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Craniometric determination of population affinity in South Africans

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Abstract A vital aspect of skeletal analysis is the determination of population affinity of an unknown individual. The aim of this paper is to develop discriminant function formulae to determine race from craniometric dimensions of South African blacks and whites. Skeletons used in this study came from the Universities of the Witwatersrand and Pretoria. The sample is composed of 53 white males and 53 white females and 45 black males and 45 black females. Using 13 standard cranial and 4 mandibular dimensions, average accuracies of 98% were obtained from the crania, which were much more discriminatory than the mandibles (74% males, 87% females). When a “leave-one-out classification” technique was applied to the sample to measure accuracy of multivariate classification, this accuracy was about the same as obtained from the multivariate function. A posterior probability of 0.80 or more was found in as much as 96% of the sample. Stepwise discriminant function formulae for incomplete remains (vault and face) were also derived. Prediction accuracy was considerably lower when North American based formulae were tested on the South Africans, indicating significant craniometric differences between these populations.

Key words Human identification · Race · Discriminant function · Skull · Mandible · South Africa

Introduction

In any analysis of a forensic case, the usual demographic characteristics of age, sex, race and ante-mortem stature need to be determined. Criteria used for the establishment of these characteristics are primarily relevant to that specific group, because standards for one group are not al-

ways applicable to another (Krogman and İscan 1986). Changing conditions in South Africa have led to the need for methods to improve identification from the skeleton (Steyn et al. 1997) and to establish specific standards for racial identification. Most African studies deal with sex determination (Washburn 1949; Keen 1950; De Villiers 1968a; Kieser and Groeneveld 1986; Macho 1990; Kieser et al. 1992; Loth 1996; Loth and Henneberg 1996; Steyn and İscan 1997) and stature estimation (Lundy 1984; Lundy and Feldesman 1987). De Villiers (1968b) completed a detailed study of the features of the skull of South African blacks, but dealt only briefly with differences from whites. Only Jacobson (1978) focused on race differences using radiographs of the craniofacial skeletons of South African blacks and whites. Kieser and Groeneveld (1989) analysed dental dimensions in South African blacks and whites and Lengua Indians of Paraguay, using discriminant function statistics.

Most attempts at craniometric differentiation of people of unknown racial origin are based upon North American standards (Giles and Elliot 1962; Howells 1970; Ayers et al. 1990; Gill and Rhine 1990; İscan and Cotton 1990). South Africans, however, are considerably different from Europeans and North Americans in their cranial dimensions (Morris 1994). Furthermore, interracial mixture between blacks and whites has been minimal when compared to, for example, North Americans. The purpose of this study is to develop specific craniometric standards for assessing population affinity of South African skeletal remains.

Materials and methods

Skulls of blacks used in this study came from the Dart collection of the University of the Witwatersrand and those of the whites were from both the Dart and University of Pretoria collections. The sample is composed of white males ($n = 53$) and females ($n = 53$) and black males ($n = 45$) and females ($n = 45$). The black sample had a younger mean age (45 years for males, 42 for females) than the whites (66 and 67 years for males and females, respectively). Birth dates of the subjects ranged from 1863 to 1936 in the Dart and 1906 to 1951 in the Pretoria Collections (Steyn and İşcan

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Table 1 Means, standard deviations and univariate F-ratios for South African whites and blacks

