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Molar Size and Shape in the Estimation of Biological Ancestry: A Comparison of Relative Cusp Location Using Geometric Morphometrics and Interlandmark Distances

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ABSTRACT Human molars exhibit varying shapes when viewed from the occlusal surface. Available methods for quantifying molar occlusal shape have historically been confined to qualitative descriptions. The present study utilized geometric morphometric analyses to capture molar shape as defined through relative cusp locations. Cusp apices of maxillary and mandibular first and second molars were digitized from 190 American Blacks and Whites to estimate biological affinity through the shape of relative cusp locations. The coordinate data were subjected to a Generalized Procrustes Analysis to generate Procrustes coordinates and calculate centroid sizes. Procrustes coordinates were then subjected to a principal component analysis to examine the direction and magnitude of shape change inherent in the sample. Centroid size and major shape component group means were compared with *t*-tests. Interlandmark distances were then calculated from the raw coordinate information and also subjected to a principal components analysis. Procrustes coordinates and the principal components derived from them with and without centroid size, along with the interlandmark distances and the principal components derived from them, were each subjected to a discriminant function analysis to examine which methods yielded the highest correct classification between population groups. Total correct classifications ranged from 62.7% to 87.9% depending on the variables forward stepwise selected for each analysis. Using a combination of the second maxillary molar and first mandibular molar yielded the most optimistic results and corroborates theoretical models of molar development. Am J Phys Anthropol 153:269–279, 2014.

Forensic anthropologists are commonly employed to establish a biological profile (age, sex, stature, population affinity, etc.) for an unknown set of remains to aid in the identification process by narrowing down a missing persons list. Given the Daubert rulings (Daubert v. Merrell Dow Pharmaceuticals, Inc., 1993), many traditional analyses for biological profile estimation have been improved to include newer techniques, known error rates, and better classification rates. Due to the Daubert rulings, new methods are continuously being developed and refined to aid in the identification process. Often the methodological improvements made in forensic anthropology are applied within the other subdisciplines of physical anthropology. While not limited by the Daubert rulings in a legal sense, accurate assessments of ancestry are equally important in bioarchaeology for demographic analyses. Teeth, and specifically molars, are well suited for ancestry estimation because of their high genetic component, i.e., low environmental impact aside from natural wear, and their general robusticity (Turner, 1984; Harris and Rathbun, 1989; Lukacs and Hemphill, 1993; Irish, 1997, 1998, 2005; Bailey, 2004; Bailey et al., 2008). Furthermore, given that enamel is the strongest material produced by the body, teeth are often better preserved than skeletal elements in both forensic and bioarchaeological contexts.

Bookstein (1982) first defined morphometrics as the integration of geometry and biology. Specifically, the geometric properties of any form must be represented by the location of homologous landmarks in either two or three dimensions using Cartesian coordinates. The use of biological homologies allows for the direct comparison of two or more different forms. Today, geometric morphometrics (GMM) have become "the study of shape variation and its covariation with other variables" (Adams et al., 2004). The most commonly employed methods in geometric morphometrics in physical and forensic

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anthropology are based on a Generalized Procrustes Analysis (GPA).

A GPA is a scaling technique used to take landmark coordinate information from a series of different specimens and derive a consensus, or mean, shape from all of the information in the study sample. While data from specimens are collected in an arbitrary coordinate system, GPA scales, translates, and rotates each of the specimens based on centroid size and location, thereby making them comparable. Size is removed by scaling all specimens to the same centroid size. Lastly, a partial least squares algorithm minimizes the differences between landmark sets. After the GPA, the coordinates are considered "size-free" Procrustes coordinates (ProCoord). A mean can then be generated from each of the specimens' ProCoords for each landmark. Thus, through the generation of each landmark mean, a consensus shape is derived. The deviations from the mean shape can be quantified for each specimen and the direction of shape changes can be measured, visualized, and further refined through principal components analysis (PCA) to generate principal component (PC) scores that reflect overall shape changes. Due to the removal of size in GPA, many researchers are applying these methodologies to investigate size-free shape changes within and between populations (cf. Rosas and Bastir, 2002; Lockwood et al., 2004; Harvati and Weaver, 2006; Perez and Monterio, 2009; Weisensee and Jantz, 2011). However, the same GMM techniques applied ubiquitously to the cranium have not been as routinely employed with the dentition.

During the 1980s a pseudogeometric morphometric technique known as occlusal polygons was developed to directly measure the lengths, angles, and areas between cusps to investigate ancestry in modern population groups (Morris, 1986). To date there has not been a GMM study of modern human teeth based simply on relative cusp locations in the maxillary and mandibular molars; however, GMM of molars has been used in paleoanthropological contexts (Bailey, 2004; Matinón-Torres et al., 2006; Bailey et al., 2008). Assuming that the morphological relationship of relative cusp location is as equally related to genetics as dental nonmetric morphologies and odontometrics, as asserted by many of the aforementioned authors, then occlusal polygons should represent a suitable genetic proxy and therefore be ideal for ancestry estimation.

MATERIALS

Coordinate data from a total of 190 individuals' first and second maxillary and mandibular molars were recorded for the present research. The American White (W) sample consisted of 109 dental casts ($F = 60$, $M = 49$) housed at the University of Alaska Fairbanks' Department of Anthropology. All dental casts were labeled with the student's name and self-recorded demographic data, which included ancestry and sex. For the present study, any cast that was identified as "European," "Caucasian," or as a specific European group was recorded as "White." The casts were made with a dental alginate, the accuracy of which has been previously demonstrated by Cohen et al. (1995). The American Black (B) sample ($F = 44$, $M = 37$) was collected at the Hamann-Todd Osteological Collection at the Cleveland Museum of Natural History. Each individual was also of documented ancestry and sex. It should be noted that the White sample was based on self-identified assessments and collapsed into a discrete group by the authors, while the Hamann-Todd collection's Black sample had individuals' ancestry assigned at autopsy by an outside observer.

METHODS

The cusp tips of each molar were digitized with a coordinate digitizer, which has an accuracy of 0.38 mm. The digitized coordinate data were collected with a modified version of 3Skull software (Ousley, 2004). Adopting the methodology of Morris (1986), the stylus of the digitizer was placed at the tips of the cusps, represented by the highest point or apex of each cusp and the three-dimensional coordinate point was collected. In the event of slight wear, the cusp locations were approximated by collecting the coordinate data at the central point of the dentine exposure. Acceptable molars demonstrated wear no greater than stage 2 as described by Smith (1984), in which only a small pinpoint apex of dentine is exposed. Molars demonstrating extensive wear, or stage 3 and above as describe by Smith (1984), were excluded from the study due to the obliteration of the cusp patterns. While the point of slight dentine exposure may not always be an appropriate analog, collecting data from specimens with no more than slight wear allowed consistent data collection by utilizing the point of dentine exposure. For each molar, only the primary cusps were observed. The primary cusps include the maxillary protocone (cusp 1), paracone (cusp 2), metacone (cusp 3), and hypocone (cusp 4), and also the mandibular protoconid (cusp 1), metaconid (cusp 2), hypoconid (cusp 3), entoconid (cusp 4), and hypoconulid (cusp 5). Any additional cusps, such as Carabelli's cusp, were not recorded. When available, the left molar was used. In the event of a missing or unsuitable left molar, the right was recorded, but did not skew the analysis due to rotation in the GPA. The left and right antimeres demonstrated no significant differences as reported previously by Kenyhercz et al. (2013). Any descriptions of shape to follow are thus based on the relative location of cusp apices and not on the outline molar shape.

