuals, as they do not reflect natural mortality. However, the BCI sample is composed entirely of individuals found dead of natural causes, and so reflects the action of selection in the sense of differential mortality. Size-based selection, depending on its type and degree, is detectable in such a found-dead sample. For example, imagine the extreme hypothetical case of a howler population under such strong adult size selection that age at death is perfectly correlated with cranial size, so that small adults invariably died at age 5, medium-sized ones died at age 10, and large ones lived until age 15 (howlers are dentally mature at ca. 3–4 years). The resulting adult skeletal sample would then exhibit a clear trend of increasing size with increasing age, as the mean size of age 5 individuals would be smaller than those of age 10 individuals, who in turn would be smaller than age 15 individuals. Knowledge of the absolute chronological ages of the skulls is not necessary, for as long as their age relative to each other can be established (i.e., with occlusal wear stages), such a trend of increasing size with increasing age will be detectable. A found-dead skeletal collection does effectively sample the entire population, including living animals, as they

all die sooner or later. The relationship of their morphology to whether they die “sooner” or “later” permits the testing of hypotheses about selection in the sense of differential mortality.

Specifically, if there is increased mortality in smaller BCI adults, then smaller individuals will (on average) die at a younger age than larger individuals. This will result in the younger adult age stage in the skeletal sample having more small individuals, while the older adult stage will have more large individuals. Significant increases in the various cranial measures between the three dentally mature age stages could therefore either indicate growth (as above) or this type of selection. An examination of dental metrics can differentiate growth from selection, assuming that tooth size is not independent of cranial size. Teeth do not grow once they are fully formed (Hillson, 1986), and all crowns are completely formed well before the youngest dentally mature age stage in this sample. Higher mortality for small individuals (selection) should produce a pattern of expansion in tooth size between age stages. Cranial growth after dental maturity, on the other hand, would not produce any significant differences in tooth size between age stages. So in addition to cranial metrics, we also examined dental metrics and suture closure in the BCI howler sample to help distinguish growth from selection.

MATERIALS AND METHODS

Sample

Barro Colorado Island, Panama (9°9'N, 79°51'W) is probably the most-studied tract of tropical forest in the world (Leigh and Wright, 1990), and detailed descriptions of the island's flora, fauna, climate, and history are available in the literature (Croat, 1978; Glanz, 1990; Hubbell and Foster, 1990). For the past 25 years, the *Alouatta palliata* population on BCI has fluctuated between some 1,250–1,350 monkeys distributed in 60–70 troops (Milton, 1996). Howlers on BCI are free-ranging, and are not provisioned, hunted, or otherwise manipulated by humans. They apparently experience no significant vertebrate predation

and are effectively isolated from mainland monkey populations (Carpenter, 1965; Milton, 1982). The population likely went through at least two bottlenecks within the last century: the island was created from 1910–1914 by the damming of the Chagres River, and a significant decrease in the number of howlers occurred in 1951, possibly due to a yellow fever epidemic (Collias and Southwick, 1952).

The sample consists of 166 adult *Alouatta palliata* skulls. Monkeys were found dead of natural causes on BCI at all times of the year from July 1986–July 1996 by K.M. and various colleagues. Skulls were obtained from all dead howlers encountered during the course of other research on BCI, and were cleaned by chemical defleshing. Most skulls were recovered from the Hubbell-Foster plot (Hubbell and Foster, 1990), Poacher's Peninsula, and the region around the laboratory, since these are the areas typically frequented by BCI researchers. The complete collection includes many immature individuals which were not included in this study because of their unknown sex. However, the fact that ~25% of all howler carcasses recovered are immature individuals, often one-third the size of an adult monkey or less, strongly suggests that the adult sample is not size-biased by the recovery method (DeGusta and Milton, 1998).

Sexing and aging

Specimens were judged "adult" if all permanent teeth were erupted, as this is the criterion used in nearly all primate craniometric studies (e.g., Schultz, 1960; Ravosa and Ross, 1994). However, as will be made clear later, the term "dentally mature" is probably more technically accurate than "adult," though the terms will be used interchangeably here for ease of expression. A tooth was considered erupted if its crown penetrated the alveolar plane, but virtually all specimens in this sample have all of their teeth fully erupted (in four individuals the canine is not quite in its final position, but excluding those specimens does not affect the results).

The adult stage was divided into three categories based on degree of occlusal wear, as per Schultz (1960): A, no noteworthy oc-

clusal wear; B, moderate to marked occlusal wear; and C, very marked to extreme occlusal wear (Fig. 1). Stages A–C correspond to Schultz's adult 0, adult 1, and adult 2 categories, respectively, and these will often be referred to here as "age stages" as shorthand for "dental age stages based on the relative degree of occlusal wear." All adult specimens were seriated by tooth wear and scored by one researcher in one session to ensure internal consistency of the subdivisions. Thus we can be sure that every stage A specimen has less occlusal wear than every stage B specimen, which will, in turn, have less wear than all stage C specimens. There is generally a close relationship between degree of occlusal wear and age (Ubelaker, 1989; Walker et al., 1991), and this should be an especially tight relationship in the BCI sample, as it represents a single population from a restricted area sampled over only about a decade. As such, it is clear that stage C individuals are older than stage B individuals, which in turn are older than stage A individuals. The rate of occlusal wear can vary between populations (Ubelaker, 1989, p. 92; Walker et al., 1991), so these subdivisions may not be strictly comparable between studies. However, for testing the hypotheses at hand, it is only necessary to have an internally consistent, *relative* measure of age (as discussed above). Whether the average absolute ages for the various stages are 5, 10, and 15 years, or 4, 8, and 12, makes little difference in this case.

Adult howlers exhibit considerable sexual dimorphism in canine size and morphology (Kay et al., 1988), which permitted the dental sexing of most adult skulls in the sample. The adult sample was seriated by canine size and shape to confirm the assignments. Even though there was typically very clear dimorphism (Fig. 2), sexing was done conservatively, with the eight doubtful cases scored as indeterminate and excluded from the sample. The age and sex composition of the sample is given in Table 1.

Methods

Thirty-four craniometric and five dental measures (defined in Appendix A) were

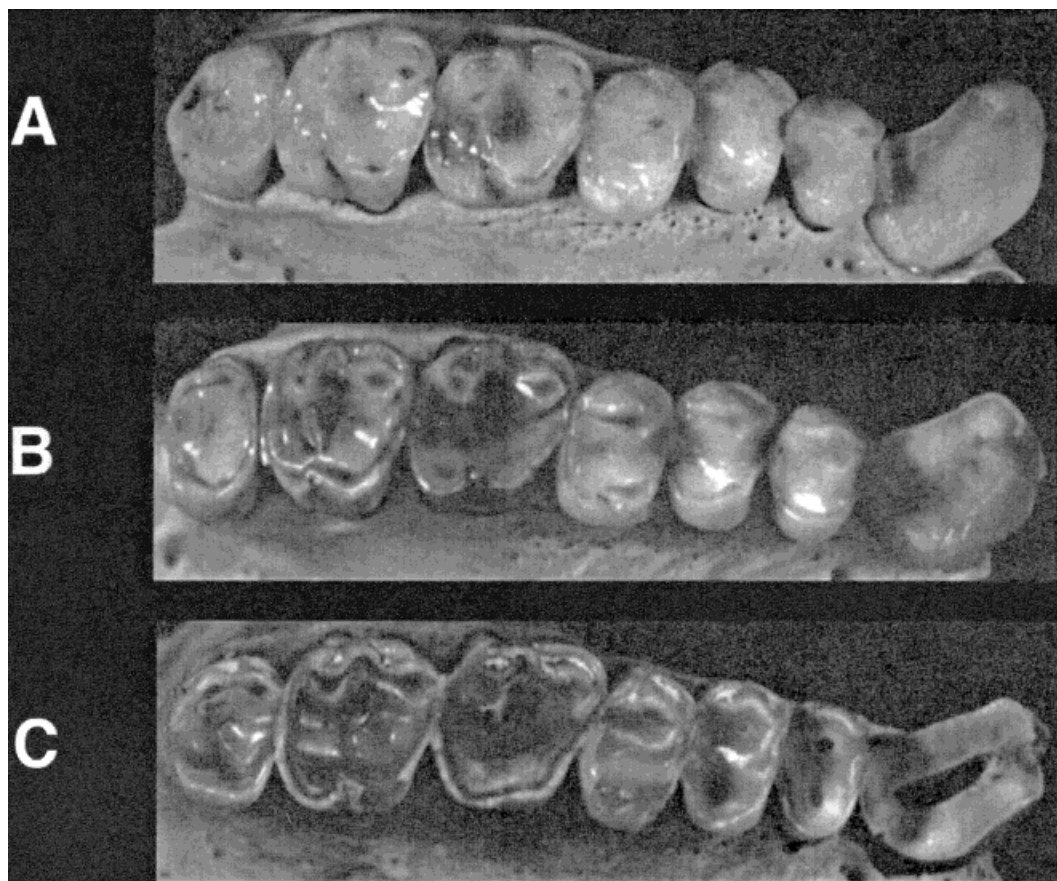


Fig. 1. Male tooth rows with occlusal wear typical of stages A, B, and C.

taken on the sample. All linear measures were taken to the hundredth of a millimeter, using digital calipers (Fowler Caliper Ultra-Call Mark III). Endocranial volume (ENCV) was measured by plugging the orbital fissures and large basicranial foramina with modeling clay, filling the cranium with solid glass beads (3-mm diameter, Fisher Scientific catalog number 11312A) to the level of the foramen magnum, and then decanting the beads into a graduated cylinder. The measures were divided into three sets, and each set of measures was taken on the entire sample by a single individual to eliminate considerations of interobserver error. Unilateral metrics were taken on the right side when possible. Fifteen skulls were measured twice, each set of measures by the original operator, with a separation of 1 month and no reference to the initial data,

and the resulting data pairs were used to calculate three indices of measurement precision (Appendix B): technical error of measurement (Dahlberg, 1940, pp. 125–126; Knapp, 1992), mean absolute difference (Utermohle et al., 1983), and percentage error (Utermohle et al., 1983). Unless otherwise noted, the magnitude of differences between age/sex groups discussed is always greater (and usually considerably greater) than the mean measurement error. Since the direction of the measurement error (i.e., whether the measurement recorded is smaller or larger than the “true” value) is random, this establishes that the differences are not an artifact of measurement methods.

