# THE PREHISTORIC KHOESAN RELATIONSHIP WITH THE MODERN POPULATION OF SOUTHERN AFRICA USING BIOLOGICAL DISTANCE

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# Declaration

I, Stacey Lander, hereby declare that this thesis is my own work and it is being submitted to the University of the Witwatersrand for the degree of Doctor of Philosophy. It has not been submitted before for any degree or examination at this or any other University.

Signed:

Date:

# Dedication

Mom:

You were my best friend and words cannot express how much I miss you. You always put family first and the sacrifices you made gave us a brighter future. Thank you for continuously supporting me and my dreams.

Dad:

Thank you for being my role model. I am the woman I am today because of you. Your love for God and those in need have always pushed me to do more and be better in all areas of my life.

Brother:

I love you and I am very proud of you.

Husband:

As we begin this new season of life together, I look forward to building the future with you.

**This PhD thesis is dedicated to YOU, mia familia.**

# Abstract

The population history of southern Africa is complex, especially with regard to the relationships between the indigenous Khoesan peoples and the migrating Bantu-speakers. Previous genetic, archaeological and bioanthropological studies suggested interactions between them, especially during the last 2,000 years. Current genetic research highlights the genetic distinctness of the Khoesan and their admixture with other South African populations, but their early population dynamics have not been fully investigated. This project used biodistance analyses to explore population interactions through time and over geographical space in southern Africa. This included Smith's Mean Measure of Divergence statistic for cranial nonmetric and dental nonmetric data, as well as R-matrix theory for the dental metric data. Samples included skeletal specimens of Later Stone Age (n=303), Iron Age (n=105), modern Khoesan peoples (n=261) and modern Bantu-speakers (n=176). Two different groups of modern Khoesan individuals were also analysed, which incorporated known-in-life crania (n=24) and dental casts of living individuals (n=237).

Substantial admixture was identified in the cranial and dental samples of modern Khoesan, with indications of both prehistoric and recent interactions with Bantu-speaking groups. The prehistoric cranial comparisons indicate the genetic exchanges began prior to 2,000 BP, with the levels of interaction increasing over time according to both the cranial and dental results. This suggests the migrating Bantu-speakers may have assimilated with other Later Stone Age groups in central Africa, implying that the morphology of the Iron Age groups may have already reflected their Khoesan admixture upon arrival in southern Africa. Once settled, these Iron Age peoples mainly interacted with those Later Stone Age groups in close geographical proximity (according to the cranial and dental results), while the more mobile Later Stone Age groups, from more distant geographical regions, show less interaction with the Iron Age peoples. Finally, differing from previous dental research, the cranial results of this study revealed two distinct geographical areas of similarity for the Later Stone Age samples.

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# A note on terminology

In early anthropological studies, a number of terms were used to describe the peoples of southern Africa. To clarify the use of terminology in biological anthropology research, a conference held in Johannesburg in 1971 suggested the terms ‘San’, ‘KhoiKhoi’ and ‘South African Negro’ be used to describe the biology of the southern African peoples of African descent, both in the past and for their living descendants (Tobias and Jenkins, 1977). The San were the peoples following a forager subsistence pattern and the KhoiKhoi (later spelled KhoeKhoe, Khoi/Khoe) were the herders. When referring to these groups as a whole, the term ‘Khoisan’ was also acceptable (Schultze, 1928; Schapera, 1930), but today this is only used for linguistic purposes. The collective term ‘Khoesan’ was later suggested to designate the combination of San and Khoe communities (Crawhall, 2006), and has been used in subsequent research. The term ‘Khoesan’ is therefore used in this study to represent the prehistoric and historic foragers and herders, as well as their descendant communities today.

Scientists no longer use the term ‘South African Negro’ when referring to non-Khoesan peoples of African descent in southern Africa. ‘Negro’ is considered to be inappropriate and offensive. ‘Bantu’ on the other hand, refers to the group of languages spoken by the peoples who constitute the majority of Sub-Saharan Africans, following their Iron Age migrations across the continent. It is also used for linguistic purposes (i.e. Bantu language speakers), but it is not recommended as a standalone descriptor (Tobias and Jenkins, 1977). In addition to this, the term has negative associations stemming from its historic use during the apartheid period. ‘Bantu-speakers’ or ‘Bantu-speaking’ is therefore used in this study to represent the majority modern-day population of southern Africa, as well as their Iron Age ancestors.

# CHAPTER 1: INTRODUCTION

The written history of the southern African peoples began approx. 500 years ago, when the Portuguese explorers and then the European colonists identified and described the Khoesan foragers and Bantu-speaking farmers they encountered (Tobias, 1985). Since that time, archaeological, bioanthropological and genetic research has shown that the Khoesan represent an indigenous population that once dominated the region, while the Bantu-speakers only arrived about 2,000 years ago from eastern Africa (Nurse *et al*., 1985; Barham and Mitchell, 2008; Schlebusch *et al*., 2013; Warren *et al*., 2015; Bostoen, 2018). Previous bioanthropological studies were predominantly interested in the biological identity of the Khoesan, but their relationships with the Bantu-speaking peoples are still not fully understood. Recent genetic research has suggested admixture between the Khoesan and Bantu-speaking populations through time (Barbieri *et al*., 2014; Schlebusch *et al*., 2017) and morphological similarity with the Bantu-speakers was further suggested for some Khoesan groups (Hausman, 1980; Morris, 1992a; Black, 2014; Irish *et al*., 2014). To better understand the population history of southern Africa, this study investigated the poorly understood relationships between the Khoesan and Bantu-speaking peoples over time and geographical space. Methods include biological distance analyses using nonmetric traits of the skull, dental nonmetric and dental metric data.

## *Historical background*

Later Stone Age foragers were predominantly located along the coastal and adjacent coastal forelands of the southern Cape (Morris, 1992b). Their absence from the southern African interior possibly due to more favourable environmental conditions or social factors between their population groups (Lazarides, 2015). A well documented continuous occupation was subsequently identified at the southern Cape coast from the Late Pleistocene to the Late Holocene. Herders were also identified in these areas post-2,000 BP, but there is still considerable debate with regards to their introduction and origin in southern Africa (Sadr, 2015; Cameron, 2019). Bioanthropologists currently suggest that the co-existing foragers and herders represent a single homogenous population that show morphological continuity for at least 12,000 years. This interpretation was derived from cranial and postcranial analyses (Stynder *et al*., 2007b; Ginter, 2008; Stynder, 2009; Pfeiffer and Harrington, 2011) and more recent dental analyses (Black, 2014; Irish *et al*., 2014). Modern Khoesan populations currently have a wide, geographical distribution from southern Angola in the North to the

Western Cape Province of South Africa in the South (Schlebusch *et al*., 2013). Within the last 5,000 years, the majority of the Khoesan populations in Africa have disappeared due to assimilation into other populations or by extinction (Henn *et al*., 2011).

The Iron Age Bantu-speaking peoples migrated into southern Africa during the 1st and 2nd millennium AD. During the 2nd millennium AD in particular, there was a further migration of Bantu-speaking peoples from eastern Africa, represented by new ceramics (Warren *et al*., 2014). The Bantu-speakers were farmers who predominantly settled in the eastern half of southern Africa, expanding to their southern limit in the Eastern Cape Province of South Africa (Mitchell and Whitelaw, 2005; Hall, 2010). They avoided areas unfavourable for Iron Age farming practices, such as the Karoo and Kalahari deserts of today, as well as the Maloti-Drakensberg mountains (Barham and Mitchell, 2008; Russell and Steele, 2009). Recent bioanthropological research indicated their morphological continuity throughout the Iron Age period (Warren *et al*., 2015). Further continuity into the present-day was also identified, whereby historic and recent Bantu-speakers were morphologically similar to Iron Age farmers (Warren *et al*., 2014). Recent genetic research suggests the modern Bantu-speakers are descendants of the Iron Age farmers (Schlebusch *et al*., 2017; Steyn *et al.*, 2019), and is supported by modern linguistic and cultural entities that are linked to specific Iron Age groups (Mitchell and Whitelaw, 2005; L'Abbé *et al*., 2006; Hall, 2010).

### *Modern genetics*

Genetic research on modern populations of southern Africa gives us new insight into the population history of the Khoesan and Bantu-speaking peoples. The large, wide-spread Bantu language speaking component is relatively homogenous, but has genetic links with both living and prehistoric Khoesan populations (Coelho *et al*., 2009; Barbieri *et al*., 2013a; Barbieri, *et al*., 2013b; Barbieri *et al*., 2014). The genetic homogeneity of recent Bantu-speaking populations are reflected in their cranial and dental morphology that display very low inter-population variation (De Villiers, 1968; Rightmire, 1970a; Irish, 1997, 1998b; Franklin *et al*., 2007; Irish, 2016). In contrast, the Khoesan populations have drastically reduced in number over time, resulting in small genetically diverse groups living in and among the Bantu-speaking peoples (Schlebusch, 2010; Schlebusch *et al*., 2013). It is estimated that all present-day Khoesan populations are influenced by 9 – 30% genetic admixture from other populations (Schlebusch *et al*., 2017). The Khoesan groups have highly variable levels of admixture from Bantu-speaking peoples, as well as admixture from prehistoric Khoesan populations and

genetically isolated living Khoesan groups (Nurse *et al*., 1985; Schlebusch, 2010; Pickrell *et al*., 2012; Schlebusch *et al*., 2013; Schlebusch *et al*., 2016; Uren *et al*., 2016; Montinaro *et al*., 2017; Schlebusch *et al*., 2017). The modern genetic picture therefore suggests a very complex population history due to the marked effects of the massive Bantu-speaker expansions and later colonisation in southern Africa. A history of marginalisation, displacement, genetic drift, severe population bottlenecks and sex-biased admixture is evident in the present-day Khoesan communities (Wood *et al*., 2005; De Filippo *et al*., 2010; Henn *et al*., 2011; Barbieri, *et al*., 2013a; Schlebusch *et al*., 2013; Bajić *et al*., 2018).

*This study*

The morphological study of Khoesan groups and their biological origins, given their complex history, has proven to be difficult. The situation is further complicated by the many poorly documented "Khoesan" specimens that currently reside in osteological collections (Morris, 1986; 1987). Assuming selected morphologies were indicative of Khoesan affinities; many prehistoric and historic individuals of unconfirmed identity were accessioned into osteological collections as "Khoesan" (and were studied as such). Researchers have subsequently tried to rectify this typological sorting by radiocarbon dating the individuals labelled as "Khoesan". This has resulted in a better understanding of Khoesan prehistoric biological identity over time and space (Stynder, 2006; Black, 2014), but their relationships with the Bantu-speaking peoples are still not fully understood.

To expand on previous work and to investigate the level of genetic and morphological diversity of the Khoesan peoples through time, this study differed from previous research in terms of the comparisons made and the samples used. Large archaeological samples (both Later Stone Age and Iron Age) from southern Africa were included, as well as a substantially larger modern Bantu-speaker comparative sample. For the first time, another modern Khoesan dental data set, which has not been previously compared with other Khoesan or Bantu-speakers, was also included. The prehistoric and modern Khoesan samples were then compared with the prehistoric and modern Bantu-speaker samples, to determine the genetic relationships between them. While a genetic analysis could potentially provide direct answers for these questions, a skeletal biology study was undertaken because aDNA is difficult to extract, has a high failure rate, and is costly to process. Furthermore, the destructive sampling of archaeological specimens is currently under ethical review in South Africa. A non-invasive approach was therefore more appropriate. This methodology captured the genetic diversity in

the populations, while investigating a level of temporal depth that was not considered in previous work. In terms of the geographical distribution of the Khoesan and Bantu-speaking peoples, a framework derived from our current understanding of southern African prehistoric population movement, was used to contextualise the study design and analysis.

Biological distance or biodistance analysis is the application of multivariate statistical methods to determine the biological relatedness or divergence between populations separated by time and and/or geography. It was well suited for this study due to its ability to reconstruct past population histories, population movement and identifying admixture (Pilloud and Hefner, 2016). Using the correlation between genotype and phenotype (Relethford and Harpending, 1994; Relethford, 2002, 2004b; Cardoso, 2007; Hubbard *et al*., 2015), assuming that the samples were representative of the populations from which they were derived, the cranial and dental similarities between the Khoesan and Bantu-speaking peoples provided a reasonable estimate of their genetic relatedness (Irish *et al*., 2014). This in turn, gave new insight into their population history and the biological identity of the Khoesan peoples.

## 1.1. RESEARCH QUESTIONS

OBJECTIVE 1

*To determine, using biodistance analyses, if the individuals from the Later Stone Age and Iron Age are more biologically similar to the modern Khoesan or modern Bantu-speaking peoples.*

OBJECTIVE 2

*To investigate how the biological relationships among the archaeological samples changed over time and geography.*

## 1.2. THESIS LAYOUT

This study consists of five chapters. Chapter 1 introduces the research by highlighting the problem and objectives. In Chapter 2, the literature concerning the population history of southern Africa is reviewed in terms of archaeology and biological identity. The archaeological record of the Khoesan and Bantu-speaking populations assists with reconstructing their prehistoric movement over time. What is currently known about the cranial and dental variation of prehistoric and living Khoesan and Bantu-speaking populations is also detailed, to provide context to previous work completed. The outcomes of the few cranial and dental studies that have investigated the biological relationships between the

Khoesan and Bantu-speaking peoples are also presented, as well as the relevant biodistance methods.

Chapter 3 describes the materials and methods used in this study. The archaeological and modern samples are summarised, and the prehistoric individuals are further categorised according to their geographical locations and time periods. The cranial and dental variables are presented in detail, while the biodistance methods are explained.

Chapter 4 is divided into three parts to present the results of the objectives investigated. Firstly, Objective 1 is addressed. This compares the biological affinity of the prehistoric Khoesan and Bantu-speaking populations with their modern descendants, to determine how biologically similar they are to one another. Objective 2 investigates the temporal and geographical relationships between the archaeological samples independently, addressed in part two and part three.

The final chapter consists of four parts. Objective 1 is discussed in part one, whereby the population history of the Khoesan peoples are discussed and compared with previous research. This includes Bantu-speaker admixture identified in recent Khoesan populations and the patterns of biological change observed in the Later Stone Age population over time and geography. Objective 2 is likewise discussed in part two, elaborating upon the biological relationships between the Later Stone Age and Iron Age groups, both over time and geography. Statistical limitations and future research are mentioned in part three and the general conclusion summarises the findings in part four.

# CHAPTER 2: LITERATURE REVIEW

This study investigated the biological relationships between the Khoesan and Bantu-speaking peoples over time and geographical space. This involved biodistance analyses using cranial nonmetric, dental nonmetric and dental metric data. In this chapter, to better understand southern African population history, the archaeological records of the Middle and Later Stone Ages, as well as the Iron Age, are reviewed. This information was used to model population movements over time, which can assist bioanthropologists when investigating biological relationships. Current knowledge about the cranial and dental variation of the prehistoric and modern Khoesan and Bantu-speaking populations are also reviewed, including morphological studies that compared Khoesan and Bantu-speaker samples. Finally, the use of biodistance analyses for understanding South African biological history, as well as the various biodistance methods, is presented.

## 2.1. ARCHAEOLOGICAL BACKGROUND

The archaeological record of southern Africa provides useful information about the indigenous Khoesan and the later Bantu-speaking migrations. Knowledge of different settlement and subsistence patterns (foragers, herders and farmers), as well as palaeoenvironmental scenarios, is crucial for reconstructing population movements over time. Understanding the archaeological history of the Khoesan and Bantu-speaking peoples is helpful in establishing their biological identities. In the following sections, the prehistoric Khoesan peoples (represented by the Later and Middle Stone Age cultures) and the prehistoric Bantu-speaking peoples (represented by the Iron Age culture) are discussed in more detail.

### 2.1.1. The Middle Stone Age (300,000 to ~20,000 BP)

The earliest San foragers are dated to the Middle Stone Age (MSA) levels at Klasies River Mouth Cave and Border Cave (Rightmire, 1979, Rightmire, 1981; Singer and Wymer, 1982). Although human remains are poorly represented in MSA sites for this time, because the record comprises of isolated teeth and postcranial fragments, a rich archaeological record gives us insight into their way of life.

The MSA is most celebrated for its technological innovations that suggest the use of complex cognitive processes (Wadley, 2015). These include the Still Bay and Howiesons Poort blade technocomplexes, beads made of seashells and discs of ostrich eggshells, ochre use and worked bone. Additionally, the remains of small and large mammals at many MSA

sites are evidence of the diversity in their subsistence, which involved terrestrial hunting, snaring, collecting and scavenging, as well as exploitation of shellfish (Wadley, 2015; Larbey *et al*., 2019). Plants were not exclusively used as food sources during the MSA, but also for making tools, medicine or poison, and for domestic purposes such as bedding.

Evidence of the MSA in southern Africa is mainly concentrated in the interior region of the African subcontinent before 130,000 BP (Wadley, 2015). Thereafter, the MSA peoples were identified in mountainous areas, as well as predominantly along the coastal areas of the southern and western Cape. Shell beads in particular, were identified along the east coast of South Africa (Sibudu Cave in KwaZulu Natal) towards the southernmost point of Africa (Blombos Cave) at approx. 100,000 to 70,000 BP. By 58,000 BP, MSA occupation began shifting away from the coastal regions, possibly due to unsuitable environmental conditions (Jacobs *et al*., 2008; Chase, 2010; Stewart *et al*., 2016) or as a result of infrequent visits of smaller groups to a particular area (Wadley, 2015). This resulted in increased habitation in the southern African interior, which contributed to MSA site distributions in the southern Cape lacking from about 50,000 to 25,000 BP. This may be due to very arid conditions that resulted in a decline in population (Klein, 2000; Klein *et al*., 2004) or the loss of sites now submerged below sea level (Barham and Mitchell, 2008). In general, the MSA record for South Africa reflects the presence of groups highly responsive to environmental change and resource distributions, using technological innovations to expand their subsistence.

The transition between the MSA and Later Stone Age (LSA) technologies does not appear to have been a simple linear process in southern Africa. Current evidence suggests it occurred at different times in the different regions. Many archaeologists argue that the MSA ended in southern Africa between 30,000 BP and 20,000 BP (McCall and Thomas, 2009), yet an early LSA industry was already present before 38,000 BP at Border Cave (Bird *et al.*, 2003; Bousman and Brink, 2018). Rose Cottage Cave, dated to 20,600 ± 250 BP (Pta-5598), also yielded a transitional assemblage containing both MSA and LSA elements (Clark, 1997). With this in mind, 20,000 BP is used in this study as an approximation date for the beginning of the LSA, but the transition possibly spanned over 20,000 years (Bousman and Brink, 2018).

### 2.1.2. The Later Stone Age (~20,000 to 0 BP)

The LSA was characterised by stone tool industries, as well as rock art, burials and other remains of the San forager lifestyle. Unlike the MSA, many LSA archaeological sites have well preserved human burials. Based on archaeological assemblages and subsistence, the LSA

has been subdivided into the Robberg Industry, the Oakhurst and Wilton Complexes, the final LSA and ceramic final LSA (Lombard *et al.*, 2012).

*a) The Robberg Industry (~18,000 to 12,000 BP: Late Pleistocene)*

The Robberg Industry, the earliest evidence of LSA peoples, is associated with the Last Glacial Maximum. This was the coldest and driest period in southern Africa during the last 125,000 years, resulting in a major decrease in population size and distribution (Mitchell, 2002). Increased aridity was observed in the interior, particularly the present-day Karoo (Partridge and Dalbey, 1986) and southern Kalahari regions (Beaumont *et al*., 1984). This climate may have played a significant role in population isolation (Lahr and Foley, 1998), by constraining natural resources and forcing the population to the southernmost coastal and near-coastal regions of the Cape (Barham and Mitchell, 2008). Very few LSA burials of this time are known beyond the western and southern coast and the coastal foreland regions (Morris, 1992b). As a warmer and wetter climate returned at approx. 14,000 BP, population growth accelerated. Deserted sites were reoccupied and new sites were established, including those in the interior regions of present-day South Africa (Mitchell, 2002; Stynder, 2006).

*b) The Oakhurst Complex (~12,000 to 7,000 BP: Terminal Pleistocene/Early Holocene)*

The Robberg Industry was gradually replaced by the Oakhurst Complex and its regional variants (Deacon, 1972). Compared with the Robberg Industry, a significant increase in population density was observed as favourable climatic conditions prevailed (Stynder, 2006). Coastal rock shelters such as Nelson Bay Cave and Elands Bay Cave show continual occupation, while previously neglected smaller shelters, including Matjes River Rock Shelter and regions of the interior, were reoccupied. By 8,000 BP the Oakhurst Complex was replaced by the Wilton Complex (Sampson, 1974).

*c) The Wilton Complex (~8,000 to 4,000 BP: Holocene)*

The mid-Holocene Wilton assemblages are found mainly south of the Cape Fold Mountains, in the SW, South and SE coastal regions of the Cape (Stynder, 2006; Black, 2014). Habitation was patchy and sparse towards the West coast region, with a few non-coastal sites identified on the outskirts of the present-day Karoo. Global temperatures increased and were consistent from around 8,000 to 6,000 BP, possibly contributing to a very arid interior in the Karoo and West coast regions (Deacon, 1972; Partridge *et al*., 1999). In comparison, the coast and coastal forelands south of the Cape Fold Mountains, including the SE coast, were better-

watered and less arid at this time (Deacon, 1974; Hall, 2000). A continuous occupation of the area is documented for the last 10,000 years.

*d) Final Later Stone Age (~4,000 to 100 BP: Holocene)*

After approx. 4,000 BP, cooler temperatures occurred in the interior and along the Cape coast, resulting in a drastic population increase, seen in the intensification of archaeological settlements up to 2,000 BP in the coastal regions (Stynder, 2006). This included both the Wilton Complex and final LSA pre-ceramic cultures. Even though a marked increase in settlements of the South African interior was noted after 4,000 BP (Deacon, 1974; Morris, 1992a; Stynder, 2006), fewer burials were identified compared with the coastal regions.

Although population movement was favoured during the mid-late Holocene, with resettlement of inland regions due to returning temperate climatic conditions, the southern coastal regions were still densely occupied by the LSA peoples (Stynder, 2006). High population density would have put pressure on the available food resources, resulting in new mobility patterns. Seasonal mobility between the coastal and inland regions was suggested to have taken place from about 4,000 to 2,000 BP (Parkington, 1976, 2001; Parkington *et al*., 1988). This did not however appear to relieve the increasing population pressures at the coast. Changes affecting the LSA population at this time included decreased mobility (Sealy and Pfeiffer, 2000; Sealy, 2006), fluctuations in cranial and body size (Pfeiffer and Sealy, 2006; Stynder, 2006; Stynder *et al*., 2007b), a subsistence strategy shift to more predictable low risk foods including tortoises, fish and mussels (Henshilwood *et al*., 1994; Barham and Mitchell, 2008), as well as artefact assemblages showing substantially greater regional diversity (Black, 2014).

*e) Ceramic final Later Stone Age (post-2,000 BP: Late Holocene)*

At this time, evidence of herding and ceramics began to appear in the archaeological record. The ceramics were typically undecorated, thin-walled, often grit-tempered wares that differ from those of the subsequent Iron Age and are thought to have developed independently from herders already in the region (Sadr, 1998, 2008; Sadr and Sampson, 2006). Current debate on the origins of herding in southern Africa considers whether herding was introduced by the immigration of herders (possibly Khoe speakers), was an indigenous development among the existing foragers, or was brought into the region by small scale population movements (Sadr, 2015; Cameron, 2019). Although archaeological differences and similarities were identified for the foragers and herders of this time, involving their burial sites, dietary remains, rock art

and occupation sites, current research supports the notion that the co-existing subsistence groups in the southern Cape region were not biologically distinct, but rather represented a single homogenous population (Stynder, 2009; Pfeiffer and Harrington, 2011; Irish *et al*., 2014). The morphological changes observed between the two groups of peoples are thought to be indicative of climatic change and increased population pressures, affecting their forager way of life.

### 2.1.3. The Iron Age

The signature archaeological development of the Iron Age involved one of the biggest population movements of Africans. The "Bantu expansion" refers to the spread of Bantu-speakers, originating from West Africa, between present-day Nigeria and Cameroon, across large parts of central and eastern Africa approx. 5,000 years ago (Franklin *et al*., 2007). According to linguistic, archaeological and genetic data, these peoples introduced the Iron Age (IA) culture to southern Africa (Huffman, 1970; Robertson and Bradley, 2000; Russell and Steele, 2009; Bostoen, 2018). The components of the IA life way included cultivating crops, herding domesticated cattle and sheep, manufacturing ceramics, settling near arable land and iron technology. The initial spread of the Bantu-speaking peoples from West Africa was a process of slow fragmentation and expansion over small distances, gaining momentum when a major climatic shift caused the destruction of the central African rainforest (Bostoen, 2018). This resulted in Bantu-speaker societies simultaneously reaching present-day Congo Basin in western central Africa and the Great Lakes of eastern Africa at approx. 2,500 BP.

The archaeological identity of the IA peoples is based upon a variety of ceramic styles identified within the Chifumbaze complex (Mitchell and Whitelaw, 2005; Parkington and Hall, 2010). These ceramics are found throughout eastern and southern Africa, and are thought to be indicative of change, migration or interaction of culturally different peoples (Warren, 2013). Their movement into southern Africa and their interactions with the indigenous Khoesan peoples can be reconstructed by assessing the material culture throughout the IA.

#### *a) The Early Iron Age (AD 200 to 900)*

During the 1st millennium AD, the Early Iron Age (EIA) was introduced to southern Africa by migrating Bantu-speaking peoples from eastern Africa (Huffman, 2007; Ribot *et al*., 2010; Warren *et al*., 2015). Two traditions of ceramics within the Chifumbaze complex, termed the Urewe and the Kalundu, indicate the areas of settlement at this time (Mitchell and Whitelaw,

2005; Huffman, 2007). The Urewe Tradition is present south of the Limpopo river, as well as in Swaziland, eastern Botswana, southeast/western Zimbabwe and southern Mozambique. Its ceramics also extend from the Mozambique border to the region south of Durban, along the coastal areas of KwaZulu Natal (KZN) (Ribot *et al*., 2010). The Kalundu Tradition is evident from Happy Rest in present-day Limpopo Province, expanding further south than the Urewe Tradition in KZN and reaching the Kei region of today's Eastern Cape (Mitchell and Whitelaw, 2005). Towards the end of the 1st millennium AD, new EIA sites are also identified in Botswana, Swaziland, the Shashe-Limpopo River Basin and today's Kruger National Park (Mitchell and Whitelaw, 2005; Warren, 2013).

The geographical distribution of the EIA peoples is therefore consistent with the palaeoenvironmental conditions most suitable for their subsistence. In KZN in particular, the EIA sites are located in areas with iron rich, arable soils that are well suited for grazing (Mitchell and Whitelaw, 2005). Their overall distribution is mainly along the coast where shellfish were accessible, as well as inland incised valleys of major rivers such as the Thukela system. They also possibly expanded their distribution to altitudes of 1000m, but remained in wooded, savannah environments (Maggs, 1984). In these regions, the summer rainfall is greater than 800mm per annum, which is ideal for tropical crops such as sorghum and millet (Russell and Steele, 2009). The farmers may not have expanded far from the KZN coast because the interior was too arid for agriculture at that time (Mitchell and Whitelaw, 2005). The present-day Eastern Cape Province was their southern limit of expansion because it had suitable summer rainfall for sorghum and millet agriculture.

During the latter part of the 1st millennium AD, there is archaeological evidence for substantial exchange between the indigenous LSA groups and the EIA communities (Hall and Smith, 2000; Robertson and Bradley, 2000; Parkington and Hall, 2010; Ribot *et al*., 2010). Ostrich eggshell beads, bone and stone artefacts were identified in EIA settlements far removed from areas thought to have been peopled by LSA populations. Likewise, EIA evidence was found in LSA deposits often far inland from the nearest EIA settlement. This suggests that the sedentary Bantu-speaking peoples were interacting with widespread mobile Khoesan groups (Ribot *et al*., 2010). Barham and Mitchell (2008) describe three phases of farmer expansion into southern Africa that illustrate the possible relationships between the Khoesan and Bantu-speaking peoples that they term the pioneer, substitution and consolidation phases. The EIA is representative of the pioneer phase. Minimal contact may have occurred as 'pioneer' farmers began to expand their areas of settlement, although the

occasional exchange of domesticates or material culture resulted (Barham and Mitchell, 2008).

*b) The Middle Iron Age (AD 900 to 1300)*

The Middle Iron Age (MIA) is the transitionary period between the EIA and the Late Iron Age (LIA). It is geographically restricted to the Shashe-Limpopo River Basin, more specifically, present-day northern South Africa and southern Zimbabwe. The establishment of larger settlements like Schroda, K2, Mapungubwe and eventually Great Zimbabwe occurred at this time (Warren, 2013). Cultural continuity with the EIA was observed at these sites, as some EIA ceramics continued to be used or were later replaced by newer wares. Internal social changes were also observed due to wealth from trading and shifting political power. This is indicative of Barham and Mitchell's (2008) substitution phase of farmer expansion. While permanent colonisation of the Bantu-speaking peoples is evident during the MIA, the Khoesan may have been threatened by their larger numbers and largely retreated from the farming areas. They may also have been absorbed into the Bantu-speaking groups through intermarriage or more structured, permanent client based relationships. In this way the Khoesan peoples would have had greater access to new technologies and products (Barham and Mitchell, 2008).

*c) The Late Iron Age (AD 1300 to 1840)*

During the 2$^{nd}$ millennium AD, the LIA was introduced to southern Africa by a further migration of Bantu-speaking peoples from eastern Africa (Warren *et al*., 2014). This is identified by the new Blackburn and Moloko ceramic wares that were unlike any ceramics dating to the EIA (Mitchell and Whitelaw, 2005; Hall, 2010). The additional movement of people may be associated with a dry climate that encouraged southern expansion (Tyson *et al*., 2002). The LIA farmers were the first to settle in the higher altitude grasslands of the KZN interior, as well as further south into today's Eastern Cape near Grahamstown. Drier conditions during the Little Ice Age would have threatened the farmer's food security which may explain the presence of LIA communities on defendable hilltops in the grasslands. Their material culture also no longer included LSA elements that may reflect a period of greater competition or conflict with the Khoesan, particularly in the KZN interior (Ribot *et al*., 2010).

With the limited availability of wood in the grassland areas for pole and daga hut construction, stone dwellings became more common in the LIA (Mitchell and Whitelaw, 2005). IA farming villages in southern Africa that had a unique internal structure and layout

are termed “central cattle pattern” (Badenhorst, 2009). These settlements are characteristic of the LIA and dominated the region south of the Zambezi River, with different types of settlements linked to specific oral histories (Warren, 2013). By approx. AD 1500, the LIA peoples west of the Drakensberg escarpment had expanded into present-day eastern Botswana and the North West Province of South Africa (Hall, 2010). They had also crossed the Vaal River to settle in the Highveld. Thereafter, low rainfall in today’s Karoo and most of the Kalahari and the cold temperatures of the Maloti-Drakensberg mountains limited further expansions (Barham and Mitchell, 2008; Russell and Steele, 2009). The Khoesan peoples may have therefore persisted longest in these areas, until their eventual dispossession after European settlement beginning in AD 1652.

European expansion from the Cape into the Bantu-speaker areas of settlement, in the interior and SE coast regions, began during the late 18$^{th}$/early 19$^{th}$ century (Warren, 2013). Larger political entities, such as the Zulu Kingdom in KZN and the Ndebele and Tswana Kingdoms in the North West Province, were already established. Khoesan groups still existed in the higher altitude grassland interior because it was unfavourable for IA farming (Mitchell and Whitelaw, 2005; Ribot *et al*., 2010). This represented the final consolidation stage of farmer expansion, involving agricultural intensification and development of greater socio-political complexities that caused further fragmentation of Khoesan communities (Barham and Mitchell, 2008).

## 2.2. BIOLOGICAL IDENTITY OF THE KHOESAN AND BANTU-SPEAKERS

In earlier bioanthropological research, cranial morphology, specifically craniometrics, was used when investigating the biological characteristics of the Khoesan and Bantu-speaking peoples. The cranium is useful for assessing the evolutionary history of a population because it is developmentally plastic and therefore reflects responses to stresses over time (Relethford and Harpending, 1994; Relethford, 2002, 2004b). At the same time, fundamental aspects of cranial morphology reflect the effects of neutral evolutionary forces such as genetic drift, gene flow and mutation (Cramon-Taudel, 2009). The analysis of Khoesan and Bantu-speaker dentition have also become more popular because of the development of standardized dental scoring methods, such as the Arizona State University Dental Anthropology System, and the recognition that teeth may be an even better proxy for genotype than crania (Dempsey and Townsend, 2001). Teeth form prior to their eruption and appear to be more shielded from environmental effects, making them ideal for investigating the broad evolutionary

development of a population (Cardoso, 2007; Hughes and Townsend, 2013; Pilloud and Hefner, 2016). In the following sections, the current literature concerning the cranial and dental morphology of the Khoesan and Bantu-speaking peoples is discussed. Postcranial studies do not fall within the scope of this study but are mentioned for comparative purposes. The intention is not to give a review of Khoesan and Bantu-speaker morphology, but rather provide a comprehensive discussion of the studies pertinent to the samples investigated in this thesis.

### 2.2.1. Khoesan cranial morphology

A common means of describing a population in early bioanthropological research was the use of racial typology. The "Khoesan skull" was described based on a physical type derived from observations of living Khoesan. They were small in size, had an infantile form, slightly developed supraorbital ridges and small mastoid processes (Wells, 1934; 1972). This was problematic because no supporting documentation was available to confirm the ancestry of these individuals. By disregarding intra-population variation and environmental conditions, this typological approach resulted in the accession of many unknown remains into osteological collections as "Khoesan" individuals (Morris, 1986; 1987).

After the 1960's, researchers began shifting away from describing cranial "types" to the use of cultural association and geographic location to identify known-in-life Khoesan individuals (Stern and Singer, 1967; Rightmire, 1970a; Howells, 1973; Hausman, 1980, Hausman, 1982). This resulted in new problems, such as assuming that material culture or subsistence and biological ancestry were linked, or that geographical areas were exclusively inhabited by a certain group of peoples. Furthermore, very few known-in-life individuals could be identified, resulting in very small sample sizes that were insufficient for statistical analyses. To overcome this, Morris (1986) noted that researchers often supplemented their samples with largely undated archaeological skeletons. This caused methodological shortcomings similar to those stemming from typology. Morris (1986, 1987) thus re-evaluated all the archaeological Khoesan individuals housed in different institutions to positively identify known-in-life Khoesan. Many of the remains were not confirmed, resulting in only seventy individuals with legitimate Khoesan identity. The individuals were from localities in the southern Kalahari and its surrounding areas, and lived during the late 19$^{th}$ to early 20$^{th}$ century. Morris (1986) therefore stressed that they did not constitute a good representative sample of all Khoesan groups, neither geographically or temporally.

Hausman (1980) was the first to conduct a large-scale investigation into the evolutionary development of the prehistoric and protohistoric Khoesan populations. Although the study had statistical shortcomings and included undated skeletons, the research did set the foundation for understanding Khoesan morphological variation over time and space. Hausman (1980) compared individuals from the Cape coastal regions and the interior regions of South Africa and found that the inland populations had greater morphological variability than the coastal populations. Their relative isolation may have resulted in a distinct biological identity due to genetic drift and unidirectional selection (Morris, 2002; 2003). Morris (1992a) supported this by investigating the legitimacy of Khoesan sites located in the Northern Cape. It was concluded that many of the crania from this interior region showed significant gene flow from neighbouring Bantu-speaking farmers, as most of them displayed traits from both the Khoesan and Bantu-speaking peoples. Morris further suggested that because many of the protohistoric Khoesan from inland South Africa had significant Bantu-speaker admixture, it was unwise to compare them directly to the pre-colonial archaeological samples from the coastal regions. Stynder (2006) subsequently agreed that the inland individuals were most likely genetically admixed, while the coastal Khoesan individuals were relatively removed from outside gene flow from Bantu-speaking farmers, because they avoided the less suitable coastal regions. This does not however rule out the possibility of gene flow between the indigenous Khoesan populations of southern Africa, particularly prior to 2,000 BP (Schlebusch *et al.*, 2017).

New data collections and statistical analyses were used to assess the biological evolution of the prehistoric Khoesan in the southern Cape regions. Stynder (2006) was the first to investigate a large radiocarbon dated LSA sample from the Cape coastal regions and adjacent coastal forelands. Using geometric morphometrics, cranial size and shape were evaluated through time and continuity in cranial form was demonstrated to span over 12,000 years, with minor cranial variability (Stynder, 2006; Stynder *et al*., 2007b). The early to mid-Holocene populations had large, robust crania. Pronounced supraorbital regions and receding frontal bones were identified, as well as long and broad upper faces with a large neurocranium relative to their facial dimensions. A decrease in cranial size and associated size-related changes in cranial shape were however observed from 4,000 BP. The supraorbital regions were more gracile and retracted, with steep and prominent frontal bones. Their upper faces were short and narrow, but the neurocranium remained large relative to their facial dimensions. This reduction in craniofacial form did not however remain and reverted at 3,000

BP to previously observed (pre-4,000 BP) dimensions (Stynder *et al*., 2007b). An overall reduction in body size and concurrent recovery in stature was also observed at these time periods (Pfeiffer and Sealy, 2006). It is unlikely that gene flow from non-Khoesan peoples caused these skeletal changes because gene flow into a population usually increases biological variability (Gonzalez-Jose *et al*., 2007) and no increase in variability was observed (Stynder *et al*., 2007b). Furthermore, environmental factors are more likely to initiate a quick morphological response, similar to those observed, should there be any change in living conditions (Eveleth, 1994; Ruff, 2002). Genetic change however, would result in long term biological consequences (Martínez-Abadías *et al*., 2006) and thus less likely the cause. With an increase in population size in this region at 4,000 BP, and evidence of limited food resources and shifts in subsistence patterns suggestive of population pressures at that time, environmental factors most likely contributed to the change in cranial morphology and stature (Stynder *et al*., 2007b). A small increase in LSA cranial variation was also observed at approx. 2,000 BP, the time when herding was introduced to the region (Stynder, 2009). Factors such as dietary stress, socially driven changes in gene flow patterns and small-scale gene flow into the indigenous Khoesan populations most likely contributed to the biological change observed.

Neuweger (2007) and Ginter (2008) also looked at Khoesan biological continuity in southern Africa, but their studies were more constrained with respect to region and time. Neuweger (2007) investigated Late Pleistocene to early Holocene Khoesan archaeological sites, with a focus on Matjes River Rock Shelter but included data from other regional sites at Fish Hoek, Cape Flats and Elands Bay Cave. The study included both radiocarbon dated and non-radiocarbon dated samples. The Matjes River sample, consisting of 43 crania dated from 11,000 to 2,000 BP were described as representing a single biological population with very little morphological variation over time. When compared with other Khoesan individuals (from similar time periods but located in different geographical regions in South Africa), no geographical differences were found between the samples. Neuweger's (2007) results supported Stynder's (2006) work in terms of finding biological continuity, as well as identifying a change in cranial size between 4,000 BP and 3,000 BP. It was not however able to comment on the recovery of cranial size to pre-4,000 BP cranial size due to the temporal framework, but also attributed the biological changes to environmental responses.

Lastly, Ginter (2008) investigated LSA individuals from the Eastern Cape dated from 8,000 to 300 BP, to assess whether the introduction of herding at 2,000 BP resulted in any

morphological changes. Genetic homogeneity in the cranial metric and nonmetric traits over time suggested that sheep herding was not introduced by foreigners but rather was due to an indigenous development. The biological continuity and the decrease in cranial and postcranial size observed between 3,500 BP and 2,000 BP in the Eastern Cape, are similar to the trends described previously for other regions (Pfeiffer and Sealy, 2006; Stynder *et al*., 2007b). The general pattern of body size reduction during the period of population stress in the Eastern Cape however, appeared to be slightly later than 4,000 to 3,000 BP and occurred for a longer duration. Factors that may have caused this temporal discrepancy are differences in regional climate, the variability of species diversity and seasonality in the Eastern Cape region (Ginter, 2008).

### 2.2.2. Bantu-speaker cranial morphology

Majority of research completed on the Bantu-speaking peoples of southern Africa was done using the individuals housed in the Raymond A. Dart Collection of Human Skeletons (Dayal *et al.*, 2009). The Bantu-speaking peoples comprise majority of this collection, providing a good database for their ethnic groups collected during the 20$^{th}$ century. Some of the earliest morphological and metric cranial studies of these individuals included De Villiers (1968) and Rightmire (1970a, 1972). De Villiers (1968) investigated the metric and nonmetric traits of the Bantu-speaker crania to assess the homogeneity between their groups, namely the Natal Nguni (Zulu, Swazi), Cape Nguni (Xhosa), Sotho (southern Sotho, Tswana, Pedi) and Shangana-Tonga. In general, no major intertribal differences were identified, suggesting cranial homogeneity for all the South African Bantu-speaking groups. When compared with other African groups however, differences were noted. De Villiers (1968) suggested Khoesan morphological characteristics (described previously) found in the South African Bantu-speakers may have distinguished them from the other groups. Similarly, Rightmire (1970a, 1972) compared Zulu, Xhosa and Sotho groups using metric and nonmetric traits of the skull. The South African populations were closely related to one another and when compared with MIA individuals (i.e. K2 archaeological site), biological similarity was observed (Rightmire, 1970a). It was later suggested that the MIA K2 individuals were broadly ancestral to the modern Bantu-speaking peoples because biological similarity was observed with both eastern and southern African groups (L'Abbé et al., 2006).

Compared with other human populations from around the world, the sub-Saharan Africans were geographically distinct (Howells, 1989). Howells (1989) investigated their craniometrics

and described them as having convex foreheads with minimal supraorbital development and upper nasal regions that were very flat and wide. Their faces were relatively short, broad across the eyes and nose, and the lower facial regions were not very projecting. Geographically, western, central, eastern and southern Africa was also investigated in more detail using discriminant function analyses (Rightmire, 1972; Ribot, 2004). Further significant differences were observed between the geographical regions. The central and western African samples clustered well together, whereas the eastern and southern African groups were biologically more distant from the other regions. The eastern Africans in particular, were also more biologically similar to the western-central region than southern Africa (Ribot, 2004). It was suggested that the southern Africans had more Khoesan admixture present due to similarity with a Khoesan sample, which resulted in their biological divergence. This was similar to conclusions made by De Villiers (1968). When southern African Bantu-speaking groups were further geographically separated, the southern populations (Swazi, Xhosa, southern Sotho and Zulu) were even more biologically similar to a Khoesan sample than the northern populations (Kalanga, Shangaan and Ndebele) (Franklin *et al.*, 2007). The cranial vault size of the Bantu-speaking groups in particular, was strongly correlated to latitude, showing larger mean values in the more southern populations. The southern African individuals were further described as having a flatter forehead contour, larger glabella, more brachycephalic cranial vault and a flatter face with an overall reduction in height (Franklin *et al.*, 2007).