Variable ^a (mm)	White		Black		F-ratio ^b
	Mean	SD	Mean	SD	
<i>Males</i>					
Cranium <i>n</i> =		46		43	
Cranial length	187.5	5.42	186.7	5.10	0.46
Cranial breadth	139.6	5.70	132.3	5.66	36.48 ^c
Max. frontal br.	119.7	4.94	114.6	6.58	16.91 ^c
Min. frontal br.	97.7	3.78	97.1	4.07	0.48
Bizygomatic br.	128.9	4.27	130.6	4.50	3.31
Basion-nasion	102.3	4.38	101.5	3.55	0.73
Basion-bregma	136.7	4.08	133.9	4.59	9.19 ^d
Basion-prosthion	95.4	5.21	104.4	6.93	48.45 ^c
Nasion-prosthion	71.2	3.82	68.3	4.71	10.18 ^d
Mastoid height	34.2	3.37	30.9	3.08	23.10 ^c
Biasterionic br.	113.4	5.09	106.9	4.31	42.09 ^c
Nasal height	53.5	3.51	48.2	4.48	38.14 ^c
Nasal breadth	24.8	2.16	27.9	2.45	39.70 ^c
Mandible <i>n</i> =		44		44	
Bicondylar length	77.2	5.54	79.1	4.65	3.28
Bicondylar br.	116.7	5.36	115.0	4.92	2.42
Bigonial breadth	99.9	5.71	97.1	5.61	5.45 ^c
Minimum ramus br.	31.3	3.61	35.4	3.29	30.25 ^c
<i>Females</i>					
Cranium <i>n</i> =		50		43	
Cranial length	179.0	5.91	178.0	6.24	0.66
Cranial breadth	137.5	4.75	129.8	7.07	39.23 ^c
Max. frontal br.	115.3	5.76	111.0	5.35	13.93 ^c
Min. frontal br.	93.5	4.60	93.4	4.52	0.02
Bizygomatic br.	122.0	3.47	121.4	5.14	0.36
Basion-nasion	96.6	4.21	95.3	3.92	2.04
Basion-bregma	130.5	5.18	126.3	6.72	11.29 ^d
Basion-prosthion	90.6	5.27	97.1	6.07	31.93 ^c
Nasion-prosthion	66.0	4.96	65.5	4.30	0.19
Mastoid height	31.4	4.15	26.2	3.00	46.06 ^c
Biasterionic br.	110.0	4.85	103.0	5.64	40.06 ^c
Nasal height	49.7	2.17	47.1	2.51	29.39 ^c
Nasal breadth	23.0	2.06	26.7	1.98	75.44 ^c
Mandible <i>n</i> =		47		45	
Bicondylar length	70.7	5.30	74.7	5.09	3.65
Bicondylar br.	111.3	5.92	108.5	5.64	5.34 ^c
Bigonial breadth	92.1	5.17	89.7	6.30	4.06 ^c
Minimum ramus br.	28.5	2.64	32.9	3.05	54.47 ^c

^aThese values are used in the calculation of Functions 1 (cranium) and 4 (mandible) with *df* 1.87 for male, and 1.91 for female skull dimensions, and 1.86 for male and 1.90 for female mandibular dimensions
^{c, d, e}Significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

1997). The subset of both groups selected for the study included specimens that were not edentulous and had no severe bone pathology. The black sample included the remains of individuals from a variety of tribes but De Villiers (1968b) has shown that they are morphologically homogenous. For this study, they were treated as a single group.

A total of 13 cranial and 5 mandibular measurements (Table 1) were taken using the standard Martin and Saller methods as described by Krogman and İşcan (1986), De Villiers (1968b) and Bräuer (1988). Stepwise discriminant function was applied to cranial and mandibular dimensions separately using the Wilks' lambda minimization procedure (with $F = 3.84$ to enter and $F = 2.71$ to remove). In addition, two combinations of cranial dimensions (vault and facial) were chosen for a stepwise discriminant procedure to create formulae that can be used on incomplete skulls.

In order to analyse effectiveness of the functions, a "leave-one-out classification" technique was applied to the sample to measure accuracy of multivariate classification. This jackknife approach takes one case aside and develops a discriminant function formula to classify that case. The process continues for all cases, one at a time. Although multivariate classification provides an understanding of within-sample assignment of individual cases, the actual affinity of a given individual may best be assessed by its posterior

probability of being reassigned to its original group (Campbell 1984; Kieser and Groeneveld 1989). A higher posterior probability confirms the percentage accuracy of a specimen's affiliation with the reference population. To confirm the need for population specific standards, the South African sample was cross-tested using discriminant function formulae developed for differentiating North American blacks and whites (Giles and Elliot 1962). The selection of this comparative group was based on the fact the present study had the same variables used in these formulae (Giles and Elliot 1962).

Results

Descriptive statistics listing the means, standard deviations and univariate F-ratios for white and black South African males and females are presented in Table 1. For crania, the F-ratios indicated that differences between the races were statistically significant for the majority of variables in both sexes. For mandibles, the most significant difference was minimum ramus breadth in both sexes.