Once the molars were digitized, the z coordinate, which corresponds to elevation, was removed to negate the effects that tooth wear would have on the relative cusp locations; teeth with greater wear would show lower elevations, which would not be directly comparable to unworn teeth. Next, the raw coordinate data were submitted to a GPA in the program MorphoJ (Klingenberg, 2011). Within MorphoJ, each specimen's raw coordinate data were converted into ProCoords to directly compare differences in cusp location from a consensus shape derived from the entire sample (Fig. 1). As mentioned above, the average of each of the landmark coordinates was used to create an arbitrary centroid for each landmark, where deviations from this arbitrary centroid can be quantified and analyzed. A subset of 25 individuals was selected via a stratified random sample and digitized at two separate times by the senior author. The data were subjected to a GPA and then the ProCoords were submitted to a Student's two-tailed t-test to test intraobserver repeatability for each molar. Additionally, centroid sizes were calculated and retained as a measure of gross size for each tooth. Centroid sizes between the two populations were subjected to a Student's two-tailed

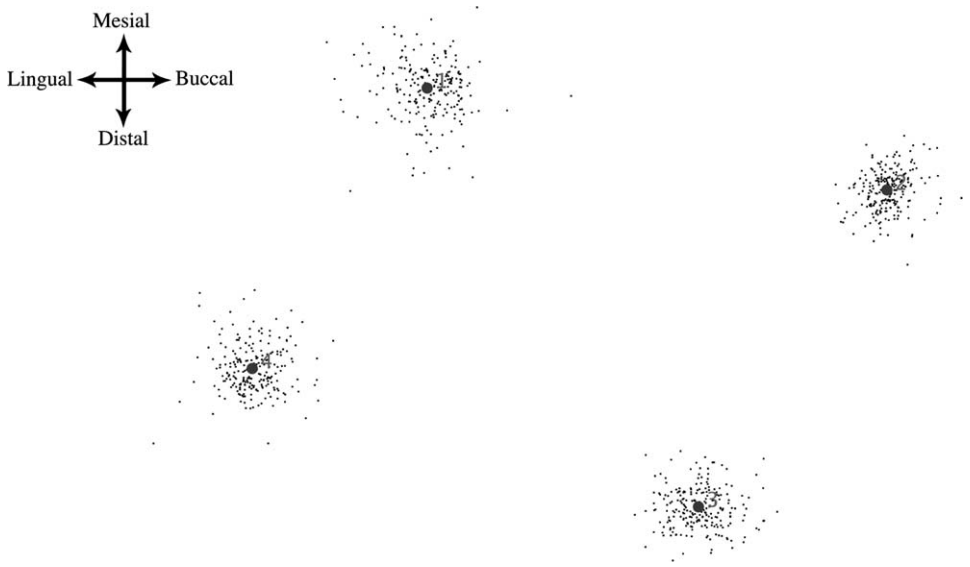

Fig. 1. Example of mean shape of M^1 derived from MorphoJ. The large circle represents the centroid size and the surrounding dots represent each individual. Cusps are numbered in order to corresponding cusp name (refer to in-text description).

TABLE 1. Descriptive statistics of centroid sizes by population group

	Mean		SD		Min		Max		Range	
Molar	B	W	B	W	B	W	B	W	B	W
M^1	**7.69**	**7.91**	0.79	0.58	5.40	6.44	10.08	9.51	4.68	3.07
M^2	7.59	7.59	0.90	0.59	5.53	6.31	10.33	8.88	4.80	2.57
M_1	8.89	8.82	0.79	0.58	6.43	7.31	10.38	10.19	3.95	2.87
M_2	**7.58**	**7.33**	0.73	0.59	5.85	5.90	9.44	8.93	3.59	3.03

Mean values in bold reflect significant difference at $P < 0.05$.

t-test to compare differences between group mean centroid sizes.

After each specimen's coordinates had been converted to ProCoords, the newly scaled coordinates were subjected to PCA because the shape and direction changes in the sample can be visualized as deviations from the landmark centroid instead of merely as differences in a single *x* or *y* coordinate value. Like centroid size, principal component one (PC1) scores, which account for the majority of the shape change information, were subjected to a Student's two-tailed *t*-test to compare group means. Additionally, centroid sizes and PC1 were subjected to a Pearson product-moment correlation test to investigate possible allometric relationships in the molars.

Next, linear discriminant function analysis (LDFA) was used to discriminate between ancestry groups. Discriminant function analysis compresses the raw data into discriminant functions that maximize the intergroup variability in relation to the intragroup variability (Albrecht, 1980). The custom database in Fordisc 3.0 (Jantz and Ousley, 2005) was used to perform LDFA between the White and Black samples using the shape variables (ProCoord and PC) with and without centroid size. Each LDFA utilized forward stepwise selection to choose the variables that best discriminated between groups. Each LDFA used leave-one-out-cross-validation (LOOCV), in which one specimen is removed from the reference group and tested against the discriminant function derived from the remainder of the sample, which is repeated for each individual in the total sample (Klecka, 1980). Leave-one-out-cross-validation yields more realistic results by comparing each individual to the discriminant function derived by every other individual in the sample excluding itself. Thus, LOOCV avoids unrealistically optimistic model performance by each individual being tested against the function derived by the rest of the sample.

Lastly, interlandmark distances (ILDs) were calculated from the raw coordinate data using the Euclidean distance function $\sqrt{((x1-x2)^2+(y1-y2)^2)}$. The ILDs were calculated to further examine the effect of overall size. Due to the nature of the centroid size's computation, a larger centroid would not indicate which dimensions were larger, simply that there are greater distances between landmark pairs. The examination of ILDs using cross-validated LDFA and stepwise selection would allow for investigation into which specific ILDs varied between groups.

RESULTS

t-Tests

Interobserver repeatability. The subset of individuals that were digitized at separate times were found to have no significant differences with the ProCoords for each molar demonstrating p values greater than $P > 0.1$.

Centroid size. The Black and White groups both demonstrated significant differences in the centroid size of the maxillary first molar (M^1) and the mandibular second molar (M_2) (Table 1). The maxillary first molar was larger in Whites than in Blacks, while the mandibular molars were larger in Blacks than Whites, however, only M_2 was significantly larger. In each of the four molars, Blacks demonstrated greater variation as shown through greater standard deviations and ranges than Whites (Table 1).

