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Ancestry estimation in South Africa using craniometrics and geometric morphometrics

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ABSTRACT

Population history and positive assortative mating directs gene flow in such a way that biological differences are recognized among groups. In turn, forensic anthropologists quantify biological differences to estimate ancestry. Some anthropologists argue that highly admixed population groups, such as South African coloureds, cannot achieve acceptable accuracies because within group variance is too large. Whereas ancestry estimation in South Africa has been limited to craniometric data from South African blacks and whites, the current study integrates craniometric and geometric morphometric data from the three largest South African groups.

Crania from 377 South African individuals (black = 158, white = 112, and coloured = 107) comprised the sample. Standard measurements were collected and the coordinate data were subjected to Generalized Procrustes Analysis (GPA), which resulted in size-free shape variables (ProCoords). A principal component analysis was used to combine the shape variation captured in the ProCoords (ProCoords PC). Linear discriminant analysis (LDA), using equal priors, stepwise variable selection and leave-one-out cross-validation, was conducted on the ProCoords, the ProCoords PCs, and the traditional craniometric data.

The LDA using 18 stepwise selected ProCoords resulted in the highest cross-validated accuracy (89%). Utilization of geometric morphometric data emphasized that the relative location of cranial landmarks was more discriminating than simple linear distances. Regardless of high levels of genetic admixture, South African coloureds are a homogeneous group and morphologically distinct from other contemporaneous South African populations. Furthermore, the present study demonstrated a correspondence between peer-reported race and morphological differences in the crania of black, white, and coloured South Africans.

1. Introduction

Throughout much of the world, social race remains a reality in which persons attribute themselves to different groups, either socially, or, in the case of the population census, legally. Social race is a concept of identification based on cultural, historical or familial affiliation and has no biological reality [1–4]. However, morphological differences are recognized among groups because positive assortative mating, geographical distances, and social forces act as barriers for gene flow, thus limiting group interaction and increasing the variation between groups [5–7]. In turn, forensic anthropologists quantify morphology to estimate ancestry, or social race, which provides practical information that is useful in a medico-legal setting [2,5].

From 1948 to 1990, South Africans were forcibly separated according to race in public, geographic locality, and education. In South Africa, the former racial classification system is maintained within all bureaucratic systems in the country but now the terms are based on self-perception and self-identification [8–10]. Institutionalized racism drastically affected gene flow in modern South Africa. However, colonization and migration shaped the unique constructs of the South African population prior to the implementation of various segregation laws and is thus considered the foundation to modern variation in South African groups.

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In 1652, the Dutch East India Company established a fueling station in what is known today as Cape Town, South Africa. After some time, Europeans, primarily Dutch with a scattering of French Huguenots and Germans, began to create permanent settlements in the area [8,11]. A large number of English settlers followed in the mid-1800s. In order to maintain the rapid expansion of Cape Town, slaves were introduced from Central Africa, Madagascar, India and Indonesia, among other countries, as well as from indigenous populations of southern Africa, such as the Khoikhoi and San [11,12]. Historical records indicated marriage among white males and free black and indigenous females was common [8,13]. During this time in history, religion influenced status more than skin color, such that the social status of black or indigenous women would increase if they were considered Christian, which often led to marriage and miscegenation [14,15]. Acceptance of children from cross-cultural relations ranged from full acceptance to slave status. However, the fluidity surrounding race relations decreased in the early 1800s [15]. Inter-racial relations became social taboo and the frequency of mixed marriages decreased and were eventually outlawed with the Prohibition of Mixed Marriages Act of 1949 [13].

Even prior to the arrival of the Europeans, admixture occurred among the indigenous groups, specifically among the Khoikhoi and San (commonly pooled and referred to as Khoe-San), and Bantu-speakers [16,17]. Nine of the 11 South African national languages are recognized as Bantu languages, a sub-group of the Niger-Congo languages. However, one of the South African Bantu languages, isiXhosa, contains clicks similar to those found within the Khoisan linguistic group that is associated with the Khoe-San. The presence of Khoisan characteristics in a Bantu language and the archaeological evidence of shared technologies suggest gene flow between Bantu-speakers and Khoe-San. Even though gene flow is evident between Bantu-speakers and Khoe-San, the groups are considered distinct in South Africa [11,18]. In sum, considerably complex interactions of different peoples and cultures form the foundation of modern South Africa.