Table 2 Stepwise discriminant function analysis of cranial and mandibular dimensions for South African whites and blacks

Step	Variables entered	Wilks' lambda	Equiv. F-ratio	Degrees of freedom
<i>Males^a</i>				
Function 1 (Cranial dimensions)				
1	Basion-prosthion	0.642	48.45	1.87
2	Nasal height	0.495	43.85	2.86
3	Biasterionic breadth	0.409	40.89	3.85
4	Nasal breadth	0.361	37.15	4.84
5	Basion-nasion	0.331	33.50	5.83
6	Mastoid height	0.316	29.59	6.82
Function 2 (Vault dimensions)				
1	Biasterionic breadth	0.649	49.71	1.92
2	Cranial breadth	0.599	30.40	2.91
3	Mastoid height	0.572	22.46	3.90
4	Minimum frontal br.	0.546	18.50	4.89
Function 3 (Facial dimensions)				
1	Nasal height	0.685	41.82	1.91
2	Nasal breadth	0.579	32.77	2.90
Function 4 (Mandibular dimensions)				
1	Minimum ramus breadth	0.740	30.25	1.86
2	Bigonial breadth	0.648	23.11	2.85
3	Bicondylar length	0.618	17.31	3.84
<i>Females^b</i>				
Function 1 (Cranial dimensions)				
1	Nasal breadth	0.547	75.44	1.91
2	Mastoid height	0.376	74.60	2.90
3	Nasal height	0.305	67.52	3.89
4	Basion-prosthion	0.277	57.35	4.88
5	Biasterionic breadth	0.251	51.91	5.87
Function 2 (Vault dimensions)				
1	Mastoid height	0.659	49.59	1.96
2	Cranial breadth	0.569	35.96	2.95
3	Cranial length	0.543	26.37	3.94
4	Biasterionic breadth	0.503	22.94	4.93
Function 3 (Facial dimensions)				
1	Nasal breadth	0.551	75.06	1.92
2	Nasal height	0.397	69.11	2.91
3	Nasion-prosthion	0.376	49.87	3.90
Function 4 (Mandibular dimensions)				
1	Minimum ramus breadth	0.623	54.47	1.90
2	Bicondylar breadth	0.558	35.31	2.89
3	Bicondylar length	0.532	25.83	3.88

^a Variables not selected for Function 1 include cranial length, cranial breadth, maximum frontal breadth, minimum frontal breadth, nasion-prosthion length, bizygomatic breadth and basion-bregma height; Function 2, cranial length, basion-bregma height and maximum frontal breadth; Function 3, bizygomatic breadth and nasion-prosthion height; Function 4, bicondylar breadth

^b Variables not selected for Function 1 include cranial length, cranial breadth, nasion-prosthion length, basion-nasion length, maximum frontal breadth, minimum frontal breadth, bizygomatic breadth, and basion-bregma height; Function 2, cranial length, maximum frontal breadth, minimum frontal breadth, and basion-bregma height; Function 3, bizygomatic breadth; Function 4, bigonial breadth

Table 2 shows the results of the stepwise discriminant function analysis of the skull and mandible. Wilks' lambda determines the order in which variables enter the function. (Variables not selected for the four functions are listed below the Table). In Function 1, 6 of the 13 cranial variables were selected in males and 5 in females. Basion-prosthion length was chosen first in males. In Function 2

(vault), 4 out of 7 variables participated and biasterionic breadth was entered first. Of the two out of four facial dimensions selected for Function 3, nasal height was first in order: three of the four mandibular variables (Function 4) contributed to race differences, with minimum ramus breadth selected first.

In females, 5 of the 13 cranial variables were selected in Function 1 in females (Table 2). Nasal breadth entered into the function first. Out of seven dimensions four were added in Function 2 and mastoid height was first. In Function 3 three variables took part with nasal breadth the most discriminatory. Of the four mandibular measurements, three were selected for females (Function 4) and as was the case for the males, minimum ramus breadth was the first chosen.

Coefficients and sectioning points appear in Table 3 for males and Table 4 for females. Standardized coefficients quantify the contribution of a variable to the overall classification. Structure coefficients are the simple product-moment correlations between the variables and the function. To calculate the discriminant score, each dimension is multiplied by its raw (unstandardized) coefficient which acts to "weigh" the variable according to its contribution to race differences. These values are then added together along with the constant. The constant has no inherent value and only serves to calibrate the sectioning point to zero if the number of cases in both groups are the same (as in Function 1 for males). When group numbers differ, as in all the other functions, the sectioning point must be calculated by averaging the two group centroids as shown in Tables 3 and 4. The discriminant score is then compared with the sectioning point. In Function 1, for example, a value greater than the sectioning point (-0.049065 in males; -0.12896 in females) is white. In contrast, Functions 4 in males and 3 and 4 in females a discriminant score greater than the sectioning point classifies as black.