A detailed study of the skeletal pathologies in this sample has been done (DeGusta and Milton, 1998), and these results were



Fig. 2. Canine dimorphism in adult mantled howler monkeys. Female on left, male on right. Bar, 0.5 cm.

TABLE 1. Age and sex composition of BCI sample

Age stage ¹	No. of females	No. of males	Total
A	22	16	38
B	56	38	94
C	18	16	34
Total	96	70	166

¹ Dental age stages are based on relative degree of occlusal wear in adult animals, and provide a relative measure of age in this sample. A, no noteworthy occlusal wear; B, moderate to marked occlusal wear; C, very marked to extreme occlusal wear. See Materials and Methods.

used to ensure that measurements potentially affected by skeletal pathology were not taken. Similarly, any measurements judged to be altered by postmortem damage were not taken.

The hypotheses to be tested required that we determine whether the skull measurements differ significantly by age and sex. This can be done in two general ways: comparison of age/sex groups examining one

measurement at a time (univariate pairwise comparison of means), and comparisons considering all measurements simultaneously (multivariate analysis). We employ both approaches.

Univariate and bivariate statistical analysis was performed using StatView 4.5 (Abacus Concepts, Berkeley, CA). The distribution of the data indicated that parametric tests were most appropriate. The data were also analyzed using nonparametric methods (i.e., Kruskal-Wallis), and the results confirmed those of the parametric analysis. There are three major parametric tests of significance for conducting multiple pairwise comparisons of means: Fisher's method, Bonferroni's method, and Scheffé's F. Fisher's method is the most liberal of the three (i.e., most likely to recognize a difference as significant), and is appropriate in cases where there are no significant differences between the variances and relatively few means to compare (Zolman, 1993; Rao, 1998). Scheffé's F test can accommodate heterogeneous variances, but is the most conservative test and can fail to recognize a truly significant difference (Howell, 1987; Zolman, 1993). Bonferroni's method is intermediate between Fisher's method and Scheffé's F in its conservatism and ability to handle unequal variances (Zolman, 1993). Given the relatively small number of mean comparisons (three per measure in the case of age stages), Bonferroni's method was selected as the appropriate test for most measures. Scheffé's F test was used in cases where the F-test of equal variance revealed a significant difference in the variances of the groups compared.

Multivariate analyses were carried out using SAS 6.12 and JMP 3.2 (SAS Institute, Cary, NC) on the subsample of specimens that had complete data sets available for all 34 craniometrics (females, $n = 35$; males, $n = 27$). All measurements were natural log-transformed. For endocranial volume, the cube root was natural log-transformed because it is a volumetric measurement. In many cases, the sample size for multivariate analysis was smaller than the number of variables. Hence, principal components analysis was used to reduce the number of variables from 34 craniometrics to a more

TABLE 2. Differences between adult age stages in females¹

Metric	Age stages ¹	Bonferroni P value	Variance ratio	Variance P value	Scheffé's P value
BZYB	A-B	<0.0001	2.064	0.813	
IBIB	A-B	0.0001	0.791	0.5354	
OBIB	A-B	<0.0001	0.914	0.8122	
UM1B	A-B	0.0009	1.055	0.7116	
BASL	A-C	0.0032	2.115	0.1330	
BCOB	A-C	0.0020	1.271	0.6916	
BZYB	A-C	<0.0001	4.366	0.0047	<0.0001
IBIB	A-C	<0.0001	0.882	0.7946	
OBIB	A-C	<0.0001	1.138	0.7879	
UM1B	A-C	<0.0001	0.835	0.5683	
ZYAL	A-C	0.0002	1.433	0.3396	
BRDT	B-C	0.0044	1.214	0.6362	
IBIB	B-C	<0.0001	1.115	0.7907	
LENG	B-C	0.0031	1.065	0.8783	
OBIB	B-C	<0.0001	1.245	0.5939	
ZYAL	B-C	0.0034	1.197	0.6602	
UCMD	C-B	0.0062	1.639	0.2640	

¹ First stage listed has the smaller mean of the pair.

manageable number of summary statistics. The first four principal components were used as dependent variables for discriminant function analysis to determine the Mahalanobis *D* distances between age stage multivariate means. Multivariate analysis of variance was also carried out on these components to obtain the Hotelling-Lawley trace (equivalent to Hotelling's *T*²; Tabachnick and Fidell, 1996) and multivariate *F* statistics to determine if the age stages differ significantly on the combined variables. Because sample sizes were smaller for the multivariate analyses, our interpretations are based primarily on the univariate and bivariate results, with the multivariate results providing additional confirmation.

RESULTS

Summary statistics

The abbreviations and definitions for all measures are provided in Appendix A. Indices of precision for each measurement are given in Appendix B. Summary statistics for each cranial metric are shown in Appendix C. The dental metric summary statistics are given in Appendix D. A computer database file (Microsoft Excel 97 format) containing all the individual measurements is available from the first author upon request.

Correlations

Correlation coefficients were used to detect any significant linear relationships be-

tween cranial measures. All pairs of measurements with correlation coefficients greater than 0.8 are listed in Appendix E. This threshold was chosen based on an examination of both full and partial correlation matrices, as virtually all correlations have significant *P*-values due to the large sample size.

Intrasexual age stage differences

A two-way analysis of variance (ANOVA) identified a significant difference between the sexes for all metrics except nasal breadth (NASB). We then used one-way ANOVA to examine differences between the three age stages within each sex. A number of metrics differed significantly (using Bonferroni's method) between the three adult age stages in both females (Table 2) and males (Table 3). The magnitude of differences, while typically on the order of a millimeter, was always notably greater than the measurement error (mean absolute difference, Appendix B), except for upper canine mesial-distal (UCMD) in females. The metrics that differ significantly between age stages in females fall into four groups, based on the correlations between measurements: 1) basal length (BASL), bizygomatic breadth (BZYB), bicondylar breadth (BCOB), and zygomatic arch length (ZYAL); 2) inner biorbital breadth (IBIB) and outer biorbital breadth (OBIB); 3) length (LENG); and 4) breadth (BRDT). In males, almost all the metrics that differ significantly

TABLE 3. Differences between adult age stages in males¹

Metric	Age stages ¹	Bonferroni P value	Variance ratio	Variance P value	Scheffé's P value
BABR	A-B	0.0017	0.974	0.9528	
BASL	A-B	<0.0001	3.433	0.0150	0.0004
BCAB	A-B	0.0075	1.172	0.7182	
BCOB	A-B	<0.0001	1.252	0.6708	
BCRB	A-B	0.0003	2.04	0.2016	
BCRL	A-B	0.0021	1.465	0.4126	
BGOB	A-B	0.0007	0.784	0.6668	
BROH	A-B	0.0062	1.55	0.3192	
BZYG	A-B	0.0001	7.286	0.0001	0.0007
GCLT	A-B	0.0002	2.31	0.0795	
IBIB	A-B	<0.0001	1.882	0.1551	
LENG	A-B	0.0007	1.862	0.1972	
LWSL	A-B	<0.0001	4.266	0.0042	0.0002
MCOH	A-B	<0.0001	1.586	0.3655	
NAPR	A-B	0.0014	0.887	0.7917	
OBIB	A-B	<0.0001	1.023	0.9581	
PLAL	A-B	<0.0001	2.276	0.0658	
POCL	A-B	0.0032	1.705	0.2423	
PZYL	A-B	0.0020	1.033	0.9412	
RAMH	A-B	0.0023	8.994	0.0005	0.0093
ZYAL	A-B	0.0002	3.463	0.0074	0.0008
BASL	A-C	<0.0068	0.849	0.7701	
BCOB	A-C	0.0034	0.839	0.7772	
BCRB	A-C	0.0009	0.481	0.2662	
GCLT	A-C	0.0010	0.577	0.3246	
IBIB	A-C	<0.0001	0.925	0.8848	
LENG	A-C	0.0014	1.118	0.8414	
LWSL	A-C	0.0034	0.678	0.4857	
MCOH	A-C	<0.0001	0.483	0.2233	
NAPR	A-C	0.0003	0.671	0.4657	
OBIB	A-C	<0.0001	0.893	0.8331	
PLAL	A-C	0.0002	1.019	0.9707	
UM1B	A-C	0.0017	0.435	0.1393	
UM1B	B-C	0.0044	0.722	0.4817	

¹ First stage listed has the smaller mean of the pair.

are linked by correlations, suggesting that changes along one or more major axes are probably responsible for the differences. For each metric, the percentage difference of the means between stage A to B and stage B to C was calculated. The means for all metrics were then averaged to elucidate the overall direction of size changes between age stages. The overall mean percentage change between age stages for females and males is shown in Figure 3.

Multivariate analyses were performed to see if age stages differ significantly within each sex, using all variables combined. For females, multivariate analysis of variance (MANOVA) shows that all age stages differ significantly from each other at the $P < 0.05$ level (Table 4). The Mahalanobis D distance is the greatest between stage A and stage C multivariate means, intermediate between stage A and stage B multivariate means, and least be-

tween stage B and stage C multivariate means (Table 5). For males, MANOVA indicates that all age stages differ significantly at the $P < 0.05$ level (Table 6), but the Mahalanobis D distances between age stage multivariate means show a different pattern than for females (Table 7). The distance between the stage A and stage C means is also the greatest, but the distance between the stage A and stage B means is the shortest, although this distance is similar to the distance between the stage B and stage C means.