Principal components of shape. Each molar's PC1 resulted in significant differences between group means for Blacks and Whites (Table 2). Blacks demonstrated greater variability in each of the molars except M_1, which demonstrated the same standard deviation between groups (Table 2, Fig. 2).

Maxillary first molar

Principal component analysis. The PCA of the maxillary first molar's ProCoords yielded four PCs, each with eigenvalues greater than 1.0. The first PC accounted for 38.9% of the variation and primarily indicated movement of the protocone (cusp 1) mesiolingually, the paracone (cusp 2) distolingually, the metacone (cusp 3) distobuccally, and the hypocone (cusp 4) mesiobuccally (Fig. 3). When subjected to a Pearson's product-moment correlation, PC1 demonstrated a nearly non-existent, non-significant, negative correlation with centroid size at $r = -0.05$ ($P = 0.48$). Principal component 2 contributed 31.2% of the variation, PC3 contributed 17.2% and PC4 contributed 12.7%.

The PCA of the ILDs resulted in six PCs. The first PC accounted for 47.6% of the variation and was most heavily loaded by the ILD between the hypocone (cusp 4) and paracone (cusp 2), followed by the hypocone-to-metacone ILD and then the metacone-to-paracone ILD.

Discriminant function analysis. The results of the DFA and associated D^2 values are presented in Tables 3 and 4, respectively. The total correct classifications for ancestral group ranged from 62.7 to 73.0% (Table 3). Each of the analyses demonstrated D^2 values significant at $P < 0.05$ (Table 4). The ProCoords of the first maxillary molar yielded a total correct classification of 72.5% (Table 3, M^1 ProCoord). The Procrustes coordinates stepwise selected for the analysis were representative of the entire tooth, with the majority of the coordinates representing the paracone (ProCoord 3-4) and hypocone (ProCoord 7-8). The shape changes represented by the discriminant function demonstrated that the mean Black M^1 shape had narrower mesiodistal dimensions and broader buccolingual dimensions, while the mean White M^1 shape was more rhomboidal and constricted in the buccolingual dimensions (Fig. 4). The inclusion of centroid size in the above analysis yielded a total correct classification of 73.0% (Table 3, M^1 ProCoord Size). The major cusp represented was the metacone (ProCoords 5-6). The centroid size of Whites (2.1 mm) was slightly larger than Blacks (2.0 mm).

The principal component scores of the ProCoords yielded a total correct classification of 70.4% (Table 3, M^1 ProCoord PC). The variables stepwise selected were

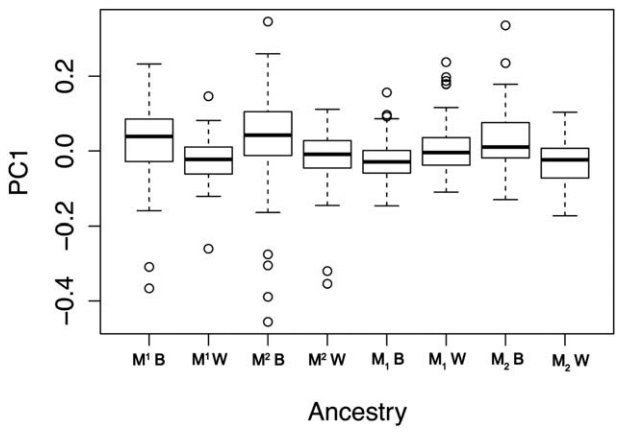

Fig. 2. Box-plots depicting range of PC1 scores between Whites and Blacks for each of the molars. Principal component 1 was significantly different between Blacks and Whites for each molar based on a Student's *t*-test ($P < 0.05$).

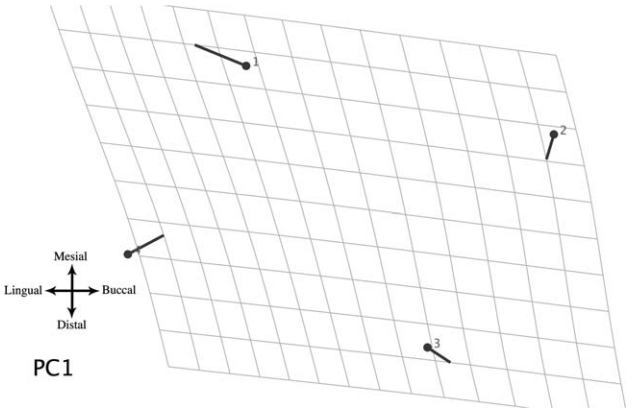

Fig. 3. Shape changes of the ProCoord PC1 associated with M^1.

TABLE 2. Descriptive statistics of PC1 by population group

	Mean		SD		Min		Max		Range	
Molar	B	W	B	W	B	W	B	W	B	W
M^1	**0.03**	**−0.02**	0.10	0.05	−0.37	−0.26	0.23	0.15	0.60	0.41
M^2	**0.03**	**−0.02**	0.13	0.08	−0.46	−0.35	0.35	0.11	0.80	0.47
M_1	**−0.02**	**0.01**	0.06	0.06	−0.15	−0.11	0.16	0.24	0.30	0.35
M_2	**0.03**	**−0.03**	0.09	0.06	−0.13	−0.17	0.34	0.10	0.47	0.28

Mean values in bold reflect significant difference at $P < 0.05$.

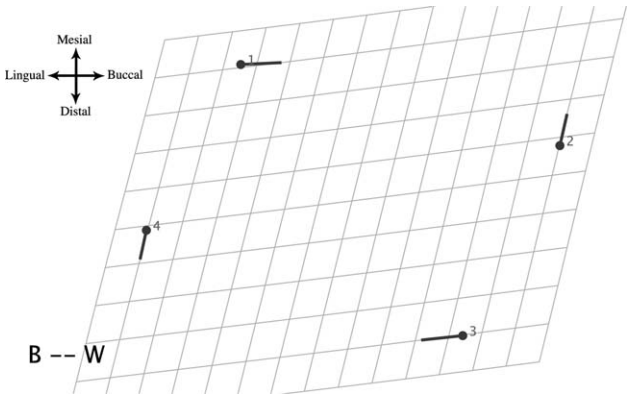

Fig. 4. Shape changes associated with the discriminant function of the ProCoords of M^1. The "lollipop" portion of the graph, demonstrating a more rectangular shape, represented blacks and the opposite tip of the "stem" represents Whites, depicting a more rhomboidal shape.

