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An anthropometric assessment of craniofacial variation in historic and modern sub-Saharan African populations

Melissa Jones

A thesis submitted to the Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy
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UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

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Co-supervisor: Dr J Hemingway

Declaration

I, Melissa Jones, declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before any other degree or examination at any other University.



Melissa Jones Date: 01/08/2022

Dad, this is for you.

In memory of my father

Eugene Pininski

1951 - 2020

Presentations arising from this thesis

Jones, M., Steyn, M. and Hemingway, J. (2017). “Anthropometric data and studies of human variation at the School of Anatomical Sciences, University of the Witwatersrand”. Oral presentation presented at the 45th Annual Conference of the Anatomical Society of Southern Africa. University of Cape Town, Western Cape, South Africa.

Abstract

Craniofacial morphology varies between populations and can be used to assess population history. As very little information is available regarding craniofacial morphology from living individuals, this study aimed to investigate craniofacial variation among historic western, eastern, southern-central and southern sub-Saharan Africa populations and a modern South African population, using anthropometric data of the head and face. From this, population variation between different sub-Saharan African groups as well as population history can be determined to gain a better understanding of the population movements throughout sub-Saharan Africa.

A historic data set of a total of 1346 individuals from various sub-Saharan communities, supplemented with 51 CT scans of the head and neck from a modern South African sample were used. The addition of CT scans allowed for a more complete dataset representing modern South Africans. The historic dataset contained anthropometric information and measurements which were recorded as hand-written documents. Twelve measurements (corresponding to the same measurements in the historic dataset) were taken from the CT scans using a three-dimensional (3D) DICOM viewer with an inbuilt measuring tool (OsiriXLite). Principal Components Analyses (PCA) were employed to assess craniofacial variation among individuals to determine which regions of the head and face are morphologically discriminative. Discriminant Function Analyses (DFA) were then employed to assess morphological differences and similarities between populations to assess the level of population separation possible. To determine whether geographic distance correlates to morphological distance, Mantel tests and Principal co-ordinate plots were used.

Overall, the Khoe and San population had smaller craniofacial morphology than Bantu-speakers while modern South Africans were the largest, particularly around the mandibular region. PCA revealed much overlap between the population groups. DFA revealed that eastern and southern Bantu-speakers shared a similar craniofacial morphology, whereas western and southern-central Bantu-speakers were more similar. The Khoe and San and modern South African populations were distinct in craniofacial morphology. There was no correlation between geographical and morphological distances, suggesting that geography and morphology are independent of one another. This is most likely because the Bantu-speaking populations had already inhabited regions where the Khoe and San lived.

The outcomes from the study suggest that anthropometric data can be used to assess population variation and population history. Sub-Saharan African populations are distinct in their craniofacial morphology and this may be due to environmental and functional responses due to

population migrations. This study supports the current theories regarding both western and eastern stream Bantu-speaker migrations, with southern Africans probably branching from eastern African population groups.

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List of abbreviations

mtDNA	mitochondrial DNA
GM	geometric morphometrics
CT scans	computerised tomography scans
KRC	Kalahari Research Committee
WIMSA	Working Group of Indigenous Minorities in Southern Africa
SASC	South African San council
NKSK	National Khoe and San Council
3D	three-dimensional
FH	Frankfort horizontal
HHM	head height
HL	head length
HB	head breadth
MFB	minimum frontal breadth
BZB	bi-zygomatic breadth
BGB	bi-gonial breadth
BOB	binocular breadth
IOB	interocular breadth
NB	nasal breadth
NH	nasal height
TFH	total facial height
UFH	upper facial height
TEM	technical error of measurement
ISAK	International Society standardization Advancement in Kinanthropometry
PCA	Principal Components Analysis
DFA	Discriminant Function Analysis
SD	standard deviation
PCoA	Principal Co-ordinate Analyses
SES	Socioeconomic status

CHAPTER 1: INTRODUCTION

Biological anthropologists have long acknowledged that morphological differences exist between populations living in different geographical areas and that cranial morphology can be used to accurately distinguish between different population groups (de Villiers, 1968; Howells, 1973; Moore-Jansen *et al.*, 1994; İşcan and Steyn, 1998; Ribot, 2004; L'Abbé *et al.*, 2006; Franklin *et al.*, 2007; 2010; Ramphaleng, 2020). Sub-Saharan Africa has a richly diverse population and one-third of the African population are recognised as Bantu-speakers (http://www.statssa.gov.za/). This diversity reflects the complex history of the people of sub-Saharan Africa (Choudhury *et al.,* 2017). Environmental, cultural, and political changes led to large historical migrations which have helped form African societies and ways of living. African populations show a range of linguistic, cultural, and phenotypic variations (Tishkoff *et al.,* 2009).

Bantu-speakers form part of a group of over 200 million people from central and southern Africa. "Bantu" languages span sub-Saharan Africa, and its origin can be traced back to west Africa (Vansina, 1995; Li *et al.,* 2014). The place of origin for the "Bantu" languages has been suggested as the Grassfields region of present-day Cameroon, near the border with Nigeria. This is the place where "Bantu" languages show the highest levels of diversity and coincide with the greatest number of related non-Bantu languages (de Maret, 2013). Bantu-speaking populations arrived in southern Africa approximately 2000 years ago following two directions; a western route and an eastern route, before further heading south into South Africa (Hammond-Tooke, 1974; Newman, 1995; Huffman, 1996; Li *et al.,* 2014). It has been suggested that present-day South Africa was first occupied by the southern eastern branch of Bantu-speakers while Namibia and western parts of South Africa were first occupied by the Khoe and San populations. As the western branch of Bantu-speakers reached northern Namibia, their movement was halted by the Khoe and San population and the need for specific climatic requirements for agriculture (Li *et al.,* 2014). Although some Khoe and San populations remained relatively untouched during this expansion, some were replaced or integrated by the Bantu-speakers (Schlebusch, 2010; Pickrell *et al.,* 2012; Li *et al.,* 2014).

While most researchers agree that the Bantu-speaker migrations originated near the borders of the current Nigeria and Cameroon (Pakendorf *et al.,* 2011; de Maret, 2013; Li *et al.,* 2014), there is debate regarding the routes, and timing taken as the populations spread through sub-Saharan Africa (Pakendorf *et al.,* 2011; Li *et al.,* 2014). Researchers have used linguistic (Vansina, 1979; de Fillipo *et al.,* 2012; de Maret, 2013; Busby *et al.,* 2016), archaeological (Huffman, 1970; 1989; de Maret, 2013), and genetic (Tishkoff *et al.,* 2009; Pakendorf *et al.* 2011; de Filippo *et al.,*

2012; Li *et al.,* 2014; Busby *et al.,* 2016; dos Santos, 2018; Schlebusch and Jakobsson, 2018) evidence for the study of Bantu-speaker migration patterns. Strong links between genetic and linguistic relationships among globally distributed populations have been noted (Wood *et al.,* 2005; Tishkoff *et al.,* 2009; Scheinfeldt *et al.,* 2010; Li *et al.,* 2014). Additionally, populations that are geographically close to one another, speak linguistically similar languages and share similar cultural traditions are more likely to exchange genes (Scheinfeldt *et al.,* 2010). This has resulted in the phenotypic and genetic adaptations and variations seen among African populations (Campbell & Tishkoff, 2010).

The movement and expansion of Bantu-speaking populations was perhaps one of the most important migrations responsible for shaping sub-Saharan African diversity. Population variation between Bantu-speaking populations and Khoe and San populations has been studied extensively (e.g., de Villiers, 1968; Howells, 1973; Hammond-Tooke, 1974; Ribot, 2004; Franklin *et al.,* 2005; 2007; 2010; L'Abbé *et al.,* 2006; Harvati and Weaver, 2006; Ramphaleng, 2020). Using crania, population specific features are evident in different African population groups. The crania of the Khoe and San present with a short and low vault with narrow orbits and a narrow vault and a highly curved occipital bone, whereas that of the west African groups present with a high long vault, high and wide orbits with a broad frontal bone (Howells, 1989; Ribot, 2004). Additionally, Bantu-speaking groups showed more homogeneity (Ribot, 2004) and generally have longer crania, have higher foreheads, higher anterior projection of the upper face and more pronounced noses and taller faces than the Khoe and San (Franklin *et al.,* 2007).

Anthropologists have long been using traditional craniometrics to study population movements and population variation (Howells, 1973; Moore-Jansen *et al.,* 1994; Ousley and Jantz, 2012; McKeowen and Schmidt, 2013). However, very little information is available regarding craniofacial morphology from living individuals. A recent study by Ramphaleng (2020) used life and death face masks to assess African population variation. The author noted differences between northern, western, eastern and southern population groups based on craniofacial morphology. North Africans exhibited narrower and longer faces and narrower noses. Similarly, eastern and central Africans had narrower and longer faces while western-central populations exhibited wider faces with a greater inner canthal distances. The Khoe and San populations were distinct from other groups having broader and shorter noses and narrower orbits.

However, most of the studies used skeletal remains and few studies (Ramphaleng, 2020) have looked at assessing craniofacial variation population in sub-Saharan Africa using information obtained from anthropometric data. During exhibitions in the 1950s, 1960s and 1970s, vast amounts of anthropometric data were collected from sub-Saharan African populations and the

records have been housed at the School of Anatomical Science, University of the Witwatersrand, Johannesburg since then. Until now, these records have not been used in research to explore historic sub-Saharan African population variation and population history. The information obtained from this historic data will aid in understanding variation between different sub-Saharan African groups as well as providing a better understanding of the population movements throughout sub-Saharan Africa. With increasing advancements in imaging modalities to assess craniofacial variation (Stull *et al.,* 2014b), historic data sets (such as this one) can be supplemented with data from modern populations to create a more complete and comparable dataset. Imaging modalities have become increasing popular over the years and studies have shown that measurements taken from crania and those taken from virtual images present with a low error rate (Decker, 2010; Stull *et al.,* 2014). Additionally, anthropometric landmarks are easy to identify and reproduce on scanned images (Stull *et al.,* 2014b).

1.1. Aims and Objectives

This study aimed to use historic and modern craniofacial anthropometric data to assess craniofacial variation among western, eastern, southern-central and southern sub-Saharan African populations. By using anthropometric data, it allows for the use of more complete data sets as well as contributing other information that is not encompassed within bone alone. Although the historic records contain invaluable information, in order to have a fully complete and comparable dataset, a sample of a modern South African population was included using modern imaging modalities and software. This allowed for a more comparable dataset and one that is representative of present-day South African individuals. Multivariate analyses were employed as it allows for a statistically robust means of evaluating morphological similarities and differences between population groups.

The objectives were as follows:

1. To assess the anthropometric craniofacial variation between individuals from historic western, eastern, southern-central and southern African population groups using historical data collected during the 1950s, 1960s and 1970s and compare this with similar data from a modern South African population.
2. Determine patterns of morphological discrimination between various population groups and assess whether it is possible to separate populations based on craniofacial morphology.
3. Assess geographical distances and morphological distances between population groups to better understand migration patterns among historic and modern sub-Saharan African populations.

4. Evaluate proposed migration routes through sub-Saharan Africa based on both geographical and morphological distances and identify possible migration barriers.

Very few studies have assessed craniofacial variation using soft tissue facial data and most studies have assessed this using dry skulls. Therefore, the information obtained from the abovementioned objectives can be compared to information obtained from cranial studies. It will also allow for the interpretation of migration patterns in sub-Saharan Africa, thereby supplementing past Bantu-migration studies.

CHAPTER 2: LITERATURE REVIEW

Cranial morphology and craniometrics have been used extensively to assess population variation (de Villiers 1968; Howells, 1973; Moore-Jansen *et al.,* 1994; L'Abbé *et al.,* 2006; Franklin *et al.,* 2007; 2010; McKeowen and Schmidt, 2013). Physical anthropologists have acknowledged that morphological differences exist between populations living in different geographical areas and that cranial morphology can be used to gain information on population variation and past population histories (Howells, 1973; Moore-Jansen *et al.,* 1994; McKeowen and Schmidt, 2013). Although there is often admixture between populations, some barriers, such as those determined by culture, geography, environment and language, continue to influence biological and genetic diversity (Edgar and Hunley, 2009).

2.1. Population movements and the populations of Africa

Population movements, or migration, is as old as humanity itself and has played a crucial role in shaping the world. Today, most people live in cities where individuals of different origins have immigrated to (Barbujani and Colonna, 2010). Gene mutation, natural selection, gene flow and genetic drift all play a role in genetic variation seen among populations. Due to these evolutionary forces, each geographically distinct population is (to some extent) biologically distinct from other populations (Relethford, 2010; Noback *et al.,* 2011; King, 2015). The population within the original area is referred to as the "parent population" and is genetically distinct from the populations formed by the migratory populations (King, 2105). Genetic variation between populations is patterned by geographic space and can be described as clinal (Barbujani and Colonna, 2010). Geographic distances from east Africa (likely an origin of anatomically modern humans), for example, are good predictors of the genetic diversity of populations throughout the world (Lui *et al.,* 2006). In fact, genetic diversity decreases with increasing geographic distance from Africa (Prugnolle *et al.,* 2005; Manica *et al.,* 2007).

Africa has more genetic diversity than anywhere else in the world (Choudhury *et al.,* 2017; Skoglund *et al.,* 2017). Present day South Africans include a major ethnolinguistic group of black south eastern Bantu-speakers (80.9% of the population), an admixed population (referred to as Coloured at 8.8% of the population), whites of European descent (7.8% of the population), an Indian population (2.6%) and small proportion of additional ethnolinguistic affiliations (http://www.statssa.gov.za/). The complex history of the people of sub-Saharan Africa is reflected in the diversity of the present populations and recent population migrations which have led to extensive regional admixture (Choudhury *et al.,* 2017).

2.1.1. Factors influencing the distribution of people and migration patterns

In any migratory scenario, there are limitations to the path a group can take. As the Bantu-speaking people would have expanded by land only, there are several regions of the African continent that would have been more difficult to navigate than others. This would have likely affected the trajectory path that the people would have travelled. The world's second largest rainforest, the Congo Basin, spans 202 3428 square kilometres across six countries: Cameroon, Central Africa Republic, Democratic Republic of Congo, Republic of Congo, Equatorial Guinea, and Gabon. This area of the African continent is much wetter and lusher than the surrounding more arid areas (Ford, 2018). Certain parts of the rainforest are conducive to farming and habitation, whereas other parts are more swamp-like and therefore less inhabitable and more difficult to navigate (Ford, 2018). As such, the Congo Basin may have very well provided a geographic boundary around which the Bantu-speaking people migrated. Additionally, along the eastern side of the continent, there are large mountain ranges. This again may have limited the migratory path of the Bantu-speaking people.

Climate and ecological changes have also played a role in migration patterns. Africa is the second largest continent in the world, spanning many latitudes and climate zones and therefore has a landscape that is subject to various climates. It has been suggested that a shift from a humid to a drier environment approximately 5000 years ago, along with the adoption of new crops suited to a drier environment, may have contributed to the widespread migration of Bantu-speaking people throughout Africa (Campbell and Tishkoff, 2010). Population migrations into new environments with different climates can directly influence anthropometric variables (Hiernaux and Froment, 1976; Beals *et al.,*1984; Harvati and Weaver, 2006).

Geography is a key element in understanding population differentiation both worldwide and within a continent (Ribot, 2004). Global human craniometric and genetic affinity patterns fit a model of isolation by distance. The isolation by distance model best describes the significant concordance between geographic distance and genetic variation. This model predicts that increased geographic distance will limit migration between populations and that genetic similarity between populations will decrease with increasing geographic distance (Relethford, 2004). Thus, the geographical distance between two populations has the strongest effect on gene flow, consequently affecting the biological diversity within and between populations (Relethford, 2004; Von Cramon-Taubadel and Lycett, 2008; Relethford, 2009). However, genetic data shows that there is some level of founder effect i.e. high level of homogeneity despite geographical distance (Pakendorf *et al.,* 2011; Rowold *et al*., 2016).

2.1.2. The Khoe and San

Africa is considered the birthplace of modern humans and is a source of geographic expansion of ancestral populations into other regions of the world (Manica *et al.,* 2007; Campbell and Tishkoff, 2010). The migration of anatomically modern humans out of Africa occurred 50 - 200 thousand years ago and eventually led to the colonization of almost the entire world with extinction of all earlier archaic forms (although with some interbreeding) (Li and Durbin, 2011; Lopez *et al.,* 2015). This expansion resulted in the genetic diversity of non-African populations as a subset of the genetic diversity present in African populations. Africa has the highest levels of human genetic variation in the world as well as a considerable amount of environmental, linguistic, and cultural diversity (Campbell and Tishkoff, 2010). African demographic history is characterized by fluctuations in population size, short- and long-term migrations and admixture which in turn has resulted in the complex variation seen in modern African populations (Campbell and Tishkoff, 2010).

Historically, African populations can be split into north Africans, west-central Africans, southern and east Africans (Tobias, 1978). Generally, the north Africans share similarities with European populations, west-central Africans are considered the original Bantu-speaking people of Africa, southern and some eastern Africans are today collectively referred to as the Khoe and San, while other east Africans show some similarities to Arab-Asian people (Bleek, 1927; Tobias, 1978). However, it must be kept in mind that admixture still occurs between population groups and as a result, genes will be exchanged between these groups. This is reflected in populations of Cameroon of west-central Africa. Chadic-speaking population groups reveal some affinities to East Africans despite the geographical distance between them (Cherný *et al.,* 2004) Additionally, northern and southern Cameroon show substantial genetic diversity, most likely from a back migration from Asia and neighbouring Bantu populations (Spínola, *et al.,* 2011).

Changes in climate led to migration of population through Africa. Approximately 9 000 years ago, some areas of the Sahara had a wet climate. However, around 3 000 years ago, the region dried up and separated the African continent into northern Africa and sub-Saharan Africa (comprising of eastern, western and southern parts) (Jurmain *et al.,* 2005; Demenocal and Stinger, 2016). This tended to result in geographical separation of the populations living in these areas.

Before colonisation, parts of southern Africa were occupied by different indigenous groups. Although there is no clear consensus on terminology, the Khoe and San is the term used to denote the KhoeKhoe and San groups. These groups have been considered to share both physical and linguistic characteristics (Thompson, 2001). However, these two groups are independent cultural groups and as such need to be individually recognised (National Khoi and San Council).

Traditionally, herders (Khoe) and hunter-gatherers (San), these indigenous groups have a long history in southern Africa (Vicente *et al.,* 2019). The current distribution of the Khoe and San groups comprises a wide geographic region from southern Angola to the Western Cape Province in South Africa. Until approximately 2000 years ago, the inhabitants of the coastal regions of western and southern Africa were hunter-gatherers (Sealy and Pfeiffer, 2000). Thereafter, some people started to keep sheep and cattle and milk and meat from domesticated animals supplemented with wild foods which they continued to gather. Only after the settlement of European colonists, was agriculture practised (Sealy and Pfeiffer, 2000).

The San did not settle in one area but rather moved around in search for game and plant foods (Nurse *et al.,* 1985; Franklin *et al.,* 2007; King, 2015; Lottering, 2020). On the other hand, the Khoe were pastoralists who reared livestock (sheep and cattle). Two theories have been proposed as to how herding reached South Africa. One theory suggests that the South African Khoe herders were descendants of the Hamitic pastoralists who moved southwards with their herds from east Africa (Stynder, 2009). A more widely accepted theory suggests that domestic stock and the knowledge associated with herding diffused down into the southern Africa from east Africa (Stynder, 2009). Archaeological evidence seems to support this, suggesting that hunter-gatherers added herding to their foraging activities rather than the arrival of immigrant herders (Sadr *et al.,* 2003). From the late 17th century onwards, the presence of European colonists in the Cape of Good Hope significantly weakened the social structure of the indigenous Khoe and San people, forcing them to either flee to the north, settle as farm workers, or blend with existing groupings of other cultures (Mountain, 2003; Botha and Steyn, 2016).

Today, the Khoe language is spoken by hunter-gatherers in parts of the Kalahari while the San are found in dry parts of Angola, Botswana and Namibia (Thompson 2001; Franklin, *et al.,* 2007; King, 2015; Lottering, 2020). For approximately two centuries, many groups were described as Khoe and San with no reference to their original lifestyle or standard of living (Botha and Steyn, 2016). Although the Khoe and San are considered biologically distinct from other Bantu-speaking populations, we now know that they also have distinct genetic markers compared to other sub-Saharan African population groups. This will be discussed later on in this chapter.

2.1.3. The Bantu-speaker migration

The Bantu-speaking people arrived in the southern regions of Africa approximately 2000 years ago from central and western Africa (Hammond-Tooke, 1974; Newman, 1995; Huffman, 1996). This migration is one of the greatest population movements in the world and because of the linguistic and cultural contributions from the Bantu-speakers, has become important in shaping

the diversity of the southern African populations (Vansina, 1995; Newman, 1995; L'Abbé *et al.,* 2006; Bostoen, 2018). As a result of this expansion, pre-existing groups across sub-Saharan Africa were largely replaced and / or assimilated by Bantu-speaking people, however, some in remote areas remained relatively untouched (Schlebusch, 2010; Pickrell *et al.,* 2012; Li *et al.,* 2014). Four main groups of Bantu languages have been identified: two in the north-western region of the Bantu-speaker distribution area, near their origins, where the highest levels of linguistic diversity are found; one west/central Bantu group; and, finally, one east/southern Bantu group (Bastin, *et al.,* 1999; de Maret, 2013). While the place and timings of the beginning of this expansion gather consensus, the way Bantu languages split between the east and west groups causes much more debate (Russel *et al.,* 2014). The literature shows very different migration routes through sub-Saharan Africa (Figure 2.1). In general, the entire eastern part of present-day South Africa was occupied by the south-eastern branch of Bantu-speakers whereas the Khoe and San occupied the western parts of South Africa and the south and central parts of Namibia (Li *et al.,* 2014). The western branch of Bantu-speakers had reached the northern part Namibia where their movement further south was limited by ecological factors (Mitchell, 2002). "The Bantu-expansion relied heavily on agriculture of millet and sorghum to support their population numbers, however, the climatic requirements for agriculture acted as actual geographical barriers to their expansion i.e., Kalahari Desert and the Cape regions, as these crops do not grow in desert or winter rainfall regions (Mitchell, 2002)."

It seems that the "Bantu" language emerged in west Africa approximately 5000 years ago, first associated with horticulture and later with iron working technology and agriculture (Newman, 1995; Mitchell, 2002; Bostoen, 2018). First proposed by Guthrie in 1967, the Bantu-speaking migration could be divided into a western and eastern stream by quite generally having a line drawn down the middle of the continent dividing it into a western and eastern side (as cited in Herbert and Huffman, 1993, p. 59). However, Huffman and Herbert (1994) noted that, culturally, some Bantu-speakers in Zambia (originally classified as eastern Bantu-speakers) were more similar to western Bantu-speakers.

Later, a "two-stream hypothesis" suggested that Bantu-speakers followed both a western and eastern path (Phillipson, 1977). All early Iron Age technologies and evidence were grouped either into a western stream centred in Zambia or an eastern stream in the eastern and southern regions of Africa. Contrary to this, Huffman (1989) proposed three streams for the "Bantu" migration. An eastern stream following similar routes to those proposed by Phillipson (1977) and a central and western steam which differ from Phillipson (1977). Originally, Huffman (1989) proposed that the western stream did not originate in north-western Angola but rather in the

wetlands of Zambia. From there the people spread to cover most of Zambia and then moved south through Zimbabwe to South Africa. Archaeological, linguistic and genetic evidence all support the migration of Bantu-speakers through sub-Saharan Africa regardless of the different views on the routes taken (Russell *et al.,* 2014).

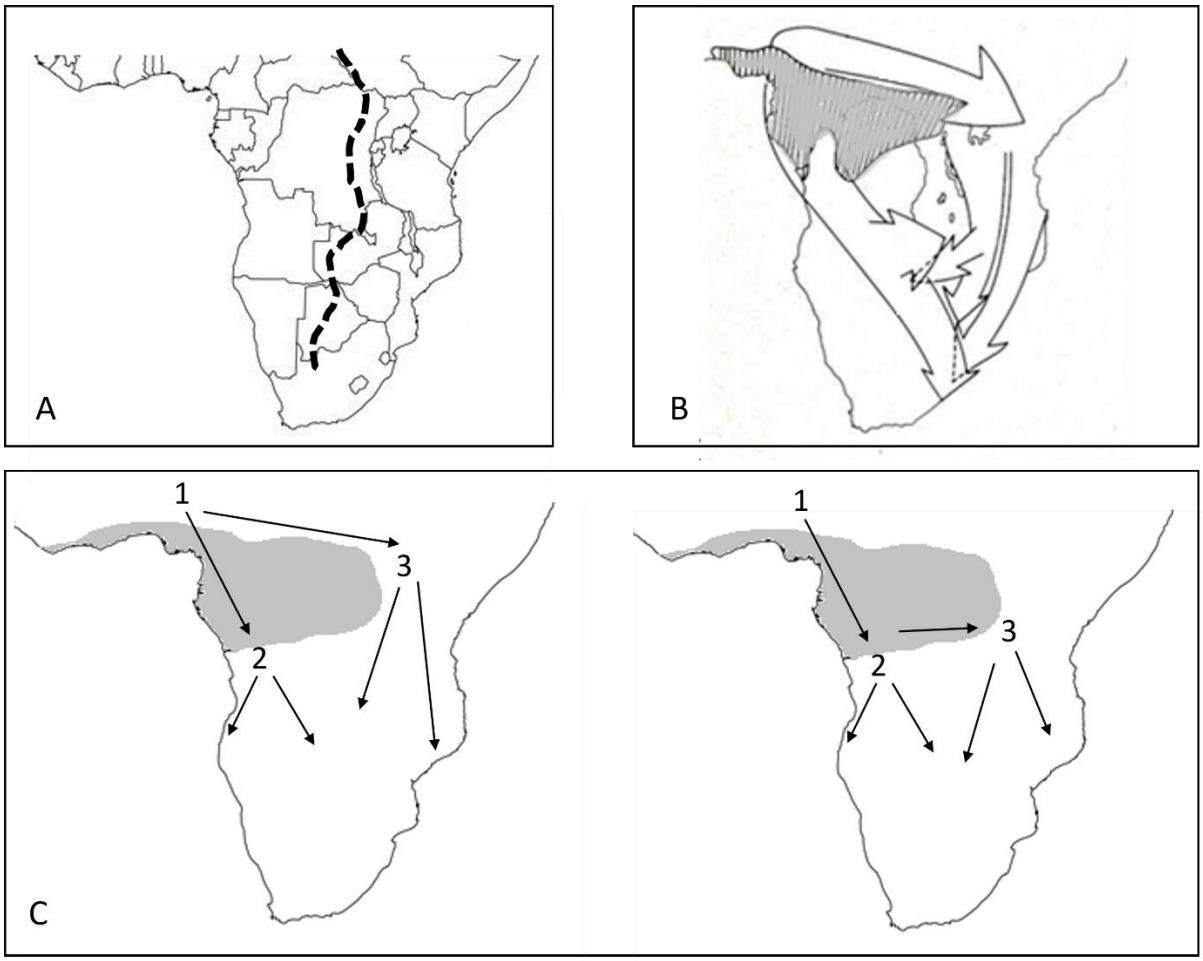


Figure 2.1: Various migration routes proposed over the years. A: Gunthries 1967 western and eastern division (adapted from Herbert and Huffman, 1993), B: Early Iron age migrations (adapted from Herbert and Huffman, 1993), C: Two models showing different proposed migration routes of the Bantu-speaker expansion (adapted from Pakendorf *et al.,* 2011)

2.1.3.1. Archaeological evidence supporting the Bantu-speaker migration

Bantu-speaking groups can be connected to various Iron Age objects by using material culture. Material culture reflects group identity and to be used and understood, material culture needs to be learned by a group of people speaking the same language (Huffman and Herbert, 1994). Ceramics, due to its variability and abundance, can be used to recognise and trace groups in the archaeological records. Early Iron Age ceramics look similar, although they diverge more as time passes into distinct streams associated with the eastern and western migrations. Therefore, ceramics would look more similar further back in time suggesting a common source (Huffman, 1970). These similarities in ceramics had to have been shared and learned from community to

community (Mitchell, 2002; Huffman, 1970). This suggests that there is an association between the distribution of the Bantu languages and Iron Age archaeological remains (Huffman, 1970).

Sub-Saharan Africa has a long history of ironworking, with examples such as Nok (in Nigeria) and Urewe (in the Great Lakes) (de Maret, 2013). In the first millennium AD, east African Bantu speakers migrated south toward East and Southern Africa from the Great Lakes region in east Africa (Schlebusch and Jakobsson, 2018). Archaeological evidence from this group is distinct from that of western African Bantu-speakers. From the Great Lakes region, there seems to have been two migration events southward; one which took an inland route, the Nkope branch, and one that took a more coastal route, the Kwale branch (Schlebusch and Jakobsson, 2018). Kalundu (another ceramic tradition) is suggested to have come from the west, south of the equatorial rainforest, across central Africa (present day Democratic Republic of the Congo and Zambia) and into present day Zimbabwe and South Africa. Western Bantu speakers are thought to be linked with a fourth ceramic tradition, Naviundu (Schlebush and Jakobsson, 2018). However, some areas of Central Africa show very sparse archaeological findings thereby hindering the interpretations of the spread of this technology through sub-Saharan Africa (de Maret, 2013).

There is evidence that Bantu-speaking populations farmed crops (Mitchell, 2012). The climatic requirements for agriculture acted as actual geographical barriers to their expansion i.e., Kalahari Desert (Mitchell, 2002). However, agriculture together with Iron Age technologies for land cultivation accelerated population growth and movements (Mitchell, 2002). It is suggested that the arrival of Bantu-speaking agriculturalists resulted in different degrees of admixture with the local populations (pastoralists and hunter-gathers) leading to isolation and/or replacement of these groups (de Fillipo *et al.,* 2012; Patin *et al.,* 2014).

2.1.3.2. Linguistic evidence supporting the Bantu migration

Languages is an important system of communication and has been used to trace population movements. Languages each have their own characteristics of speech; however, effective communication is achieved when an individual's linguistic code is understood by others. This creates a community where members can understand one another, creating a dialect. A dialect community is often regional. A language is a collection of dialects that are mutually understandable. Speakers exposed to a dialect influence each other, so changes in speech occur continuously, usually starting with the dialect (on an individual level). These changes are adopted by a household and will subsequently appear in the wider community: idiolect to dialect (Vansina, 1995). To understand past population movements, historical linguists can use language to classify or reconstruct vocabulary.

Languages in the African continent are a key component of most individuals' self-identity and identification as members of a population is deeply rooted in the languages that someone speaks (dos Santos, 2018). Today, approximately one third of the African continents' population speak a Bantu language. Several hundreds of dialects of Bantu languages exist, and the close relatedness makes it difficult to determine the origin, evolutionary history, and relationships between the languages (de Fillipo *et al.,* 2012; de Maret, 2013; Busby *et al.,* 2016).

Excluding languages non-native to the continent, African languages can be divided into four main groups: the Niger-Congo, Afroasiatic, Nilo-Saharan, and KhoeSan languages (Sheinfeldt *et al.,* 2010). As seen in Figure 1, the Niger-Congo languages are spoken throughout the western central, eastern, and southern region of Africa. The Niger-Congo group shows a clear dominance over the southern half of the African continent (Figure 2.2), and includes the Bantu languages (Scheinfeldt *et al.,* 2010: Santos, 2018). The Afro-Asiatic languages are spoken throughout northern, central, and eastern Africa, whereas the Nilo-Saharan languages are spoken in central and eastern Africa (Scheinfeldt *et al.,* 2010; Santos, 2018). Finally, the Khoe and San language (representing the smallest of the groups) which involves click consonants, was spoken by the original hunter-gatherer and hunter-herder populations in eastern and southern Africa, and their descendants (Scheinfeldt *et al.,* 2010; Santos, 2018).

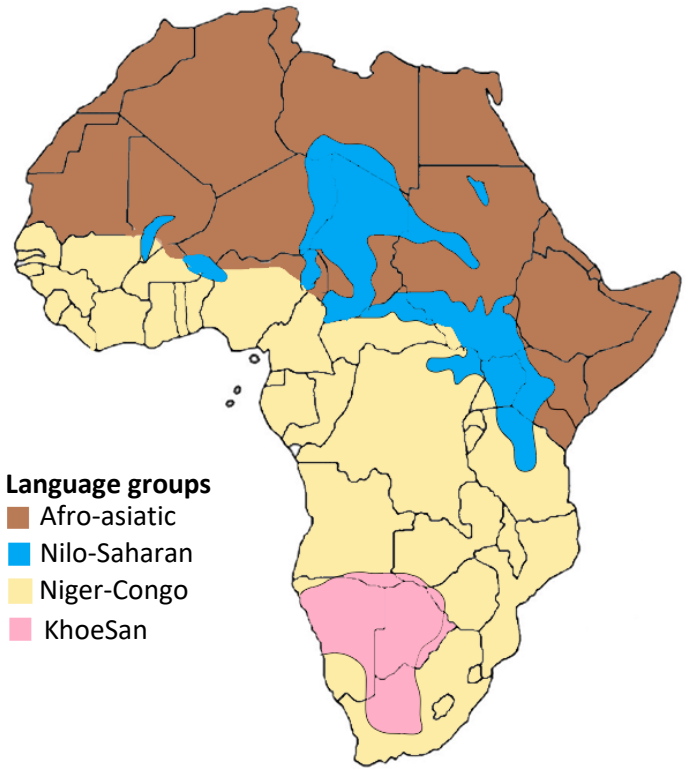


Figure 2.2: Map of Africa showing the distribution of the four main language groups (adapted from Scheinfeldt *et al.,* 2010). The Afroasiatic shown in brown, Nilo-Saharan shown in blue, Niger-Congo shown in yellow and KhoeSan shown in pink.

The close relatedness of the Bantu languages has generated extensive discussions about the origin, evolutionary history, and relationships between the languages (de Fillipo *et al.,* 2012; de Maret, 2013; Busby *et al.,* 2016; Choudhury *et al.,* 2017; Patin *et al.,* 2017). Linguistic evidence suggests that the Bantu language spread and diversified along with the expansion of agriculture and possibly the use of iron (Huffman, 1970; Holden, 2002; Li *et al.,* 2014). The Bantu language first differentiated and dispersed from a primary "Bantu" centre, and spread in western and eastern directions (Herbert and Huffman, 1993; Vansina, 1995; Ribot, 2004). Bantu-speaker expansion began approximately 3000 – 5000 years ago. Two hypotheses have been proposed as to how the eastern and western dispersal of language occurred (Figure 2.2). An early split suggests that the Bantu-speakers divided into a western and eastern stream and that the eastern Bantu-speaking populations would have migrated directly eastwards out of Nigeria and Cameroon reaching the Great Lakes region in eastern Africa approximately 3000 years ago (Pakendorf *et al.,* 2011; Li *et al.,* 2014). The Bantu-speakers would have expanded further southwards, approximately 1000 years ago, and this would have resulted in the current distribution of eastern Bantu-speaking people across most of the eastern and southern parts of Africa. On the other hand, the western Bantu-speaking people are proposed to have migrated directly south through the rainforests of Cameroon. The second hypothesis suggests a late split of the eastern and western branches of Bantu-speaking people. This late-split hypothesis proposes that the eastern and western branches split after passing through the central African rainforest (Pakendorf *et al.,* 2011; Li *et al.,* 2014). Recent studies have shown that the 'late-split' hypothesis shows a better match with the current distribution of the available linguistic evidence (Currie *et al.,* 2013; Grollemund *et al.,* 2015; dos Santos, 2018).