Differences between sexes

Metric differences between sexes were considered between each age stage as well as between the composite adult female and adult male samples. The t -test was employed to test significance of differences. The composite adult sample showed significant differences ($P < 0.005$) be-

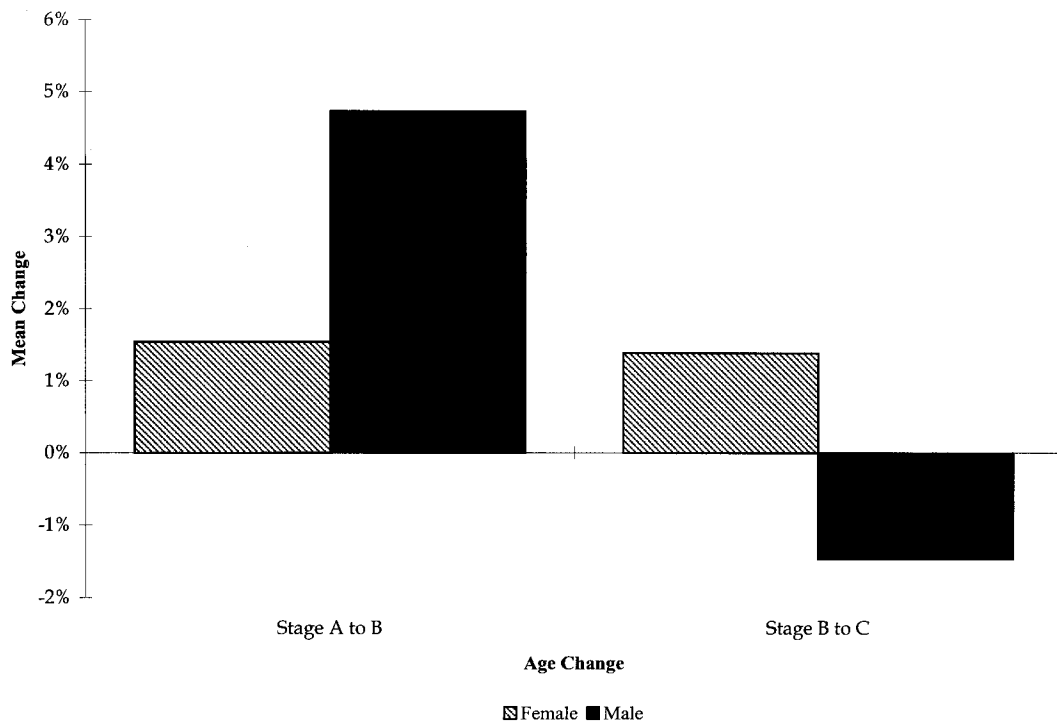


Fig. 3. Overall percentage change in mean value for cranial metrics between age stages in females and males.

TABLE 4. Differences between adult age stages in females (MANOVA)

Age stages	Hotelling-Lawley trace	df1	df2	Multivariate F	P value
A-B	0.727	4	29	5.268	0.0026
A-C	1.204	4	29	8.730	0.0001
B-C	0.385	4	29	2.790	0.0448

TABLE 5. Mahalanobis D distance between female age stages

	Age stage A	Age stage B	Age stage C
Age stage A			
Age stage B	4.484		
Age stage C	10.321	2.155	

tween females and males in every measure except nasal breadth (NASB, $P = 0.140$). For age stage A, though, there were several metrics that did not differ significantly between the sexes (Table 8). For age stage B, all measures again differed significantly. For age stage C, some metrics failed to differ significantly between the sexes (Table 9).

Suture closure

Nonmetric data on the state of ectocranial suture closure were gathered for the sample. The sutures examined were the coronal, sagittal, lambdoidal, parietosquamosal, zygomaticotemporal, zygomaticomaxillary, and intermaxillary. The ectocranial aspect of each suture was scored as either “open” (identical to the immature condition), “intermediate” (in between open and closed), “closed” (edges of suture physically bonded to each other), or “obliterated” (closed and its course obscured for the majority of its length). These stages are recognized to be somewhat subjective, but the entire sample was scored in the course of 2 days by one observer with frequent cross-checking to en-

TABLE 6. Differences between adult age stages in males (MANOVA)

Age stages	Hotelling-Lawley trace	df1	df2	Multivariate F	P value
A-B	0.560	4	21	2.942	0.0446
A-C	0.890	4	21	4.674	0.0074
B-C	0.772	4	21	4.050	0.0138

TABLE 7. Mahalanobis D distances between male age stages

	Age stage A	Age stage B	Age stage C
Age stage A			
Age stage B	3.082		
Age stage C	7.835	4.860	

TABLE 8. Nonsignificant differences between stage A females and males

Metric	P value
ENCV	0.1155
HEIG	0.0504
IBIB	0.0879
NASB	0.5215
OBIB	0.0674
ORBH	0.3719
PZYL	0.1134

TABLE 9. Nonsignificant differences between stage C females and males

Metric	P value
HEIG	0.4958
IBIB	0.0735
NASB	0.4351
NEHT	0.0935
ORBH	0.0960
UM1M	0.1913

sure internal consistency of scoring. The results are shown as means in Table 10. We recognize that means of discrete measures are of dubious biological meaning, but they convey the overall trend in a concise manner.

DISCUSSION

Sexual dimorphism

Previous studies, by using samples composed of individuals from different populations, implicitly assumed that sexual dimorphism does not vary between populations of *Alouatta palliata* (Ravosa and Ross, 1994; Miller, 1997; Masterson and Hartwig, 1998). Sexual dimorphism ratios (male mean/female mean) were used in these studies to assess the level of craniometric

sexual dimorphism in the various species of *Alouatta*. If cranial sexual dimorphism is uniform within a species, then these ratios should not vary notably between different samples of the same species.

Masterson and Hartwig (1998) examined the cranial sexual dimorphism in 13 New World monkey species (including *A. palliata*), using five of the measures also employed in our study. The BCI *A. palliata* sample's sexual dimorphism ratio does not group with the sample ratio in Masterson and Hartwig (1998) for any of those measures. Instead, it typically clusters with various *Cebus* and *Saimiri* species. In the rank order lists of 13 species in Masterson and Hartwig (1998), the BCI sample is anywhere from 1-4 places below (less dimorphic) than the *A. palliata* sample in Masterson and Hartwig (1998).

Ravosa and Ross (1994) examined the sexual dimorphism in *Alouatta palliata* and *Alouatta seniculus*, using 19 of the measures also employed in our study. In 6 of the 19 measures, the BCI *A. palliata* sample has a sexual dimorphism ratio closer to the *A. seniculus* sample than to the *A. palliata* sample in Ravosa and Ross (1994).

Miller (1997) compared sexual dimorphism ratios in all six recognized species of *Alouatta* (*belzebul*, *caraya*, *fusca*, *pigra*, *palliata*, and *seniculus*), using eight measures also utilized in our study. In seven of the measures, the BCI *A. palliata* ratio is closer to the ratio of another *Alouatta* species than it is to the *A. palliata* sample in Miller (1997). In the remaining measure, the BCI *A. palliata* ratio is equidistant from both Miller's *A. palliata* sample and two non-*palliata* species. The BCI *A. palliata* ratio grouped with each one of the non-*palliata* species in at least one metric, so the disparity between the BCI and *A. palliata* samples of Miller (1997) is not due to a tight correspondence between one of them and a single

TABLE 10. Suture closure mean values¹

Group	Coronal	Sagittal	Lambdoidal	Parieto-squamosal	Zygomatico-temporal	Zygomatico-maxillary	Intermaxillary
F (all stages)	3.67	3.36	3.34	3.58	1.64	3.33	3.01
F stage A	2.75	2.30	2.15	2.65	1.26	1.95	1.65
F stage B	3.92	3.58	3.59	3.81	1.54	3.64	3.25
F stage C	4.00	3.94	4.00	4.00	2.35	4.00	3.88
M (all stages)	3.31	2.82	2.67	3.25	1.36	2.47	2.35
M stage A	1.33	1.20	1.00	1.87	1.00	1.00	1.00
M stage B	3.82	3.18	2.90	3.53	1.27	2.55	2.47
M stage C	4.00	3.53	3.67	3.93	1.93	3.73	3.40
Total	3.52	3.13	3.05	3.44	1.52	2.96	2.73

¹ 1, open; 2, intermediate; 3, closed; 4, obliterated. We recognize that means of discrete measures are of dubious meaning, but they summarize these data concisely.

non-*palliata* species. The mean dimorphism ratio for all eight common metrics shows the BCI *A. palliata* sample (1.094) to be closer to Miller's *A. fusca* (1.093) and *A. pigra* (1.110) samples than to her *A. palliata* sample (1.135).

Sexual dimorphism ratios can also be calculated from the data of Schultz (1960) on a sample of 378 adult *A. palliata* skulls from five Central American countries (Costa Rica, Guatemala, Mexico, Nicaragua, and Panama). Nine of the metrics used by Schultz (1960) were also employed in the present study. For 6 of the 9 metrics, the sexual dimorphism ratio of the BCI *A. palliata* sample is closer to the ratio of one of Schultz's non-Panamanian samples than to the ratio of his Panamanian sample. Depending on the metric, different samples were closest to the BCI sample, so the disparity is not due to a close correspondence between the BCI sample and just one of Schultz's non-Panamanian samples.

One metric, lower skull length (LWSL), was used in both this study and all the above-mentioned studies (Schultz, 1960; Ravosa and Ross, 1994; Miller, 1997; Masterson and Hartwig, 1998). Various *A. palliata* samples of Schultz (1960) have ratios which match those of the *A. fusca* and *A. pigra* samples of Miller (1997), as does the *A. palliata* sample of Masterson and Hartwig (1998). The *A. seniculus* ratio of Ravosa and Ross (1994) is more similar to four of Schultz's *A. palliata* samples and Miller's *A. palliata*, *A. belzebul*, and *A. pigra* samples than it is to Miller's *A. seniculus* sample. The LWSL ratio for the BCI *A. palliata* sample is closest to that of a *Cebus capucinus* sample (Schultz, 1960).