TABLE 3. Correct classifications of each discriminant function for the maxillary first molar

Analysis	% Correct Black	% Correct White	% Total Correct
M^1 ProCoord	66.3	77.1	72.5
M^1 ProCoord Size	65.0	78.9	73.0
M^1 ProCoord PC	63.8	75.2	70.4
M^1 ProCoord PC Size	61.3	78.9	71.4
M^1 ILD	48.8	73.4	62.7
M^1 ILD PC	51.2	71.6	62.7

PC1 and PC3. Principal component one was most heavily loaded with ProCoords 1 and 2 (protocone) and also 7 and 8 (hypocone), while PC3 was most heavily loaded by ProCoords 5 (metacone) and 7 (hypocone). As noted above, PC1 represented a more square shaped M^1 in Blacks and a more rhomboidal shape in Whites. Principal component three demonstrated a constriction of the distal aspect of the tooth in Whites as compared with Blacks. The addition of centroid size to the above analysis slightly improved total correct classification to 71.4% (Table 3, M^1 ProCoord PC Size).

The ILDs resulted in a total correct classification of 62.7% (Table 3, M^1 ILD). The variables stepwise selected for the analysis included hypocone-to-paracone, hypocone-to-metacone, and metacone-to-paracone. Hypocone-to-metacone carried the most weight in the discriminant function at 60.9% and demonstrated that Blacks had greater values in this ILD with a mean of 6.5 mm compared with the White mean of 6.3 mm, corroborating the shape changes found in PC3 above.

The principal components of the ILDs resulted in a total correct classification of 62.7% (Table 3, M^1 ILD PC). Principal component three accounted for 94.7% of the relative weight in the discriminant function and was most heavily loaded by metacone-to-protocone, then hypocone-to-paracone, and then hypocone-to-protocone.

Maxillary second molar

Principal component analysis. The PCA of the maxillary second molar's ProCoords yielded four PCs, each with eigenvalues greater than 1.0. The first PC accounted for 44.1% of the variation and primarily indicated movement of cusp 1 distobuccally, cusp 3 mesiobuccally, and cusp 4 mesiolingually; cusp 2 showed no movement (Fig. 5). When subjected to a Pearson's product-moment correlation, PC1 demonstrated a nearly non-existent, non-significant, positive correlation with centroid size at $r = 0.02$ ($P = 0.74$). Principal component two contributed 27.5% of the variance, PC3 provided 20.7%, and PC4 7.7%.

TABLE 4. Malanobis D^2 values and corresponding significance for each M^1 analysis

Analysis	Mahalanobis D^2	Significance (P)
M^1 ProCoord	1.161	<0.001
M^1 ProCoord Size	1.220	<0.001
M^1 ProCoord PC	0.990	<0.001
M^1 ProCoord PC Size	1.068	<0.001
M^1 ILD	0.221	0.017
M^1 ILD PC	0.278	0.002

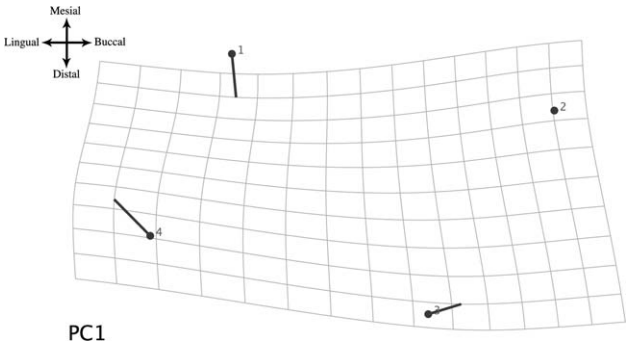

Fig. 5. Shape changes of ProCoord PC1 associated with M^2.

TABLE 5. Correct classifications of each discriminant function for the maxillary second molar

Analysis	% Correct Black	% Correct White	% Total Correct
M^2 ProCoord	75.7	84.1	80.1
M^2 ProCoord Size	74.3	84.1	79.5
M^2 ProCoord PC	75.7	86.6	81.4
M^2 ProCoord PC Size	77.9	87.8	82.7
M^2 ILD	64.1	67.1	65.6
M^2 ILD PC	64.1	67.1	65.6

The PCA of the ILDs of the second maxillary molar yielded six PCs. The first PC accounted for 40.5% of the variation and was most heavily loaded by the ILDs for metacone-to-protocone, followed by paracone-to-protocone, and then hypocone-to-paracone.

Discriminant function analysis. Total correct classifications achieved through the LDFAs for the maxillary second molar ranged from 65.6% to 82.7% (Table 5). The D^2 values were all significant at $P < 0.05$ (Table 6). The ProCoords for the maxillary second molar yielded 80.1% total correct classification (Table 5, M^2 ProCoord). The Procrustes coordinates stepwise selected for the analysis represented the paracone (ProCoord 1-2) and the metacone (ProCoord 5). Procrustes coordinate 5 contributed

TABLE 6. Malanobis D^2 values and corresponding significance for each M^2 analysis

Analysis	Mahalanobis D^2	Significance (P)
M^2 ProCoord	2.029	<0.001
M^2 ProCoord Size	2.191	<0.001
M^2 ProCoord PC	1.924	<0.001
M^2 ProCoord PC Size	1.906	<0.001
M^2 ILD	0.497	<0.001
M^2 ILD PC	0.578	<0.001

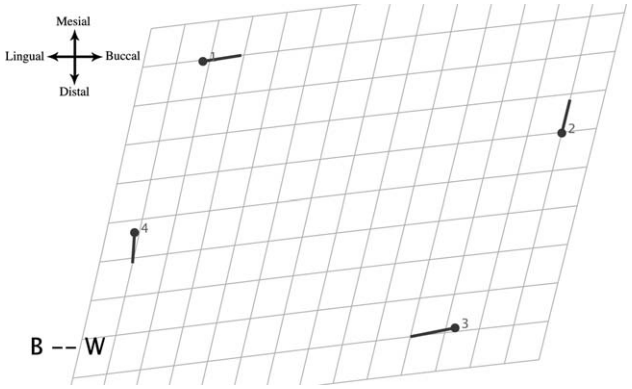

Fig. 6. Shape changes associated with the discriminant function of the ProCoords of M^2. Just as with M^1, Blacks demonstrated a more rectangular shape and Whites demonstrated a more rhomboidal shape.

the greatest relative weight to the discriminant function at 67.6%. The shape differences between Blacks and Whites based on the discriminant function scores were similar to the M^1; Blacks demonstrated broader teeth buccolingually, while Whites again demonstrated more of a rhomboidal shape (Fig. 6).

The inclusion of centroid size in the above analysis yielded a total correct classification of 79.5% (Table 5, M^2 ProCoord Size). The variables stepwise selected for in the analysis included the paracone that was represented by ProCoord 1, the paracone by ProCoord 3, and the metacone by ProCoord 5. Again, ProCoord 5 (metacone) contributed the most relative weight to the discriminant function at 75.2%. Both population groups demonstrated the same group mean for centroid size.

When the PC scores of the ProCoords were subjected to LDFA, a total of 81.4% correct classification between groups was achieved (Table 5, M^2 ProCoord PC). Principal component two contributed the most to the relative weight of the discriminant function and was most heavily loaded by coordinates of the metacone, followed by coordinates of the paracone. The shape change demonstrated narrowing between the protocone and metacone and lengthening between the paracone and hypocone. In total, the shape changes reflected a more exaggerated rhomboidal shape in Whites and a more rectangular shape in Blacks. The inclusion of centroid size in the above analysis of PC scores yielded a greater total correct classification of 82.7% (Table 5, M^2 ProCoord PC Size). Just as in the above M^2 analysis, PC2 contributed most heavily to the discriminant function at 60.5%.