Figure 2.3: Map showing the two main models of migration based on linguistic evidence. The shaded area shows the extent of the rainforest. (A) "Early" split hypothesis (B) "Late" split hypothesis (adapted from de Filippo et al., 2012).

Along with the spread of Bantu languages came the interaction with pre-Bantu populations, especially in the southern areas (Isern and Fort, 2019). The Khoe and San inhabited southern Africa before the arrival of the Bantu-speaking populations and are often considered to be a homogenous group based on their highly distinctive click languages (Rocha and Fehn, 2016). However, these groups are quite diverse and the click languages from southern Africa are thought to belong to three independent lineages: Tuu, Kx'a and Khoe-Kwadi (Güldemann, 2004). The Khoe-Kwadi population show much cultural and biological variation. The Tuu and Kw'a speaking populations are preferentially hunter-gathers, whereas the Khoe-Kwadu people are both pastoralist and foraging communities and often present levels of admixture with the Bantu-speaking populations (Rocha and Fehn, 2016). Supporting this, linguistic evidence has shown that Bantu herding vocabulary, with words such as sheep, cattle and milk, came from local KhoeKhoe languages (Ishern and Fort, 2019).

2.1.3.3. Genetic evidence for Bantu-speaker migration

Genetic variation among African populations has been studied extensively. Genetic variation in Africa is structured geographically and linguistically (Scheinfeldt *et al.,* 2010). Several studies have indicated strong associations between genetic and linguistic relationships among globally distributed populations (Wood *et al.,* 2005; Tishkoff *et al.*, 2009; Scheinfeldt *et al.,* 2010; Li *et al.,* 2014). Populations in close proximity as well as populations that speak linguistically similar languages are more likely to exchange genes (Scheinfeldt *et al.,* 2010).

Bantu-speaking populations share genetic similarities across a vast area of sub-Saharan Africa. The geographic and genetic distinction between north African and sub-Saharan African populations support the pattern of genetic variation in Africa when geographic barriers limit gene flow (Scheinfeldt *et al.,* 2010). The shared genetic ancestry of Bantu-speakers has been used to support the Bantu-speaker expansion being an actual movement of people across Africa and not just a cultural spread of languages through neighbouring populations (Tishkoff *et al.,* 2009; Pakendorf *et al.* 2011; de Filippo *et al.,* 2012; Li *et al.,* 2014; Busby *et al.,* 2016; dos Santos, 2018). If the expansion of Bantu languages did not involve the actual movement of people and was only the result of cultural diffusion, it would not be expected that the present-day Bantu populations would be genetically similar. However, if the Bantu expansion was the result of a southwards and eastwards migration of people from central west Africa and their settlement across sub-Saharan Africa, the opposite would be true and Bantu-speaker populations would be genetically closer to each other than their neighbouring populations. The available genetic data support the latter option (Tishkoff *et al.,* 2009; Pakendorf *et al.,* 2011; de Filippo *et al.,* 2012; Li *et al.,* 2014; Busby *et al.,*

2016; dos Santos, 2018). Furthermore, studies have shown a clear genetic separation of sub-Saharan African populations from North African populations (Salas *et al.*, 2002; Luis *et al.*, 2004).

Studies using mitochondrial DNA (mtDNA) were one of the first studies to assess genetic variation in Bantu-speaking populations and are widely used to measure the genetic effects of expansion of Bantu-speaking individuals. mtDNA studies of African populations show that genetics is more closely associated with geographic traits than with linguistic associations (Neuweger, 2007). The frequency and distribution of some mtDNA lineages (such as L0a, L2a, L3b and L3e) in Bantu-speakers and non-Bantu-speaker populations are believed to be genetic footprints of the Bantu-speaker expansion (Pereira *et al.,* 2001; Wood *et al.,* 2005). Most of the lineages spread out along the eastern route of the Bantu-speaker expansion (Periera *et al.,* 2001; Salas *et al.,* 2002; Schlebusch *et al.,* 2012) while only a few lineages are believed to have been carried along the western route (Salas, *et al.,* 2002; Plaza *et al.,* 2004).

Bantu-speakers' genes were introduced to the southern parts of Africa as a result of the Bantu-speaking migration (Rowold, *et al.,* 2013). Early genetic studies noted that Bantu-speakers were genetically homogenous, in contrast to the genetic differentiation between west African Niger-Congo populations and east African Nilo-Saharan populations. Specific haplogroups have been linked to Bantu-speaking populations based on Y-chromosome markers and single locus mitochondrial DNA (mtDNA) (de Fillipo *et al.,* 2012; Li *et al.,* 2014). Y-chromosomes from paternal lineages are particularly useful to infer the spread of Bantu-speaker populations. Gene flow from displaced groups is less affected by paternal lines (Li *et al.,* 2014). The majority of men in Bantu-speaking populations possess the NRY defined haplogroup E3a (Cruciani *et al.,* 2002) spanning from Cameroon and Nigeria to southern Africa (Periera *et al.,* 2002) suggesting the Bantu-speaker expansion of males through sub-Saharan Africa. Additionally, mtDNA lineages have also shown a distinct pattern of migration for both males and females. High Bantu-speaker mtDNA diversity suggests that the expansion involved lots of short bursts and involved numerous women being absorbed into groups of incoming Bantu-speaking men (Salas *et al.,* 2002). The low diversity in the NRY haplogroup suggests that male Bantu-speaking farmers migrated larger distances and had lower effective population sizes (Wood *et al.,* 2005; Warren *et al.,* 2015).

East Africa shows more genetic and linguistic diversity than west central and central sub-Saharan Africa (Salas *et al.,* 2002; Wood *et al.,* 2005). This suggests that the movement and replacement of existing populations by Bantu-speaking farmers was less complete in this region as well as having genetic interactions from Asian populations (Salas *et al,* 2002; Rowold *et al.,* 2014). Populations from Mozambique and Tanzania have shown greater proportions of more ancestral NRY and mtDNA types (Pereira *et al.,* 2001; Salas *et al.,* 2002; Wood *et al.,* 2005).

Mozambicans and Kenyans (Brandstätter *et al.,* 2004), Rwandan Hutus (Tofanelli *et al.,* 2003), Zimbabweans and Ugandans (Gené *et al.,* 2001) have all demonstrated substantial differences with each other and/or populations further to the west at some molecular level.

As the Bantu-speaking people migrated through sub-Saharan Africa, they not only assimilated many elements of the indigenous cultures but also expanded their gene pool by intermarriage with the autochthonous people (Tishkoff *et al.,* 2007; Rowold *et al.,* 2014). Studies on people from the central western Africa rainforest have consistently shown that Bantu groups had a substantial impact on the genetic composition of Pygmy hunter-gathers, for example (Berniell-Lee *et al.,* 2009; Patin *et al.,* 2014). This suggests that there may have been some assimilation with previous populations of hunter-gathers as well (Sikora *et al.,* 2011). Admixture and gene flow between South African populations and the Khoe and San has affected the enlargements of some groups (South African Bantu-speakers) and the shrinkage of others (Khoe and San) (Exoffier *et al.,* 1991). Despite the fact that modern Khoe and San groups show conservable genetic diversity, suggesting a complex population history (Schlebusch *et al.,* 2012), morphology does not always provide the same results. For example, studies based on craniometric variation of both modern and Later Stone Age individuals have failed to provide conclusive evidence that the San and KhoeKhoe populations are biologically distinct from one another after 2000 B.P. (Howells, 1973; Stynder, 2009).

Genetic studies have identified Khoe and San groups as the most divergent group of modern humans and studies have suggested that there is a deep separation between northern and southern Khoe and San population groups dating to -35kya (Schlebusch *et al.,* 2012). Moreover, genome-wide data has allowed the identification of genetic structure among the KhoeSan populations. However, this genetic structure does not appear to correlate with linguistic affiliation or subsistence strategy, but correlating instead with geography (Neuweger, 2007; Montinaro *et al.,* 2017). Among Niger-Congo populations, it was found that geography is the main factor explaining genetic differences, with a similarity to western African populations (Sikora *et al.,* 2011). This reflects the expansion to the west from the north together with the spread of iron metallurgy and the Niger-Congo languages. South-eastern Bantu-speakers from Mozambique were found to be remarkably different from the western Niger-Congo populations as well as from the geographically closer eastern Bantu-speaker populations (Sikora *et al.,* 2011). Li and colleagues (2014) found that the movement of southeast Bantu-speakers to the south of Africa followed the eastern route of migration and this finding fits well with the linguistic evidence where speakers of south-eastern Bantu languages are related to or descendent from the east Africa Bantu languages. The east African origin of the southern African Bantu-speakers is supported by studies that have found up

to 22% genetic admixture from east Africa or Eurasian pastoralists on modern-day Khoe and San groups (Schlebusch *et al.,* 2017; Skoglund *et al.,* 2017).

2.2. Craniofacial morphology in recognising populations

Facial appearance is the most distinctive and recognisable human characteristic, as well as the most morphologically variable (Cole *et al.,* 2017; Cole and Spritz, 2017). The bones, muscles, cutaneous and subcutaneous layers of the face all contribute to the unique morphology in a single person (Sforza and Ferrario, 2006). The overall form (size, shape, and shared arrangement of parts) and function of the face and head is strongly determined by a multiplicity of genes, with environmental variables such as nutrition exerting increasing influence over the lifespan of an individual. Similarities in facial appearance within families, across generations, suggest that key genes exert particularly large effects on facial shape and appearance and that facial morphology is highly heritable (Fitzgerald *et al.,* 2010; Cole *et al.,* 2017; Cole and Spritz, 2017). In contrast, the loss of muscle mass and soft tissue elasticity with age will also influence the dimensions of the face (Fitzgerald *et al.,* 2010).

Specific dimensions of the face are coded for by genes (Cole *et al.,* 2017; Richmond *et al*., 2018). There are several recognised genetic variants that are associated with facial morphology and genes are likely to influence more than one facial trait (Richmond *et al.,* 2018). For instance, the PAX3 gene is associated with eye to nasion distance, prominence of nasion and eye width and side walls of the nose (Cole *et al.,* 2017; Richmond *et al.,* 2018). PRDM16 is linked to the length and the prominence of the nose as well as the width of the alae, whereas SOX9 is thought to be related to the shape of the alae and nose tip (Cole *et al.,* 2017; Richmond *et al.,* 2018).

Cranial modularity and integration of the cranium are affected by development, genes and the environment (Klingenberg, 2013). Cranial modularity refers to the small “modules” or anatomical regions of the cranium that contribute to cranial morphology. The change of one module of the cranium that leads to change in another is referred to as integration of the cranium. Due to the high level of covariance between adjacent modules, modularity is often studied in combination with integration (Bruner, 2007). It has been suggested that the entire craniofacial region functions as a module and changes significantly compared to the components of neurocranium (Bastir and Rosas, 2005). The nasal bones, maxillae and zygomatic bones have tightly integrated morphological shapes and sizes (Holton *et al.,* 2013). Variations in mid-craniofacial morphologies between populations are indicative of craniofacial integration. Broader maxillae, zygomae and nasal bones are found among African populations whereas narrower

maxillae, zygomae and nasal bones are seen in European populations (Gillick, 2012). The close morphological association between the maxilla and zygoma may be due to the similar developmental origins as both these are derived from the same neural crest cells (Heuze *et al.,* 2016). However, Mitteroeker and Bookstein (2008) suggest that the association between the enlarged laterally projecting zygomae and enlarged, prognathic maxillae is mainly related to mastication and force. Therefore, genetic, developmental and functional factors need to be considered when interpreting craniofacial population morphology.

Plasticity in the craniofacial skeleton has been studied extensively (Jantz and Jantz, 2000; Simpson and Henneberg, 2002; Cole *et al.,* 2017) and it has been found that there is a predictable and direct influence of the facial skeleton on the overlying soft tissues (Simpson and Henneberg, 2002). Facial dimensions change relative to the muscle pressures caused by dietary preferences. An example of this regards the muscles of mastication which exert extensive force on underlying skeletal features relative to dietary preferences (Cole *et al.,* 2017).

Heritable features of the head and face are thought to be genetic adaptations to specific environments and can be traced back to specific geographic populations affected by environmental factors (King, 2015). Human morphology responds adaptively to combined effects of air, temperature, and humidity. Hiernaux and Froment (1976) found that head and facial anthropometric features are sensitive to climatic changes with the head and face being narrower in hot and dry climates. Nasal shape is also affected by climatic changes with noses tending to be narrower and higher in hot environments (Hiernaux & Froment, 1976). Populations affected by similar climatic conditions are often geographically close to each other, thus complicating the assessment of the effects of climate on craniometric traits (Betti *et al.,* 2010). Therefore, when populations from similar climates share craniometric traits, one cannot imply that this is a result of natural selection but could also reflect common ancestry and/or recent genetic exchange due to proximity (Betti *et al.,* 2010).

Population movements can affect craniofacial variation in several ways. Movement into a different area can lead to developmental plasticity, especially when movement occurs at a young age. This could lead to immediate effects on craniofacial development. Movement into a different environment can lead to long-term changes through natural selection. Lastly, changes within and among populations and genetic distance, because of gene flow, will increase variation within groups while decreasing genetic distances between groups (Relethford, 2004). Therefore, populations that were once quite distinct from one another, may now show craniofacial similarities.

2.2.1. Cranial morphology in sub-Saharan African populations

There is no one single factor that determines cranial morphology, and it is rather the result of the complex relationship of both genetic and environmental factors (González-José *et al.,* 2004; Neuweger, 2007). These factors include neutral evolutionary forces of mutation, migration, and random genetic drift as well as natural selection and environmental factors such as climate (Roseman, 2004). Population specific traits of the cranium are established in early ontogeny and are accentuated during development. Cranial elements are developmentally flexible and vulnerable to epigenetic interactions with the environment (Timbrell and Plomp, 2019). Specifically, responses to the environment have been known to affect cranial morphology. Trait variation can be limited to particular cranial areas due to specific adaptive responses (Timbrell and Plomp, 2019). Craniofacial characteristics, for example nasal shape and the size and shape of the neurocranium, have been linked to climatic adaptations (Beals *et al.,* 1984; Roseman, 2004; Harvati & Weaver, 2006; McDowell, 2012).

South Africa has an incredibly diverse population representing a vast heritage and many different cultures. Morphological differences seen between South Africa populations are the result of colonialism, migration and forced separation (Stull *et al.,* 2014a). Various authors have studied crania of indigenous South Africans (e.g., De Villiers, 1968; Howells, 1973; Hammond-Tooke, 1974; Franklin *et al.,* 2005; 2007; 2010; L'Abbé *et al.,* 2006; Harvati and Weaver, 2006; Morris and Ribot, 2006; Ribot *et al.,* 2010; Botha *et al.,* 2017). Facial features are thus genetically inherited and are evident in populations groups that admix. Genetic studies have shown that individuals that formed part of the Bantu-speaking expansion have strong similarities in their cranial and dental morphology (Wood *et al.,* 2005; Warren *et al*, 2015). Diet, due to mastication, can exert mechanical strain on the cranium and that cranial vault has also been correlated to population history (Timbrell and Plomp, 2019).

A large amount of research within biological anthropology has looked at distinguishing between major populations using the skull and craniofacial skeleton. West Africans and Bantu-speakers of southern Africa display maxillary and mandibular prognathism and pronounced cheekbones, these features are genetically determined but also affect mastication (Tobias, 1970; L'Abbe *et al.,* 2011; Sforza *et al.,* 2016). The Khoe and San (the original southern African population groups) have ancient facial features that make them distinct from other African groups (Tobias, 1970; Sforza *et al.,* 2016). The crania of the Khoe and San present with a short and low vault with narrow orbits and a narrow vault and a highly curved occipital bone, whereas that of the west African group present with a high long vault, high and wide orbits with a broad frontal bone (Ribot, 2004).

2.2.2. Craniometry

Populations from specific regions share skeletal traits that are similar while others have different features due to adaptation of those populations to their specific environment (Beals *et al.,* 1984; Roseman, 2004; Harvati & Weaver, 2006). Determining population differences generally comprises visual and metric examination of morphological differences. This includes the bone shape, the absence or presence of a trait, the protrusion or prominence of a feature and bony morphology (Simpson and Henneberg, 2002; Lottering, 2020). These morphological differences are recognisable between different population groups due to factors such as geographical distances, language and cultural differences (Stull *et al.,* 2014a).

Craniometry involves taking metric measurements of the skull. Traditional craniometrics uses standardised linear measures between cranial landmarks found on specific locations of the cranium that occur in relatively the same place on each individual (King, 2015). Initially, craniometrics focused on biological distance – using craniometric data to measure biological relatedness or to reconstruct past populations histories (Relethford, 2004). Measurements are generally taken using callipers; however, the same measurements can also be calculated when landmarks are digitally mapped by a Microscribe. Using various statistical analyses, the differences among the measures are used to explore variation between individuals (King, 2015). Both size and shape of the cranium is reflected in these linear measurements, however, size differences among individuals are often due to sexual dimorphism. This requires analysis of the linear data to be size corrected before both males and females can be included in the analysis (Ross *et al.,* 2011; McKeon and Schmidt, 2013; Kimmerle *et al.,* 2008; King, 2015). However, when using the Microscribe and geometric morphometrics (GM), size can be separated from shape and therefore, size correction is not needed.

When studying the face and skull, anthropologists also examine the shape of certain morphological characteristics and their relation to each other in the attempt to extract important biological information (Gillick, 2012; King, 2015). Morphometrics refers to the quantitative analysis of form, consisting of both size and shape, where mathematics and statistics play an important role in the analyses (Bookstein *et al.,* 2004; Gillick 2012). Morphometric studies attempt to quantify variations between different populations statistically using linear distance measurements, angles and/ or ratios (Gillick, 2012).

Geometric morphometrics (GM) uses three-dimensional co-ordinates of homologous landmarks. GM focusses on two – or three-dimensional Cartesian coordinates of anatomical landmarks rather than a collection of distance measurements, ratios and angles (Slice, 2007; Gillick, 2012;). This allows for variability due to both size and shape to be quantified (Kimmerle

et al., 2008). Landmark-based analyses provides a repeatable and reliable method that retains information on shape (Slice, 2007). Developed in the 1980s and 1990s, GM allows scientists to virtually view the shape variation by creating a three-dimensional map of the cranium or other objects studied on a coordinate grid system (Adams *et al.,* 2004). This allows researchers to study a greater amount of shape variation between individuals as size has been removed from the analysis (King, 2015; McKeowen and Schmidt, 2013).

Landmark co-ordinates are critical to GM approaches (Gillick, 2012). Landmarks are distinct anatomical points which are recognised as the same points in all individuals (Zelditch *et al.,* 2004). Landmarks can be identified using a number of set criteria. Landmarks should be "1) homologous anatomical loci that 2) do not alter their typological positions relative to other landmarks, 3) provide adequate coverage of the morphology, 4) can be found repeatedly and reliably, and 5) lie within the same plane" (Zelditch *et al.,* 2004:25). It is also suggested that landmarks should be chosen specifically to answer the research question but not be so specific as to take away from the potential to discover novel shape information (Zelditch *et al.,* 2004).

Landmarks are commonly classified into three types (Bookstein *et al.,* 2004). Type I landmarks are homologous, meaning they have the same relative position on the bone across all populations, for example, the intersection between sutures of the cranium (i.e., pterion). This makes them easily locatable and repeatable. Type II landmarks are not based on locally defined biology but rather are landmarks whose morphology from population to population is maintained by geometric or shape evidence (i.e. mastoidale or frontomalare orbitale along the orbit). Type III landmarks usually lack proper definition across populations and are therefore much more difficult to locate (i.e., euryon) (Bookstein *et al.,* 2004; Hallgrímson *et al.,* 2007; Wärmländer *et al.,* 2019).

2.2.2.1. Craniometry in sub-Saharan Africa populations

Among the first to describe differences in the crania of southern African groups was Professor Hertha de Villiers in 1968. Analysing approximately 750 skulls from different black South African Bantu-speaking populations groups (namely the Natal Nguni, Cape Nguni, Shangana-Tonga and Sotho), de Villiers found no major population differences and, for practical purposes, found that these populations could be considered part of a single population, the black South African population (de Villiers, 1968).

Later, Howells undertook two major studies (Howells, 1973; 1989) that assessed cranial differences between current human populations. Having analysed 57 linear measurements and 12 angles from 17 populations worldwide, Howells (1973) attempted to find out which measurements

would be of use in discriminating different populations groups from skeletal remains. Of particular interest to this study, Howells concluded that the discriminating features for the "Bushmen" were "*Flatness across the interorbital space and nasal saddle, with relatively broad nasal aperture. Low skull with flattish short parietal. Moderate relative breadth of upper face"* (Howells, 1973, p.147). In 1989 (and building on his work in 1973), Howells used 28 populations to determine specific geographical differentiation between populations. He found that size is not determined by geographic location, with shape differences found mainly in the upper face and upper nose, particularly around the orbits.

Ribot (2003; 2004) set out to investigate morphological variability of African populations with a focus on geography and population history. A large sample of skulls from various modern African populations were assessed. These were collated into four groups based on geographic regions (western, eastern, southern central) and two other groups, the Pygmies and the Khoe and San. Morphological features reflected the differences between Khoe and San and west African groups (Ribot 2003; 2004). The crania of the Khoe and San presented with a short and low vault with narrow orbits and a narrow vault and a highly curved occipital bone, whereas that of the west African group present with a high long vault, high and wide orbits with a broad frontal bone. Additionally, Bantu-speaking groups showed more homogeneity, and those from central Africa and Eastern Africa showed similarities in facial and vault features (Ribot, 2003; 2004). This study also noted that population history and geography are difficult to distinguish from one another.

Franklin *et al*. (2007) examined cranial variation in twelve modern indigenous groups in South Africa. This included both Bantu-speaking populations and the Khoe and San populations. Using 96 cranial landmarks on 298 male crania, the authors found that although Bantu-speaking and Khoe and San individuals are morphologically distinct, the groups show population specific features that may be attributed to differential admixture with the Bantu-speaking population. Generally, the crania of Bantu-speaking populations are more dolichocephalic, have higher forehead contours, higher anterior projection of the upper face and more prominent noses and taller faces (Franklin, *et al.,* 2007). The authors also found clear morphological differences between the southernmost population groups and other sub-Saharan populations. Additionally, they found that accuracy rates for distinguishing between southern African Bantu-speaking groups range from below 50% for the Xhosa to almost 90% for the Swazi. They found that the southern-dwelling Xhosa are the most similar Bantu-speaking people to the Khoe and San (reflecting an extended period of admixture) while the northern Malawi and Kalanga are the most dissimilar. Extending their study in 2010, Franklin *et al*. included crania from central, western, and eastern Africa. The authors found that Pygmies had the smallest cranial size, while the Khoe and San also had

significantly smaller crania than other population groups. Central African populations were significantly smaller than eastern, western, or southern populations groups.

L'Abbé *et al*. (2006) explored cranial variation in a modern Venda population group. The study found that morphologically the Venda are most similar to modern sub-Saharan African groups, (both southern and eastern), and least similar to the historical San group. Due to the large number of similarities between the Venda and other sub-Saharan African groups, the Venda contribute to diversity present within the modern eastern and southern African populations (L'Abbé *et al.,* 2006). It was also noted that Venda have distinct cranial features particulary in the cranial vault and face, with narrow high cranial vaults, tall face with high orbits and long nasal apertures. This was similar to other Bantu- speaking populations. In contrast, the Khoe and San presented with wide short vaults, short faces with low orbits and short nasal apertures. Despite increasing admixture during the last 2000 years, craniometrics show that the Khoe and San are considerably different from other sub-Saharan African populations (L'Abbé *et al.,* 2006).

Assessing mid-craniofacial characteristics of 329 crania from skeletal collections in South Africa, Dinkele (2018) found that the nasal and maxillary regions showed population diversity. It has been noted that population variations in each component of the mid-craniofacial regions area are associated with functional, regional and developmental proximities of the regions (Paschetta *et al.,* 2010; Cunningham *et al.,* 2016; Dinkele, 2018).

Anthropologists have long been using traditional craniometrics to study population movements and population variation (Howells, 1973; Moore-Jansen *et al.,* 1994; Ousley and Jantz, 2012; McKeowen and Schmidt, 2013). While craniometry uses measurements from bones, anthropometry uses observations and measurements from living individuals. Craniofacial anthropometry provides objective means to assess facial shape and changes over time, whether during an individuals' life or through generations (Fourie *et al.,* 2011).

2.2.3. Anthropometry

Although anthropometric craniofacial data has been collected on living individuals and face masks (Houlton and Billings, 2017; Ramphaleng, 2020), it has not been used extensively for studies of craniofacial variation. One of the most recent studies is that of Ramphaleng (2020), where face masks of various African populations were used to assess morphological variation. The author also assessed crania that were associated with the face masks. It was found that African morphology is distinct between different populations and can be grouped geographically. Bantu-speaking populations had broader and taller faces that were more prognathic while the Khoe and

San has narrower shorter noses and were broader across the face. Western-central Bantu-speaking populations had wider faces with eyes that were further apart (Ramphaleng, 2020). This is contrary to Ribot (2004) who suggested western Africans to have narrower faces. Ramphaleng (2020) also found that east Africans had shorter and broader faces while southern Africans and central Africans had narrower and longer faces. However, Ramphaleng (2020) used GM (which removes size) to analyse variation in the shape of the craniofacial morphology whereas Ribot (2004) used linear measurements. Linear measurements (unless otherwise corrected for) describes absolute differences, independent of size. Furthermore, Ramphaleng (2020) and Ribot (2004) used different samples and this may have accounted for the differences observed between the two studies.

Soft tissue patterns and dimensions has shown to be a better indicator of the relationship between primate groups than bone alone and as such may provide a better understanding into the relationship among humans too – in this case modern sub-Saharan African populations (Diogo & Wood, 2011). Soft tissue characteristics are not as prone to homology as skeletal characters (Gibbs *et al.,* 2002). Homology refers to shared character states which result from similarities in the way the genotypes interact with the environment. As bone is a dynamic tissue, many of the morphological features of bone may be homologous, however, this may not be the case with soft tissue (Gibbs *et al.,* 2002).

The face is one of the most individualistic parts of the human body, however, certain features of the face are often shared among populations groups. Farkas (1994) published a widely used set of landmarks and measurements for describing the face. The system uses 47 landmark points across the face and head, some of which are shown in Appendix A. Many of these landmarks can be identified visually, while palpation is required to locate some of the landmarks related to underlying skeletal structures. Using these landmarks, several anthropological measurements can be recorded. The direct method most commonly used to collect craniofacial anthropometric data has been manual anthropometry with the use of tools such as callipers and tape measures (Weinberg, 2019).

There are, however, limitations when it comes to measuring soft tissue structures. Palpation of faces of living individuals is limited by the inability to accurately locate bony landmarks, particularly in the areas of the face with the greatest soft tissues. Clinical imaging modalities allow one to visualise soft and hard tissues simultaneously. However, different imaging modalities suffer from gravitational problems (i.e., the individual is usually supine), artifacts may occur, and bone visibility may be limited. Direct anthropometry from a living individual is perhaps the most reliable form of data collection (Damas, *et al.,* 2019). However, there are some drawbacks. Direct anthropology requires direct contact with the participant which may be uncomfortable and can also

be time consuming. Measurements can be relatively invasive and therefore inappropriate, particularly for small children or those that do not prefer direct contact for cultural or personal reasons (Jayaratne and Zwahlen, 2014; Weinberg, 2019). The need to repeatedly locate landmarks for each measurement can introduce errors and prolong the time it takes to take measurements from a single individual. As this technique does not leave an archival record on the facial appearance, other than a set of numbers, some errors become permanent. Additionally, the researcher is unable to remeasure measurements that are not collected at the time of participation (Jayaratne and Zwahlen, 2014; Weinberg, 2019).

Imaging modalities have become increasingly popular. Anatomists and anthropologists now use 3D data and models to detect phenotypic variation among different population groups (Decker, 2010). Studies have shown that measurements taken from dry skulls and those taken from virtual images present with a low error rate and that the anthropometric landmarks are easy to identify and reproduce on scanned images (Decker, 2010; Stull *et al.,* 2014). Researchers argue that the virtual images are more accurate, and measurements obtained from the computerised tomography (CT) scans can be used in forensic application. CT images allow for a more efficient and less invasive way to obtain data (Stull *et al.,* 2014). However, it must be kept in mind that there may be differences in soft tissue measurements taken in a supine position and those taken in an erect position. While some studies have addressed the effects of gravity and its effects on soft tissue facial measurements (Manhein *et al.,* 2000; De Greef *et al.,* 2006; Baillie *et al.,* 2016), there are conflicting results on how much these gravitational influences affect the soft tissue measurements. Baillie and colleagues (2016) found that individual results for differences between supine and erect positions were varied suggesting that there is no clear prediction for postural facial soft tissue differences for any one individual.

2.2.3. Anthropometry in Southern Africa

Craniometry is a major field of research within biological anthropology. As far back as the 1800s, physical anthropologists were recording biological data of living individuals of southern Africa (Tobias, 1985). At the time anthropologists believed that humans could be categorised as distinct racial types and that each racial type could be classified by physical characteristics (Birdsell, 1987). However, at that time, concepts of clinal variation were limited. An Italian physical anthropologist, Professor Lidio Cipriani, was involved in research across Africa, including the Italian Scientific Expedition of Cape to Cairo from 1927 to 1930 (Houlton and Billings, 2020). During this expedition, racial typological face masks, anthropometric data, and photographs of individuals from several African communities were collected. In 1930, Raymond

A. Dart (who headed the Department of Anatomy at the University of the Witwatersrand from 1922 to 1958) joined the Italian Scientific Expedition. Among the many researchers involved in the studies of living individuals of sub-Saharan African populations, Tobias believed that measurements such as brain size, skull shape, facial features, skin colour, hair texture and bone length were fundamental in the search for racial differences in the human population (Tobias, 1985). The search for "pure racial types" that represented groups described as the "Bantu", "Bushmen" and Hottentot" using typological methods was the core of biological anthropology during this time (Tobias, 1985; Kuljian, 2016). In 1936, the University of Witwatersrand's Kalahari Bushmen Expedition began. The main interest of the expedition lay in the physical characteristics of the "Bushmen" and to learn more about the last surviving individuals of an "ancient racial type" (Kuljian, 2016). Physical characteristics included skin and eye colour, hair features, cranial and facial measurements, body measurements as well as casting of face masks. After analysing all the data, it was believed that "Bushmen" were the most primitive race (Kuljjan, 2016). Racial typology continued until the mid 20th century (Morris 2012; Houlton and Billings, 2017). Although the concept of race has been scientifically challenged and shown to not biologically exist, debates regarding the use of racial terminology persist today. While some physical anthropologists recommend that the terms used in research reflect self-identification and community (eg. white/black) (İşcan and Steyn, 1999; Konigsberg et al., 2009; Stull et al., 2014a), others prefer terms related to ancestry (African/European) or ty to distance themselves from the social, political, and methodological implications of race (Sauer, 1992; Ross and Williams, 2021).

In 1951, Phillip V. Tobias, joined the Panhard-Capricorn expedition as an anthropologist taking measurements and observations. During this expedition, the group travelled through Botswana, Namibia, Mozambique, and South Africa along the line of the Tropic of Capricorn (Kuljian, 2016). During this expedition Tobias stated that "[he] encountered teeming humanity, from light yellow-brown San to the taller dark-skinned Africans, from hunter and gatherers to pastoralists, agriculturalists, and urbanites" (as cited by Kuljian, 2016). For much of the 1950s, Tobias focussed his research on living individuals and human measurements and in the late 1950s, Tobias was involved in a survey of the people living in the Tonga Valley around the Zambezi River (Tobias, 1970; Kuljian, 2016). He studied over 400 adult males and 600 children. It is unclear why no women were measured at the time, and it wasn't until the early 1960s that he began gathering information on the women. During this survey, over 200 physical measurements were recorded on a specific individual (Tobias, 1970; Kulijan, 2016). Five years after Tobias' involvement in the Panhard-Capricorn Expedition, the University of the Witwatersrand established the Kalahari Research Committee (KRC). The expedition went on to produce 25 publications. When comparing observations form the tonga Valley survey and KRC expeditions, Tobias found

clear distinctions between the "Bushmen" and the Tonga groups and began to explore the possibility whether these distinctions were due to environmental factors or genetic variations (Kulijan, 2016).

In 1985, Tobias published the "History of Physical Anthropology in Southern Africa". In this paper, Tobias describes the history of the discipline of physical anthropology in South Africa through the years. Many of Tobias' students were involved in expeditions and research involving sub-Saharan African populations. Two of the most outstanding craniological studies to emerge from South Africa are those from Hertha de Villiers (1968) and Alan Morris (1984). De Villiers analysed approximately 750 skulls using a combination of craniometric, cranioscopic and genetic approaches. It was established that both male and female skulls of black South Africans showed no major population differences and could be considered a single population, namely the Bantu-speaking South African population (de Villiers, 1968). This finding was supported by several other doctoral studies using the same skeletal collection, i.e., on permanent teeth (Jacobson, 1968). on paranasal sinuses (Wolfowitz, 1974) and the sacrum (de Beer Kaufman, 1975). Instead of classifying individuals into a racial type, de Villiers explained that there is a range of variation in a group of closely related individuals. Ahead of her time, de Villiers moved away from typological thinking and classification of populations. In 1984, Morris analysed three skeletal references populations, a Southern Sotho and Tswana sample, "Caucasoid" sample and Khoe and San sample. In the compilation of the Khoe and San sample, Morris set extremely stringent criteria and this provided a reference point for future research on Khoe and San osteology (Tobias, 1985). This was perhaps one of the first its kind in this region of the world and would later provide future insights in population variation and movements in southern regions of Africa.

In his 1985 publication, Tobias expands on initial studies which investigated population movements but were later expanded to also study morphological characteristics of the Khoe and San and other Bantu-speaking populations. Mid-20th century, South African researchers Dr W.H. Brodie and Dr G.A. Turner recorded measurements on black miners in the Witwatersrand. The miners were most likely migrants from other regions of the African continent, thereby having data that was more representative of sub-Saharan Africa (Tobias 1985). These data provide mean statures and weights for male African individuals from the 1900s. Data such as this are important when investigating secular trends as it is used as a baseline to which to compare more recent data (Tobias, 1985). Another major field study on the anthropometry of living black South Africa populations was conducted in 1951 by Frederick W. Strydom. Using data from 970 adult males from black South African populations, the author documented admixture between the KhoeSan

and other Bantu speaking population groups. Tobias' 1985 publication elaborates on the many researchers involved in the study of African populations not only from South Africa but globally.

As previously discussed, in the 1950s, 1960s and 1970s, several expeditions were initiated in order to observe and collect physical anthropological records, demographic information, human genetic data and ecological observation on living individuals and their environment in southern Africa (Tobias, 1985). The School of Anatomical Sciences at the University of the Witwatersrand curates the anthropometric data that were recorded during these expeditions. These data sets contain vast amounts of anthropometric and anthroposcopic information of sub-Saharan African communities and remain largely unexplored. It is a valuable resource for historic and modern human variation studies.