Sexual dimorphism ratios of cranial metrics vary notably between populations and groups of *A. palliata*. Different composite samples of *A. palliata* have quite different sexual dimorphism ratios for the same cranial metrics. The sexual dimorphism ratios of the BCI *A. palliata* sample differ from those of *A. palliata* samples from different regions (Schultz, 1960), and from those of composite *A. palliata* samples (Ravosa and Ross, 1994; Miller, 1997; Masterson and Hartwig, 1998). This indicates that craniometric sexual dimorphism ratios vary between different populations of this species.

Age stage changes

In the BCI howler monkey sample, the female stage A means are significantly smaller than the female stage B means for three cranial measures. In turn, the female stage B means are significantly smaller than the female stage C means for five measures. The male stage A means are significantly smaller than the male stage B means for 21 cranial measures. In both sexes, the stage A means are often significantly smaller than the stage C means (7 measures in females, 12 in males). The multivariate results also reveal a similar pattern of differentiation between these age/sex groups, though such results are variably sensitive to both size and shape.

There is, then, cranial expansion between the three adult age stages in females and between the first two (A-B) in males. Therefore, it is possible that BCI howlers experience cranial growth past dental maturity, and/or selection for larger size. However, it is also possible that this expansion is due to other causes, such as a cohort effect, or to a

relationship between size and the *rate* of occlusal wear that confounds the relative aging method.

Different generations of howler monkeys likely experience at least somewhat different environments (Froehlich et al., 1981), so differences in food availability could lead to different mean sizes between generations. Theoretically, then, it is possible that the cranial expansion seen in the BCI skeletal sample is due to a cohort-based effect, with an older, larger generation being followed by a younger, smaller generation. This is only possible, though, if the sample contains just a few discrete cohorts. If many cohorts are represented, then each age stage is composed of individuals from a variety of different generations, precluding the "old large generation, young small generation" cohort effect hypothesized above. So the only way that a cohort-based effect could be responsible for the observed cranial expansion is if all (or almost all) of the stage C adults found were from one generation of howlers, whereas all stage B adults were from one other generation, and all the stage A adults from a third generation.

The chronological age range of individuals in the BCI skeletal sample is from roughly 3 years of age to over 15 years of age (DeGusta and Milton, 1998). The interbirth interval of *Alouatta palliata* is about 2 years (Milton, 1982), so even if the skulls were all collected in 1 year, at least six cohorts would be represented. However, the skulls were collected over a period of 10 years. Therefore, at least 30 cohorts (six every 2 years) are represented in the sample. This is a rough approximation, but the BCI sample is clearly composed of numerous cohorts, and so the observed expansion between age stages cannot be due to a cohort-based effect.

The adult age stages of the BCI sample are based on degree of occlusal wear. This assumes that, for an individual howler, its general degree of occlusal wear is proportional to its chronological age (more wear in older howlers). As discussed in Materials and Methods, this is a well-supported and widely employed assumption (Ubelaker, 1989; Walker et al., 1991). However, given the cranial expansion across age stages in

the BCI sample, it is necessary to consider whether the degree of wear might instead be a function of an individual's size, rather than age. In other words, would a large howler have more heavily worn teeth than a small howler of the same chronological age? If so, if larger howlers wear their teeth down faster than smaller howlers, then this would obviously create a correlation between size and "age" as assessed by degree of wear.

The general theory of tooth wear argues against this: larger individuals may generate greater forces in chewing, but they also have larger teeth which resist excessive wear better than smaller teeth (Benfer and Edwards, 1991). If this theory did not hold for the BCI sample, we would expect to see a ubiquitous pattern of increased size with increased wear. In males, though, there are no significant differences in cranial metrics between age stages B and C. So males with marked occlusal wear are not any larger than those with moderate wear. If larger howlers wear their teeth down faster, then the distribution of individuals across wear stages (age stages) should differ between the sexes: the larger males should have relatively more occlusally worn individuals (stage C) than the smaller females. This is not the case, as the distribution between wear stages is almost identical in males and females (Table 1). The expansion in cranial size across age stages seen in the BCI sample is therefore not due to a correlation between size and *rate* of occlusal wear.

We propose that the cranial expansion seen in the BCI howlers must then be due to either growth or selection. Accepting that suture closure is roughly, though not precisely, correlated with the end of significant cranial growth (Herring, 1974; Cohen, 1993), it is possible that at least a portion of the expansion seen in the BCI sample is due to growth. The suture closure data suggest that significant growth is physically possible only in age stage A, since most sutures are open at that stage but closed at stage B and obliterated by stage C. The zygomaticotemporal suture is the only suture observed that stays open in the later age stages, so the difference in zygomatic arch length (ZYAL) between female stages B and C could be due to growth. In general, then,

growth might explain the differences between age stages A and B–C in both sexes, but not the differences between stages B and C.

Since the BCI sample is composed of individuals found dead of natural causes, the expansion between age stages could be due to size-based selection rather than growth. If small individuals have a higher mortality rate than large individuals, they will (on average) die at a younger age than larger individuals. In this case, the younger age stage in the resulting skeletal sample would have more small individuals than large ones, whereas the older age stage would have more large individuals than small ones. Selection against small size would thus produce essentially the same pattern of craniometric expansion as would growth.

Dental metrics can differentiate growth from selection: teeth do not grow once they are fully formed (Hillson, 1986), and all crowns are completely formed well before the youngest adult age stage in this sample. Higher mortality for small individuals should produce a pattern of expansion in tooth size between age stages, assuming that tooth size is not independent of cranial size. Occlusal wear complicates the analysis, as it leads to the shrinkage of most dental metrics between age stages (Appendix D). However, the buccal-lingual dimension of the upper first molar (UM1B) was found to be unaffected by occlusal wear. This is based both on observation of the course of dental wear in the sample and an experimental “aging” of a molar with a dental drill (repeated measures of the same tooth revealed no change in UM1B from no wear to extreme wear). The high correlation of UM1B with most cranial measures indicates that this dental metric is representative of the general size of the skull.

The UM1B mean for stage A females is significantly smaller than the means for female stages B and C (Table 2). This indicates that the molar size (and, by correlation, cranial size) expansion seen in females between stages A and B–C is due to selection. The difference in mean UM1B between female stages B and C is significant using Fisher’s method ($P = 0.024$), but not with Bonferroni’s or Scheffé’s.

In males, the mean UM1B for stage A is not significantly different than that of stage B. This indicates that selection is not the cause of expansion between male stages A and B. The mean UM1B of male stage C is significantly larger than the mean for stages A and B, but no cranial metrics are significantly different between stages B and C.

For females, the expansion of tooth size across the three age stages and the closure of sutures in stage A–B indicates selection rather than growth. The cranial expansion of females throughout all three age stages can thus be attributed to a higher mortality rate among smaller individuals. For males, the lack of a significant increase in tooth size between age stages A and B, and the lack of suture closure in stage A, argues for growth rather than selection. The generally larger size of stage B males relative to stage A males can be attributed to growth in stage A, despite the dental maturity of those individuals.

The growth inferred in the adult male BCI skeletal sample is consistent with previous work on *Alouatta* development. Schultz (1960) noted some increase in the means of various cranial metrics in *A. palliata* between his adult 0 and adult 1 categories (broadly equivalent to our stages A and B). Froehlich et al. (1981) studied the body weights of living BCI howlers and concluded that expansion in body weight continued well past dental and sexual maturity. Ravosa and Ross (1994) found that male *A. palliata* continue growing after females have stopped. Data on postcranial element size, organ weights, and body part dimensions from a population of *Alouatta caraya* suggest that males might undergo growth after dental maturity (Lusted et al., 1966; Malinow et al., 1966). In a longitudinal study of adult *A. palliata* females, Zucker et al. (1998) found weight to increase with age in 7 of 8 individuals.

The pattern of expansion seen between the age stages of females and males affects the analysis of sexual dimorphism, since females are fully grown at age stage A, while males do not finish their growth until age stage B. That some measures do not differ significantly between the sexes at age stage

A is attributable to males not having completed their growth. The lack of significant differences between the sexes in some measures at age stage C is due to older females having undergone notable cranial size-based selection, while males of a similar age have not.

CONCLUSIONS

The level of cranial sexual dimorphism, at least as expressed by the commonly used sexual dimorphism ratio, is not uniform within *Alouatta palliata* due to variation between populations. Different composite samples of *A. palliata* (those which pool individuals from different populations) also differ notably in their levels of cranial sexual dimorphism. It is clearly inappropriate, then, to attribute differences in sexual dimorphism between *Alouatta* species to phylogeny (Miller, 1997; Masterson and Hartwig, 1998). Until the uniformity of sexual dimorphism within other primate species can be assessed, the validity of sexual dimorphism ratios derived from composite samples is unclear.

Cranial growth continues past dental maturity in male BCI *A. palliata*. Placing all dentally mature individuals into a single age category can thus introduce a bias in comparisons of different populations or taxa. If, for example, the craniometrics of different *Alouatta* species are compared (Ravosa and Ross, 1994; Miller, 1997; Masterson and Hartwig, 1998), differences in the adult male age structures of the samples (perhaps introduced by collection methods) could create artificial size differences between them or obscure real differences. Differing adult age structures may also explain some of the variation observed in sexual dimorphism ratios.

Female BCI howlers appear to be under selection for increased size, since there is evidence that females with smaller crania, on average, die at a younger age than females with larger crania. Cranial size in this sample is partially correlated with body weight, and other studies of *A. palliata* have found similar correlations (Ravosa and Ross, 1994). This suggests that the selection may be for greater overall body size, rather than just for larger heads.