In summary, the cranial morphology of the Bantu-speaking peoples of southern Africa show biological divergence compared with other regions within Africa (De Villiers, 1968; Rightmire, 1972; Ribot, 2004). They are also not biologically homogenous, as previously thought (De Villiers, 1968), because geographical differences were identified between their population groups (Franklin *et al.*, 2007). The biological variation observed in the Bantu-speaking African peoples was suggestive of their interactions with the Khoesan peoples that varied across Africa (Ribot, 2004), as well as within southern Africa (Franklin *et al.*, 2007). Previous research also showed specific IA individuals were possible ancestors to the modern Bantu-speaking peoples (Rightmire, 1970a; L'Abbé *et al*., 2006) and recent craniomandibular metric research (Warren, 2013; Warren *et al*., 2014) supports this. A large southern African IA sample was compared with the modern Bantu-speaking peoples and although significant differences were observed for some of their measurements, substantial biological similarity was identified.

### 2.2.3. Khoesan and Bantu-speaker dental morphology

Early dental anthropology research on the indigenous southern African peoples was mainly concerned with the frequencies of specific morphological traits and tooth size (Sperber, 1958; Van Reenen, 1961; Van Reenen, 1964; Kieser, 1979). Larger morphological and metric analyses of recent Bantu-speaking peoples in particular, also became more popular, especially with regards to comparisons made with other dental complexes (Jacobson, 1967, 1982; Haeussler *et al.*, 1989; Irish, 1993; 1997; 1998a; 1998b). The different Bantu-speaking groups in South Africa were shown to be morphologically homogenous and the sub-Saharan Africans in particular, were unique compared with other worldwide populations. Similar to the early anthropological investigations of Khoesan cranial morphology, conclusions about Khoesan teeth were often based on unreliable samples of unconfirmed biological identity.

The Arizona State Dental Anthropology System was developed to standardise the use of dental nonmetric traits for the classification of human populations (Turner *et al*., 1991; Scott and Irish, 2017). This included a series of rank-scaled reference plaques and corresponding descriptions defining a number of dental crown and root complexes, with varying expressions among human populations. Dental nonmetric traits of samples from many different regions of Africa were therefore compared and marked dental homogeneity was identified within the North African and sub-Saharan African areas (Irish, 1997). The Sub-Saharan African Dental Complex (SSADC) was subsequently established to characterize sub-Saharan African peoples, of which the modern Khoesan were a recognised subgroup. Although differences were identified between the Khoesan sample included in the SSADC and a Bantu-speaking group from sub-Saharan Africa (Haeussler *et al*., 1989), the similarities between the populations were considered to outweigh their differences (Irish, 1997). Recently, the SSADC, also known as Afridonty, was revisited with the inclusion of much larger regional samples over a greater time interval (Irish, 2013). Overall trait consistency was identified from the Pleistocene until the present across sub-Saharan Africa, with 11 distinct traits identified. These included high frequencies of the “Bushman canine” (mesial canine ridge), two-rooted upper first premolars, upper first molar Carabelli’s trait, three-rooted upper second molars, lower second molar Y-groove, lower first molar cusp 7, lower first premolar Tome’s root, two-rooted lower second molar and upper third molar presence. Low frequencies were observed for the upper first incisor double shovelling and upper first molar enamel extension. Relatively high frequencies of upper first incisor labial curvature and midline diastema were also identified, but these traits are not commonly recorded in other populations and therefore

are not considered part of the SSADC (Irish, 2013). Importantly, southern African dentition was described as unique compared with the western, central and eastern regions of Africa, similar to their cranial morphology (Ribot, 2004). This geographical difference was observed for several traits, possibly due to the inclusion of modern Khoesan and early Holocene individuals (presumably LSA) in the southern African sample (Irish, 2013). Temporal differences were also observed, whereby trait variation between the ancient and recent individuals from Irish's (2013) study was identified. If only the recent Khoesan and Bantu-speaking peoples were considered, they were more or less identical, suggesting gene flow between their population groups over time in sub-Saharan Africa.

As documented by the above mentioned studies, dental anthropology research was mainly concerned with modern Khoesan and Bantu-speaking populations of sub-Saharan Africa, while the prehistoric Khoesan and Bantu-speaking peoples remained understudied. Warren (2013) was therefore the first to investigate the population variation of the IA peoples in southern Africa using dental nonmetrics and metrics. Biological continuity was observed from the EIA to LIA (Warren *et al*., 2015) and when compared with a historic and modern Bantu-speaker sample, further continuity was identified into present day (Warren *et al*., 2014). The few dental differences that were noted showed the IA individuals were more biologically similar to the historic sample than the modern Bantu-speaking peoples. This suggested increased gene flow into the Bantu-speaking population with time, particularly after AD 1800 (Warren *et al*., 2014).

Similarly, Black (2014) was the first to investigate the evolutionary development of the prehistoric Khoesan using their dental metrics and nonmetrics. A large radiocarbon dated LSA dental sample from the Cape coastal regions and adjacent coastal forelands was assessed, similar to Stynder's (2006) cranial study. The LSA samples were subdivided into geographical regions within South Africa and temporal groups throughout the Holocene period. To extend the analysis deeper in time and geographical space, Black also included an inland South African sample of more recent Khoesan (±500 BP) to compare with the other Cape coastal regions, as well as a prehistoric mid-late Pleistocene sample consisting of the Mumbwa Cave, Border Cave and Klasies River Mouth Cave remains. In general, little regional variation was seen among the Khoesan groups within South Africa, however minor dental variation was identified (Black, 2014). The inland sample showed statistically significant differences in dental size and shape compared with all the other regions. It was also most biologically distant from the south and south-west coast regions. Black's inland sample was dated to more

recent times (±500 BP), consisting of archaeological sites known to have been in contact with IA peoples, according to Morris (1992a). These biological differences were therefore suggestive of genetic admixture, even though the sample itself was identified as Khoesan due to its overall dental similarity to the other Khoesan samples. A similar study by Irish *et al.* (2014) compared these suspected inland admixed Khoesan samples from Riet River and Kakamas to the same coastal regions of South Africa. Significant differences were observed between the Kakamas and the early to mid Holocene Khoesan samples from the west and south coast, further suggesting genetic admixture with the Bantu-speaking peoples for the inland regions.

Black's (2014) dental results also revealed biological continuity of Khoesan characteristics throughout the Holocene, as well as deeper in time. Much of the Holocene Khoesan remains showed dental similarity with the mid-late Pleistocene sample. Although overall, biological continuity of the Khoesan peoples was observed through time, minor dental variation was identified. A number of dental traits showed significant changes pre- and post-3,000 BP (Black, 2014), similar to what was observed for the crania and postcrania at 4,000 BP (Pfeiffer and Sealy, 2006; Stynder *et al*., 2007b). Although a millennium later than the rest of the skeleton, these changes in tooth morphology observed at 3,000 BP also recovered to previously observed levels at 2,000 BP (Black, 2014). This difference in timing of the dental changes observed, compared with the rest of the skeleton, was unclear because dentition is reasonably shielded from environmental effects and research has not conclusively demonstrated environmental plasticity of nonmetric traits. Whether or not the biological change observed for the crania and dentition are linked, Black (2014) agreed with Stynder (2009) that it was unlikely due to gene flow from non-Khoesan peoples.

Similar patterns were presented by Ginter (2008) for the dental size of LSA individuals in the Eastern Cape, but caution is given to the results. Certain male and female cervical dental measurements suggested a decrease in size between 3,500 BP and 2,000 BP, after which it recovered to the dental size observed pre-3,500 BP. Males and females did not however show statistical significant differences for the same tooth measure, their sample sizes in general were very small, and no corresponding shape changes were observed (Ginter, 2008). Overall, no significant change in the size and shape of the dentition was identified over time. This corresponded with Black's (2014) results, whereby no change in dental morphology was observed when herding was introduced at 2,000 BP. Although the dental morphology from 2,000 to 1,000 BP was variable, it was less so than the dentitions from 3,000 to 2,000 BP. The

dental morphology post-2,000 BP was therefore similar to that observed pre-4,000 BP (Black, 2014).

Lastly, Black (2014) also compared her prehistoric Khoesan data to the Afridonty complex, which included the dental traits identified by Irish (1997, 2013) as characteristic of the sub-Saharan African peoples, but they did not appear to fit entirely with one another. Twelve new Khoesan dental traits were therefore suggested by Black (2014) based on her prehistoric data. This included high frequencies of upper second incisor interruption grooves, "Bushman canines" (mesial canine ridge), lower second premolar Y-grooves, number of roots on the lower second molar, three-rooted upper second molars, upper first molar metaconules and the presence of midline diastemae. Low frequencies of the upper first incisor double shovelling, upper canine distal accessory ridges, lower first molar protostylids, lower first molar distal trigonid crests and lower second molar cusp number with an ASU score of 4, were also identified. Additionally, Black (2014) also compared the modern Khoesan sample included in the Afridonty complex to her prehistoric Khoesan sample and 53% of the dental traits differed. This was most likely due to temporal differences because the modern Khoesan sample (Haeussler *et al.*, 1989; Irish, 1997) was most similar to Black's (2014) inland regional sample, dated to a similar time period. Modern Khoesan are therefore not representative of their past populations and although Khoesan dentition have important links with the Afridonty complex compared with other worldwide complexes, significant differences are observed between and within their archaeological and modern populations.

## 2.3. KHOESAN AND BANTU-SPEAKER BIOLOGICAL INTERACTIONS

To date, few cranial and dental studies have investigated the biological relationships between the Khoesan and Bantu-speaking populations in southern Africa. Previous research was mainly interested in the biological identity of specific population groups and samples of Khoesan or Bantu-speaking individuals were only included for comparison purposes. These comparative samples were usually from a particular geographic region or a specific time period, which did not take into account the population diversity over time and space. In this section, the cranial and dental studies that have investigated Khoesan and Bantu-speaker interactions are reviewed. Cranial studies include, but are not limited to, Rightmire (1970b), L'Abbé *et al*. (2006), Morris and Ribot (2006), Stynder *et al*. (2007a), Franklin *et al*. (2007), Ginter (2008), Ribot *et al*. (2010) and Botha *et al*. (2017).

Rightmire (1970b) was one of the first to use a non-typological approach when addressing Khoesan identity, using multivariate statistics to assess the biological differences between Khoesan and Bantu-speaking peoples. The study included a historic Khoesan sample that was selected based on reliably documented known-in-life individuals, after assessing a number of specimens found in museums or collections housed in South Africa (Rightmire 1970a). When comparing the Khoesan sample (n=55) to a modern Bantu-speaking sample, consisting of Zulu (n=62), Xhosa (n=24) and Sotho (n=65) individuals, a significant difference was found between the two (Rightmire, 1970b). This was mainly due to the relative cranial size and shape differences observed between them, which lead the way for future research on classifying individuals of unknown origin in South African populations.

Two modern Bantu-speaking groups and two South African archaeological samples were compared with 20$^{th}$ century Venda speakers (n=96) using craniometrics (L'Abbé *et al*., 2006). The modern Bantu-speakers included eastern Africans (Hutu, Rwanda; Teita, Kenya; Haya, Tanzania; n=154) and southern Africans (Sotho-Tswana and Nguni; n=61), while the archaeological samples included historic Riet River Khoesan (n=38) and a few IA individuals from the K2 archaeological site (n=3). The Venda speakers were least biologically related to the historic Khoesan and most biologically related to both the eastern and southern Bantu-speaking groups. This suggested cranial homogeneity among Bantu-speaking sub-Saharan Africans, and a different biological and historical origin of the Khoesan from other Bantu-speaking groups (L'Abbé *et al*., 2006). The historic Riet River Khoesan in particular, are believed to have strong Khoesan characteristics, with very little gene flow from the Bantu-speaking peoples (Morris, 1992a). This particular sample of Khoesan was often included in subsequent studies for comparison purposes to illustrate "Khoesan-like" morphology.

Morris and Ribot (2006) investigated the Holocene populations of Malawi in south-central Africa using craniometrics to assess their biological identity. The prehistoric Malawians selected were from seven archaeological sites dated to the Middle Holocene (5,000 to 2,000 BP, n=15) and the Late Holocene (2,000 to 500 BP, n=9). They were subsequently compared with modern sub-Saharan Bantu-speaking peoples from four geographical regions (west-central Africa, n=61; central Africa, n=135, eastern Africa, n=97 and southern Africa, n=61), as well as the historic Riet River Khoesan (n=41, mentioned previously). The results suggested biological continuity for the prehistoric Malawians from the Middle to Late Holocene and showed biological similarities with both the historic Khoesan and modern Bantu-speaking groups, especially those located in west-central Africa. Their results suggest

that the prehistoric Malawians were not exclusively affiliated with Khoesan ancestry, but rather shared a common biological heritage with Bantu-speaking peoples originating in west-central Africa (Morris and Ribot, 2006).

Stynder *et al*. (2007a) investigated five pre-5,000 BP LSA individuals and a post-5,000 BP LSA sample (n=100) from South Africa's Cape coast and coastal forelands. They were subsequently compared with a modern Bantu-speaking group (n=50), to assess their biological affinities. Previous research had suggested dissimilarity of the early LSA crania to more recent Khoesan crania, as well as their possible cranial similarity to Bantu-speaking peoples. Although the pre-5,000 BP LSA crania were relatively large, they fell well within the range of variation of the post-5,000 BP sample in terms of both cranial size and shape. Three of the five pre-5,000 BP LSA individuals in particular, fell outside or on the edge of the range of variation of the Bantu-speaking peoples, further confirming their Khoesan affinities (Stynder *et al*., 2007a). The post-5,000 BP LSA crania were generally smaller than the modern Bantu-speakers, indicating dissimilarity.

To expand on the traditional cranial morphometric research done previously on southern African population variation, Franklin *et al.* (2007) assessed a large modern Bantu-speaker sample of crania (n=298, consisting of a number of Bantu-speaking groups) with a small historic Khoesan sample (n=25) using geometric morphometrics. The Khoesan sample only included documented known-in-life individuals or archaeological remains with adequate cultural evidence and/or radiocarbon dating to affirm their ethnic identity. The Khoesan and Bantu-speaker crania were morphologically distinct and clearly distinguishable from one another. Similar to previous research done by Rightmire (1970b) and Howells (1973), the Khoesan crania were also shown to be considerably smaller. The modern Xhosa speaking group was the most biologically similar to the Khoesan, followed by the southern Sotho, Swazi and Zulu speaking groups of South Africa. In contrast, the northern Bantu-speaking populations of southern Africa from Malawi and Kalanga were the least biologically related to the Khoesan group. This suggested a gradient of Khoesan admixture with Bantu-speaking populations that decreased from the south to the north of southern Africa (Franklin *et al.,* 2007). Historical evidence of the Xhosa speakers in particular, suggest assimilation into the Khoesan population during their early southward migration (Peires, 1982). Genetics also indicated as much as 60% Khoesan admixture may be present in the Xhosa individuals (Jenkins et al., 1970). This may explain why this particular Bantu-speaking group was the most biologically similar to the Khoesan sample.

LSA individuals in today's Eastern Cape Province of South Africa were investigated to determine if any significant changes in skeletal morphology were indicative of the appearance of pastoralism (Ginter, 2008). This included metric variables of the cranium, postcranium and dentition, as well as cranial discrete traits. Pre- and post-2,000 BP LSA samples were compared with previously investigated Khoesan groups (Morris, 1992a), as well as previously investigated modern Bantu-speakers from different geographical regions in Africa (west-central, central, eastern and southern; Morris and Ribot, 2006). Overall, minor size changes of the LSA skeleton were noted through time but population continuity was observed pre- and post-2,000 BP. The LSA crania were biologically similar to the South African Khoesan and significant differences were observed in their cranial size compared with the Bantu-speaking peoples (Ginter, 2008). The differences identified between the LSA samples and the comparative Bantu-speaker samples were less for the post-2,000 BP group than the pre-2,000 BP group, suggesting increased biological similarity between them with time.

Ribot *et al.* (2010) investigated the craniometrics of archaeological and modern remains from KZN. The individuals from the last 6,000 years were assessed, to determine possible population changes within the region at the time of the first IA settlement, AD 400. The archaeological samples were small and included LSA (earlier than AD 400, n=7), EIA (AD 400 to 1000, n=12) and LIA (AD 1000 to colonial times, n=7) individuals. The modern samples included two Bantu-speaking groups (Nguni (n=101) and Sotho-Tswana (n=61)), as well as a historic Khoesan sample (n=131). The majority of the Khoesan individuals were not well documented in terms of their geographical origin, except the 31 previously investigated Riet River individuals. The results showed a greater similarity between the pre-AD 400 LSA group and the groups with Khoesan ancestry. The EIA and LIA groups were more biologically similar to the modern Bantu-speaking groups. Small sample sizes prohibited statistical testing of differences between the time periods. The preliminary results, however, suggested the change was progressive, as the indigenous Khoesan were partly assimilated and replaced by the migrating Bantu-speaking peoples in the KZN region. The cranial morphology reflected possible gene flow between the Khoesan and Bantu-speaking peoples between AD 400 and AD 1000, becoming more variable as the Bantu-speaking population increased during the 2$^{nd}$ millennium AD. This suggested increased genetic diversity as Khoesan morphological characteristics became less identifiable during the latter period (Ribot *et al*., 2010).

Lastly, a number of historic Khoesan specimens in European collections recently came into question and were investigated using craniometrics to assess their biological affinities (Botha

*et al*., 2017). They were also compared with the historic Riet River Khoesan (n=31) and other modern and historic Bantu-speaking groups from southern (n=61), central (n=66) and eastern (n=77) Africa. The historic Khoesan sample, although not homogenous, was the most biologically similar to the Riet River Khoesan. It also had some biological resemblance to the eastern African group, the central African group and the southern African group, in that order. This reaffirmed their biological affinity with Khoesan groups, but also revealed their morphological variability.

As documented by the above mentioned studies, the cranial size and shape of the Khoesan and Bantu-speaking populations of southern Africa are better understood. They are morphologically distinct from one another and the Khoesan in particular, have a much smaller cranial size (Rightmire, 1970b; Howells, 1973; Franklin *et al*., 2007). This has helped validate the biological affinity of individuals (Botha *et al*., 2017) and population groups (L'Abbe *et al*., 2006) in southern Africa. Gene flow between the Khoesan and Bantu-speakers was also suggested through time (Ginter, 2008; Franklin *et al.,* 2007; Ribot *et al*., 2010), but more research is needed to establish their relationships temporally and geographically. To enhance these earlier studies, large prehistoric and modern samples of Khoesan and Bantu-speakers are included in this study to capture the genetic diversity in the population groups. Cranial nonmetric traits are also investigated in more detail in the current study because a problem with previous cranial research on Khoesan populations, particularly for the prehistoric samples, was small sample sizes due to incomplete specimens. Cranial nonmetric traits are more widely available and should increase the sample sizes, to better assess the biological relationships between the Khoesan and Bantu-speakers. Dentition is also useful in these particular circumstances, as teeth are often well preserved and in relative abundance compared with skeletal remains. A few dental studies have also investigated the biological relationships between the Khoesan and Bantu-speaking peoples and include, but are not limited to, work by Haeussler *et al.* (1989), Ginter (2008), Irish (1997, 2013) and Warren (2013).

Metric and nonmetric dental comparisons were made by Haeussler *et al.* (1989) to compare a modern Khoesan sample (n=287) from Botswana with a modern central Sotho speaking group (n=443) from northern South Africa. Similar to the cranial studies, significant dental differences were noted between the Khoesan and Bantu-speaking peoples. The Khoesan had very small teeth (microdont), whereas the Bantu-speakers had slightly larger teeth (mesodont) (Haeussler *et al*., 1989). The frequency of specific dental nonmetric traits also differed

between the population groups. A similar study done by Ginter (2008) also described larger Bantu-speaker teeth when comparing a prehistoric LSA sample from the Eastern Cape with modern South African Bantu-speaking peoples.

A modern and prehistoric Khoesan sample was included in the Sub-Saharan African Dental complex, as described previously. This complex is a suite of dental morphological traits believed to be unique to sub-Saharan Africans and was described as distinct from other global populations (Irish, 1997; 2013). Even though differences were observed between the modern Khoesan and Bantu-speaking peoples, Haeussler *et al.*'s (1989) samples were included in the data set used by Irish. Their regional similarity in the selected traits compared with the other sub-Saharan populations appeared to outweigh any of their differences. When, however, the sub-Saharan African samples were later stratified by time (after the inclusion of a prehistoric Khoesan sample), the more recent populations were biologically very much the same, whereas increased diversity was observed otherwise (Irish, 2013). Similarly, when stratifying the sub-Saharan African samples by geography (western, central, eastern and southern), the southern sample was the most biologically diverse. Although precise information about sample size, provenance and radiocarbon dates of the individuals included were not given, the increased dental diversity, both geographically and temporally, was thought to be due to the inclusion of many prehistoric and modern Khoesan groups (Irish, 2013).

Finally, although not the main aim of her study, Warren (2013) did compare a small modern Bantu-speaking group (n=39) with an IA sample (n=142) and a small LSA sample (n=35). The study used dental metric and nonmetric data, as well as craniomandibular measures. The results showed dissimilarity between the LSA compared with the IA and modern Bantu-speaking peoples. The LSA individuals were also found to be as biologically similar to the modern Bantu-speakers as they were to the IA individuals. This suggested the amount of Khoesan admixture present in modern Bantu-speaking groups (Barbieri *et al*., 2014) may be similar to what existed between the IA and LSA peoples (Warren, 2013). Recently, Khoesan admixture was identified in four LIA individuals from KZN (Steyn *et al.*, 2019), which possibly supports this.

The development of the biological relationships between the Khoesan and Bantu-speaking peoples are still not fully understood. Gene flow over time between the Khoesan and Bantu-speakers is evident and reflected in cranial size and shape, as well as dental variation. These genetic relationships however, have not been elaborated upon in detail until this study. Previous craniometric studies mainly compared different modern Bantu-speaking groups,

from various geographical locations, to small historic Khoesan and LSA samples. In this study, large samples of prehistoric and modern Khoesan are compared with large samples of prehistoric and modern Bantu-speakers. In addition to this, a new modern Khoesan sample, which has not been previously compared with other Khoesan or Bantu-speakers, is included for comparison purposes. Besides Warren (2013), little is known about the prehistoric relationships between the LSA and IA peoples in southern Africa; hence these particular groups are investigated further in this study, stratified by time and geography. Finally, considering that cranial and dental morphology are seen as a proxy for the underlying patterns of genetic affinity, multivariate statistics like biological distance should give insight into the dynamic nature of Khoesan and Bantu-speaker relationships.

## 2.4. BIOLOGICAL DISTANCE ANALYSIS

Biological distance or biodistance analysis uses morphological information to assess the biological relatedness or divergence among or within populations using multivariate statistical methods (Hefner *et al.*, 2016). The patterns of morphological variability in the cranium and dentition in particular, are often seen as a proxy for genetic relatedness and can be used to reconstruct population histories (Pilloud and Hefner, 2016). Although a number of studies have suggested that craniometric data reflect patterns of genetic neutrality, some argue that they are too plastic to be effectively used for population history research (Dudzik and Kolatorowicz, 2016). This is because under extreme climatic conditions, evidence of environmental selection responses in the dimensions of the cranium were previously identified (Beals *et al.*, 1984; Hubbe *et al*., 2009). Specific areas of the skull were also shown to be more susceptible to environmental effects compared with other areas (Hollo *et al.*, 2010). Nonmetric traits of the skull were therefore employed in this study, also marking the first time they contribute to the study of Khoesan and Bantu-speaker relationships.

Cranial nonmetrics have been established as viable proxies for genetic data (Hefner *et al.*, 2016; Pink *et al.*, 2016). They may even be superior to craniometric studies because they can be obtained from fragmentary remains, are easy to collect and are relatively free from age and sex differences (Berry and Berry, 1967; Buikstra, 1974). They might also be more stable over time because they are less affected by natural selection and genetic drift, and thus better indicators of population affinity (Rightmire, 1972). Hauser and De Stefano (1989) expanded on the cranial nonmetric trait list used by Berry and Berry (1967) to define, standardize and explore their heritability and function. Ossenberg (2013) later increased its popularity, making

them ideal measures to use in this study to assess the biological interactions between the Khoesan and Bantu-speaking populations.

Similarly, teeth are believed to be an even better proxy for the genotype compared with the skull, because they form prior to eruption and appear more shielded from environmental effects (Cardoso, 2007). Biological distance analysis of dental nonmetrics have also shown similar relationships between population groups as the DNA analysis (Hubbard *et al*., 2015). The Arizona State Dental Anthropology System encouraged future dental anthropology research by standardising the scoring of dental nonmetric traits (Turner *et al*., 1991; Scott and Turner, 1997; Scott and Irish, 2017). In addition to this, the consideration of dentometric variation expanded the sample sizes far beyond what are typically available for traditional craniometric analyses (that are dependent upon complete specimens). The definitions for the maximum dimensions of the tooth crown (Moorrees and Reed, 1954), and the more recent alternative measurements on the cervical aspect of the tooth and the maximum diagonals of the molar crown (Hillson *et al*., 2005), have made dental metrics more popular. Using a combination of the different types of data, more specifically, the nonmetric traits of the skull, dental morphology and dental metrics, the population history of the southern African peoples was investigated using biodistance.

Different biodistance methods are used for nonmetric and metric data and are referred to as model-free or model-bound. Using population history to describe patterns of morphological variability is model-free, whereas utilising a population's genetics and evolutionary framework is model-bound (Relethford and Harpending, 1994). Smith's Mean Measure of Divergence statistic or a modified version of the Mahalanobis $D^2$ distance statistic can be used to analyse nonmetric cranial or dental data. The Euclidean distance, original Mahalanobis $D^2$ distance statistic or R-matrix theory can be used to analyse dental metric data. The results are represented in a distance matrix, where the greater the distance value between two groups, the less biologically similar they are to one another. The history and development of each of these biodistance methods is reviewed in the following sections and summarised in Table 2.1.

Table 2.1: A summary of the different biological distance methods.

| Method | Data Type | Description | Considerations |
|---|---|---|---|
| Smith's Mean Measure of Divergence | Nonmetric Model-free* | A formula that converts frequencies into a numerical value of similarity, using Freeman and Tukey (1950) or Anscombe (1948) transformation to account for very high and very low trait frequencies, as well as small sample size. | Ensure no correlation between traits.<br>Only include traits with sufficient variability (significance).<br>Negative MMD values can occur due to very small sample sizes. |
| Pseudo-Mahalanobis | Nonmetric Model-free* | A modified version of the Mahalanobis $D^2$ statistic that uses dichotomous data by individual and adjusts for correlations between traits. | Formula adjustments are not made for small sample sizes. |
| Euclidean | Metric Model-free* | A simple distance formula, similar to the Mahalanobis $D^2$ statistic, but does not account for the intercorrelation between traits. | Ensure no correlation between traits. |
| Mahalanobis $D^2$ | Metric Model-free* | A formula that adjusts for the correlation between traits and small sample size. | No missing data allowed, but this can be determined using data imputation methods.<br>Negative $D^2$ values can occur due to very small sample sizes. |
| R-matrix theory | Metric Model-bound* | A genetic distance formula that makes assumptions about a given population and corrects for small sample sizes. | No missing data allowed, but this can be determined using data imputation methods.<br>Dependent on population size and heritability estimates. |

*Model-free uses the populational history to describe patterns of morphological variability, whereas model-bound uses the populational genetics and evolutionary framework.

### 2.4.1. Nonmetric data

Biodistances can be calculated for nonmetric data using Smith's Mean Measure of Divergence (MMD) or a modified version of the Mahalanobis $D^2$ distance statistic (Grewal, 1962; Sjøvold, 1977; Williams-Blangero and Blangero, 1989; Konigsberg, 1990; Harris and Sjøvold, 2004). Both are considered a model-free distance because their origin is based on statistical concerns and not any model of population genetics. The MMD formula converts the nonmetric trait frequencies to a numerical value to reflect similarity, and has been used extensively to explore biological relationships within and among human populations using both cranial and dental data (Berry and Berry, 1967, 1972; Irish, 1997, Hanihara *et al*., 2003; Sutter and Mertz, 2004; Ullinger *et al.*, 2005; Irish, 2006, 2010). It was first used by Grewal (1962) on mice, but later applied to human biological affinity by Berry and Berry (1967). Harris and Sjøvold (2004) made adjustments to the original formula because an overestimate of the true variance between samples was identified by Green and colleagues (Green and Suchey, 1976; Green *et al*., 1979). The new formula incorporated the Freeman and Tukey (1950) transformation to account for very high (>0.95) and very low (<0.10) trait frequencies. Other researchers still preferred to use the Anscombe (1948) transformation due to its mathematical simplicity (Irish, 2010), but the results were essentially identical when using either of these two formulas (Harris and Sjøvold, 2004). Although significant improvements were made to Smith's MMD formula, it still did not account for the correlation between traits and negative MMD values could still occur. A negative MMD value was due to the sample size of a trait being too small or a given trait not differentiating between the samples (Harris and Sjøvold, 2004; Irish, 2010; Soltysiak, 2011). It was therefore suggested that as many traits as possible be used with the MMD and to account for intertrait correlations, only those traits with sufficient variability be included (Harris and Sjøvold, 2004; Irish, 2010; Santos, 2016).

A modified version of the Mahalanobis $D^2$ distance statistic, known as pseudo-Mahalanobis distance, was originally used on uncorrelated metric variables. This was later extended to nonmetric traits by Williams-Blangero and Blangero (1989) and Konigsberg (1990). Unlike the MMD, which required positive counts of the observations from the total number of individuals, the Mahalanobis $D^2$ used dichotomous data per individual (Irish, 2010). To ensure there were no correlated nonmetric traits included for each individual, tetrachoric correlations were calculated within each group and pooled using the sample size for each pair of traits, to find the weighted average correlation (Konigsberg, 1990). The

formula therefore adjusted for phenotypic correlations between traits (which the MMD did not do), but unlike the generalized $D^2$ statistic for metric variables or the MMD statistic, there was no bias correction for small sample sizes (Konigsberg *et al*., 1993; Irish, 2010).

To summarise, a good correlation between the MMD and modified Mahalanobis $D^2$ methods was found after improvements were made to Smith's MMD formula (Irish, 2010; Nikita *et al*., 2012). Although the Mahalanobis $D^2$ is the preferred method for assessing biological distance today (Pink *et al.*, 2016), its sensitivity to small sample sizes is problematic when dealing with archaeological samples. The MMD statistic was therefore used in this study because of its user friendliness and preferred application to samples that had incomplete data sets, often resulting in small sample sizes (Harris and Sjøvold, 2004; Irish, 2010; Santos, 2016). In addition to this, the tetrachoric correlation coefficient used with the Mahalanobis $D^2$ was also applied to the MMD data. This was because it was more appropriate for traits with an underlying continuous distribution (Pink *et al.*, 2016), like the nonmetric traits of the skull investigated in this study. This assisted with data editing for the biodistance analysis, especially when differentiating the most variable nonmetric traits to include in the MMD statistic, thereby reducing the occurrence of negative MMD values.

### 2.4.2. Metric data

Biodistances can be calculated on metric data by using the Euclidean distance, Mahalanobis $D^2$ distance statistic or R-matrix theory (Mahalanobis, 1936; Rao, 1952; Rightmire, 1970b; Sneath and Sokal, 1973; Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Van Vark and Schaafsma, 1992; Relethford, *et al*., 1997). The Euclidean distance statistic is a simple multivariate distance measure, similar to the $D^2$ statistic, but does not take into account the intercorrelation of traits. For this reason, the generalized Mahalanobis $D^2$ distance statistic is commonly used because of the refinements made to the formula that account for the correlation of traits and small sample size (Rao, 1952; Rightmire, 1970b). The Mahalanobis $D^2$ statistic does however have its drawbacks, particularly in bioarchaeological studies. It requires no missing data, which is difficult to achieve when dealing with fragmentary archaeological remains and it can be biased by small sample size. This can be rectified using data imputation methods for the former, if the number of missing values for a given trait is relatively small (Kenyhercz and Passalacqua, 2016), and a formula correction for the latter, following Rightmire (1970b). Like the nonmetric multivariate methods discussed in

the previous section, the Mahalanobis distance is also considered a model-free distance statistic.

A model-bound approach, R-matrix theory, either assumes or estimates specific population sizes and the heritability of traits to compare patterns in the data to assumptions given about a population (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990). This not only provides information about a population's distance from other populations, but also reveals a population's heterogeneity, allowing for a more direct measure of gene flow between populations. The development of R-matrix theory can be found in Harpending and Jenkins (1973) and Workman *et al.* (1973), and the Harpending-Ward model (1982) was the first to compute the expected relationship between the population's heterozygosity and its genetic distance from a regional mean. This population genetic approach was later modified by Williams-Blangero and Blangero (1989) and Relethford and Blangero (1990), to suit metric methods. The R-matrix therefore consisted of scaled variances and covariances around the regional mean, estimating the distance of each population from the regional centroid (Konigsberg, 2006; Irish, 2010). The regional centroid is the mean of all the samples and can be thought of as a hypothetical group if the samples were not separated from each other (Irish, 2010). The elements of the R-matrix can also be used to estimate other useful population genetic measures like the genetic $D^2$ distance matrix and Wright's $F_{ST}$ (Harpending and Jenkins, 1973; Workman *et al.*, 1973).

R-matrix theory and its relative components has been used to explore population structure and the genetic history of a population or populations using both cranial and dental metric data (Relethford, 2002; Schillaci and Stojanowski, 2005; Ginter, 2008; Pawn, 2012; Byrd, 2014; Botha *et al.*, 2017). A bias correction for small sample sizes is also available (Relethford, 1991; Relethford, *et al*., 1997). Similar to the Mahalanobis $D^2$ statistic, missing values should be estimated to maximise the sample size without compromising the integrity of the data (Kenyhercz and Passalacqua, 2016).

To summarise, although the generalized Mahalanobis $D^2$ distance statistic has been the preferred method used with metric data (Relethford, 2016), R-matrix theory may be more applicable to this study. It provides a more accurate reflection of the underlying genetic distances that allow for the assessment of the effects of genetic drift. Compared with the other biodistance methods that only assess the morphological patterns of variability between populations, the R-matrix provides further insight into population genetics beneficial for understanding Khoesan and Bantu-speaker relationships.

# CHAPTER 3: MATERIALS AND METHODS

## 3.1. SAMPLES

This study was based upon 845 specimens from archaeological and modern contexts that are curated in eight South African institutions (Appendix A). Access to the collections was granted based on successful applications submitted. LSA individuals are housed at the University of the Witwatersrand, the McGregor Museum, the Florisbad Quaternary Research Station, the Iziko Museum of South Africa and the University of Cape Town. IA individuals are housed at the University of Pretoria, the University of the Witwatersrand, the Ditsong Museum, the KwaZulu-Natal Museum and the University of Cape Town. The modern Bantu-speakers and modern Khoesan dental casts are curated in the School of Anatomical Sciences at the University of the Witwatersrand. The modern Khoesan individuals identified by Morris (1986) are housed at the McGregor Museum, the Florisbad Quaternary Research Station and the University of Cape Town.

### 3.1.1. Geographical regions

The archaeological samples include human remains from sites across southern Africa, that are associated with either LSA (n=303) or IA (n=105) material culture (Appendix A, Table A1). Archaeological samples were only included if they were assigned a locality and were dated by radiocarbon or archaeological association. The localities were allocated to seven regions based on Heydorn and Flemming's (1985) division of the South African coastline, the environmental biome borders defined by Morris (1992b) and consideration of previous researcher's subdivisions (Stynder, 2006; Ginter, 2008; Warren, 2013; Black, 2014) (Figure 3.1). Each region consisted of either LSA or IA individuals, with the exception of the Inland central and SW coast groups that included one IA individual with LSA individuals. Two LSA individuals from Ladybrand and Lesotho were excluded from the geographical analyses because they were outliers and did not fall within the selected regions. They were however used for the temporal comparisons. It is important to note that the samples within each geographical region range in time from 12,000 BP to approx. AD 1900. The Inland central group is the exception because the majority of the specimens are dated to ±500 BP. For the biodistance analyses, some geographical regions were not included due to small sample sizes.


Figure 3.1: The geographical regions of the LSA (dots) and IA (stripes) groups (W – West coast, SW – South West coast, S – South coast, SE – South East coast).

The following regions were designated:

1. **LSA Inland central** (n=75) is situated north of the Great Escarpment extending from the Richtersveld to Koffiefontein. Specimens are dated from approx. 1,000 to 0 BP but the majority of the individuals are dated to 500 BP.
2. **LSA West coast** (n=17) includes the western coastal strip of South Africa from Port Nolloth to Stompneusbaai. Specimens are dated from approx. 4,000 to 500 BP, with one individual dated to an earlier period (UCT378: 10,860 BP). The majority of the individuals are however dated to between approx. 3,000 BP and 2,000 BP.
3. **LSA SW coast** (n=84) includes all the samples from Stompneusbaai to Mossel Bay. Specimens are dated from approx. 6,500 to 100 BP with the majority dated between approx. 3,000 BP and 1,000 BP.

4. **LSA South coast** (n=109) is situated in the area from Mossel Bay to Cape St. Francis. This group covers the greatest time range, with individuals from approx. 12,000 to 150 BP.
5. **LSA SE coast** (n=18) extends along the eastern coast of South Africa from Cape St. Francis to Widenham, south of Durban. Specimens are dated from approx. 4,800 to 600 BP however the majority of individuals are dated within the last 2,000 years.
6. **IA North East** (n=80) includes the western inland area of the Great Escarpment, extending from Skutwater to Vrede, as well as the area east of the Great Escarpment from the Durban and extending north to Phalaborwa. Individuals represent the last 2,000 years, dating from the EIA to the LIA.
7. **IA South Zambia** (n=23) consists of IA samples obtained from southern Zambia.

### 3.1.2. Temporal groups

To compare the Khoesan and Bantu-speaking peoples over time, the archaeological samples were divided into six temporal groups. These divisions were based on previous archaeological and bioanthropological research suggesting periods of change in the environment, subsistence or population size (Stynder, 2006; Stynder *et al*., 2007b). At 8,000 BP the Oakhurst complex was replaced by the Wilton complex. At 4,000 BP, the archaeological record showed an increased population size due to favourable environmental conditions (Stynder, 2006). This resulted in a decrease in stature and cranial size, thought to be due to limited mobility (Sealy and Pfeiffer, 2000; Sealy, 2006). A subsistence strategy shift from foraging to more predictable, low risk foods like fish was also observed at this time (Barham and Mitchell, 2008). Stynder (2006) noted that the decrease in cranial size began to recover at approx. 3,000 BP to previous levels. Black (2014) noted a similar change in the dentition from 3,000 BP, in what appears to be a delayed response to the increase in population size observed in the previous time period. A new subsistence strategy involving herding of domesticates appeared in southern Africa at approx. 2,000 BP (Ginter, 2008). IA technology appeared shortly thereafter, introducing farming to the region by Bantu-speakers from eastern Africa (Warren, 2013). The transition between the EIA and LIA at approx. 1,000 BP is represented by new ceramic wares (Warren, 2013; Warren *et al*., 2015). These ceramics are described as indicative of a new wave of Bantu-speaking peoples from eastern Africa. To capture these transitionary periods that may or may not have resulted in biological change, the following temporal groups were designated:

1. **LSA: 12,000 BP – 8,000 BP** (n=19)
2. **LSA: 8,000 BP – 4,000 BP** (n=32)
3. **LSA: 4,000 BP – 3,000 BP** (n=34)
4. **LSA: 3,000 BP – 2,000 BP** (n=67)
5. **LSA: 2,000 BP – 1,000 BP** (n=42)
6. **EIA: 2,000 BP – 1,000 BP** (n=11)
7. **LSA: 1,000 BP – 0 BP** (n=103)
8. **LIA: 1,000 BP – 0 BP** (n=48)

For statistical purposes, some of the temporal groups were combined for the biodistance analyses or removed due to small sample sizes. Fifty-two individuals that were included in the geographical comparisons were excluded in the temporal analysis because their archaeological associations were too broad or non-specific. As suggested by Relethford (2016), the contemporaneous LSA and IA groups were investigated separately for a more accurate biodistance analysis. To strengthen the biodistance analysis, the EIA and LIA groups were also subsequently combined because Warren and colleagues (Warren, 2013; Warren *et al*., 2015) used similar IA samples and described cranial and dental homogeneity, with limited gene flow throughout the IA period.

### 3.1.3. Modern comparative samples

The modern samples were composed of dental casts and skeletal remains of historic to contemporary individuals. Crania of Khoesan individuals from the late 19$^{th}$ and early 20$^{th}$ century (Morris, 1986) were included in this group (n=24, Appendix A, Table A2). The dental casts (n=237) were made by Van Reenen in the 1980's to document remnant Khoesan groups and consist of both the maxillary and mandibular dentition (Appendix A, Table A3). They are part of the Dental Cast Collection of the School of Anatomical Sciences, University of the Witwatersrand. The dental casts were majority of Barakwena (n=162), with smaller groups of Vassekela (n=39), !Kung (n=19) and Lake Chrissie (n=17) individuals. The Vassekela and Barakwena casts were made of Khoesan originally from Angola but mainly found in Omega, a settlement in the Caprivi strip of Namibia (Reid *et al*., 1991; Navsa, 1992). They are Khoesan and Bantu-speaking hybrids, often referred to as black bushmen or river bushmen, and several of these casts had cultural dental modifications in a style associated with Bantu-speaking groups in the region (De Almeida, 1965). The Lake Chrissie casts were from Khoesan living in the Lake Chrissie region in the Eastern Transvaal, near Ermelo (today's

Mpumalanga Province). These particular Khoesan have genetic ancestry from both the Khoesan and Bantu-speaking peoples (Schlebusch *et al.*, 2016, 2017).

The modern Bantu-speaker sample (n=176, Appendix A, Table A4) was selected from the Raymond A Dart Collection of Human Skeletons (Dayal *et al.*, 2009) and included Zulu and Xhosa speakers because they have a high degree of Khoesan admixture (Jenkins *et al*., 1970; Hitzeroth, 1986; Mitchell, 2010; Barbieri *et al*., 2014), as well as Ndebele and Tsonga speakers who have a low degree of Khoesan admixture (Hitzeroth, 1986; Esterhuysen *et al*., 2009). Individuals in the Dart Collection were randomly selected males and females aged between 10 and 60 years (Ref: W-CJ-140604-1).