CHAPTER 3: MATERIALS AND METHODS

3.1 Introduction

This study used two sources of data. The first source comprises of previously collected historic data housed in the School of Anatomical Sciences at the University of the Witwatersrand. These comprise of handwritten files of anthropometric data collected in the 1950s, 1960s and 1970s throughout sub-Saharan African communities. Research on materials housed in the School of Anatomical Sciences is covered by an ethics waiver (Appendix B). As the data are historic, it is useful to understand the terminology. Bantu-speaking populations refer to the groups of Sub-Saharan Africa groups that were part of the Bantu-speaker migration and who share similar linguistic characteristics.

On these old documents reference is also made to “Bushmen”, which is not a currently acceptable term. In this instance it refers to the Khoe and San people. Today, the Khoe language is spoken by hunter-gatherers in parts of the Kalahari while the San are found in dry parts of Angola, Botswana and Namibia (Thompson, 2010; King, 2015; Lottering, 2020). The word “Khoe’ means “person” in Nama and the word “San” is the Khoe word for “foragers” or “bushmen” (Chebanne, 2012). In 2002, at a meeting attended by the Working Group of Indigenous Minorities in Southern Africa (WIMSA) and the South African San council (SASC), the San people decided that they wanted to be referred to by their individual community names or collectively as the San. When collectively referring to the San and the Khoe, the term KhoeSan was suggested (Chebanne, 2012). However, the National Khoe and San Council (NKSK) recognise these two groups as being culturally independent and as such they should be referenced as two separate groups and therefore will be referred to as the Khoe and San in this study. While debates as to the most appropriate terminology is ongoing, these are the terms that will be used through this study.

The second source of data comprises of computerised tomography (CT) scans of a modern South African population. These CT scans were collected at the Department of Diagnostic Radiology at Charlotte Maxeke Academic Hospital, Johannesburg. All the scans used in the study were collected retrospectively and accessed via hospital records. Individuals that were recorded as black South Africans were used. As the ethnicity of these individuals were not always known, this sample was treated as a single group of black South Africans. The CT scans were collected and archived by the hospital between 2016 and 2018. The Human Research Ethics Committee (Medical) granted approval for the use of the CT scans in 2017 (clearance certificate no. M170339)

(Appendix C). Additionally, access to the CT scans was granted by the Department of Diagnostic Radiology (Appendix D).

3.2. Materials

3.2.1. Historic anthropometric data

Several multidisciplinary scientific expeditions were carried out during the 1950s, 1960s and 1970s throughout sub-Saharan Africa to collect anthropometric data from various populations (Figure 3.1). During these expeditions, anthropometric data from communities in Zambia, Mozambique, Malawi, Tanzania, Angola, Botswana and South Africa were collected and documented. These data are archived, as individual paper scoring sheets, in the School of Anatomical Sciences at the University of the Witwatersrand. Data from a total of approximately 2000 individuals (male and female) from various communities and population groups around sub-Saharan Africa were collected and assessed, of which 1345 were found to be complete and usable enough to include in the current study (Table 3.1). The majority of the individuals were male with very few recorded female data. This did not allow for an adequate comparison between the sexes and therefore it was decided to only use male data for the study.

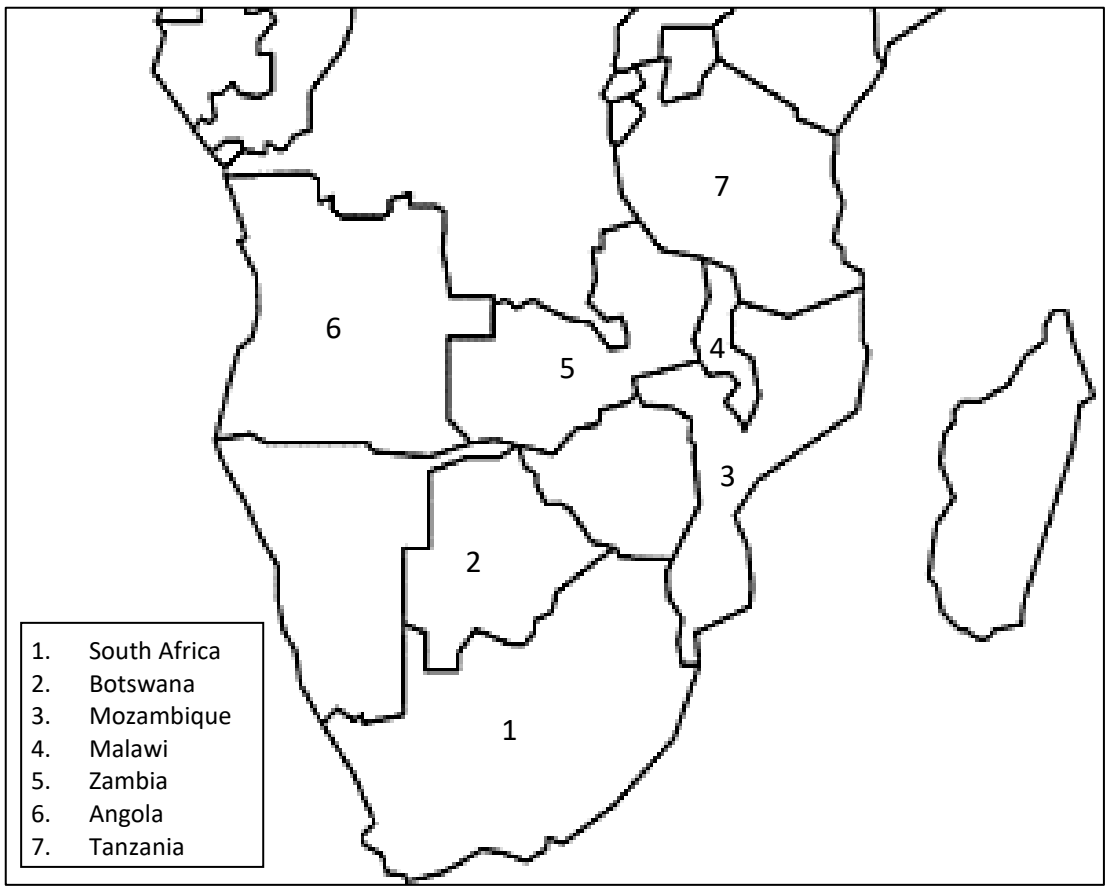


Figure 3.1: Map indicating the countries of the represented population groups throughout sub-Saharan Africa.

Table 3.1: Number of adult male individuals (n) for each sub-Saharan African group included in the historic data.

Population	N
Angola	34
Botswana (Bantu-speaking)	45
Botswana (Khoe and San)	
Central	41
Hybrid	39
Southern Sarwa	48
Malawi	113
Mozambique	56
South Africa (Pedi)	
Rural	95
Urban	217
South Africa (Venda)	
Rural	201
Urban	146
Tanzania	165
Zambia	46
Total (n)	1346

For each individual, a range of characteristics was measured, recorded and scored on individual scoring sheets. This information included anthropometric measurements throughout the body, fingerprints, blood samples and, in some instances, photos were also included, and face masks obtained. For this study, only craniofacial measurements were used. Most individuals were adults; however, it is difficult to provide age ranges as specific ages of the individuals were not always included. The records would often only state whether an individual was an adult or not. The handwritten data were transferred to Excel spreadsheets. During this exercise, all demographic information (such as name, birthplace, etc). and the full range of measurements from the complete body were recorded in Excel. This database is now available for research purposes and is stored at the School of Anatomical Sciences, University of the Witwatersrand.

3.2.1.1. History of sample

Records of the expeditions are unfortunately limited. Tobias (1985) noted that many South African researchers were involved in such expeditions in the 20th century, and he speaks specifically of Raymond A. Dart. In 1951, Dart suggested that Tobias represent Wits University and join the French Panhard Capricorn Expedition that was crossing southern Africa (Tobias 1985). Tobias would particularly study Bushmen of the Kalahari, taking anthropometric data and face masks. In the 1950s, Tobias led the University of the Witwatersrand Kalahari Research committee. Over approximately 15 years, he generated a considerable amount of data on the so called "Bushmen" cultures. These multidisciplinary expeditions embraced physical anthropology under Tobias (1956; 1957; 1961; 1962) and de Villiers (1961; 1969). Human population genetics were studied under supervision of Jenkins and Nurse and many collaborators that continued well after the Kalahari Research Committee ceased to operate in 1970 (Jenkins, 1965; 1968; 1972; Jenkins *et al.,* 1968; 1971; Jenkins and Nurse, 1974; 1976; Nurse and Jenkins, 1975). Wyndham studied physiological adaptability (Wyndham and Morrison 1956; 1958; Wyndham, 1965), and investigated black miners from many subequatorial African territories ranging up to Tanzania in the northeast and Angola in the Northwest (Fleming *et al.,* 1964; Wyndham *et al.,* 1964; Wyndham, 1965; Morrison *et al.,* 1986). Nurse extended this program of field studies of the living Southern African populations and studied the physical characteristics of the Maravi and other people of Malawi. This formed the substance for his doctoral thesis. In Angola, de Almeida was the director of the Anthropobiological survey during which he and other collaborators studied a wide range of Angolans, particularly the San and non-Bantu speakers (de Almeida, 1965).

Upholding ethical integrity towards scientific research is fundamental. Historical collections, such as the one used in the study, where no formal research participant consensus is available, presents a problem (Houlton and Billings, 2017). Although the collection of measurements (and in some instances, face masks) may possibly offer a form of consent, it is impossible to differentiate willing participants from manipulated participants. Access to the data and collections at the University of the Witwatersrand is controlled. Applications for research using such sensitive data is reviewed and cleared depending on the ethical and practical appropriateness by the Head of School and Collections Committee. Recently, traditional leaders from !Xun, Khwe and !Khomani groups of the San, issued a San research-ethics code to scientists that actively requests such engagement (Callaway, 2017). However, gaining ethical clearance can be challenging, particularly when the population origins are unknown or whether there is uncertainty around the population information recorded in historical data sets. It is imperative that any future research at Wits is led by a passion in promoting continuity between the peoples of

Africa and the world, benefiting both society and science (Houlton and Billings, 2017). In the current research, no names of individuals will be given and no photographs will be shown. Unfortunately, very little information is available regarding the history of the sample, however, a brief description and history of the communities that were assessed during the field work is provided. The total historic sample used in this study is shown in Table 3.1. Very few female records are available and hence they were not included in this study.

Angola

Anthropometric measurements were collected on mine labourers from Angola. The participants were contracted mine labourers working on the mines in South Africa but who were originally from Angola. The study of African gold miners was done by the Human Sciences Laboratory Transvaal and the Orange Free State Chamber of Mines, Johannesburg, Transvaal, successively headed by Wyndham and Strydom (Wisner, 1989). The data set comprises of 34 individuals and it was noted that these were Bantu-speaking individuals.

Botswana

From 1956 to 1966, a series of expeditions studied the Kalahari 'Bushmen' of Botswana. These expeditions were multidisciplinary and brought together several scientists from different fields under the Kalahari Research Committee (Tobias, 1970). In 1964, an expedition to the central and southern Kalahari in Botswana was carried out. Interest lay in the study of three groups of KhoeSan in the Ghanzi/Kang districts of Botswana. Two of the groups numbered about 60 individuals each (including men, women, and children) and the third was much smaller, consisting of only 20 people. Anthropometric and anthroposcopic findings were recorded. Along with the observations of "Bushmen", several Bantu-speaking males were also studied. The collection currently includes 128 male "Bushmen" individuals and 45 Bantu-speaking male individuals.

Malawi

During 1969 and 1970, anthropometric surveys were carried out by Nurse on men in Malawi. The "tribe", district or village of origin, and clan names of both parents were recorded (Nurse, 1975). The sample comprised of a large number of adult men made up of smaller samples thought to be representative of various divisions of the population of Malawi (Nurse, 1975). The current data set comprises of 132 individuals.

Mozambique

Much like the sample from Angola, and under the supervision of Morrison *et al.* in 1968, anthropometric measurements were collected on contracted mine labourers working in South Africa but originating from Mozambique. This study was also conducted by the Human Sciences

Laboratory Transvaal and Orange Free State Chamber of Mines, Johannesburg, Transvaal. The current data set comprises 74 individuals.

Tanzania

Wyndham collected data from black miner labourers in South Africa from Tanzania (Tobias, 1985), similarly to those from Mozambique and Angola. The sample comprises of 165 individuals.

Zambia

Tobias' field studies in 1957 and 1958 of the Tonga in southern Zambia comprised a demographic survey and detailed biological observations on a series of 500 adult males. In 1957, Tobias invited Desmond Clark and H. A. Fosbrooke to be involved in the Gwembe valley survey of the Plateau Tonga of the then Northern Rhodesia. The land was to be flooded by the Kariba Dam and some 54 000 people would be affected. As a member of the survey, Tobias was responsible for studies of physical anthropology. Numerous metric and non-metric observations were recorded, along with photographs of each individual. The field work included studies in 59 villages (Tobias, 1970).

Studies focused on the Zambian Tonga who lived on a high plateau and the low-lying Grebe valley. Historically, the Valley Tonga population had been clearly distinguished from other groups on higher ground. For centuries there was a constant coming and going of Bantu-speaking groups on the Plateau where numerous cultural contacts were made. The Grebe Valley, on the other hand, was difficult to access, and thus the Valley Tonga has remained largely isolated. Tobias (1970) noted that the cattle owning plateau Tonga exceed the Valley Tonga significantly in stature and weight along with other measurements. Although anthropometric data may differ between the Valley and Plateau Tonga, these two groups were assessed as a single group.

South Africa

Two individual South African groups were studied – the Venda and Pedi. As part of the South African Multidisciplinary Human Adaptability Project of the International Biological Programme, field studies under the supervision of De Villiers were carried out on the Venda in 1968 (de Villiers, 1979). Approximately 348 adult male Venda individuals, of which 201 were from a rural area in Chief Lwamondo's District and 148 in an urban environment at Tshiawelo township, southeast of Johannesburg, were observed (Tobias, 1970; de Villiers, 1979). For the purpose of this study, individuals from the rural and urban areas will be treated as a single Venda population group.

In 1970, as part of the same study mentioned above, approximately 437 adult male Pedi, of which 227 resided in an urban environment and 210 residing in a rural environment at were observed (de Villiers, 1979). Once more, individuals from rural and urban areas were treated as a single population group.

3.2.2. Modern South African data

In addition to the historic anthropometric data previously collected and documented on the abovementioned population groups, a modern black South African sample was added to the analysis. This reflects the current modern population variation in South Africa.

Computerised tomography (CT) scans of 51 self-identified black male South African individuals from the Department of Diagnostic Radiology at the Charlotte Maxeke Johannesburg Academic Hospital were used. Ages ranged between 20 – 60 years of age. No distinctions were made between these individuals as far as language or origin was concerned, as they were seen as a homogeneous population representing black South Africans (de Villiers, 1968). Data were collected retrospectively and only head and neck CT scans from a pre-existing database were used as this allowed for a complete scan of the head. This was necessary, as all the anthropometric measurements which are mentioned in Table 3.3 needed to be taken. Any scans that showed signs of trauma or pathology which may have obstructed landmarks necessary for the measurements were excluded from the study. The total sample used in this study thus comprised 1397 individuals, as shown in Table 3.2.

Table 3.2: Total sample

Populations	N
Historic sub-Saharan populations	1346
CT scans of modern South Africans	51
Total (n)	1397

3.3. Methods

During the anthropometric surveys, several measurements were taken of the head and face, of which 12 measurements were used in this study. This was decided due to a large number of missing values for specific measurements such as those around the mouth. All these measurements are standard anthropometric measurements described in several texts (Farkas, 1994). Table 3.3

provides descriptions of the included measurements while Appendix A provides illustrations of the craniofacial landmarks. Measurements were taken using spreading and sliding callipers and were recorded to the nearest millimetre. The same descriptions were used to locate craniofacial landmarks and take measurements from CT scans of the modern South African sample.

3.3.1. Historical data

The historical data which were collected during the 1950s, 1960s and 1970s by individuals such as Dart, Tobias and de Villiers were catalogued. All the data collected during the expeditions were on hand-written records which are housed at the School of Anatomical Sciences, University of the Witwatersrand. All the old documents were sorted through, and the archival records updated and entered into a computer database using Microsoft Excel. Information pertaining to the expeditions was recorded where available. The capturing of this data provides access to this information which will be made readily available for future research, pending ethics clearance.

3.3.2. CT Scans

All measurements (Table 3) were taken from CT scans from a modern South African population of African origin. A three-dimensional (3D) DICOM viewer with an inbuilt measuring tool (OsiriXLite) was used to collect all 12 measurements from soft tissue dimensions. OsiriX is a multidimensional image navigation and display software that allows for the display and interpretation of large sets of multidimensional images (Rosset *et al.,* 2004). OsiriXLite is a free downloadable demonstration version of OsiriX. Although there are some limitations in functionality with OsirxLite, it had all the available functions needed for the study.

The CT scans were imported into OsirixLite. Once imported, scans from the selected individual were 3D surface rendered (Figure 3.2). From the surface rendered image, landmarks were plotted on the image (Figure 3.3). Following this, the image was 3D volume rendered in order to take the measurements from the images. Figure 3.4 shows the scans rendered in 3D and demonstrates how measurements were taken. Two measurements (BZB and BGB) were taken from the CT slices as it proved easier to locate the position of the landmarks and gauge the soft tissue thickness around these areas (Figure 3.5).

In OsiriXLite, measurements are taken in centimetres (cms), however, all measurements were converted to millimetres (mm) to correlate with the historic data. All scans were positioned in the Frankfort Horizontal plane before measurements were taken. All measurements were repeated by the primary and a different observer on 20 randomly selected CT scans, which have

been rendered in 3D, to test inter- and intra-observer repeatability. The details of the measurements and measuring techniques were discussed among the primary and independent researcher to provide the most precise definitions for replicability of the landmarks and measurements.

Table 3.3: Descriptions and abbreviations of the anthropometric measurements for the face and head

Measurements	Descriptions	Abbreviations
Head height	The height of the apex above the bitragial axis. This measurement is taken on both the left and right sides and an average head height is calculated.	HHM
Head length (g-op)	The maximum length from the glabella to the opisthocranion measured in the midsagittal plane	HL
Head breadth (eu-eu)	The maximum breadth from euryon to euryon.	HB
Minimum frontal breadth (ft-ft)	The shortest distance between the fronto-temporale on both sides	MFB
Bizygomatic breadth (zy-zy)	The distances between the most laterally projecting points on the zygomatic arches on both sides	BZB
Bigonial breadth (go-go)	The distance between the gonial points	BGB
Binocular breadth (ex-ex)	The distance from ectocanthion to ectocanthion	BOB
Interocular breadth (en-en)	The distance from endocanthion to endocanthion	IOB
Nasal breadth (al-al)	The distance from alare to alare.	NB
Nasal height (n-sn)	The distance from nasion to subnasale	NH
Total facial height (n-gn)	The distance from the nasion to the gnathion.	TFH
Upper facial height	The distance from nasion to alveolare	UFH

(Farkas, 1994)

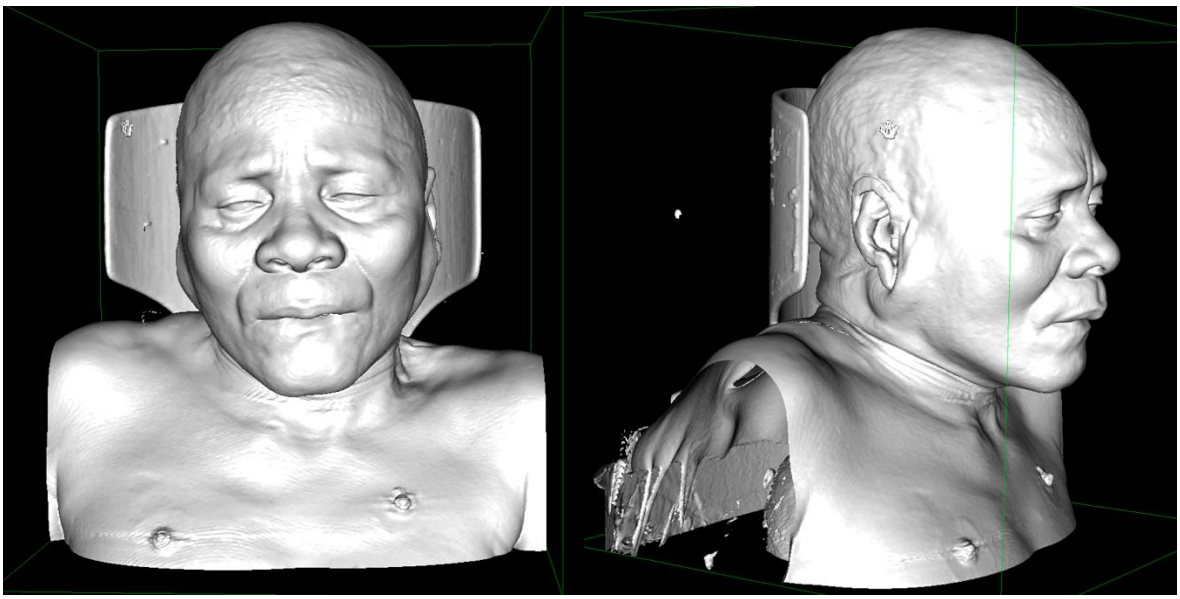


Figure 3.2: Images showing the 3D surface rendering of CT scans using OsiriXLite.



Figure 3.3: A 3D surface rendered image (zoomed in) showing plotted landmarks (red dots) for facial measurements.

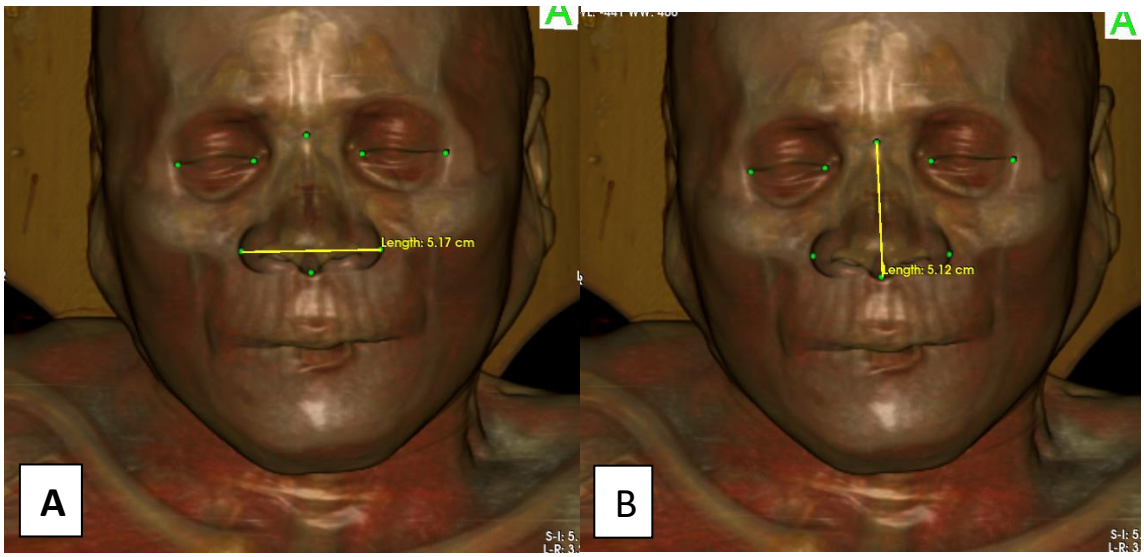


Figure 3.4: Two images that were 3D volume rendered after landmarks were plotted (green dots). This allowed for measurements to be taken between each plotted landmark. Image A indicates nasal width and image B indicates nasal height taken in centimetres.

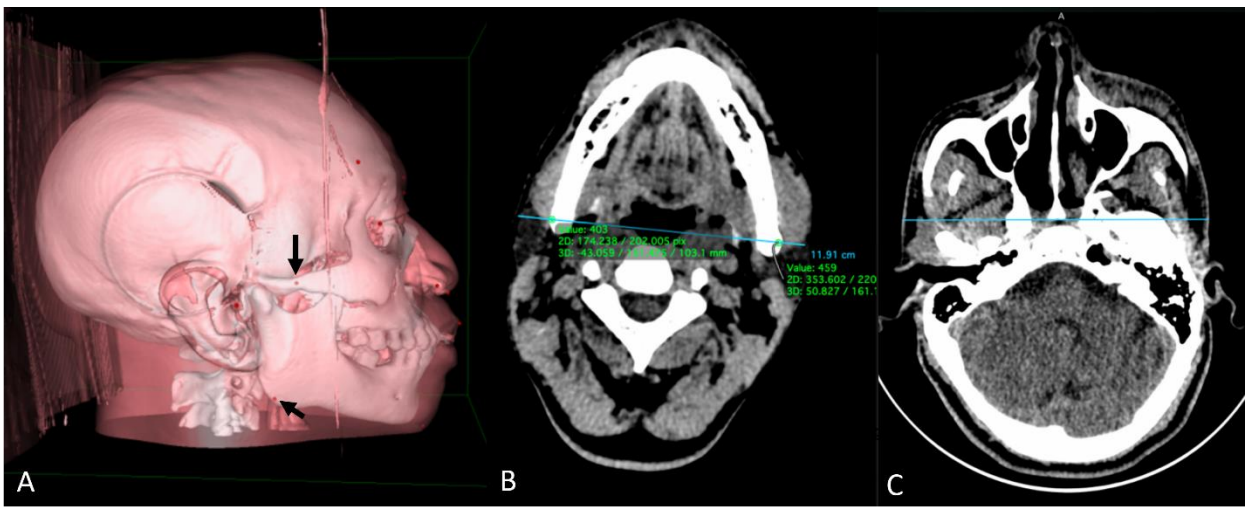


Figure 3.5: A: surface rendered CT scan showing underlying bony landmarks of BZB and BGB (black arrows). B: CT slice showing BGB measurement after the landmarks were plotted, C: CT slice showing BZB measurement after the landmarks were plotted.

3.4. Groupings and comparisons

Due to the large dataset and to make comparisons between various groupings possible, populations were initially allocated into three sets. The first set (set 1) consists of the historic Bantu-speaking population groups only. It includes individuals from Angola, Malawi, Mozambique, Tanzania, Zambia, Botswana (Bantu-speakers only) and South Africa. The population groups were further grouped into geographic populations representing the west, east, south-central and south of sub-Saharan Africa (Table 3.4)

Table 3.4: Populations grouped according to geographic regions in set 1

Geographic region	Population group
West	Angola
East	Malawi
	Mozambique
	Tanzania
South-Central	Zambia
South	Botswana (Bantu-speakers only)
	South Africa

Set 2 consists of historic Bantu-speaking population groups but with the Khoe and San populations added. The population groups have been further grouped into populations representing the West, East, South, South central and Khoe and San (Table 3.5). The data from the Kalahari originates from Khoe and San populations and as such, it is expected they will prove to be different from all the other population groups. Although they will act as outliers, it can also be assessed whether the populations from the western or eastern geographic regions are more similar to those from the Kalahari.

Table 3.5: Populations grouped according to geographic location in set 2

Geographic region	Population group
West	Angola
East	Malawi
	Mozambique
	Tanzania
South-Central	Zambia
South	Botswana (Bantu-speakers only)
	South Africa
Kalahari	Khoe and San

Set 3 consists of historic Bantu-speaking population groups, the Khoe and San populations and the modern South African sample (Table 3.6). This was done in order to evaluate and compare the historic data and modern data. This will allow for the interpretation of possible migration

patterns through sub-Saharan Africa to southern Africa, thereby supplementing existing information on the Bantu expansion.

Table 3.6: Populations grouped according to geographic location in set 3

Geographic region	Population group
West	Angola
East	Malawi
	Mozambique
	Tanzania
South-Central	Zambia
South	Botswana (Bantu-speakers only)
	South Africa (historic)
Kalahari	Khoe and San
South Africa	South Africa (modern)

For certain statistical analyses, these three sets were not informative enough and it was decided to further separate the sets into geographic regions based on the demographic information recorded in the datasets. Table 3.7 indicates the regions the populations as recorded as from the dataset. Most of the populations were grouped according to their country of origin. The Khoe and San populations were further divided into three groups: 1) Khoe and San central 2) Khoe and San "hybrid" and 3) Khoe and San southern Sarwa. These three Khoe and San groups come from various regions of the Kalahari and the Khoe and San "hybrid populations were documented as being a mixture of the Khoe and San and Bantu-speaking populations. Furthermore, the historic South African populations were also further divided into three groups: 1) South African Venda, 2) South African Pedi and 3) South African individuals from Limpopo. Again, these represented different areas in South Africa that the individuals came from.

Table 3.7: Further geographic grouping of populations in sub-Saharan African based on recorded information in the datasets.

Geographic region	Population group	Region as recorded in the datasets
West	Angola	Angola
East	Malawi	Malawi
	Mozambique	Mozambique
	Tanzania	Tanzania
South-Central	Zambia	Zambia
South	Botswana (Bantu-speakers only)	Botswana
	South Africa (historic)	South Africa Venda
		South Africa Pedi
		South Africa Limpopo
Kalahari	Khoe and San	KhoeSan (central)
		KhoeSan (hybrid)
		KhoeSan (Southern Sarwa)
South Africa	South Africa (modern)	Modern SA

3.5. Statistical Analyses

All statistical analyses were performed using the statistical program PAST (version 4.1) (https://www.nhm.uio.no/english/research/infrastructure/past/) and SPSS (Version 26). Repeatability of measurements on CT scans were tested using the technical error of measurement (TEM). The most common way to express the error margin in anthropometry is to calculate the technical error measurement (TEM) and associated metrics (Ulijaszek and Kerr, 1999). TEM is an accuracy index which represents the measurement quality. It allows anthropologists to assess the degree of accuracy when performing and repeating anthropological measurements (intra-observer error) and when comparing their measurements with measurements from other observers (inter-observer error) (Perini *et al.,* 2005). This index is approved by the International Society standardization Advancement in Kinanthropometry (ISAK) for the accreditation of anthropometrists in Australia (Ulijaszek and Kerr, 1999). Acceptable levels of agreement are often difficult to ascertain because TEM is age dependent and related to anthropometric characteristics of the group or population under investigation. However, a reliability coefficient (R) of 0.95 should be sought where possible (Ulijaszek and Kerr, 1999). Specific figures of acceptable levels of agreement are rare in the literature and are often related to the specific aims of a given study and how the data will be applied (Franklin, *et al.,* 2013). Therefore, it was decided that an r value

greater than 0.90 would be acceptable for the current study. This follows the Franklin *et al.* (2013) study where traditional osteometric and volume rendered MSCT cranial measurements were assessed.

Following this, descriptive statistics for each population group was calculated using the raw data sets. Descriptive statistics included the total number of individuals (n), as well as the mean and standard deviations (SD) for each population group. The raw dataset had less than 1% missing values. Therefore, the dataset was cleaned and any missing values were imputed for a more complete data set. Imputation is the process of replacing missing data with substituted values. To achieve this, a multiple imputation method was used. Multiple imputation has become an important and influential approach to dealing with missing data and has been shown to be a valid tool for handling missing data (Schafer, 1999; Kenward and Carpenter, 2007). If any individuals had more than 50% of variables i.e., more than 6 of the 12 variables missing, those individuals were excluded from the final analysis as there would have been too much missing information to impute missing values. All missing values were imputed using SPSS (version 26). Most multiple statistical methods, such as those used in this study, require complete datasets. Following the imputation, statistical analyses were performed for each of the sets mentioned above and to meet each objective set out at the beginning of the study.

3.5.1. Objective 1

To assess anthropometric variation within each set, a Principal Components Analysis (PCA) and ANOVA, incorporating pairwise post-hoc tests, was performed. PCA allows one to extract pertinent information from a large data set. PCA is a dimension-reduction technique that is used to reduce a large set of variables to a small set of variables while still retaining most of the information from large set (Harris, 1975). By doing so, any trends, groupings, key variables, or outliers could be noted. PCA displays variation within a sample and characterises the main features of size and shape variation (Jolicoeur and Mosiman, 1960). PCAs were performed on all the groupings (set1, set 2, and set 3) mentioned above. PCAs and ANOVA were run separately for each group in order to assess the variation between individuals from different geographic locations. All twelve measurements of the head and face were analysed to determine which measurements were associated with craniofacial variation among the population groups. PCA produces loading scores which determine the strength of association a particular variable has on size and shape. In order to visually represent the results, scatterplots were used.

3.5.2. Objective 2

To determine patterns of morphological discrimination between the population groups for group separation, a Discriminant Function Analysis (DFA) was used. DFA is used to show differences among variables to maximise inter-group differences and to determine whether a variable or a combination of variables is useful in predicting group / population membership (Green and Salkind, 2008). Once again, DFA was run on all three sets of groups and all twelve measurements were included in the analysis. This was done to determine which regions of the head and face are morphologically distinct or similar between groups of populations.

3.5.3. Objective 3

The third objective aimed to assess geographic and morphological distances among the populations. During this stage of the analysis, the three sets were further divided into geographic regions (Table 3.7) as this would provide more information on morphological distance among the populations. Mahalanobis distance (D^2) was used to determine morphological distances between individual faces, to identify possible populations and outliers and measure levels of homogeneity and heterogeneity in and between the groups. As Mahalanobis distances represent dissimilarities, the greater the Mahalanobis distance between two groups, the greater the morphological distance (Xing, *et al.,* 2008).

The geographic co-ordinates (longitude and latitude) for the villages and regions were obtained from google maps and the longitude and latitude finder of the My NASA data website (Https://landlook.usgs.gov/landlook/viewer.html). For those individuals that were gold miners (i.e., from Angola, Mozambique, and Tanzania) that were observed in South Africa but stated that they were from a different country, the co-ordinates for the approximate centres of the region / country were obtained. The co-ordinates were used to calculate a geographical distance matrix.

A Mantel test was then calculated using the morphological distance matrix and geographical distance matrix to determine a correlation between the two. The Mantel test measures the strength of the relationship between the two matrices using an r value (Diniz-Filho *et al.,* 2013). R values will range from -1 to 0 to +1. Negative 1 (-1) indicates a strong negative correlation, zero (0) indicates no correlation and positive one (+1) indicates a strong positive correlation. Following this, Principal Co-ordinate Analyses (PCoA) were conducted and scatterplots used to visually represent mean morphological differences between sub-Saharan African populations.

3.5.4. Objective 4

Based on the results of the abovementioned statistical analyses, proposed migration routes through sub-Saharan African can be evaluated and possible geographic and other barriers identified. No additional statistical analyses were needed for this step.

CHAPTER 4: RESULTS

The results of the study are described in the order of the statistical analyses and objectives provided in the previous chapter. The Technical Error of Measurement (TEM) and descriptive statistics will be discussed first. These statistical analyses describe the entire sample (historic data and modern data).

As described in the previous chapter, the populations were divided into three sets. Set 1 is composed of the historic Bantu-speaking populations only, set 2 is composed of the historic Bantu-speaking populations and Khoe and San group, and set 3 is composed of the historic Bantu-speaking populations, the Khoe and San group and the modern South African population. The statistically analyses were then performed on each of these sets. The results of the Principal Components Analysis (PCA) will be presented first. All three sets were compared to assess the greatest variation among individuals. Following this, the results of the Discriminant Function Analysis (DFA) will be presented to assesses patterns of morphological discrimination between the population groups. Again, this will be performed independently for each of the three data sets. Lastly, the results of the Mantel tests and Principal co-ordinate plots, for each of the sets, will be presented. This will show whether there is a correlation between craniofacial variation and geographic distance. As described in Chapter 3, all measurements are standard anthropometric measurements of the face and head. Table 3.3 shows the abbreviations for each of the measurements used in the study and in the statistical analyses. The abbreviations will be used throughout the results and discussion.