Multivariate and cross-validation classifications are given in Table 5. Multivariate accuracies were very high in the cranium (Function 1), reaching 98% and 96% for males and females, respectively. Average discrimination from facial measurements ranged from 87% to 93% (Function 3). The vault and mandible were less racially dimorphic (Functions 2 and 4), ranging from 77% (males) to 83% accuracy (females). The same table also shows cross-validation percentages after using the leave-one-out classification. It is clear that the results were not considerably different from the multivariate discrimination classification.

Posterior probability of correct group membership increases with distance from the sectioning point. In order to measure posterior probability in a set of intervals, Table 6 was constructed. It is clear that the majority of the individuals in both sex groups had 80% or more posterior probability of being members of their original populations. For example as in Function 1, of correctly classified males, 91% of whites and 86% of blacks had a posterior probability of more than 80% to be a member of their actual white and black populations, respectively. Corresponding figures are less for the other functions. However, there were no correctly classified individuals who

Table 3 Canonical discriminant function coefficients and sectioning points for cranial and mandibular variables selected by the stepwise sub-routine for males

Functions and variables	Unstandardized coefficient	Stand. coeff.	Structure coeff.	White and Black group centroids
Function 1 (cranial dimensions)				
Basion-nasion	0.1036361	0.41	0.06	W = 1.40659
Basion-prosthion	-0.1166638	-0.71	-0.51	B = -1.50472
Mastoid height	0.0873897	0.28	0.35	
Biasterionic br.	0.0915375	0.43	0.47	
Nasal height	0.0644897	0.26	0.45	
Nasal breadth	-0.1830582	-0.42	-0.46	
Constant	-10.3308953			
Sectioning point	-0.049065 ^a			
Function 2 (Vault dimensions)				
Biasterionic br.	0.1005717	0.48	0.81	W = 0.82826
Cranial breadth	0.0988918	0.58	0.74	B = -0.98236
Min. frontal br.	-0.0863091	-0.35	0.50	
Mastoid height	0.1045828	0.34	0.57	
Constant	-19.6635113			
Sectioning point	-0.07705 ^a			
Function 3 (Facial dimensions)				
Nasal height	0.1663298	0.66	0.79	W = 0.81735
Nasal breadth	-0.2704951	-0.62	-0.77	B = -0.87184
Constant	-1.3765213			
Sectioning point	0.027245 ^a			
Function 4 (Mandibular dimensions)				
Bicondylar length	-0.0893011	-0.46	0.25	W = -0.77727
Bicondylar br.	-0.1060704	-0.60	-0.32	B = 0.77727
Minimum ramus br.	0.3540254	1.82	0.75	
Constant	5.6254967			
Sectioning point	0.0 ^b			

^a A discriminant score higher than the sectioning point classifies as white, lower as black

^b A discriminant score higher than the sectioning point classifies as black, lower as white

Table 4 Canonical discriminant function coefficients and sectioning points for cranial and mandibular variables selected by the stepwise sub-routine for females

Functions and variables	Unstandardized coefficient	Stand. coeff.	Structure coeff.	White and black group centroids
Function 1 (Cranial dimensions)				
Basion-prosthion	-0.0759954	-0.43	-0.34	W = 1.58438
Mastoid height	0.1405740	0.51	0.41	B = -1.84230
Biasterionic br.	0.0716162	0.37	0.38	
Nasal height	0.1963076	0.46	0.33	
Nasal breath	-0.3248690	-0.66	-0.53	
Constant	-6.0918283			
Sectioning point	-0.12896 ^a			
Function 2 (Vault dimensions)				
Cranial length	-0.0756214	-0.46	0.07	W = 0.90589
Cranial breadth	0.0687569	0.40	0.67	B = -1.06694
Biasterionic br.	0.0879088	0.47	0.65	
Mastoid height	0.1769011	0.64	0.72	
Constant	-10.2480112			
Sectioning point	-0.080525 ^a			
Function 3 (Facial dimensions)				
Nasal breadth	0.4532151	0.92	0.70	W = -1.19656
Nasion-prosthion	0.0734427	0.34	-0.03	B = 1.35973
Nasal height	-0.3670842	-0.86	-0.43	
Constant	1.7702316			
Sectioning point	0.081585 ^b			
Function 4 (Mandibular dimensions)				
Bicondylar length	-0.0860992	-0.45	0.21	W = -0.90817
Bicondylar br.	-0.0620960	-0.36	-0.26	B = 0.94853
Minimum ramus br.	0.4253305	1.21	0.83	
Constant	-0.1324754			
Sectioning point	-0.02018 ^b			