While this sort of selection for larger body size (or cranial size) has not, to our knowledge, previously been suggested for female howler monkeys, it is readily accommodated by available information on howler diet and reproduction. Howlers are thought to experience periodic annual food stress when key species of young leaves and fruits are unavailable (Glander, 1980; Milton, 1980, 1982; Otis et al., 1981). Since lactating females require significantly more calories than nonlactating females, nursing mothers may experience difficulties in meeting their caloric requirements (Milton, 1980; Froehlich et al., 1981). Larger folivorous animals have greater gut capacities than smaller folivorous animals, and can process more food and extract more energy from the environment (Demment, 1983). Metabolic costs and caloric needs, however, scale as a fraction of body size (Kleiber, 1961; Martin, 1990). Smaller lactating females thus have disproportionately higher metabolic requirements for their gut capacity relative to larger lactating females, and must compensate for this by eating more food or a greater proportion of high-quality food (Demment, 1983). During times of food stress, larger females can more easily subsist on lower quality food (Demment, 1983) and, in *A. palliata*, can displace smaller females from high-quality food patches (Milton, 1982). The selection for larger size in adult females might thereby be driven by the energetic demands of pregnancy and lactation (cf. Ralls, 1976), coupled with periodic food stress. Further investigation of these possibilities is needed.

Alouatta palliata is generally less dimorphic than other *Alouatta* species, but *A. palliata* social groups have the highest ratio of adult females to adult males (Crockett, 1987). This is an exception to the general trend in primates, where the socioeconomic sex ratio is positively correlated with the level of sexual dimorphism (Clutton-Brock et al., 1977; Crockett, 1987). *Alouatta palliata* has one of the largest mean body weights among *Alouatta* and other platyrrhines (Hartwig, 1996; Milton, 1996), and so is also an exception to the usually tight correlation between absolute body weight and level of sexual dimorphism in body weight (Clutton-Brock

et al., 1977; Leutenegger and Cheverud, 1985). Based on the results from this study, it seems likely that the unexpectedly low level of sexual size dimorphism in *A. palliata* is due to larger females rather than smaller males. The selection for larger size in adult females would partially mask any dimorphism that might have been created via intramale competition or foraging niche separation (cf. Plavcan and van Schaik, 1997; Masterson and Hartwig, 1998). If selection for larger female size occurs in other primate taxa, it has the potential to confound attempts to correlate social structure with levels of sexual dimorphism (e.g., Kay et al., 1988; Leigh, 1995).

The variation in sexual dimorphism across samples of *A. palliata*, the size selection inferred for females, and the growth seen in dentally mature males also challenge the core assumptions underlying a substantial body of work on primate craniometrics. Elaborate theoretical classifications of ontogeny (e.g., heterochrony, hypermorphosis, paedomorphosis, and peramorphosis; Shea, 1983) have been applied to a wide range of primates based on craniometric studies which assume that skeletal growth ceases with dental maturity and that intraspecific variation is negligible (e.g., Shea, 1981, 1992; Ravosa, 1992, 1998). If the *A. palliata* pattern is present in other taxa, then these confounding factors may compromise such results. While considering the theoretical aspects of ontogeny and allometry understandably has great attraction, such findings are limited by the samples employed. As such, it is crucial to investigate whether the intraspecific variation and postdental-maturity growth documented here for *A. palliata* are also present in other primate taxa.

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APPENDIX A

Definitions of measures

BABR: Basicranial breadth. Greatest breadth of braincase measured between the

inferior midline of the external auditory meati.

BASL: Basal length. Basion to nasion.

BCAB: Bicanine breadth. Distance between the outer lateral surfaces of the canine alveolus at the septum between the canine and second premolar.

BCOB: Bicondylar breadth. Condylion laterale to condylion laterale.

BCRB: Bicornoid breadth. Coronion to coronion.

BCRL: Basicranial length. Basion to the posterior spine of the vomer.

BGOB: Bigonial breadth. Gonion to gonion (the point on the inferior border of the ascending ramus, where a line drawn from the most anterior point of the mandibular condyle to the inferior border of the ramus intersects the tangent of the body of the mandible at a right angle).

BPTB: Bipterygoid breadth. Distance between the outer lateral surfaces of the lateral pterygoid plates.

BRDT: Breadth. Greatest breadth of braincase perpendicular to midsagittal plane above the roots of the zygomatic arches on the temporal squamae or parietals.

BROH: Browridge height. The inner orbital midpoint perpendicular to the inferior surface of the superior orbital rim to the outer surface of the orbital rim.

BZYG: Bizygomatic breadth. Distance between the outer lateral surfaces of the zygomatic arches, measured at the inferior-most aspect of the temporozygomatic suture.

ENCV: Endocranial volume. Volume of the endocranial cavity (see Materials and Methods).

GCLT: Greatest cranial length. Opisthocranion (disregarding processes or crests) to prosthion.

HEIG: Height. Basion to vertex (disregarding possible sagittal crests).

IBIB: Inner biorbital breadth. Frontomolare orbitale to frontomolare orbitale.

LENG: Length. Nasion to opisthocranion (disregarding processes or crests).

LWSL: Lower skull length. Prosthion to basion.

MCOH: Mandibular corpus height. Height from the alveolus of the second molar, taken at the septum between the mesial

and distal roots, to the inferior border of the mandible.

MCOV: Mandibular corpus width. Buccolingual width of the mandible taken at the widest point on the perpendicular to MCOH.

NAPR: Nasion to prosthion height.

NASB: Nasal breadth. Width of the nasal aperture measured at the medial nasal protuberances.

NEHT: Neurocranial height. Basion to bregma.

OBIB: Outer biorbital breadth. Frontomolare temporale to frontomolare temporale.

ORBH: Orbital height. Greatest vertical distance between the inner aspect of the right superior and inferior orbital rims perpendicular to the outer biorbital breadth.

PALL: Palatine length. Prosthion to the midline point on a tangent between the most aboral (posterior) portions of the right and left alveolar processes.

PLAL: Pterygoid lever arm length. The inner inferior midline of the external auditory meatus to the junction of the sphenopterygoid suture and the medial pterygoid crest.

POCL: Postcanine length. Greatest straight distance from the septum between the right upper canine and second premolar to the distal border of the right upper third molar alveolus.

PZYL: Posterior zygomatic root length. The length of the posterior zygomatic root from the anterior midline of the external auditory meatus to the point at which the sphenozygomatic suture crosses the crest of the zygomatic root.

RAMH: Ramus height. Height of the mandibular ramus from the superior condylar surface to the gonion.

SYMH: Symphysis height. Infradentale to the inferior symphyseal border.

SYMW: Symphysis width. Labiolingual width of the symphysis measured from the infradentale to the most posterior point of the superior transverse torus.

UCBL: Upper canine buccal-lingual. Maximum buccal-lingual dimension of maxillary canine tooth.

UCMD: Upper canine mesial-distal. Maximum mesial-distal dimension of maxillary canine tooth.

UCM2: Upper canine to second molar. Distance between the mesial-most point of the maxillary canine alveoli to the middle distal edge of the second molar tooth.

UM1B: Upper first molar buccal-lingual. Buccal-lingual dimension of the maxillary first molar crown taken at the occlusal level at the mesial-distal midpoint.

UM1M: Upper first molar mesial-distal. Mesial-distal dimension of maxillary first molar crown taken at the occlusal level, in line with the buccal cusps.

UPPB: Upper palate breadth. Greatest breadth of the palate between the outer superior alveoli at the septa separating the first and second molars.

ZYAL: Zygomatic arch length. The anterior-most inner surface of the external auditory meatus to the anterior root of the zygomatic arch at the maxillozygomatic suture.

ZYAW: Zygomatic arch width. Width of the zygomatic arch at the inferior zygomaticotemporal suture.

APPENDIX B. Indices of precision for metrics (in mm)¹

Metric	Technical error of measurement	Mean absolute difference	Percentage error
BABR	0.282	0.329	0.78%
BASL	0.159	0.175	0.28%
BCAB	0.083	0.078	0.28%
BCOB	0.053	0.061	0.10%
BCRB	0.059	0.072	0.14%
BCRL	0.678	0.780	2.05%
BGOB	0.139	0.175	0.43%
BPTB	0.060	0.065	0.21%
BRDT	0.361	0.297	0.58%
BROH	0.114	0.132	5.00%
BZYP	0.277	0.284	0.38%
ENCV	0.567	0.500	0.93%
GCLT	0.660	0.673	0.65%
HEIG	1.037	0.796	2.05%
IBIB	0.845	0.523	1.03%
LENG	0.956	1.159	1.64%
LWSL	0.293	0.299	0.35%
MCOH	0.024	0.033	0.17%
MCOW	0.146	0.181	2.15%
NAPR	1.071	1.134	2.93%
NASB	0.282	0.302	2.63%
NEHT	1.128	1.101	2.53%
OBIB	1.097	0.938	1.73%
ORBH	0.359	0.387	1.66%
PALL	0.172	0.219	0.51%
PLAL	0.508	0.555	1.79%
POCL	0.182	0.179	0.54%
PZYL	0.632	0.547	2.53%
RAMH	0.329	0.386	0.66%
SYMH	0.061	0.071	0.24%
SYMW	0.548	0.647	2.28%
UCBL	0.082	0.086	1.58%
UCM2	0.238	0.176	0.52%
UCMD	0.205	0.207	3.01%
UM1B	0.125	0.126	1.70%
UM1M	0.198	0.215	3.17%
UPPB	0.135	0.133	0.35%
ZYAL	0.352	0.366	0.77%
ZYAW	0.096	0.095	3.59%

¹ See Utermohle et al. (1983) for definitions of indices.