### 3.1.4. Condition of specimens and incomplete data

The crania and dentition of the LSA (n=303) and IA (n=105) individuals were relatively well preserved, with most of their dentition *in situ*. Of the 408 archaeological specimens investigated, 78% (n=318) had crania (complete or incomplete with missing portions of skull or dentition that could not be assessed) available for assessment and only 20% (n=63) had no lower dentition available to score or measure (missing mandibles). Although the archaeological samples often had incomplete dentition, 66% (n=269) of the individuals had measureable teeth and 56% (n=230) had observable dental nonmetric traits. Dental nonmetrics were observed on all the modern Khoesan dental casts, but only 83% (n=197) of the teeth were measurable. The other modern Khoesan individuals had well preserved crania, with only three individuals having no lower dentition present (missing the mandible). Eleven (46%) individuals had measurable teeth and nine (38%) had observable dental nonmetric traits. Most of the modern Bantu-speaker crania were complete and thus all cranial nonmetric traits could be assessed, but some individuals had missing teeth or substantial tooth wear that precluded a full dental assessment. A high proportion of the sample, 92% (n=162), had cranial nonmetric traits present, with 13 missing mandibles that prevented the assessment of the lower dentition. Dental measurements were possible for 91% (n=161) of the modern Bantu-speaker sample and dental nonmetrics for 89% (n=156).

## 3.2. METHODS

### 3.2.1. Data collection

Discrete cranial and mandibular traits were evaluated on all adult skulls for the LSA, IA, modern Bantu-speaker and modern Khoesan groups. If any dental material was available for

these samples (including any subadult remains identified), discrete dental traits were also scored and dental measurements taken for permanent dentition. The other modern Khoesan material consisted of dental casts, so only discrete dental traits and dental measurements were collected for permanent dentition. To reduce error, due to the subjectivity of scoring the nonmetric traits, calibration of the scoring was initially done by two observers for the same specimen. It resulted in 90% accuracy for the cranial nonmetrics and 99% accuracy for the dental nonmetrics. In the subsequent sections, the quantitative methods used to assess the nonmetric cranial and mandibular traits, dental nonmetric traits and dental metrics of the dentition are described.

When possible, age and sex was assessed from all available skeletal material for each archaeological skeleton, using a combination of techniques described by Buikstra and Ubelaker (1994) and White and Folkens (2005). The Dart Collection database provided the age and sex for each individual, and the sex of the Khoesan individuals was taken from Morris (1986). The ages for the archaeological, historic and modern samples were categorised as subadult (<20yrs) or adult (≥20yrs) (Appendix A - Tables A1, A2 and A4). Only adult material was scored for cranial nonmetric traits because sex based differences and age related changes showed non-significant levels of variability related to these attributes in adult remains (Hauser and De Stefano, 1989; Hefner, 2003; Ginter, 2008; Pink, 2016). Subadult, as well as adult remains were included in the dental analysis because permanent dentition can occur from the age of 6 (White and Folkens, 2005). Due to the non-significant levels of variability related to dental nonmetrics and metrics (Garn *et al*., 1966; Brown and Townsend, 1979; Kieser, 1990; Turner *et al*., 1991; Scott and Turner, 1997; Hanihara and Ishida, 2005; Hanihara, 2008; Moreno-Gómez, 2013; Luna, 2015), sex based differences and age related changes were not of concern. It is therefore common practice to pool the cranial and dental data when sex and age are not contributing factors (Irish, 1997; Hefner, 2007; Irish, 2010; Black, 2014).

### 3.2.2. Nonmetric traits of the skull

Discrete cranial and mandibular traits were scored using explanations and illustrations given by De Villiers (1968) and/or Hauser and De Stefano (1989). Population specific nonmetric traits were identified for South African Bantu-speakers by De Villiers (1968) and others were used to differentiate global populations (Hauser and De Stefano, 1989). Each trait (n=48) was scored according to its level of expression as either a categorical value (i.e. 0 – 4) or as

present/absent. Breakpoints were determined for those traits scored as a categorical value by assessing the range of expression of each trait in the samples. Due to the complexity of some of the traits (shape of the orbits, positions of the nasion and the completeness of the metopic suture), additional categories were used to adequately describe the range of their expression to retain as much information as possible, by scoring their variations as separate traits. Some traits were scored only if they were bilaterally expressed (i.e. orbital shape and the supra-asterionic region), based on the assumption that bilateral expression of a trait is under stronger genetic control (Molto, 1983; De Laurier and Spence, 2003). Other traits, such as the supraorbital notch and hypoglossal canal bridging, were scored independently for both sides of the skull to prevent loss of important information due to laterality, as well as prevent exclusion of an individual when dealing with fragmentary remains. Both the left and right scores for each trait were analysed separately due to the understanding that while a trait may be expressed more strongly on one side, the predominant side is not consistent from one population to another (Hauser and De Stefano, 1989). Once scored, all the traits were dichotomised as present or absent according to the breakpoints given, for input into the biodistance statistic. The frequencies of each trait were subsequently determined according to the groups investigated for each study objective. Repeatability of the cranial scores was evaluated on 13 individuals using Cohen's Kappa, where excellent agreement (k=0.85) was found for the intraobserver scoring and good agreement (k=0.63) was found between two different observers. The descriptions of each trait are found below with their degree of expression, as well as the additional categories of the trait (if applicable) and the breakpoints used if the trait was not initially scored as present or absent.

FACIAL

1. Metopic suture (De Villiers, 1968; Hauser and De Stefano, 1989)

The frontal suture dividing the two halves of the frontal bone of the skull (Figure 3.2) are present in infants and children but generally fused in adults. If it does persist, it can either be complete (extending from nasion to bregma) or incomplete (only partially present at either the nasal or parietal end).

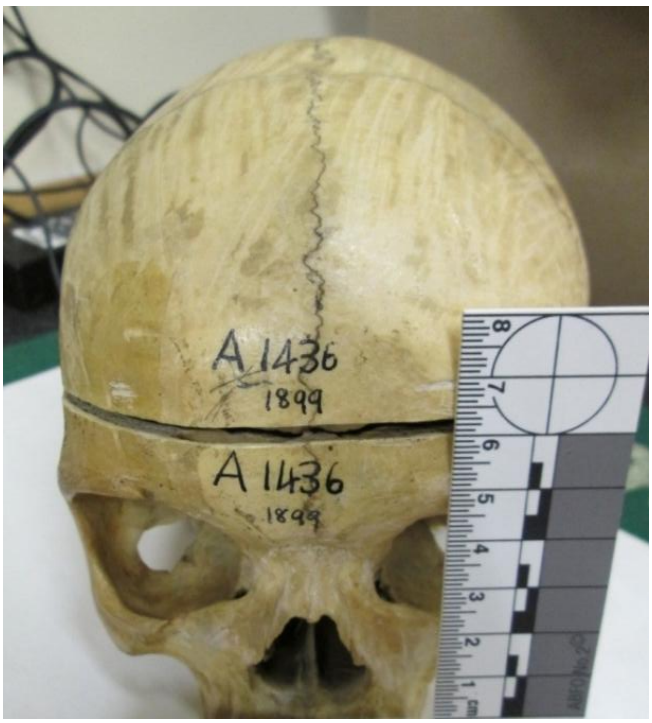


Figure 3.2: A complete metopic suture in a modern adult.

Score:

0 – Absence of metopic suture
1 – Incomplete (nasal part) metopic suture
2 – Complete metopic suture

Additional categories:

1. Incomplete (nasal part) metopic suture, *0 & 2 – Absent, 1 – Present*
2. Complete metopic suture, *0 & 1 – Absent, 2 – Present*

2. Metopic ridge (De Villiers, 1968)

A low vertical elevation located along a fused metopic suture (Figure 3.3). This elevation is not continuous along the sutural line, but varies in position from the anterior to middle region of the suture. It is best seen in the frontal view running a finger along the suture area from left to right.

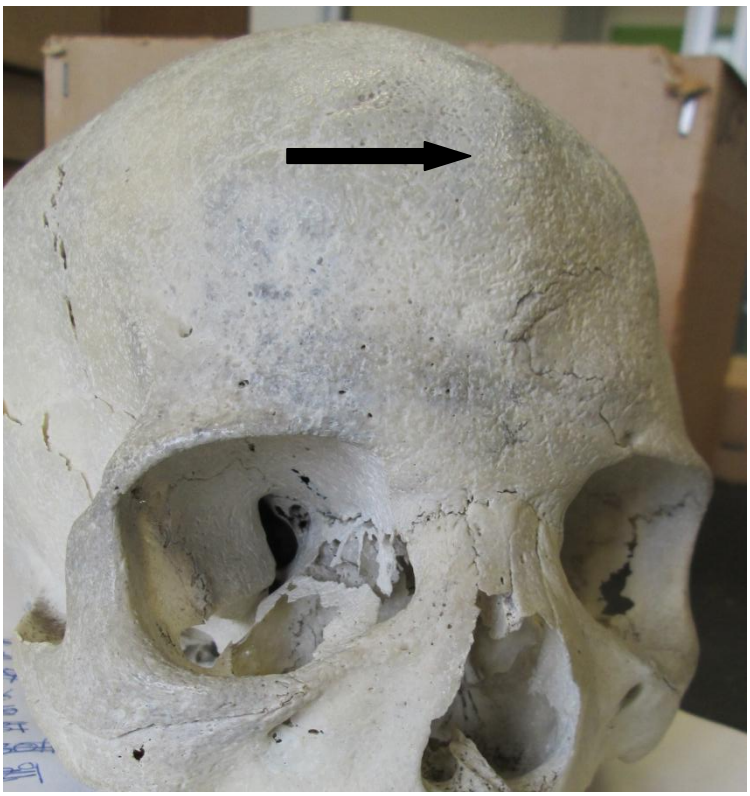

Figure 3.3: Frontal bone highlighting a metopic ridge.

Score:

*0 – Absent, 1 – Present*

3. Orbital shape (De Villiers, 1968)

This trait involves the shape of both the left and right orbits (Figure 3.4). If the shape of the orbits is not bilaterally the same, a score was not given (as per De Villiers). Similarly, if only a single orbit is presented in fragmentary remains, the shape was not scored.

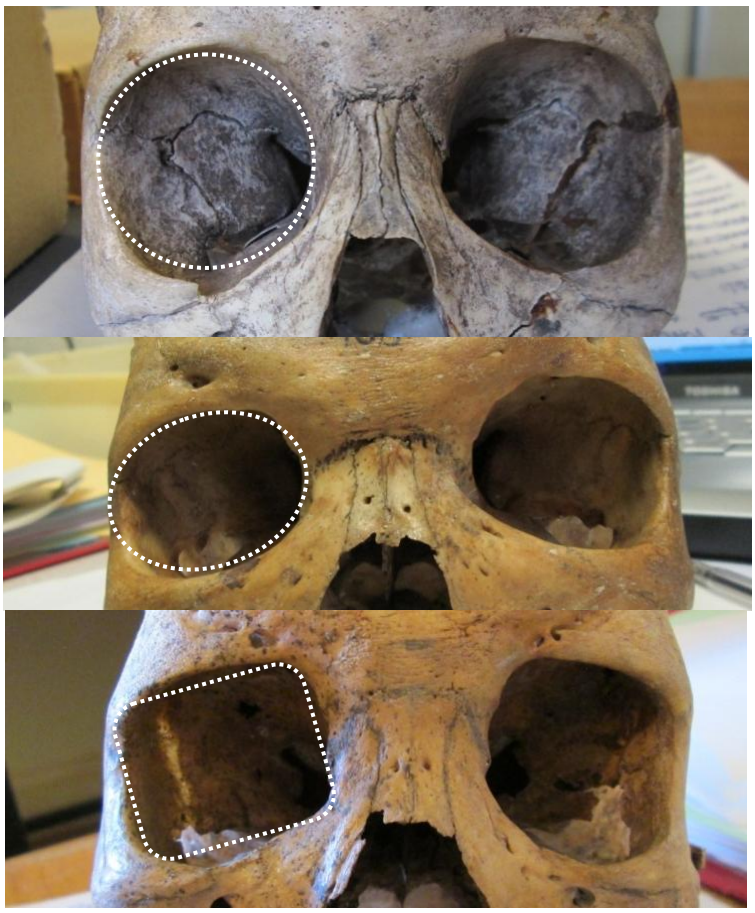

Figure 3.4: Shapes of the orbits: round (top), quadrilateral/oval (middle) and rectangular/square (bottom).

Score:

1 – Round
2 – Quadrilateral/oval
3 – Rectangular/square/rhomboid

Additional categories:

1. Round, *2 & 3 – Absent, 1 – Present*
2. Oval, *1 & 3 – Absent, 2 – Present*
3. Square, *1 & 2 – Absent, 3 – Present*

4. Supraorbital notch or supraorbital foramen (De Villiers, 1968)

A small opening along the medial edge of the superior orbital margin of the frontal bone (Figure 3.5), sometimes converted into a foramen (Figure 3.6). When scoring, these two traits were separated to capture the most variation and the left and right sides were scored independently.

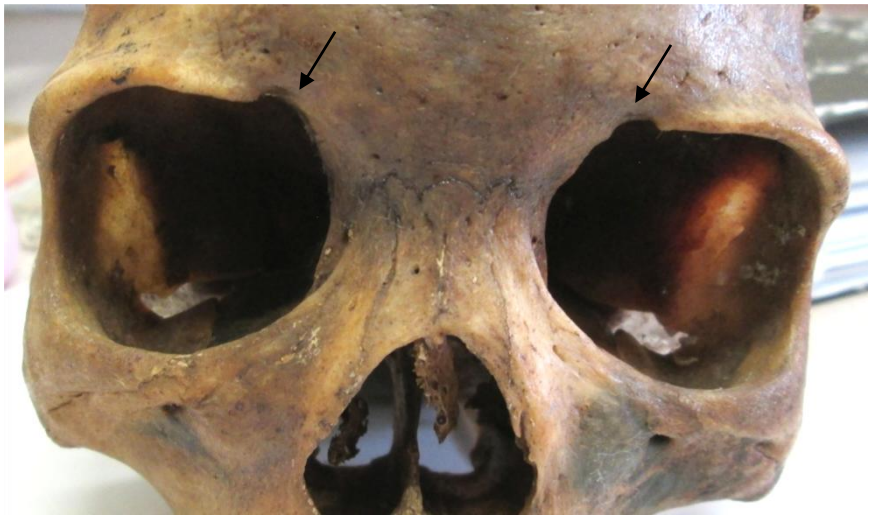

Figure 3.5: Left and right supraorbital notch.

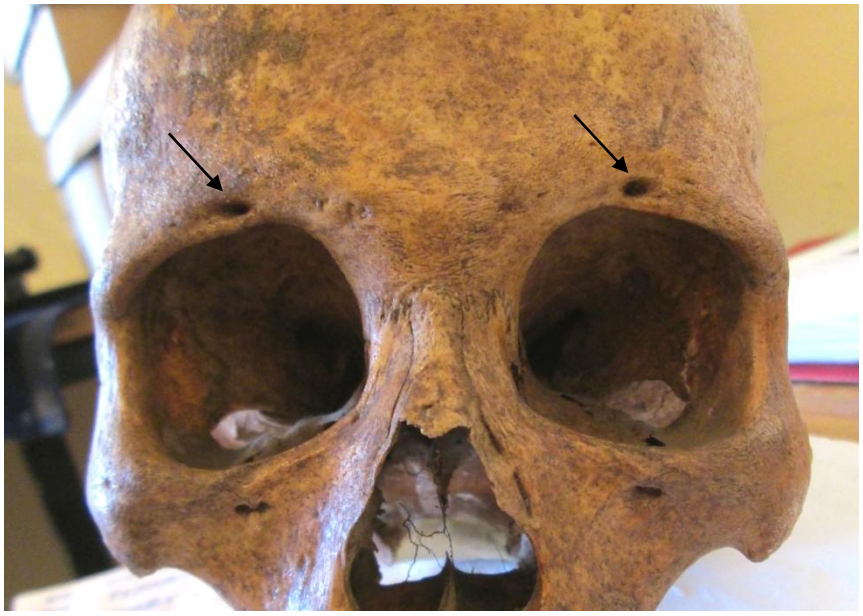

Figure 3.6: Left and right supraorbital foramina.

Score:

*0 – Absent, 1 – Present*

5. Ethmoidal foramina (De Villiers, 1968)

One or more foramina are present along the line of the suture between the orbital plate of the ethmoid and the orbital plate of the frontal bone (within the orbit, Figure 3.7). The left and right sides were scored independently.

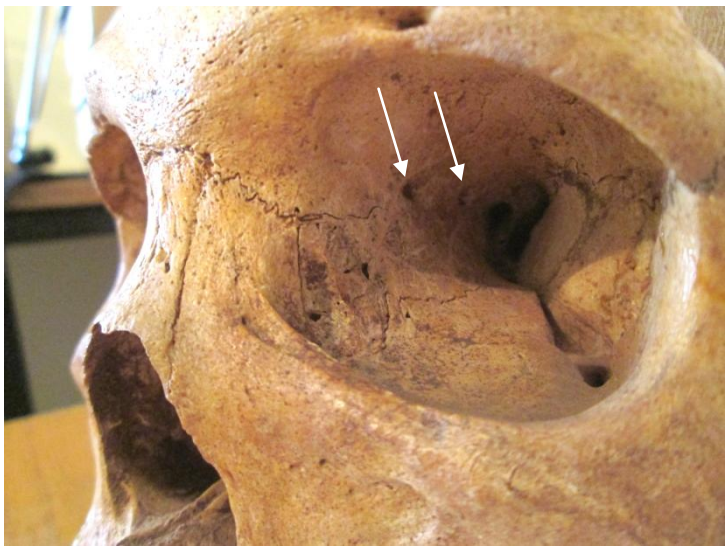

Figure 3.7: Two foramina present along the line of the suture within the left orbit.

Score:

1 – 1 foramen
2 – 2 foramina
3 – 3 foramina

Breakpoints: *1 – Absent, 2 & 3 – Present*

6. Infraorbital foramen (Hauser and De Stefano, 1989)

One or more openings in the maxillary bone, below the inferior margin of the orbit (Figure 3.8). The left and right sides were scored independently.

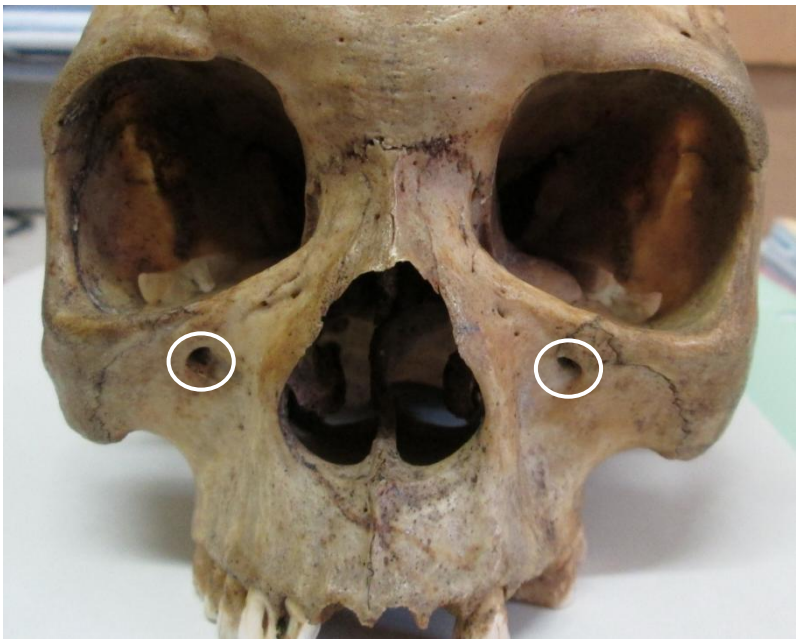

Figure 3.8: Left and right infraorbital foramen.

Score:

1 – 1 foramen
2 – 2 foramina
3 – 3 foramina
4 – 4 foramina

Breakpoints: *1 – Absent, 2, 3 & 4 – Present*

7. Infraorbital form (De Villiers, 1968)

The region limited superiorly by the inferior margin of the orbit and laterally by the prominence of the zygomatic bone, as well as the frontal curve of the maxilla and medially by the nasal aperture (Figure 3.9).

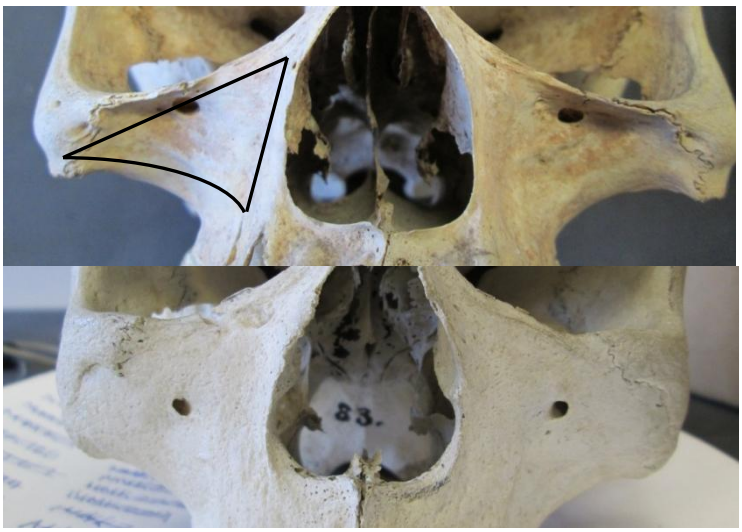


Figure 3.9: Infraorbital region: moderate degree of excavation (top) and no excavation (bottom).

Score:

0 – No excavation, the maxilla is slightly convex but the frontal curve is present
1 – Slight degree of excavation and is curved in the horizontal, sagittal and frontal planes
2 – Moderate degree of excavation and the horizontal, sagittal and frontal curves are more pronounced
3 – Marked degree of excavation with 3 pronounced curves

Breakpoints: *0 & 1 – Absent, 2 & 3 – Present*

8. Infraorbital suture (Hauser and De Stefano, 1989)

A suture running from the infraorbital foramen towards the inferior margin of the orbit or zygomaxillary suture.

Score:

0 – Absent
1 – Blending with the zygomaxillary suture for some distance
2 – Touching the zygomaxillary suture at the infraorbital margin
3 – Running medial to the zygomaxillary suture

Breakpoints: *0 – Absent, 1, 2 & 3 – Present*

9. Profile curves of nasal bones (De Villiers, 1968)

Median curve of the nasal bones in the lateral view, determined by describing an imaginary straight line from the nasion to the rhinion that assesses: the length of the bones, the depth of the curve and whether the straight line makes direct contact with the rhinion or not (Figure 3.10).

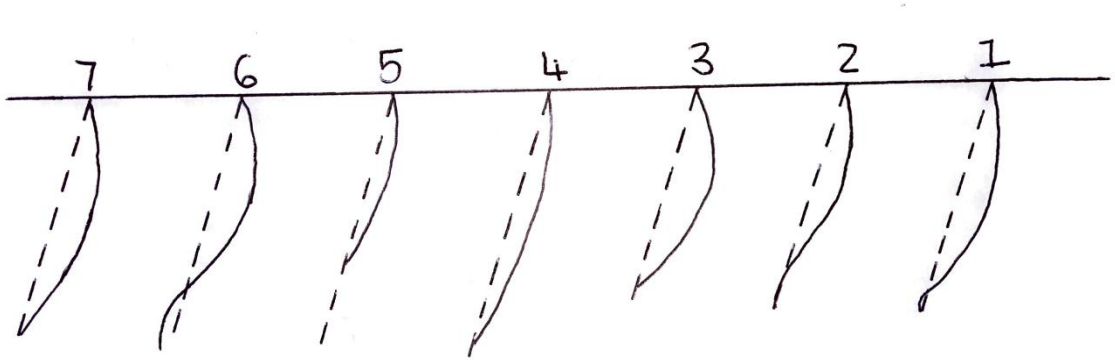


Figure 3.10: Profile curves of the nasal bones, redrawn from De Villiers (1968) - Figure 37.

Score:

1 – Deeply curved profile recurving slightly before rhinion
2 – Shallow curves produced by short nasal bones recurving slightly before rhinion
3 – A short, relatively deep profile curve
4 – Shallow curves produced by long nasal bones
5 – Shallow curves produced by short nasal bones
6 – Moderately curved profiles recurving slightly before rhinion
7 – Moderately curved profiles ending abruptly at rhinion

Breakpoints: *1, 2, 3, 4 & 5 – Absent, 6 & 7 – Present*

10. Position of nasion (De Villiers, 1968)

In the lateral view, an imaginary line joins the glabella to the rhinion (Figure 3.11). The nasion therefore may be inset and thus lie at a greater or lesser distance from the line, or it may be superficial and lie either on or immediately below the line.

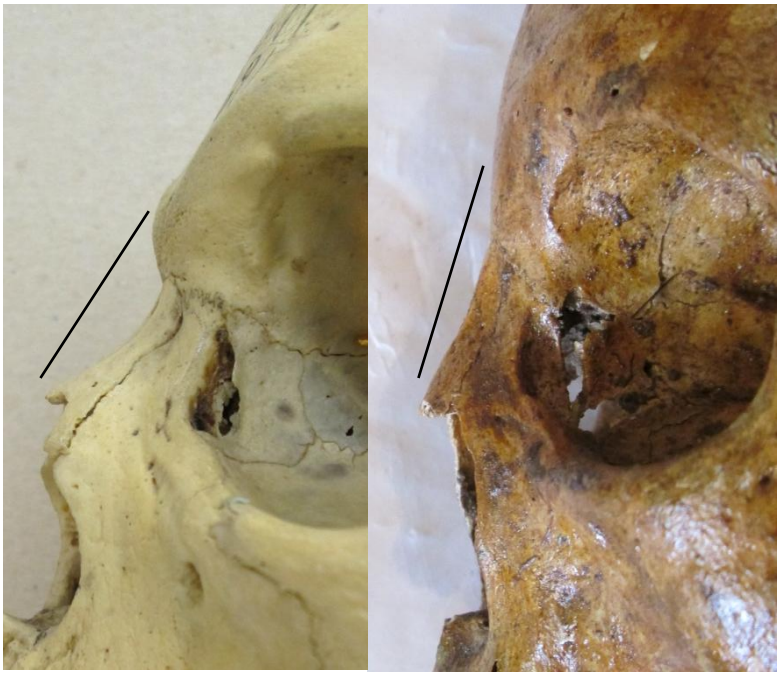

Figure 3.11: Position of nasion: marked depression of nasion (left) and superficial nasion (right).

Score:

1 – Superficial nasion and a flat/slightly curved glabella
2 – Moderately depressed nasion and a moderately curved glabella
3 – Depressed nasion and marked curvature of the glabella. The depression of the nasion is accentuated by the deep median curve of the nasal bones

Additional categories:

1. Superficial nasion, *2 & 3 – Absent, 1 – Present*
2. Moderately depressed nasion, *1 & 3 – Absent, 2 – Present*
3. Marked depression of nasion, *1 & 2 – Absent, 3 – Present*

11. Angle of nasal bones (De Villiers, 1968)

The angle at which the two nasal bones meet is determined by comparing the angle to a 90 degree angle ruler.

Score:

1 – Acute: an angle of 90 degrees or less
2 – Obtuse minus: an angle substantially greater than 90 degrees but the resulting ridge is still pronounced
3 – Obtuse: angle between the nasal bones is wide
4 – Obtuse plus: Nasal bones lie in the same transverse plane, the angle between them approximating 180 degrees

Breakpoints: *1 – Absent, 2, 3 & 4 – Present*

12. Nasal bone shape (De Villiers, 1968)

The often symmetrical nasal bones can differ in shape, particularly with regards to their width and height compared with the nasal aperture. Some of the variations identified in the samples are illustrated in Figure 3.12.

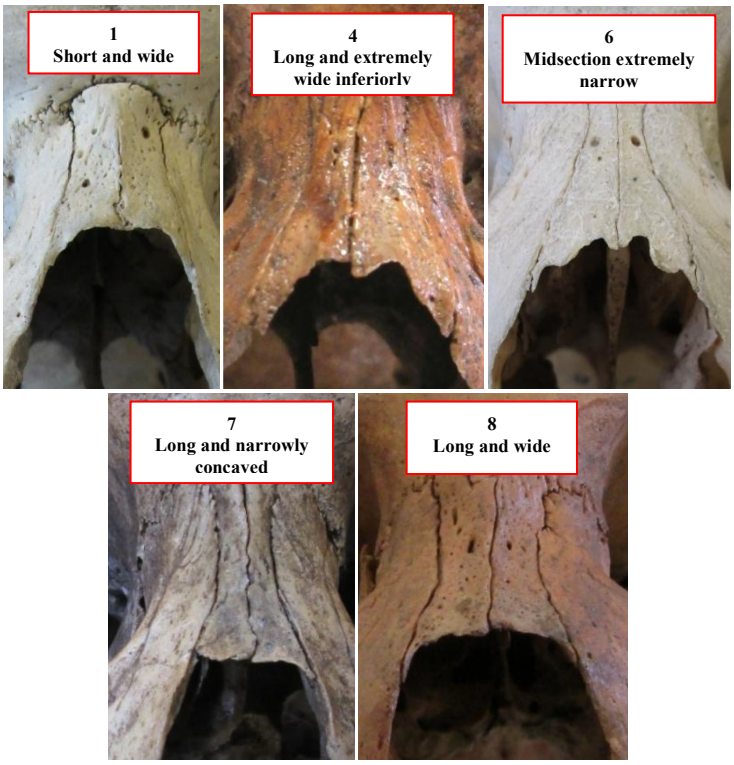


Figure 3.12: Examples of different nasal bone shapes: short and wide (1), long and extremely wide inferiorly (4), midsection extremely narrow (6), long and narrowly concaved (7), long and wide (8).

Score:

1 – Short, wide nasal bones
2 – Short, extremely wide nasal bones
3 – Long nasal bones, narrow superiorly becoming gradually wider inferiorly
4 – Long nasal bones, narrow superiorly becoming extremely wide inferiorly
5 – Long nasal bones, superiorly and inferiorly extremely wide with a moderate width midsection due to lateral border concavity
6 – Long, narrow nasal bones with the midsection extremely narrow due to distinct lateral concavity
7 – Long, narrow nasal bones with the lateral border distinctly concaved
8 – Long, wide nasal bones with the lateral border only slightly concaved

Breakpoints: *1, 2, 3, 4 & 5 – Absent, 6, 7 & 8 – Present*

13. Extension of nasal bones (De Villiers, 1968)

In lateral view, the extension of the anterior extremity of the nasal bones is assessed in relation to the maxillary border of the nasal aperture. Some of the non-normal variations are illustrated in Figure 3.13.

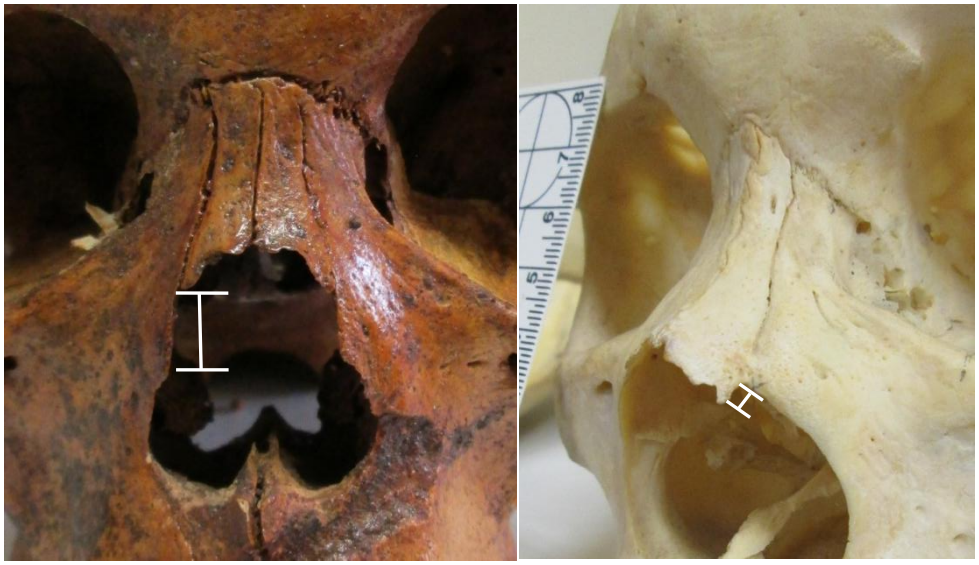

Figure 3.13: Undergrowth of nasal bones (left) and overgrowth of nasal bones (right).

Score:

1 – Normal growth of nasal bones: inferior margins of the nasal bones are level with the superior maxillary border of the nasal aperture
2 – Overgrowth: nasal bones extend beyond the superior maxillary border of the nasal aperture
3 – Undergrowth: inferior margins of the nasal bones do not meet the superior maxillary border at the nasal aperture
4 – Lateral overgrowth: nasal bones extend inferolaterally along the margins of the nasal aperture on both the left and right side

Breakpoints: *1– Absent, 2, 3 & 4 – Present*

14. Development of anterior nasal spine (De Villiers, 1968)

The anterior nasal spine is assessed from the lateral view to determine the size and how pronounced the spine is (Figure 3.14).

Figure 3.14: A marked anterior nasal spine.

Score:

0 – Absent: No protrusion present
1 – Slight: A very small protrusion
2 – Moderate: Moderately sized anterior nasal spine
3 – Marked: Large anterior nasal spine
4 – Extremely marked: Extremely large anterior nasal spine

Breakpoints: *0 & 1 – Absent, 2, 3 & 4 – Present*

15. Zygomaxillary tubercle (Hauser and De Stefano, 1989)

On the inferior margin of the zygomatic bone, a protruding bony tubercle of varying size and shape can occur (Figure 3.15). The left and right zygomaxillary tubercles were scored independently.

Figure 3.15: Expression of a medium zygomaxillary tubercle (left) and a strong zygomaxillary tubercle (right).

Score:

0 – Absence of zygomaxillary tubercle
1 – Weak expression of zygomaxillary tubercle
2 – Medium expression of zygomaxillary tubercle
3 – Strong expression of zygomaxillary tubercle

Breakpoints: *0 & 1 – Absent, 2 & 3 - Present*

16. Subnasal region (De Villiers, 1968)

Variations in face shape can result in different degrees of jaw protrusion. The maxillary region inferior to the nasal aperture can therefore have corrugations caused by the tooth roots depending on their direction related to the maxilla (Figure 3.16). The extent of these corrugations is scored in association with their degree of jaw protrusion.

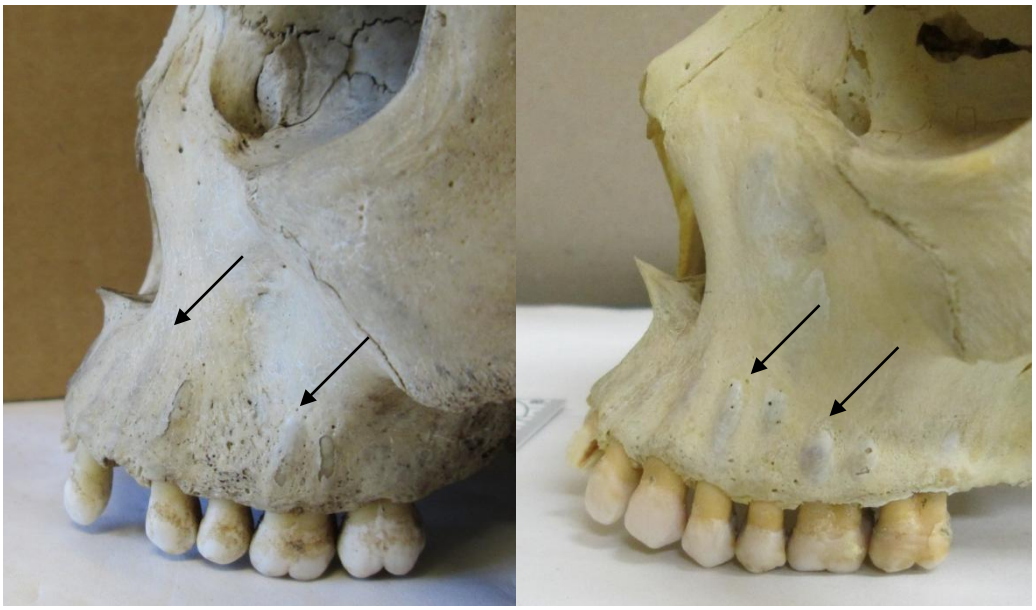

Figure 3.16: Slight subnasal corrugations (arrows) with a mesognathic jaw (left) and strong subnasal corrugations (arrows) with a prognathic jaw (right).

Score:

1 – Smooth subnasal region associated with orthognathic jaws
2 – Slight vertical subnasal corrugations associated with mesognathic jaws
3 – Strong delineated subnasal corrugations associated with prognathic jaws

Breakpoints: *1 & 2 – Absent, 3 - Present*

BASILAR

17. Dental arcade shape (De Villiers, 1968)

The shape of the dental arcade is dependent upon the position of the tooth sockets (Figure 3.17). When the shape could not be determined due to missing teeth or bone resorption after tooth removal (particularly in older individuals), the contour of the dental arcade was not scored.

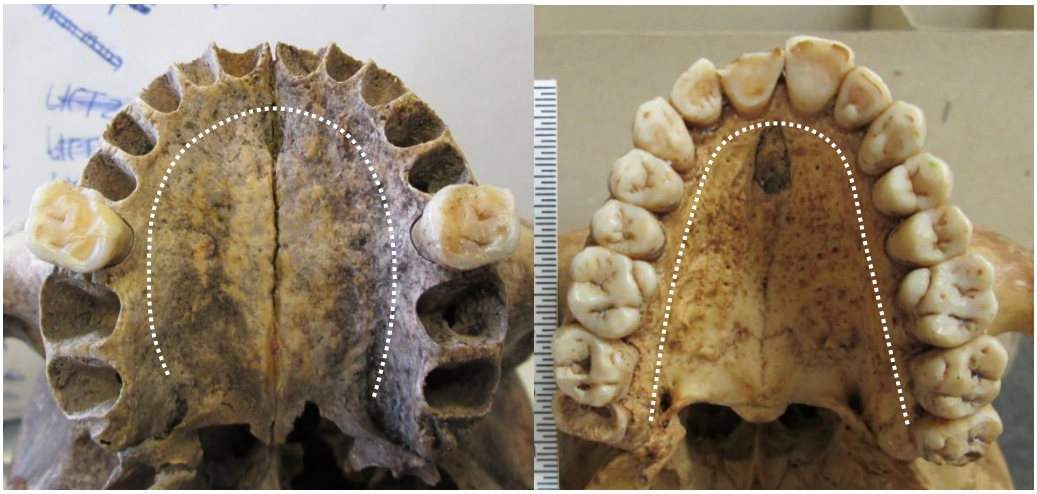

Figure 3.17: Horseshoe-shaped dental arcade (left) and divergent U-shaped dental arcade (right).

Score:

1 – U-shaped or hyperbolic dental arcade: summit is round and the sides are approximately parallel
2 – Horseshoe-shaped or elliptical dental arcade: anterior arc is round and the sides converge slightly
3 – Divergent U-shaped dental arcade: anterior arc is rectilinear and the sides diverge slightly

Breakpoints: *1 & 2 – Absent, 3 – Present*

18. Anterior palate form (De Villiers, 1968)

The anterior alveolar region of the hard palate can be horizontally flat or curved towards the anterior teeth (incisors). A curved anterior alveolar region is illustrated in Figure 3.18.

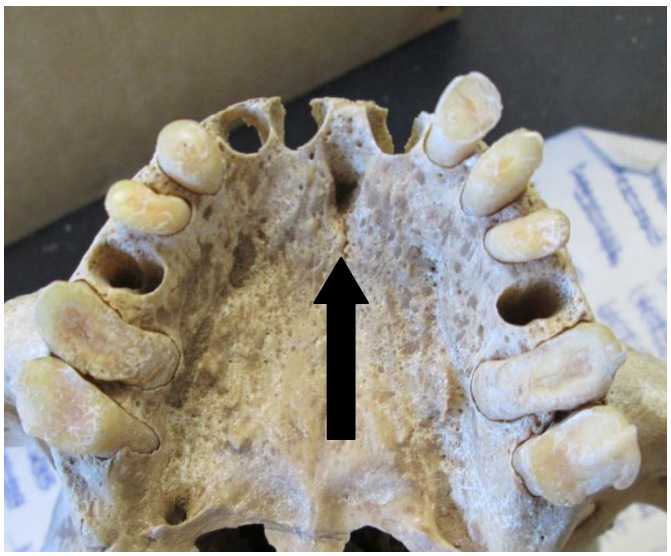

Figure 3.18: A curved anterior alveolar region of the hard palate.

Score:

1 – Flat anterior region of the palate
2 – Curved anterior region of the palate

Breakpoints: *1 – Absent, 2 – Present*

19. Torus palatinus (De Villiers, 1968)

Two different types of tori can be present on the hard palate along the median palatine suture (Figure 3.19).

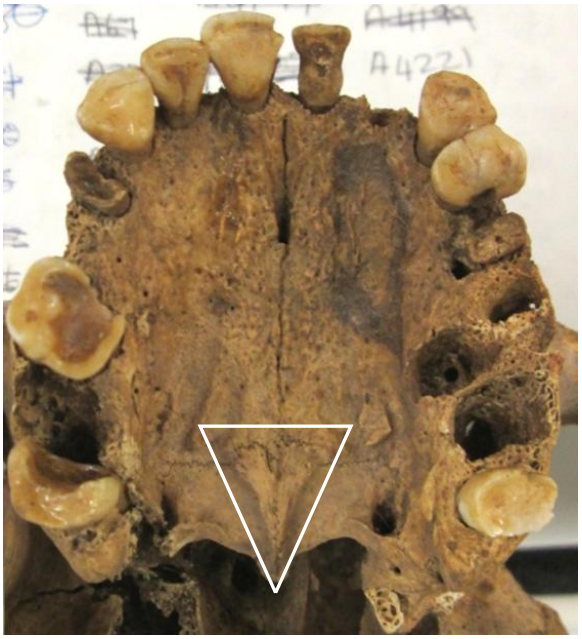

Figure 3.19: The 'mound' type of palatine torus.

Score:

0 – Neither the ‘ridge’ or ‘mound’ type palatine torus is present
1 – Small ‘mound’ type palatine torus. This torus is confined to the palatine portion of the hard palate
2 – Small ‘ridge’ type palatine torus. This torus extends from the posterior edge of the palatine portion to the maxillary portion of the hard palate

Breakpoints: *0 – Absent, 1 & 2 – Present*

20. Torus maxillaris (De Villiers, 1968)

Torus maxillaris is described as an occasional hyperostosis on the alveolar portion of the maxilla and is usually confined to the lingual aspect of the molar region (Figure 3.20).