The ILDs resulted in a total correct classification of 65.6% (Table 5, M^2 ILD). The variables stepwise selected for in the analysis included hypocone-to-protocone, hypocone-to-metacone, and metacone-to-paracone. Hypocone-to-metacone carried the most weight in the discriminant function at 60.9%, just as in the ILD discriminant function for the maxillary first molar. However, the group means for the ILD hypocone-to-metacone showed greater disparity than with the first maxillary molar; Blacks demonstrated a mean value of 6.3 mm compared to Whites with a mean value of 5.8 mm. Principal components of the ILDs from the above analysis yielded exactly the same results with a total correct classification of 65.6% (Table 5, M^2 ILD PC). Principal component one contributed the majority of the weight to the discriminant function at 65.0% and again was most heavily loaded by the ILD for metacone-to-protocone, followed by paracone-to-protocone, and then hypocone-to-paracone.

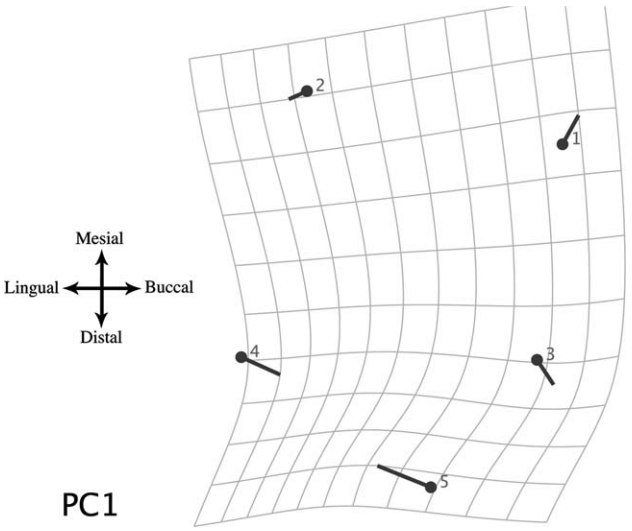

Fig. 7. Shape changes of the ProCoord PC1 associated with M_1.

Mandibular first molar

Principal component analysis. The PCA using the subset of data utilizing the mandibular first molar yielded six principal components, each with eigenvalues greater than 1.0. The first principal component accounted for 36.2% of the variation and indicated movement of the protoconid in the mesiobuccal direction, the metaconid in the distolingual direction, the hypoconid in the distobuccal direction, the entoconid in the distobuccal direction, and the most marked change in the hypoconulid in the mesiolingual direction (Fig. 7). When subjected to a Pearson's correlation, PC1 demonstrated a moderate, significant, negative correlation of $r = -0.32$ ($P < 0.001$). Principal component 2 provided 19.1% of the variance, PC3 contributed 14.9%, PC4 added 12.8%, PC5 with an additional 10.5%, and PC6 with 6.5%.

Principal component analysis of the ILDs yielded ten PCs. The first principal component accounted for 42.2% of the variation and was most heavily loaded by the ILDs hypoconulid-to-metaconid, hypoconulid-to-protoconid, entoconid-to-hypoconulid, hypoconid-to-hypoconulid, and then nearly evenly by the remaining ILDs.

Discriminant function analysis. The LDFA for the mandibular first molar resulted in total correct classifications ranging from 69.6% to 82.1% (Table 7). Each of

TABLE 7. Correct classifications of each discriminant function for the mandibular first molar

Analysis	% Correct Black	% Correct White	% Total Correct
M_1 ProCoord	76.5	84.8	82.1
M_1 ProCoord Size	74.5	82.9	80.1
M_1 ProCoord PC	74.5	81.9	79.5
M_1 ProCoord PC Size	76.5	82.9	80.8
M_1 ILD	62.5	73.3	69.6
M_1 ILD PC	62.5	76.2	71.4

TABLE 8. Malanobis D^2 values and corresponding significance for each M_1 analysis

Analysis	Mahalanobis D^2	Significance (P)
M_1 ProCoord	2.540	<0.001
M_1 ProCoord Size	2.505	<0.001
M_1 ProCoord PC	2.308	<0.001
M_1 ProCoord PC Size	2.320	<0.001
M_1 ILD	0.879	<0.001
M_1 ILD PC	0.964	<0.001

the Mahalanobis D^2 values for the analyses were significant at $P < 0.05$ (Table 8). The LDFA for the ProCoords of the mandibular first molar resulted in 82.1% total correct classification (Table 7, M_1 ProCoord). The variables stepwise selected represented the hypoconid (6), entoconid (7), and the hypoconulid (9-10). Procrustes coordinate seven (entoconid) held the greatest weight in the discriminant function. The shape changes associated with the discriminant function showed that Blacks had reduced mesiodistal dimensions and increased lingual-buccal breadths when compared with Whites (Fig.8). The inclusion of size on the aforementioned analysis decreased total correct classification to 80.1% (Table 7, M_1 ProCoord Size). The ProCoords selected for the analysis represented the metaconid (3), hypoconid (6), entoconid (8), and hypoconulid (9-10). Procrustes coordinate 10 (hypoconulid) accounted for the majority of the weight in the discriminant function at 41.3%. Blacks showed slightly larger mean centroid sizes than Whites at 8.9 mm^2 versus 8.8 mm^2.

When the PCs of the ProCoords were subjected to a LDFA, there was a 79.5% total correct classification (Table 7, M_1 ProCoord PC). Principal component four contributed the most weight to the discriminant function at 49.9% and was most heavily loaded by ProCoords 7-8, which represented the entoconid. The overall shape change demonstrated by PC4 was a wider distal aspect of the tooth in Blacks, especially in the buccolingual elongation of the entoconid and hypoconid and the more centrally oriented hypoconulid, whereas Whites had a more bucally oriented hypoconulid. The addition of centroid size to the above analysis slightly improved total correct classification to 80.8% (Table 7, M_1 ProCoord PC Size). Just as before, PC4 contributed the greatest weight to the discriminant function (49.4%).

The ILDs resulted in a total correct classification of 69.6% (Table 7, M_1 ILD). The variables stepwise selected included entoconid-to-hypoconulid, hypoconid-to-metaconid, hypoconid-to-protoconid, hypoconulid-to-metaconid, and hypoconulid-to-protoconid. The ILD entoconid-to-metaconid contributed the greatest relative weight to the discriminant function at 60.0% with the Black mean value of 6.8 mm compared with the White mean value of 4.5 mm.