^a A discriminant score higher than the sectioning point classifies as white, lower as black.

^b A discriminant score higher than the sectioning point classifies as black, lower as white

were in lower posterior probability interval categories, that is, for example, less than 40%.

The last table (Table 7) shows the results of cross-testing discriminant function formulae derived from North American blacks and whites on South Africans. While

these formulae were almost as effective on South African blacks (96% in males, 98% in females) as in the original populations, they were much less accurate in whites (83% in males, 76% in females).

Table 5 Racial classification accuracy for the cranium and mandible

Functions	Total <i>n</i>	Whites		Blacks		Average %
		%	<i>n</i>	%	<i>n</i>	
<i>Multivariate discrimination</i>						
Males						
1. Cranium	89	97.8	45/46	97.7	42/43	97.8
2. Vault	95	78.8	41/52	83.7	36/43	81.1
3. Face	98	84.9	45/53	88.9	40/45	86.7
4. Mandible	90	73.9	34/46	79.5	35/44	76.7
Females						
1. Cranium	96	98.0	50/51	93.3	42/45	95.8
2. Vault	98	83.0	44/53	80.0	36/45	81.6
3. Face	94	96.0	48/50	88.6	39/44	92.6
4. Mandible	92	87.2	41/47	77.8	35/45	82.6
<i>Cross-validation</i>						
Males						
1. Cranium	89	93.5	43/46	95.3	41/43	94.4
2. Vault	95	78.8	41/52	83.7	36/43	81.1
3. Face	98	84.9	45/53	86.7	39/45	85.7
4. Mandible	90	71.7	33/46	79.5	35/44	75.6
Females						
1. Cranium	96	96.1	49/51	91.1	41/45	93.8
2. Vault	98	83.0	44/53	80.0	36/45	81.6
3. Face	94	94.0	47/50	88.6	39/44	91.5
4. Mandible	92	83.0	39/47	77.8	35/45	80.4

Table 6 Percentages of posterior probability intervals of correct classification for South African blacks and whites

Probability intervals	Male		Female	
	White	Black	White	Black
Function 1				
0.00–0.19	–	–	–	–
0.20–0.39	–	–	–	–
0.40–0.59	4.4	2.4	–	–
0.60–0.79	4.4	11.9	4.0	4.8
0.80–1.00	91.1	85.7	96.0	95.2
Function 2				
0.00–0.19	–	–	–	–
0.20–0.39	–	–	–	–
0.40–0.59	–	2.8	–	2.8
0.60–0.79	29.3	19.4	22.7	13.9
0.80–1.00	70.7	77.8	77.3	83.3
Function 3				
0.00–0.19	–	–	–	–
0.20–0.39	–	–	–	–
0.40–0.59	13.3	15.0	4.2	2.6
0.60–0.79	37.8	35.0	12.5	10.3
0.80–1.00	48.9	50.0	83.3	87.2
Function 4				
0.00–0.19	–	–	–	–
0.20–0.39	–	–	–	–
0.40–0.59	14.7	8.6	12.2	–
0.60–0.79	17.6	40.0	17.1	28.6
0.80–1.00	67.6	51.4	70.7	71.4

Discussion

This research has resulted in the development of effective osteometric standards for distinguishing South African whites from blacks. The significantly lower accuracy for race prediction using North American standards under-

Table 7 Race classification from South African crania using Giles and Elliot (1962) formulae derived from North American whites and blacks^a

Sex	Total <i>n</i>	Blacks		Whites	
		%	<i>n</i>	%	<i>n</i>
Males	91	95.5	42/44	83.0	39/47
Females	93	97.7	42/43	76.0	38/50