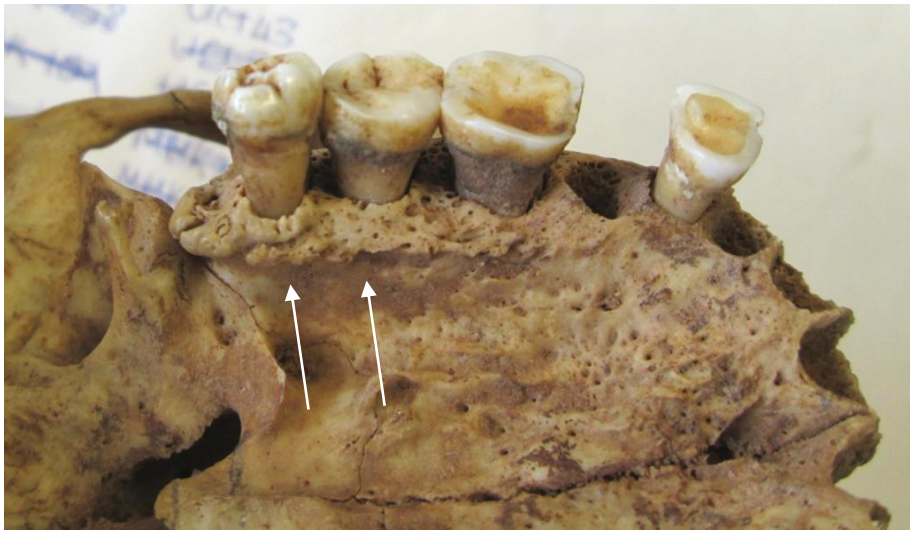

Figure 3.20: Torus maxillaris on the lingual aspect of the right molars.

Score:

*0 – Absent, 1 – Present*

21. Foramen of Huschke (De Villiers, 1968; Hauser and De Stefano, 1989)

Also known as a tympanic dehiscence, where the anterior and posterior portions of the floor of the external acoustic meatus (tympanic part of the temporal bone) incompletely fuse and remain as a foramen later in life (Figure 3.21). The left and right expressions were scored independently.

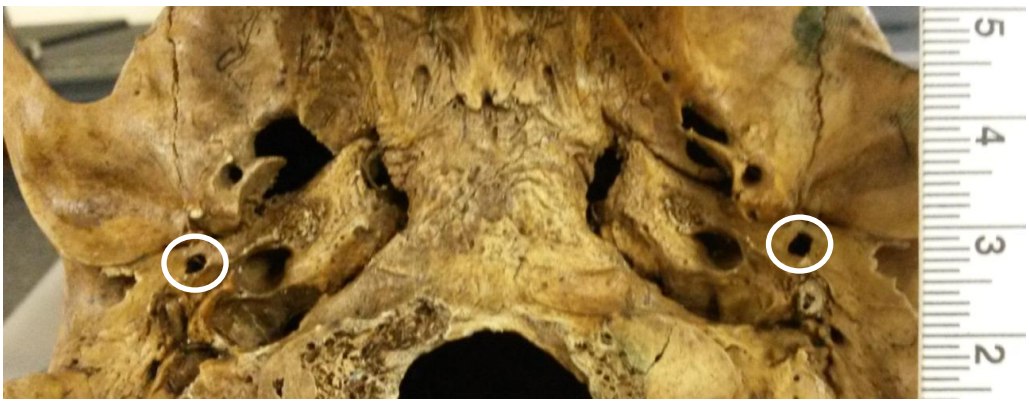

Figure 3.21: Left and right foramen of Huschke.

Score:

0 – Absence of tympanic dehiscence (complete closure of tympanic floor)
1 – Trace expression of tympanic dehiscence (thin translucent area on tympanic floor)
2 – Medium expression of tympanic dehiscence (foramen present)

Breakpoints: *0 & 1 – Absent, 2 – Present*

22. Encroachment of occipital condyles (De Villiers, 1968)

In relation to the foramen magnum, condyles may encroach (obscure/extend over) the outline of the foramen (Figure 3.22). Encroachment occurs when the boundary of the foramen magnum is no longer visible.

Figure 3.22: No encroachment of occipital condyles (left) and encroaching occipital condyles (right).

Score:

*0 – Absent, 1 – Present*

23. Hypoglossal canal bridging (Hauser and De Stefano, 1989)

Viewed internally through the foramen magnum, a canal passes in a medio-lateral direction through the base of the occipital condyle (Figure 3.23). The inner orifice of the canal can be single, double or even multiple. Small osseous spines, seen as a minor expression of division, may also be present. The left and right hypoglossal canals were scored independently.


Figure 3.23: A thick osseous septum dividing the hypoglossal canal (left) and two spines protruding into the hypoglossal canal (right).

Score:

1 – Completely undivided hypoglossal canal
2 – One small spine protrudes from the margin of the aperture
3 – One spine (from above) and one spine from below protrude into the internal aperture of the hypoglossal canal
4 – A thick osseous septum divides symmetrically the internal aperture of the hypoglossal canal
5 – A thick osseous septum divides asymmetrically the internal aperture of the hypoglossal canal
6 – Similar to (4) but in addition, the hypoglossal canal is divided by the septum for some distance

Breakpoints: *1, 2 & 3 – Absent, 4, 5 & 6 – Present*

24. Condylar canal (Hauser and De Stefano, 1989)

Posterior to the occipital condyle is the condylar fossa that may contain the external orifice of the condylar canal, generally situated close to the medial edge of the jugular foramen (Figure 3.24). This canal can be divided by a thin bony bridge, may be double, or absent. The left and right condylar canals were scored independently.


Figure 3.24: Posterior aspect of the occipital condyles with bilateral condylar canals.

Score:

0 – Condylar canal is absent (blind ending external orifice)
1 – Condylar canal is present and undivided
2 – Condylar canal is divided by a thin bony bridge
3 – Multiple condylar canals occur

Breakpoints: *0 – Absent, 1, 2 & 3 – Present*

POSTERIOR

25. Inca bone (Hauser and De Stefano, 1989)

A complete Inca bone is defined as a transverse suture from the left and right asterion dividing the occipital bone (Figure 3.25). Incomplete variations of the Inca bone exist and are illustrated in Hauser and De Stefano (1989). Both complete and incomplete variations of the Inca bone are scored as present in this study.

Figure 3.25: Posterolateral view of the left and right side of the same individual, highlighting a complete Inca bone.

Score:

*0 – Absent, 1 – Present*

SUPERIOR

26. Interparietal groove (De Villiers, 1968)

A groove located in the region of obelion where the parietal foramen/foramina are situated, when present (Figure 3.26).

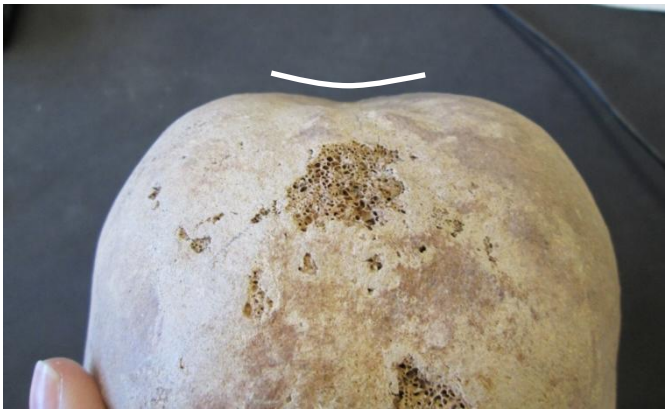

Figure 3.26: Posterior aspect of the skull illustrating a wide interparietal groove.

Score:

0 – Interparietal region is evenly rounded/flat, groove is absent
1 – Postcoronal grooving associated with narrow interparietal grooving
2 – Wide interparietal groove encroaching on the parietal bone on either side of sagittal suture

Breakpoints: *0 – Absent, 1 & 2 – Present*

27. Parietal foramina (De Villiers, 1968)

Near the sagittal suture at the posterior aspect of the parietal bones, parietal foramina are usually present.

Score:

1 – Absence of parietal foramina
2 – Numerous minute foramina in the posterior part of the parietal bones
3 – Three parietal foramina, two on one side and one on the other (indicate left or right)
4 – A median parietal foramen
5 – A single foramen on one side (indicate left or right)
6 – Two parietal foramina, one on each side

Breakpoints: *1, 2 & 3 – Absent, 4, 5 & 6 – Present*

28. Zygomatic arch (De Villiers, 1968)

The zygomatic arch is either hidden from the superior view (cryptozygous) or clearly visible from the superior view (phaenozygous).

Score:

1 – Phaenozygous arch associated with a relatively narrow cranial vault
2 – Cryptozygous arch associated with a somewhat broader cranial vault

Breakpoints: *1 – Absent, 2 – Present*

29. Wormian bones (De Villiers, 1968)

Sutural bones arising as separate ossifications between the main cranial elements (Figure 3.27).


Figure 3.27: Superior view of the skull showing multiple wormian bones in the sagittal and lambdoid sutures (A – Anterior, P – Posterior).

Scoring:

0 – No wormian bone/s present in all cranial sutures
1 – Wormian bone/s present in one or more cranial suture/s

30. Ophryonic groove (De Villiers, 1968)

A groove found on the forehead just above the orbit and glabella, generally associated with marked development of the superciliary ridges (Figure 3.28).

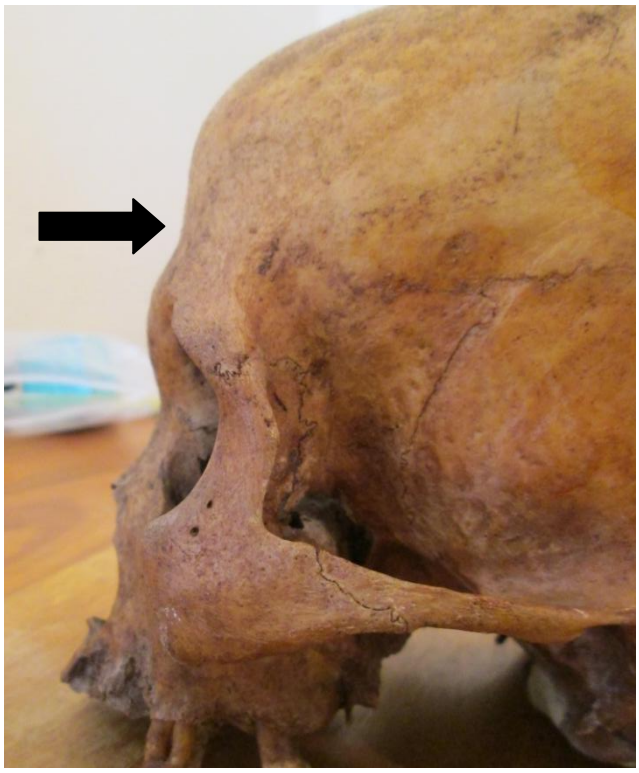

Figure 3.28: Lateral view of the ophryonic groove of the forehead.

Score:

*0 – Absent, 1 – Present*

LATERAL

31. Sutural variations at pterion (De Villiers, 1968)

The pattern exhibited where the frontal bone, greater wing of the sphenoid, temporal bone and parietal bone meet (Figure 3.29). Scores were not given when one or more sutures at this point had completely fused. The left and right sides were scored independently.

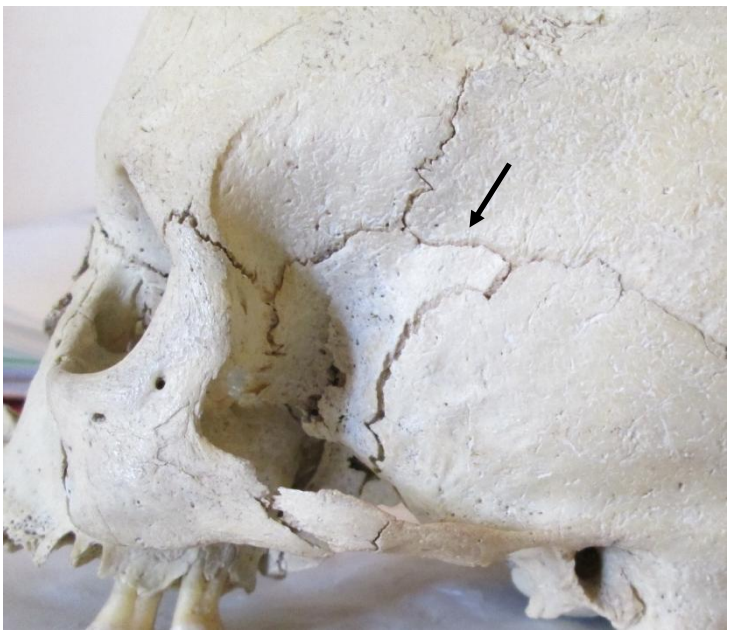

Figure 3.29: Lateral view of a wide sphenoparietal suture.

Score:

1 – Junction point of the frontal, temporal, parietal and sphenoid bones, pterion as an X
2 – Narrow sphenoparietal suture, pterion as a narrow H
3 – Slender frontal process of temporal, almost meeting a similar process from frontal bone, pterion as a K
4 – Epipteric bone, a wormian bone present at pterion
5 – Frontotemporal articulation, pterion as an I
6 – Wide sphenoparietal suture, pterion as an H

Breakpoints: *1, 2, 3, 4 & 5 – Absent, 6 – Present*

32. Inferior frontal eminence (De Villiers, 1968)

An oval projection of the frontal bone, immediately posterior to the anterior extremity of the superior temporal line. This elevation corresponds to the fossa in which the inferior frontal convolution of the brain is lodged in the interior of the cranium. The left and right sides were scored independently.

Score:

*0 – Absent, 1 – Present*

33. Superior temporal line (De Villiers, 1968)

The superior line present on the parietal bones due to the attachment of the temporal fascia, commonly forming an arch that is convex superiorly and posteriorly (Figure 3.30). The left and right sides were scored independently.

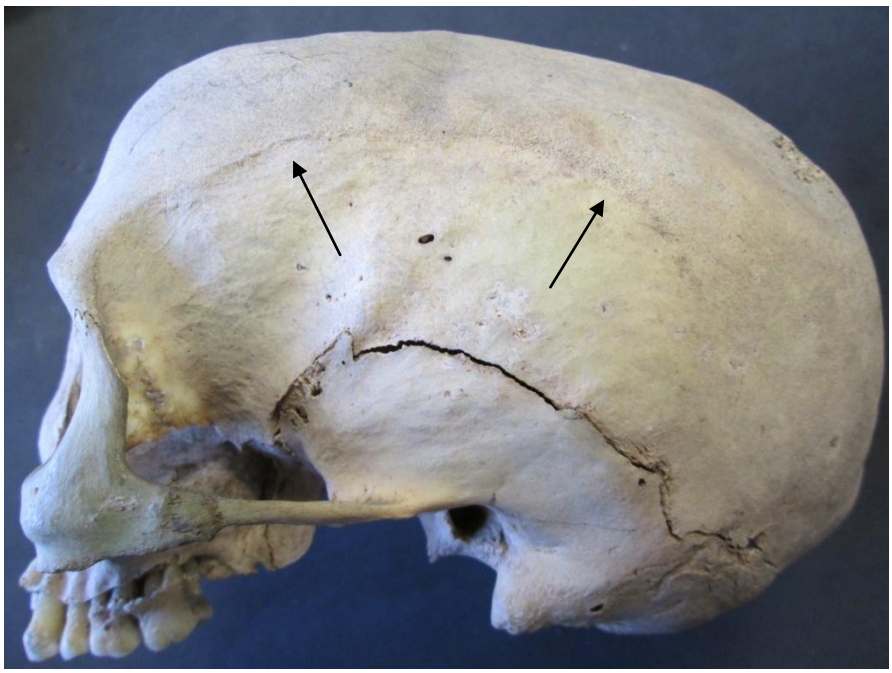

Figure 3.30: Left superior temporal line following a moderately high course.

Score:

1 – Superior temporal line that turns sharply posteriorly at the junction of the angular and cranial portions of the frontal bone to pursue an almost horizontal and low course
2 – Superior temporal line that passes superiorly and posteriorly to pursue a moderately high course
3 – High superior temporal line with a forward convexity of the anterior extremity

Breakpoints: *1 & 2 – Absent, 3 – Present*

34. Mons temporosphenoidalis (De Villiers, 1968)

Viewed superolaterally, a marked temporosphenoidal swelling can be seen resulting from the temporal fossa being diminished posteroinferiorly. This swelling is caused by the relative exaggeration of the temporal lobe of the brain. The left and right sides were scored independently.

Score:

*0 – Absent, 1 – Present*

35. Parietotemporal suture (De Villiers, 1968)

The pattern of the parietotemporal suture, describing the shape or direction of its superior and posterior limb (Figure 3.31). The left and right sides were scored independently.

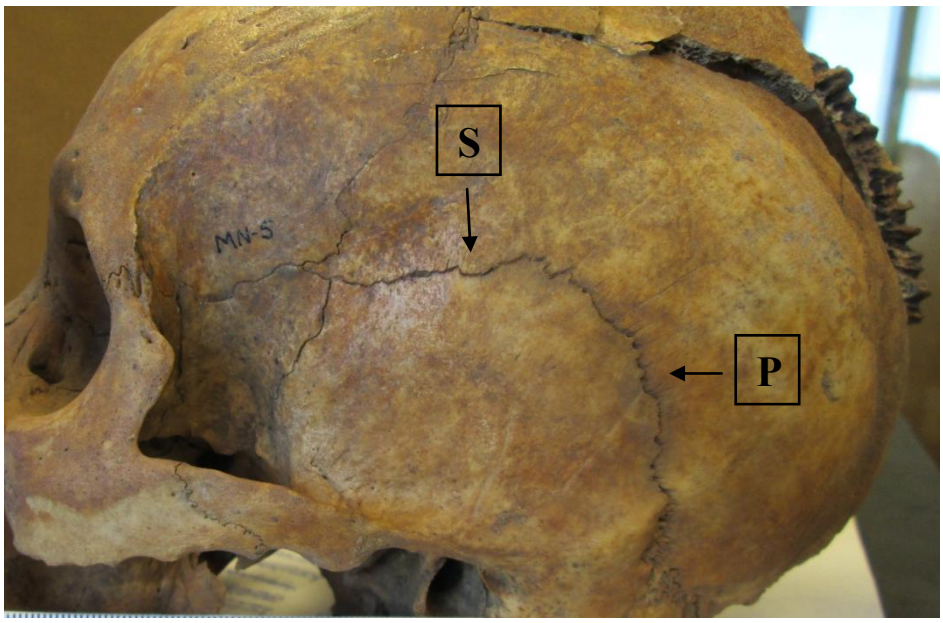


Figure 3.31: Lateral view of a parietotemporal suture with the superior limb (S) rising above the pterion and the posterior limb (P) at an even curvature.

Score:

1 – Superior limb is horizontal and does not rise above the level of pterion, posterior limb is low and oblique
2 – Superior limb is horizontal and does not rise above the level of pterion, posterior limb is low and curved
3 – Superior limb is convex, rising above the level of pterion, while the posterior limb descends as an oblique line
4 – Superior limb of the parietotemporal suture is convex, rising above pterion and the posterior limb continues the even curvature

Breakpoints: *1, 2 & 3 – Absent, 4 - Present*

36. Tympanic plate of temporal bone (De Villiers, 1968)

The thickness of the tympanic plate compared to the relative size of the external auditory meatus (Figure 3.32). The left and right sides were scored independently.

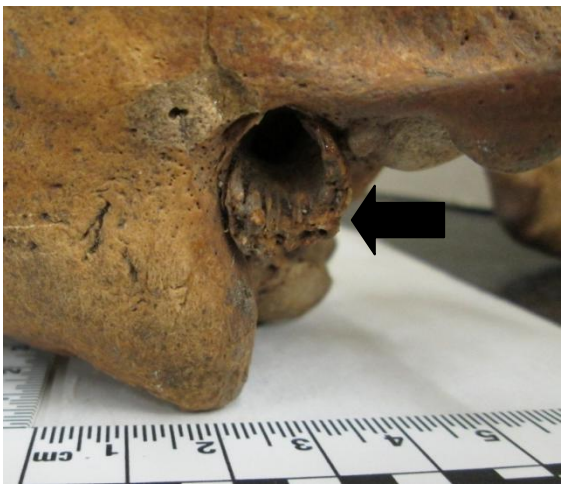

Figure 3.32: Moderate development of the tympanic plate.

Score:

0 – Delicate or foetal type of tympanic plate
1 – Moderate development of the tympanic plate
2 – Massive tympanic plate

Breakpoints: *0 – Absent, 1 & 2 - Present*

37. Supra-asterionic region (De Villiers, 1968)

The curvature of the parietal bones above asterion, as viewed from the posterior (Figure 3.33).

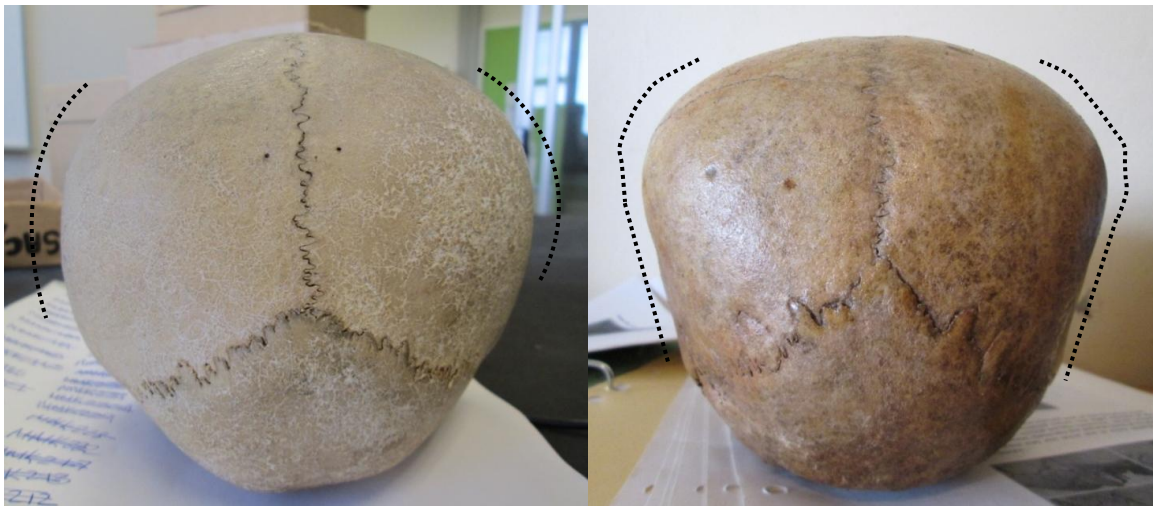

Figure 3.33: Posterior view of the skull illustrating an evenly curved supra-asterionic region (left) and moderate flattening associated with marked bossing of the parietal bones (right).

Score:

1 – An evenly rounded supra-asterionic region
2 – Slight flattening of the supra-asterionic region associated with moderate bossing of the parietal bones
3 – Moderate flattening of the supra-asterionic region associated with marked bossing of the parietal bones

Breakpoints: *1 – Absent, 2 & 3 - Present*

38. Parietal notch bone (Hauser and De Stefano, 1989)

A wormian bone found in the notch whereby the parietal bone extends into the temporal bone (Figure 3.34). The left and right sides were scored independently.

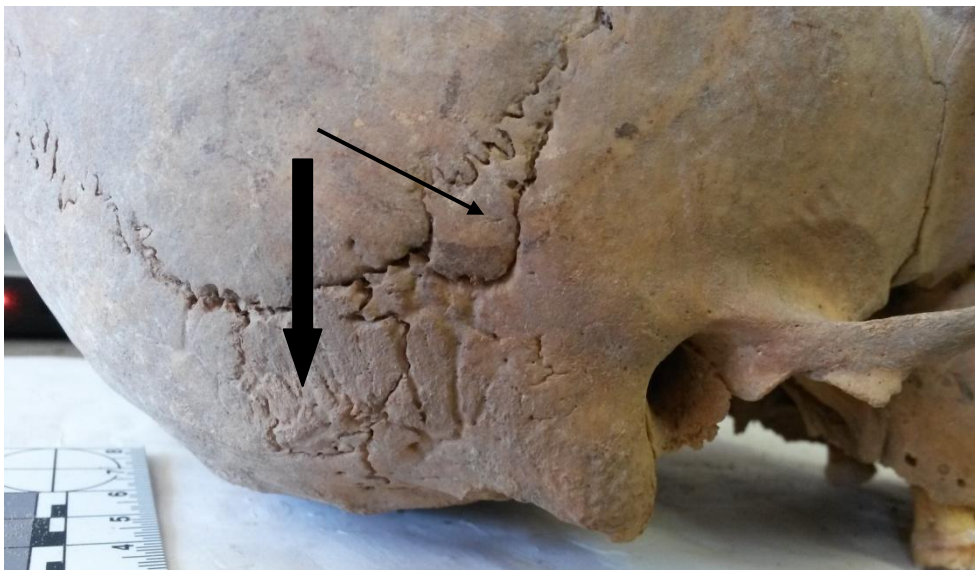

Figure 3.34: Lateroposterior view of the skull highlighting a parietal notch bone (thin arrow) and an asterion ossicle (thick arrow).

Score:

*0 – Absent, 1 – Present*

39. Sutura mendosa (biasterionic suture) (Hauser and De Stefano, 1989)

An incomplete Inca bone is when two bilateral sutures extend horizontally from the region of the left and right asterion, but do not bisect the occipital bone. These sutures can originate inferior to, at or superior to the asterion. Although they can occur unilaterally, this trait is only scored when present bilaterally.

Score:

0 – Sutura mendosa absent
1 – Bilaterally originating below asterion
2 – Bilaterally originating from asterion
3 – Bilaterally originating above asterion

Breakpoints: *0 – Absent, 1, 2 & 3 - Present*

40. Os japonicum (De Villiers, 1968)

Division of the zygomatic bone by a horizontal suture into a larger upper and smaller lower division (Figure 3.35). The left and right zygomatic bones were scored independently.

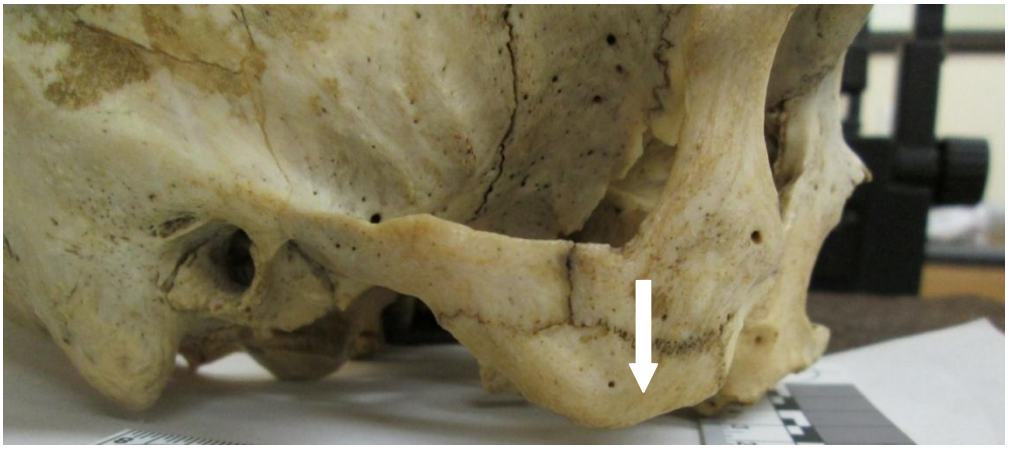

Figure 3.35: Lateral view of a zygomatic bone with an os japonicum.

Score:

*0 – Absent, 1 – Present*

41. Asterion ossicle (Hauser and De Stefano, 1989)

A wormian bone situated at asterion (Figure 3.34). The left and right sides were scored independently.

Score:

*0 – Absent, 1 – Present*

42. Occipitomastoid wormian bone (Hauser and De Stefano, 1989)

A wormian bone situated in the occipitomastoid suture (Figure 3.36). The left and right sides were scored independently.

Figure 3.36: Postero-lateral view of an occipitomastoid wormian bone.

Score:

*0 – Absent, 1 – Present*

MANDIBLE

43. Chin shape (De Villiers, 1968)

The shape of the chin when viewed inferiorly, that results from the development of the mental protuberance and mental tubercles (Figure 3.37).

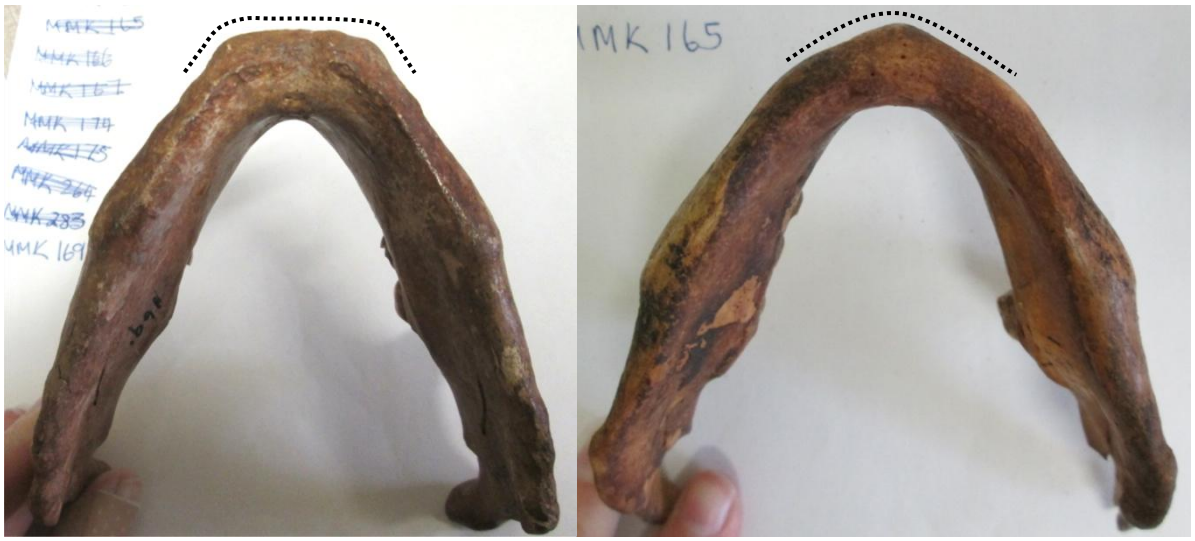


Figure 3.37: Inferior view of the square-shaped chin (left) and the pointed-shaped chin (right).

Score:

1 – Round chin: moderate development of the mental protuberance and slight development of the mental tubercles
2 – Round chin: both mental protuberance and tubercles show equal but moderate development
3 – Square chin: marked development of the mental tubercles and slight development of the mental protuberance
4 – Square chin: marked development of the mental tubercles and moderate development of the mental protuberance
5 – Pointed chin: marked development of the mental protuberance and slight development of the mental tubercles
6 – Pointed chin: marked development of the mental protuberance and moderate development of the mental tubercles

Breakpoints: *1, 2, 3 & 4 – Absent, 5 & 6 - Present*

44. Mental foramen (De Villiers, 1968)

One or more foramina located on the anterior surface of the mandible (Figure 3.38). The left and right sides were scored independently.

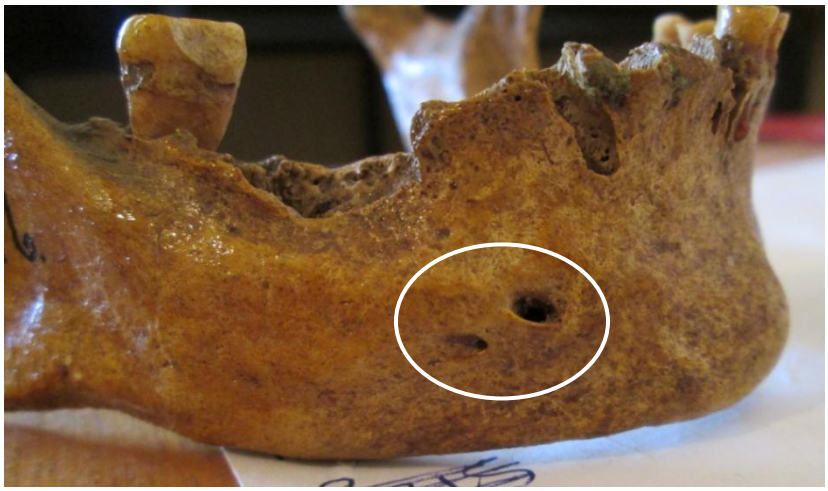

Figure 3.38: Right side of the mandible with multiple mental foramina.

Score:

1 – One mental foramen
2 – Multiple mental foramina

Breakpoints: *1 – Absent, 2 – Present*

45. Genial tubercles (De Villiers, 1968)

Located on the internal surface of the mandible near the lower end of the midline, a variation of bony tubercles or pits (depressions) attach to the genioglossus muscle (Figure 3.39).

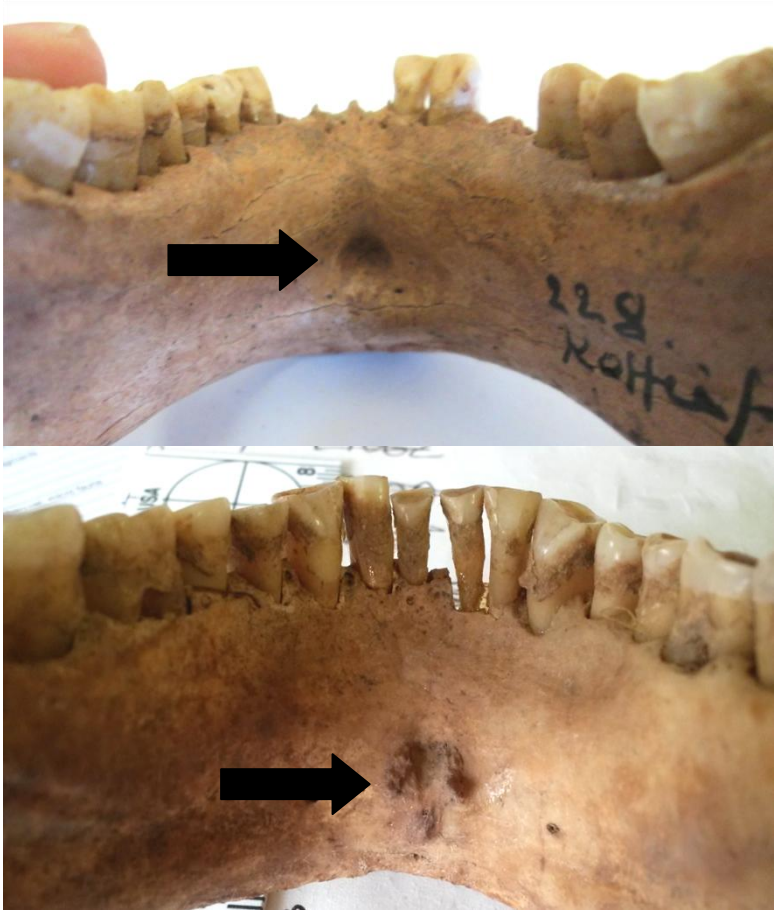

Figure 3.39: A single pit (top) and two superior and one inferior tubercle (bottom) on the internal surface of the mandible.

Score:

1 – One tubercle
2 – Superior pit and two inferior tubercles
3 – Absent: mandible showing neither tubercles nor pit
4 – Common median spine
5 – Superior and an inferior pit
6 – Single pit
7 – Superior pit and an inferior tubercle
8 – Two superior tubercles only
9 – Two superior and one inferior tubercle
10 – Two superior and two inferior genial tubercles

Breakpoints: *1, 2, 3, 4, 5, 6 & 7 – Absent, 8, 9 & 10 - Present*

46. Torus mandibularis (De Villiers, 1968)

On the lingual surface of the mandible, near the roots of the canine and premolar teeth and above the mylohyoid line, a bone hyperostosis of normal bone can occur.

Score:

*0 – Absent, 1 – Present*

47. Mylohyoid bridge (Hauser and De Stefano, 1989)

The mylohyoid groove may be covered by an osseous roof of varying length, transforming the groove into a canal (Figure 3.40). This canal may begin at the upper or central part of the groove, resulting in one or more "bridges". The left and right sides were scored independently.

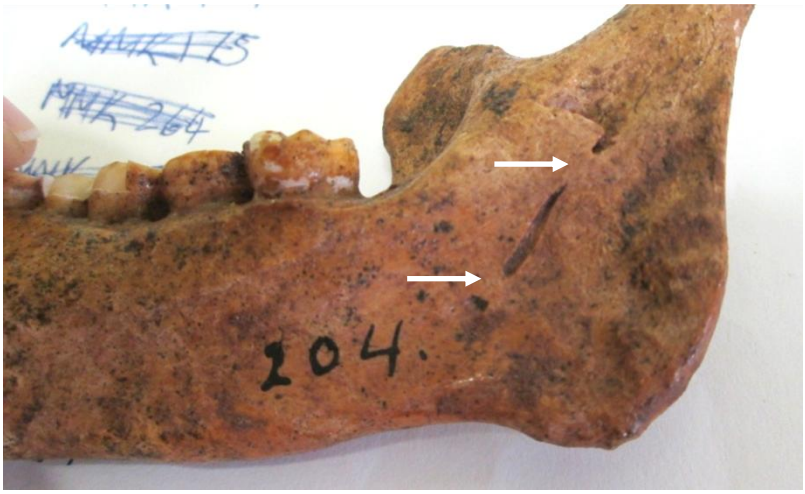


Figure 3.40: Right internal ramus of the mandible with two mylohyoid bridges.

Score:

*0 – Absent, 1 – Present*

### 3.2.3. Dental nonmetrics

The Arizona State University Dental Anthropology System (ASUDAS) (Turner *et al*., 1991; Wu and Turner, 1993; Scott and Turner, 1997; Burnett *et al*., 2010; Scott and Irish, 2017) was used to assess the dental nonmetric traits of each permanent tooth present in the archaeological and modern samples. Using rank-scale reference plaques in conjunction with descriptions given in the literature, each trait (n=34) was scored according to the degree of expression (Table 3.1). Two additional traits were also included and scored: the midline diastema and the mandibular molar pit-tubercle. The midline diastema is commonly found in African populations (Irish, 1998a; Black, 2014) and the mandibular molar pit-tubercle was investigated because it has a high rate of occurrence in ancient populations but was not previously investigated in Africa (Weets, 2009). Root traits were not evaluated as they could not be assessed for teeth in sockets or for the dental casts. Teeth from both sides of the dental arcade were investigated to include as many individuals as possible and to maximise potential genetic differences. The side that had the highest expression of the trait was used in the statistical analysis, as recommended by Turner *et al.* (1991), Scott and Turner (1997) and Irish (2010). Standardized breakpoints from the literature (Irish and Konigsberg, 2007; Hanihara, 2008; Irish, 2016) were used to dichotomise each trait scored as present or absent (Table 3.1). The frequencies of each trait were determined according to the groups investigated for each objective. Repeatability of the dental scores was evaluated on 12 individuals using Cohen's Kappa, resulting in excellent agreement (k=0.86) for the intraobserver scoring and good agreement (k=0.69) between two different observers.

Table 3.1: Dental nonmetric traits scored (n=34) and their breakpoints.

| **Trait** | **Teeth** | **Breakpoints** |
|---|---|---|
| Midline diastema | UI1 | P(>0.5mm)/A |
| Lateral incisor variants | UI2 | P/A |
| Winging | UI1, LI1 | P(ASU 1)/A |
| Shovelling | UIs, LIs, UC, LC | P(ASU 2-6)/A |
| Double shovelling | UIs, LIs UC, UP1 | P(ASU 2-6)/A |
| Interruption groove | UIs | P/A |
| Tuberculum dentale | UIs, UC | P(ASU 2-6)/A |
| Peg-shaped | UI2, UM3 | P/A |
| Labial convexity | UIs | P(ASU 2-4)/A |
| Congenital absence | UI2, LI1, UP2, LP2, UM3, LM3 | P/A |
| Mesial ridge (Bushman canine) | UC | P(ASU 1-3)/A |
| Distal accessory ridge | UC, LC | P(ASU 2-5)/A |
| Mesial & Distal premolar accessory ridges | UPs, LPs | P(ASU 1-4)/A |
| Odontome | UPs, LPs | P/A |
| Mesial and Distal accessory cusps | UPs | P/A |
| Distosagittal ridge | UP1 | P/A |
| Tricusped | Ups | P/A |
| Lingual cusp variation | LPs | P(ASU 2-9)/A |
| Hypocone | Ums | P(ASU 3-5)/A |
| Carabelli's trait | Ums | P(ASU 2-7)/A |
| Cusp 5 (Metaconule) | Ums | P(ASU 2-5)/A |
| Cusp 5 (Hypoconulid) | LMs | P(ASU 2-5)/A |
| Groove pattern | LMs | P(ASU Y)/A |
| Cusp 6 (Entoconulid) | LMs | P(ASU 1-5)/A |
| Cusp 7 (Metaconulid) | LMs | P(ASU 2-4)/A |
| Deflecting wrinkle | LM1 | P(ASU 2-3)/A |
| Distal trigonid crest | LMs | P/A |
| Middle trigonid crest | LMs | P/A |
| Metacone | Ums | P(ASU 3.5-5)/A |
| Parastyle | Ums | P(ASU 1-5)/A |
| Anterior fovea | LM1 | P(ASU 2-4)/A |
| Cusp number | LMs | P(ASU 5+, 6+)/A |
| Protostylid | LMs | P(ASU 2-7)/A |
| Mandibular molar pit-tubercle | LMs | P(1-3)/A |

*UI – upper incisor, LI – lower incisor, UC – upper canine, LC – lower canine, UP – upper premolar, LP – lower premolar, UM – upper molar, LM – lower molar, P – present, A – absent, ASU – Arizona State University score.*

### 3.2.4. Dental metrics

Using a digital calliper accurate to the nearest hundredth of a centimetre (0.01mm), three repeat measures of the two maximum crown diameters (mesiodistal and buccolingual; Hillson *et al*., 2005: 418) were taken for each permanent tooth in the samples. Where possible, areas of interproximal attrition were avoided when taking the mesiodistal measurements, but this was difficult when dealing with teeth *in situ*. Alternative measurements proposed by Hillson *et al*. (2005: 419) to overcome this, specifically with regards to the molars, are the mesiobuccal-distolingual and mesiolingual-distobuccal crown diameters. These diagonal measures for the molars were therefore also included.

Considering that the occlusal surface size is dependent upon wear, Smith's (1984) occlusal surface wear index was used to standardize the samples to the same rate of wear. The different occlusal wear patterns are described by Smith from stages 0 to 8 for each tooth. The more severely worn the tooth was, the greater the value given. The mesiodistal maximum crown diameters for incisors were only measured with a stage 3 or less of occlusal attrition, and for the other tooth classes with stage 4 or less. Above these limits occlusal wear began to involve the maximum mesial and distal bulges of the crown side, irrespective of approximal wear effects (Hillson *et al*., 2005). Buccolingual maximum crown diameters were measured in teeth with more occlusal wear up to Smith stage 5 because similarly, if wear was relatively even, the maximum bulges of the respective crown sides were still present. Individual discretion was used for the diagonal molar diameters using Smith stage 4 and 5 as a guide. Diagonal measures were not taken for occlusal wear greater than stage 5. Cervical measurements were not possible due to the inclusion of dental casts in this study. To maximise the sample sizes, teeth from both the left and the right sides of the dental arcade were measured. The side with the most measures was subsequently selected for the statistical analysis to correct for asymmetry. Repeatability of the tooth measurements was evaluated on 15 individuals using Lin’s concordance correlation coefficient. This resulted in an almost perfect agreement between the same observer (Pc=0.996) and very high agreement between two different observers (Pc=0.956).