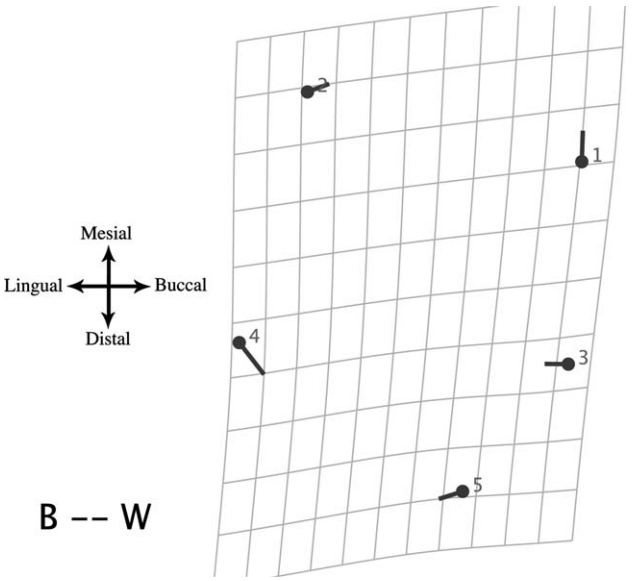

Fig. 8. Shape changes associated with the discriminant function of the ProCoords of M_1. Blacks demonstrated broader buccolingual and compressed mesiodistal shape compared with Whites, with the greatest shape changes occurring in the distal aspect of the tooth.

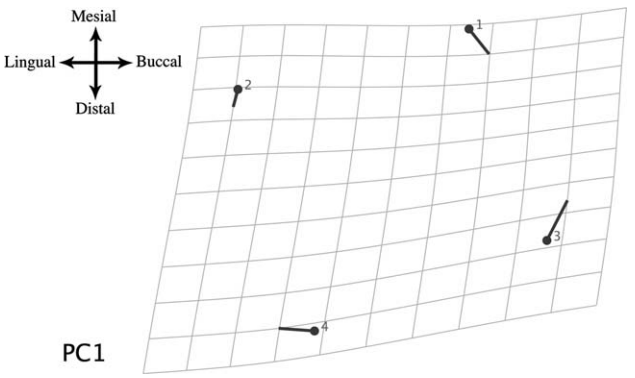

Fig. 9. Shape changes of the ProCoord PC1 associated with M_2.

The PC scores of the ILD resulted in a total correct classification of 71.4% (Table 7, M_1 ILD PC). Principal component three accounted for most of the relative weight of the discriminant function at 59.5% and was most heavily loaded by the ILD hypoconulid-to-protoconid.

Mandibular second molar

Principal component analysis. The PCA of the ProCoords of the mandibular second molar resulted in four PCs, each with eigenvalues greater than 1.0. The first principal component accounted for 36.0% of the variation and indicated movement of the protoconid in the distobuccal direction, the metaconid in the distobuccal direction, the hypoconid in the mesiobuccal direction, and the entoconid in the distolingual direction, indicating that Whites had a comparatively longer and narrower M_2 as

TABLE 9. Correct classification of each discriminant function for the mandibular second molar

Analysis	% Correct Black	% Correct White	% Total Correct
M_2 ProCoord	62.8	71.6	67.8
M_2 ProCoord Size	61.5	69.6	66.1
M_2 ProCoord PC	62.8	71.6	67.8
M_2 ProCoord PC Size	62.8	73.5	68.9
M_2 ILD	65.8	76.5	71.8
M_2 ILD PC	68.4	75.5	72.4

TABLE 10. Malanobis D^2 values and corresponding significance for each M_2 analysis

Analysis	Mahalanobis D^2	Significance (P)
M_2 ProCoord	1.169	<0.001
M_2 ProCoord Size	2.505	<0.001
M_2 ProCoord PC	2.308	<0.001
M_2 ProCoord PC Size	2.320	<0.001
M_2 ILD	0.879	<0.001
M_2 ILD PC	0.964	<0.001

compared with Blacks (Fig. 9). When subjected to a Pearson's correlation, PC1 demonstrated a very weak, significant, correlation of $r = 0.14$ ($P = 0.04$). Principal component two offered an additional 24.0%, PC3 provided 22.2%, and PC4 contributed 17.8%.

The PCA of the ILDs yielded six PCs, which accounted for 100% of the variance. The first principal component represented 47.4% of the variation and was most heavily loaded by the ILD entoconid-to-protoconid, followed by hypoconid-to-metaconid, and then loaded relatively evenly across the remaining ILDs.

Discriminant function analysis. The total correct classification of the mandibular second molar ranged from 66.1% to 72.4% (Table 9). Each of the Mahalanobis D^2 values were significant at $P < 0.001$ (Table 10). The ProCoords resulted in a 67.8% total correct classification (Table 9, M_2 ProCoord). ProCoord 8 (entoconid) contributed the greatest weight to the discriminant function at 50.0%. The shape changes associated with the discriminant function illustrated that Blacks had comparatively broader mandibular second molars than Whites (Fig.10). The addition of size to the aforementioned analysis resulted in a lower total correct classification of 66.1% (Table 9, M_2 ProCoord Size). Again, ProCoord 8 (entoconid) contributed the most to the discriminant function at 50.0%. Blacks again demonstrated a greater mean centroid size of 7.6 mm^2, compared with Whites at 7.3 mm^2.

The LDFA of the PC scores of the ProCoords resulted in comparable results as the ProCoords with a total correct classification of 67.8% (Table 9, M_2 ProCoord PC). Principal component one contributed 76.0% of the relative weight of the discriminant function, with the corresponding shape changes having been described above under PCA for the mandibular second molar. However, the most marked shape change in PC1 was in the hypoconid, which was more mesial and buccal in Blacks as compared with Whites (Fig. 10). The addition of centroid size to the above analysis slightly improved total correct classification to 68.9% (Table 9, M_2 ProCoord PC Size). Again, PC1 accounted for the greatest relative weight of the discriminant function at 65.0%. Blacks demonstrated greater mean centroid sizes than Whites (Table 1).

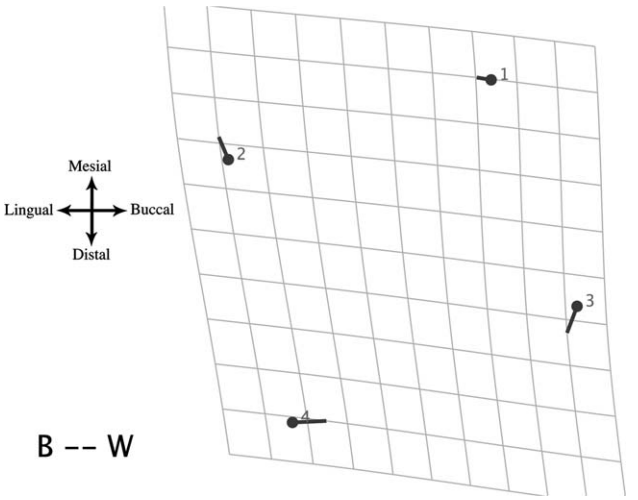

Fig. 10. Shape changes associated with the discriminant function of the ProCoords of M_2. Again, Blacks demonstrated broader shapes buccolingually and more compressed mesiodistally than Whites.