4.1. Technical Error of Measurement (TEM)

The precision and accuracy of the measurements of the modern individuals was calculated using 20 randomly selected CT scans. Table 4.1a and b shows the TEM, the relative TEM (%TEM) and the R coefficient for both the inter observer and intra observer measurements. An r coefficient of > 0.90 is considered reliable (Ulijaszek and Kerr, 1999). Ulijaszek and Kerr (1999) state that %TEM provides no information for comparison of studies in which more than one observer is used, and where both intra- and inter-observer TEM are reported. Therefore, it was decided to not report the %TEM in the following study.

Generally, most of the measurements obtained R-values above 0.9 when repeated by the author (intra-observer). Mid facial measurements (IOB, NB, NH, TFH and UFH) are shown to be most repeatable and reliable. Measurements of the cranial vault (HHM and HL) and craniofacial

breadth (MFB, BGB and BOB) had moderate reliability. The lowest repeatability was for BZB (R=0.68).

Most of the measurements repeated by a second observer obtained R-values that show moderate to good reliability and repeatability (R>0.8). Similar to results obtained from the intra-observer measurements, IOB, NB and NH had the highest repeatability (R>0.9). The least repeatable, was once again BZB (R=0.67). Although BZB obtained the lowest r-value, it was decided to use all measurements (including BZB) in the study as these were the same measurements taken during the expeditions and was needed for comparability. It must be kept in mind that the measurements taken when determining TEM and repeatability, were all done on CT scans. As such, these would only have had an influence on the results of set 3 when the CT scans are being compared to the historic data. Therefore, statistical analyses conducted on sets 1 and 2 were not influenced by these measurements.

4.2. Descriptive statistics

Summary statistics were calculated for each population group on the raw data, before the missing data were imputed. Table 4.2 shows the mean, standard deviation (SD) and total number of individuals (n) in each population. Populations from the eastern side of the continent (Malawi, Mozambique and Tanzania) and those from South Africa had longer HL measurements and wider BZB measurements compared to all the other population groups. All other measurements are comparable between these groups. As expected, the Khoe and San population groups showed much smaller measurements than the other groups, except for the Botswana Bantu-speaking population who had smaller measurements than any other population group.

Figure 4.1 visually represents the mean values for each measurement across the entire sample. Certain measurements in the modern South African sample (HL, HB, BZB, and BGB) were significantly larger when compared to the other population groups. Interestingly, a decrease in size can be seen in MFB in the modern South African sample. All other population groups seem to follow a similar trend line with individuals from Botswana and the Khoe and San having the smallest mean measurements.

Following the analysis of the descriptive statistics, the data was imputed to make for a more complete and comparable data set. Once all the data was imputed and complete, PCA, DFA, Mantel tests and PCoA were run.

Table 4.1a: Intra-observer repeatability for 20 randomly selected CT scans

	HHM	HL	HB	MFB	BZB	BGB	BOB	IOB	NB	NH	TFH	UFH
n	20	20	20	20	20	20	20	20	20	20	20	20
TEM	1.86	1.76	1.21	0.95	3.56	4.48	1.47	0.87	0.86	1.01	2.71	1.68
%TEM	1.45	0.87	0.78	0.94	2.56	3.60	1.48	2.31	1.81	1.92	2.19	2.47
R coeff	0.82	0.86	0.97	0.87	0.68	0.80	0.88	0.92	0.91	0.92	0.93	0.90

Table 4.1b: Inter-observer error for 20 randomly selected CT scans

	HHM	HL	HB	MFB	BZB	BGB	BOB	IOB	NB	NH	TFH	UFH
n	20	20	20	20	20	20	20	20	20	20	20	20
TEM	1.86	1.76	1.98	1.33	3.93	5.53	1.76	1.08	0.85	1.15	4.181	1.91
%TEM	1.45	0.87	1.29	1.32	2.83	4.48	1.77	2.87	1.79	2.24	3.44	2.80
R coeff	0.82	0.85	0.92	0.70	0.67	0.74	0.84	0.90	0.91	0.90	0.85	0.86

Table 4.2: Descriptive statistics for each population group and measurement in millimetres (mean(±SD) and n = total number of individuals)

Population Group	HHM	HL	HB	MFB	BZB	BGB	BOB	IOB	NB	NH	TFH	UFH
Angola	121.9(±5.8)	190.3(±6.9)	141.0(±5.8)	107.6(±5.8)	131.7(±6.9)	100.7(±6.2)	100.0(±5.9)	36.5(±3.6)	42.0(±3.2)	50.6(±5.1)	115.8(±8.0)	71.2(±6.2)
n	32	33	33	32	33	33	33	33	33	33	33	33
Botswana	111.1(±7.2)	189.6(±5.3)	140.1(±5.2)	102.3(±3.7)	130.1(±6.0)	99.2(±5.9)	90.7(±5.2)	34.7(±3.6)	41.8(±2.9)	48.3(±5.6)	111.1(±9.7)	65.4(±6.5)
n	43	43	43	43	43	43	43	43	43	43	43	42
Malawi	121.7(±6.2)	194.0(±5.9)	141.9(±5.4)	107.6(±7.8)	137.4(±5.2)	104.6(±6.1)	97.3(±5.8)	36.3(±2.8)	44.5(±2.9)	50.7(±4.6)	117.1(±7.0)	69.8(±5.0)
n	109	110	110	110	110	110	110	110	110	110	110	110
Mozambique	122.5(±7.1)	193.3(±5.9)	142.2(±4.9)	105.8(±5.0)	135.3(±6.5)	101.9(±6.1)	94.7(±4.7)	36.2(±3.5)	43.7(±2.9)	48.5(±3.9)	113.9(±7.7)	68.4(±4.7)
n	51	53	53	53	53	53	52	53	53	53	53	50
Tanzania	121.7(±6.3)	192.9(±6.4)	143.9(±5.3)	110.1(±7.1)	135.2(±5.3)	102.9(±6.9)	96.6(±5.3)	35.9(±3.5)	43.5(±2.7)	49.7(±4.8)	115.9(±6.4)	68.9(±6.1)
n	165	165	166	166	166	165	165	165	165	165	165	160
Zambia	121.3(±7.4)	190.8(±7.0)	140.0(±5.5)	107.0(±4.6)	131.8(±6.6)	101.9(±5.4)	97.6(±6.8)	36.6(±3.4)	44.1(±2.9)	50.0(±5.5)	116.7(±9.0)	70.8(±6.0)
n	45	46	46	45	46	46	46	46	46	46	46	45
South Africa (historic)	122.1(±6.1)	195.9(±6.3)	142.5(±5.3)	109.1(±6.3)	136.9(±5.7)	103.5(±6.1)	97.9(±5.5)	36.3(±3.3)	43.9(±3.5)	51.3(±4.7)	120.0(±7.3)	70.5(±5.7)
n	734	735	737	736	736	735	736	736	737	737	736	672
KhoeSan	115.5(±5.9)	190.1(±6.1)	142.4(±5.2)	104.1(±4.9)	133.2(±4.1)	101.5(±5.4)	92.5(±5.7)	36.5(±4.0)	40.9(±2.7)	50.9(±5.1)	112.6(±7.6)	66.8(±5.9)
n	127	127	127	127	127	127	127	127	126	125	126	124
South Africa (modern)	128.4(±5.4)	201.9(±6.0)	156.5(±6.9)	101.4(±4.3)	141.6(±6.3)	125.1(±8.6)	99.8(±4.8)	38.0(±2.9)	48.1(±3.3)	50.7(±4.0)	124.8(±7.7)	66.3(±5.5)
n	36	50	49	49	48	45	43	49	50	51	30	48

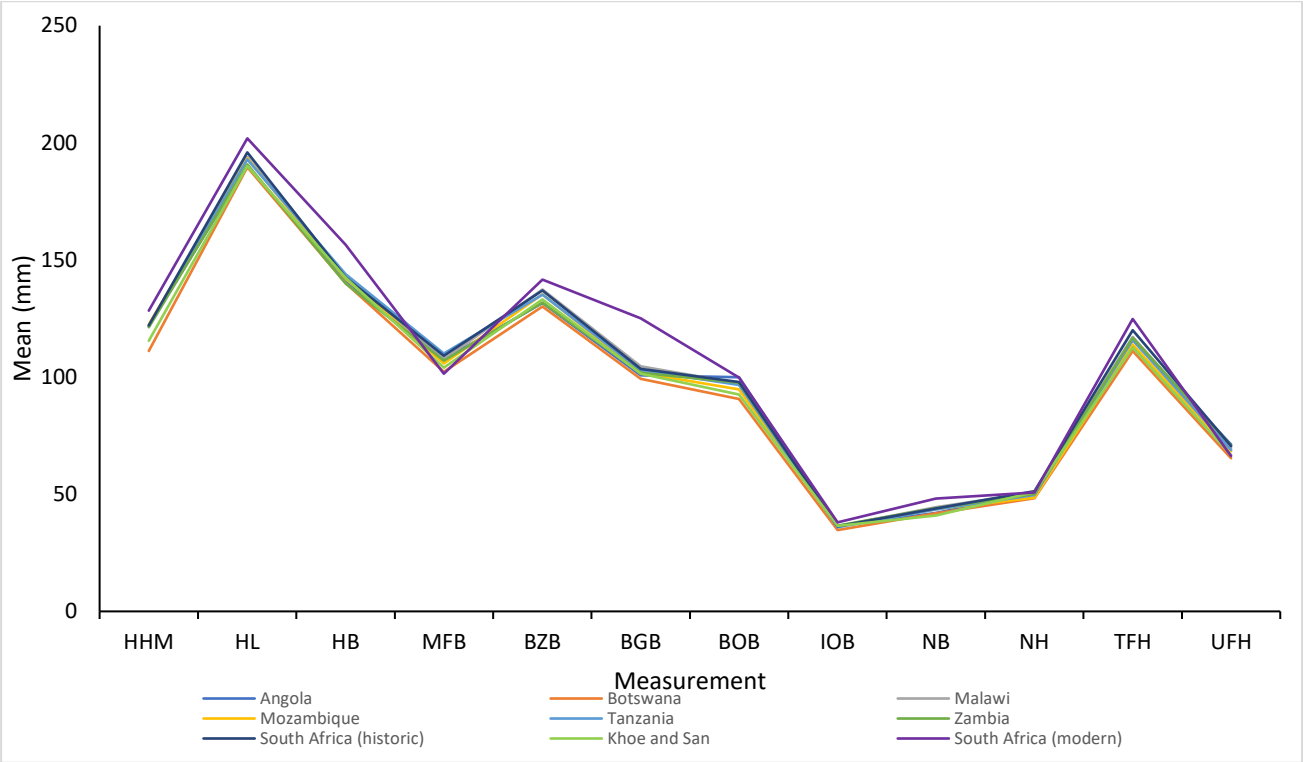


Figure 4.1: Line graph showing mean values (mm) for each measurement across the entire sample.

4.3 Principal Components Analysis

The first objective was to assess the maximum amount of variance among west, east, south-central and South African individuals. This was done by conducting a principal component analysis (PCA) and Kruskal-Wallis (Kruskal-Wallis results are shown in Appendix E in support of the PCA findings). PCA displays variation within a sample and characterises the main features of size and shape variation (Jolicoeur and Mosiman, 1960). PCA and Kruskal-Wallis was performed on all three sets. Results for set 1 will be discussed first, followed by results for set 2 and lastly the results of set 3. For each set, the results of the summary statistics will be discussed first, followed by the loadings and the scatterplots.

4.3.1: Summary statistics and loadings

Summary statistics included the total number of principal components (PC) calculated, eigenvalues and percentage total variance. In all three sets, the eigenvalues and percentage total variance for each of the 12 possible PCs were computed as all 12 measurements (variables) were used in the analysis. If all 12 variables contributed equally to the PCs, then each variable would contribute 8.33% to the total variance. This value was used as a cut off value when determining the number of PCs to include in the results (Peres-Neto *et al.*, 2003).

PC scores were interpreted by examining the loadings for each variable. Loadings indicate the strength of the association between the variables and the principal component. A positive loading indicates that a variable and a PC are positively correlated i.e., an increase in one is associated with in an increase in the other. Negative loadings indicate a negative correlation. Large loadings (whether positive or negative) indicate that a variable has a strong association with the PC. The first PC of traditional morphometric measures usually represents size variation (if all loading scores are positive), while the remaining PCs with negative and positive loading scores usually represent shape variation (Jolicouer and Mossiman, 1960).

4.3.1.1: Set 1: Historic Bantu-speaking groups

Table 4.3 represents the summary statistics for the PCA for the historic Bantu-speaking population groups (set 1). Three principal components accounted for the greatest variation among the individuals (Figure 4.2 and Table 4.3). The first principal component accounted for 34.18% of the total variance, whereas principal components 2 and 3 accounted for 16.05% and 9.61% respectively. As function 4 accounted for 8.64%, it was decided to exclude this function due to it being very close to the cut off value of 8.33% and would therefore barely contribute to the total amount of variance seen within set 1. Principal components 1, 2 and 3 account for almost 60% of the variance.

Table 4.3: PCA summary statistics for Set 1

PC	Eigenvalue	% Variance	Cumulative variance
1	138.14	34.18	34.18
2	64.87	16.05	50.23
3	38.86	9.61	59.84
4	34.92	8.64	68.48
5	28.04	6.94	75.42
6	25.56	6.33	81.75
7	20.88	5.17	86.92
8	15.68	3.88	90.8
9	13.13	3.25	94.05
10	9.55	2.36	96.41
11	7.53	1.86	98.27
12	7.00	1.73	100

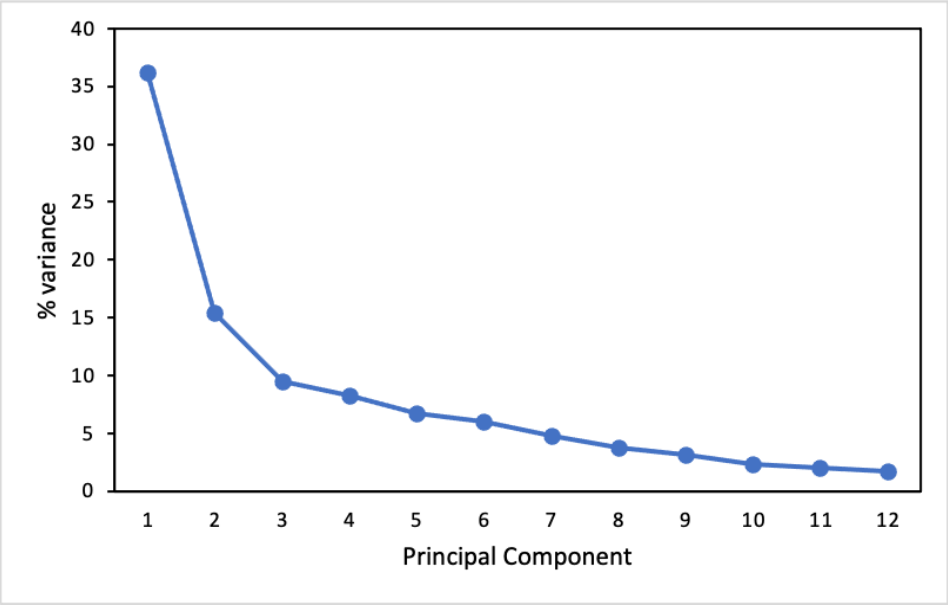


Figure 4.2: Scree plot showing PCA for set 1. PC1, PC2 and PC3 account for most of variance in set 1

The loadings for PC1, PC2 and PC3 are shown in Figures 4.3a - 4.3c. In PC1 (Figure 4.3a), all measurements had positive loadings, suggesting that PC1 represents size and size related shape changes (allometry). TFH had the highest loading (0.5) whereas NB (0.07) had the lowest loading. Values above 0.289 are positively allometric while values below 0.289 are negatively allometric (Somers, 1989). TFH, HL and UFH are significantly above the 0.289 scale and therefore are positively allometric. IOB, NB (and to some extent HB and NH) are below the 0.289 scale and are therefore negatively allometric. Therefore, with increasing size, the head becomes relatively taller and longer with the breadth across the nasal apertures becoming relatively smaller. Variables related to height and breadth of the cranial vault and face (HHM, MFB, BZB, BGB, BOB, TFH and UFH) indicated the greatest association with size and size related changes amongst individuals, while variables related to the breadth of nose and orbits (IOB and NB) showed the least association with size and size related changes amongst individuals. This suggests that elements of the height of the face account for the most variation in size differences, particularly TFH.

PC2 and PC3 show differences in shape-related changes. PC2 had both positive and negative loadings (Figure 4.3b). The largest loading was TFH (-0.52) and the smallest loading was NB (0.05). Variables related to facial height (NH, TFH and UFH) all had negative loadings on PC2. Variables associated with the cranial vault (HHM and HL), the breadth of the face, zygomatics and mandible (MFB, BZB, BGB, and BOB) and the breath of orbits and nose (IOB and NB), on the other hand, all had positive loadings. This suggests that as the face gets shorter

(negative loadings), the cranial vault and face get wider (positive loadings). However, it seems that the greatest association with shape related changes among historic individuals is related to the height of the face and nose. Once again, variables of the midface (IOB and NB) accounted for the least association with shape-related changes seen among individuals in set 2.

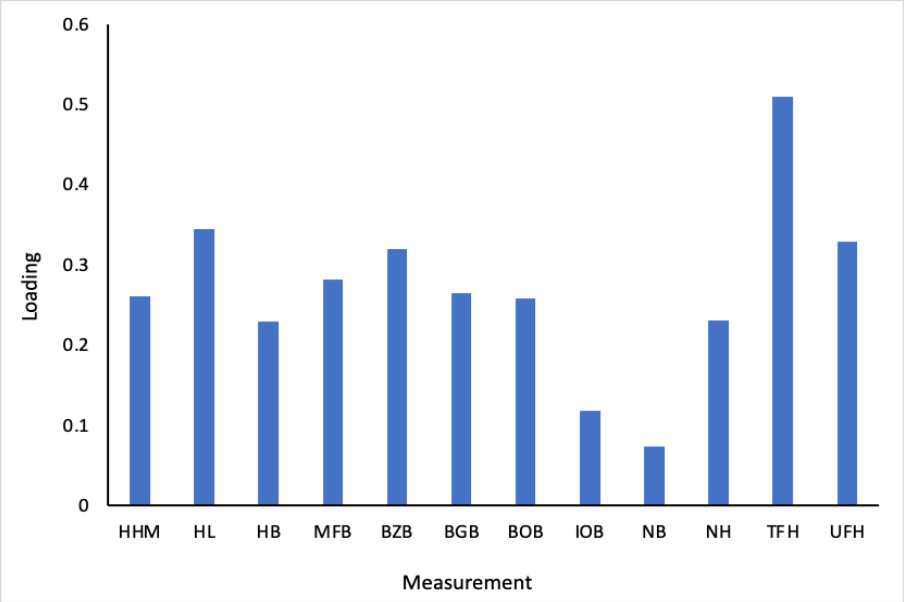


Figure 4.3a: Loadings for each measurement in PC1 in set 1.

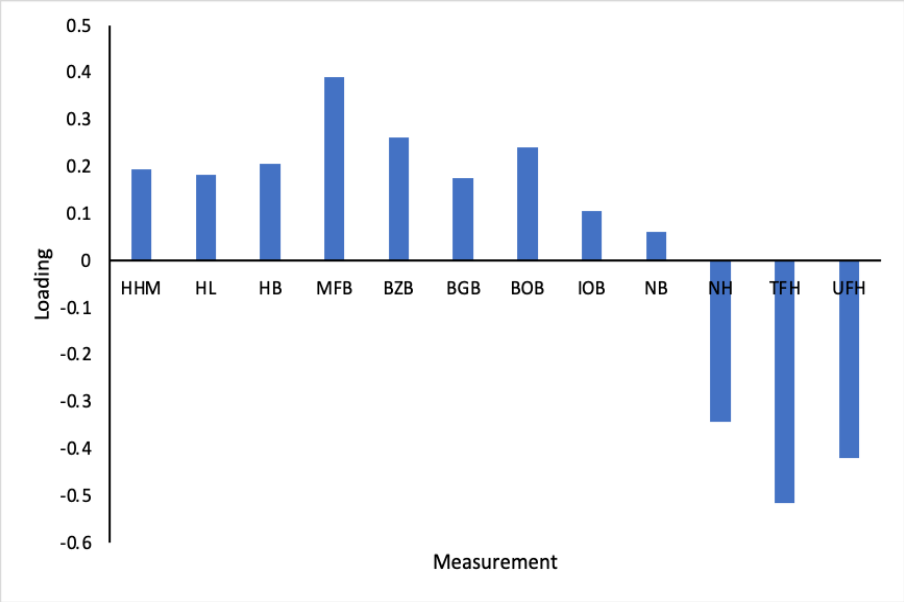


Figure 4.3b: Loadings for each measurement in PC2 in set 1.

PC3 also had both negative and positive loadings (Figure 4.3c). The largest loading was HHM (-0.73), and the smallest loading was MFB (0.004). Variables of the cranial vault (HHM and HL) indicated strong negative loadings on PC3 whereas variables associated with breadth of the face and jaw (BZB and BGB) had the second strongest positive loadings on PC3. This suggests that the shape of the cranium gets relatively smaller as the mandibular region of the face gets bigger. All other measurements (HB, MFB, BOB, IOB, NB, NH TFH and UFH) in PC3 had very little association with shape related changes among individuals.

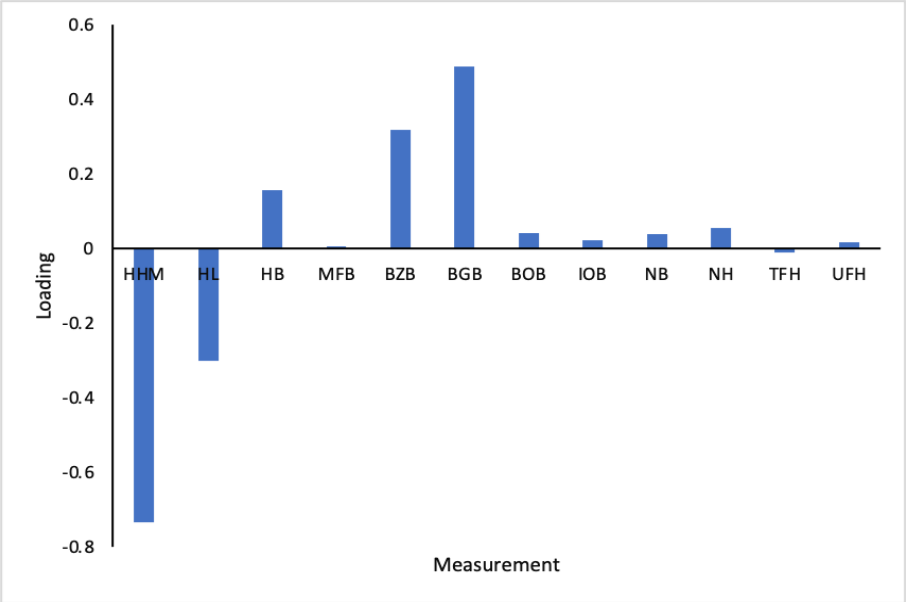


Figure 4.3c: Loadings for each measurement in PC3 in set 1

4.3.1.2: Set 2: Historic Bantu-speaking and Khoe and San groups

The summary statistics for PCA for set 2 are shown in Table 4.4. Set 2 comprises of historic Bantu-Speaking populations grouped according to geographic region (set 1) plus Khoe and San population groups. As described in set 1, a cut off value of 8.33% was used to determine the number of PCs to include in the results. Three principal components accounted for the greatest variation between the populations (Table 4.4 and Figure 4.4). The first principal component accounts for 36.19% of the variance, whereas principal components 2 and 3 account for 15.42% and 9.52% respectively. Principal components 1, 2 and 3 account for almost 61% of the variance.

Table 4.4: PCA summary statistics for Set 2

PC	Eigenvalue	% Variance	Cumulative variance
1	149.36	36.19	36.19
2	63.65	15.42	51.61
3	39.32	9.52	61.13
4	33.89	8.21	69.34
5	27.78	6.73	76.07
6	24.87	6.02	82.09
7	19.90	4.82	86.91
8	15.47	3.75	90.66
9	13.14	3.18	93.81
10	9.69	2.34	96.18
11	8.49	2.05	98.23
12	7.04	1.77	100

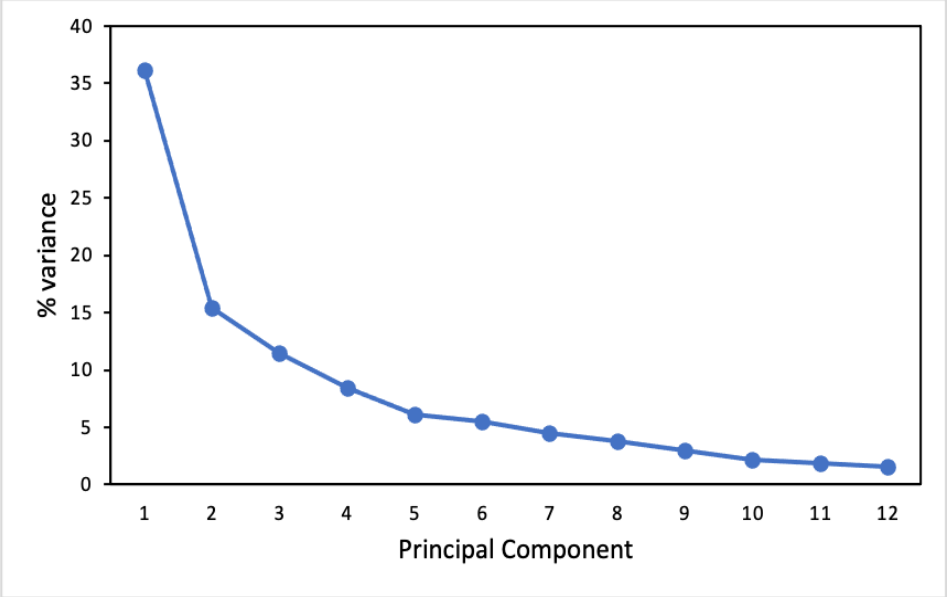


Figure 4.4: Scree plot showing PCA for set 2. PC1, PC2 and PC3 account for most of the variance seen within the sample.

The first principal component, as previously discussed, relates predominantly to size (all positive loadings) and will therefore show size and size-related shape differences among individuals. The loading scores for PC1, PC2 and PC3 are seen below (Figures 4.5a - 4.5c) and are very similar to the loadings seen in set 1. In PC1 (Figure 4.5a), all measurements had positive

loadings. Once again, a value of 0.289 can be used to differentiate between positive allometry and negative allometry (Somers, 1989). TFH had the highest loading (0.51) whereas NB (0.08) had the lowest loading. PC1. TFH, UFH and HL were significantly above 0.289 value scale and as such suggests positive allometry. IOB, NB, HB and NH are below the 0.289 scale and are therefore negatively allometric. Therefore, with increasing size, the head becomes relatively taller and longer with the breadth across the nasal apertures becoming relating smaller. Variables related to height and breadth of the cranial vault and face (HHM, MFB, BZB, BGB, BOB, TFH and UFH) indicated the greatest association with size and size related changes amongst individuals, while variables related to the breadth of nose and orbits (IOB and NB) showed the least association with size and size related changes amongst individuals. This suggests that elements of the height of the face account for the most variation in size differences, particularly TFH.

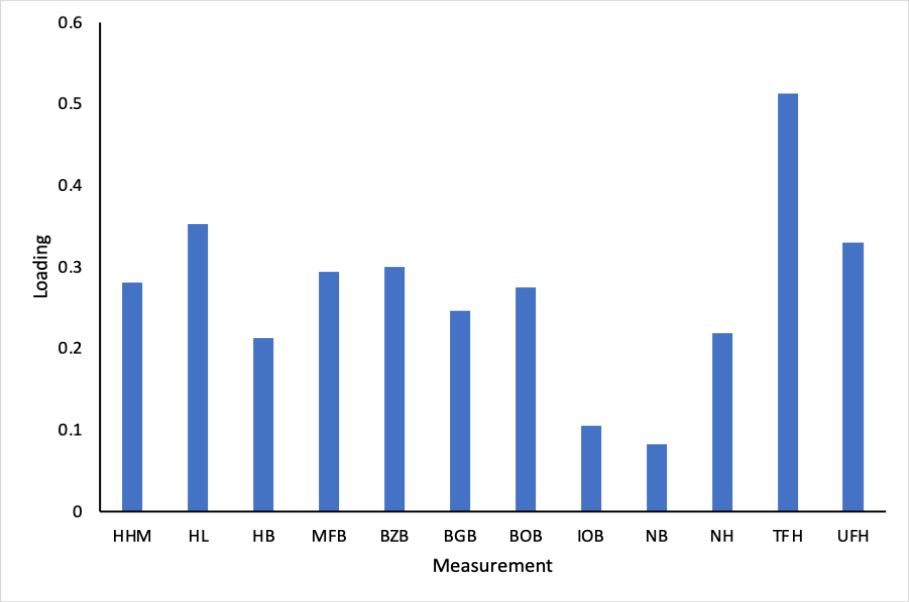


Figure 4.5a: Loading for each measurement in PC1 in set 2.

PC2 has both positive and negative loadings (Figure 4.5b). The largest loading was TFH (-0.51) and the smallest loading was NB (0.06). NH, TFH and UFH all had negative loadings on PC2 whereas all other measurements had positive loadings on PC2. PC2 is associated with shape change. These negative measurements are correlated to the height of the face. Similar to that seen in set 1, this suggests that as the face gets shorter (negative loadings), the cranial vault and face get wider (positive loadings). Once again, variables of the midface (IOB and NB) accounted for the least association with shape related changes seen amongst individuals in set 2.

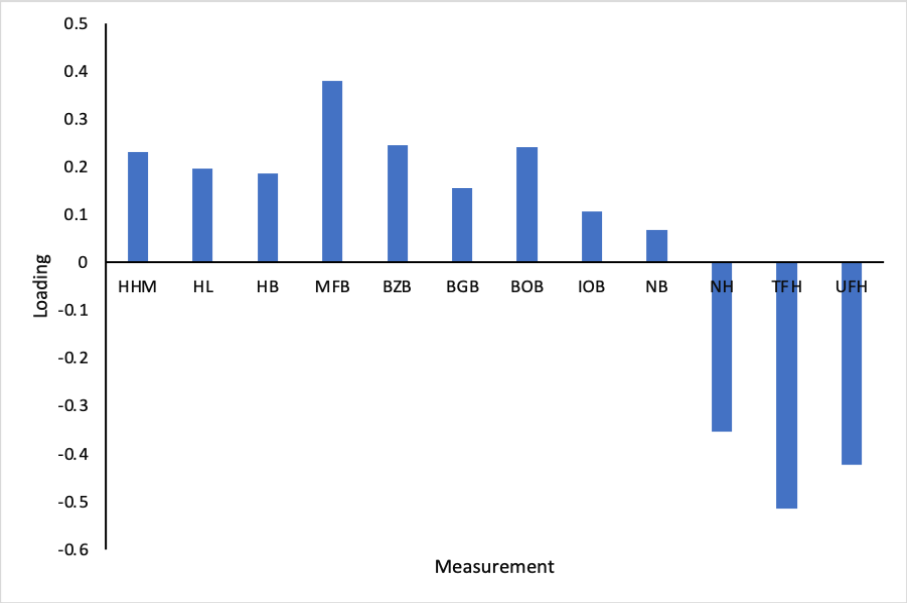


Figure 4.5b: Loadings for each measurement for PC2 in set 2.

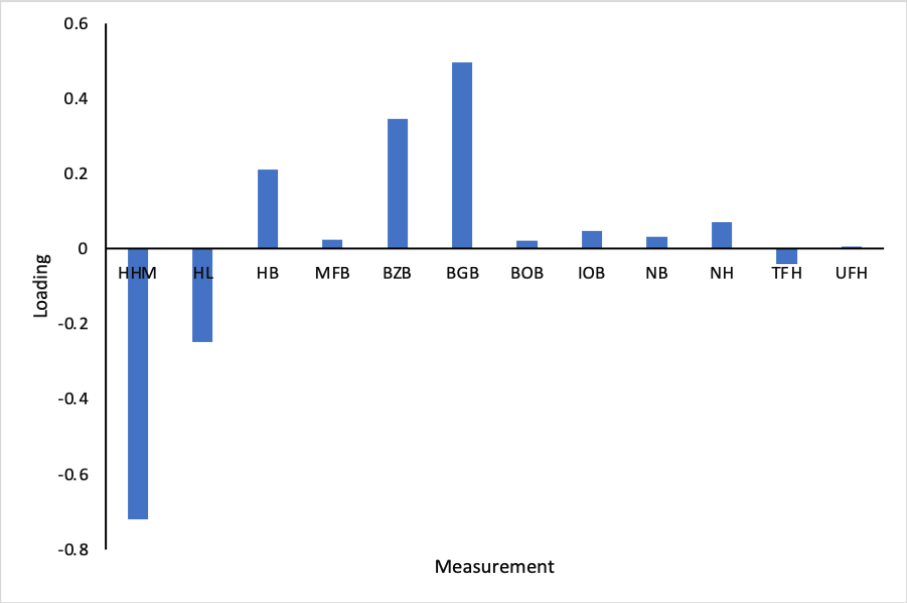


Figure 4.5c: Loadings for each measurement for PC3 in set 2

PC3 also has both negative and positive loadings (Figure 4.5c). The largest loading was HHM (-0.72) and the smallest loading was UFH (0.006). Once more, similar to set 1, variables of the cranial vault (HHM and HL) indicated strong negative loadings on PC3 whereas variables associated with breadth of the face and jaw (BZB and BGB) had the second strongest positive loadings on PC3. MFB, BOB, IOB, NH, TFH and UFH all had small loading scores and therefore did not contribute to much of the shape differences in PC3.

4.3.1.3: Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

Table 4.5 shows the summary statistics for the PCA for all individuals within the study (historic Bantu-speaking, Khoe and San and modern South African) (set 3). The first three principal components accounted for the greatest amount of sample variance (Table 4.5 and Figure 4.6).