APPENDIX C. Summary statistics for cranial metrics (in mm; ENCV in ml)

Metric	Group	Mean	S.D.	Median	Minimum	Maximum	Variance	Count
BABR	F (all stages)	40.54	1.36	40.62	37.51	44.71	1.85	92
	F stage A	40.21	1.55	40.04	37.57	44.71	2.41	21
	F stage B	40.61	1.32	40.71	37.51	43.36	1.74	54
	F stage C	40.76	1.25	40.97	38.16	43.21	1.56	17
	M (all stages)	44.68	1.87	44.73	39.16	48.82	3.50	70
	M stage A	43.60	1.50	43.54	40.68	46.18	2.25	16
	M stage B	45.30	1.52	45.22	41.37	48.82	2.31	38
	M stage C	44.28	2.40	44.73	39.16	47.26	5.75	16
	F (all stages)	60.99	1.68	61.02	56.51	65.67	2.81	89
BASL	F stage A	60.19	2.22	60.52	56.51	64.58	4.94	19
	F stage B	61.01	1.37	61.00	57.70	65.67	1.87	53
	F stage C	61.82	1.53	61.61	59.30	64.40	2.34	17
	M (all stages)	66.46	2.29	66.66	57.45	69.92	5.24	66
	M stage A	64.37	2.57	64.42	57.45	67.97	6.61	13
	M stage B	67.17	1.39	67.05	63.90	69.69	1.93	37
	M stage C	66.52	2.79	67.62	61.11	69.92	7.78	16
	F (all stages)	26.67	0.87	26.69	24.93	29.45	0.76	87
	BCAB	F stage A	26.27	1.03	26.12	24.93	29.19	1.06
F stage B		26.73	0.74	26.81	25.32	28.23	0.55	51
F stage C		26.95	0.94	26.70	25.51	29.45	0.88	17
M (all stages)		30.30	1.49	30.44	26.36	33.81	2.23	68
M stage A		29.43	1.19	29.30	26.99	31.47	1.43	16
M stage B		30.61	1.10	30.59	28.32	33.27	1.22	37
M stage C		30.44	2.21	31.10	26.36	33.81	4.86	15
F (all stages)		56.97	2.06	57.02	52.27	61.22	4.24	65
BCOB		F stage A	55.78	2.02	55.77	52.27	58.77	4.08
	F stage B	56.91	1.95	56.71	53.72	60.69	3.80	40
	F stage C	58.28	1.79	58.01	54.61	61.22	3.21	13
	M (all stages)	61.76	2.61	61.66	56.24	66.58	6.79	54
	M stage A	59.14	2.35	59.33	56.24	63.61	5.52	11
	M stage B	62.61	2.10	62.37	58.74	66.54	4.41	30
	M stage C	62.00	2.56	61.61	57.37	66.58	6.58	13
	F (all stages)	51.10	1.80	51.19	47.09	55.37	3.23	63
	BCRB	F stage A	50.27	1.63	49.57	48.20	53.61	2.66
F stage B		51.31	1.94	51.40	47.09	55.37	3.75	36
F stage C		51.44	1.35	51.69	48.43	53.13	1.82	13
M (all stages)		55.96	2.04	55.95	51.19	59.59	4.17	52
M stage A		53.85	1.85	53.67	51.19	56.91	3.41	10
M stage B		56.42	1.29	56.26	52.27	59.27	1.67	30
M stage C		56.58	2.67	57.14	52.29	59.59	7.10	12
F (all stages)		36.16	1.73	36.04	32.56	39.84	2.98	86
BCRL		F stage A	35.57	1.77	35.54	32.69	39.84	3.13
	F stage B	36.30	1.72	36.23	32.56	39.68	2.97	51
	F stage C	36.34	1.65	35.94	34.05	39.20	2.72	17
	M (all stages)	39.90	1.81	40.11	34.54	43.13	3.26	67
	M stage A	38.62	1.87	38.68	34.54	41.46	3.51	14
	M stage B	40.33	1.55	40.47	37.56	43.13	2.40	37
	M stage C	40.03	1.88	40.82	36.28	42.36	3.55	16
	F (all stages)	39.42	3.31	38.98	32.10	46.86	10.93	55
	BGOB	F stage A	37.55	2.65	38.36	33.90	41.61	7.01
F stage B		39.90	3.69	39.05	32.10	46.86	13.63	29
F stage C		40.22	2.31	40.02	37.16	46.07	5.33	13
M (all stages)		44.58	4.41	44.82	36.10	53.49	19.47	44
M stage A		41.04	3.51	41.22	36.10	45.13	12.33	10
M stage B		46.36	3.97	46.98	39.37	53.49	15.72	25
M stage C		43.59	4.11	43.75	38.30	49.12	16.92	9
F (all stages)		28.28	1.66	28.16	25.04	34.00	2.74	68
BPTB		F stage A	28.09	1.54	28.37	25.04	30.47	2.38
	F stage B	28.43	1.79	28.00	26.00	34.00	3.20	41
	F stage C	28.03	1.36	28.17	25.30	30.26	1.86	13
	M (all stages)	32.76	2.83	32.28	26.23	40.36	7.98	59
	M stage A	32.99	2.78	32.02	28.49	38.12	7.74	13
	M stage B	33.35	2.62	33.00	28.47	40.36	6.87	32
	M stage C	31.22	2.94	31.25	26.23	36.04	8.65	14
	F (all stages)	50.58	1.28	50.43	47.28	53.95	1.63	91
	BRDT	F stage A	50.57	1.27	50.31	48.45	53.95	1.61
F stage B		50.33	1.25	50.21	47.28	53.75	1.56	53
F stage C		51.34	1.13	51.29	49.07	53.63	1.29	17

(Continued)

APPENDIX C. (Continued)

Metric	Group	Mean	S.D.	Median	Minimum	Maximum	Variance	Count
BROH	M (all stages)	52.31	1.41	52.36	48.75	55.42	1.97	70
	M stage A	51.66	1.49	52.04	48.75	54.45	2.21	16
	M stage B	52.58	1.29	52.55	50.31	55.42	1.67	38
	M stage C	52.34	1.45	52.60	50.16	54.52	2.11	16
	F (all stages)	2.33	0.44	2.38	1.37	3.38	0.19	89
	F stage A	2.16	0.38	2.05	1.56	2.92	0.14	21
	F stage B	2.35	0.48	2.38	1.37	3.38	0.23	51
	F stage C	2.48	0.31	2.44	1.75	3.12	0.10	17
	M (all stages)	3.09	0.58	3.14	1.77	4.19	0.34	70
	M stage A	2.77	0.60	2.71	1.83	3.96	0.36	16
	M stage B	3.24	0.49	3.22	2.13	4.19	0.24	38
	M stage C	3.07	0.66	3.08	1.77	3.99	0.44	16
BZYB	F (all stages)	70.66	2.23	70.71	63.32	74.67	4.95	79
	F stage A	68.55	2.57	68.84	63.32	72.41	6.58	18
	F stage B	71.03	1.79	70.77	67.44	74.67	3.19	44
	F stage C	71.92	1.23	71.95	70.24	73.88	1.51	17
	M (all stages)	79.61	3.84	80.07	67.09	86.85	14.73	62
	M stage A	76.71	4.57	77.38	67.09	85.18	20.85	15
	M stage B	81.04	1.69	81.35	77.03	83.36	2.86	34
	M stage C	79.22	5.12	79.85	70.02	86.85	26.17	13
	F (all stages)	52.77	3.27	53.00	46.00	65.00	10.71	87
	F stage A	52.85	3.07	52.00	49.00	60.00	9.40	20
	F stage B	52.34	3.22	52.00	46.00	59.00	10.39	50
	F stage C	53.94	3.54	53.00	50.00	65.00	12.56	17
ENCV	M (all stages)	56.21	3.18	56.00	50.00	63.00	10.14	67
	M stage A	54.50	2.71	55.00	50.00	58.00	7.35	14
	M stage B	56.54	2.94	56.00	52.00	63.00	8.64	37
	M stage C	56.94	3.73	57.00	50.00	63.00	13.93	16
	F (all stages)	100.80	2.78	100.90	92.31	106.97	7.73	86
	F stage A	100.43	2.67	99.75	95.41	106.00	7.13	19
	F stage B	100.45	2.79	100.91	92.31	106.06	7.76	51
	F stage C	102.36	2.49	102.19	97.67	106.97	6.18	16
	M (all stages)	108.95	3.37	109.33	97.46	115.29	11.39	64
	M stage A	105.95	3.27	106.16	97.46	111.43	10.71	14
	M stage B	109.76	2.15	110.03	105.23	113.58	4.64	35
	M stage C	109.85	4.31	110.85	100.61	115.29	18.56	15
GCLT	F (all stages)	38.29	1.23	38.18	35.54	41.26	1.52	90
	F stage A	38.17	1.25	38.03	36.44	41.20	1.57	20
	F stage B	38.14	1.17	38.05	35.54	41.23	1.38	53
	F stage C	38.88	1.30	38.74	36.98	41.26	1.68	17
	M (all stages)	39.19	1.28	39.09	36.71	42.44	1.63	67
	M stage A	39.08	1.32	39.10	36.71	41.68	1.74	14
	M stage B	39.21	1.12	39.09	37.23	41.72	1.26	37
	M stage C	39.23	1.63	39.02	36.83	42.44	2.65	16
	F (all stages)	51.04	1.88	51.06	47.31	55.34	3.55	89
	F stage A	49.45	1.42	49.40	47.31	52.56	2.01	21
	F stage B	51.08	1.59	51.09	47.41	54.91	2.54	51
	F stage C	52.85	1.51	52.80	49.94	55.34	2.27	17
IBIB	M (all stages)	52.51	2.18	52.43	46.73	58.08	4.74	68
	M stage A	50.46	2.08	50.66	46.73	53.79	4.31	16
	M stage B	52.77	1.51	52.56	50.14	56.75	2.29	37
	M stage C	54.06	2.16	53.73	51.42	58.08	4.65	15
	F (all stages)	70.04	2.24	69.94	63.19	76.12	5.04	88
	F stage A	69.91	2.28	69.47	66.56	74.22	5.18	19
	F stage B	69.63	2.14	69.80	63.19	74.74	4.56	52
	F stage C	71.46	2.07	71.12	68.14	76.12	4.29	17
	M (all stages)	73.76	2.16	73.91	68.37	77.83	4.67	67
	M stage A	71.88	2.35	72.07	68.37	76.49	5.54	13
	M stage B	74.16	1.73	74.20	70.43	77.73	2.97	38
	M stage C	74.36	2.23	74.64	70.84	77.83	4.95	16
LENG	F (all stages)	82.51	2.39	82.69	75.88	87.37	5.73	87
	F stage A	81.39	3.09	82.25	75.88	87.37	9.57	19
	F stage B	82.72	2.04	82.88	76.63	86.87	4.14	52
	F stage C	83.15	2.26	83.28	79.83	87.16	5.11	16
	M (all stages)	92.25	3.47	92.71	77.69	97.44	12.04	63
	M stage A	89.08	3.67	89.78	77.69	92.45	13.49	14
	M stage B	93.43	1.78	93.56	90.50	97.44	3.16	34
	M stage C	92.54	4.46	93.31	82.31	97.38	19.88	15