The LDFA of the ILDs of the second mandibular molar resulted in a total correct classification of 71.8% (Table 9, M_2 ILD). The variables stepwise selected for the analysis included the ILDs for entoconid-to-hypoconid, entoconid-to-metaconid, entoconid-to-protoconid, hypoconid-to-metaconid, and metaconid-to-protoconid. The ILD that had the most weight in the discriminant function was entoconid-to-hypoconid, which accounted for 60.9%. Blacks demonstrated a greater mean value with the aforementioned ILD at 6.1 mm compared with the White's mean value of 5.3 mm.

The PC scores of the ILDs yielded a correct classification of 72.4% (Table 9, M_2 ILD PC). Principal component two accounted for most of the relative weight of the discriminant function at 46.8% and was most heavily loaded by the ILDs hypoconid-to-protoconid, followed by entoconid-to-hypoconid, while the remaining ILDs loadings were relatively evenly distributed.

Combined molars

Principal component analysis. When subjected to a PCA, the ProCoords yielded 18 PCs, of which the first nine contained eigenvalues greater than 1.0 and accounted for 92.6% of the total variance. The first PC accounted for 20.8% of the variation and was most heavily loaded, in order, by ProCoords 5 (metacone) and 8 (hypocone) of the maxillary second molar, followed by ProCoords 10 (hypoconulid) and 7 (entoconid) of the mandibular first molar.

Principal component analysis of the ILDs yielded 27 PCs, the first 11 of which contained eigenvalues greater than 1.0. The first principal component accounted for 27.8% of the variation and was most heavily loaded by the ILD hypoconulid-to-metaconid of the mandibular first molar, followed by entoconid-to-hypoconid of the mandibular second molar, then entoconid-to-protoconid of the mandibular second molar, then entoconid-to-hypoconid of the mandibular first molar.

Discriminant function analysis. The LDFA for the combined molar data resulted in total correct

TABLE 11. Correct classification of each discriminant function for combined molars

Analysis	% Correct Black	% Correct White	% Total Correct
Combined ProCoord	78.9	92.3	87.9
Combined ProCoord PC	81.6	89.7	87.1
Combined ILD	75.9	81.6	80.0
Combined ILD PC	79.3	82.9	81.9

TABLE 12. Malanobis D^2 values and corresponding significance for each combined molar analysis

Analysis	Mahalanobis D^2	Significance (P)
Combined ProCoord	4.780	<0.001
Combined ProCoord PC	4.691	<0.001
Combined ILD	4.051	<0.001
Combined ILD PC	2.787	<0.001

classifications ranging from 81.6% to 87.9% (Table 11). Each of the Mahalanobis D^2 values were significant at $P < 0.001$ (Table 12). When the ProCoords were combined and subjected to a DFA, total correct classification was 87.9% (Table 11, Combined ProCoord). The variables stepwise selected for the analysis included ProCoords from the maxillary second molar and the mandibular first molar. From the maxillary second molar, ProCoords 2 and 4 were selected, which represented the protocone and paracone, respectively. From the mandibular first molar, ProCoords 1, 6, and 7 were selected, which represented the protoconid (1), hypoconid (6), and entoconid (7). The variable that had the single most weight in the discriminant function was ProCoord 4, which represented the paracone, from the maxillary second molar at 43.7%; however, the mandibular first molars ProCoords combined for more than half of the discriminant function.

The LDFA of the PCs of the ProCoords resulted in a total correct classification of 87.1% (Table 11, Combined ProCoord PC). Principal component 1 offered the most relative weight to the discriminant function and was most heavily loaded by ProCoords 5 (metacone) and 8 (hypocone) of the M^2, followed by ProCoords 10 (hypoconulid) and 7 (entoconid) of the mandibular first molar.

The LDFA of the ILDs resulted in 80.0% total correct classification (Table 11, Combined ILD). The variables stepwise selected for the analysis included: entoconid-to-hypoconid, hypoconid-to-protoconid, and metaconid-to-protoconid from the mandibular first molar; hypoconid-to-metaconid, entoconid-to-hypoconid, entoconid-to-metaconid, and entoconid-to-protoconid from the mandibular second molar; and metacone-to-protocone, metacone-to-paracone, and paracone-to-protocone from the maxillary first molar. The ILD that had the most weight in the discriminant function (24.8%) was entoconid-to-hypoconid of the mandibular second molar, in which Blacks demonstrated a greater mean of 6.1 mm compared with the 5.4 mm mean of the Whites.

The LDFA of the PCs of the ILDs resulted in a total correct classification of 81.9% (Table 11, Combined ILD PC). The discriminant function was most heavily weighted by PC5 at 37.9%, which was most heavily loaded by metacone-to-protocone of the first maxillary molar, followed by entoconid-to-hypoconulid of the first mandibular molar, and then by hypocone-to-protocone of the first maxillary molar.

DISCUSSION

Blacks demonstrated greater variability in both centroid sizes and PC1 scores based on the ProCoords (Tables 1 and 2). However, there were only significant differences between centroid sizes in two molars: $M^1$and M_2. Interestingly, the molars that demonstrated no significant difference between size (M^2 and M_1) resulted in the greatest correct classifications for individual teeth and were the only molars that were stepwise selected for in the combined analyses. The greater variability in both size and shape of the Black sample's molars may be the result of more varied historical diversity and gene flow with American White populations, or, as an older ancestral group, Blacks may have developed greater variability in tooth form through a comparatively longer evolutionary development.

The different data reduction techniques, PCA and LDFA, elucidated varying trends in intercuspal shape patterns. The PCA demonstrated shape changes in every aspect of the tooth, while the LDFA focused on the distal aspects of the tooth, which was true for the ProCoords, ProCoord PCs, and ILDs. The differences observed between the techniques are likely due to the fact that PCA accounts for the shape variation in the entire sample while the LDFA maximizes the variation between samples for classification purposes. Potential reasons for the distal tooth variability are detailed below.