According to the 2011 South African census, the three largest groups in South Africa are blacks (79%), whites (9%), and coloureds (9%) [10]. The remainder of the population consists of Indians and Asians. Individuals who were a product of the Bantu expansion and who were not Khoe-San, were grouped into a single entity and considered black South Africans underneath the apartheid government [13]. Thus, contemporary black South Africans are comprised of individuals from numerous ethnic groups that largely self-identify with language. Coloureds are a self-identified group unique to South Africa [8,11], whose history and genetic admixture are often relayed through documents on slavery, marriage, and personal accounts of the settlement of Cape Town in the 17th and 18th centuries. The term coloured dates back to 1808, following the abolishment of slavery [8,12]. The distinct group, which emerged as a result of this complex history, displays the highest levels of intra- and inter-continental genetic admixture compared to all other populations in the world [11,19,20]. On average, the genetic composition of coloureds is an equal contribution from four groups, namely European, Bantu-speakers, Khoe-San and Indian [19,20]; however, genetic contributions vary between the sexes, at the individual level, and in geographic location within South Africa [21].

Historical circumstances contribute to cultural and social behavior, which subsequently modifies the range of human variation within a population. Specifically, positive assortative mating alters trait frequencies and biologically modifies social groups. Although the genetic structure of South Africa's populations demonstrates past admixture, institutionalized racism and positive assortative mating has left these groups largely segregated from one another and subsequently has decreased variation within groups and increased variation between groups. South African whites, blacks, coloureds and Asians all have high rates (>96%) of homogamy, even after the termination of institutionalized racism [13]. Though apartheid is likely the most prominent force driving separation among South Africans, other cultural barriers, such as the polylinguistic society, reduces the rate of heterogamy [13]. Thus, South Africa's history, and specifically South Africa's race history, can be used to identify differences among groups [22–24]. Similarly, race relations were used to interpret modern craniometric variation among black and white North Americans. In North America, a strong concordance exists between cranial morphology and social race, seen by correct classifications as high as 97% [5,25].

Yet, some anthropologists assume that high levels of genetic admixture, as found amongst coloured South Africans, will present with such a wide spectrum of variation that attempts to estimate ancestry will fail and the unidentified remains will be meaninglessly cast into white and non-white divisions [26,27]. Theoretically, this abovementioned assumption is flawed because panmixia does not exist; as described earlier, cultural, social, and legal barriers have restricted gene flow among groups in South Africa and elsewhere. Previous studies using modern South African crania have been limited to standard craniometric analyses between black and white South Africans. When modern South African craniometric data were explored by group and sex, accuracies of 71% were achieved [23], but when mid-facial variables were explored by group only, accuracies increased to 95% [22]. The purpose of this study is to estimate ancestry and to evaluate craniometric patterns in the three largest social groups of South Africa through craniometric and geometric morphometric techniques. Because craniometric data reflects genetic relationships, multivariate statistical analyses should reveal three largely unique social groups [5,7,28,29].

2. Materials and methods

A total of 377 crania were used in the analyses and included South African (SA) black (n = 158), white (n = 112), and coloured (n = 107) individuals. Because the same landmarks were not available on every cranium, the sample sizes for the geometric morphometric analyses were reduced to a total of 209 individuals (black = 101, white = 58, and coloured = 50). The skeletal remains were housed in different skeletal collections in South Africa, including the Pretoria Bone Collection at the University of Pretoria, the Raymond A. Dart Collection of Human Skeletons at the University of Witwatersrand, and the Kirsten Skeletal Collection at the University of Stellenbosch. Although males and females comprised the sample, the sexes were pooled for all analyses because the aim was to explore population differences. All individuals were older than 18 years of age and did not exhibit signs of pathology, traumatic injuries or extensive antemortem tooth loss.

Coordinate data were collected with a three-dimensional digitizer and 3Skull [30]. In an effort to retain large sample sizes, 44 cranial landmarks were chosen to represent the entire cranium with special reference to the mid-face, which previously achieved high accuracies distinguishing modern South African groups (Table 1) [22].

Coordinate data were subjected to Generalized Procrustes Analysis (GPA) in the program MorphoJ [31]. A GPA is a superimposition technique that translates, scales, and rotates the landmark combinations upon the centroid size and location for each specimen [32]. Because GPA minimizes the squared difference between homologous landmarks, the resultant Procrustes coordinates (ProCoords) are size-free shape variables. A principal component analysis (PCA) was used to combine the shape variation captured in the ProCoords for the entire cranium. The PCA of the ProCoords (ProCoords PCs) yielded 125 principal