(Continued)

APPENDIX C. (Continued)

Metric	Group	Mean	S.D.	Median	Minimum	Maximum	Variance	Count
MCOH	F (all stages)	20.21	1.15	20.18	17.17	22.46	1.32	74
	F stage A	19.96	1.28	19.55	18.44	22.30	1.65	16
	F stage B	20.14	1.10	20.15	17.17	22.42	1.20	44
	F stage C	20.71	1.10	20.76	19.01	22.46	1.21	14
	M (all stages)	23.02	1.58	23.34	19.24	25.40	2.48	57
	M stage A	21.20	1.24	21.05	19.24	23.50	1.54	12
	M stage B	23.60	0.99	23.71	21.38	25.19	0.97	31
	M stage C	23.31	1.79	23.95	20.06	25.40	3.20	14
	MCOW	F (all stages)	7.18	0.59	7.15	5.98	8.97	0.34
F stage A		6.99	0.47	7.05	6.28	7.82	0.22	15
F stage B		7.21	0.53	7.20	6.09	8.97	0.28	44
F stage C		7.27	0.82	7.21	5.98	8.64	0.67	14
M (all stages)		8.68	0.62	8.58	7.35	10.31	0.39	57
M stage A		8.56	0.47	8.49	7.91	9.62	0.22	12
M stage B		8.74	0.61	8.60	7.71	10.31	0.37	31
M stage C		8.64	0.79	8.58	7.35	10.15	0.63	14
NAPR		F (all stages)	37.59	1.63	37.53	33.36	41.80	2.64
	F stage A	37.24	1.81	37.19	33.36	39.70	3.27	20
	F stage B	37.82	1.62	37.67	34.42	41.80	2.64	52
	F stage C	37.29	1.33	37.48	34.65	39.17	1.76	16
	M (all stages)	41.47	2.32	41.61	34.78	45.79	5.37	65
	M stage A	39.64	1.93	39.83	34.78	42.41	3.72	15
	M stage B	41.80	2.05	42.09	37.17	45.54	4.20	35
	M stage C	42.55	2.35	43.01	35.84	45.79	5.54	15
	NASB	F (all stages)	11.16	0.88	11.26	9.13	13.24	0.77
F stage A		11.33	0.99	11.26	9.74	13.24	0.98	11
F stage B		11.11	0.79	11.16	9.21	12.49	0.63	43
F stage C		11.18	1.05	11.71	9.13	12.27	1.10	15
M (all stages)		11.39	0.87	11.36	9.39	13.92	0.75	58
M stage A		11.62	1.19	11.68	9.39	13.92	1.41	13
M stage B		11.48	0.69	11.33	10.51	13.21	0.47	33
M stage C		10.89	0.79	10.97	9.39	12.04	0.62	12
NEHT		F (all stages)	43.23	1.42	43.27	39.55	46.62	2.00
	F stage A	43.26	1.36	43.19	40.86	46.62	1.84	20
	F stage B	43.10	1.26	43.22	39.55	45.74	1.59	53
	F stage C	43.60	1.89	43.49	39.75	46.24	3.58	17
	M (all stages)	44.50	1.58	44.57	39.69	49.36	2.49	66
	M stage A	44.27	1.30	44.41	41.75	46.69	1.68	14
	M stage B	44.50	1.62	44.66	39.69	49.36	2.62	36
	M stage C	44.70	1.77	44.81	41.77	47.84	3.14	16
	OBIB	F (all stages)	54.13	2.31	53.71	47.86	59.33	5.36
F stage A		52.14	1.80	52.40	47.86	55.47	3.23	21
F stage B		54.13	1.88	53.71	49.67	58.02	3.53	51
F stage C		56.57	1.68	56.72	52.48	59.33	2.84	17
M (all stages)		56.77	3.34	56.51	47.81	64.48	11.17	68
M stage A		53.56	2.79	53.76	47.81	57.64	7.80	16
M stage B		57.36	2.76	56.78	53.00	64.48	7.62	37
M stage C		58.72	2.95	58.73	54.29	64.21	8.73	15
ORBH		F (all stages)	22.77	0.94	22.68	20.29	25.05	0.89
	F stage A	22.50	0.92	22.32	20.93	25.05	0.85	21
	F stage B	22.85	0.98	22.76	20.29	24.88	0.96	52
	F stage C	22.84	0.85	22.83	21.21	24.09	0.72	17
	M (all stages)	23.25	1.11	23.31	20.95	26.26	1.22	70
	M stage A	22.81	0.96	23.04	21.19	24.17	0.92	16
	M stage B	23.36	1.15	23.39	20.95	26.26	1.33	38
	M stage C	23.42	1.08	23.49	21.32	25.23	1.17	16
	PALL	F (all stages)	41.25	1.16	41.32	39.14	44.40	1.34
F stage A		41.20	1.21	41.28	39.55	44.30	1.46	19
F stage B		41.36	1.10	41.50	39.14	44.10	1.21	51
F stage C		40.99	1.31	40.59	39.19	44.40	1.70	16
M (all stages)		44.78	1.60	44.81	37.99	48.51	2.55	64
M stage A		43.94	1.96	44.17	37.99	45.88	3.82	14
M stage B		45.03	1.24	44.95	42.40	48.51	1.53	34
M stage C		44.99	1.79	45.12	41.74	47.49	3.20	16
PLAL		F (all stages)	30.12	1.26	30.21	27.00	33.14	1.58
	F stage A	29.84	1.13	30.02	27.50	31.80	1.27	20
	F stage B	30.15	1.33	30.24	27.00	33.14	1.76	51
	F stage C	30.34	1.19	30.25	28.96	32.37	1.41	17

(Continued)

APPENDIX C. (Continued)

Metric	Group	Mean	S.D.	Median	Minimum	Maximum	Variance	Count
	M (all stages)	33.60	1.93	33.98	28.81	37.95	3.71	70
	M stage A	31.61	1.92	31.36	28.81	34.32	3.70	16
	M stage B	34.36	1.28	34.36	31.25	37.95	1.63	38
	M stage C	33.81	1.91	33.66	31.06	37.77	3.63	16
POCL	F (all stages)	32.08	0.96	31.92	30.07	34.07	0.92	89
	F stage A	32.05	0.83	32.10	30.56	33.61	0.69	20
	F stage B	32.06	0.94	32.00	30.32	34.02	0.89	52
	F stage C	32.19	1.17	31.85	30.07	34.07	1.37	17
	M (all stages)	34.00	1.14	33.95	30.80	37.44	1.31	66
	M stage A	33.23	1.12	33.40	30.80	34.86	1.25	15
	M stage B	34.24	0.86	34.10	32.53	36.16	0.73	36
	M stage C	34.21	1.47	34.19	31.99	37.44	2.17	15
PZYL	F (all stages)	21.07	1.18	21.20	18.32	24.69	1.40	91
	F stage A	20.99	1.09	21.20	19.10	23.39	1.19	21
	F stage B	20.97	1.15	21.07	18.32	23.16	1.31	53
	F stage C	21.49	1.38	21.25	19.73	24.69	1.90	17
	M (all stages)	22.56	1.41	22.56	19.05	25.64	1.99	70
	M stage A	21.62	1.28	21.80	19.05	24.40	1.64	16
	M stage B	22.90	1.26	22.84	19.88	25.19	1.59	38
	M stage C	22.72	1.52	22.22	20.75	25.64	2.32	16
RAMH	F (all stages)	57.53	3.64	58.14	49.03	66.20	13.23	67
	F stage A	56.50	4.31	57.26	50.24	66.20	18.57	13
	F stage B	57.35	3.76	57.66	49.03	64.28	14.11	40
	F stage C	58.99	2.06	58.48	56.09	64.54	4.24	14
	M (all stages)	68.07	5.64	69.81	49.48	74.43	31.85	50
	M stage A	64.13	7.35	67.07	49.48	73.54	53.96	11
	M stage B	70.11	2.45	70.27	64.96	74.43	6.00	27
	M stage C	67.12	7.21	69.42	53.92	73.66	51.93	12
SYMH	F (all stages)	28.25	1.43	28.30	23.97	31.86	2.05	71
	F stage A	27.93	1.57	28.32	23.97	30.21	2.47	15
	F stage B	28.16	1.19	28.19	25.44	30.47	1.42	42
	F stage C	28.84	1.84	28.49	25.90	31.86	3.37	14
	M (all stages)	31.56	1.92	31.57	27.06	36.89	3.68	50
	M stage A	30.57	0.92	30.65	29.20	32.03	0.85	12
	M stage B	32.06	1.77	32.25	28.65	36.89	3.12	29
	M stage C	31.27	2.82	31.94	27.06	36.26	7.95	9
SYMW	F (all stages)	26.86	1.39	26.88	22.64	30.57	1.92	71
	F stage A	26.49	1.42	26.56	22.64	28.48	2.02	15
	F stage B	26.76	1.35	26.81	23.88	29.89	1.82	42
	F stage C	27.54	1.33	27.52	25.51	30.57	1.76	14
	M (all stages)	30.47	1.82	30.59	26.80	35.99	3.31	50
	M stage A	29.91	1.22	30.08	27.85	31.86	1.48	12
	M stage B	30.89	1.68	30.98	27.84	35.99	2.83	29
	M stage C	29.86	2.60	29.97	26.80	34.56	6.78	9
UPPB	F (all stages)	36.54	1.00	36.60	34.13	39.11	0.99	87
	F stage A	36.25	1.20	36.28	34.40	39.11	1.44	19
	F stage B	36.52	0.93	36.60	34.13	38.43	0.86	51
	F stage C	36.92	0.88	37.08	35.16	38.87	0.77	17
	M (all stages)	39.38	1.26	39.49	36.00	42.24	1.58	66
	M stage A	39.01	1.23	39.41	36.00	40.67	1.52	16
	M stage B	39.64	1.02	39.57	37.23	41.70	1.03	37
	M stage C	39.12	1.77	39.50	36.11	42.24	3.14	13
ZYAL	F (all stages)	45.58	1.53	45.55	41.61	48.76	2.34	91
	F stage A	44.89	1.66	44.43	42.10	47.47	2.74	21
	F stage B	45.49	1.38	45.37	41.61	48.46	1.91	53
	F stage C	46.69	1.26	46.48	43.46	48.76	1.60	17
	M (all stages)	51.19	2.23	51.49	43.40	55.22	4.98	69
	M stage A	49.55	2.29	50.19	43.40	52.83	5.23	16
	M stage B	51.98	1.23	52.00	49.60	55.13	1.51	37
	M stage C	50.99	3.04	51.65	45.66	55.22	9.26	16
ZYAW	F (all stages)	2.19	0.30	2.16	1.52	2.95	0.09	84
	F stage A	2.14	0.33	2.13	1.52	2.67	0.11	18
	F stage B	2.22	0.30	2.20	1.70	2.95	0.09	49
	F stage C	2.15	0.24	2.15	1.59	2.59	0.06	17
	M (all stages)	2.90	0.43	2.93	2.04	3.75	0.19	68
	M stage A	2.89	0.42	2.96	2.27	3.73	0.18	15
	M stage B	2.98	0.40	2.96	2.11	3.75	0.16	37
	M stage C	2.72	0.49	2.63	2.04	3.64	0.24	16