### 3.2.5. Biodistance analysis

The statistical method of biodistance analysis uses the patterns of morphological variability described previously as a proxy for genetic relatedness. A combination of the different types of data collected (nonmetric and metric) was subjected to this analysis to compare the

Khoesan and Bantu-speaking groups. In the subsequent sections, the biodistance methods used for the nonmetric and metric data are discussed.

*a) Nonmetric data*

Descriptive statistics were determined for the discrete cranial and dental trait data to provide an overall summary of the samples investigated for each objective. Smith's Mean Measure of Divergence (MMD) statistic was used to calculate the biodistances between the groups. To calculate the MMD biodistance statistic, the data was edited to select the most informative traits (Irish, 2010). Factors to bear in mind when dealing with trait selection were firstly, to include as many traits as possible to provide a broad overview of how the groups were phenotypically related. This allowed for objective biodistances (Harris and Sjøvold, 2004). Traits that contained contributory information or showed a significant difference between at least one pair of the groups was also used, as non-significant variables had little use in biodistance studies (Harris and Sjøvold, 2004; Irish, 2010). Secondly, it was necessary to demonstrate that none of the traits were highly correlated because the MMD statistic did not account for this and it results in redundancies (Sjøvold, 1977). Thirdly, it was important to reconsider using groups or traits with small sample sizes because they can lead to negative MMD values in the biodistance results. This is a statistical artefact with no biological meaning (Harris and Sjøvold, 2004; Irish, 2010; Soltysiak, 2011).

The chi square statistic or Fisher's Exact test in the PAST software package (Hammer *et al*., 2001) was used to determine which discrete traits were significantly different between the groups. Tetrachoric correlations were calculated using TetMat v.1.0.3 (Uebersax, 2006) to determine which traits were highly correlated to one another. This was done by investigating traits with $r > 0.5$, $r < -0.5$, in conjunction with $p < 0.05$ (Pawn, 2012). Both correlated traits were not removed but rather individually assessed to determine which trait to select. The trait with the smaller number of observations was generally eliminated, unless the correlated trait showed significance or previous literature indicated that the specific trait was important to include, based on its relevance in distinguishing populations. Lastly, to correct for small sample sizes, it was recommended that variables totalling less than 60% of the maximum number of observations for any trait in the total sample be eliminated (Pawn, 2012). This included examining the individual samples and removing traits with fewer than 10 observations to reduce bias.

The AnthropMMD package (Soltysiak, 2011; Santos, 2016) was used in R (R Core Team, 2018) to calculate the MMD statistic. The Freeman and Tukey angular transformation was

used because it was essentially identical to the Anscombe transformation (Harris and Sjøvold, 2004) and it stabilized the variance more quickly with the small samples commonly found in archaeological studies (Green and Suchey, 1976). This angular transformation also accounted for low (<5%) and high (>95%) trait frequencies, as well as small sample sizes – even as small as 10 (Green and Suchey, 1976; Green *et al*., 1979; Irish, 2010; Santos, 2016). The negative MMD values were generally corrected once trait selection was finalised and sample sizes strengthened. However, if they did persist thereafter they were set to zero as recommended by Konigsberg *et al*. (1994), Relethford *et al*. (1997) and Harris and Sjøvold (2004). The MMD was calculated using the following formula:

$$MMD = \frac{\sum_{i=1}^{r}(\theta_{1i} - \theta_{2i})^2 - \left(1/\left(n_{1i} + \frac{1}{2}\right) \middle| + 1/\left(n_{2i} + \frac{1}{2}\right)\right)}{r}$$

Where

r = The number of uncorrelated traits

θ = angular transformation, where

$$\theta = \left[\frac{1}{2}\right] sin^{-1}\left(1 - \frac{2k}{n+1}\right) + \left[\frac{1}{2}\right] sin^{-1}\left(1 - 2\frac{k+1}{n+1}\right)$$

k = number of positive counts for trait i

n = number of individuals examined for trait i

Once calculated, the biodistances between the groups for each objective were inserted into a matrix and graphically represented using multidimensional scaling. Significance ($p<0.025$) was assessed using the standardised method established by Sjøvold (1977), by comparing the MMD value to the standard deviation [the square root of the variance of the MMD]. If the MMD was greater than two times the standard deviation, the populations were significantly different from each other. The following formula was used to calculate the variance of the MMD:

$$Var(MMD) = \frac{2}{r^2}\sum_{i=1}^{r}\left(\frac{1}{n_{1i}} + \frac{1}{n_{2i}}\right)^2$$

*b) Metric data*

Descriptive statistics were determined for the dental metric data to provide an overall summary of the population groups investigated for each objective. The data was subsequently edited to select the ideal tooth measures to use for the biodistance analysis. Similar to analysing the nonmetric data in this study, there were a few factors to bear in

mind when dealing with trait selection. Including as many traits as possible allowed for objective rather than subjective biodistances and provided a broad overview of how the groups were phenotypically related (Harris and Sjøvold, 2004). Traits that showed significance between at least one pair of the groups were important to include because they contained contributory information useful in biodistance studies (Harris and Sjøvold, 2004; Irish, 2010). Using PAST software (Hammer *et al*., 2001), an ANOVA or Kruskal Wallis test was used to identify the tooth measures that were significantly different at the 5% level. Lastly, evaluating the sample size of the groups and their individual traits prevented statistical bias. As suggested by Pawn (2012), variables totalling less than 60% of the maximum number of measures in the total sample were eliminated, whereas individual tooth measures that had fewer than 10 cases were also removed when possible.

R-matrix theory was used to investigate the biodistances between the groups for each objective. RMET 5.0 (http://employees.oneonta.edu/relethjh/programs/), developed by Relethford, was used to calculate the R-matrix from which the levels of gene flow between the groups were estimated. To calculate the R-matrix, it was important to take into consideration missing values in the data (which are statistically not allowed), the population size of the sample, and the heritability of the traits selected. To account for the missing values often encountered when dealing with archaeological material, individuals with little to no data were removed until the sample contained 70% or more data. This is common practice when dealing with missing data (Clavel *et al*., 2014). The MICE package in R (R Core Team, 2018) then estimated the missing data 100 times using the Bayesian linear regression, and the average was subsequently used to run the biodistance analysis. This method was selected because it performed relatively well with larger proportions of missing data and had low error (Clavel *et al*., 2014). The actual population size of the archaeological samples was unknown and in such circumstances a default estimate of one is used (Relethford and Harpending, 1994; Relethford *et al*., 1997; Irish, 2010; Pawn, 2012). The estimate of trait heritability used in this study was $h^2$=0.55 based on standard procedure used by dental researchers (Kieser, 1990; Scott and Turner, 1997; Stojanowski, 2004; Scherer, 2007; Pawn, 2012).

A genetic $D^2$ distance matrix, derived from the R-matrix in RMET, was also estimated to explore the genetic relationships between the groups. For populations i and j:

$$D_{ij}{}^2 = r_{ii} + r_{jj} - 2r_{ij}$$

The $r_{ij}$ values are defined as average kinship coefficients between the groups, while the $r_{ii}$ values are the coefficients within (Konigsberg, 2006). The $r_{ij}$ values can either be positive or negative. Positive $r_{ij}$ values indicate greater similarity than expected between the groups and negative $r_{ij}$ values indicate they are less genetically alike (Relethford and Harpending, 1994; Relethford *et al*., 1997). Sample size bias correction was selected to correct for sampling error due to small sample size (Relethford, 1991; Relethford *et al*., 1997). Further explanations on formulae used in RMET can be found in Williams-Blangero and Blangero (1989), Relethford and Blangero (1990), Relethford and colleagues (1997) and Relethford (2016). Lastly, the $D^2$ matrix that showed the genetic distances between the population groups was graphically represented using multidimensional scaling, and subsequently compared with the MMD statistic calculated for the nonmetric data.

The Relethford-Blangero analysis and Wright's $F_{ST}$ values were not calculated in this study. Their results can lead to over-interpretation, especially when dealing with small sample sizes, rates of local and long-range gene flow and time depth (Relethford, 2016). Considering the long time spans and wide geographical dispersion of the groups investigated in this study, these additional population genetic measures were not included. The small archaeological samples investigated, may have also significantly affected the results.

# CHAPTER 4: RESULTS

This chapter is divided into three parts. Firstly, objective 1 addressed the relationships between the prehistoric and modern Khoesan and Bantu-speaking groups. For the second objective, the LSA and IA groups were further stratified by time and geographical regions within southern Africa, to explore how these two factors affected their biological relationships. The temporal and geographical results were addressed separately, in part two and part three of this chapter.

## 4.1. BIODISTANCES BETWEEN THE PREHISTORIC AND MODERN GROUPS OF BOTH KHOESAN AND BANTU-SPEAKERS

Cranial and dental nonmetric data, as well as dental metric data was investigated when comparing the LSA (prehistoric Khoesan), IA (prehistoric Bantu-speakers), modern Khoesan and modern Bantu-speaking samples. Their biodistances were assessed to ascertain if the LSA and IA were more similar to the modern Khoesan or modern Bantu-speakers. It is important to note that the modern Khoesan samples represent two different groups of peoples depending on the data type. The cranial Khoesan data was derived from late 19$^{th}$ to early 20$^{th}$ century Khoesan identified by Morris (1986, 1987). The dental Khoesan data on the other hand, was derived from living Khoesan in the 1980's (Reid *et al*., 1991; Navsa, 1992). The biological affinities of the cranial and dental modern Khoesan samples were therefore assessed independently, because their relationships may have differed when compared with the prehistoric and modern Bantu-speakers.

### 4.1.1. Cranial nonmetrics

The frequencies of the 73 nonmetric cranial traits investigated for the LSA, IA, modern Khoesan and modern Bantu-speaking samples are shown in Appendix B, Table B1. Significant differences ($p<0.05$) were observed for 41 traits (56%). Of the 73 cranial traits, only 36 traits were finally selected for the biodistance analysis (Table 4.1). This was because four traits were present in less than 60% of the samples, 15 traits were highly correlated with another trait and 18 traits had negative meanMMD values that were subsequently removed during data editing.

Table 4.1: Cranial nonmetric traits selected (n=36) for the biodistance statistic ($p<0.05$).

| | Chi - squared | | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **$X^2$** | **p** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Metopic ridge | 7.69 | 0.05 | 238 | 37 | 43 | 26 | 24 | 21 | 145 | 26 |
| Oval shaped orbits | 27.83 | **0.00** | 213 | 53 | 38 | 29 | 21 | 29 | 142 | 27 |
| Supraorbital notch (Left) | 11.50 | **0.01** | 236 | 68 | 44 | 86 | 24 | 67 | 153 | 80 |
| Supraorbital foramen (Right) | 17.57 | **0.00** | 233 | 42 | 46 | 15 | 24 | 33 | 153 | 27 |
| Ethmoidal foramina (Left) | 18.04 | **0.00** | 241 | 46 | 15 | 60 | 21 | 81 | 129 | 64 |
| Ethmoidal foramina (Right) | 19.21 | **0.00** | 141 | 82 | 14 | 86 | 19 | 100 | 130 | 64 |
| Infraorbital foramen (Left) | 4.11 | 0.25 | 191 | 88 | 36 | 97 | 24 | 88 | 144 | 92 |
| Infraorbital form | 11.38 | **0.01** | 215 | 5 | 44 | 16 | 24 | 17 | 144 | 6 |
| Infraorbital suture | 14.67 | **0.00** | 124 | 24 | 22 | 23 | 14 | 0 | 127 | 9 |
| Superficial nasion | 22.53 | **0.00** | 158 | 66 | 28 | 29 | 22 | 41 | 121 | 44 |
| Moderately depressed nasion | 9.32 | **0.03** | 158 | 27 | 28 | 54 | 22 | 45 | 121 | 34 |
| Marked depression of nasion | 13.81 | **0.00** | 158 | 7 | 28 | 18 | 22 | 14 | 121 | 22 |
| Angle of nasal bones | 5.77 | 0.12 | 198 | 91 | 37 | 100 | 22 | 95 | 149 | 95 |
| Nasal bone shape | 2.54 | 0.47 | 157 | 54 | 26 | 65 | 18 | 44 | 112 | 50 |
| Zygomaxillary tubercle (Left) | 12.91 | **0.00** | 213 | 45 | 34 | 59 | 24 | 67 | 149 | 62 |
| Zygomaxillary tubercle (Right) | 15.94 | **0.00** | 211 | 43 | 39 | 46 | 23 | 74 | 150 | 60 |
| Subnasal region | 40.22 | **0.00** | 204 | 36 | 34 | 50 | 19 | 32 | 115 | 72 |
| Anterior palate form | 27.09 | **0.00** | 229 | 85 | 45 | 98 | 22 | 91 | 151 | 99 |
| Foramen of Huschke (Left) | 27.31 | **0.00** | 220 | 29 | 48 | 13 | 22 | 9 | 150 | 9 |
| Foramen of Huschke (Right) | 23.55 | **0.00** | 221 | 30 | 48 | 10 | 23 | 13 | 151 | 11 |
| Encroachment of occipital condyles | 76.54 | **0.00** | 185 | 27 | 28 | 21 | 22 | 91 | 151 | 9 |
| Condylar canal (Left) | 11.79 | **0.01** | 137 | 45 | 17 | 76 | 22 | 50 | 131 | 62 |
| Inca bone | 1.09 | 0.78 | 224 | 1 | 38 | 0 | 24 | 0 | 146 | 68 |
| Interparietal groove | 7.37 | 0.06 | 225 | 27 | 43 | 42 | 24 | 42 | 147 | 24 |
| Parietal foramina | 3.38 | 0.34 | 201 | 94 | 30 | 97 | 23 | 100 | 137 | 91 |

Table 4.1: continued.

| | Chi - squared | | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **$X^2$** | **p** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Zygomatic arch | 24.66 | **0.00** | 200 | 29 | 29 | 7 | 24 | 8 | 145 | 43 |
| Inferior frontal eminence (Left) | 4.83 | 0.18 | 217 | 47 | 36 | 36 | 23 | 65 | 147 | 46 |
| Mons temporosphenoidalis (Left) | 81.17 | **0.00** | 211 | 56 | 32 | 38 | 24 | 79 | 151 | 14 |
| Parietotemporal suture (Left) | 35.29 | **0.00** | 176 | 47 | 26 | 65 | 22 | 18 | 127 | 73 |
| Tympanic plate of temporal bone (Right) | 16.37 | **0.00** | 226 | 43 | 48 | 60 | 24 | 46 | 151 | 63 |
| Parietal notch bone (Left) | 10.28 | **0.02** | 202 | 10 | 33 | 6 | 24 | 0 | 144 | 18 |
| Parietal notch bone (Right) | 3.38 | 0.34 | 204 | 12 | 31 | 10 | 24 | 0 | 145 | 12 |
| Occipitomastoid wormian bone (Left) | 10.61 | **0.01** | 196 | 8 | 28 | 21 | 23 | 4 | 141 | 17 |
| Genial tubercles | 3.75 | 0.29 | 127 | 43 | 38 | 50 | 20 | 60 | 117 | 39 |
| Mylohyoid bridge (Left) | 54.21 | **0.00** | 183 | 46 | 38 | 5 | 21 | 33 | 147 | 14 |
| Mylohyoid bridge (Right) | 63.36 | **0.00** | 181 | 45 | 40 | 8 | 21 | 29 | 145 | 8 |

Table 4.2: MMD-SD matrix displaying the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups, using cranial nonmetrics.

| **Population** | **Later Stone Age** | **Iron Age** | **Modern Khoesan** | **Modern Bantu-speakers** |
|---|---|---|---|---|
| Later Stone Age | 0 | 0.009 | 0.012 | 0.003 |
| Iron Age | 0.137* | 0 | 0.019 | 0.010 |
| Modern Khoesan | 0.155* | 0.165* | 0 | 0.013 |
| Modern Bantu-speakers | 0.242* | 0.136* | 0.372* | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

The biodistance matrix comparing the LSA, IA, modern Khoesan and modern Bantu-speaking samples is provided in Table 4.2 and the plot of the multidimensional scaling (MDS) of these distances is shown in Figure 4.1. All the samples were significant at a p-value less than 0.025 when comparing the MMD to the standard deviation of the MMD (Table 4.2). The LSA sample was most similar to the IA group, while the modern Khoesan sample was more similar to the LSA group for the modern comparisons. The LSA group was therefore least similar to the modern Bantu-speaking sample. The IA group was most similar (equidistant) to the LSA sample (MMD=0.137) as the modern Bantu-speaking sample (MMD=0.136). The IA group was therefore least similar to the modern Khoesan sample. In comparison, the modern Khoesan group was the most distant from the modern Bantu-speakers and when compared with the LSA and IA samples respectively, were very similar, but slightly more similarity was observed with the LSA sample. Lastly, the modern Bantu-speaking sample was more similar to the LSA group than the modern Khoesan group (Table 4.2 and Figure 4.1).

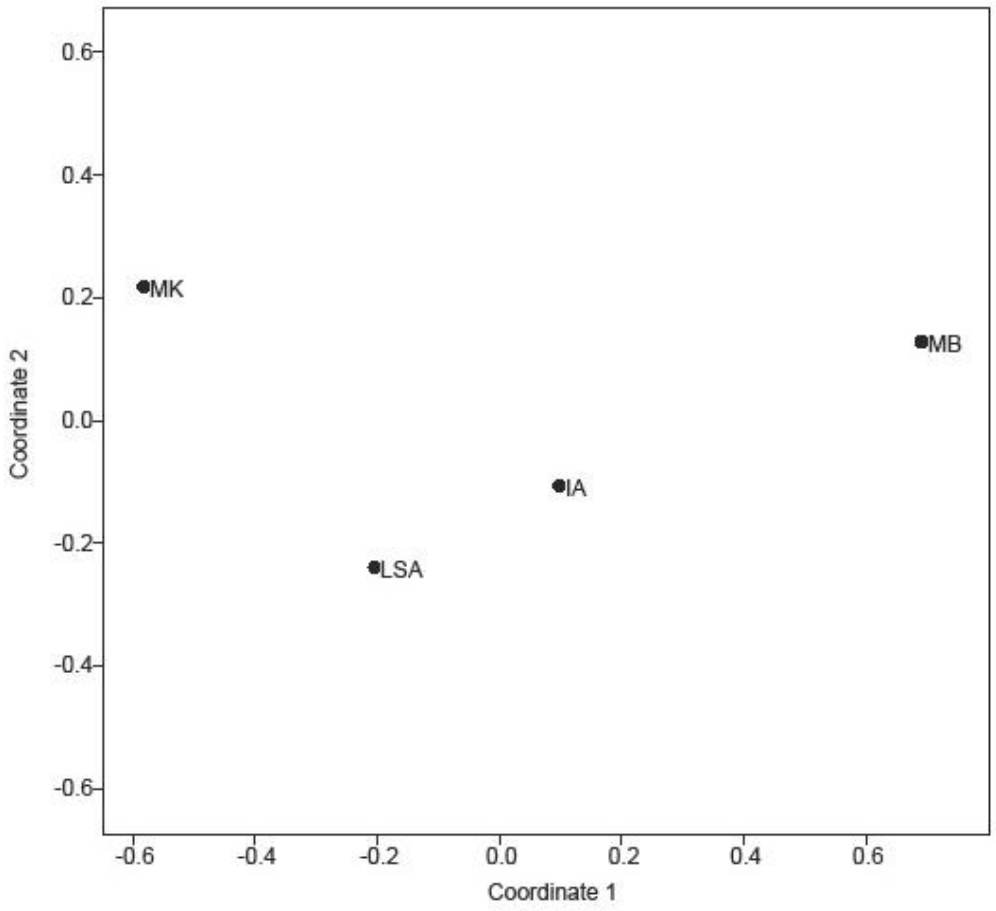


Figure 4.1: MDS illustrating the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups, using cranial nonmetrics (LSA – Later Stone Age, IA – Iron Age, MK – Modern Khoesan, MB – Modern Bantu-speakers).

### 4.1.2. Dental nonmetrics

The frequencies of the 100 dental nonmetric traits investigated for the LSA, IA, modern Khoesan and modern Bantu-speaking samples are shown in Appendix B, Table B2. When comparing these samples, significant differences ($p<0.05$) were identified for 31 of the 100 traits (31%). Of the 100 dental traits investigated, only 17 were finally selected for the biodistance analysis after data editing (Table 4.3). This was because 36 traits were present in less than 60% of the samples, 39 traits were highly correlated with another trait and eight traits had negative meanMMD values.

The biodistances when comparing the LSA, IA, modern Khoesan and modern Bantu-speaking groups are displayed as a matrix (Table 4.4) and are graphically represented in the resulting MDS plot (Figure 4.2). All the groups were significant at the 0.025 level when comparing the MMD to the standard deviation of the MMD. The LSA sample was most similar and equidistant from the IA and modern Khoesan samples, the least similar to the modern Bantu-speakers. In comparison, the IA group was most similar to the modern Khoesan group than the modern Bantu-speaking group, showing least similarity to the LSA group. Thus, both the modern Khoesan and modern Bantu-speaking groups were most similar to the IA sample. The modern Khoesan individuals in particular, also more similar to the IA and modern Bantu-speaking groups than the LSA sample (Table 4.4 and Figure 4.2).

Table 4.3: Dental nonmetric traits selected (n=17) for the biodistance statistic ($p<0.05$).

| Dental Trait | Chi - squared | | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | p | N | Freq (%) | N | Freq (%) | N | Freq (%) | N | Freq (%) |
| Shovelling UC (ASU 2-6) | 4.27 | 0.23 | 52 | 83 | 40 | 93 | 187 | 79 | 70 | 81 |
| Shovelling LI2 (ASU 2-6) | 12.42 | **0.01** | 34 | 18 | 42 | 2 | 191 | 5 | 63 | 2 |
| Shovelling LC (ASU 2-6) | 33.95 | **0.00** | 58 | 84 | 48 | 67 | 209 | 51 | 84 | 38 |
| Double shovelling UC (ASU 2-6) | 13.53 | **0.00** | 61 | 51 | 46 | 48 | 196 | 29 | 81 | 40 |
| Double shovelling UPM1 (ASU 2-6) | 39.69 | **0.00** | 67 | 46 | 51 | 71 | 204 | 28 | 107 | 53 |
| Congenital absence UM3 | 6.89 | 0.08 | 106 | 4 | 52 | 0 | 200 | 4 | 119 | 0 |
| Congenital absence LM3 | 3.54 | 0.32 | 83 | 0 | 50 | 2 | 201 | 1 | 108 | 0 |
| Mesial and Distal accessory cusps UPM1 | 3.87 | 0.28 | 42 | 7 | 38 | 0 | 187 | 3 | 77 | 3 |
| Lingual cusp variation LPM1 (ASU 2-9) | 6.31 | 0.10 | 43 | 23 | 44 | 39 | 188 | 21 | 77 | 23 |
| Hypocone UM2 (ASU 3-5) | 3.87 | 0.28 | 86 | 98 | 52 | 90 | 217 | 95 | 117 | 94 |
| Cusp 5 UM2 (ASU 2-5) | 13.70 | **0.00** | 67 | 45 | 46 | 22 | 170 | 22 | 91 | 30 |
| Cusp 5 LM1 (ASU 2-5) | 2.80 | 0.42 | 56 | 1 | 50 | 98 | 176 | 99 | 91 | 100 |
| Cusp 5 LM2 (ASU 2-5) | 18.51 | **0.00** | 74 | 92 | 41 | 71 | 174 | 66 | 68 | 74 |
| Metacone UM3 (ASU 3.5-5) | 34.84 | **0.00** | 78 | 71 | 45 | 96 | 107 | 62 | 96 | 91 |
| Parastyle UM2 (ASU 1-5) | 1.97 | 0.58 | 96 | 1 | 58 | 3 | 212 | 1 | 113 | 89 |
| Protostylid LM1 (ASU 2-7) | 6.08 | 0.11 | 49 | 8 | 42 | 0 | 186 | 4 | 79 | 1 |
| Mandibular molar pit-tubercle LM2 (P=1-3) | 27.9 | **0.00** | 54 | 15 | 39 | 0 | 199 | 2 | 85 | 1 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.4: MMD-SD matrix displaying the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups, using dental nonmetrics.

| **Population** | **Later Stone Age** | **Iron Age** | **Modern Khoesan** | **Modern Bantu-speakers** |
|---|---|---|---|---|
| Later Stone Age | 0 | 0.014 | 0.008 | 0.010 |
| Iron Age | 0.517* | 0 | 0.009 | 0.012 |
| Modern Khoesan | 0.517* | 0.116* | 0 | 0.006 |
| Modern Bantu-speakers | 0.863* | 0.277* | 0.343* | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

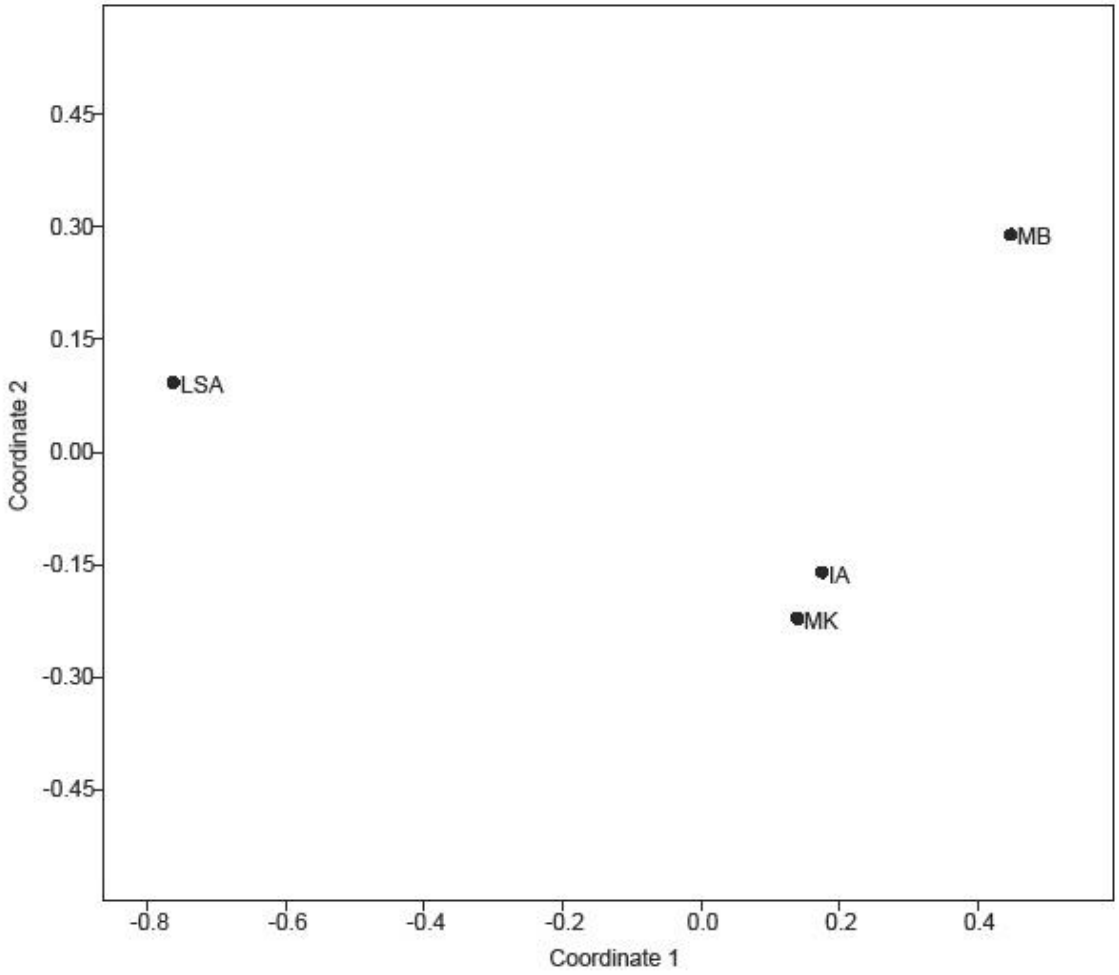


Figure 4.2: MDS illustrating the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups, using dental nonmetrics (LSA – Later Stone Age, IA – Iron Age, MK – Modern Khoesan, MB – Modern Bantu-speakers).

### 4.1.3. Dental metrics

Descriptive statistics of the upper and lower dental measurements for the LSA, IA, modern Khoesan and modern Bantu-speaking groups are presented in Appendix B, Table B3. The means of the dental measurements between the samples were compared and significant differences were observed for all 44 dental variables. Of these variables, only 34 were finally selected for the biodistance analysis (Table 4.5) because 10 dental variables had less than 60% of their data present and were therefore removed during data editing.

Table 4.6 shows the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups that are visually represented in the resulting MDS plot in Figure 4.3. The differences between the biodistances of the LSA sample compared with the other groups are small. Nonetheless, the LSA group was slightly more similar to the modern Khoesan group, when compared with the modern Bantu-speaking group, and was least similar to the IA group. In contrast, the IA sample was closely related to the modern Bantu-speaking sample compared with the modern Khoesan sample. The modern Khoesan sample in particular, was also more similar to the IA and Bantu-speaking groups than the LSA sample (Table 4.6 and Figure 4.3).

Table 4.5: Descriptive statistics for the dental measurements selected (n=34) for the biodistance statistic to compare the prehistoric and modern Khoesan and Bantu-speaking groups.

| | LATER STONE AGE | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 36 | 29 | 38 | 52 | 68 | 61 | 70 | 67 | 75 | 69 | 77 | 71 | 77 | 102 | 108 | 106 | 109 |
| **Min** | 6.03 | 5.41 | 4.86 | 6.28 | 5.94 | 5.72 | 7.11 | 5.49 | 6.82 | 8.65 | 9.67 | 10.81 | 9.60 | 8.15 | 9.68 | 10.20 | 8.65 |
| **Max** | 7.80 | 7.70 | 7.12 | 8.30 | 8.81 | 7.90 | 9.83 | 7.48 | 9.93 | 12.12 | 12.43 | 13.54 | 12.63 | 11.21 | 12.57 | 13.78 | 12.09 |
| **Mean** | 6.76 | 6.80 | 6.10 | 7.37 | 7.67 | 6.74 | 8.60 | 6.43 | 8.56 | 10.18 | 11.00 | 12.24 | 11.04 | 9.74 | 11.02 | 11.93 | 10.57 |
| **SD** | 0.50 | 0.58 | 0.49 | 0.46 | 0.51 | 0.48 | 0.53 | 0.41 | 0.60 | 0.61 | 0.57 | 0.56 | 0.62 | 0.60 | 0.62 | 0.71 | 0.62 |
| | **IRON AGE** | | | | | | | | | | | | | | | | |
| | UI1 | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 21 | 33 | 26 | 39 | 41 | 51 | 52 | 50 | 51 | 43 | 45 | 42 | 44 | 53 | 54 | 53 | 53 |
| **Min** | 5.83 | 6.07 | 5.82 | 6.65 | 7.60 | 6.27 | 8.36 | 5.94 | 8.20 | 9.21 | 10.15 | 11.27 | 10.24 | 8.91 | 10.13 | 10.61 | 9.02 |
| **Max** | 7.92 | 8.26 | 7.50 | 8.37 | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 11.35 | 12.71 | 14.28 | 12.39 | 12.03 | 13.46 | 13.89 | 13.54 |
| **Mean** | 7.15 | 7.14 | 6.58 | 7.67 | 8.49 | 7.18 | 9.56 | 6.84 | 9.53 | 10.58 | 11.48 | 12.63 | 11.55 | 10.12 | 11.55 | 12.28 | 11.26 |
| **SD** | 0.52 | 0.57 | 0.40 | 0.41 | 0.50 | 0.45 | 0.58 | 0.43 | 0.54 | 0.44 | 0.56 | 0.57 | 0.47 | 0.63 | 0.77 | 0.82 | 0.76 |
| | **MODERN KHOESAN** | | | | | | | | | | | | | | | | |
| | UI1 | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 160 | 152 | 146 | 178 | 174 | 159 | 183 | 145 | 181 | 163 | 171 | 134 | 155 | 137 | 167 | 92 | 154 |
| **Min** | 5.69 | 5.01 | 4.72 | 5.66 | 6.37 | 5.88 | 7.58 | 5.57 | 7.69 | 8.71 | 9.63 | 10.76 | 9.47 | 7.83 | 9.35 | 10.22 | 8.31 |
| **Max** | 8.78 | 9.09 | 7.58 | 8.94 | 9.96 | 7.90 | 10.68 | 7.90 | 10.86 | 12.11 | 13.25 | 14.22 | 13.48 | 11.14 | 13.01 | 14.63 | 13.06 |
| **Mean** | 6.85 | 6.55 | 6.16 | 7.47 | 8.04 | 6.85 | 9.04 | 6.52 | 9.06 | 10.38 | 11.12 | 12.45 | 11.24 | 9.51 | 11.14 | 11.98 | 10.69 |
| **SD** | 0.57 | 0.61 | 0.59 | 0.48 | 0.67 | 0.45 | 0.65 | 0.46 | 0.66 | 0.61 | 0.64 | 0.68 | 0.73 | 0.72 | 0.77 | 0.86 | 0.83 |
| | **MODERN BANTU-SPEAKERS** | | | | | | | | | | | | | | | | |
| | UI1 | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 36 | 46 | 54 | 83 | 92 | 87 | 103 | 77 | 95 | 91 | 92 | 94 | 85 | 95 | 99 | 87 | 98 |
| **Min** | 6.43 | 5.71 | 5.29 | 6.67 | 6.97 | 6.03 | 8.17 | 5.84 | 8.40 | 8.87 | 10.23 | 10.89 | 9.16 | 8.35 | 10.08 | 10.73 | 9.80 |
| **Max** | 8.13 | 8.44 | 7.45 | 8.83 | 10.46 | 8.11 | 11.02 | 8.02 | 11.36 | 11.91 | 12.97 | 13.76 | 13.11 | 11.30 | 13.68 | 14.41 | 13.03 |
| **Mean** | 7.20 | 7.00 | 6.54 | 7.66 | 8.57 | 7.19 | 9.60 | 6.71 | 9.52 | 10.45 | 11.41 | 12.57 | 11.40 | 9.92 | 11.62 | 12.33 | 11.04 |
| **SD** | 0.39 | 0.57 | 0.49 | 0.48 | 0.67 | 0.44 | 0.60 | 0.39 | 0.64 | 0.56 | 0.62 | 0.63 | 0.71 | 0.63 | 0.74 | 0.86 | 0.71 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.5: continued.

| | LI1 | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **LATER STONE AGE** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 33 | 30 | 37 | 38 | 48 | 72 | 75 | 76 | 82 | 60 | 68 | 61 | 65 | 85 | 96 | 88 | 93 |
| **Min** | 4.66 | 4.73 | 4.86 | 5.92 | 6.03 | 5.84 | 6.45 | 5.52 | 6.54 | 10.01 | 9.29 | 10.39 | 10.03 | 9.64 | 9.33 | 10.40 | 10.22 |
| **Max** | 6.54 | 6.61 | 6.57 | 7.82 | 7.73 | 8.05 | 8.59 | 8.23 | 9.07 | 12.42 | 11.78 | 13.20 | 12.35 | 12.94 | 12.43 | 13.50 | 13.21 |
| **Mean** | 5.29 | 5.73 | 5.65 | 6.91 | 6.88 | 6.84 | 7.62 | 6.99 | 7.97 | 11.10 | 10.52 | 11.72 | 11.44 | 11.01 | 10.50 | 11.57 | 11.54 |
| **SD** | 0.41 | 0.45 | 0.44 | 0.53 | 0.47 | 0.49 | 0.50 | 0.52 | 0.53 | 0.55 | 0.48 | 0.53 | 0.49 | 0.67 | 0.61 | 0.60 | 0.65 |
| **IRON AGE** | **LI1** | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | |
| | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 34 | 37 | 37 | 40 | 48 | 43 | 50 | 42 | 48 | 38 | 43 | 42 | 42 | 53 | 51 | 51 | 46 |
| **Min** | 5.05 | 5.25 | 5.61 | 6.34 | 6.66 | 6.13 | 7.22 | 6.28 | 7.45 | 9.63 | 9.47 | 10.85 | 10.49 | 9.37 | 9.38 | 10.39 | 10.39 |
| **Max** | 7.35 | 7.37 | 6.80 | 8.03 | 9.04 | 8.06 | 9.52 | 8.26 | 9.61 | 12.77 | 12.19 | 13.24 | 12.91 | 12.82 | 11.94 | 13.92 | 13.06 |
| **Mean** | 5.86 | 6.14 | 6.22 | 7.06 | 7.60 | 7.30 | 8.27 | 7.30 | 8.58 | 11.67 | 10.87 | 12.15 | 11.90 | 11.08 | 10.62 | 11.96 | 11.72 |
| **SD** | 0.43 | 0.46 | 0.33 | 0.44 | 0.52 | 0.41 | 0.57 | 0.56 | 0.58 | 0.61 | 0.56 | 0.60 | 0.60 | 0.73 | 0.63 | 0.75 | 0.69 |
| **MODERN KHOESAN** | **LI1** | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | |
| | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 134 | 142 | 145 | 161 | 163 | 177 | 174 | 151 | 175 | 158 | 165 | 153 | 152 | 123 | 149 | 106 | 101 |
| **Min** | 4.24 | 4.60 | 4.72 | 5.48 | 6.06 | 5.46 | 6.49 | 5.68 | 6.61 | 8.97 | 9.30 | 10.58 | 10.06 | 8.87 | 8.13 | 9.69 | 9.85 |
| **Max** | 7.17 | 7.16 | 7.37 | 8.26 | 9.20 | 8.28 | 9.19 | 8.76 | 9.61 | 13.22 | 12.27 | 13.83 | 13.72 | 12.22 | 12.11 | 13.30 | 12.85 |
| **Mean** | 5.46 | 5.75 | 5.84 | 6.83 | 7.28 | 6.95 | 7.73 | 7.03 | 8.04 | 11.28 | 10.41 | 11.82 | 11.77 | 10.41 | 10.23 | 11.48 | 11.32 |
| **SD** | 0.49 | 0.49 | 0.49 | 0.50 | 0.61 | 0.49 | 0.55 | 0.57 | 0.58 | 0.71 | 0.58 | 0.64 | 0.68 | 0.73 | 0.70 | 0.73 | 0.63 |
| **MODERN BANTU-SPEAKERS** | **LI1** | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | |
| | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 56 | 63 | 63 | 70 | 78 | 98 | 100 | 83 | 97 | 94 | 96 | 91 | 90 | 82 | 84 | 83 | 79 |
| **Min** | 4.86 | 4.92 | 5.27 | 5.89 | 6.06 | 6.43 | 7.17 | 6.09 | 7.51 | 10.16 | 9.51 | 10.86 | 10.44 | 9.34 | 9.37 | 10.13 | 10.13 |
| **Max** | 6.54 | 6.63 | 6.85 | 7.95 | 9.04 | 8.31 | 9.50 | 8.74 | 10.00 | 13.30 | 11.89 | 13.44 | 12.72 | 13.08 | 12.43 | 14.01 | 13.66 |
| **Mean** | 5.68 | 6.03 | 6.14 | 7.07 | 7.78 | 7.33 | 8.32 | 7.39 | 8.69 | 11.50 | 10.75 | 12.04 | 11.68 | 11.15 | 10.55 | 11.95 | 11.67 |
| **SD** | 0.34 | 0.38 | 0.33 | 0.48 | 0.62 | 0.45 | 0.56 | 0.57 | 0.55 | 0.57 | 0.50 | 0.57 | 0.55 | 0.76 | 0.66 | 0.77 | 0.70 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.6: $D^2$ matrix showing the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups using dental metrics.

| **Population** | **Later Stone Age** | **Iron Age** | **Modern Khoesan** | **Modern Bantu-speakers** |
|---|---|---|---|---|
| Later Stone Age | 0 | | | |
| Iron Age | 0.395 | 0 | | |
| Modern Khoesan | 0.337 | 0.182 | 0 | |
| Modern Bantu-speakers | 0.361 | 0.076 | 0.212 | 0 |

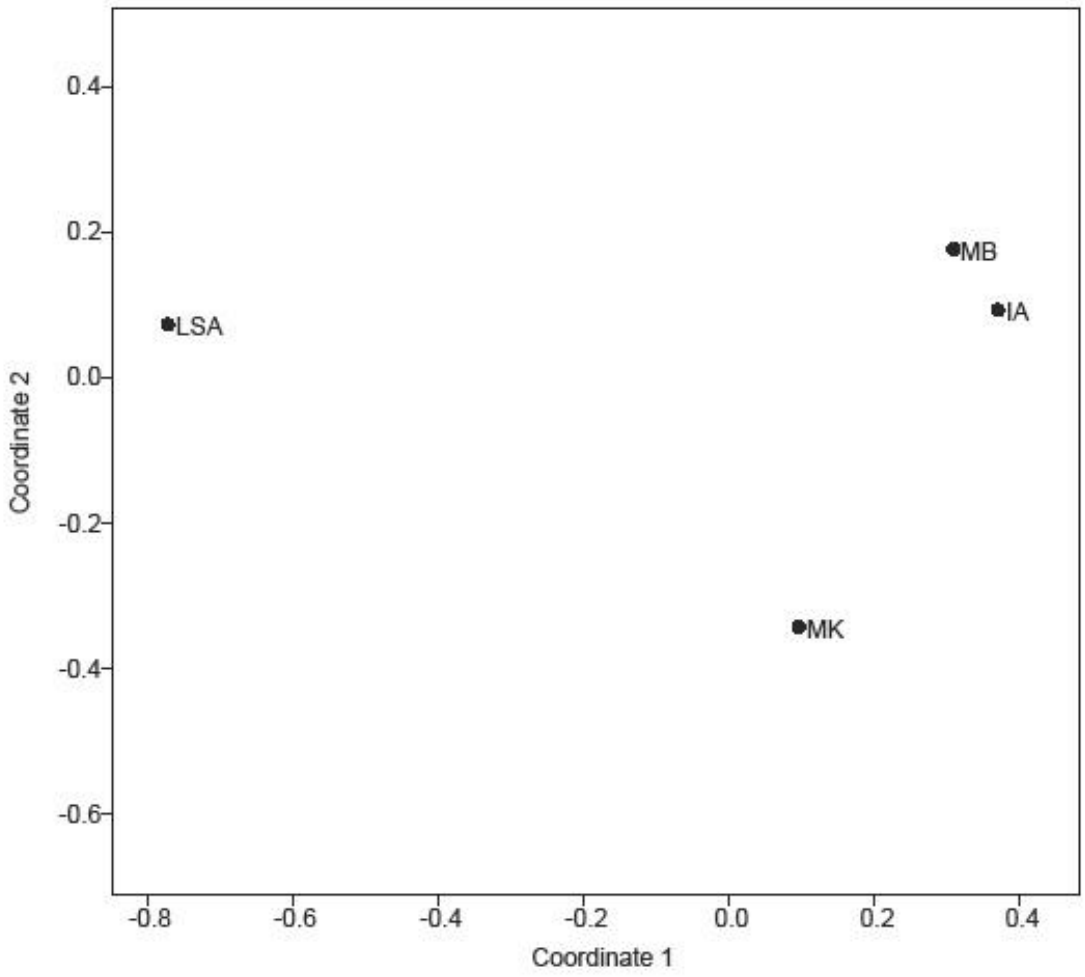


Figure 4.3: MDS of the $D^2$ matrix illustrates the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups using dental metrics (LSA – Later Stone Age, IA – Iron Age, MK – Modern Khoesan, MB – Modern Bantu-speakers).