^aMale formula: basion-prosthion × 3.06 + cranial length × 1.6 – cranial breadth × 1.9 – basion-bregma × 1.79 – basion-nasion × 4.41 – bizygomatic × 0.1 + nasion-prosthion × 2.59 + nasal breadth × 10.56 (sectioning point = 89.27)
 Female formula: basion-prosthion × 1.74 + cranial length × 1.28 – cranial breadth × 1.18 – basion-bregma × 0.14 – basion-nasion × 2.34 + bizygomatic × 0.38 – nasion-prosthion × 0.01 + nasal breadth × 2.45 (sectioning point = 92.20). These are sectioning points as corrected in Krogman and İşcan (1986)

scores the need for population specific standards. These results are supported by earlier studies (Snow et al. 1979; Ayers et al. 1990), reporting that the Giles and Elliot (1962) formulae did not work very well in a sample of modern North American forensic specimens. The differences in cranial dimensions of the various groups were attributed to the possible existence of secular changes (Giles and Elliot 1962). In the case of South Africa, crania are generally narrower than those from the Hamann-Todd and Terry collections and forensic specimens (Giles and Elliot 1962; Ayers et al. 1990). This is true for South African males of both races and for black females, but not for white females. A trend towards brachycephalization has been demonstrated in many areas of the world (e.g., Weidenreich 1945; Henneberg 1976; Nakashima 1986), but this has not been observed in subsaharan Africa (Hen-

neberg and Steyn 1993). Thus, different evolutionary processes on various continents may have resulted in different expressions of this temporal trend in head shape.

Apart from indicators of cranial breadth, most dimensions for South Africans are comparable to the American forensic sample (Ayers et al. 1990), or fall between them and the Hamann-Todd and Terry collections (Giles and Elliot 1962). A possible exception is nasion-prosthion length, which is shorter in South African blacks.

Accuracy obtained in this research for crania (96%–98%) surpasses that reported in most studies of American whites and blacks. Cross-validation tests were carried out by the jackknife procedure similar to that utilized by Kieser and Groeneveld (1989) which represents more realistic, unbiased estimates. The resulting cross-validation tests provided classification accuracies not considerably different from those obtained from the multivariate classification. Howells (1970) reached 100% accuracy, using several additional measurements. Giles and Elliot (1962) obtained 83%–89% accuracy, while Ayers et al. (1990) attained an average accuracy of 74%. Gill and Gilbert (1990), using only the midfacial skeleton, obtained accuracies ranging from 82% to 94%. However, none of these studies used the jackknifing approach to obtain more realistic estimates.

Discriminant function classification is based on whether the discriminant score of a given individual is above or below the sectioning point. However, posterior probability provides information about the probability of an assigned person's correct placement in its original population. Of the correctly classified individuals more than 86% had a posterior probability of 0.8 or higher for Function 1. This clearly suggests that discriminant functions provide important means to identify the population affiliation of unknown individuals in South Africa.

In this study, width dimensions of the vault, nasal morphology and prognathism seem to separate blacks from whites. In the entire cranium prognathism, biasterionic breadth and the nasal dimensions are the most divergent. In the vault itself mastoid height also played a role. Facial differences were more apparent in the nose. South African mandibles are not considerably distinct from each other from these dimensions used. Minimum ramus breadth was the dimension most different between the races. In their study of four populations, males and females combined, Johnson et al. (1989) also achieved higher accuracies from the viscerocranium than the neurocranium, with best results from a combination of variables (100% in Caucasoids, 73% in Negroids). Race differences in the facial skeleton were also observed in South Africans by Jacobson (1978).

This study also tested the current data with standards developed for another population. It was discovered that formulae developed for North Americans were less effective in determining the race of South Africans. The North American standards misclassified many of the South African whites as blacks because the South African blacks have the smallest cranial dimensions of all four race groups. The high level of accuracy obtained in this study

may also be attributed to the low degree of interpopulation mixture in South Africa.

This study produced discriminant function formulae that accurately classify skeletal remains of unknown race. Osteometric standards are population specific and it has often been demonstrated that they are not interchangeable between groups. It can therefore be concluded that standards based on South African samples will result in a more accurate assessment of those inhabitants than standards derived from geographically distant populations.

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