Table 4.5: PCA summary statistics for set 3

PC	Eigenvalue	% Variance	Cumulative variance
1	161.80	36.18	36.18
2	68.76	15.37	51.55
3	51.14	11.43	62.98
4	37.85	8.46	71.44
5	27.58	6.16	77.60
6	24.55	5.48	83.08
7	19.92	4.45	87.53
8	17.01	3.80	91.33
9	13.18	2.94	94.27
10	9.78	2.18	96.45
11	8.44	1.88	98.33
12	7.15	1.67	100

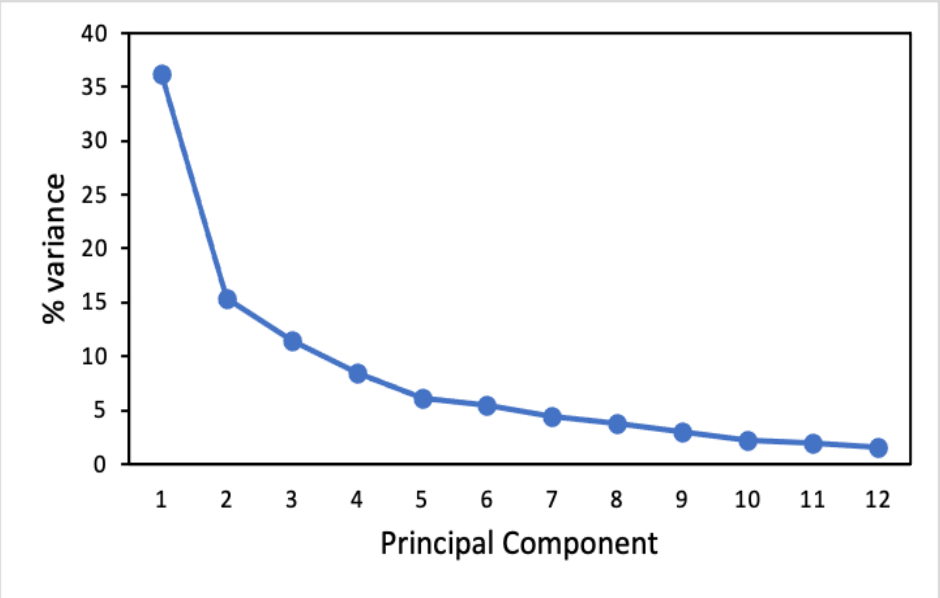


Figure 4.6: Scree plot showing PCA for set 3. PC1, PC2 and PC3 account for most of the variance seen within set 3.

The first principal component accounts for 36.18% of the variance, whereas principal components 2 and 3 account for 15.37% and 11.43% respectively. Again, a cut off value of 8.33% was used to determine the number of PCs used in the analysis. As PC4 accounted for 8.46% of the variance, it was decided to exclude this from the results and discussion. Principal components 1, 2 and 3 account for almost 63% of the variance.

The loadings for PC1, PC2 and PC3 are seen below (Figures 4.7a-4.7c). PC1 and PC2 are very similar to that seen in sets 1 and 2. In PC1 (Figure 4.7a), all measurements had positive loadings. TFH had the highest loading (0.47) whereas NB (0.1) had the lowest loading. Once again, a value of 0.289 can be used to differentiate between positive allometry and negative allometry (Somers, 1989). TFH, UFH, HL, HHM, BGB and BZB all had strong positive allometric associations in PC1. IOB, NB and NH all had negative allometric associations. Therefore, the head, face and mandibular will increase relatively with an increase in size while the midfacial region (nose and eyes) will become relatively smaller. Variables related to height and breadth of the cranial vault and face (HHM, MFB, BZB, BGB, BOB, TFH and UFH) indicated the strongest association with size among individuals, while variables related to the breadth of nose and orbits (IOB and NB) showed the least association with size among individuals. However, in comparison with sets 1 and 2, MFB had a weaker association with PC1 and BGB had a stronger association with PC1.

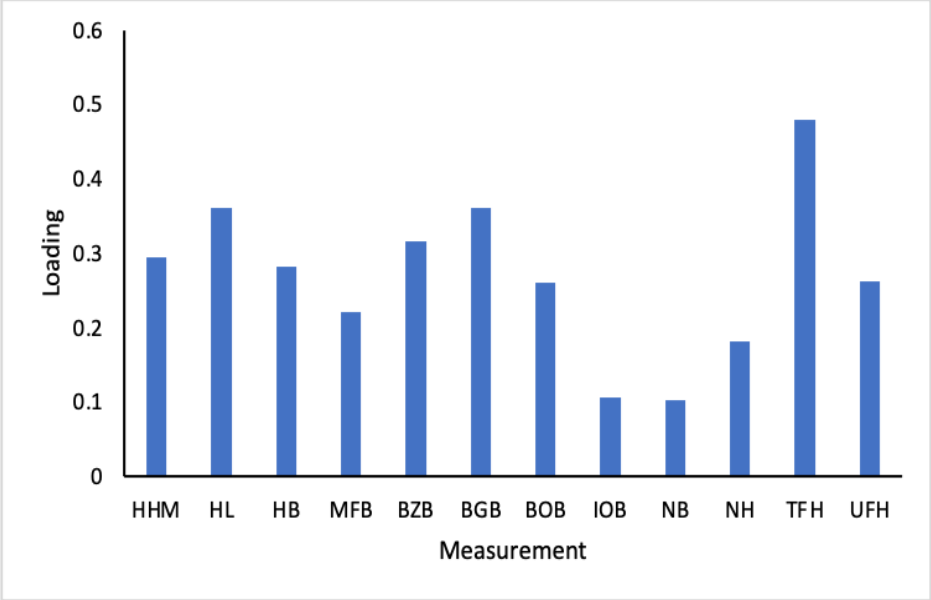


Figure 4.7a: Loadings for each measurement for PC1 in set 3.

PC2 has both positive and negative loadings (Figure 4.7b). The largest loading was TFH (-0.52) and the smallest loading was IOB (0.06). NH, TFH and UFH all had negative loadings on

PC2. Similar to what was seen in set 1, this suggests that as the face gets shorter (negative loadings), the cranial vault and face get wider (positive loadings). In this set (set 3), BGB has a stronger positive association among individuals while MFB had a weaker positive association in PC2. This differs from sets 1 and 2 where MFB had a stronger positive association and BGB had weaker positive association on PC2. Once again, variables of the midface (IOB and NB) accounted for the least association among individuals.

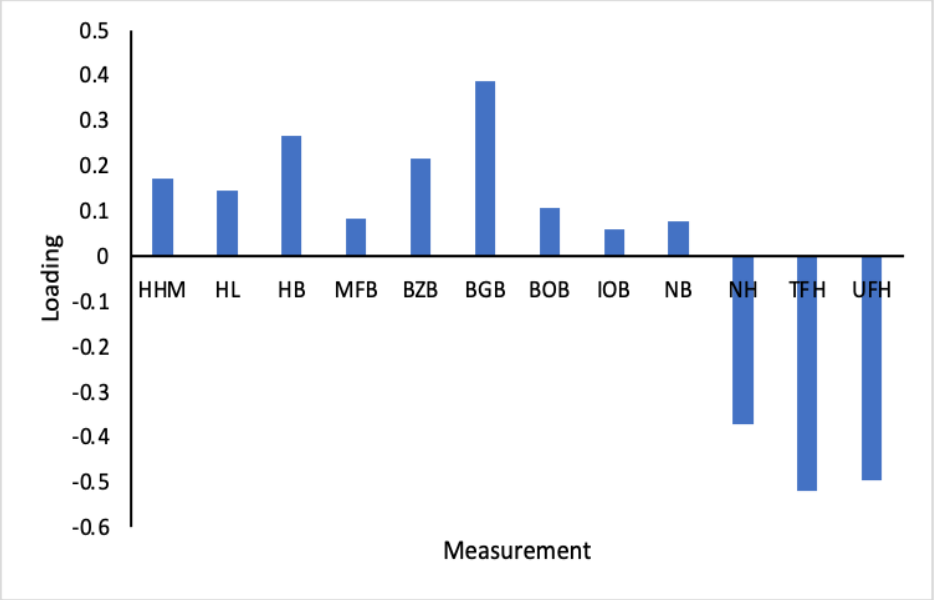


Figure 4.7b: Loadings for each measurement for PC2 in set 3

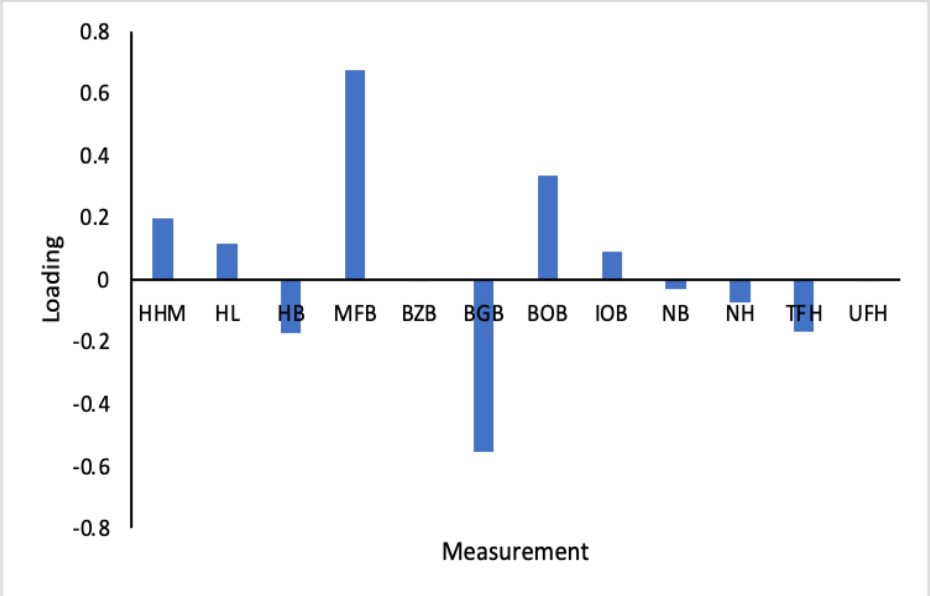


Figure 4.7c: Loadings for each measurement for PC3 in set 3.

PC3 also has both negative and positive loadings (Figure 4.7c). The loadings from this set (set 3) are greatly different than those seen in sets 1 and 2. The largest loading was MFB (0.67) and the smallest loading was UFH (0.001). BGB had the second strongest negative loading (-0.55). Based on the descriptive statistics, this is not surprising as BGB in the modern South African sample was one of the measurements which deviated from the other trends lines (Figure 4.1). These results suggest MFB and BGB have the greatest association with shape-related changes indicated by PC3 in this set.

4.3.2. Scatterplots

In order to visualise the distribution of the variation seen within the sets, the scores were shown as scatterplots. The most significant pair of PCs (PC1 and PC2) will be discussed first, followed by subsequent scatterplots. As PC1 resulted in positive loadings for all variables, it is assumed to represent size and size-related shape changes. Therefore, PC2 and PC3 are assumed to represent only shape differences.

4.3.2.1. Set 1: Historic Bantu-speaking groups

Figure 4.8a represents a scatterplot of PC1 (size and size-related shape change) and PC2 (shape-related change). Although the graph shows much overlap, it can be seen that there tends to be groupings of individuals from the east and south, whereas those from the west and south-central Africa tend to group together. However due to the overlap of population groups, very little difference can be seen, and further group separation will be discussed under the DFA results.

Figure 4.8b shows a plot of PC2 and PC3. Both these principal components account for shape-related differences. The principal components do not adequately separate the population groups due to the amount of overlap seen between the population groups. The variation in west sub-Saharan Africa populations is widely spread across the scatterplot, suggesting that this group has the largest amount of variation. Figure 4.8c shows a scatter plot of PC1 and PC3. PC3 only accounted for 9.61% of the variation within the sample. Again, there is much overlap between the population groups and it is difficult to discern any group separation.

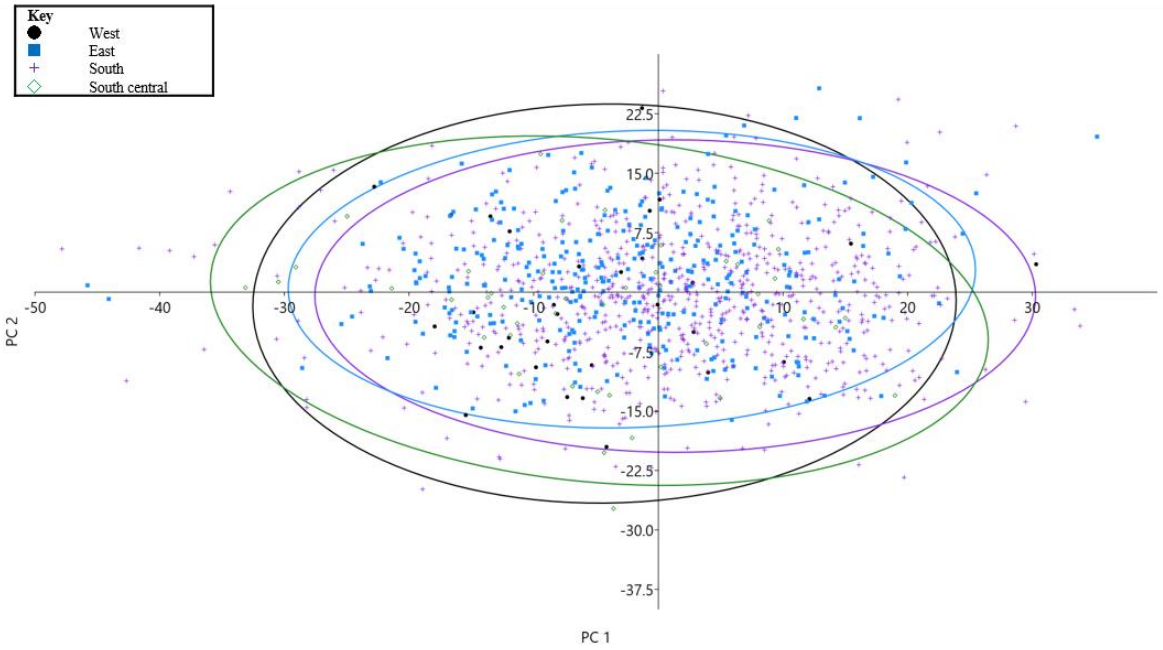


Figure 4.8a: Scatterplot of PC1 and PC2 scores with 95% ellipses in set 1. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south and green represents populations from the south-central region.

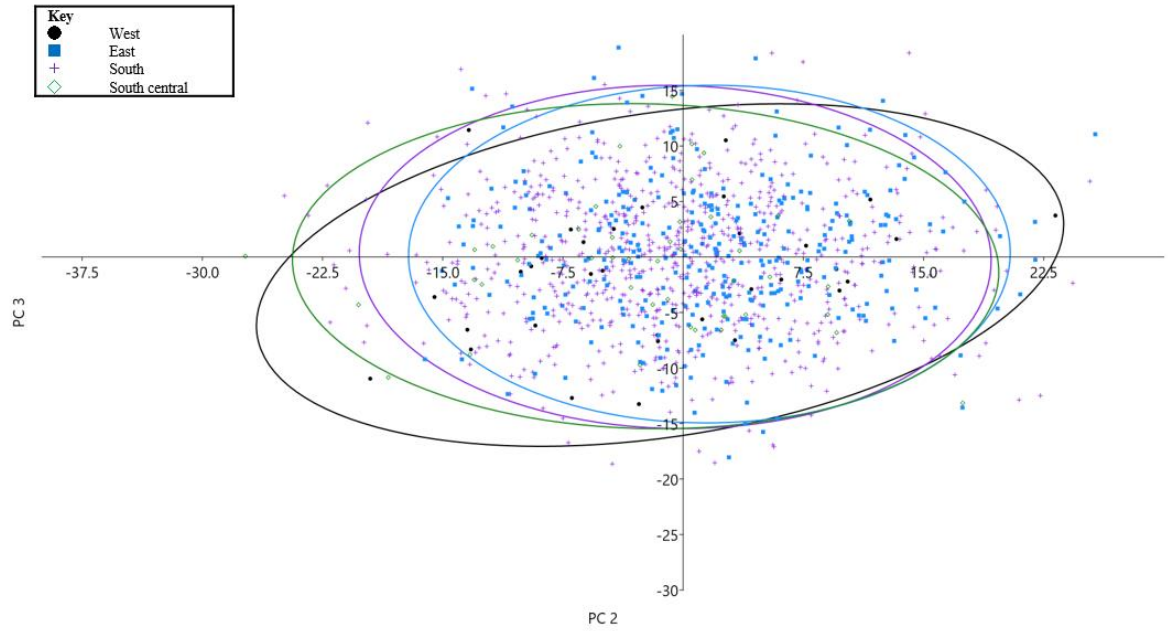


Figure 4.8b: Scatter plot of PC2 and PC3 scores with 95% ellipses in set 1. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south and green represents populations from the south-central region.

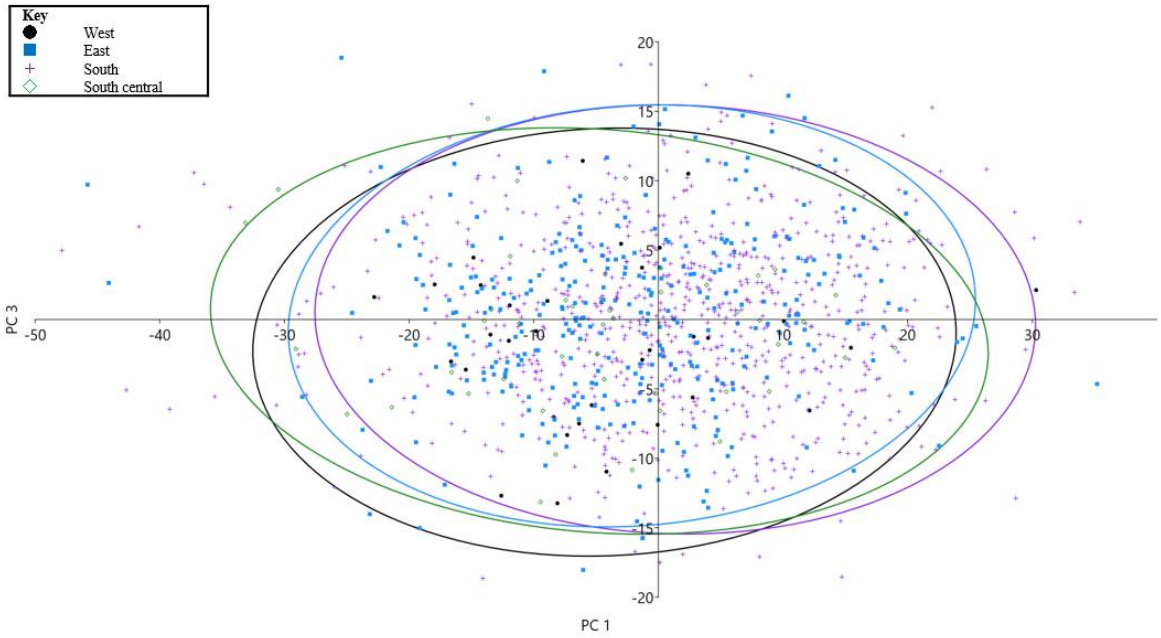


Figure 4.8c: Scatter plot of PC1 and PC3 scores with 95% ellipses in set 1. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south and green represents populations from south-central.

4.3.2.2. Set 2: Historic Bantu-speaking and Khoe and San groups

Set 2 comprises of historic Bantu-speaking population groups from the west, east, south and south-central part of sub-Saharan Africa plus the Khoe and San population groups from the Kalahari. Based on the percentage of variance for PCA in set 2, three principal components were plotted against each other and are represented in scatterplots (Figures 4.9a – 4.9c). Once more, all scatterplots show overlap between the population groups, however there is a clear separation of the Khoe and San population group (Appendix E).

Figure 4.9a shows PC1 (size and size-related shape changes) and PC2 (size and shape-related changes). The scatterplot indicates that the Khoe and San group has the least amount of variation compared to other groups. In addition, the Khoe and San are positioned more towards the left of the axis for PC1. This suggests that these individuals are smaller than other population groups.

Figure 4.9b shows a scatterplot of PC2 and PC3 (shape related variation between populations). The overlap of the population groups makes it difficult to separate them, however it appears that the Khoe and San have the least amount of shape variability within their population group compared to the other population groups.

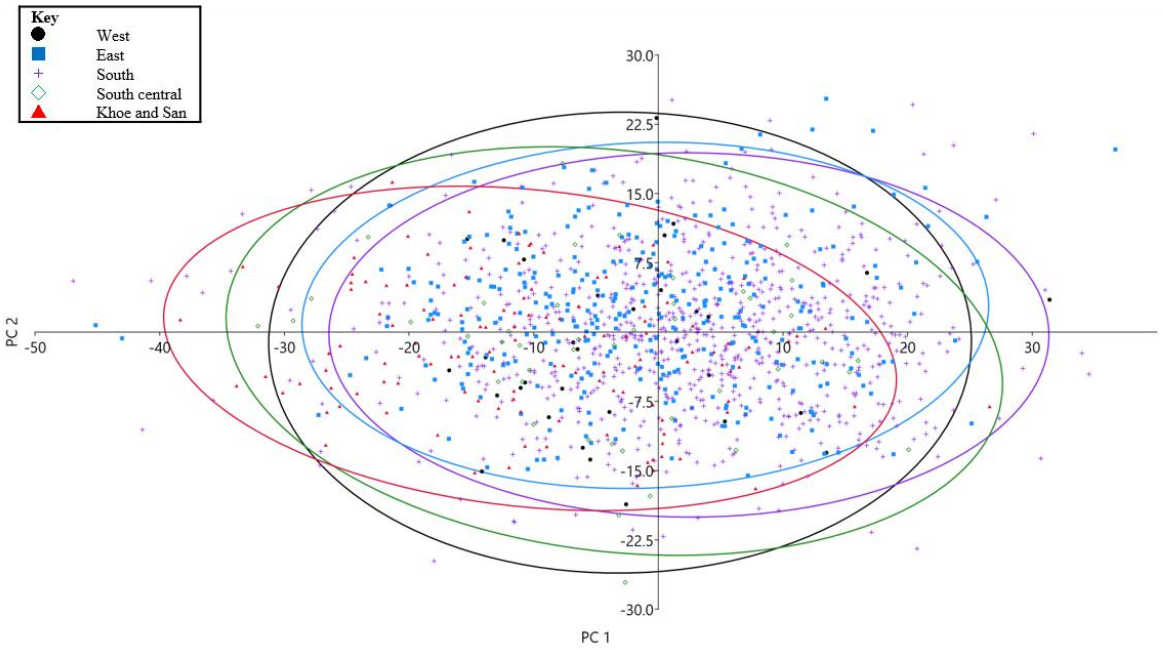


Figure 4.9a: Scatter plot with 95% ellipses indicating PC1 versus PC2 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari.

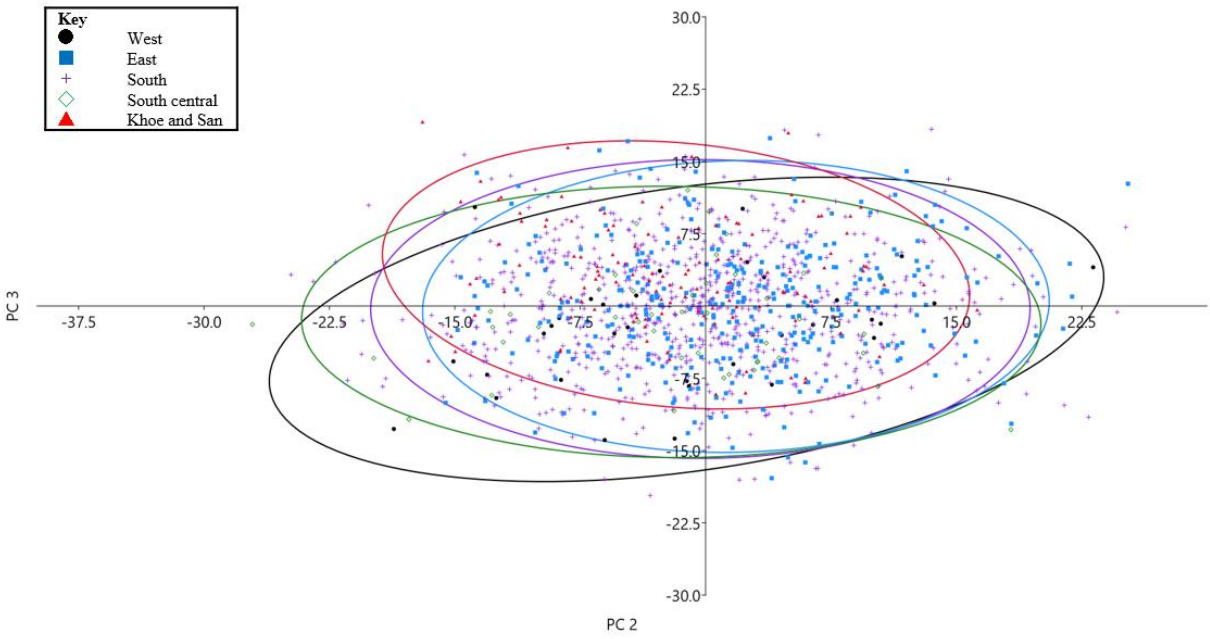


Figure 4.9b: Scatter plot with 95% ellipses indicating PC2 and PC3 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari.

Figure 4.9c shows a scatterplot of PC1 and PC3 (size and shape related differences between populations). There is separation of the Khoe and San groups from all other population groups. The separation of Khoe and San is more evident and there is clear variability in size- and shape-changes between Khoe and San individuals compared to other historic Bantu-speaking individuals. There is a shift along the PC1 axis which suggests that the crania of the Khoe and San individuals is smaller than other Bantu-speaking individuals. Additionally, the shift along the PC3 axis suggests shape related changes. Variables in PC3 associated with the cranial vault (HHM and HL) and those associated with breadth of the face and jaw (BZB and BGB) contributed to differences seen among the historic individuals.

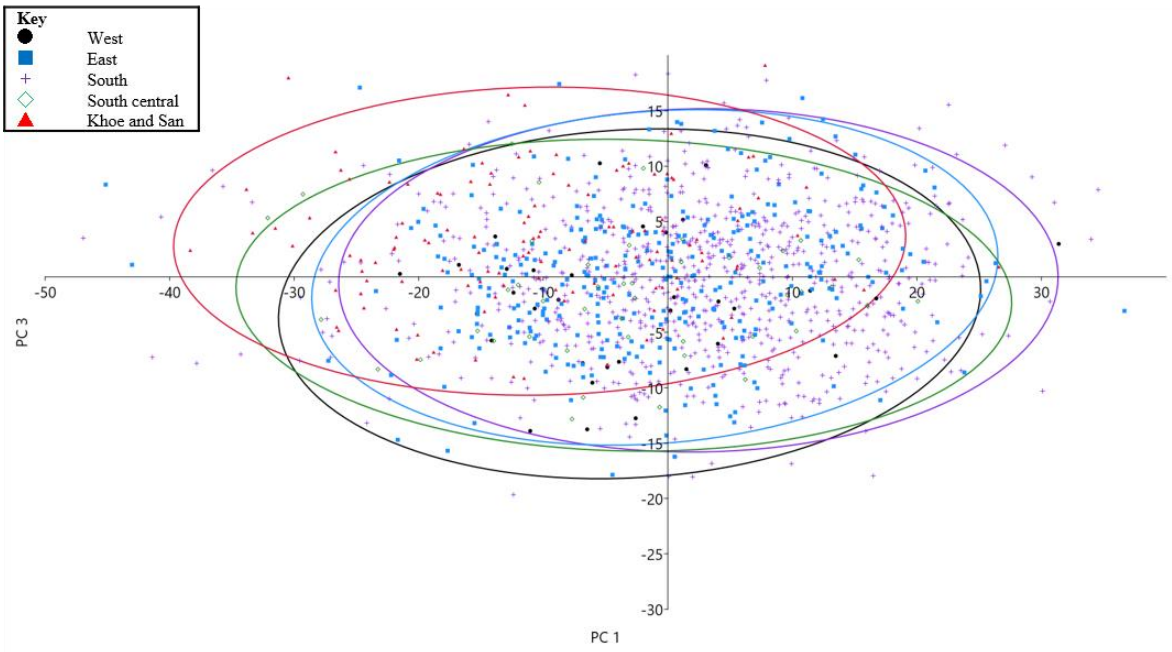


Figure 4.9c: Scatter plot with 95% ellipses indicating PC1 and PC3 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari.

4.3.2.3. Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

Set 3 comprises set 2 (historic Bantu-speaking populations and Khoe and San) plus a modern South African sample. Once more, the first three principal components analysis were plotted against each other and are represented in scatterplots (Figures 4.10a - 4.10c). In all three scatterplots, there is clear separation of the South African modern group from all other population groups. Overall, it appears that the craniofacial morphology of the modern South African group is significantly different in size and shape. Figure 4.10a represents PC1 versus PC2. From the

scatterplot, a shift of the modern South Africa sample along the PC 1 and PC2 axes can be seen. This shift suggests that as the cranium of the modern South African sample increases, the shape changes relative to this. From the loadings, measurements associated with the head (HHM and HL), face (TFH, UFH and BZB) and mandibular region (BGB) had the strongest association on differences seen among individuals. Therefore, modern south African individuals would tend to have larger crania, faces and mandibular regions.

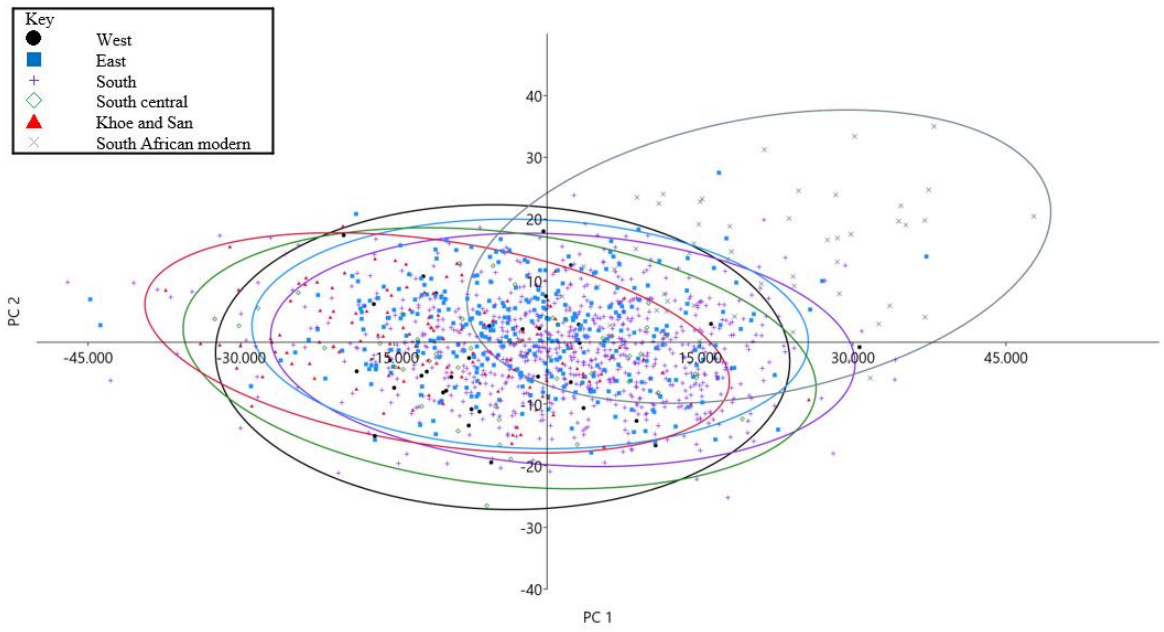


Figure 4.10a: Scatter plot with 95% ellipses indicating PC1 versus PC2 in set 3. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central, red represents the Khoe and San populations from the Kalahari and grey represents a modern South African population.

Figures 4.10b and 4.10c show similar representation of group separation. Loadings from the PCs suggest that measurements associated with facial height (TFH) and the mandibular region (BGB) have the strongest association for differences seen between individuals. Therefore, modern South Africans are shown to have significantly larger mandibular regions with relatively smaller facial heights, whereas the opposite is true for individuals from other population groups.

In all three sets, the scatterplots show much overlap between the groups. Any differences seen between the principal components is overshadowed by intra-group variability. Further group separation will be determined by the results of the discriminant function analyses (DFA) discussed later in this chapter.

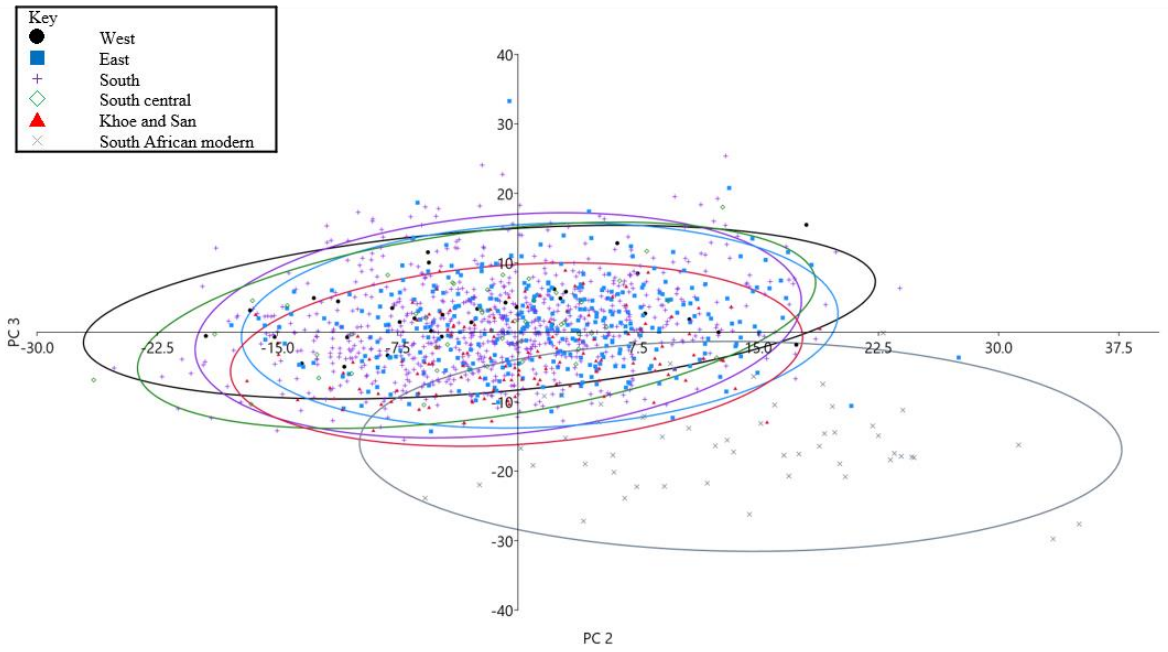


Figure 4.10b: Scatter plot with 95% ellipses indicating PC2 versus PC3 in for set 3. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central, red represents the Khoe and San populations from the Kalahari and grey represents a modern South African population.