Table 4.7 and Figure 4.4 show the relative regional gene flow between the prehistoric and modern Khoesan and Bantu-speaking groups, estimated from the dental metrics. Slightly more than expected gene flow was observed between the IA and modern Bantu-speaking sample, whereas slightly less than expected gene flow was observed between all the other population groups (Table 4.7). The R-matrix plot (Figure 4.4) shows similar relationships between the groups investigated, as described previously for the $D^2$ matrix.

Table 4.7: R-matrix showing the average kinship coefficients ($r_{ij}$) between the prehistoric and modern Khoesan and Bantu-speaking groups using dental metrics.

| **Population** | **Later Stone Age** | **Iron Age** | **Modern Khoesan** | **Modern Bantu-speakers** |
|---|---|---|---|---|
| Later Stone Age | 0 | -0.080 | -0.039 | -0.062 |
| Iron Age | -0.080 | 0 | -0.017 | 0.025 |
| Modern Khoesan | -0.039 | -0.017 | 0 | -0.032 |
| Modern Bantu-speakers | -0.062 | 0.025 | -0.032 | 0 |

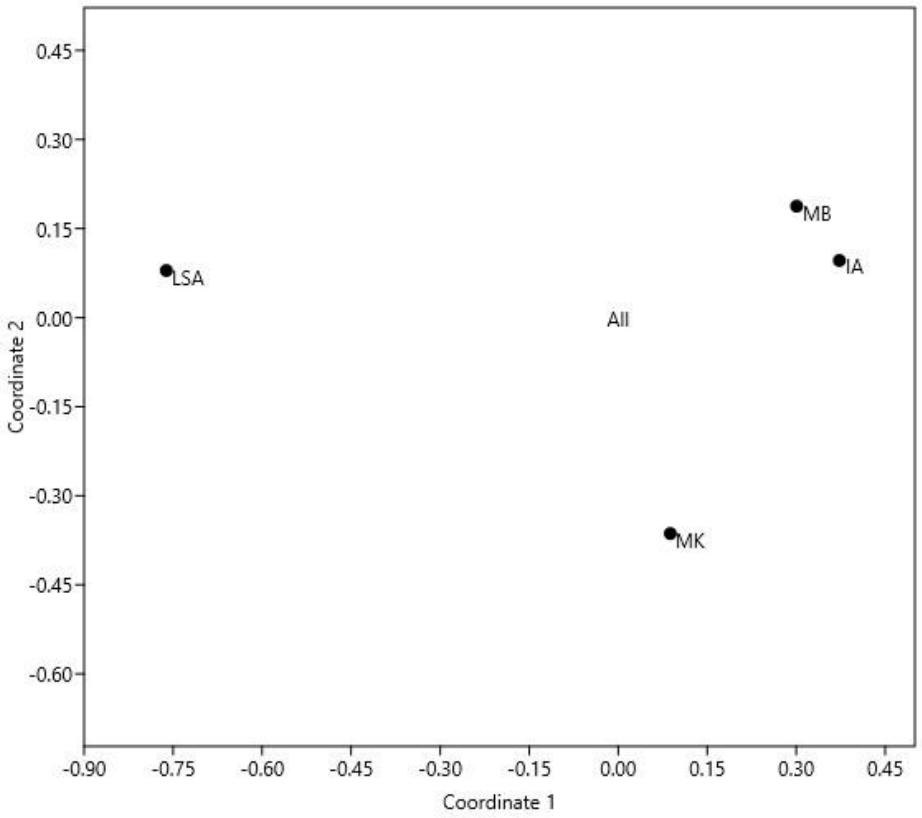


Figure 4.4: MDS of the R-matrix illustrates the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups using dental metrics (LSA – Later Stone Age, IA – Iron Age, MK – Modern Khoesan, MB – Modern Bantu-speakers).

### 4.1.4. Summary

The biodistances between the LSA, IA, modern Khoesan and modern Bantu-speaking groups were significantly different for their cranial and dental morphological characteristics. When comparing the biodistances between the prehistoric and modern Khoesan and Bantu-speaking groups to address objective 1, similarities and differences were observed for the cranial and dental data. The cranial nonmetrics and dental metrics revealed a closer relationship between the IA sample and the modern Bantu-speaking group, compared with the modern Khoesan group. The dental nonmetrics however, demonstrated that the IA group was more similar to the modern Khoesan sample, than the modern Bantu-speaking sample. When comparing the LSA sample to the modern Khoesan and Bantu-speaking groups, cranial and dental similarity was observed with the modern Khoesan group.

When assessing the cranial sample of a modern Khoesan group and the dental sample of another modern Khoesan group, biological differences were noted for their comparisons. The cranial modern Khoesan group showed the most similarity with the LSA sample (MMD=0.155), as well as the IA sample (MMD=0.165). The dental modern Khoesan group on the other hand, was more similar to the IA and Bantu-speaking groups for both their dental metrics and nonmetrics, showing dissimilarity to the LSA sample.

## 4.2. BIODISTANCES BETWEEN THE PREHISTORIC GROUPS OF KHOESAN AND BANTU-SPEAKERS OVER TIME

The archaeological samples investigated are dated from 12,000 to 0 BP and were subdivided into seven temporal groups: LSA: 12ka – 8ka, LSA: 8ka – 4ka, LSA: 4ka – 3ka, LSA: 3ka – 2ka, LSA: 2ka – 1ka, LSA: 1ka – 0ka and IA: 2ka – 0ka. The cranial nonmetrics, dental nonmetrics and dental metrics of these samples were investigated to assess the relationships between the LSA and IA groups over time.

### 4.2.1. Cranial nonmetrics

The frequencies of the 73 cranial nonmetric traits investigated between the LSA and IA groups over time are shown in Appendix C, Table C1. The sample size of the LSA: 12ka – 8ka group was very small (n<10) and subsequently excluded from the biodistance analysis to prevent statistical bias. It was not combined with any other LSA group, like the LSA: 8ka – 6ka, because a change in the size of LSA crania was previously observed at this time (Stynder, 2006). After the exclusion of the LSA: 8ka – 6ka group, 16 of 73 (22%) traits were found significantly different between the groups (Appendix C, Table C1). Moreover, after final data editing for the biodistance analysis, only 18 nonmetric cranial traits were selected (Table 4.8). Fifty-five traits were removed from the analysis because 36 traits were highly correlated with another trait, 10 traits were present in less than 60% of the samples and nine traits had negative meanMMD values.

The resulting biodistance matrix comparing the LSA and IA groups over time is presented in Table 4.9 and the plot of the MDS of these distances is provided in Figure 4.5. When comparing the MMD to the standard deviation of the MMD, significant differences were observed between many of the groups. The IA: 2ka – 0ka group was significantly different from all the LSA groups. The LSA: 3ka – 2ka group was also only significantly different from the post-2,000 BP groups (LSA: 2ka – 1ka and LSA: 1ka – 0ka), whereas the LSA: 4ka – 3ka group was only significantly different from the LSA: 8ka – 4ka, LSA: 2ka – 1ka and LSA: 1ka – 0ka groups (Table 4.9).

Table 4.8: Cranial nonmetric traits selected (n=18) for the biodistance statistic to compare the Later Stone Age (LSA) and Iron Age (IA) groups over time ($p<0.05$).

| Cranial Trait | Chi - squared | | LSA (8ka – 4ka) | | LSA (4ka – 3ka) | | LSA (3ka – 2ka) | | IA (2ka – 0ka) | | LSA (2ka – 1ka) | | LSA (1ka – 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | p | N | Freq (%) | N | Freq (%) | N | Freq (%) | N | Freq (%) | N | Freq (%) | N | Freq (%) |
| Incomplete (nasal part) metopic suture (B) | 5.00 | 0.42 | 21 | 0 | 24 | 8 | 60 | 7 | 21 | 10 | 38 | 0 | 80 | 5 |
| Metopic ridge | 19.89 | **0.00** | 22 | 36 | 27 | 59 | 61 | 51 | 22 | 23 | 40 | 25 | 79 | 25 |
| Supraorbital notch (Left) | 8.77 | 0.12 | 21 | 67 | 23 | 52 | 63 | 70 | 23 | 91 | 40 | 73 | 79 | 71 |
| Supraorbital notch (Right) | 12.53 | **0.03** | 22 | 77 | 22 | 73 | 63 | 67 | 26 | 92 | 39 | 67 | 80 | 85 |
| Infraorbital foramen (Right) | 9.11 | 0.10 | 17 | 100 | 21 | 86 | 51 | 84 | 16 | 75 | 37 | 86 | 62 | 95 |
| Infraorbital form | 18.75 | **0.00** | 21 | 5 | 20 | 0 | 55 | 2 | 21 | 24 | 39 | 0 | 74 | 11 |
| Profile curves of nasal bones | 10.48 | 0.06 | 9 | 44 | 18 | 33 | 42 | 45 | 12 | 67 | 29 | 66 | 44 | 68 |
| Moderately depressed nasion | 10.33 | 0.07 | 10 | 30 | 19 | 26 | 43 | 21 | 12 | 67 | 30 | 37 | 52 | 27 |
| Foramen of Huschke (Left) | 25.31 | **0.00** | 14 | 14 | 23 | 61 | 61 | 33 | 26 | 4 | 36 | 33 | 80 | 20 |
| Foramen of Huschke (Right) | 11.22 | **0.05** | 16 | 25 | 19 | 53 | 60 | 28 | 26 | 8 | 39 | 31 | 78 | 28 |
| Hypoglossal canal bridging (Left) | 4.01 | 0.55 | 15 | 7 | 17 | 0 | 55 | 11 | 16 | 0 | 36 | 11 | 61 | 8 |
| Interparietal groove | 5.55 | 0.35 | 17 | 41 | 27 | 33 | 59 | 25 | 22 | 41 | 38 | 18 | 77 | 27 |
| Zygomatic arch | 19.79 | **0.00** | 16 | 38 | 20 | 35 | 54 | 46 | 15 | 13 | 38 | 18 | 68 | 15 |
| Ophryonic groove | 10.75 | 0.06 | 23 | 39 | 24 | 21 | 62 | 11 | 26 | 12 | 39 | 21 | 81 | 26 |
| Parietotemporal suture (Right) | 6.45 | 0.29 | 13 | 31 | 23 | 57 | 42 | 52 | 17 | 71 | 27 | 52 | 61 | 44 |
| Tympanic plate of temporal bone (Right) | 9.16 | 0.10 | 18 | 50 | 22 | 41 | 60 | 45 | 25 | 72 | 39 | 36 | 80 | 43 |
| Mylohyoid bridge (Left) | 25.57 | **0.00** | 16 | 31 | 18 | 67 | 48 | 63 | 17 | 12 | 32 | 47 | 59 | 27 |
| Mylohyoid bridge (Right) | 30.84 | **0.00** | 16 | 38 | 18 | 72 | 47 | 66 | 19 | 16 | 32 | 34 | 59 | 25 |

Table 4.9: MMD-SD matrix showing the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups over time, using cranial nonmetrics.

| **Time** | **LSA (8ka – 4ka)** | **LSA (4ka – 3ka)** | **LSA (3ka – 2ka)** | **IA (2ka – 0ka)** | **LSA (2ka – 1ka)** | **LSA (1ka – 0ka)** |
|---|---|---|---|---|---|---|
| LSA (8ka – 4ka) | 0 | 0.037 | 0.028 | 0.040 | 0.031 | 0.027 |
| LSA (4ka – 3ka) | 0.097* | 0 | 0.022 | 0.034 | 0.025 | 0.021 |
| LSA (3ka – 2ka) | 0.049 | 0.003 | 0 | 0.024 | 0.016 | 0.011 |
| IA (2ka – 0ka) | 0.154* | 0.423* | 0.306* | 0 | 0.028 | 0.023 |
| LSA (2ka – 1ka) | 0.016 | 0.095* | 0.052* | 0.189* | 0 | 0.014 |
| LSA (1ka – 0ka) | 0.000 | 0.189* | 0.129* | 0.098* | 0.020 | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

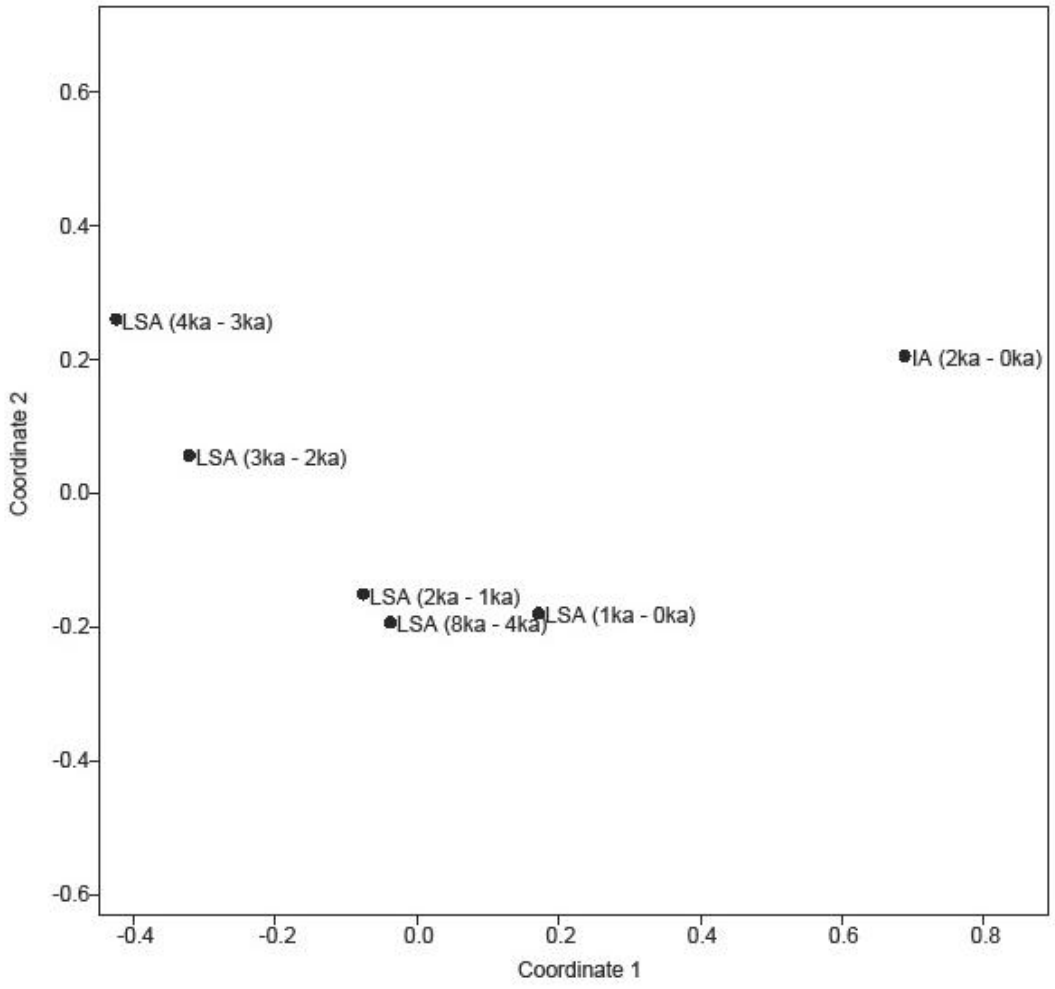


Figure 4.5: MDS illustrating the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups over time, using cranial nonmetrics.

When comparing the biodistances between the post-2,000 BP IA sample and the LSA groups dated from 4,000 to 0 BP, an increase in similarity was observed with time (Table 4.9 and Figure 4.5). The LSA group most similar to the IA was the LSA: 1ka – 0ka, followed by the LSA: 2ka – 1ka, LSA: 3ka – 2ka and LSA: 4ka – 3ka successively, becoming more dissimilar deeper in time. The rate of biological change between their biodistances was also consistent with time. Contrary to the above mentioned dissimilarity observed deeper in time between the LSA and IA groups, the LSA: 8ka – 4ka group was the exception. It had a similar biodistance to the LSA: 2ka – 1ka sample rather than the LSA: 4ka – 3ka sample. This biological change is further elaborated upon below.

When looking at the relationships among the LSA groups, the LSA: 8ka – 4ka group was most similar to the LSA: 2ka – 1ka and LSA: 1ka – 0ka groups, becoming more dissimilar later in time (2,000 to 4,000 BP) (Table 4.9 and Figure 4.5). The negative MMD value between the LSA: 8ka – 4ka and LSA: 1ka – 0ka groups was set to zero, which suggests the groups were biologically identical. The LSA: 4ka – 3ka group was also indistinguishable from the LSA: 3ka – 2ka group, with a very small biodistance between them (MMD=0.003). Both the LSA: 4ka – 3ka and the LSA: 3ka – 2ka groups were therefore equally distant from LSA: 8ka – 4ka and LSA: 2ka – 1ka groups, and were least similar to the LSA: 1ka – 0ka group.

### 4.2.2. Dental nonmetrics

The frequencies of the 100 dental nonmetric traits investigated between the LSA and IA groups are shown in Appendix C, Table C2. Similar to the cranial nonmetric data, the LSA: 12ka – 8ka sample had a very small sample size ($n<10$), as well as the LSA: 8ka – 4ka, LSA: 4ka – 3ka and LSA: 2ka – 1ka groups. Based on previous dental research (Black, 2014), the LSA samples dated from 12,000 to 3,000 BP were combined, as well as those dated from 2,000 to 0 BP, because dental homogeneity was identified during these time periods. This subsequently strengthened the biodistance analysis by increasing the sample sizes. When comparing the combined temporal groups (LSA: 12ka – 3ka, LSA: 3ka – 2ka, LSA: 2ka – 0ka and IA: 2ka – 0ka), significant differences were observed for eight of the 100 dental traits (8%) (Appendix C, Table C2). Once the dental data was finally edited, only six traits were selected for the biodistance analysis (Table 4.10). This was because seven traits were highly correlated with another trait, 70 traits were present in less than 60% of the samples and 17 traits had negative meanMMD values that resulted in a total of 94 traits removed.

The biodistances between the LSA and IA groups are displayed as a matrix in Table 4.11 and graphically represented in the resulting MDS plot in Figure 4.6. Although the results are limited, they do show a clear biological distinction between the LSA and IA groups. When comparing their relationships, the LSA: 12ka – 3ka group was least similar and showed the greatest distance from the IA: 2ka – 0ka group. This difference was significant at $p<0.025$. The biodistances between the LSA: 3ka – 2ka and LSA: 2ka – 0ka groups were also similar compared with the IA: 2ka – 0ka sample, the former LSA group only slightly more similar to the IA group. The LSA: 2ka – 0ka was significantly different from the IA group at $p<0.025$. We also expected the LSA: 3ka – 2ka group to be significant, based on previous results of this study, but this was not the case. Finally, when looking at the relationships among the LSA groups, no biological differences were observed. Negative MMD values were set to zero (biologically identical) when comparing the LSA: 12ka – 3ka and LSA: 2ka – 0ka groups with the LSA: 3ka – 2ka sample. Similarly, the LSA: 12ka – 3ka and LSA: 2ka – 0ka groups were also closely related (MMD=0.001).

Table 4.10: Dental nonmetric traits selected (n=6) for the biodistance statistic to compare the Later Stone Age (LSA) and Iron Age (IA) groups over time ($p<0.05$).

| | Fisher's Exact | | LSA (12ka – 3ka) | | LSA (3ka – 2ka) | | IA (2ka – 0ka) | | LSA (2ka – 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **$X^2$** | **p** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Shovelling LI2 (ASU 2-6) | 5.63 | 0.13 | 15 | 40 | 13 | 38 | 30 | 70 | 37 | 51 |
| Mesial premolar accessory ridges UPM2 (ASU 1-4) | 5.53 | 0.13 | 15 | 100 | 16 | 94 | 32 | 88 | 53 | 98 |
| Odontome UPM1 | 4.15 | 0.25 | 12 | 58 | 14 | 50 | 29 | 28 | 41 | 39 |
| Mesial and Distal accessory cusps UPM1 | 7.66 | **0.03** | 12 | 75 | 14 | 71 | 25 | 96 | 49 | 67 |
| Cusp 6 LM2 (ASU 1-5) | 4.75 | 0.22 | 23 | 96 | 12 | 92 | 25 | 76 | 37 | 89 |
| Distal trigonid crest LM2 | 5.48 | 0.20 | 18 | 28 | 15 | 7 | 24 | 8 | 36 | 8 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.11: MMD-SD matrix showing the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups over time, using dental nonmetrics.

| Time | LSA (12ka – 3ka) | LSA (3ka – 2ka) | IA (2ka – 0ka) | LSA (2ka – 0ka) |
|---|---|---|---|---|
| LSA (12ka – 3ka) | 0 | 0.080 | 0.060 | 0.053 |
| LSA (3ka – 2ka) | 0.000 | 0 | 0.063 | 0.056 |
| IA (2ka – 0ka) | 0.213* | 0.097 | 0 | 0.035 |
| LSA (2ka – 0ka) | 0.001 | 0.000 | 0.113* | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

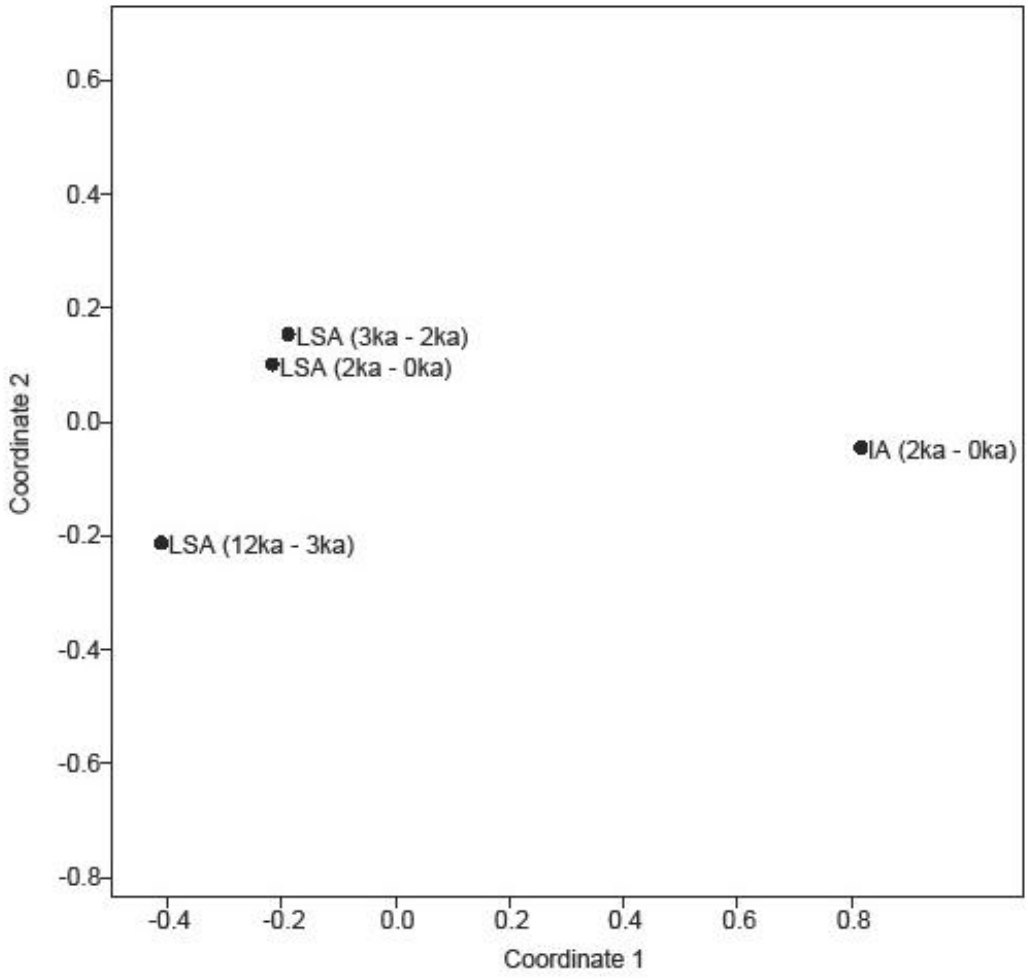


Figure 4.6: MDS illustrating the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups over time using dental nonmetrics.

### 4.2.3. Dental metrics

Descriptive statistics of the upper and lower dentition for the LSA and IA samples separated by time are displayed in Appendix C, Table C3. Like the previously described dental nonmetric analyses, the LSA samples dated from 12,000 to 3,000 BP were combined, as well as those dated from 2,000 to 0 BP, based on earlier dental research (Black, 2014). This strengthened the biodistance analysis by increasing the sample sizes. The means of the dental measures compared between the resulting temporal groups (LSA: 12ka – 3ka, LSA: 3ka – 2ka, LSA: 2ka – 0ka and IA: 2ka – 0ka) showed 35 of the 44 variables (80%) differed significantly (Table 4.12). Once data editing was complete, the final variables selected for the biodistance analysis included 26 of the 44 variables (59%) investigated (Table 4.13). This was because 12 dental variables had less than 60% of their data present and six of the remaining variables were removed due to non-significance.

Table 4.12: Significant differences observed between the Later Stone Age and Iron Age groups over time ($p<0.05$).

| **Variable** | **F** | ***p*** | **Variable** | **F** | ***p*** |
|---|---|---|---|---|---|
| UI1 M-D | 2.85 | 0.06 | LI1 M-D | 2.77 | 0.07 |
| UI1 B-L | 4.84 | **0.01** | LI1 B-L | 8.87 | **0.00** |
| UI2 M-D | 1.34 | 0.27 | LI2 M-D | 4.03 | **0.01** |
| UI2 B-L | 6.25 | **0.00** | LI2 B-L | 9.60 | **0.00** |
| UC M-D | 2.92 | **0.04** | LC M-D | 3.48 | **0.02** |
| UC B-L | 15.46 | **0.00** | LC B-L | 13.46 | **0.00** |
| UPM1 M-D | 6.06 | **0.00** | LPM1 M-D | 8.73 | **0.00** |
| UPM1 B-L | 22.55 | **0.00** | LPM1 B-L | 12.45 | **0.00** |
| UPM2 M-D | 9.35 | **0.00** | LPM2 M-D | 2.51 | 0.06 |
| UPM2 B-L | 28.05 | **0.00** | LPM2 B-L | 7.80 | **0.00** |
| UM1 M-D | 5.15 | **0.00** | LM1 M-D | 9.77 | **0.00** |
| UM1 B-L | 6.96 | **0.00** | LM1 B-L | 5.48 | **0.00** |
| UM1 MB-DL | 2.79 | **0.05** | LM1 MB-DL | 7.56 | **0.00** |
| UM1 ML-DB | 6.87 | **0.00** | LM1 ML-DB | 7.07 | **0.00** |
| UM2 M-D | 3.33 | **0.02** | LM2 M-D | 0.40 | 0.75 |
| UM2 B-L | 8.32 | **0.00** | LM2 B-L | 0.83 | 0.48 |
| UM2 MB-DL | 1.58 | 0.20 | LM2 MB-DL | 3.07 | **0.03** |
| UM2 ML-DB | 9.42 | **0.00** | LM2 ML-DB | 0.69 | 0.56 |
| UM3 M-D | 4.39 | **0.01** | LM3 M-D | 8.86 | **0.00** |
| UM3 B-L | 3.53 | **0.02** | LM3 B-L | 2.73 | **0.05** |
| UM3 MB-DL | 2.43 | 0.07 | LM3 MB-DL | 5.05 | **0.00** |
| UM3 ML-DB | 16.44 | **0.00** | LM3 ML-DB | 6.44 | **0.00** |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.13: Descriptive statistics for the dental measurements (n=26) selected for the biodistance statistic to compare the Later Stone Age (LSA) and Iron Age (IA) groups over time.

| | LSA (12ka – 3ka) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UC | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | UM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | ML-DB | M-D | B-L | ML-DB |
| N | 16 | 18 | 19 | 20 | 19 | 17 | 20 | 19 | 20 | 19 | 22 | 22 | 14 | 16 | 16 |
| Min | 6.68 | 5.72 | 7.11 | 5.52 | 7.70 | 8.65 | 9.81 | 10.81 | 9.78 | 8.15 | 9.85 | 9.03 | 6.94 | 8.63 | 8.23 |
| Max | 8.52 | 7.72 | 9.51 | 7.48 | 9.16 | 11.28 | 11.97 | 13.07 | 12.10 | 11.21 | 12.30 | 12.09 | 10.22 | 12.06 | 10.71 |
| Mean | 7.59 | 6.77 | 8.42 | 6.48 | 8.41 | 9.95 | 10.96 | 12.19 | 10.96 | 9.67 | 11.19 | 10.66 | 8.35 | 10.19 | 9.09 |
| SD | 0.46 | 0.49 | 0.53 | 0.48 | 0.43 | 0.54 | 0.54 | 0.58 | 0.54 | 0.78 | 0.68 | 0.74 | 0.89 | 1.07 | 0.74 |
| | LSA (3ka – 2ka) | | | | | | | | | | | | | | |
| | UC | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | UM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | ML-DB | M-D | B-L | ML-DB |
| N | 14 | 15 | 16 | 16 | 19 | 16 | 19 | 17 | 20 | 23 | 25 | 24 | 20 | 20 | 20 |
| Min | 6.59 | 6.04 | 7.80 | 5.84 | 6.82 | 9.41 | 9.92 | 11.27 | 10.00 | 8.47 | 9.85 | 9.43 | 6.59 | 9.54 | 8.00 |
| Max | 8.81 | 7.69 | 9.40 | 7.02 | 9.45 | 10.98 | 12.43 | 13.54 | 12.63 | 10.84 | 12.20 | 11.38 | 9.16 | 11.97 | 10.69 |
| Mean | 7.46 | 6.67 | 8.51 | 6.36 | 8.23 | 10.13 | 10.84 | 12.19 | 10.81 | 9.66 | 10.81 | 10.35 | 8.13 | 10.62 | 9.21 |
| SD | 0.53 | 0.53 | 0.45 | 0.30 | 0.64 | 0.47 | 0.62 | 0.63 | 0.64 | 0.66 | 0.59 | 0.49 | 0.75 | 0.68 | 0.69 |
| | IA (2ka – 0ka) | | | | | | | | | | | | | | |
| | UC | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | UM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | ML-DB | M-D | B-L | ML-DB |
| N | 21 | 29 | 28 | 27 | 28 | 24 | 26 | 24 | 25 | 29 | 31 | 30 | 23 | 25 | 24 |
| Min | 7.60 | 6.27 | 8.36 | 6.28 | 8.49 | 9.21 | 10.15 | 11.27 | 10.24 | 8.91 | 10.35 | 9.02 | 8.03 | 9.65 | 9.25 |
| Max | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 11.35 | 12.71 | 14.28 | 12.21 | 11.40 | 13.46 | 13.54 | 9.89 | 12.69 | 11.35 |
| Mean | 8.52 | 7.21 | 9.59 | 6.94 | 9.59 | 10.61 | 11.57 | 12.62 | 11.53 | 10.12 | 11.64 | 11.26 | 8.86 | 11.01 | 10.32 |
| SD | 0.55 | 0.50 | 0.63 | 0.45 | 0.57 | 0.48 | 0.65 | 0.64 | 0.50 | 0.62 | 0.81 | 0.84 | 0.50 | 0.75 | 0.47 |
| | LSA (2ka – 0ka) | | | | | | | | | | | | | | |
| | UC | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | UM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | ML-DB | M-D | B-L | ML-DB |
| N | 34 | 25 | 31 | 29 | 34 | 34 | 37 | 34 | 36 | 58 | 59 | 61 | 49 | 52 | 46 |
| Min | 5.94 | 5.81 | 7.78 | 5.55 | 7.68 | 9.06 | 9.67 | 11.22 | 9.60 | 8.33 | 9.68 | 8.65 | 7.04 | 9.09 | 7.68 |
| Max | 8.76 | 7.90 | 9.83 | 7.45 | 9.93 | 12.12 | 12.24 | 13.35 | 12.45 | 10.72 | 12.57 | 11.77 | 9.77 | 14.05 | 10.81 |
| Mean | 7.80 | 6.77 | 8.77 | 6.46 | 8.84 | 10.35 | 11.08 | 12.27 | 11.18 | 9.77 | 11.05 | 10.62 | 8.37 | 10.41 | 9.57 |
| SD | 0.52 | 0.45 | 0.53 | 0.41 | 0.56 | 0.66 | 0.56 | 0.52 | 0.59 | 0.51 | 0.59 | 0.61 | 0.69 | 0.96 | 0.64 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.13: continued.

| | LSA (12ka – 3ka) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | LPM1 | | LPM2 | LM1 | | | LM2 | LM3 | | | |
| | M-D | B-L | B-L | B-L | MB-DL | ML-DB | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 20 | 22 | 27 | 27 | 24 | 24 | 29 | 18 | 19 | 19 | 19 |
| **Min** | 5.85 | 6.59 | 7.18 | 9.29 | 10.39 | 10.03 | 10.40 | 7.92 | 8.97 | 9.08 | 8.04 |
| **Max** | 7.55 | 8.39 | 8.97 | 11.32 | 12.67 | 12.15 | 13.34 | 11.52 | 10.93 | 11.80 | 12.44 |
| **Mean** | 6.80 | 7.50 | 7.97 | 10.50 | 11.55 | 11.36 | 11.58 | 9.84 | 9.83 | 10.40 | 10.35 |
| **SD** | 0.45 | 0.51 | 0.54 | 0.50 | 0.54 | 0.49 | 0.70 | 0.95 | 0.61 | 0.70 | 0.98 |
| | **LSA (3ka – 2ka)** | | | | | | | | | | |
| | LPM1 | | LPM2 | LM1 | | | LM2 | LM3 | | | |
| | M-D | B-L | B-L | B-L | MB-DL | ML-DB | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 13 | 15 | 14 | 13 | 10 | 12 | 16 | 13 | 14 | 12 | 14 |
| **Min** | 6.03 | 6.87 | 7.38 | 9.58 | 10.96 | 10.36 | 10.74 | 8.56 | 7.94 | 9.12 | 8.51 |
| **Max** | 7.86 | 8.33 | 8.58 | 11.46 | 12.46 | 12.35 | 12.68 | 12.72 | 11.55 | 12.81 | 12.51 |
| **Mean** | 6.66 | 7.49 | 7.84 | 10.33 | 11.53 | 11.26 | 11.37 | 10.03 | 9.85 | 10.67 | 10.27 |
| **SD** | 0.51 | 0.49 | 0.38 | 0.47 | 0.48 | 0.57 | 0.55 | 1.12 | 0.97 | 0.94 | 0.99 |
| | **IA (2ka – 0ka)** | | | | | | | | | | |
| | LPM1 | | LPM2 | LM1 | | | LM2 | LM3 | | | |
| | M-D | B-L | B-L | B-L | MB-DL | ML-DB | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 26 | 31 | 27 | 26 | 26 | 26 | 28 | 22 | 22 | 21 | 21 |
| **Min** | 6.13 | 7.22 | 7.45 | 10.00 | 11.11 | 10.96 | 10.39 | 10.04 | 8.80 | 9.76 | 10.33 |
| **Max** | 8.06 | 9.52 | 9.61 | 12.19 | 13.24 | 12.91 | 13.47 | 12.03 | 11.25 | 12.18 | 12.34 |
| **Mean** | 7.35 | 8.30 | 8.57 | 10.96 | 12.23 | 11.93 | 11.95 | 11.08 | 10.32 | 11.27 | 11.25 |
| **SD** | 0.40 | 0.64 | 0.64 | 0.60 | 0.64 | 0.58 | 0.76 | 0.60 | 0.64 | 0.60 | 0.56 |
| | **LSA (2ka – 0ka)** | | | | | | | | | | |
| | LPM1 | | LPM2 | LM1 | | | LM2 | LM3 | | | |
| | M-D | B-L | B-L | B-L | MB-DL | ML-DB | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 35 | 35 | 37 | 25 | 24 | 26 | 40 | 43 | 44 | 44 | 40 |
| **Min** | 5.84 | 6.45 | 6.54 | 9.83 | 11.01 | 10.54 | 10.48 | 8.79 | 8.69 | 8.31 | 9.54 |
| **Max** | 8.05 | 8.59 | 9.07 | 11.78 | 13.20 | 12.29 | 13.50 | 12.01 | 11.34 | 12.14 | 12.41 |
| **Mean** | 6.93 | 7.76 | 8.05 | 10.63 | 11.94 | 11.56 | 11.64 | 10.34 | 10.20 | 10.76 | 10.84 |
| **SD** | 0.50 | 0.49 | 0.57 | 0.47 | 0.50 | 0.44 | 0.55 | 0.74 | 0.62 | 0.72 | 0.68 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

The biodistances between the LSA and IA groups over time are displayed in Table 4.14 and the resulting MDS plot in Figure 4.7. A clear biological distinction between the temporally separated LSA groups and the IA sample was observed. When comparing the IA: 2ka – 0ka group with the LSA groups, the IA was most similar to the LSA: 2ka – 0ka and least similar to the LSA: 3ka – 2ka. The LSA: 12ka – 3ka was also more similar to the IA than the LSA: 3ka – 2ka. When assessing the relationships among the LSA groups, on the other hand, the LSA: 2ka – 0ka group was more similar to the LSA: 12ka – 3ka than the LSA: 3ka – 2ka group.

Table 4.14: $D^2$ matrix showing the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups over time using dental metrics.

| Time | LSA (12ka – 3ka) | LSA (3ka – 2ka) | IA (2ka – 0ka) | LSA (2ka – 0ka) |
|---|---|---|---|---|
| LSA (12ka – 3ka) | 0 | | | |
| LSA (3ka – 2ka) | 0.116 | 0 | | |
| IA (2ka – 0ka) | 0.472 | 0.572 | 0 | |
| LSA (2ka – 0ka) | 0.108 | 0.161 | 0.300 | 0 |

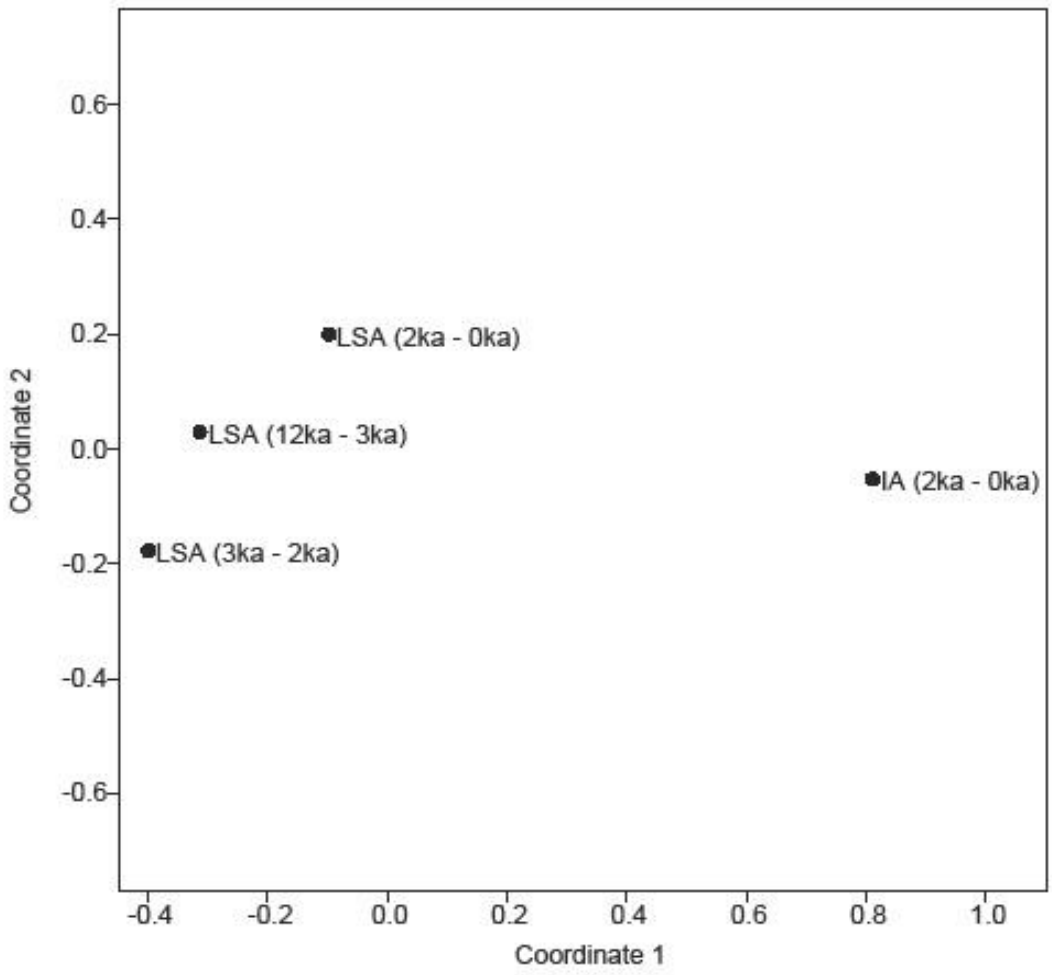


Figure 4.7: MDS of the $D^2$ matrix illustrates the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups using dental metrics.

Table 4.15 and Figure 4.8 show the relative regional gene flow between the LSA and IA groups over time. Slightly more gene flow than expected was observed between the LSA: 12ka – 3ka and LSA: 3ka – 2ka groups. Considerably less gene flow than expected was observed between the IA sample and all the LSA samples, but particularly less so for the LSA: 2ka – 0ka sample (Table 4.15). Slightly less gene flow than expected was also observed for the LSA: 12ka – 3ka and LSA: 3ka – 2ka groups, when compared with the LSA: 2ka – 0ka group. The R-matrix plot (Figure 4.8) shows similar relationships between the groups investigated, as described previously for the $D^2$ matrix.