APPENDIX D. Summary statistics for dental metrics (in mm)

Metric	Group	Mean	S.D.	Median	Minimum	Maximum	Variance	Count
UCBL	F (all stages)	4.73	0.33	4.68	4.01	5.80	0.11	76
	F stage A	4.78	0.31	4.75	4.30	5.55	0.10	16
	F stage B	4.75	0.36	4.69	4.01	5.80	0.13	45
	F stage C	4.61	0.19	4.59	4.38	5.00	0.04	15
	M (all stages)	6.26	0.63	6.23	4.73	8.60	0.39	50
	M stage A	6.07	0.41	6.14	5.39	6.66	0.17	11
	M stage B	6.41	0.64	6.25	5.46	8.60	0.40	28
	M stage C	6.05	0.72	6.10	4.73	7.05	0.52	11
	UCMD	F (all stages)	6.05	0.35	6.00	5.39	7.20	0.12
F stage A		6.02	0.34	5.96	5.53	6.85	0.11	16
F stage B		6.13	0.36	6.04	5.50	7.20	0.13	45
F stage C		5.84	0.28	5.85	5.39	6.35	0.08	15
M (all stages)		8.03	0.74	8.12	5.73	9.55	0.54	50
M stage A		8.25	0.50	8.23	7.64	9.18	0.25	11
M stage B		7.94	0.68	8.12	5.73	8.80	0.47	28
M stage C		8.07	1.03	8.06	6.40	9.55	1.07	11
UCM2		F (all stages)	32.81	0.76	32.80	31.19	35.25	0.58
	F stage A	32.98	0.85	33.02	31.74	35.25	0.73	19
	F stage B	32.87	0.69	32.99	31.30	34.35	0.48	51
	F stage C	32.44	0.79	32.30	31.19	34.54	0.62	17
	M (all stages)	35.91	1.23	35.89	32.71	39.91	1.51	65
	M stage A	35.97	1.20	36.02	33.29	38.22	1.43	14
	M stage B	36.13	0.93	36.02	33.10	38.41	0.86	37
	M stage C	35.24	1.73	35.10	32.71	39.91	2.99	14
	UM1B	F (all stages)	7.32	0.37	7.31	6.50	8.28	0.14
F stage A		7.04	0.33	7.04	6.50	7.65	0.11	20
F stage B		7.34	0.32	7.34	6.60	7.90	0.10	52
F stage C		7.56	0.36	7.51	6.82	8.28	0.13	17
M (all stages)		7.77	0.41	7.74	7.00	9.28	0.17	67
M stage A		7.61	0.30	7.60	7.08	8.08	0.09	15
M stage B		7.72	0.39	7.68	7.00	8.73	0.15	38
M stage C		8.07	0.45	7.89	7.65	9.28	0.21	14
UM1M		F (all stages)	6.73	0.33	6.75	5.55	7.47	0.11
	F stage A	6.79	0.26	6.75	6.41	7.33	0.07	20
	F stage B	6.75	0.26	6.75	5.99	7.47	0.07	52
	F stage C	6.60	0.51	6.55	5.55	7.47	0.26	17
	M (all stages)	7.03	0.34	7.06	6.20	7.76	0.12	67
	M stage A	7.12	0.27	7.14	6.56	7.62	0.08	15
	M stage B	7.08	0.31	7.09	6.40	7.76	0.09	38
	M stage C	6.83	0.43	6.80	6.20	7.43	0.18	14

APPENDIX E. Correlations of >0.8 between craniometric measures¹

Metrics	Correlation	Z-value	95% lower	95% upper
BABR-BZYB	0.836	14.17	0.778	0.879
BABR-GCLT	0.827	14.30	0.769	0.872
BABR-LWSL	0.824	14.19	0.765	0.870
BABR-ZYAL	0.803	13.87	0.740	0.852
BASL-BABR	0.809	13.84	0.746	0.857
BASL-BCAB	0.859	15.60	0.811	0.896
BASL-BCRB	0.828	12.22	0.758	0.879
BASL-BCRL	0.864	15.96	0.817	0.899
BASL-BZYB	0.879	15.82	0.834	0.912
BASL-GCLT	0.878	16.46	0.835	0.910
BASL-LWSL	0.952	22.44	0.935	0.965
BASL-MCOH	0.812	12.46	0.742	0.864
BASL-PALL	0.803	13.28	0.737	0.854
BASL-PLAL	0.862	15.87	0.814	0.898
BASL-RAMH	0.814	11.90	0.741	0.869
BASL-ZYAL	0.917	19.28	0.887	0.939
BCAB-BZYB	0.851	14.68	0.797	0.891
BCAB-GCLT	0.834	14.36	0.777	0.877
BCAB-LWSL	0.901	17.66	0.865	0.928
BCAB-PALL	0.865	15.69	0.817	0.901
BCAB-RAMH	0.824	12.21	0.754	0.876
BCAB-UPPB	0.863	15.81	0.815	0.899
BCAB-ZYAL	0.861	16.01	0.814	0.897
BCOB-BCRB	0.813	11.85	0.738	0.867
BCOB-BZYB	0.836	12.37	0.768	0.885
BCRB-BZYB	0.889	14.31	0.841	0.923
BCRB-LWSL	0.860	13.21	0.802	0.903
BCRB-ZYAL	0.842	12.77	0.778	0.889
BCRL-LWSL	0.859	15.47	0.809	0.896
BCRL-ZYAL	0.808	13.67	0.744	0.857
BZYB-GCLT	0.841	13.90	0.782	0.884
BZYB-LWSL	0.902	16.86	0.865	0.930
BZYB-MCOH	0.804	11.69	0.728	0.861
BZYB-PLAL	0.826	13.82	0.766	0.872
BZYB-RAMH	0.871	13.62	0.816	0.910
BZYB-UPPB	0.837	14.00	0.778	0.881
BZYB-ZAYL	0.914	18.21	0.882	0.937
GCLT-LENG	0.874	16.33	0.830	0.908
GCLT-LWSL	0.921	19.30	0.893	0.942
GCLT-MCOH	0.821	12.59	0.753	0.872
GCLT-NAPR	0.818	13.89	0.756	0.865
GCLT-PALL	0.847	14.89	0.794	0.887
GCLT-PLAL	0.832	14.34	0.775	0.876
GCLT-RAMH	0.812	11.66	0.736	0.867
GCLT-ZYAL	0.884	16.91	0.843	0.915
IBIB-OBIB	0.912	19.12	0.881	0.935
LWSL-MCOH	0.821	12.60	0.753	0.872
LWSL-NAPR	0.829	14.30	0.770	0.873
LWSL-PALL	0.901	17.68	0.865	0.928
LWSL-PLAL	0.861	15.56	0.812	0.898
LWSL-RAMH	0.854	13.09	0.794	0.898
LWSL-SYMH	0.807	11.73	0.731	0.863
LWSL-SYMW	0.836	12.65	0.770	0.884
LWSL-UPPB	0.826	14.00	0.766	0.872
LWSL-ZYAL	0.946	21.71	0.926	0.961
MCOH-RAMH	0.853	13.55	0.795	0.896
MCOH-ZYAL	0.801	12.28	0.729	0.856
MCOW-UPPB	0.807	12.15	0.734	0.861
PALL-POCL	0.828	14.27	0.769	0.872
PALL-SYMW	0.801	11.44	0.722	0.859
PALL-ZYAL	0.809	13.63	0.745	0.858
PLAL-ZYAL	0.884	17.28	0.844	0.914
RAMH-ZYAL	0.840	12.86	0.776	0.887
SYMH-SYMW	0.900	15.96	0.859	0.929
SYMW-ZYAL	0.801	11.75	0.724	0.858
UPPB-ZYAL	0.809	13.78	0.747	0.858

¹ All P values < 0.0001.