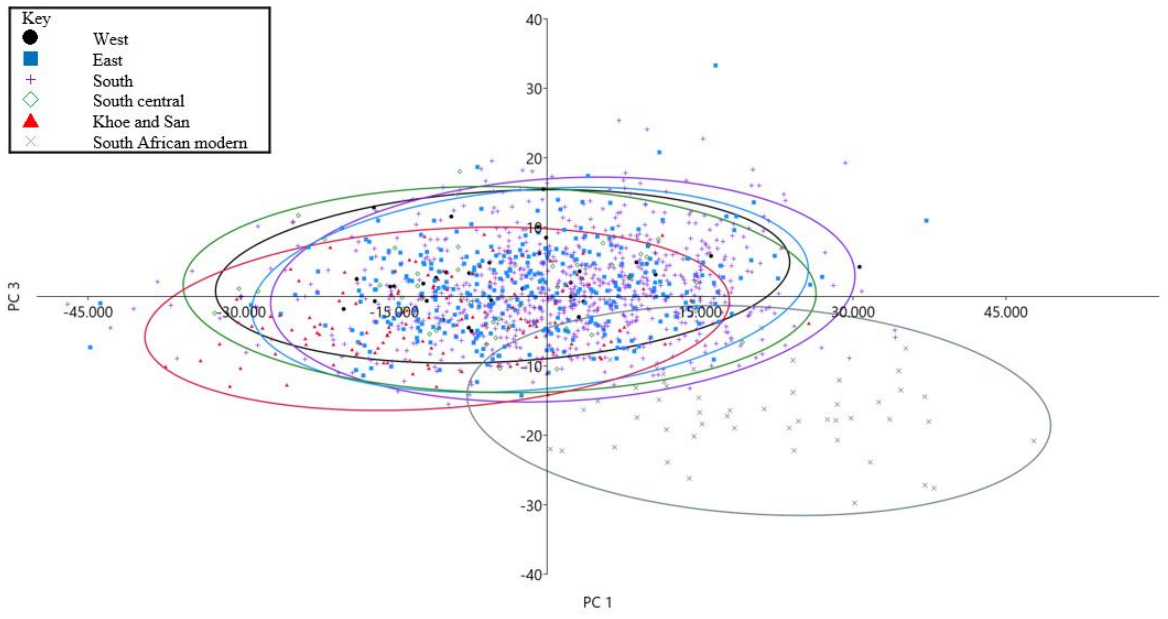


Figure 4.10c: Scatter plot with 95% ellipses indicating PC1 versus PC3 in set 3. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the East, black represents populations from the west, purple represents populations from south, green represents populations from south-central, red represents the Khoe and San populations from the Kalahari and grey represents a modern South African population.

4.4. Discriminant Function Analysis

The second objective was to employ Discriminant Function Analyses (DFA) to assess patterns of morphological discrimination between the population groups. DFA is used to maximise inter-group differences and to determine whether a variable or a combination of variables is useful in predicting group or population membership. The results will discuss the summary statistics and loadings for each set first, the percentage correctly classified (with actual versus predicted classification in Appendix F), followed by scatterplots.

4.4.1. Summary statistics and loadings

Summary statistics included the total number of DFAs calculated, eigenvalues and percentage total variance. The number of functions created using DFA is determined by the number of groups minus one (N-1). For the purposes of this study, all variables were used when calculating DFA. This was done in order to compare morphological differences between the groups rather than creating equations to optimally predict group membership. DFA was conducted on each set. DFA scores were interpreted by examining the loading scores for each variable. Loadings indicate the strength of the association of variables on the DFAs. Scores were then plotted as scatterplots to visualise group separation between population groups.

4.4.1.1: Set 1: Historic Bantu-speaking groups

Table 4.6 shows the summary statistics for the DFA for set 1. As there are only four groups in set 1 (west, east, south-central and south), DFA calculated 3 functions. Furthermore, all variables were used. Function 1 and Function 2 accounted for most of the variance (71.01% and 24.89% respectively) between the groups. As function 3 accounted for very little of the variance (4.04%), it was excluded from the results. Overall, 49.83% of individuals were correctly classified. Appendix F shows the results for actual versus predicted groupings.

Table 4.6: Summary statistics for DFA in set 1

	Eigenvalue	**% Variance**
Function 1	0.160	71.07
Function 2	0.056	24.89
Function 3	0.009	4.04

The loadings for each discriminant function are shown in bar graphs (Figures 4.11a – 4.11b). Function 1 (Figure 4.11a) has both positive and negative loadings. The largest loading is UFH (0.15) and the smallest loading is BGB (0.02). This suggests that UFH accounts for the largest amount of variation among populations and BGB accounts for the least amount of variation among populations. HHM, HB, BGB, BOB, IOB, NB and UFH all had positive loadings whereas HL, MFB, BZB, NH and TFH had negative loadings in Function 1. Function 1 accounts for differences in facial height (TFH and UFH) and cranial vault length (HL), with some influence of measurements involving the breadth of the midface (BZB). Overall, this function suggests that among the historic Bantu-speaking populations, taller upper faces (UFH), together with wider interorbital breadths (IOB), shorter cranial vaults (HL) and narrower zygomatic regions (BZB) appears to best separate some of the groups.

Figure 4.11b shows the loadings for Function 2. It can be seen that BOB (-0.2) had the strongest negative loading in the function whereas NH (0.003) has the weakest loading. HHM, HB, MFB, BZB, BGB and NH all had positive loadings whereas HL, BOB, NB, TFH and UFH all had negative loadings on function 2. Function 2 accounts mostly for differences seen in the breadth of the cranial vault (HB) and breadth of the upper face (BOB and BZB).

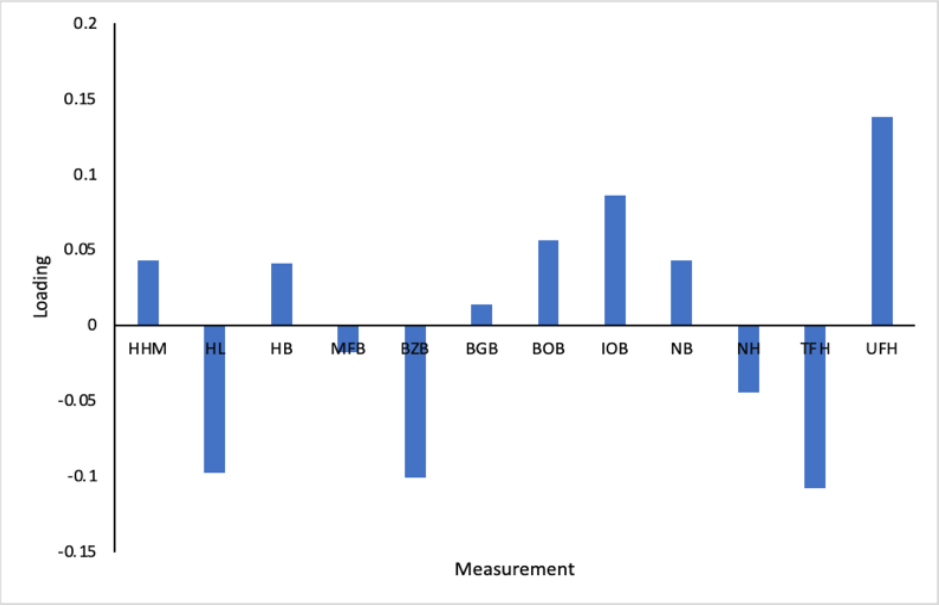


Figure 4.11a: Loading scores for each measurement in DF1 in set 1.

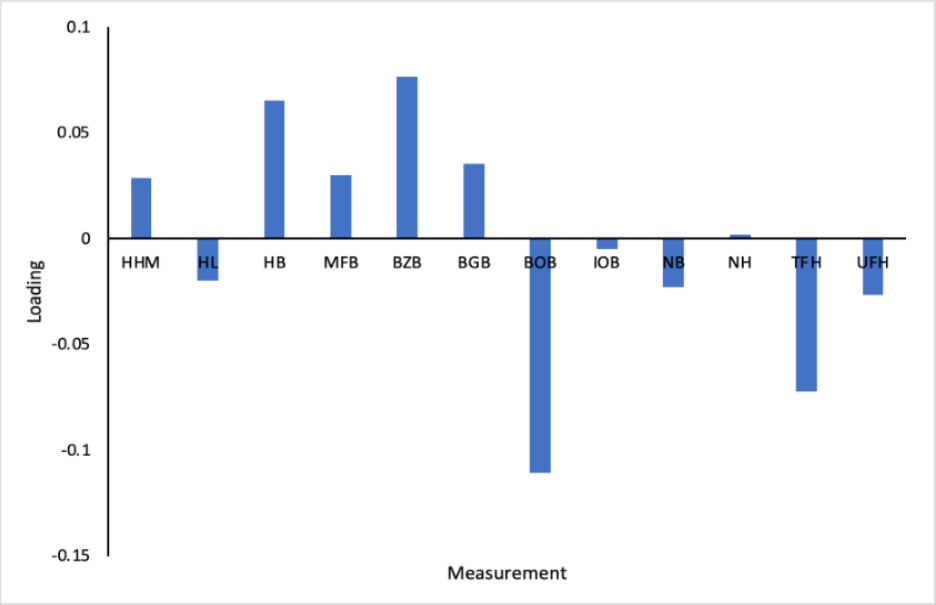


Figure 4.11b: Loading scores for each measurement in DF2 in set 1.

4.4.1.2: Set 2: Historic Bantu-speaking and Khoe and San groups

Table 4.7 shows the summary statistics for DFA in set 2. Set 2 includes set 1 plus the Khoe and San groups and therefore, four functions were calculated. Function 1 (62.19%) and function 2 (25.84%) account for most of the variance seen between the groups. Function 3 accounted for 10.2% of the variance whereas function 4 (1.77%) accounted for the least amount. Therefore, function 4 was excluded from the results and discussion. Overall, 47.91% of individuals were correctly classified. Appendix F shows the results for actual versus predicted groupings.

Table 4.7: Summary statistics for DFA in set 2

	Eigenvalue	**% Variance**
Function 1	0.308	62.19
Function 2	0.128	25.84
Function 3	0.051	10.20
Function 4	0.008	1.77

The loadings for each discriminant function are shown in Figures 4.12a to 4.12c. Figure 4.12a represents Function 1 in set 2. The measurements which had the strongest loading on group separation were NB (0.14), NH (-0.11) and IOB (-0.13). BGB (-0.01) had the weakest loading on

group separation. Based on these loadings, Function 1 accounts for differences in the height and breadth of the nose and the distance between the orbits (NH, NB and IOB).

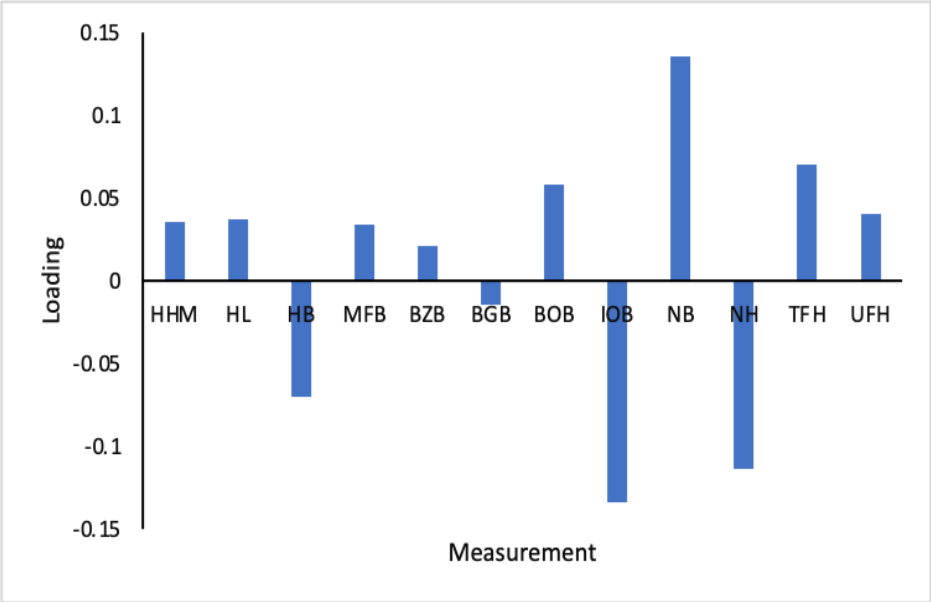


Figure 4.12a: Loading scores for each measurement in DF1 in set 2.

Figure 4.12b shows both negative and positive loadings on group separation for function 2. UFH (0.16) had the strongest loading whereas MFB (-0.009) and BGB (0.008) both had weak loadings on groups separation. Function 2 accounts for differences in upper facial height (UFH). The breadth of the zygomatics (BZB), head length (HL), nasal breadth (NB) and breadth of the obits (BOB) may also account for differences seen between population but to a lesser degree.

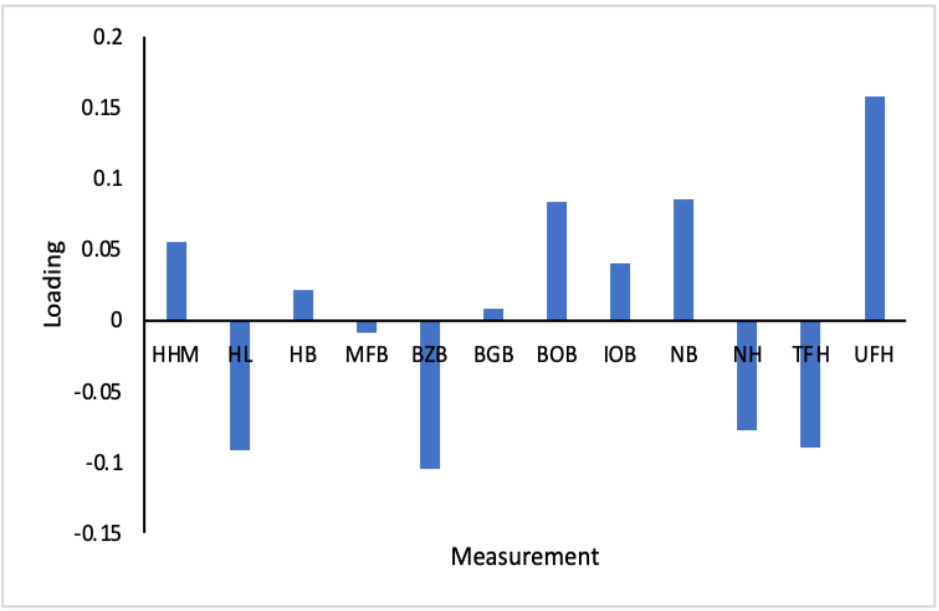


Figure 4.12b: Loading scores for each measurement in DF2 in set 2.

Figure 4.12c shows the loadings for Function 3. Most of the measurements had negative loadings. However, measurements of the obits (BOB and IOB) and measurements associated with the height of the nose and face (NH and TFH) had positive loadings of group separation. BOB (0.08) had the strongest loading whereas UFH (-0.018) height had the weakest loading on group separation. This suggest that function 3 accounts for differences in the height of the face (TFH), width of the orbits and zygomatics (BOB, IOB and BZB).

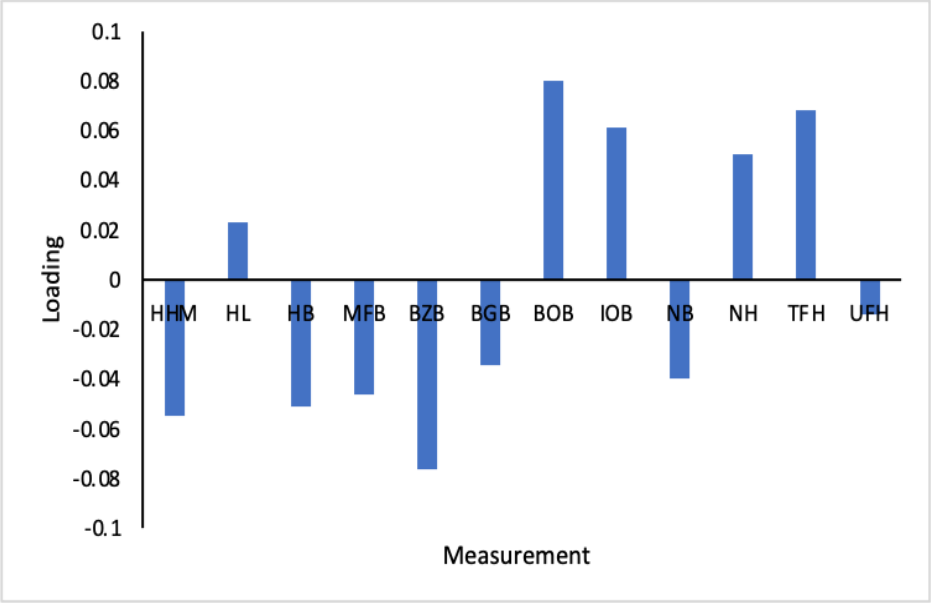


Figure 4.12c: Loading scores for each measurement in DF 3 in set 2.

4.4.1.3: Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

The summary statistics for set 3 are represented in Table 4.8. Five functions were calculated for set 3 as there are six groups within set 3. Function 1 and Function 2 accounted for most of the variance seen with set 3 (66.73% and 21.14% respectively). All other functions accounted for very little of the variation and were therefore excluded from the results and discussion. Overall, 49.63% of individuals were correctly classified. Appendix F shows the results for actual versus predicted groupings.

Table 4.8: Summary statistics for DFA in set 3

	Eigenvalue	% Variance
Function 1	0.939	66.73
Function 2	0.297	21.14
Function 3	0.116	8.26
Function 4	0.046	3.27
Function 5	0.001	0.58

The loadings for each discriminant function are shown in bar graphs (Figures 4.13a–4.13b). Function 1 (Figure 4.13a) has both positive and negative loadings. The highest loadings were UFH (0.108) and BGB (-0.105). HL, BGB and IOB had the weakest loading on function 1. Function 1 accounts for differences in the height and breadth of the upper face (HB, MFB and UFH) as well as differences across the mandible (BGB). There were negative and positive loadings in function 2 (Figure 4.13b). NB (0.13) and IOB (-0.13) both had a strong loading on function 2 whereas BGB (-0.01) and BZB (0.02) both have a weak loading on function 2. Function 2 mainly represents differences in the height and breadth of the nose and orbits (IOB, NB and NH).

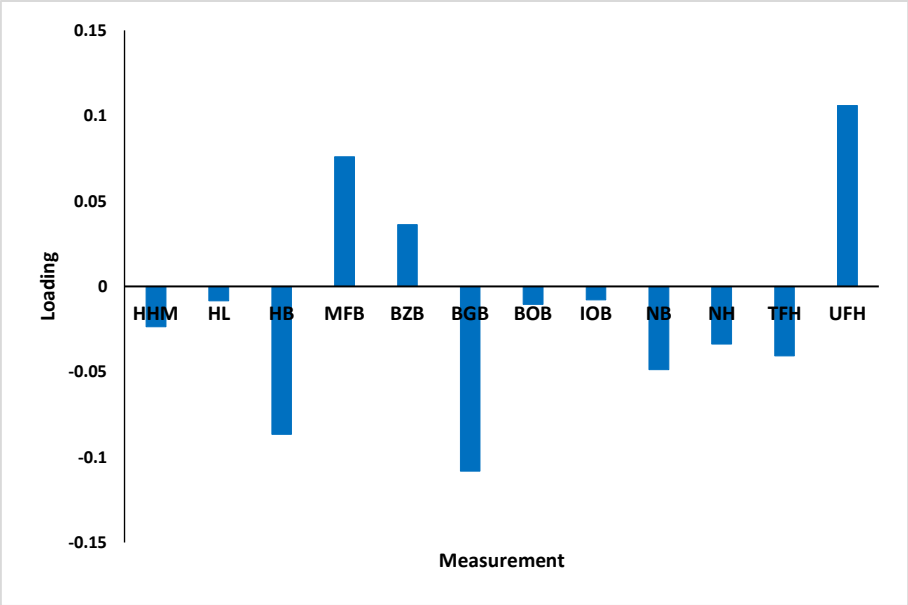


Figure 4.13a: Loading scores for each measurement in DF1 in set 3.

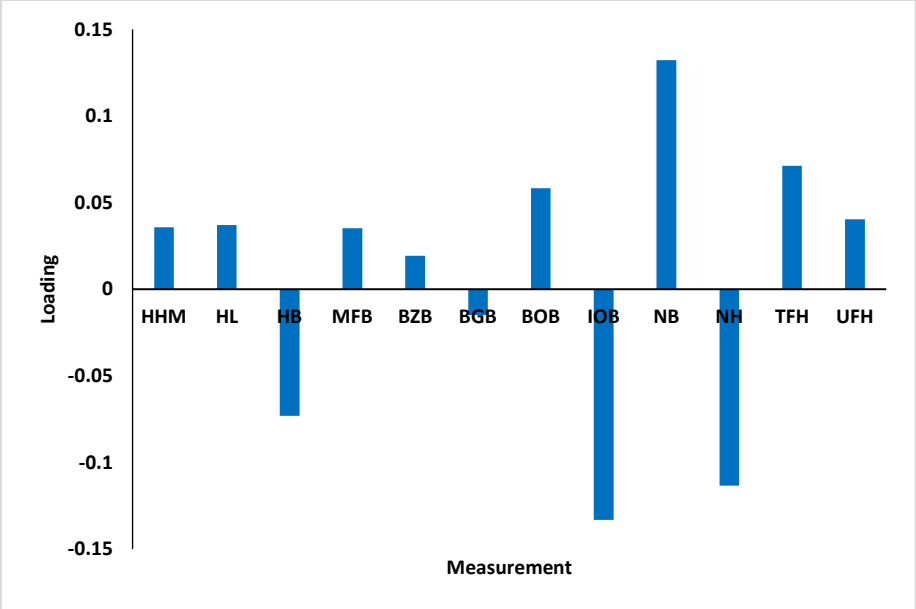


Figure 4.13b: Loading scores for each measurement in DF2 in set 3.

4.4.2: Scatterplots

In order to visualise group separation, the scores were plotted as scatterplots. Set 1 contains geographically grouped historic Bantu-speaking population groups, set 2 comprises of set 1 plus Khoe and San population groups and set 3 comprises set 2 plus a modern South African population group.

4.4.2.1: Set 1: Historic Bantu-speaking groups

As previously mentioned, two discriminant functions were calculated in set 1. This is represented as a scatterplot in Figure 4.14a. Based on the loadings for set 1, Function 1 is mainly accounting for differences in upper facial height (UFH), cranial length (HL), zygomatic breadth (BZB) and interorbital breadth (IOB) whereas Function 2 is mainly accounting for cranial breadth (HB) and facial breadth (BZB and BOB).

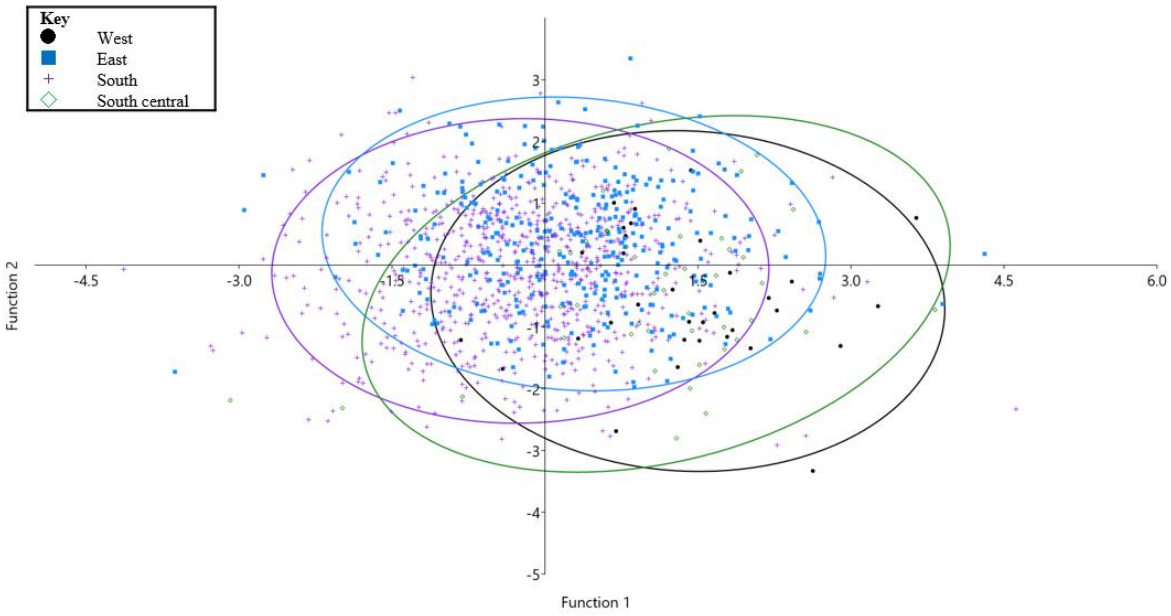


Figure 4.14a: Scatter plot of discriminant functions 1 and 2 with 95% ellipses. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the east, black represents populations from the west, purple represents populations from south and green represents populations from the south-central region.

There appears to be a clear separation between the east and south population groups and the west and south-central population groups. Populations from the western (Angola) and southern central (Zambia) parts of sub-Saharan Africa, will have taller faces, longer craniums broader zygomatics and wider intercanthal distances than those from the eastern (Tanzania, Malawi and

Mozambique) and southern (Botswana and South Africa) parts of sub-Saharan African. Very little differences can be seen along the Function 2 axis. However, it does seem that the eastern and southern populations have slightly wider faces and wider cranial vaults.

4.4.2.2: Set 2: Historic Bantu-speaking and Khoe and San groups

The discriminant functions for set 2 were plotted against each other (Figures 4.15a – 4.15c). Based on the loadings, differences in the breadth and height of the nose (NH and NB) and interocular breadth (IOB) are represented in Function 1. Function 2 represents differences in upper facial height (UFH). Lastly, function 3 accounts for differences in facial height (TFH) and breadth of the orbits and zygomatics (BOB, IOB and BZB).

Figures 4.15a and 4.15c show clear separation of the Khoe and San from other population groups. Individuals from the west (Angola) and south-central (Zambia) parts of the continent are more similar in craniofacial morphology, while individuals from the east (Tanzania, Malawi and Mozambique) and south (Botswana and historic South Africans) are more similar in craniofacial morphology and individuals from the Kalahari (the Khoe and San) are separate from the other populations.

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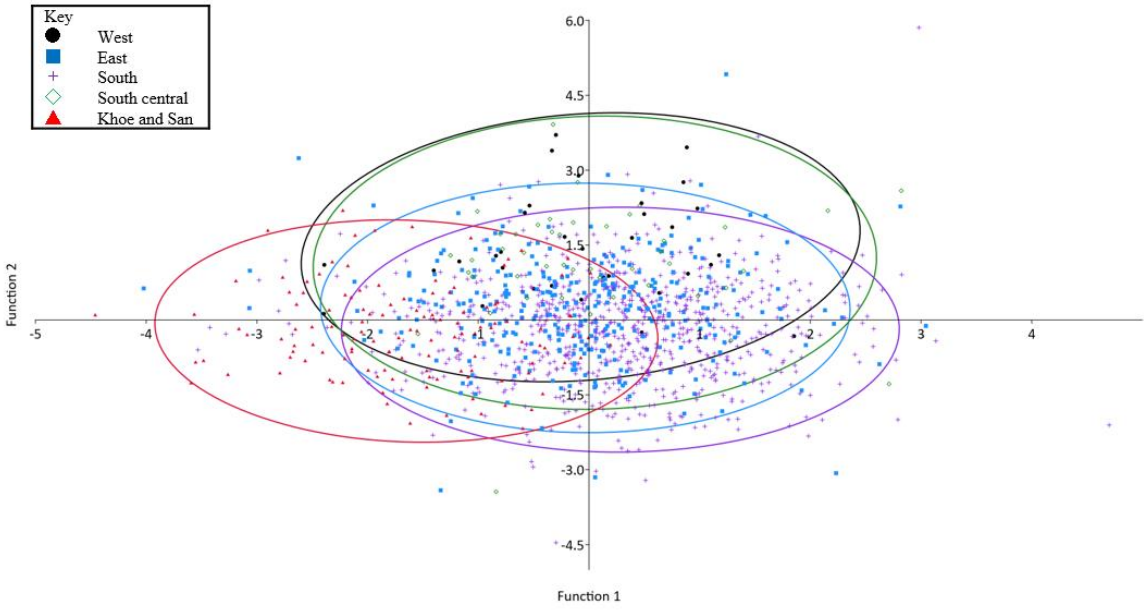


Figure 4.15a: Scatter plot with 95% ellipses indicating Function 1 versus Function 2 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the east, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari

Figure 4.15a represents differences in breadth and height of measurements associated with the midface (particularly those of the nose and orbits). Populations from the Kalahari (Khoe and San) have similar cranial morphology around the nose and orbits compared to Bantu-speaking populations from the east and south of Africa, but significantly different nasal and orbital regions from those populations from the west and south-central regions. Western and southern-central population groups tend to have wider and broader nasal apertures than those from the eastern, southern and Kalahari regions. Individuals from the western and south-central regions have significantly taller faces than those from the eastern and southern regions. The Khoe and San are more similar to the eastern and southern Bantu-speaking populations in relation to facial height

Figure 4.15b shows overlap between all the population groups. Broader and taller faces and wider interorbital breadths are found in populations from the western and southern-central regions. However, the Khoe and San (Kalahari) are more closely grouped with the eastern and southern population groups. This suggests that craniofacial morphology of the upper face, zygomatic and orbits is more similar between the populations from the Kalahari (Khoe and San) and those from the east (Tanzania, Malawi and Mozambique) and south (Botswana and South Africa).

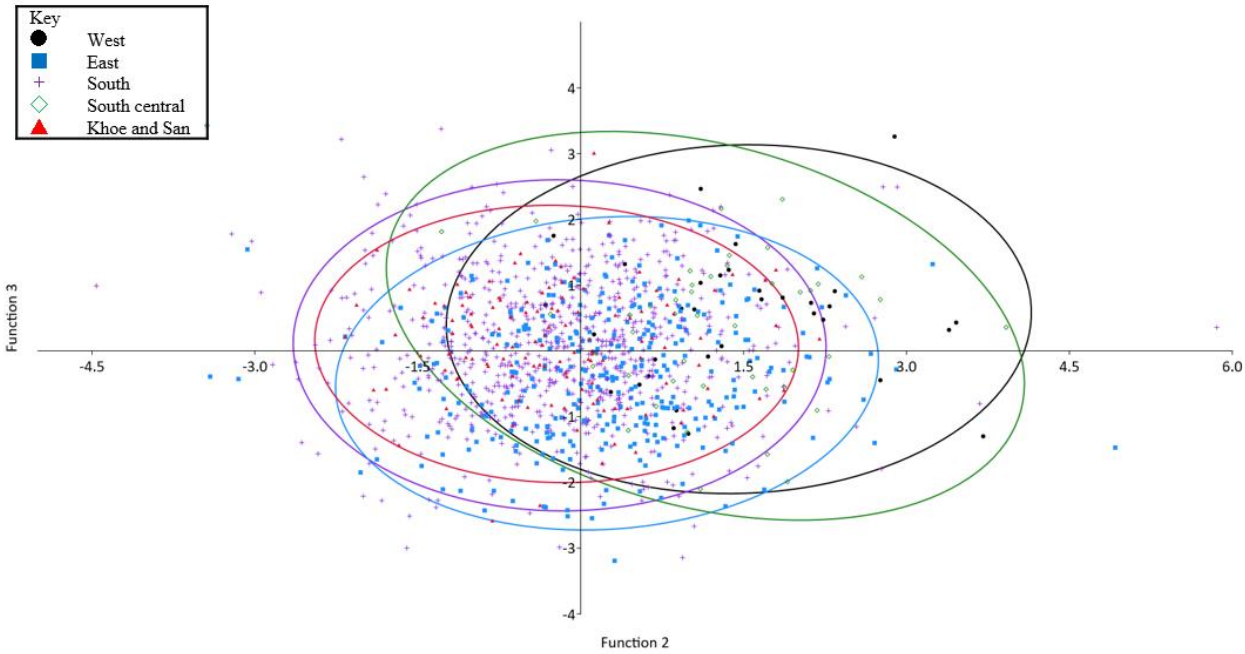


Figure 4.15b: Scatter plot with 95% ellipses indicating Function 2 versus Function 3 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the east, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari.

Figure 4.15c represents DF1 and DF3. Based on the loadings, these functions account for differences in facial height, nasal height and breadth and orbital breadth (measurements closely associated with the midface). Once more, there is clear separation of the Khoe and San from other population groups. The Khoe and San midfacial morphology is significantly smaller than other population groups.

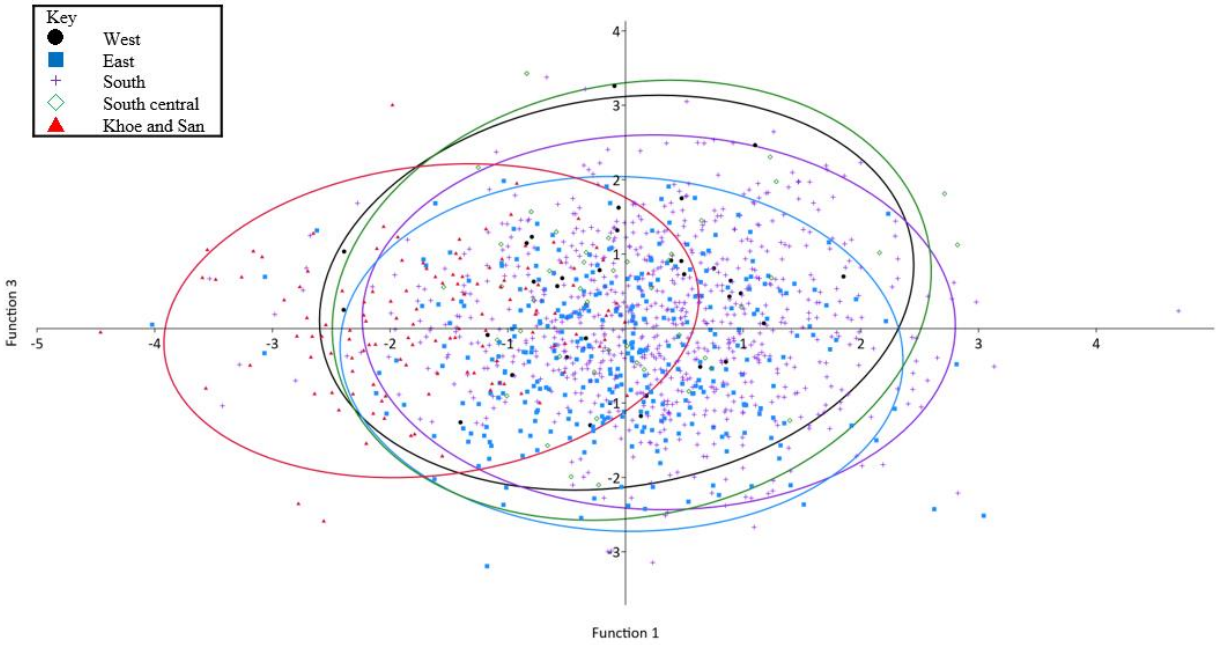


Figure 4.15c: Scatter plot with 95% ellipses indicating Function 1 versus Function 3 in set 2. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the east, black represents populations from the west, purple represents populations from south, green represents populations from south-central and red represents the Khoe and San populations from the Kalahari.

4.4.2.3: Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

In set 3, only DF 1 and DF2 were discussed as these accounted for the greatest variance seen among population groups. All other functions accounted for very little of the variation and were therefore excluded from the results and discussion. Figure 4.16 represents DF1 and DF2. Based on the loadings for set 3, differences in the breadth of the upper face (UFH) and jaw (BGB) were represented in Function 1 whereas Function 2 represented differences in morphology around the nose (NB and NH) and breadth between the orbits (IOB). There is clear group separation of the modern South Africa population from the rest of the population groups along the first function. UFH had a positive loading and BGB had a negative loading on Function 1, suggesting that as one measurement increases the other with decrease (and vice versa). As there is a left sided shift along the axis (Function 1 axis), this may suggest that as the height of the face decreases the breadth of

the jaw increases. Additionally, BGB and BZB (regions associated with masticatory processes) were among the measurements that deviated from the others when discussing the descriptive statistics. Although there is clear separation along the Function 1 axis, the modern South African sample has similar craniofacial morphology to historic Bantu-speaking populations along the Function 2 axis. Function 2 accounted from variation in morphology across the nose (NH and NB) and the inner canthal distances (IOB). Therefore, this suggest that modern South African population groups share similar nasal and orbital morphology to historic Bantu-speaking populations. The Khoe and San individuals are still separated from the Bantu-speaking population groups, however it is now more difficult to distinguish separation between the western, southern-central, eastern and southern Bantu-speaking population groups.