Table 4.15: R-matrix showing the average kinship coefficients ($r_{ij}$) between the Later Stone Age (LSA) and Iron Age (IA) groups over time using dental metrics.

| **Time** | **LSA (12ka – 3ka)** | **LSA (3ka – 2ka)** | **IA (2ka – 0ka)** | **LSA (2ka – 0ka)** |
|---|---|---|---|---|
| LSA (12ka – 3ka) | 0 | 0.020 | -0.094 | -0.010 |
| LSA (3ka – 2ka) | 0.020 | 0 | -0.125 | -0.017 |
| IA (2ka – 0ka) | -0.094 | -0.125 | 0 | -0.022 |
| LSA (2ka – 0ka) | -0.010 | -0.017 | -0.022 | 0 |

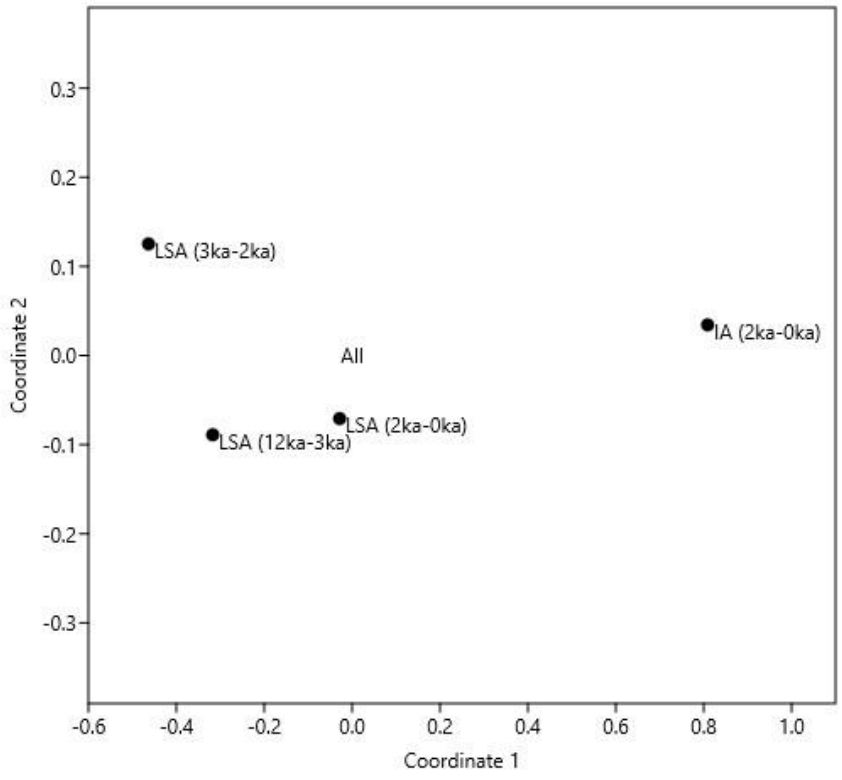


Figure 4.8: MDS of the R-matrix illustrates the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups using dental metrics.

### 4.2.4. Summary

To understand the relationships between the LSA and IA groups over time, the relationships among the LSA peoples are summarised beforehand. The cranial results showed substantial biological change for the LSA samples at 4,000 BP and similarly, a slight change in dental size was observed at 3,000 BP. Please note that these values are arbitrary temporal divisions based on the subdivisions of the samples. The LSA crania dated from 4,000 to 3,000 BP were most dissimilar from the LSA crania dated from 8,000 to 4,000 BP, as well as the post-2,000 BP LSA groups. The LSA cranial results also indicated that the LSA: 4ka – 3ka and LSA: 3ka – 2ka groups were biologically alike, with significant differences observed when compared with the LSA: 8ka – 4ka and post-2,000 BP LSA groups. The biodistances between the LSA: 8ka – 4ka and LSA: 2ka – 1ka groups, in particular, compared with either the LSA: 4ka – 3ka or LSA: 3ka – 2ka groups, were relatively equidistant, which further supported their biological relatedness. The cranial change observed at 4,000 BP therefore appeared to return at 2,000 BP to previous cranial morphology (pre-4,000 BP). The pre-4,000 BP LSA individuals were thus similar to the post-2,000 BP LSA individuals and their relationships strengthened with time. The LSA: 2ka – 1ka group was slightly more distant (MMD=0.016) from the LSA: 8ka – 4ka group, than the LSA: 1ka – 0ka group, which was biologically identical (MMD=0.000) to the LSA: 8ka – 4ka group.

Similar to the cranial results, a slight dental change was also observed for the metric results of the LSA samples at 3,000 BP. Their tooth dimensions dated from 12,000 to 3,000 BP were more similar to the LSA: 2ka – 0ka group than the LSA: 3ka – 2ka group. This suggested dental change in the LSA samples from 3,000 BP. With so few LSA samples investigated, it was impossible to say when the dental change observed at 3,000 BP may have recovered to the previously observed dental morphology (like the cranial nonmetrics). However, bearing in mind the similarity between the LSA: 12ka – 3ka group and the LSA: 2ka – 0ka group, the results suggested morphological recovery from 2,000 BP or thereafter. Lastly, the dental nonmetrics did not provide any useful information about the dental change of the LSA samples through time because very little dissimilarity was observed between the groups.

With a greater understanding of the cranial and dental pattern of variability within the LSA peoples over time, the temporally-separated LSA groups are considered with respect to the IA sample. This addressed the first part of objective 2. The crania and dentition of the IA sample (post-2,000 BP) was significantly different from all the temporally-separated LSA groups.

The LSA crania and dentition also became more similar to the IA sample over time, the rate of cranial change increased consistently. The IA: 2ka – 0ka group was therefore least similar to the LSA: 4ka – 3ka and most similar to the LSA: 1ka – 0ka group. Although the LSA: 4ka – 3ka group was biologically identical to the LSA: 3ka – 2ka group (mentioned previously), their biodistances from the IA group were quite different. The LSA: 3ka – 2ka had an MMD of 0.306 and the LSA: 4ka – 3ka had an MMD of 0.423 from the IA: 2ka – 0ka sample. In addition to this, a cranial change over time was identified from 4,000 BP, when assessing the relationships among the LSA samples in this study. In particular, similarity was observed between the LSA: 8ka – 4ka and post-2,000 BP LSA groups. These relationships were similar when the LSA groups were compared with the IA sample. The LSA: 8ka – 4ka group was as biologically alike from the IA group as the LSA post-2,000 BP groups.

Finally, although the dental results were limited, especially for the dental nonmetrics, they were in keeping with the cranial results when comparing the LSA and IA groups over time. The dental metrics indicated the IA (post-2,000 BP) group was most similar to the LSA: 2ka – 0ka group and least similar to the LSA: 3ka – 2ka group. Due to the dental change observed at 3,000 BP in this study, when assessing the relationships among the LSA samples, the LSA: 12ka – 3ka was also more similar to the IA sample than the LSA: 3ka – 2ka group. In comparison, the dental nonmetric results showed the same overall picture, except the LSA: 3ka – 2ka group was not significantly different or more dissimilar to the IA sample. This did not correspond with the cranial or dental metric results.

## 4.3. GEOGRAPHICAL BIODISTANCES BETWEEN THE PREHISTORIC GROUPS OF KHOESAN AND BANTU-SPEAKERS

The archaeological samples in this study were geographically divided into seven regions within southern Africa: LSA Inland central, LSA West coast, LSA SW coast, LSA South coast, LSA SE coast, IA North East and IA South Zambia. The samples are dated from 12,000 to 0 BP, so it is important to note that the different regions are not temporally identical. The LSA Inland central group is however the exception, because the individuals represented are dated to a more recent time (±500 BP). In addition to this, the IA North East group consists of EIA and LIA individuals, the latter making up the majority of the sample. These geographical regions were investigated for their cranial nonmetrics, dental nonmetrics and dental metrics to assess the relationships between the LSA and IA groups over geographical space.

To strengthen the biodistance analysis, some of the geographical regions were removed, particularly for the dental comparisons, to prevent statistical bias due to small sample size. The LSA West coast and LSA SE coast samples in particular, had few individuals present ($n<10$) for their dental nonmetric and dental metric data (Appendix D, Table D2 and D3), and were thus removed. Based on previous research that investigated similar samples in these regions (Stynder, 2006; Ginter, 2008; Black, 2014), the LSA samples on the West and SE coasts were not combined with any other geographical areas. This was because these particular regions are described as unique in terms of population movement or their relationships with other geographical areas are noteworthy (biological differences observed). On the other hand, the IA South Zambia sample also had relatively small sample sizes ($n<10$) for both the cranial and dental comparisons (Appendix D, Table D1 – 3), yet the sample was included in the biodistance analysis for comparison purposes. This was due to elimination of most of the extremely small sample sizes during data editing (when selecting the variables for the biodistance analysis) and a correction for small sample size was used in this study. It was also not combined with the IA North East group because biological differences were noted when comparing their dentition in a similar study by Warren, *et al.* (2015).

### 4.3.1. Cranial nonmetrics

The frequencies of the 73 cranial traits investigated for the geographical regions within southern Africa are presented in Appendix D, Table D1. When comparing the cranial traits between all the regions, significant differences ($p<0.05$) were observed for 21 of the 73 traits (29%). For the biodistance analysis however, only 18 nonmetric cranial traits were finally selected after data editing (Table 4.16). Fifty-five traits were removed from the analysis because 10 traits were present in less than 60% of the samples, 37 traits were highly correlated with another trait and eight traits had negative meanMMD values.

The resulting biodistance matrix that compared the geographical regions of southern Africa is displayed in Table 4.17 and the plot of the MDS of these distances is represented in Figure 4.9. When comparing the MMD to the standard deviation of the MMD, most of the regions were significantly different from one another at $p<0.025$, except when comparing the LSA West coast to the Inland central and SW coast samples, the LSA South coast to the LSA SE coast samples, and the IA North East to the IA South Zambia samples. The biodistances between these groups were small, indicating biological homogeneity of these areas. The IA samples in particular, were biologically identical (negative MMD value set to zero), even though they were somewhat distant from one another geographically. The LSA samples on the other hand, showed greatest similarity between the West coast and the neighbouring Inland central (MMD=0.001) and SW coast (MMD=0.008) regions. In comparison, the LSA samples from the South and the SE coast regions, that were also geographical neighbours, differed slightly, but were more similar (MMD=0.019) when compared with the regions that showed significant differences.

Table 4.16: Cranial nonmetric traits selected (n=18) for the biodistance statistic to compare the geographical regions of southern Africa ($p<0.05$).

| | Chi - squared | | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **$X^2$** | **p** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Incomplete (nasal part) metopic suture (B) | 8.67 | 0.19 | 53 | 8 | 11 | 0 | 76 | 3 | 68 | 6 | 17 | 0 | 29 | 14 | 5 | 20 |
| Metopic ridge | 11.90 | 0.06 | 52 | 29 | 12 | 42 | 77 | 38 | 74 | 49 | 18 | 17 | 33 | 24 | 8 | 25 |
| Oval shaped orbits | 15.98 | **0.01** | 43 | 37 | 13 | 54 | 74 | 49 | 62 | 65 | 17 | 65 | 27 | 26 | 9 | 44 |
| Round shaped orbits | 14.15 | **0.03** | 43 | 2 | 13 | 15 | 74 | 3 | 62 | 0 | 17 | 0 | 27 | 0 | 9 | 0 |
| Supraorbital notch (Right) | 11.73 | 0.07 | 53 | 83 | 12 | 67 | 77 | 66 | 73 | 75 | 17 | 88 | 36 | 89 | 9 | 89 |
| Supraorbital foramen (Left) | 26.69 | **0.00** | 50 | 44 | 11 | 73 | 76 | 49 | 74 | 50 | 18 | 17 | 34 | 12 | 9 | 22 |
| Superficial nasion | 24.47 | **0.00** | 36 | 78 | 9 | 67 | 54 | 74 | 46 | 54 | 10 | 30 | 19 | 26 | 8 | 38 |
| Anterior palate form | 11.60 | 0.07 | 53 | 83 | 14 | 71 | 70 | 86 | 69 | 84 | 18 | 94 | 32 | 100 | 11 | 100 |
| Foramen of Huschke (Right) | 12.19 | 0.06 | 53 | 26 | 13 | 23 | 70 | 24 | 63 | 40 | 16 | 31 | 39 | 10 | 8 | 13 |
| Ophryonic groove | 5.89 | 0.44 | 54 | 24 | 11 | 18 | 77 | 17 | 73 | 26 | 17 | 18 | 36 | 14 | 9 | 0 |
| Tympanic plate of temporal bone (Left) | 14.97 | **0.02** | 54 | 43 | 12 | 50 | 73 | 52 | 67 | 27 | 17 | 29 | 37 | 54 | 9 | 67 |
| Tympanic plate of temporal bone (Right) | 19.18 | **0.00** | 55 | 47 | 12 | 50 | 70 | 54 | 67 | 27 | 17 | 29 | 37 | 57 | 9 | 78 |
| Supra-asterionic region | 25.05 | **0.00** | 47 | 57 | 13 | 46 | 73 | 23 | 67 | 21 | 18 | 44 | 30 | 43 | 8 | 13 |
| Os japonicum (Left) | 23.83 | **0.00** | 46 | 0 | 13 | 15 | 75 | 1 | 67 | 0 | 16 | 0 | 24 | 0 | 7 | 0 |
| Occipitomastoid wormian bone (Left) | 5.15 | 0.52 | 40 | 5 | 12 | 0 | 65 | 11 | 57 | 11 | 17 | 6 | 22 | 18 | 5 | 20 |
| Mental foramen (Right) | 6.55 | 0.36 | 40 | 83 | 12 | 75 | 59 | 73 | 51 | 78 | 12 | 75 | 30 | 90 | 9 | 100 |
| Mylohyoid bridge (Left) | 34.38 | **0.00** | 45 | 31 | 12 | 25 | 58 | 52 | 53 | 57 | 10 | 70 | 27 | 7 | 10 | 0 |
| Mylohyoid bridge (Right) | 29.58 | **0.00** | 45 | 31 | 11 | 27 | 58 | 47 | 50 | 60 | 12 | 50 | 29 | 10 | 10 | 0 |

Table 4.17: MMD-SD matrix showing the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups, using cranial nonmetrics.

| Region | LSA Inland central | LSA West coast | LSA SW coast | LSA South coast | LSA SE coast | IA North East | IA South Zambia |
|---|---|---|---|---|---|---|---|
| LSA Inland central | 0 | 0.035 | 0.012 | 0.013 | 0.030 | 0.019 | 0.049 |
| LSA West coast | 0.001 | 0 | 0.033 | 0.034 | 0.050 | 0.040 | 0.070 |
| LSA SW coast | 0.035* | 0.008 | 0 | 0.010 | 0.027 | 0.016 | 0.047 |
| LSA South coast | 0.097* | 0.093* | 0.041* | 0 | 0.028 | 0.017 | 0.048 |
| LSA SE coast | 0.075* | 0.120* | 0.065* | 0.019 | 0 | 0.034 | 0.064 |
| IA North East | 0.137* | 0.236* | 0.231* | 0.314* | 0.173* | 0 | 0.054 |
| IA South Zambia | 0.164* | 0.198* | 0.216* | 0.347* | 0.284* | 0.000 | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

When comparing the biodistances between the LSA and IA groups, their distances appeared to be associated with their geographical distributions, except for the LSA sample located on the south coast of South Africa. The IA North East sample was most similar to the LSA groups located closest (Inland central and SE coast), followed by those most geographically distant (West coast and SW coast). The LSA South coast sample however, was the most dissimilar from the IA North East sample, even though it was geographically closer than the LSA samples located on the West and SW coasts. In addition to this, even though the other IA sample (South Zambia) was biologically identical to the IA North East sample, slightly different relationships were observed when compared with the LSA groups. The LSA group most similar to the IA South Zambia group was the Inland central group, followed closely by the West, SW and slightly more dissimilar SE coast regions. Like with the IA North East group, the IA South Zambia group was also most dissimilar from the LSA South coast group. Finally, in general, the IA North East sample was more similar to all the LSA groups than the IA South Zambia sample. This somewhat agreed with their geographical distances.

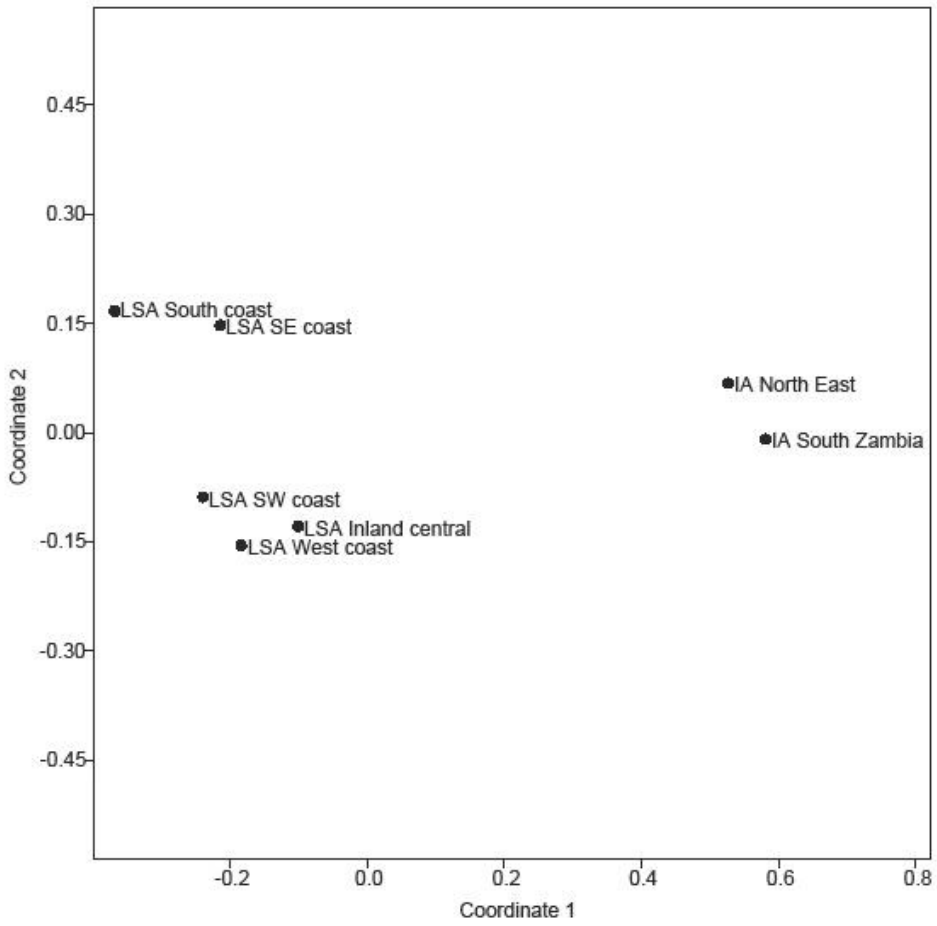


Figure 4.9: MDS illustrating the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups using cranial nonmetrics.

When looking at the relationships among the LSA groups, a further association between the sample's location and their biological similarity with the other LSA samples was observed. Yet again, the South coast group was the exception. Those LSA samples in the Inland central, West coast and SW coast regions, which were similar to one another (mentioned previously), were more dissimilar and geographically distant from the South and SE coast regions. More specifically, the LSA sample located on the SW coast was most similar to its western neighbour (West coast) and least similar to the SE coast sample. The Inland central and South coast samples were somewhat between these two groups when comparing their relationships with the SW coast group. Given their geographical proximity, it was interesting that the Inland central sample was slightly more similar to the SW than the South coast group. In comparison, the South coast sample was also more similar to the samples located to the east (SE coast, mentioned previously) than the samples located to the west (SW coast), the Inland central region most dissimilar from the South coast region. Lastly, the LSA SE coast sample was more similar to the SW coast and Inland central groups than the West coast group, which was the most geographically distant sample.

### 4.3.2. Dental nonmetrics

The frequencies of the 100 dental nonmetric traits investigated for the geographical regions of southern Africa are displayed in Appendix D, Table D2. Significant differences ($p<0.05$) were observed for 12 of the 100 traits (12%). Once data editing was complete, only eight dental nonmetric traits were finally selected for the biodistance analysis (Table 4.18). This was because 60 traits had less than 60% data present, 13 traits were highly correlated with another trait and 19 traits had a negative meanMMD value.

The resulting biodistances that compared the geographical regions of southern Africa are displayed as a matrix in Table 4.19 and visually represented as an MDS plot in Figure 4.10. When comparing the MMD to the standard deviation of the MMD, significant differences were observed at $p<0.025$. Majority of the IA samples were significant when compared with the LSA groups. The IA North East sample was significantly different from all the LSA groups considered for this analysis. The IA South Zambia sample on the other hand was also significantly different from the LSA groups, except for the SW coast LSA group. When compared with one another, the IA samples were also significantly different, while the LSA samples were not significantly different. Lastly, the biodistance between the IA samples (MMD=0.318) suggested they were as similar to one another as the LSA Inland central group was to the IA South Zambia group (MMD=0.312).

When investigating the relationships between the LSA and IA groups, the biodistances between the samples (like the cranial nonmetrics for this study) appeared to be associated with their geographical distributions. The LSA sample located on the South coast was however, the exception. The IA North East group was most similar to the LSA Inland central group, which was geographically closest. Slightly less similarity was then observed for the more geographically distant LSA groups along the SW and South coast regions, the latter being least similar to the IA North East group. Similarly, the IA South Zambia sample was the most similar to the LSA Inland central sample and least similar to the LSA South coast sample. The biodistance between the IA South Zambia and the LSA SW coast groups however, was questionable due to its non-significance and close similarity to one another. This was contrary to the relationship observed between these groups for the cranial results and the dental metric results (see section 4.3.3). In general, the IA South Zambia sample was more dissimilar from all the LSA samples than the IA North East sample, the exception being the LSA SW coast sample. These relationships corresponded with their geographical distances.

Table 4.18: Dental nonmetric traits selected (n=8) for the biodistance statistic to compare the geographical regions of southern Africa ($p<0.05$).

| | Fisher's exact | | LSA Inland central | | LSA SW coast | | LSA South coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **$X^2$** | **p** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Shovelling LI1 (ASU 2-6) | 11.47 | 1.00 | 28 | 61 | 11 | 18 | 19 | 47 | 36 | 56 | 9 | 11 |
| Distal premolar accessory ridges LPM1 (ASU 1-4) | 4.24 | 0.31 | 31 | 6 | 11 | 18 | 11 | 18 | 38 | 5 | 8 | 0 |
| Odontome UPM2 | 9.36 | 0.05 | 30 | 60 | 14 | 64 | 15 | 80 | 31 | 35 | 11 | 55 |
| Mesial and Distal accessory cusps UPM1 | 13.22 | **0.00** | 32 | 66 | 19 | 74 | 16 | 75 | 33 | 100 | 11 | 82 |
| Hypocone UM1 (ASU 3-5) | 20.07 | **0.03** | 23 | 87 | 8 | 63 | 24 | 92 | 38 | 76 | 9 | 22 |
| Cusp 6 LM2 (ASU 1-5) | 12.67 | **0.01** | 29 | 86 | 13 | 92 | 22 | 100 | 34 | 74 | 6 | 50 |
| Cusp 6 LM3 (ASU 1-5) | 13.06 | **0.02** | 22 | 100 | 13 | 100 | 21 | 95 | 30 | 77 | 9 | 100 |
| Distal trigonid crest LM2 | 8.08 | 0.10 | 25 | 8 | 13 | 8 | 24 | 29 | 33 | 6 | 10 | 20 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.19: MMD-SD matrix showing the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups, using dental nonmetrics.

| **Region** | **LSA Inland central** | **LSA SW coast** | **LSA South coast** | **IA North East** | **IA South Zambia** |
|---|---|---|---|---|---|
| LSA Inland central | 0 | 0.061 | 0.047 | 0.033 | 0.076 |
| LSA SW coast | 0.038 | 0 | 0.070 | 0.057 | 0.099 |
| LSA South coast | 0.056 | 0.048 | 0 | 0.044 | 0.086 |
| IA North East | 0.214* | 0.236* | 0.340* | 0 | 0.072 |
| IA South Zambia | 0.312* | 0.057 | 0.496* | 0.318* | 0 |

Values above the diagonal (shaded): SD values, values below the diagonal (clear): MMD values
*Significant values at $p<0.025$

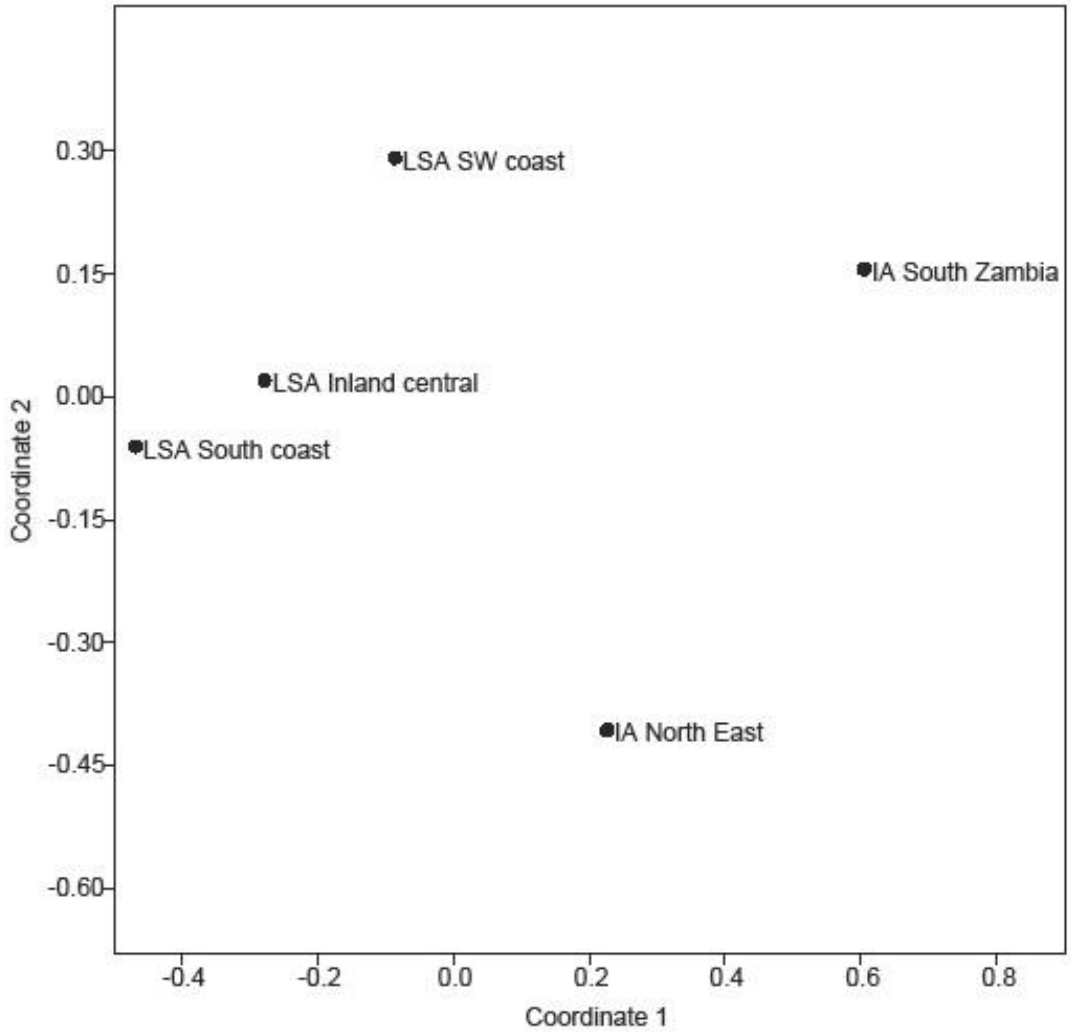


Figure 4.10: MDS illustrating the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups using dental nonmetrics.

When looking at the relationships among the LSA samples, their biodistances also appeared to be associated with their geographical locations, with the exception of the South coast sample. The Inland central group was most similar to the SW coast group and least similar to the South coast group. Similarly, the SW coast sample was most similar to the Inland central sample and least similar to the South coast sample, even though the LSA Inland central sample was more geographically distant from the SW than the South coast samples. Lastly, the South coast group was most similar to the SW coast group and least similar to the Inland central group, indicative of their geographical distances.

### 4.3.3. Dental metrics

Descriptive statistics of the upper and lower dentition of the geographical regions of southern Africa are displayed in Appendix D, Table D3. The means of the dental measures compared between the different regions within southern Africa showed 40 of 44 variables (91%) were significantly different (Table 4.20). Of the 44 variables investigated, only 20 variables were finally selected for the biodistance analysis (Table 4.21). This was because 10 variables had less than 60% of the data present, 11 variables had less than 10 individuals present (in any of the regions investigated) and three of the remaining variables were not significant.

Table 4.20: Significant differences observed between the geographical regions of southern Africa for their dental metrics ($p<0.05$).

| **Variable** | **F** | ***p*** | **Variable** | **F** | ***p*** |
|---|---|---|---|---|---|
| UI1 M-D | 3.76 | **0.02** | LI1 M-D | 2.21 | 0.09 |
| UI1 B-L | 4.28 | **0.00** | LI1 B-L | 8.10 | **0.00** |
| UI2 M-D | 3.49 | **0.02** | LI2 M-D | 3.88 | **0.01** |
| UI2 B-L | 6.39 | **0.00** | LI2 B-L | 10.21 | **0.00** |
| UC M-D | 6.69 | **0.00** | LC M-D | 2.79 | **0.03** |
| UC B-L | 19.76 | **0.00** | LC B-L | 15.64 | **0.00** |
| UPM1 M-D | 6.32 | **0.00** | LPM1 M-D | 8.79 | **0.00** |
| UPM1 B-L | 21.96 | **0.00** | LPM1 B-L | 14.62 | **0.00** |
| UPM2 M-D | 8.70 | **0.00** | LPM2 M-D | 4.65 | **0.00** |
| UPM2 B-L | 25.60 | **0.00** | LPM2 B-L | 10.29 | **0.00** |
| UM1 M-D | 7.93 | **0.00** | LM1 M-D | 8.22 | **0.00** |
| UM1 B-L | 6.66 | **0.00** | LM1 B-L | 3.16 | **0.02** |
| UM1 MB-DL | 4.98 | **0.00** | LM1 MB-DL | 5.28 | **0.00** |
| UM1 ML-DB | 9.97 | **0.00** | LM1 ML-DB | 5.54 | **0.00** |
| UM2 M-D | 5.76 | **0.00** | LM2 M-D | 0.71 | 0.58 |
| UM2 B-L | 7.07 | **0.00** | LM2 B-L | 1.15 | 0.33 |
| UM2 MB-DL | 2.95 | **0.02** | LM2 MB-DL | 3.60 | **0.01** |
| UM2 ML-DB | 11.42 | **0.00** | LM2 ML-DB | 0.99 | 0.41 |
| UM3 M-D | 7.89 | **0.00** | LM3 M-D | 12.64 | **0.00** |
| UM3 B-L | 4.87 | **0.00** | LM3 B-L | 4.27 | **0.00** |
| UM3 MB-DL | 4.70 | **0.00** | LM3 MB-DL | 7.43 | **0.00** |
| UM3 ML-DB | 20.39 | **0.00** | LM3 ML-DB | 9.88 | **0.00** |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.21: Descriptive statistics for the dental measurements selected (n=20) for the biodistance statistic to compare the Later Stone Age (LSA) and Iron Age (IA) groups geographically.

| | LSA INLAND CENTRAL | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UC | UPM1 | | UPM2 | | UM2 | | | | UM3 | | | | LPM1 | LPM2 | LM2 | LM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | B-L | B-L | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 25 | 18 | 23 | 23 | 25 | 34 | 35 | 34 | 34 | 24 | 27 | 28 | 21 | 27 | 26 | 27 | 24 | 25 | 24 | 23 |
| **Min** | 7.24 | 5.93 | 7.78 | 5.55 | 7.91 | 9.02 | 9.68 | 10.36 | 9.54 | 7.04 | 9.26 | 9.15 | 8.15 | 7.09 | 7.01 | 10.48 | 8.79 | 8.69 | 9.35 | 9.76 |
| **Max** | 8.76 | 7.90 | 9.83 | 7.45 | 9.93 | 10.72 | 11.88 | 13.01 | 11.70 | 9.59 | 14.05 | 13.53 | 10.47 | 8.59 | 9.07 | 13.50 | 12.01 | 11.12 | 11.67 | 12.37 |
| **Mean** | 7.93 | 6.80 | 8.77 | 6.51 | 8.89 | 9.95 | 11.04 | 11.93 | 10.70 | 8.24 | 10.46 | 10.91 | 9.48 | 7.83 | 8.10 | 11.64 | 10.41 | 10.12 | 10.77 | 10.83 |
| **SD** | 0.40 | 0.45 | 0.52 | 0.40 | 0.52 | 0.42 | 0.54 | 0.57 | 0.50 | 0.77 | 1.06 | 0.97 | 0.59 | 0.41 | 0.49 | 0.56 | 0.76 | 0.51 | 0.60 | 0.62 |
| | LSA SW COAST | | | | | | | | | | | | | | | | | | |
| | UC | UPM1 | | UPM2 | | UM2 | | | | UM3 | | | | LPM1 | LPM2 | LM2 | LM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | B-L | B-L | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 17 | 18 | 19 | 18 | 19 | 31 | 30 | 30 | 33 | 27 | 27 | 27 | 26 | 21 | 25 | 24 | 24 | 23 | 23 | 21 |
| **Min** | 5.94 | 5.72 | 7.11 | 5.49 | 7.68 | 8.15 | 9.85 | 10.36 | 8.65 | 6.59 | 9.16 | 8.99 | 7.68 | 6.45 | 6.54 | 10.74 | 8.79 | 8.85 | 8.31 | 9.54 |
| **Max** | 8.81 | 7.69 | 9.40 | 7.02 | 9.55 | 10.80 | 12.53 | 13.30 | 11.86 | 9.77 | 12.26 | 12.45 | 10.81 | 8.52 | 8.97 | 12.68 | 12.72 | 11.55 | 12.81 | 12.51 |
| **Mean** | 7.42 | 6.63 | 8.51 | 6.26 | 8.43 | 9.60 | 10.99 | 11.76 | 10.34 | 8.35 | 10.40 | 10.72 | 9.40 | 7.43 | 7.96 | 11.49 | 10.35 | 10.09 | 10.74 | 10.70 |
| **SD** | 0.61 | 0.59 | 0.59 | 0.41 | 0.57 | 0.67 | 0.70 | 0.76 | 0.70 | 0.69 | 0.85 | 0.91 | 0.63 | 0.51 | 0.63 | 0.52 | 0.78 | 0.72 | 0.85 | 0.79 |
| | LSA SOUTH COAST | | | | | | | | | | | | | | | | | | |
| | UC | UPM1 | | UPM2 | | UM2 | | | | UM3 | | | | LPM1 | LPM2 | LM2 | LM3 | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | B-L | B-L | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 20 | 18 | 20 | 20 | 20 | 24 | 28 | 27 | 28 | 25 | 25 | 25 | 25 | 23 | 28 | 28 | 22 | 24 | 23 | 23 |
| **Min** | 6.68 | 6.04 | 7.80 | 5.75 | 6.82 | 8.36 | 10.25 | 10.72 | 9.75 | 6.76 | 8.63 | 8.82 | 8.23 | 6.83 | 7.19 | 10.40 | 7.92 | 7.94 | 9.08 | 8.04 |
| **Max** | 8.69 | 7.72 | 9.51 | 7.18 | 9.19 | 11.21 | 12.04 | 13.40 | 12.09 | 10.22 | 11.97 | 12.61 | 10.71 | 8.39 | 8.82 | 13.34 | 11.52 | 10.93 | 11.80 | 12.44 |
| **Mean** | 7.56 | 6.76 | 8.54 | 6.46 | 8.29 | 9.70 | 11.00 | 11.98 | 10.66 | 8.34 | 10.36 | 10.63 | 9.23 | 7.53 | 7.87 | 11.51 | 9.75 | 9.67 | 10.34 | 10.13 |
| **SD** | 0.44 | 0.46 | 0.46 | 0.32 | 0.56 | 0.69 | 0.52 | 0.66 | 0.57 | 0.83 | 0.89 | 0.97 | 0.73 | 0.48 | 0.42 | 0.63 | 0.99 | 0.78 | 0.76 | 1.02 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

Table 4.21: continued.

| | IA NORTH EAST | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UC | UPM1 | | UPM2 | | UM2 | | | | UM3 | | | | LPM1 | LPM2 | LM2 | LM3 | | | |
| | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | B-L | B-L | MB-DL | M-D | B-L | MB-DL | ML-DB |
| **N** | 28 | 40 | 39 | 37 | 36 | 39 | 40 | 39 | 40 | 29 | 30 | 31 | 30 | 38 | 36 | 38 | 27 | 27 | 27 | 26 |
| **Min** | 7.60 | 6.27 | 8.36 | 5.94 | 8.49 | 8.91 | 10.13 | 10.61 | 9.02 | 8.03 | 9.65 | 10.10 | 8.93 | 7.22 | 7.45 | 10.39 | 10.04 | 8.80 | 9.76 | 10.33 |
| **Max** | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 12.03 | 13.46 | 13.85 | 13.54 | 10.32 | 12.71 | 13.03 | 12.10 | 9.25 | 9.60 | 13.92 | 13.06 | 11.23 | 13.21 | 12.34 |
| **Mean** | 8.49 | 7.21 | 9.62 | 6.87 | 9.57 | 10.21 | 11.65 | 12.32 | 11.33 | 9.04 | 11.12 | 11.44 | 10.42 | 8.29 | 8.62 | 12.02 | 11.13 | 10.34 | 11.33 | 11.28 |
| **SD** | 0.51 | 0.47 | 0.54 | 0.45 | 0.51 | 0.66 | 0.77 | 0.78 | 0.79 | 0.62 | 0.75 | 0.77 | 0.65 | 0.55 | 0.58 | 0.79 | 0.68 | 0.59 | 0.71 | 0.57 |
| | **IA SOUTH ZAMBIA** | | | | | | | | | | | | | | | | | | | |
| | **UC** | **UPM1** | | **UPM2** | | **UM2** | | | | **UM3** | | | | **LPM1** | **LPM2** | **LM2** | **LM3** | | | |
| | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **B-L** | **B-L** | **MB-DL** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 12 | 11 | 12 | 13 | 14 | 13 | 13 | 13 | 12 | 13 | 13 | 13 | 13 | 11 | 11 | 12 | 11 | 11 | 11 | 11 |
| **Min** | 7.82 | 6.47 | 8.45 | 6.09 | 8.20 | 9.16 | 10.19 | 10.79 | 10.03 | 7.97 | 10.45 | 10.06 | 9.57 | 7.36 | 7.49 | 11.09 | 9.66 | 9.16 | 9.78 | 9.94 |
| **Max** | 9.27 | 7.66 | 10.80 | 7.32 | 10.57 | 10.50 | 12.78 | 13.89 | 12.51 | 10.12 | 12.23 | 12.77 | 11.43 | 9.52 | 9.61 | 13.13 | 12.24 | 11.27 | 12.04 | 12.62 |
| **Mean** | 8.48 | 7.07 | 9.39 | 6.75 | 9.44 | 9.88 | 11.31 | 12.21 | 11.08 | 9.15 | 11.14 | 11.51 | 10.56 | 8.28 | 8.52 | 11.80 | 11.37 | 10.46 | 11.39 | 11.58 |
| **SD** | 0.50 | 0.39 | 0.68 | 0.37 | 0.65 | 0.48 | 0.78 | 0.99 | 0.67 | 0.52 | 0.65 | 0.86 | 0.53 | 0.62 | 0.59 | 0.62 | 0.73 | 0.64 | 0.65 | 0.73 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73.

The resulting biodistances comparing the geographical regions between the LSA and IA groups are displayed in Table 4.22 and visually presented in the MDS plot in Figure 4.11. Similarities were observed for both the IA samples when compared with the LSA groups. The North East and South Zambia IA groups were most similar to the LSA Inland central group, followed by the South coast and SW coast LSA groups. The IA groups were also biologically identical when compared with one another (MMD=0.000). Although their geographical distances appeared to correspond with their biodistances (i.e. LSA Inland central sample was the closest geographical sample and had the smallest biodistance from the IA samples), the geographically distant IA South Zambia group did not have greater biodistances from the LSA groups compared with the IA North East group.

When looking at the relationships between the LSA groups on the other hand, their biological differences were very small compared with one another, resulting in subtle but not clear geographical relationships. The SW coast sample in particular, was the most similar to the South coast sample (its geographical neighbour) and least similar to the Inland central sample, located some distance away.

Table 4.22: $D^2$ matrix displaying the biodistances between the Later Stone Age (LSA) and Iron Age (IA) groups geographically using dental metrics.

| **Region** | **LSA Inland central** | **LSA SW coast** | **LSA South coast** | **IA North East** | **IA South Zambia** |
|---|---|---|---|---|---|
| LSA Inland central | 0 | | | | |
| LSA SW coast | 0.063 | 0 | | | |
| LSA South coast | 0.054 | 0.056 | 0 | | |
| IA North East | 0.271 | 0.446 | 0.393 | 0 | |
| IA South Zambia | 0.228 | 0.382 | 0.357 | 0.000 | 0 |

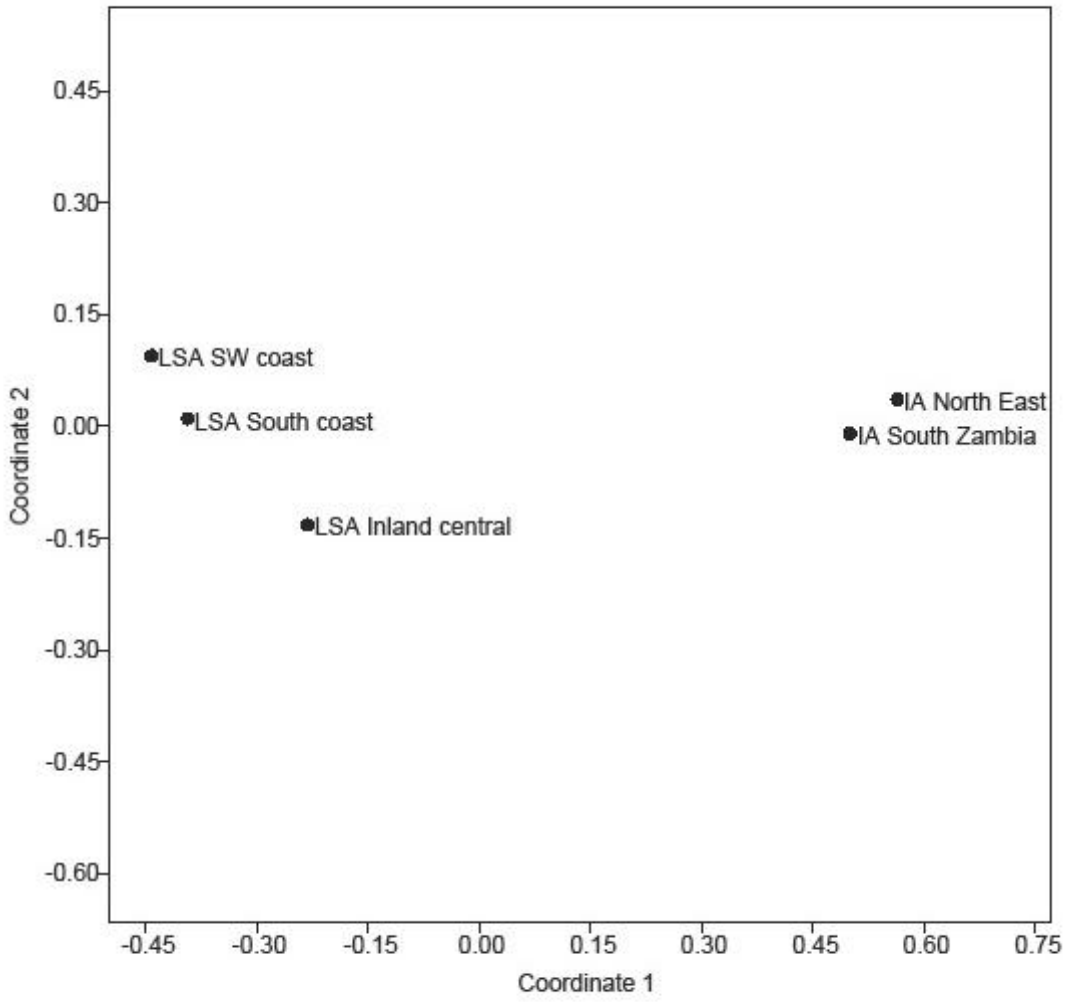


Figure 4.11: MDS of the $D^2$ matrix illustrates the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups using dental metrics.