Overall, correct classifications of analyses between ProCoords and ProCoord PCs varied, with the highest total correct classification from the combined ProCoords. The greater classification of the combined ProCoords, as compared with the PCs based on the ProCoords (Table 11), may be due to the fact that the PCs took into account overall shape variation of the relative cusp locations instead of changes in just certain aspects, namely the distal aspects of the molars, which may have introduced noise or redundancy in the analysis. However, the greatest positive predictive value, or precision, in any of the analyses for Blacks was in the combined ProCoord PCs analysis (Table 11). Due to the more balanced classifications in the ProCoord PC, i.e., more comparable correct classifications in Blacks and Whites, it may be the case that examining overall occlusal polygon shape is more appropriate, in terms of classification, than simply isolated x or y coordinates. The raw ILDs showed less total correct classifications than the PCs based upon them. The improved classification achieved through the PCs of the ILDs is unsurprising because while the first PC is generally attributed to size, the remaining PCs are generally attributed to shape (Jolliffe, 2002). It has previously been demonstrated that individual tooth length and width dimensions, traditionally buccolingual and mesiodistal values, were poor discriminators between groups alone, but shape information could be extracted using PCA and elucidate group differences (Harris and Bailit, 1988; Harris and Rathbun, 1989; Harris, 1997; Hanihara and Ishida, 2005). Given the sexual dimorphism in males and females, in conjunction with the pooled sexes for analyses, raw measures of size were likely to introduce noise to the analyses. Principal components were able to negate any noise by getting at the finer grained "shape" information based on the differing combination of loadings. However, PC1, which is generally regarded to represent overall size, was continually stepwise selected for the separate LDFAs using ILDs. Regardless, Harris (1997) pointed out that while

PC1 generally accounts for gross size, as determined through the positive loadings of each of the variables on the component, there is also useful shape information in PC1.

The only ProCoords analysis that demonstrated improved classification with the inclusion of size was the maxillary first molar (Table 3). Following Dahlberg's (1945) field concept theory, in which the first, and in the case of the molars, polar, tooth in any morphogenetic field will be the largest and most stable tooth, while distal teeth will become smaller, demonstrate less morphology, and contain the highest degree of phenotypic variability; it would follow that the size of the polar tooth would be stable between populations and thus contribute more to the discriminant function. However, each of the analyses based on the ProCoords PCs demonstrated improved classification with the inclusion of size. Harris and Rathbun (1989) previously reported on the importance of tooth size apportionment in discriminating between Whites and Blacks, and the above results corroborate the importance of size in conjunction with shape.

The distal aspect of the molars demonstrated the greatest variability and shape change. The distal molar regions were consistently stepwise selected in the analyses, contributed heavily to the ProCoord PCs, comprised the majority of the stepwise selected ILDs, and provided the greatest loadings to the PC of the ILDs. As the distal cusps of the teeth developed later throughout embryological development, and thus evolution (Kraus and Jordan, 1965), it makes evolutionary sense that the mesial aspects of the teeth are more stable than the distal aspects. Harris and Dinh (2006) also noted that the distal aspects of the first and second maxillary molars demonstrated greater variability than the mesial cusps and that these cusp locations were largely independent of overall tooth size, which is corroborated by the above analyses.

The maxillary second molar and mandibular first molar showed the greatest discriminating power and also accounted for the majority of the variables in the combined molar analyses. The analysis with the PCs of the ProCoords and centroid size of the second maxillary molar demonstrated the single highest classification of any single tooth analysis (82.7%), whereas the ProCoords of the mandibular first molar showed the greatest discriminating power independent of size (82.1%). The inclusion of size makes sense, again, in accordance with Dahlberg's (1945) field concept theory. Harris and Dinh (2006) noted that more distal molars vary more in size; therefore, while the second maxillary molar is more phenotypically variable in shape, it is also in size, which may lead to its greater discriminating power. The ILDs for the mandibular and maxillary second molars confirm Harris and Dinh's (2006) observation about size variability, as these molars both demonstrated greater correct classifications than those achieved by the first molars using ILDs. Further, M_2 was the only tooth to have the ILDs outperform the shape variables. However, M_1 demonstrated the most shape variation independent of size. Assuming Dahlberg (1945) was correct in his assessment that the polar tooth received the most genetic information, or demonstrates the genetic potential of morphology, it would follow that the polar tooth would contain the most useful information in discriminating between populations. While the M^2 and M_1 might seem to be at theoretical odds at their ability to discriminate populations, Alvesalo and Tigerstedt (1974) demonstrated that M^2 and M_1 exhibited the greatest heritability in twin studies.

Lastly, using a combination of molars achieved the highest total correct classifications for each of the analyses (Table 11). Again, each of the analyses focused on the distal aspects of the teeth. The combined ProCoords demonstrated the highest total correct classification at 87.9%, followed by the PCs of the ProCoords at 87.1%. The ProCoords likely classified higher than the PCs based upon them due to noise and redundancy in the transformation; some aspects just did not vary much in the molar, particularly the paracone, which demonstrated no movement in the PCA of M^2 (Fig. 5). The ILDs, however, showed greater classification of the PCs based upon them than the raw ILDs. The greater classification of the ILD PCs was likely due to the transformation and orthogonal rotation of the PCA being able to more adequately express the "shape" of the molars by using differing combinations of loadings.

The percent correct classification based upon the shape variables for M^1 is higher than results for *Homo sapiens* (68.8% correct classification) reported by Gómez-Robles et al. (2007), though their analysis also included the occlusal outline and examined different hominin species. The results of the present study are also on par with a similar study by Klales et al. (2012), which included an Asian population group along with American Blacks and Whites. The association of ILDs, and odontometrics in general, with ancestry estimation has been demonstrated in previous studies (Lukacs, 1985; Lukacs and Hemphill, 1993), as has the utility of LDFA and odontometrics with sex estimation (Ditch and Rose, 1972). Further, the total correct classification results are similar to those achieved by Edgar (2005) using dental morphological traits. The present study demonstrated the utility of bridging the gap between size and shape in the estimation of biological ancestry using human molars. Molar intercusp relationships can be used in a forensic context to aid in the creation of the biological profile and can also give insight into evolutionary relationships without the influence of gross size.

CONCLUSIONS

The utility of modern geometric morphometric analyses using the first and second molars, both maxillary and mandibular, has been demonstrated and can significantly discriminate between modern population groups, as was observed by Morris (1986) in modern world populations using occlusal polygons. However, the utility of this method only currently extends to modern American Whites and Blacks; the usefulness of this method on other modern American groups (Asians and Hispanics) is currently being investigated. After a General Procrustes Analysis, which translated, scaled, and rotated each of the specimen's coordinate points to a common coordinate system, significant shape differences were found between American Whites and Blacks. As demonstrated through LDFA, the maxillary second molar proved to be the single tooth with the greatest discriminating power. The ILDs for both the maxillary and mandibular molars demonstrated lower correct classifications than the corresponding shape analyses, with the exception of the mandibular second molar. The addition of centroid size in the shape analyses only improved classification of the maxillary first molar using the ProCoords, and then generally improved the analyses of the PCs based on the ProCoords. The current results are congruent with previous studies on biological affinity as

assessed through the teeth (Lukacs, 1985; Harris and Rathbun, 1989; Lukacs and Hemphill, 1993; Irish, 1997, 2005; Hanihara and Ishida, 2005; Edgar, 2005). Bailey (2004) and Bailey et al. (2008) have demonstrated the utility of morphometrics on molars in the evolutionary context using the first molar. However, the present study indicated that using a combination of all of the molars might elucidate information with higher fidelity. The incorporation of geometric morphometric analyses in dental studies has promise and has proven to be just as useful as overall size or nonmetric dental morphology by bridging the gap between purely metric or nonmetric analytical pursuits.

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