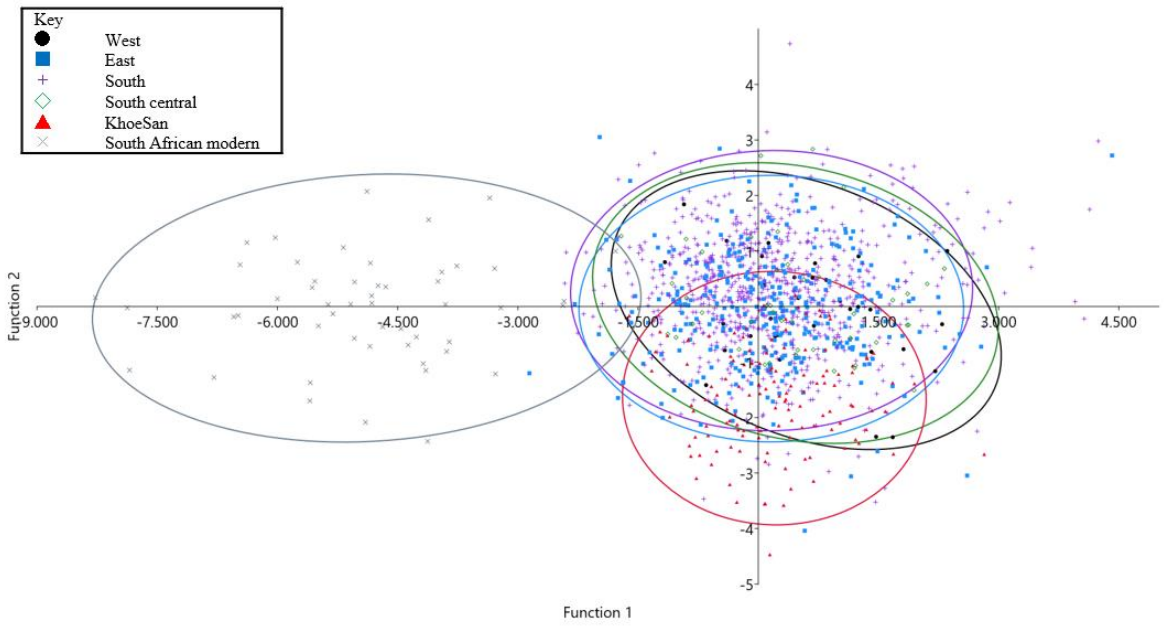


Figure 4.16: Scatter plot with 95% ellipses indicating Function 1 versus Function 2 in set 3. The colours represent different population groups within sub-Saharan Africa; blue represents populations from the east, black represents populations from the west, purple represents populations from south, green represents populations from south-central, red represents the Khoe and San populations from the Kalahari and grey represents a modern South African population.

4.5. Mantel test and Principal coordinate plot

The third objective aimed to assess the relationship between facial morphology and geography or the biological and geographical distances. In each set, the population groups were further separated into geographic regions (as seen in Tables 3.7), to allow for a better comparison between the different population groups. Firstly, a Mantel test was used to assess whether an association exists between facial and geographic distance. Secondly, in order to visualise the similarity or dissimilarity of the population groups to one another, a principal co-ordinate analysis was conducted (PCoA) using the Mahalanobis distances between group means of craniofacial morphology.

4.5.1: Set 1: Historic Bantu-speaking groups

Results for the Mantel test for set 1 are shown in Table 4.9. The weak r value and associated p value suggest that there is no correlation between morphology and geographic distance. This indicates that morphological distance and geographic distance were independent. There is no evidence of association between morphological distance and geographic distance. Populations that are more distant from each other may still be morphologically similar to populations that are geographically close to one another. However, it may also suggest that populations that are closer are morphologically distant.

Table 4.9: Results of the Mantel Test for set 1

P value	0.3907
r correlation	0.0538

Figure 4.17a shows a principal co-ordinate plot of the mean morphology between the population groups using Mahalanobis distance. Based on craniofacial morphology, it can be seen that the mean craniofacial morphology from Botswana (south) appears to be an outlier. Additionally, the other population groups from South Africa (SA Pedi, SA Venda and SA Limpopo) do not cluster together but are instead spread across the plot. It can also be seen that the means from samples of the eastern part of Africa (Tanzania, Malawi and Mozambique) are clustering.

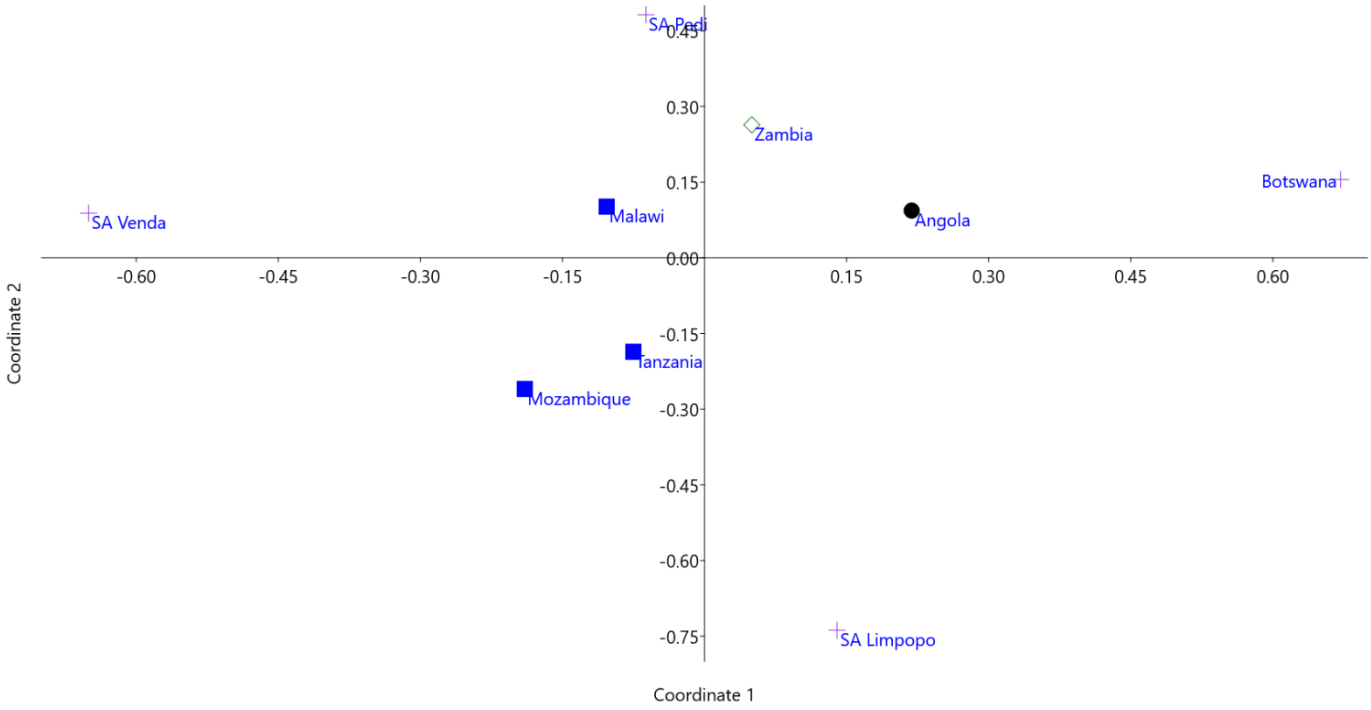


Figure 4.17a: Principal co-ordinate analysis of mean morphology using Mahalanobis distances for set 1.

4.5.2: Set 2: Historic Bantu-speaking and Khoe and San African groups

Results of the Mantel test are shown in Table 4.10. The non-significant p value suggests no correlation between morphology and geographic distance. This is interesting, as the Khoe and San population groups are known to be morphologically and geographically distant from other Bantu-speaking population groups. However, these results suggest that populations from the Kalahari (which are geographically distant from other populations) may still be morphologically similar to other population groups.

Table 4.10: Results of the Mantel test for set 2

P value	0.8082
r correlation	-0.14

Figure 4.17b shows a principal co-ordinate plot of the mean morphology between the population groups in set 2. Based on craniofacial morphology, the Khoe and San are grouping with the Botswana population group. Interestingly, craniofacial morphology of individuals from Limpopo (South Africa) seem to be more closely related to west (Angola) and south-central populations (Zambia).



Figure 4.17b: Principal co-ordinate analysis of mean morphology using Mahalanobis distance for set 2.

4.5.3: Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

Results of the Mantel test for set 3 are shown in Table 4.11. Once more, the test was not significant suggesting no correlation between morphological distance and geographic distance.

Table 4.11 Results of the Mantel test for set 3

P value	0.924
r correlation	-0.371

Figure 4.17c below shows a principal co-ordinate plot of the mean morphology between all the population groups. Based on craniofacial morphology, it can be seen that individuals from a modern South African sample are completely separate from all other population groups. It can

also be seen that the Khoe and San individuals and those from Botswana are grouping together based on facial morphology and those population groups that were classified as Bantu-speakers (with the exception of the Botswana sample) all tend to group together.

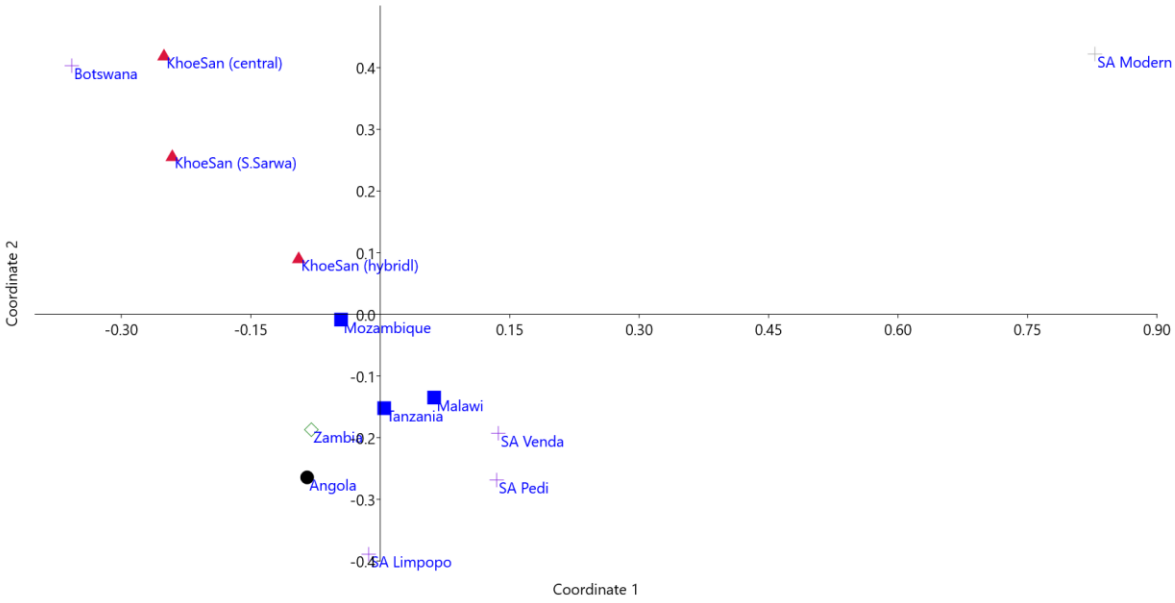


Figure 4.17c: Principal co-ordinate analysis of mean morphology using Mahalanobis distance for set 3.

Chapter 5 Discussion

Cranial morphology and craniometrics have been used extensively to assess population variation (de Villiers, 1968; Howells, 1973; Franklin *et al.,* 2007; 2010; Ousley and Jantz, 2012; McKeowen and Schmidt, 2013) and migration patterns (Ribot, 2004; Ousley and Jantz, 2012; McKeowen and Schmidt, 2013). Biological anthropologists have acknowledged that morphological differences exist between populations living in different geographical areas and that cranial morphology can be used to accurately distinguish between different population groups (Ousley *et al.,* 2009). Although there is often intermixing between population groups, certain barriers, such as those defined by culture, geography, ecology, and language, continue to influence biological and genetic variation (Edgar and Hunley, 2009).

Studies have traditionally used dimensions recorded from crania (de Villiers, 1968; Howells, 1973; Moore-Jansen *et al.,* 1994; Ribot, 2004; Ousley and Jantz, 2012; McKeowen and Schmidt, 2013) and more recently, life and death face masks have been used to investigate craniofacial morphology and their ability to distinguish between populations (Ramphaleng, 2020). The current study used anthropometric craniofacial measurements, something which has not been used extensively in the past, to determine population variation and population history among sub-Saharan African populations. Anthropometric studies have been used to assess head and face climatic adaptations (Hiernaux and Fremont, 1976; Beals *et al.,*1984; Harvati and Weaver, 2006), secular trends (Katzmarzyk and Leonard, 1998; Hawley *et al.,* 2009) and plan surgical interventions (Fitzgerald *et al.,* 2010; Fourie *et al.,* 2011). However, studies using anthropometric measurements of the head and face from living individuals to assess craniofacial variation and population history are limited. One of the aims of this study was therefore to establish whether anthropometry can be used for this purpose, and if it is as reliable and informative as craniometry.

This chapter will begin by discussing the reliability of the measurements. Both the historic data and CT scans will be discussed in terms of 1) using measurements from living individuals from a historic data set and 2) the reliability of using CT scans to replicate the same measurements taken from living individuals. Following this, descriptive statistics will be discussed. The overall similarities and differences will be described between individuals from various regions of sub-Saharan Africa. The chapter will go on to interpret of the results obtained from the PCAs, DFAs and Mantel tests and compare these to the literature. Craniofacial features from populations from the western, eastern, southern-central and southern regions of sub-Saharan Africa will be compared. Evidence supporting the population history of sub-Saharan and southern Africa as well as observed population variation will be discussed, and comments made with regards to

geographical distance and barriers and if it influenced the current patterns observed. The chapter will end off by addressing the limitations of the study as well as future directions.

5.1. Reliability of the measurements

5.1.1. Historic data set

The historic population groups were measured using manual anthropometric measuring techniques. This involved taking measurements directly from the individual using callipers and measuring tapes. Direct anthropometry using callipers can yield varying results (Sforza *et al.*, 2004; Weinberg *et al.*, 2004; Ghoddousi *et al.*, 2007). The reliability of measurements depends on the researchers' measuring skills and the participants physical and psychological condition at the time the measurements are being taken. The researcher needs to accurately identify the anatomical landmarks, be familiar with the anthropometric measuring techniques and have experience in using the instruments correctly. In addition to this, the age, morphological quality of the head and face, the quality of landmark location and willingness to cooperate from the examinee all influences the variability of the outcomes of accuracy and reproducibility of anthropometric measurements (Jayaratne and Zwahlen, 2014; Weinberg, 2019). However, there is no demonstrable evidence for the accuracy and precision of these recordings, as well as the reproducibility across the expeditions. The only assurance is that the expeditions and studies were conducted under the auspices of Phillip Tobias, who was renowned for his attention to detail and methodology (see Tobias, 1967, for example). It can only be assumed that the researchers used these definitions as a reference for all data collection, and all dimensions seemed to be within the ranges as expected.

Based on the information obtained from the historic dataset and the limited information available in the records and publications, the reliability of these measurements could not be assessed. The historic data set was collected in the 1950s, 1960s and 1970s during expeditions through sub-Saharan Africa. The data from various communities were all recorded as handwritten documents and have been housed at the School of Anatomical Sciences, University of the Witwatersrand over the years. Large amounts of information were recorded during the expeditions ranging from anthropometric measurements, blood type and fingerprints to obtaining face masks and photographs. However, one has to keep in mind that the information recorded might not be accurate or truly representative of the observations and information observed. Additionally, it may be that many of these populations (both Bantu-speaking and Khoe and San) have been recently displaced, that there is a barrier to gene flow between living groups (cultural or physical) or both. During the documentation of the records into an Excel spreadsheet, it was noted that information

and measurements would often been missing with no explanation as to why it may not have been recorded. Each facial measurement would have been taken individually and as such, any missing values, errors in recordings or miscalculations could not be corrected as the individual is no longer present (Sforza *et al.*, 2012). Furthermore, records and publications on the expeditions were also very limited. Often, the records would not state who collected the data and exactly when the data was collected. However, these records containing vast amount of information have not been used in research to explore historic sub-Saharan African population variation and population history.

As already mentioned, the full range of measurements from the complete body were recorded and an electronic database established through the work of this thesis. This database is now available for research purposes and is stored at the School of Anatomical Sciences, University of the Witwatersrand. The database contains large amounts of information that can be used in future research interested in sub-Sharan population history and population variation. Such a dataset obtained from historic populations will aid in understanding variation between different sub-Saharan African groups as well as providing a better understanding of the population history in sub-Saharan Africa.

5.1.2. CT Scans

In contrast to the historic data, the measurements for the modern South African sample were taken from CT scans. As such, the data from the CT scans could be used to conduct reliability tests. The assessment of the technical error of measurement (TEM) was conducted on 20 randomly selected CT scans representing a modern South African population. All measurements (when repeated by both the author and second observer) obtained moderate to high reliability except for BZB (with a value of less than 0.7). However, BZB measurements taken from the author were more reliable than those repeated by a second observer. The results obtained for BZB are not surprising. Both the author and second observer had difficulties identifying the landmarks used for measuring BZB from the CT scans. This was often due to the position or angle of the head and neck when the scan was taken, making it difficult to pin-point the most lateral aspects of the zygomatics. Stull *et al.* (2014b) noted that landmark identification and location uncertainty can have a powerful impact on the interpretation of the results. Although BZB had the lowest reliability, the score was still within the moderate range.

The decision to keep BZB in the current study can be explained for a number of reasons. The number of measurements available from CT scans was limited. CT scans of the head and neck are often taken due to trauma and hence trying to find “normal” head and neck scans was difficult.

This in turn, often resulted in only a portion of the head or neck being scanned, thereby limiting the ability to take all the required measurements from a single CT scan. Additionally, the measurements obtained from CT scans were being compared to the same measurements obtained from the historic data set, to make for a more comparable analysis, However, given the difficulties associated with landmark location, caution is advised when using this measurement and the difficulties of taking this measurement from CT scans.

As expected, the author obtained more reliable measurements than the second observer. Several reasons may be responsible for the variability of the measurements. This may be due to the experience of the person taking the measurements, the time interval between measurements and the variation on the marking of anatomical landmarks (Perini *et al.,* 2005). There may also have been some memory bias associated with landmark placement of the author (Gwilliam *et al.,* 2006). Memory bias may not truly represent the repeatability of measurements, and this has been noted as a possible shortcoming. Due to the varying thickness and projections of the soft tissue of the head and face, craniofacial features are one of the most difficult components of the body to measure in living individuals (Kim and Shin, 2018). The basic requirements for accuracy and precision of measurements relies on the ability to locate craniofacial landmarks and having a high-quality set of measuring tools. It was found that measurements of the mid face such as those associated with nose and eyes were most reliable when repeated by the author and the second observer. This may be due to the ease of location and clear definition of the measurements.

The measurements were taken from 3D volume rendered images. It has been found that it is easier to take measurements from 3D CT reconstructions and most landmarks can be located as quickly as they can from the dry skull (Hildebolt *et al.,* 1990). However, there are limitation to volume rendered images. To approximate the natural position of the head, the Frankfort horizontal (FH) plane is used. This is an imaginary horizontal line running through the inferior border of the orbits and the external auditory meatus on either side of the skull (Jayaratne and Zwahlen, 2014). However, in most cases the individual's head will not be positioned in the FH plane when taking the scan. This makes it difficult to identify landmarks and reliably take the same measurements as those taken during manual anthropometry techniques. Additionally, CT scans are often conducted with the individual lying in a supine position and as such this can change the gravitational effects on the soft tissues (Caple *et al.,* 2016). The gravitational effects plus the position of the head made it somewhat difficult to identify landmarks and reliably repeat the measurements.

Although there were some limitations to the reliability and repeatability of the measurements, most of the measurements have moderate to good reliability. This is comparable

to studies that assessed the use of 3D images of underlying bone (Sholtz *et al.,* 2011; Stull *et al.,* 2014b) as well as soft tissue measurements from 3D images (Perini *et al.,* 2005; Fourie *et al.,* 2010).

5.2. Descriptive statistics

The descriptive statistics from the current study are in line with that seen in the literature. The Khoe and San are distinguished by their small body size (Wilson and Lundy, 1994; Franklin *et al.,* 2007; Kurki *et al.,* 2010) and as expected, the Khoe and San population groups showed much smaller craniofacial morphology than the Bantu-speaking populations (except for those individuals from Botswana). Certain environmental stressors such as dietary insufficiencies and climatic adaptations have been known to affect growth (Sealy and Pfeiffer, 2000; Pfeiffer, 2012). The Khoe and San were hunter-gatherers and would need to navigate different landscapes in the search for food. It is suggested that the need to be more mobile and have lighter and small bodies outweigh the need to be particularly strong (Sealy and Pfeiffer, 2000; Pfeiffer, 2012). Genetic factors also play a role in the selection for small body size. The favoured smallness of Khoe and San could be the result of the removal of selection for larger size combined with isolation. Cultural practices and sexual selection could have suggested the removal of selection for larger males. Likewise, the selection for larger females through fertility was probably reduced through adaptations for larger pelvises for the birth of larger children (Pfeiffer, 2012). Interestingly, the Botswana Bantu-speaking population (as identified in the historic data set) had smaller measurements than any other population group and were more similar in size to the Khoe and San. Geographically, these two populations are close to one another and share a similar environment. It is possible that there was considerable genetic exchange between these two groups.

Overall, modern South African individuals (measured from CT scans) had much larger craniofacial measurements than the historic populations. Certain measurements (Figure 4.2) (HL, HB, BZB, and BGB) were considerably larger when compared to the other population groups. Socioeconomic factors over time could possibly account for the overall size differences seen in the modern South African sample, although the fact that they were recorded in a different manner than the other dimensions could also have played a role. The improvement in healthcare, social environments and nutrition and well as migration and move from a lower socioeconomic status to a higher socioeconomic status could all account for increased size of the modern South African sample (Hawley *et al.,* 2009). One factor that could account for the overall larger size seen in the modern South African population is obesity. Between 1980 and 2014 there has been an increase

in mean body mass index (BMI) from 21kg/m^2 to 23kg/m^2 in men (NCD Risk Factor Collaboration, 2016). The NCD Risk Factor Collaboration (African Working Group) report a higher mean BMI than global average in northern and southern Africa and lower mean BMI in central, eastern and western Africa.

Rate of growth has generally increased worldwide over the past few centuries. The rate of secular change has been correlated with socio-economic status (SES) of different populations, however the trend is neither widespread nor does it display similar rates in all populations (Grine *et al.,* 2020). SES of a group of individuals, such as diet restrictions, access to health care, levels of physical labour and industrialization to name a few, all influence the growth of the group (Mybrugh, 2016; Grine *et al*., 2020). Long bones and skulls have displayed different trends in size (Jantz and Jantz, 2000; Myburgh 2016). Assessing secular trends among black South Africans through the 20th century, Grine *et al.* (2020) noted an absence in secular trend in cranial length but a negative secular trend in cranial breadth. The current study found notable size differences in the crania among the population groups, particularly between the small size of the Khoe and San and Bantu-speaking Botswana craniofacial morphology and large size in modern South African craniofacial morphology. These differences are probably due to SES of the population groups. For centuries, Bantu-speaking populations and the Khoe and San have been economically disadvantaged (Grine *et al.,* 2020). The increase in the overall size of the cranium in the modern South African sample, particularly around the mandible (BGB) and that fact the measurements taken using CT scans, could account for the differences between the modern South African sample and the historic data set. Additionally, soft tissue thickness may influence the overall results. The sample was that of a modern population and again socioeconomic factors can play a role in affecting size and growth of individuals overtime and as such can have an effect on the thickness of soft tissue on overlying bone (Grine *et al,* 2020).

5.3. Craniofacial variation among sub-Saharan African populations

Craniofacial morphology can be used to distinguish between populations. Based on the idea that genes contribute considerably to craniofacial morphology within a population, craniometric studies have assessed change in variation in skull morphology between different populations (Beals *et al.,* 1984; Roseman, 2004; Relethford, 2004, 2010). Not only does the anatomy of the human skull correlate well with genetics and geography, but also with population history and (to some extent) climate (Beals *et al.,* 1984; Harvati and Weaver, 2006). The overall form (size, shape, and shared arrangement of parts) and function of the face and head is strongly

determined by a multiplicity of genes, with environmental variables such as nutrition exerting increasing influence over time. Similarities in facial appearance within families, across generations, suggest that key genes exert particularly large effects on facial shape and appearance and that facial morphology is highly heritable (Fitzgerald *et al.,* 2010; Cole *et al.,* 2017; Cole and Spritz, 2017). Craniofacial variation among modern humans develops very early in ontogeny further supporting its relatively high heritability (Vidarsdottir *et al.,* 2002). Consequently, craniofacial morphology can be used to supplement information for genetics, population history and archaeology (Ribot, 2004; Von Cramon-Taubadel, 2014).

5.3.1. Size and shape differences in sub-Sharan African morphology

The study set out to assess variation between populations from different regions of sub-Saharan Africa using Principal Components Analysis (PCA). PCA using morphometric data can be interpreted as co-variation between size and shape (Somers, 1986). Allometry refers to size-related shape changes and is an important concept when studying human evolution and development (Klingenberg, 2016) and should be taken into account when assessing the variations observed in this study. Allometry is variation in several traits that is explained by or associated with variation in size and size-related shape changes (Mosimann, 1970; Bookstein *et al.,* 1985; Klingenberg, 1998).

Variations in the size and size-related shape changes of the cranium and face among the historic Bantu-speaking populations, the Khoe and San and modern South Africans were observed. Specific features of the face were strongly associated with changes in size and shape of the craniofacial morphology. In all three sets, the first PC displayed positive loadings for all craniofacial features. The first PC of traditional morphometric measures usually represents size variation (if all loading scores are positive) and that morphological traits are well correlated with size (Jolicouer and Mosimann, 1960). Therefore, if the PC1 can be interpreted as size, the other components can be interpreted as a mixture of size and shape (Mosimann, 1970; Sundberg, 1989).

While there seemed to be a considerable amount of overlap in the variation across the population groups, specific regions of the head and face seemed to be associated with this variation. Measurements associated with the height of the face (TFH and UFH), cranial vault length (HL), nasal breadth (NB) and inner canthal distances (IOB) all had strong associations with size related variation among the populations when considering PC1. Generally speaking, an increase in the overall size of the craniofacial morphology was found to be associated with taller faces and longer cranial vaults with relatively narrower noses and narrower inner canthal distances.

Additionally, when considering size and size-related shape changes, that is PC2 and PC3, measurements related to the height of the face (TFH and UFH), breadth of the head and face (HB and MFB) and breadth of the mandible (and to some extent zygomatics) (BGB and BZB) were strongly associated with the variation seen in craniofacial morphology among the populations. The loadings of these measurements were, however, slightly different among the sets. PC2 within the historic sample (including both Bantu-speaking and Khoe and San individuals (i.e., sets 1 and 2) suggests that as the face gets broader (an increase in MFB) the face gets shorter (a decrease in TFH and UFH). Additionally, PC3 suggests there will also be an increase in the breadth of the zygomatics (BZB) and mandible (BGB) as the cranial vault gets shorter. Slightly different to this was set 3 when a modern South African sample was included. There was a strong association between facial measurements and the mandible suggesting that as the face gets shorter the mandible will increase in width (PC2), However, PC3 suggested that as the face gets broader, BGB will decrease.

Craniofacial morphology varies in size and shape (Mitteroecker *et al.,* 2013; Freidline *et al.* 2015) and is influenced by genes and development (Freidline *et al.,* 2015). Allometry can be viewed as a form of integration where traits covary because of variation in the developmental process (Hallgrímsson *et al.,* 2009). Bruner and Manzi (2004) noted that the whole face undergoes a structural development where components of the face are rearranged. The authors found that individuals from sub-Saharan African population undergo "enlargement, widening and flattening of interorbital and nasal areas, prognathism and vertical shortening" (Bruner and Manzi, 2004, p. 55). The current study aligns with this. Regions associated with facial height influence the size and shape of the nasal and interorbital regions. In other words, as the face gets shorter and broader, nasal breadth and inner canthal distances will increase (and vice versa).

Nutritional and environmental adaptations also play a role in size and shape of craniofacial morphology. Changes in growth due to adaptations in the environment result in different allometric trajectories, particularly in the mid-facial regions (Bastir *et al.,* 2006). The wide and more prognathic maxillae in Khoe and San are associated with a rapid growth in anterior and lateral planes of the maxillae (Freidline *et al.,* 2015) and this is most likely due to mechanical adaptation in response to diet and climate changes (von Cramon-Taubadel, 2014). Such studies have shown that differences in the craniofacial morphology of different populations may be associated with different growth trajectories, and that small growth in one region may influence growth in a neighboring region. This means that adjacent craniofacial modules may have similar growth trajectories (Dinkele, 2018).

Variation in cranial morphology is also related to genes that code for specific features of the face. For example, the maxilla, mandible and zygomae contribute to the length and breadth of the face and specific genes code for a combination of facial features (Cole *et al,* 2017; Cole and spritz, 2017; Cha *et al.*, 2018). In the current study, measurements mainly associated with the facial height, nasal regions and inner canthal distances and facial breadth accounted for the variation seen among the populations. Studies have shown that specific genes code for different regions of the face (Cole *et al.,* 2017; Cole and Spritz, 20017; Cha *et al*., 2018). For example, PAX3 has been shown to code for regions around the nose and inner canthal distances (Cole *et al*., 2017) whereas the PARK2 gene has been associated with facial height (Cha *et al.,* 2018). However, these genes do not act alone and often there are numerous genes acting together. It must also be kept in mind that in some populations, these genes code for wider and shorter features while the opposite can occur in other populations (Roosenboom *et al.,* 2016; Cole *et al.,* 2017).

In the current study, the historic Bantu-speaking individuals have shorter cranial vaults and broader faces than the Khoe and San while mid facial features (IOB and NB) were relatively smaller. Similar to this, Ramphaleng (2020) noted broader faces among Bantu-speaking populations using face masks. Additionally, Howells (1989) found that populations from sub-Saharan Africa had shorter faces but larger breadths across the nose, eyes and face. The current study also noted overall smaller craniofacial morphology in individuals from the Kalahari (Khoe and San). This supports previous literature where studies found the Khoe and San to have significantly smaller crania than other sub-Saharan African populations (de Villiers, 1968; Ribot, 2004; Franklin *et al.,* 2010). The modern South African individuals had narrower facial breadths (MFB) with relatively larger bi-gonial breadths (BGB) relative to all other populations. Although the current study shows some similarities between that of Ramphaleng (2020) it must be noted that Ramphaleng (2020) only compared shape differences whereas the current study looked at both size and shape differences.

The current study found that elements associated with masticatory processes seemed to influence the size and shape of the craniofacial morphology. Bi-gonial breadth (BGB) seemed to have the strongest association on the overall shape of the cranium, particularly among historic Bantu-speaking individuals (set 1) and the Khoe and San (set 2). Cranial regions under masticatory stress, have higher variability than those regions less affected by mastication, such as the upper face and cranial vault, indicating higher plasticity in the masticatory regions of the cranium (von Cramon-Taubadel, 2014).

Since the 17th century, colonialism, war, genocide, forced migrations of individuals and gene flow has resulted in the composition and distribution of the population of the world (Botha

et al., 2017) and morphological differences seen between South Africa populations are the result of colonialism, migration and forced separation (Stull *et al.,* 2014a). Hence, variation in the size and shape of craniofacial morphology play an important role in understanding and explaining population history. Different regions of the face are influenced by several factors and studies, such as this one, can supplement other studies on population variation and population history.

5.3.2. Craniofacial morphology for group separation

Although different regions of the face show variation among individuals in the current study, there was much overlap between the population groups and therefore, it was difficult to separate populations using PCA alone. However, DFA did show a clear separation between the populations. While PCA is used to show the greateast amount of variance in cranial morphology among individuals and which measurements have the strongest association with that variation, independent of group separation. However, DFA, allows one to determine craniofacial similarities and differences for group separation. Therefore, the second objective of the study was to assess craniofacial similarities and differences between sub-Saharan African populations using Discriminant Function Analysis (DFA).

Bantu-speaking individuals from Malawi, Mozambique, and Tanzania (eastern region) and South Africa and Botswana (southern region) were found to be morphologically distinct from individuals from Zambia (south-central region) and Angola (western region) (Figure 4.11a). Aspects of the head and face which seemed to be more variable between populations included the upper face, inner canthal distances, cranial length and breadth and zygomatic breadth. Western and southern-central population groups had taller faces with longer cranial vaults, and wider inner canthal distances and zygomatics. Eastern and southern populations had wider faces and wider cranial vaults and narrower inner canthal distances. Ramphaleng (2020) reported similar findings using face masks. Shorter and broader faces were noted in east Africans while central Africans had longer and narrower faces. The author also noted that individuals from western-central regions of Africa had wider faces with eyes being more apart. In contrast to the current study, Ramphaleng (2020) noted longer and narrower faces in individuals from southern African regions. The current study is comparable to studies that have used crania to assess variations in sub-Saharan African populations. Using a large sample size (Ribot, 2004) found the Khoe and San presented with a short and low vault with narrow orbits and a narrow vault and a highly curved occipital bone, whereas west Africans presented with a high long vault, high and wide orbits with a broad frontal bone (Ribot, 2004). Franklin *et al.* (2007) found that Bantu-speaker crania are generally more

dolichocephalic, having higher foreheads, higher anterior projecting upper faces and more prominent noses with taller faces.

The modern South African sample was morphologically distinct from the historic populations. Modern South Africans did not tend to group with any other population. Generally, the historic Bantu-speaking populations (from all regions) had taller faces with narrower mandibular regions (BGB). The opposite is suggested for the modern South African sample, with this group having wider mandibular regions and shorter faces. However, when separating the historic Bantu-speaking populations into geographic regions, broad and short noses and narrower inner canthal distances that are seen in eastern and southern Bantu-speaking populations are similar to that found in the modern South African sample. The literature assessing genetics has suggested that South Africans come from eastern regions of the continent and therefore this could account for the similarities between modern South Africans and historic eastern and southern Bantu-speaking populations (Li *et al.,* 2014).

The Khoe and San were also found to be morphologically distinct from the Bantu-speaking populations in this study. They had significantly smaller craniofacial features than Bantu-speaking populations (both historic and modern). Bantu-speaking individuals seemed to have broader and shorter noses with narrower inner canthal distances. Similarly, Ramphaleng (2020) noted broader and more prognathic faces with thicker lips in Bantu-speaking populations. The Khoe and San, although smaller in size, shared similarities in facial height and inner canthal distances to historic Bantu-speaking individuals from eastern and southern regions. The Khoe and San exhibited wider faces with slightly narrower inner canthal distances. L'Abbé *et al.* (2006) noted that San populations had wide low vaults, low faces with low orbits and short nasal apertures. Similar results were found for the current study with the Khoe and San having longer craniums and relatively smaller orbits and nasal apertures. However, Ramphaleng (2020) noted San individuals to have broader, shorter noses and narrower and longer faces, which differs from the findings in the current study. The current study treated the Khoe and San as a single group. If these two populations were to be separated, it may have resulted in differences in craniofacial morphology between the two populations.

There is no one single factor that determines cranial morphology, and it is rather the result of the complex relationship of both genetic and environmental factors (Gonzalez-Jose *et al.,* 2004; Neuweger, 2007). These factors include neutral evolutionary forces of mutation, migration, and random genetic drift as well as natural selection and environmental factors such as climate (Roseman, 2004).

Stress exerted during mastication could also influence craniofacial morphology. However, the current study found larger mandibular widths (BGB), particularly in modern South Africans. Cranial regions under masticatory stress, such as the zygotemporal region, have higher variability than those regions less affected by mastication, such as the upper face and cranial vault, indicating higher plasticity in the masticatory regions of the cranium (von Cramon-Taubadel, 2009). However, Mitteroeker and Bookstein (2008) suggest that the association between the enlarged laterally projecting zygomae and enlarged, prognathic maxillae is mainly related to mastication and force distribution. Plasticity in the craniofacial skeleton has been studied extensively (e.g., Jantz and Jantz, 2000; Simpson and Henneberg, 2002; Cole *et al.,* 2017) and there is a predictable and direct influence of the facial skeleton on the overlying soft tissues (Simpson and Henneberg, 2002). Facial dimensions change relative to the muscle pressures caused by dietary preferences (Collard and Wood, 2007; von Cramon-Taubadel, 2014). Researchers have long theorised that there is an interaction between subsistence behaviour and the growth and development of the skull and lower jaw. Major changes in cranial robusticity and shape were accompanied by the shift from hunter-gathering to farming (von Cramon-Taubadel, 2014; Noback and Harvati, 2015). Agriculturists have a softer more processed diet than hunter-gathers, which in turn places less mechanical stress on the masticatory muscles and underlying bone. However, cranial shape is not influenced by diet alone. Often migration into new areas and changes to the environment would lead to the introduction of new subsistence behaviour.

Research suggests adaptive selection due to the relationship between climatic factors and morphology of the face (Roseman, 2004; Harvati and Weaver, 2006), the midface (Evteev *et al.,* 2014) and cranial size (Beals, *et al.,* 1984; Harvati and Weaver, 2006). Changes in temperature and humidity can influence soft tissue and facial features (Harvati and Weaver 2006; Maddux *et al.,* 2016; Zaidi *et al.,* 2017; Wroe *et al.,* 2018). Adaptations of the nasal region to certain climates have been reported (McDowell, 2012). In this study, measurements around the nasal region (i.e, NB, IOB and NH) were least associated with craniofacial variation among the groups. Additionally, facial height and head length seemed to have the strongest association with variation in craniofacial morphology in historic Bantu-speaking and Khoe and San individuals in the current study. This may be due to the fact that the current study included individuals from indigenous African communities only. It has been noted that other population groups, such as Europeans, have longer and narrower noses while African populations have broader and shorter nasal apertures due to climatic adaptations (McDowell, 2012). Roseman (2004) noted two facial elements (nasal and zygomatic height) that were closely related to climatic distances. Higher and wider zygomatic bones seen in Bantu-speaking and Khoe and San population are thought to be

adaptations to hot sub-Saharan climates (Twaha *et al.,* 2020). In the current study, bi-zygomatic breadth (BZB) did not seem to have a strong association with craniofacial morphology.

It has been reported that the neurocranium tends to be larger in cooler environments and smaller in hot environments, to allow the brain to cool down quicker and easier (Irmak *et al.,* 2004). This may be one explanation for the larger cranial sizes seen in the modern South African population, as South Africa is cooler and dry with low atmospheric pressure (Lawal *et al.,* 2009). However, it is unlikely that these adaptations would have been able to develop over such a short time period, and more likely other factors, such as genetic exchange with other groups, may have played a role. Changes over time in the morphology of the face and neurocranium of sub-Saharan Africans should be investigated in future studies. Africa has a wide range of climates and research has shown that craniofacial morphology is sensitive to climatic changes, particularly changes in the mid face and the nose (Heirnaux and Fremont, 1976; Roseman, 2004), and these adaptations in more recent times have hardly been explored.

Populations affected by similar climatic conditions are often geographically close to each other, thus complicating the assessment of the effects of climate on craniometric traits (Betti *et al.,* 2010). Natural selection, gene flow and genetic drift are all factors that influence craniofacial morphology. Therefore, when populations from similar climates share craniometric traits, one cannot imply that this is a result of natural selection but could also reflect common ancestry and/or recent genetic exchange due to proximity (Betti *et al.,* 2010). In the current study, western and southern-central Bantu-speaking populations shared similar craniofacial morphology while eastern and southern Bantu-speaking populations shared similar craniofacial morphology, with modern South Africans closely resembling eastern historic Bantu-speaking populations. This may be the result of gene flow during population movements through sub-Saharan Africa. Genes were most likely introduced into different parts of the continent when individual settled during this time, thereby increasing the variation in geographically close populations (Lynch *et al.,* 2016; Skoglund *et al.,* 2017).

The current study noted distinct cranial facial morphology in the Khoe and San population groups which differed from other Bantu-speaking populations. Genetic studies have shown considerable diversity within various modern Khoe and San population groups (Schlebusch *et al,* 2012). In the current study, the Khoe and San population was a historic sample that was treated as a single population group. Botha *et al.* (2017) conducted a study using historic Khoe and San collections to propose interpretations of population history. The study found that although the Khoe and San specimens used from two European museums are closer to some historic San groups, they are not homogenous at all and as such historical data should not be treated a single group.

The authors also noted that east and central African cranial morphology was more similar to the Khoe and San (Both *et al.,* 2017). The Khoe and San individuals in the current study, although historic, are more representative of a recent population rather than an ancient Khoe and San population. Studies have shown that older crania from ancient Khoe and San populations are very different from recent Khoe and San populations (Botha *et al.,* 2017). Genetic studies have identified the Khoe and San as the most divergent group of modern humans and studies have suggested that there is a deep separation between northern and southern Khoe and San populations (Schlebusch *et al.,* 2012). In the current study, the Khoe and San did not show much variation and were treated as a single group. This may be due to the composition of the sample.

These regional differences in craniofacial morphology among sub-Saharan African populations can be used to supplement the literature on population history and population movements. Although the differences and similarities in craniofacial morphology are subtle, there is separation between Bantu-speaking populations that live along the western side of the sub-Saharan African continent and those along the eastern side of the continent. Additionally, eastern and southern populations are more similar in their craniofacial morphology. This could be explained by different environments and climates. Western regions have a more desert or semi-arid climatic conditions whereas eastern and southern regions have a more subtropical temperate climate. These differences in climate would result in differences in agricultural needs and approaches (von Cramon-Taubadel, 2014). The modern South Africa sample shared similar craniofacial morphology to the eastern and southern historic populations. This could be due to gene flow between these groups.

5.4. Geographic and morphological distances

The third objective aimed to assess geographic and morphological distances among the population groups using a Mantel test. For this analysis, it was decided to expand the sets into regional groups based on geographic location, as the grouping in sets would not have been informative to assess geographic and morphological distances. The regional groups are shown in Tables 3.7.

The current study found no correlation between craniofacial morphology and geographic distance. This suggests that morphological distance and geographical distance were independent of one another. Populations that are more distant from each other may be morphologically similar to populations that are geographically close to one another. In contrast, it may also suggest that populations that are geographically closer are morphologically distant from each other. To better

understand this a Principal co-ordinate Analysis (PCoA) was employed. Using mean morphology, the PCoA allowed for a visual representation of craniofacial morphology between populations and some clustering was observed.

When comparing mean morphology between historic Bantu-speaking population groups (Figure 4.17a) it was noted the populations from the southern regions of sub-Saharan Africa, were widely spread across the PCoA plot. This is interesting as it shows a wide range of variation among these groups. Research has assessed variation among southern Bantu-speaking populations. L'Abbé *et al.* (2006) explored cranial variation in a modern Venda population group. The authors found that Venda are morphologically most like modern sub-Saharan African groups both southern and eastern and least like the historical San group. The large number of similarities between the Venda and other sub-Saharan African groups indicates that the Venda are part of the diversity present within the majority of living eastern and southern Africans (L'Abbé *et al.,* 2006). It was also noted that the most distinct cranial features within the Venda are found in the cranial vault and face. The narrow high cranial vaults, high face with high orbits and long nasal apertures of the Venda population are like other Bantu-speaking populations (L'Abbé *et al.,* 2006). These are similar to the findings in the current study. The South African populations from the southern region of the continent, of which Venda individuals were a part of in set 2, were closely related to those populations from the eastern region.

There seemed to be better groups separation when the Khoe and San and modern South African sample were included in the analysis (Figure 14.7b and 14.7c) Populations from the eastern region of the continent (Mozambique, Malawi and Tanzania) were grouped more closely with population from the southern regions of the continent (South African Venda, Pedi and Limpopo) (Figure 14.7a). Similar to these findings, L'Abbé *et al.,* (2006) found craniofacial morphological similarities between the southern Bantu-speaking populations and east Africans. The authors noted that this was most likely the result of historical processes and geographical proximity.

Individuals from the Kalahari were composed of three Khoe and San groups; 1) individuals from central Kalahari, 2) individuals considered "hybrid" and 3) individuals from southern Kalahari. The Khoe and San populations (named according to regions in the Kalahari i.e., central, "Hybrid" and Southern Sarwa in Figure 4.17b) were clustered together based on mean cranial facial morphology and interestingly, individuals from Botswana were closely grouped with the Khoe and San. These groups are from the same region geographically and could account for the results seen in the current study. This clustering of Khoe and San with individual from Botswana is not surprising. Several studies have noted distinct morphological differences between the Khoe

and San and other African populations (Ribot, 2004; de Villiers, 1968; Jenkins, 1982; Excoffier, 1987; Cavalli-Sforza *et al.,* 1994; L'Abbe, 2006). The Khoe and San are distinguished by their small body size (Wilson and Lundy, 1994; Kurki, 2007; Franklin *et al.,* 2007). This was also found in the current study in that the Khoe and San populations overall exhibited smaller craniofacial morphology than other population groups. Individuals from Botswana, and which were identified as Bantu-speakers, were more similar in size to the Khoe and San. This could be due to admixture of the groups and gene flow between the populations. One needs to keep in mind that perhaps documentation of the "Bantu-speaking" individuals from Botswana was not accurate and may have been individual more closely associated with the Khoe and San.

The Khoe and San "hybrid" population, which were documented as being a mixture of the Khoe and San and Bantu-speaking populations, was more closely related to individuals from Mozambique (Figure 14.7c). This connection with the eastern parts of the continent is unexpected. In general, the south-eastern branch of Bantu-speakers occupied the entire eastern part of present-day South Africa while the Khoi and San people occupied the western parts of southern Africa as well as the southern and central parts of Namibia (Li *et al.,* 2014). Using mtDNA haplogroups, Pereira *et al.* (2001) found that a population from Mozambique had clear resemblances with populations both to the north and south. This was most likely due to the Bantu-speaker expansion as well as interaction and admixture with the Khoe and San.

Additionally, individuals from Zambia and Angola were more closely grouped with the eastern and southern regions and the modern South African sample was completely separate from all other populations. These findings are similar to those reported in the literature. Jenkins (1982) and Exoffier (1987) both reported a clear separation of populations into genetic distances that followed closely with their relative geographical locations in sub-Saharan Africa. It was noted that genetically the sub-Saharan Africa populations clustered into distinct groups: the Khoe and San; southern African Bantu-speaking groups; eastern African Bantu-speaking groups and west African groups.

Based on the findings, there is much overlap in the mean craniofacial morphology among historic Bantu-speaking populations. This makes it difficult to make any conclusions about population history and population movements within this group. However, there is clear shared craniofacial morphology among individuals from the Kalahari and Botswana. Additionally, modern South Africans show distinct morphological distance from the historic populations. While there is still some uncertainty in the morphological distances among the sub-Saharan groups, studies using anthropometric data of the face can complement genetics and archaeological studies.

5.4. Population history and movements

The last objective aimed to describe possible migration patterns through sub-Saharan Africa based on craniofacial morphology. There were subtle morphological distinctions among different regional population groups. Western and southern-central populations shared similar craniofacial morphology. Eastern and southern populations were more similar in craniofacial morphology with the modern South African population being more similar to individuals from these regions as well. The Khoe and San were completely distinct from all other population groups. The current study therefore supports the notion of South Africans being more similar to eastern-Bantu speakers and being more dissimilar to western Bantu-speakers. The findings of the current study thus support linguistic, archaeological and genetic evidence for population movements through sub-Saharan Africa.

5.4.1. Linguistic and archaeological evidence

Linguistic and archaeological evidence suggests that the Bantu language spread and diversified along with the expansion of agriculture and possibly the use of iron (Huffman, 1970; Holden, 2002; Li *et al.,* 2014). The Bantu language first differentiated and dispersed from a primary "Bantu" origin, and spread in western and eastern directions (Newman, 1995; Mitchell, 2002; Bostoen, 2018). A number of hypotheses have been proposed as to how the eastern and western dispersal of language occurred. (Packendorf *et al.,* 2011; Currie *et al.,* 2013; Li *et al.,* 2014; Grollemund *et al.,* 2015; dos Santos, 2018). Of interest for this study is the late split hypothesis. This late-split hypothesis proposes that the eastern and western branches split after passing through the central African rainforest and that southern African populations share similar linguistic, archaeological and genetics as the eastern branches (Pakendorf *et al.,* 2011; Li *et al.,* 2014). The current study noted that craniofacial morphology of modern South Africans is similar to that of eastern Bantu-speakers. Unfortunately, the current study cannot add much to this debate. However, the study cannot say whether the craniofacial morphology follows the early or late split hypotheses. Anthropometric data from northern and central African regions would be needed to better aid our understanding of proposed migration routes through sub-Saharan Africa.

Along with the spread of Bantu languages came the interaction with pre-Bantu-speaking populations, especially in the southern areas (Isern and Fort, 2019). The Khoe and San inhabited southern Africa before the arrival of the Bantu-speaking populations and are often considered to be a homogenous group based on their highly distinctive click languages (Rocha and Fehn, 2016).

This is evident in the current study, where the populations from the Kalahari (the Khoe and San (set 2)) were morphologically distinct from the other Bantu-speaking populations.

Modern South Africans share similar craniofacial morphology to eastern and southern historic Bantu-speaking populations. In contrast to this, Vincente *et al.* (2019) found that archaeological individuals from KwaZulu Natal in South Africa, clustered with those from western Africa. When considering the Bantu-speaker migration, one must keep in mind that all Bantu-speakers originated from a common western African origin (Huffman, 1970; Mitchell, 2002). From this origin, populations expanded into regions south of the Sahara, however, the routes taken is debated in the literature and often makes it difficult to trace migration routes decisively. Studies, such as Vincente *et al.* (2019) use reference samples (i.e. FORDISC) that are often limited and not fully representative of population variation and population history. In saying this, it is not bad to use such references sample as this is what is usually available. However, using other data (such as anthropometric data in this study) can make for a more representative comparison between studies.

Geological barriers can affect the expansion of populations. The climatic requirements for agriculture may have acted as actual geographical barriers to Bantu-speaking migration and expansion i.e., Kalahari Desert (Mitchell, 2002). It is suggested that the arrival of Bantu-speaking agriculturalists resulted in different degrees of admixture with the local populations (pastoralists and hunter-gatherers) leading to isolation and replacement of these groups (Mitchell *et al.,* 2009; de Fillipo *et al.,* 2012; Patin *et al.,* 2014). However, unravelling population history from dietary factors is difficult. Geography facilitates evolutionary processes responsible for population history while subsistence economy is also to some extent related to geography (von Cramon-Taubadel, 2011). Areas where there is an abundance of water, sunlight and good soil for growing crops would allow for the spread of prehistoric farmers while areas such as deserts or dense rainforests would make it difficult for farmers to grow crops thereby halting the expansion of populations into these areas (von Cramon-Taubel, 2011).

5.4.2. Genetic evidence

Bantu-speaking populations share a strikingly genetic similarity across a vast area of sub-Saharan Africa. Based on genetics, it has been suggested Bantu-speaking expansion was the actual movement of people and just simply the infusion of cultural tradition and languages through neighbouring populations (Tishkoff *et al.,* 2009; Pakendorf *et al.* 2011; de Filippo *et al.,* 2012; Li *et al.,* 2014; Busby *et al.,* 2016; dos Santos, 2018). Furthermore, studies have shown a clear genetic

separation of sub-Saharan African populations from north African populations (Salas *et al.,* 2002; Luis *et al.,* 2004).

East Africa shows more genetic and linguistic diversity than west central and central sub-Saharan Africa (Salas *et al.,* 2002; Wood *et al.,* 2005). This may be due to the influence of travellers or the possibility that movement and replacement of existing populations by Bantu-speaking farmers was less complete in this region (Salas *et al.,* 2002). Mozambiquans (Brandstatter *et al.,* 2004), Kenyans (Brandstatter *et al.,* 2004), Rwandan Hutus (Tofanelli *et al.,* 2003), Zimbabweans (Gené *et al.,* 2001) and Ugandans (Geneé *et al.,* 2001) have all demonstrated substantial differences with each other and/or populations further to the west at some molecular level. This is supported by findings from the current study, where eastern and southern Africans had different craniofacial morphology to western and southern-central Africans.

As the Bantu-speaking people migrated through sub-Saharan Africa, they not only integrated many elements of the indigenous cultures but also expanded their gene pool by intermarriage with the Khoe and San (Tishkoff *et al.,* 2007; Rowold *et al.,* 2014). This is often highlighted in studies on the impact of Bantu-speakers on the genetic composition of Pygmy hunter-gatherers (Berniell *et al.,* 2009; Patin *et al.,* 2014) and this suggests that there may have been some assimilation with previous populations of hunter-gatherers as well (Sikora *et al.,* 2011). Due to admixture of genes, South African populations and the Khoe and San has affected the enlargements of some groups (South African Bantu-speakers) and the shrinkage of others (Khoe and San) (Exoffier *et al.,* 1991).

According to genetic evidence, most Khoe and San populations show some degree of east African admixture (Schlebusch *et al.,* 2017). The findings of the current study support the genetic evidence in that craniofacial morphology is distinct between the Khoe and San populations groups and other Bantu-speaking population groups. There is clear separation from the eastern (Malawi, Mozambique and Tanzania) and western region (Angola) of the continent and clear separation of the Khoe and San populations from the other populations based on mean craniofacial morphology, except for the Botswana population which could be explained by the geographic closeness to the Kalahari.

The current study used anthropometric data from past living historic Bantu-speaking populations and Khoe and San populations as well as CT scans from a modern South African sample. From the results, it can be determined that using information from living individuals is useful and can help researchers assess population history and population variation. This, in combination with information obtained from craniometry, can help reinforce our understanding of population similarities and differences between populations around the world. Anthropometric

data from living individuals also allow one to look at new influences from better healthcare and living standards, something which is continuously changing overtime.

5.5. Limitations and future directions

Several limitations and shortcomings can be identified. The number of individuals in each sample ranged from 34 to 300. This difference in sample sizes is a relatively large range and may have affected the outcomes. Population groups with smaller numbers may not have truly reflected the population. In general, however, these sample sizes, with a total sample size of 1397, are probably on par if not larger than most studies using crania only.

The Khoe and San populations groups may also not have truly reflected early populations of southern Africa. Over time there has been a steady decrease in the population numbers of the Khoe and San and at the time the historic data was collected there were not many Khoe and San populations left. This in turn may reduce the overall variation and probably does not reflect what may have been seen a few hundred years earlier.

It must be kept in mind that the information written recorded in the hand-written documents of the historic data set may not be accurate or truly representative of the observations and information recorded during the time of the expeditions. Furthermore, records and publications on the expeditions were also very limited making it difficult to gain insight into the populations being assessed. Even though there are limitations to the historic dataset, it does contain vast amount of information that can be used in future studies. The historic data not only recorded craniofacial anthropometric measurements but included a wide range of postcranial anthropometric measurements, blood types, phenotypic features and photographs of these historic populations. Further studies could incorporate these observations with the current study to further assess population history in sub-Saharan Africa. The historic (handwritten) data has now been digitally recorded and is available for possible future research in the School of Anatomical Sciences, University of Witwatersrand.

CT scans were obtained from the Department of Diagnostic Radiology at Charlotte Maxeke Academic Hospital, Johannesburg from handwritten hospital records. This again proved challenging as each individual had limited demographic information and it was assumed (based on name) that all individuals were black South African. The method of repeating the same measurement on CT scans also proved challenging. Landmark description, landmark location and the position of the head and neck at the time the scan was taken all could have played a role in low reliability of some measurements. Additionally, overestimation of the measurements may have

occurred when taking measurements from the CT scans. However, imaging modalities are now the forefront of many anthropological studies. Although there have been a low error margins on measurements taken from different imaging modalities, most of these involve measurements of the underlying bone tissue. Measurements from soft tissue are beneficial and interesting to use as it can complement studies that use bone alone.

There were some notable size and shape differences among the sub-Saharan African populations. However, the current study only used data from male individuals. Future research that includes data from females could be used to assess sexual dimorphism and size and shape variation among male and female historic sub-Saharan African populations. Furthermore, the current study only used anthropometric data from to the head and face. Postcranial anthropometric data could be used to further assess population history and population variation. In addition to this, including modern data from other regions of sub-Saharan Africa may provide better insight into secular changes over time.

An electronic database was established through the work of this thesis and until now this information has not been used to explore variation among sub-Saharan Africa populations. It is now available for research purposes and is stored at the School of Anatomical Sciences, University of the Witwatersrand.

CHAPTER 6: CONCLUSION

This study aimed to evaluate craniofacial variation among historic and modern sub-Saharan African populations using anthropometric data. Four objectives were stated. The first objective assessed anthropometric variation between western, eastern, southern-central and southern Bantu-speaking population groups and Khoe and San population groups and compared this to the modern South African sample. The second objective aimed to determine patterns of morphological discrimination for group separation. The third objective assessed geological and morphological distances to better understand population history. Lastly, based on these results, the fourth objective was to evaluate possible migration routes through sub-Sahara Africa.

The following conclusions can be drawn from the study.

- Craniofacial morphology is distinct for different population groups throughout sub-Saharan Africa. Taller faces and longer crania with narrower and broader noses are shared among Bantu-speaking individuals, while larger bi-gonial breadths are common among modern South Africans.
- The head and face morphology of the Khoe and San are smaller than other Bantu-speaking population groups. However, historic Bantu-speaking individuals from Botswana are similar in size to the Khoe and San and this is most likely due to geographical closeness and gene flow, resulting in morphological plasticity.
- Sub-Saharan African populations can be distinguished based on certain regions of the face. Western and south-central Bantu-speaking individuals have taller faces and longer crania while southern and eastern Bantu-speaking populations have wider faces and broader cranial vaults. The Khoe and San have narrower inner canthal distances and overall smaller nasal apertures. Modern South African have wider mandibular and zygomatic regions.
- Southern African populations share similar cranial facial variation to those from the eastern side of the continent while western and southern-central share similar craniofacial morphology form the western side of the continent. Although migratory patterns could be speculated, it is difficult to decide which route the populations best fit.
- Certain measurements of the midface can be reliably repeated using CT scans. This can aid in future anthropometric studies where different 3D imaging modalities can been used to supplement research using bone alone.

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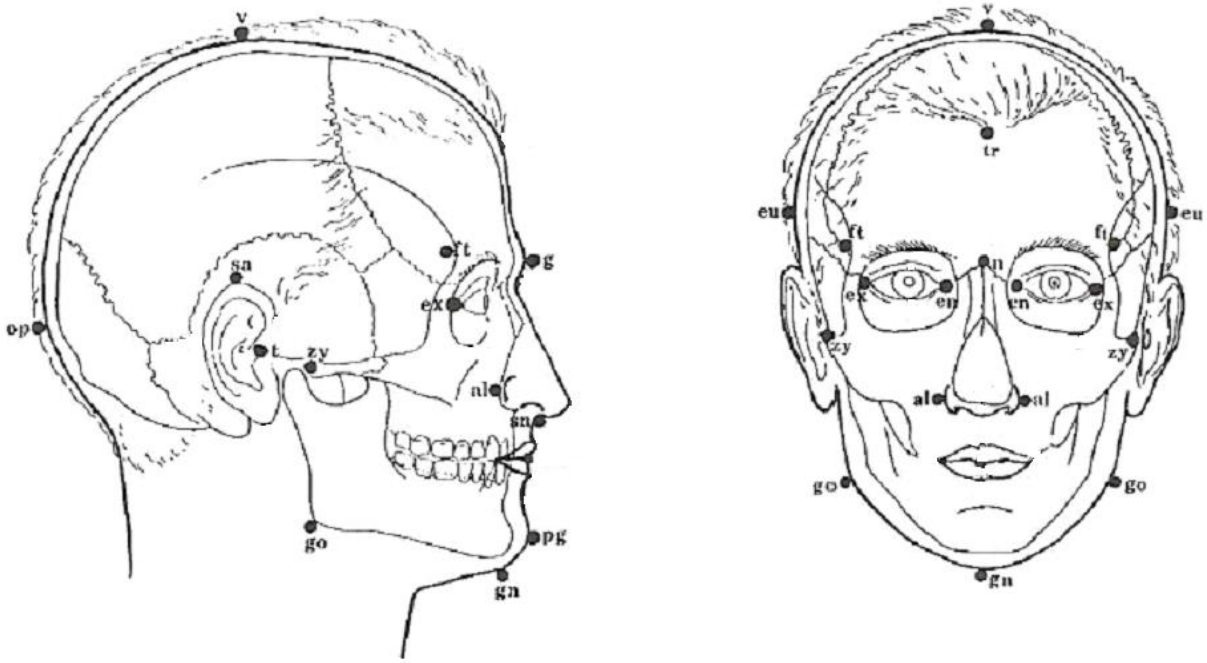
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APPENDIX A



Frontal and lateral aspects of the craniofacial landmarks of the head and face used in the current study (Illustration adapted from Farkas, 1994).

APPENDIX B

Human Research Ethics Committee (Medical)

Research Office Secretariat: Senate House Room SH 10005, 10th floor. Tel +27 (0)11-717-1252
Medical School Secretariat: Medical School Room 10M07, 10th Floor. Tel +27 (0)11-717-2700
Private Bag 3, Wits 2050, www.wits.ac.za. Fax +27 (0)11-717-1265

Ref: W-CJ-140604-1 25/01/2016

TO WHOM IT MAY CONCERN:

Waiver: This certifies that the following research does not require clearance from the Human Research Ethics Committee (Medical).

Investigator: School of Anatomical Sciences (Head: Prof M Steyn - Previously Prof T J M Daly, initial approval 04/06/2014 – recertified 27/01/2016).

Project title: Research on Cadaveric Material.

Reason: In terms of Chapter 8, sections 62-64 of the National Health Act No 61 of 2003 donated bodies and their tissues may be used for, among other purposes, health, and research. Use of such Material is subject only to permission from the responsible person in the School of Anatomical Sciences – the Head or person designed by the Head.

Professor Peter Cleaton-Jones

Chair: Human Research Ethics Committee (Medical)

UNIVERSITY OF THE WITWATERSRAND
OFFICE OF THE DEPUTY VICE CHANCELLOR RESEARCH
29 JAN 2016
RESEARCH OFFICE HREC (Medical)
JOHANNESBURG

Copy - HREC (Medical) Secretariat: Rhulani Mkansi, Zanele Ndlovu.

APPENDIX C

R14/49 Melissa Jones

HUMAN RESEARCH ETHICS COMMITTEE (MEDICAL)

CLEARANCE CERTIFICATE NO. M170339

NAME: (Principal Investigator)	Melissa Jones
DEPARTMENT:	School of Anatomical Sciences Charlotte Maxeke Johannesburg Academic Hospital
PROJECT TITLE:	An Anthropometric Assessment of Cranial Variation in Historic and Modern Sub-saharan African Populations
DATE CONSIDERED:	31/03/2017
DECISION:	Approved unconditionally
CONDITIONS:	
SUPERVISOR:	Prof Maryna Steyn and Mr Jason Hemingway
APPROVED BY:	Professor P. Cleaton-Jones, Chairperson, HREC (Medical)
DATE OF APPROVAL:	08/05/2017

This clearance certificate is valid for 5 years from date of approval. Extension may be applied for.

DECLARATION OF INVESTIGATORS

To be completed in duplicate and **ONE COPY** returned to the Research Office Secretary 3rd floor, Phillip Tobia Building, Parktown, University of the Witwatersrand. I/We fully understand the the conditions under which I am/we are authorised to carry out the above-mentioned research and I/we undertake to ensure compliance with these conditions. Should any departure be contemplated, from the research protocol as approved, I/we undertake to resubmit to the Committee. I agree to submit a yearly progress report. The date for annual re certification will be one year after the date of convened meeting where the study was initially reviewed in this case, the study was initially review in March and will therefore be due in the month of March each year. Unreported changes to the application may invalidate the clearance given by the HREC (Medical).

Principal Investigator Signature

Date 11/05/2017

PLEASE QUOTE THE PROTOCOL NUMBER IN ALL ENQUIRIES

APPENDIX D

UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

FACULTY OF HEALTH SCIENCES

DEPARTMENT OF DIAGNOSTIC RADIOLOGY

08 September 2016

Dear Dr/ Ms Melissa Jones

Re:Request for permission to access the CT scans in our department
Study Title: An anthropometric assessment of craniofacial variation in historic and modern sub-Saharan african populations

Permission is granted to Melissa Jones to access our CT records for her study.

Please liaise with the relevant Consultant and Radiography manager in charge of CT with regard to the logistics and practical aspects of obtaining this information.

I hope you find the above order.

Yours Sincerely,

Victor Mngomezulu MB BCh (Wits), FC Rad Diag (SA), MBA (Wits)
Adjunct Professor and Academic Head
Division of Diagnostic Radiology
University of the Witwatersrand and Charlotte Maxeke Johannesburg Academic Hospital

Diagnostic Radiology: Department of Radiation Sciences
7 York road, Parktown, 2193, South Africa | Tel: +27 11 488-3368/4590 | Fax2Email: +27 86-238-9963 | E-mail: diagnostic.radiology@wits.ac.za

APPENDIX E

This appendix shows the results obtained from the statistical analyses of the principal components. A Kruskal-Wallis test was run for each principal component in each set. The results shown here further support the findings discussed in the thesis.

Set 1: Historic Bantu-speaking groups

Using Kruskal-Wallis analyses, PC1 and PC2 both resulted in p-values <0.0001, whereas PC3 resulted in a p value of 0.2594. The tables below highlight the p-values for each PC for the different geographic population groups. A p-value <0.05 is considered significant and highlights differences among population groups based on the PCs.

Table 1: Bonferroni corrected p values for PC1 in set 1.

	West	**East**	**South**
East	0.7688		
South	0.004	<0.0001	
South Central	1	1	0.006

Table 2: Bonferroni corrected p values for PC2 in set 1.

	West	**East**	**South**
East	0.2683		
South	1	0.0001	
South Central	1	0.0321	1

Table 3: Bonferroni corrected p values for PC3 in set 1.

	West	**East**	**South**
East	0.5248		
South	0.8166	1	
South Central	1	1	1

Set 2: Historic Bantu-speaking and Khoe and San groups

Using Kruskal-Wallis analyses, all three PCs resulted in p-values <0.0001. The tables below highlight the p-values for each PC for the different geographic population groups. A p-value <0.05 is considered significant and highlights differences among population groups based on the PCs.

Table 4: Bonferroni corrected p values for PC1 in set 2.

	West	East	South	South Central
East	1			
South	0.0090	<0.0001		
South Central	1	1	0.0112	
Khoe and San	0.0328	<0.0001	<0.0001	0.0138

Table 5: Bonferroni corrected p values for PC2 in set 2.

	West	East	South	South Central
East	0.05138			
South	0.4891	0.0002		
South Central	0.9355	0.0634	1	
Khoe and San	0.891	0.0001	0.6858	1

Table 6: Bonferroni corrected p values for PC3 in set 2.

	West	East	South	South Central
East	0.3657			
South	0.6491	1		
South Central	1	0.6214	1	
Khoe and San	<0.0001	<0.0001	<0.0001	<0.0001

Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

Using Kruskal-Wallis analyses, all three PCs resulted in p-values <0.0001. The tables below highlight the p-values for each PC for the different geographic population groups. A p-value <0.05 is considered significant and highlights differences among population groups based on the PCs.

Table 7: Bonferroni corrected p values for PC1 in set 3.

	West	East	South	South Central	Khoe and San
East	1				
South	0.0076	<0.0001			
South Central	1	1	0.0123		
Khoe and San	0.0134	<0.0001	<0.0001	0.0424	
Modern South African	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 8: Bonferroni corrected p values for PC2 in set 3.

	West	East	South	South Central	Khoe and San
East	0.1688				
South	1	<0.0001			
South Central	1	0.0818	1		
Khoe and San	1	0.9047	1	1	
Modern South African	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 8: Bonferroni corrected p values for PC2 in set 3.

	West	East	South	South Central	Khoe and San
East	1				
South	0.683	1			
South Central	1	1	1		
Khoe and San	<0.0001	<0.0001	<0.0001	<0.0008	
Modern South African	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

APPENDIX F

This appendix highlights the percentage correctly classified within each geographic population group. Each table shows the confusion matrix where the rows represent the recorded/given groupings, and the columns represent the predicted groupings.

Set 1: Historic Bantu-speaking groups

The percentage correctly classified for set 1 was 49.83%. The table below shows the recorded versus predicted groupings.

Table 1: Confusion matrix indicating the recorded group and the predicted groups for set 1

		Predicted groups				
		West	**South**	**East**	**South Central**	**Total**
Recorded groups	**West**	12	2	7	8	33
	South	63	415	210	92	780
	East	47	92	143	48	330
	South Central	13	4	10	18	45
	Total	139	513	370	166	1188

Set 2: Historic Bantu-speaking and Khoe and San groups

The percentage correctly classified for set 2 was 47.91%. The table below shows the recorded versus predicted groupings.

Table 2: Confusion matrix indicating the recorded groups and the predicted groups for set 2

		Predicted groups					
		West	**South**	**East**	**South Central**	**Khoe and San**	**Total**
Recorded groups	**West**	15	2	7	7	2	33
	South	59	386	160	77	98	780
	East	42	82	117	45	44	330
	South Central	14	3	9	16	3	45
	Khoe and San	6	14	4	7	96	127
	Total	136	487	370	166	166	1188

Set 3: Historic Bantu-speaking, Khoe and San and modern South African groups

The percentage correctly classified for set 3 was 49.63%. The table below shows the recorded versus predicted groupings.

Table 3: Confusion matrix indicating the recorded groups and the predicted groups for set 3

		Predicted groups						
		West	**South**	**East**	**South Central**	**Khoe and San**	**Modern South Africa**	**Total**
Recorded groups	**West**	16	2	6	7	2	0	33
	South	60	384	159	76	100	1	780
	East	42	82	116	44	45	1	330
	South Central	14	3	9	16	3	0	45
	Khoe and San	6	14	4	7	96	0	127
	Modern South Africa	0	0	1	0	0	50	51
	Total	138	485	295	150	246	52	1188

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