Table 4.23 and Figure 4.12 show the relative regional gene flow between the geographical regions of LSA or IA samples in southern Africa. More than expected gene flow was observed between all the LSA samples, more so between the SW coast and South coast samples. Considerably more gene flow than expected was also observed between the IA groups from the North East of South Africa and southern Zambia. In addition to this, both IA samples showed similar levels of reduced gene flow with all the LSA samples. The LSA samples located on the SW and South coast in particular, showed considerably less gene flow with both IA samples. In comparison, slightly less than expected gene flow was observed between the LSA Inland central and IA groups (Table 4.23). The R-matrix plot (Figure 4.12) shows similar relationships between the groups investigated, as described previously for the $D^2$ matrix.

Table 4.23: R-matrix showing the average kinship coefficients ($r_{ij}$) between the Later Stone Age (LSA) and Iron Age (IA) groups geographically, using dental metrics.

| **Region** | **LSA Inland central** | **LSA SW coast** | **LSA South coast** | **IA North East** | **IA South Zambia** |
|---|---|---|---|---|---|
| LSA Inland central | 0 | 0.031 | 0.026 | -0.056 | -0.052 |
| LSA SW coast | 0.031 | 0 | 0.058 | -0.110 | -0.095 |
| LSA South coast | 0.026 | 0.058 | 0 | -0.092 | -0.092 |
| IA North East | -0.056 | -0.110 | -0.092 | 0 | 0.115 |
| IA South Zambia | -0.052 | -0.095 | -0.092 | 0.115 | 0 |

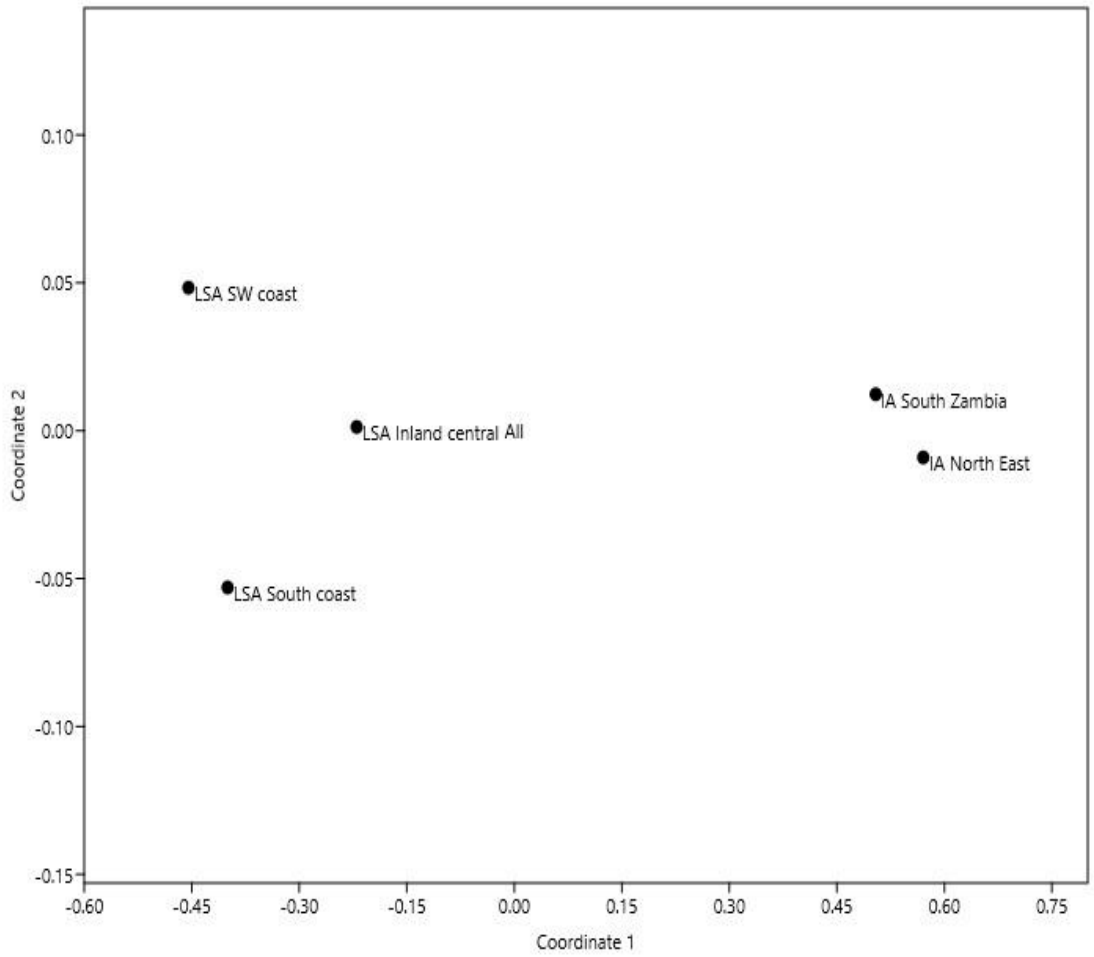


Figure 4.12: MDS of the R-matrix illustrates the biodistances between the geographical regions of the Later Stone Age (LSA) and Iron Age (IA) groups using dental metrics.

### 4.3.4. Summary

Both the dental and cranial results showed significant differences between the geographically distributed IA and LSA groups in southern Africa (Figure 3.1). The cranial nonmetrics and dental metrics also revealed that the North East and South Zambia IA groups were biologically identical and the cranial results in particular, showed no significant differences between their samples. To address the second part of objective 2, the regional variation between the LSA and IA groups in southern Africa was also investigated. Similarities were observed for the cranial and dental nonmetric results, but a few discrepancies were identified for the dental metric results. All cranial and dental results showed the North East and South Zambia IA samples were most similar to the LSA Inland central group and least similar to the LSA South coast group. The dental metric result in particular, only showed both IA groups most similar to the LSA Inland central group, but was least similar to the LSA SW coast sample than the LSA South coast group. The biodistances between the SW and South coast LSA samples however, were very similar (MMD=0.382, MMD=0.357, respectively) when compared with the IA South Zambia group. Overall, when assessing the geographical relationships between the LSA and IA groups, their geographical distance appeared to be associated with their biodistances for the cranial and dental results. The LSA individuals on the South coast of South Africa were however the exception and the IA South Zambia sample, although geographically more distant than the IA North East sample, did not always show greater biodistances from the LSA groups compared with the IA North East sample.

When looking at the geographical relationships between the LSA samples themselves, contradictory results were shown for their crania and dentition. The cranial results demonstrated two distinct geographical areas of biological similarity (Figure 4.13). The West coast sample showed more similarity and non-significance with its regional neighbours, the Inland central and SW coast samples, whereas the South coast sample showed similarity and non-significance with its regional neighbour, the SE coast sample. When, for example, the West and South coast samples were compared with the other LSA groups, significant differences were observed for their biodistances. Although the dental results were limited, the dental nonmetric results showed similar relationships to those described for the cranial results. No significant differences were however observed between the LSA groups and their biodistances were very similar to one another. The dental metric results on the other hand, also had very similar biodistances when comparing the LSA groups, but their relationships differed compared with the cranial and dental nonmetric

results. Overall, the geographical distances between the LSA samples appeared to be associated with their biodistances. The LSA groups were similar to their regional neighbours, except where the South coast group was concerned, and were most dissimilar or significant from those geographical groups located furthest away.

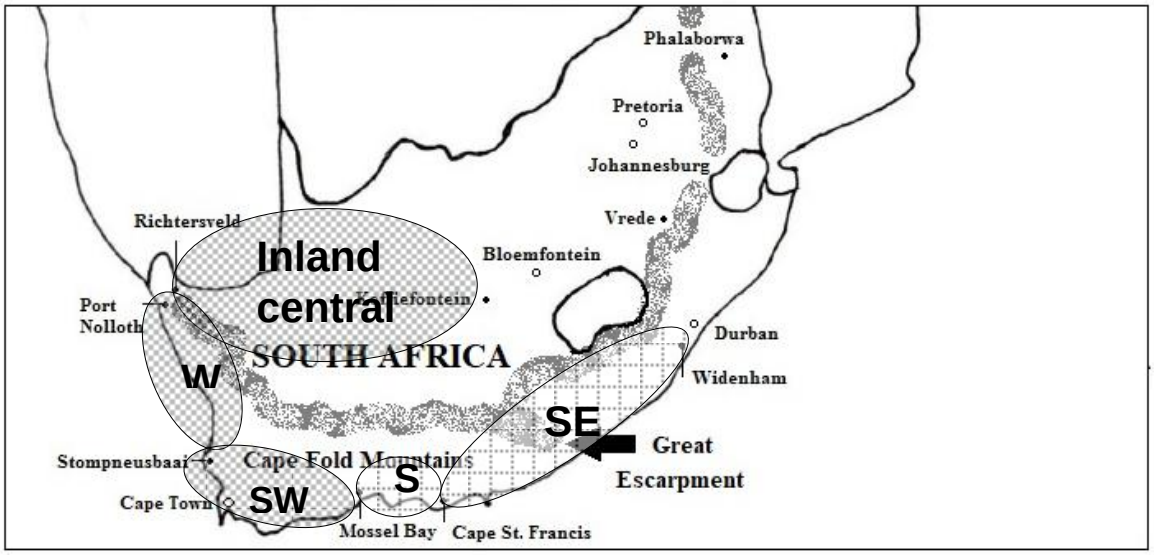


Figure 4.13: Map showing the geographical areas of similarity for the cranial nonmetric traits of the Later Stone Age groups.

# CHAPTER 5: DISCUSSION AND CONCLUSION

This chapter is divided into four parts. Firstly, the population history of the Khoesan peoples are discussed and compared with previous research. This includes the evidence of Bantu-speaker admixture identified in modern Khoesan individuals, as well as the relationships between the LSA peoples over time and geographical space. Secondly, the prehistoric relationships between Khoesan and Bantu-speakers are discussed in detail. The LSA and IA populations are compared according to their groups separated by time and their subdivided geographical regions within southern Africa. Thirdly, the statistical limitations noted in this study are presented, followed by suggestions for future research. Finally, the general conclusion summarises the major study outcomes.

## 5.1. POPULATION HISTORY OF THE KHOESAN PEOPLES

The first objective of this study was to investigate if the individuals from the LSA and IA were more similar to the modern Khoesan or modern Bantu-speaking peoples of southern Africa. As expected, the cranial and dental results for this study supported recent genetic research that suggested present-day Khoesan and Bantu-speakers are descendants of the LSA and IA peoples respectively (Schlebusch *et al.*, 2017; Bodiba *et al.*, 2019; Steyn *et al.*, 2019). The LSA samples were most similar to the modern Khoesan groups and the IA sample was most similar to the modern Bantu-speaking group. This expanded on previous cranial research that suggested MIA individuals from South Africa were broadly ancestral to modern Bantu-speaking groups (Rightmire, 1970a; L'Abbé, *et al*., 2006). It also further supported the biological continuity identified for craniomandibular and dental research that compared similar IA and Bantu-speaking groups (Warren, 2013; Warren *et al*., 2014), as well as dental research that compared a similar LSA sample with a different modern Khoesan sample (Black, 2014). On the contrary though, the dental nonmetric results of this study showed the IA group had greater similarity to the modern Khoesan sample than the modern Bantu-speakers. This may be due to the fact that, after further assessment of the cranial and dental samples of modern Khoesan, substantial admixture with prehistoric and/or modern Bantu-speakers was identified.

The precise start time of the relationships between the indigenous Khoesan and migrating Bantu-speakers in southern Africa is difficult to determine due to the fact that population sizes were probably small and their initial interactions may have been limited. Collectively however, archaeological, bioanthropological and genetic analyses have suggested interactions between them from approx. 2,000 years ago. The archaeological record provides

evidence for substantial material culture exchange between the LSA peoples and the EIA communities from the latter part of the 1st millennium AD (Hall and Smith, 2000; Robertson and Bradley, 2000; Parkington and Hall, 2010; Ribot *et al.*, 2010). Morphological studies on the other hand, by several scholars, found the Khoesan peoples were less similar to Bantu-speakers pre-2,000 BP compared with post-2,000 BP (Ginter, 2008; Irish, 1997, 2013; Black, 2014). Lastly, present-day Khoesan groups were recently shown to have between 9 and 30% genetic admixture from East Africans or Eurasians (Schlebusch *et al.*, 2017). The admixture process itself was further reconstructed for specific living Khoesan groups. The results predicted that interactions with the Eurasian/East African group began approx. 1,500 years ago or thereafter (Pickrell *et al.*, 2012; Uren *et al.*, 2016; Montinaro *et al.*, 2017; Schlebusch *et al.*, 2017). This is not to say that genetic exchange between the LSA and IA peoples did not occur prior to this time, because Khoesan groups were absorbed into the Bantu-speaking population (Barbieri *et al*., 2013a; Barbieri, *et al*., 2013b; Barbieri *et al*., 2014). Instead, it may indicate that our current data cannot detect the beginnings of the population interactions because they were of low magnitude.

### 5.1.1. Bantu-speaker admixture in recent Khoesan populations

Two different modern Khoesan data sets were investigated in this study: nonmetric cranial data, and a second set of dental nonmetric and metric data from dental casts. Together, they provided a more nuanced picture of later Khoesan biological diversity. The cranial sample consisted of historic Khoesan individuals that represented the dynamic distribution of their population throughout southern Africa during the late 19th to early 20th century (Morris, 1986; 1987). These individuals had sufficient supporting documentation to positively identify them as "Khoesan", but according to Morris (1987), they were poor representatives of prehistoric Khoesan groups because genetic interactions may have occurred with other populations over the last few millennia. A similar sample of Khoesan individuals from the same time period, but mostly from the northern regions of South Africa, were assessed by Botha *et al.* (2017) who agreed with Morris's view (1987). Botha and colleagues' (2017) Khoesan sample, although similar to another historic Khoesan sample (i.e. Riet River), also showed similarity with modern Bantu-speakers. The present study also concurred with Morris (1987). The modern Khoesan individuals were more similar (equidistant) to both the LSA and IA samples, and were least similar to the modern Bantu-speaking sample. This further implied that gene flow between the Khoesan and Bantu-speakers was more important during prehistoric times than in the modern time period. The Bantu admixture identified in

the modern Khoesan individuals was therefore possibly reflecting their past relationships with the IA peoples, rather than new interactions with the modern Bantu-speakers.

Previous bioanthropological research suggested greater gene flow between the LSA and IA peoples, especially for the LIA period, compared with the modern time period. A similar sample of Khoesan individuals to those investigated in this study, were compared with a series of modern southern African Bantu-speaking groups (Franklin *et al.*, 2007). The results suggested the modern Xhosa language speakers in particular, were most similar to the Khoesan compared with the other Bantu-speaking groups. Archaeological evidence has been used to associate the modern Nguni (Xhosa) language speakers with Blackburn ceramics that were found in the LIA at around AD 1100 (Mitchell and Whitelaw, 2005; Warren *et al*., 2014). It was during that time period that LIA farmers expanded into the Eastern Cape Province of South Africa for the first time (Hall, 2010) and possibly came into contact with the LSA peoples already living in that region (Ginter, 2008). It is therefore highly likely that the LSA peoples assimilated with the ancestors of the Xhosa speakers. This is because the Xhosa have a high degree of Khoesan admixture (De Wit *et al.*, 2010), possibly as much as 60% compared with other modern Bantu-speaking groups (Jenkins *et al*., 1970). This may also explain why the other modern Bantu-speaking groups, investigated by Franklin *et al.* (2007), had less similarity with the Khoesan peoples. Firstly, the Xhosa possibly had more opportunities for gene flow with Khoesan groups over time. Secondly, as the Bantu-speaking population increased in the KZN region during the LIA, the LSA individuals may have been largely replaced by IA farmers, resulting in fewer interactions with the Khoesan peoples (Ribot *et al.*, 2010).

The modern Khoesan cranial data used in the current study may therefore represent descendants of LSA individuals who initially interacted with IA farmers upon their arrival from the north. These groups later felt threatened by the ever-increasing Bantu-speaking population and avoided them as best as possible. This would have also involved movement into less optimal regions. In response to this, the size of the Khoesan population decreased and the small groups of Khoesan became genetically isolated from the Bantu-speaking population (Schlebusch, 2010).

The other modern Khoesan dataset investigated in this study consisted of dental casts made from living Khoesan individuals in the 1980's. These individuals were mainly living in the Caprivi strip of Namibia, but there was also a smaller group from the Lake Chrissie region. The Lake Chrissie Khoesan represent one of the few remaining Khoesan groups in the south-eastern region of southern Africa and a genetic study suggested their admixture

with Bantu-speakers (Schlebusch *et al.*, 2016). Similarly, the Barakwena (also known as Khwe) and the Vassekela (also known as !Xun) Khoesan from Namibia, appeared morphologically similar to the Bantu-speakers but spoke the Khoisan language (De Almeida, 1965). This was suggestive of a Khoesan and Bantu-speaking hybrid community and was viewed as such by researchers (Reid *et al*., 1991; Navsa, 1992), before genetic research indicated links with Bantu-speaking groups (Chen *et al.*, 2000).

The results from this study demonstrated that the Khoesan dental cast sample had similarities with Bantu-speakers, and was thus in-line with previous research. Unlike the cranial Khoesan sample that only reflected past relationships with the IA peoples, the dental Khoesan sample reflected both their past and present relationships with Bantu-speakers. More specifically, the dental nonmetrics and metrics showed that the dental cast Khoesan sample was more similar to the IA and modern Bantu-speaking groups than the LSA peoples. This suggests sustained genetic interaction over time between the Khoesan and Bantu-speakers, and considering the locations of the Barakwena, Vassekela and Lake Chrissie groups in southern Africa, this was not surprising. Recent genetic research on Khoesan groups still living in the Kalahari Desert, showed those groups located towards the south were the last to interact with the migrating Bantu-speakers (Pickrell *et al.*, 2012; Uren *et al.*, 2016). This implies that due to the location of the Khoesan groups on the Caprivi strip in the northern-most part of the Kalahari Desert, increased gene flow with the Bantu-speakers possibly occurred over time. Similarly, considering that IA farmers settled predominantly on the eastern part of southern Africa (Mitchell and Whitelaw, 2005), the Lake Chrissie individuals were most likely completely surrounded by Bantu-speakers, encouraging gene flow between them with time.

The Caprivi strip individuals may therefore represent descendants of LSA individuals who were forced into the Kalahari region due to its unsustainability for IA farming, or groups who moved into the Desert due to later colonisation events that pushed them further north. Their biological diversity may reflect their movements in southern Africa, with interactions with other populations until the modern time period. The individuals who interbred with Bantu-speakers or European colonists may have subsequently become isolated from the Khoesan gene pool.

The gene flow between the LSA and IA peoples, as well as between the modern Khoesan and modern Bantu-speaking groups, are therefore important contributors to shaping modern Khoesan diversity. The results from this study also showed the Bantu expansion and later colonisation events in southern Africa, greatly impacted the Khoesan population groups. The

modern Khoesan individuals thus had the most internal genetic variation, compared with the LSA, IA and modern Bantu-speaking samples in this study, further supporting recent genetic analyses (Schlebusch *et al.*, 2013, 2016, 2017).

### 5.1.2. Patterns of biological change in the LSA population

A number of studies have investigated the biological continuity or discontinuity of the LSA population during the Holocene, particularly in the Cape coastal regions and surrounding areas in South Africa (Stynder, 2006, 2009; Pfeiffer and Sealy, 2006; Stynder, *et al*., 2007b, Ginter, 2008; Black, 2014; Irish *et al.*, 2014). A pattern of morphological variation was identified in these particular areas that reflected the dynamic effects of natural selection, mutation, genetic drift and genetic isolation. These trends of significant skeletal variation over time also appeared to differ regionally in South Africa, possibly reflecting the adaptations of smaller LSA populations to different habitats with diverse vegetation or genetic drift. A reduction in craniofacial form was identified between 4,000 BP and 3,000 BP, compared to a previous time in the SW and South coast areas (Figure 3.1) (Neuweger, 2007; Stynder, *et al*., 2007b). Thereafter, craniofacial form reverted to previously observed (pre-4,000 BP) dimensions. This decrease in craniofacial form was also supported by an overall reduction in body size (estimated from femoral length) and concurrent recovery in stature at these time periods (Pfeiffer and Sealy, 2006). In comparison, the SE coast (Figure 3.1) also showed a decrease in cranial and postcranial size between 3,500 BP and 2,000 BP, but appeared to be slightly later and occurred for a longer duration (Ginter, 2008), compared with the previously described coastal areas. It was argued that the discrepancies in Ginter's results compared with the other studies (Stynder, 2006, 2009; Pfeiffer and Sealy, 2006; Stynder, *et al*. 2007b), may have been due to regional differences such as climate, the variability of species diversity and seasonality (Ginter, 2008).

In this study, a similar pattern of cranial variation over time was identified for the LSA population. Interestingly though, the period of cranial nonmetric change was most similar to Ginter's (2008) findings. The LSA individuals dated from 4,000 to 2,000 BP were biologically indistinguishable and significantly different from the pre-4,000 BP and post-2,000 BP LSA individuals. The pre-4,000 BP and post-2,000 BP LSA individuals also appeared to be biologically similar to one another. The majority of the LSA individuals investigated in this study were located on the SW coast (37%) and South coast (48%) regions of the southern Cape, and the sample included many of the same individuals studied previously (Pfeiffer and Sealy, 2006; Neuweger, 2007; Stynder, *et al*., 2007b). Only a few individuals (8% of the LSA individuals in the current study) represented the SE coast region,

similar to those investigated by Ginter (2008). It is generally assumed that nonmetric cranial traits reflect high heritability and less environmental influence compared with cranial metrics (Pink *et al.*, 2016). The cranial nonmetric traits may have therefore differed in their expression of genetic change in these particular regions, which may also explain the different timing of the biological change. Ginter (2008) was the only other study that also looked at cranial nonmetric traits in this context, in conjunction with cranial and postcranial metric analyses. Only pre-2,000 BP and post-2,000 BP LSA individuals were investigated, but no major significant differences were identified over time. Majority of the cranial nonmetric traits selected for the analysis however, differed compared with this study. This suggests some cranial nonmetric traits may be more sensitive to environmental influences than others.

The pattern described previously for the LSA crania and postcrania, is similarly expressed in the dentition, but occurred a millennium later. Nonmetric dental change was observed between 3,000 BP and 2,000 BP, compared to a previous time, and reverted back to pre-3,000 BP levels at 2,000 BP (Black, 2014). According to Black (2014), this was a delayed genetic response to the environmental factors affecting the population at 4,000 BP. Black's (2014) dental metric results on the other hand, showed no substantial biological change in size or shape over time. Minor temporal variations were however identified, but this was thought to be due to intra-population variation caused by individual outliers, or was an artefact of sample size because there was considerable overlap between the temporal groups. Although no statistically significant differences were found between the different groups, t-tests did show that only the 3,000 to 2,000 BP group differed (43% of the 175 dental metric variables) when compared with the other time periods (ranging from 8,000 to 300 BP). This suggested that the individuals from 3,000 to 2,000 BP were biologically unique in some way and supported the dental nonmetric results (Black, 2014).

Similar results were observed in this study, but only for the dental metrics. The LSA individuals dated from 12,000 to 3,000 BP were more similar to the LSA individuals dated from 2,000 to 0 BP, than those from 3,000 to 2,000 BP. Considering that the majority of the LSA (2,000 to 0 BP) group consisted of individuals from the LIA, the dentition may have returned to pre-3,000 BP dental size from 1,000 BP. The dental nonmetric results however, showed no biological change over time, possibly due to statistical limitations.

In conclusion, both the cranial and dental data were in line with previous research concerning the pattern of morphological variation identified within the LSA population over time. The cranial nonmetric results showed a biological change at approx. 4,000 BP, similar

to previous cranial metric studies (Neuweger, 2007; Stynder *et al*., 2007b; Ginter, 2008) and postcranial metric research (Pfeiffer and Sealy, 2006). The similarity observed between the LSA crania pre-4,000 BP and post-2,000 BP, instead of the 3,000 to 2,000 BP LSA individuals, may be indicative of how the cranial nonmetric traits reflected the genetic or non-genetic adaptations to environmental change. In comparison, the LSA dentition also reflected this pattern of variation over time, but with a delayed response at 3,000 BP. This further agreed with previous dental research (Black, 2014), but the return of the LSA dentition to previously observed dental size, was inconclusive in this study. This may be due to statistical limitations, but nonetheless, the results suggested similarity of the pre-3,000 BP individuals with those LSA individuals dated to between 2,000 BP and 1,000 BP, similar to previous research (Black, 2014). Understanding the cranial and dental pattern of variation in the LSA population assisted with the interpretations of the interactions between them and the IA peoples over time (see section 5.2.1). In the current study, the IA (2,000 to 0 BP) crania were as similar to the LSA (8,000 to 4,000 BP) crania as the LSA (2,000 to 1,000 BP) crania. This reflected the pattern of cranial change at 4,000 BP and 2,000 BP. Similarly, the LSA (12,000 to 3,000 BP) and LSA (2,000 to 0 BP) dentition was more similar to the IA (2,000 to 0 BP) dentition than the LSA (3,000 to 2,000 BP) dentition. This also reflected the pattern of dental change at 3,000 BP and approx. 2,000 BP.

Finally, this study also supported the argument that the biological changes observed at 4,000 BP in the LSA crania and 3,000 BP in the LSA dentition were not due to external gene flow into the population (discussed in section 5.2). The best explanation is that the changes were due to genetic changes and *in situ* factors such as natural selection, mutation, genetic drift and genetic isolation, as suggested by other researchers (Stynder, *et al*., 2007b; Ginter, 2008; Black, 2014), because morphological variability increases when gene flow into a population occurs (Gonzalez-Jose *et al.*, 2007), yet biological continuity was observed in this study between the LSA groups over time.

### 5.1.3. Geographical interactions between the LSA peoples

When comparing the LSA individuals by their geographical distributions, the cranial and dental results showed general similarities across South Africa. Two distinct geographical areas of similarity were observed for the cranial nonmetric data (Figure 4.10) and although fewer geographical regions were investigated for the dental nonmetrics, the results concurred with the cranial results. The LSA individuals located in the Inland central, West and SW coast areas were biologically alike and significantly different from the LSA

individuals located in the South and SE coast areas. These areas of biological similarity possibly reflect the population dynamics of the LSA peoples over time.

During the mid-Holocene, the archaeological record suggests that the LSA peoples were living south of the Cape Fold Mountains in the present-day Western Cape Province (Stynder, 2006; Black, 2014). Their population size drastically increased after 4,000 BP and population movement from these areas (SW, South and SE coastal regions) into the South African interior was suggested (Deacon, 1974; Morris, 1992a; Stynder, 2006). The results from this study implied that the earlier LSA individuals living in the SW coast area may have migrated, or later interacted, with populations toward the west coast of South Africa, around the Cape Fold Mountains. Thereafter, further migration or interaction may have occurred with the populations in the Inland central region at a later time (±500 BP). The same can be said for the relationships between the South and SE coast areas, suggesting population movement or interaction with the populations toward the east coast of South Africa, around the Cape Fold Mountains. The similarity between the LSA groups over time was therefore dependent upon their geographical distance, whereby increased gene flow occurred between the LSA groups that were geographical neighbours. The Cape Fold Mountains acted as a geographical barrier and may have lead to population movements toward the west and east coasts, but this does not however explain the dissimilarity between the SW and South coast LSA samples.

Considering that the SW and South coast LSA groups are geographical neighbours, increased gene flow is to be expected, similar to the other regional relationships mentioned previously. Prior research is inconclusive with regard to this matter and further investigation is needed. Researchers have questioned the extent of possible interactions between the western and southern Cape LSA individuals over time and have generally treated them as distinct (Pfeiffer and Sealy, 2006). Some cranial metric support for population interactions was given by Stynder *et al*. (2007b), who suggested similarity between the groups because only minor size and shape differences were identified between the SW and South coast regions. In contrast, Irish *et al.*'s (2014) more recent dental analysis revealed a clear separation between the western and southern Cape LSA samples. Other possible scenarios include the geographical barrier of the Cape Fold Mountains, which may have prevented the interactions between these two coastal areas. The population dynamics of the LSA groups on the west and east coasts may have also been different over time, contributing to their dissimilarity. An increase in population size and subsequent gene flow between the migrating LSA groups could have resulted in significant intra-population genetic and

biological variation. On the other hand, a decrease in population size over time could have resulted in an increase in genetic drift that could have led to a significant reduction in intra-population genetic and biological variation. The structure of the LSA population on the west and east coasts were dependent upon the balance that existed between mutation, gene flow and genetic drift, which could have affected the inter-population diversity (Relethford, 2001; Relethford, 2004a). Another possibility is the temporal differences of the samples. More specifically, the South coast group represents a greater span of time than the other geographical regions, representing individuals from approx. 12,000 to 150 BP. Many of the LSA individuals included in this region are also older than 3,000 BP (Appendix 1, Table A1). The morphological variation identified over time in the LSA population may have therefore contributed to high biological diversity within the South coast group in particular, compared with the other regions.

Lastly, the results from this study were similar to Black's (2014) study, that also separated the LSA peoples into comparable geographical groups. Black's dental nonmetric results showed that the Inland central sample was significantly different from the West, SW, South and SE coast samples. This is somewhat similar to the cranial results from this study, whereby significant differences were observed between the Inland central group and the SW, South and SE coast samples. However, the Inland central sample in this study was biologically indistinguishable from the West coast group. Even though Black (2014) did use a correction for sample size in her biodistance analysis, the West coast region may have been problematic because many of the traits had very few cases and thus gave poor estimates of population ranges, possibly affecting the MMD results. In comparison, the majority of the cranial traits selected for the West coast sample in this study had larger sample sizes (Table 4.16), that strengthened the biodistance result. The West coast region was not included in the biodistance analysis for the dental comparisons in this study and thus cannot be compared with Black's (2014) dental results.

Another explanation for the discrepancies observed between the cranial results in this study and Black's (2014) dental results are regional differences between the West coast and Inland central areas. The Inland central region is made up of the Nama Karoo, which is a vast, open area that is quite arid with low vegetation (Low and Rebelo, 1996). The West coast region is made up of the Succulent Karoo, also arid or semi-arid like the Nama Karoo, but has more succulents and wildlife. These areas are quite different to the Fynbos regions of the SW and South coast areas (Low and Rebelo, 1996). Due to the fact that teeth may be more shielded from environmental effects (Cardoso, 2007), the cranial nonmetric traits may

be more sensitive to the environment than the dentition. This may explain why Black (2014) observed similarity and non-significance between the West, SW, South and SE coast regions, unlike the present study, where the West and SW coast areas were significantly different from the South and SE coast areas. Ginter (2008) also previously suggested the LSA individuals from the SE coast area in particular, responded to the environment differently than the SW and South coast regions, which the present study reflects as well.

## 5.2. INTERACTIONS BETWEEN THE PREHISTORIC KHOESAN AND BANTU-SPEAKERS

The second objective of this study was to investigate the relationships between the LSA and IA groups over time and geographical space within southern Africa. The results also suggested gene flow between the Khoesan and Bantu-speaking groups was more important during prehistoric times than in the modern time period. These prehistoric relationships are therefore elaborated upon here.

### 5.2.1. Relationships between the LSA and IA over time

Archaeological, bioanthropological and genetic research suggested the Bantu-speakers only arrived in southern Africa after 2,000 BP (see section 5.1), but the cranial results from this study suggested gene flow occurred between the LSA and IA peoples prior to this. The LSA population was predominantly settled along the coastal edges of the southern Cape before 2,000 BP, with little evidence of populations in the interior regions (Parkington, 1976, 2001; Parkington *et al*., 1988; Morris, 1992a; Stynder, 2006). The geographical distance between the migrating Bantu-speakers at this time and the coastal LSA population make it unlikely that there were interactions between them. It may be possible however, that the Bantu-speakers from the north came into contact with other groups of LSA individuals, not represented in this analysis, living in those areas of present-day Angola, Zambia and Malawi. Gene flow may have occurred as suggested by genetic research (Wood *et al.*, 2005; Schlebusch *et al.*, 2017; Bajić *et al.*, 2018), resulting in hunter-gather/hunter-herder lineages being introduced into the IA population. This could explain why the LSA individuals dated from 3,000 to 2,000 BP in this study were more similar to the IA group, compared with the LSA individuals dated from 4,000 to 3,000 BP, while the LSA population in the southern Cape regions from 4,000 to 2,000 BP still remained morphologically indistinguishable. Morris and Ribot (2006) provided some support for this by showing that Middle Holocene Malawians were similar to both Khoesan and Bantu-speaking peoples. If the migrating Bantu-speakers from the north interacted with these LSA individuals, the IA peoples that

eventually settled in South Africa may have already had admixture from these Khoesan groups. Larger archaeological samples are however needed to confirm the suggestions made by Morris and Ribot (2006).

Lastly, previous bioanthropological research suggested that the Khoesan peoples gradually became more similar to the Bantu-speakers, especially after 2,000 BP (Irish, 1997, 2013; Ginter, 2008; Black, 2014). Similarly, the cranial and dental results from the current study also showed increased similarity between the LSA and IA groups over time. More specifically, the cranial results suggested the LSA individuals became more similar to the IA peoples after each millennium, starting from 4,000 BP until 0 BP. This supports work by Warren (2013) who suggested that the Khoesan admixture present in modern Bantu-speakers was similar to what existed between the IA and LSA peoples.

### 5.2.2. Regional variation between the LSA and IA groups

The IA groups in the North East region of South Africa and South Zambia, as well as the LSA groups in the Inland central, West, SW, South and SE coast areas of South Africa, were compared in this study (Figure 5.1). The IA samples were biologically identical to one another for the cranial and dental metric results, similar to previous dental research by Warren *et al.* (2015). When comparing the IA groups to the geographical distribution of LSA groups, both IA samples were most similar to the LSA Inland central sample, for the cranial and dental results, and least similar to the LSA South coast sample, mostly for the cranial results but some dental results. The LSA individuals dating to the LIA period (1,000 to 0 BP) were also most similar to the IA group. Considering that the Inland central sample consisted of more recent LSA individuals dating to ±500 BP (Appendix 1, Table A1), this group is expected to be most similar to the IA peoples. This is in line with previous cranial (Hausman, 1980; Morris, 1992a) and dental (Black, 2014; Irish *et al.*, 2014) research that suggested inland LSA individuals had significant gene flow from Bantu-speakers. In comparison, as discussed in section 5.1.3, the South coast group encompasses the largest time span compared with the other geographical regions occupied by the LSA peoples. This may explain its dissimilarity to the IA peoples because the other LSA groups (West, SW and SE coast – excluding the Inland central group) had very few individuals older than 3,000 BP. Depending on the individuals selected for the biodistance analysis, the variability identified between the LSA groups and the IA peoples over time, may have resulted in high biological diversity in the LSA South coast sample. Further investigation is however needed.

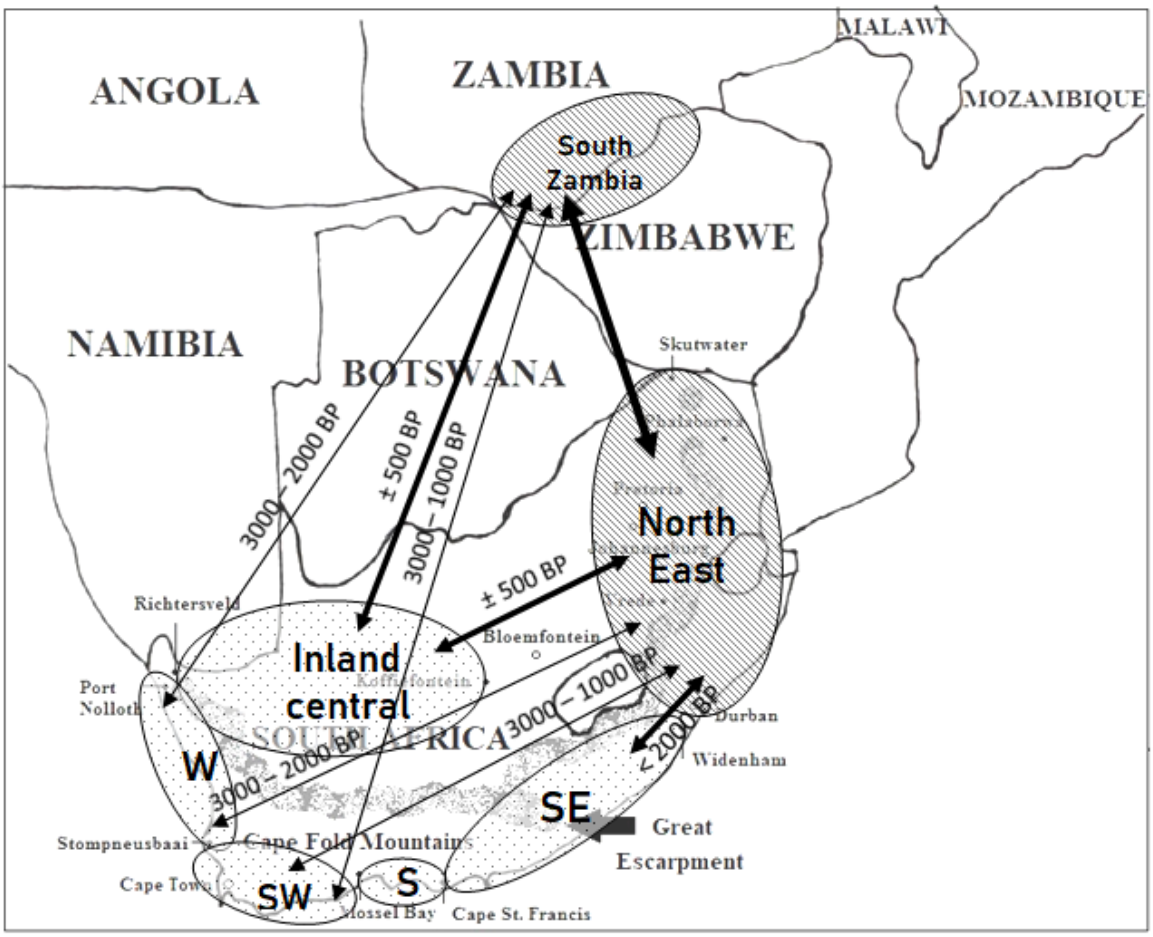


Figure 5.1: Population movement and subsequent interactions between the Later Stone Age (dots) and Iron Age (stripes) peoples. Arrow thickness indicates relative degree of genetic similarity.

Besides time, the other factor that may have affected the interactions between the LSA and IA peoples was the geographical distance between the groups based on population movement. More specifically, the geographical pattern was consistent with the isolation-by-distance model (Wright, 1943; Relethford, *et al.*, 1981; Konigsberg, 1990). This model predicts that genetic similarity between populations decreases exponentially as their geographical distance increases (Relethford, 2002). This only occurs in the absence of natural selection and is due to the limiting effect of geographical distance on the amount of gene flow between them. The geographical pattern observed in the cranial and dental results of this study was in line with this, as the biodistances between the groups were greater the further they were from one another. The Inland central and SE coast LSA samples were geographically closest to the IA peoples in the North East and therefore most similar (Figure 5.1). In comparison, the LSA peoples located on the West or SW coast had similar biodistances (Table 4.19) and were geographically most distant, showing slightly less genetic similarity to the IA North East peoples. This supports the conclusion of Stynder

(2006), who found that the coastal areas of South Africa, particularly the SW and South coast areas, were relatively free from outside gene flow because Bantu-speaking farmers avoided those less suitable areas. Based on the results from this study, the LSA individuals in the West coast region were also possibly isolated from the North East Bantu-speakers.

The isolation-by-distance model does not explain the LSA South coast sample and the comparisons between the IA South Zambia sample and some of the LSA groups. Although the LSA South coast group is geographically closer to the North East IA peoples compared with the West and SW coast LSA groups (Figure 5.1), it was most dissimilar from the IA sample in the current study. This may be due to high biological diversity for this particular sample, mentioned previously. Similarly, although the IA South Zambia sample was more geographically distant from the LSA groups, compared with the IA North East sample, their biodistances were not always greater when compared with the LSA groups. A larger Zambian sample is however needed to explore this further.

The biodistances between the Zambians and LSA groups did however suggest a different relationship with the LSA peoples, compared with the IA individuals that were located on the North East of South Africa. The cranial and dental results revealed that the Zambian individuals were most similar to the Inland central and West coast LSA samples, followed by the SW, SE and South coast LSA samples (Figure 5.1). Geographically, the Kalahari Desert separates the Zambian individuals from the closest LSA groups (i.e. Inland central, West coast) and was not conducive to IA farming. Therefore, the LSA population may have expanded into the Kalahari regions during the LIA or prior to this. The Kalahari populations may have interacted with the groups represented by the IA Zambians in central southern Africa, as well as other LSA populations in the south-western areas of southern Africa. Archaeological evidence from KZN for the EIA suggests the Bantu-speakers were relatively sedentary, interacting with a more widespread and mobile Khoesan population (Ribot *et al*., 2010). It is therefore not likely that the Zambian IA individuals migrated much further south than where they settled but rather, LSA groups were more widely spread in the south-western areas of southern Africa.

## 5.3. STATISTICAL LIMITATIONS AND FUTURE RESEARCH

Three types of data were investigated in the current study: cranial nonmetrics, dental nonmetrics and dental metrics. When calculating the biodistance statistic, there are two procedures that increased the accuracy of their results (Harris and Sjøvold, 2004; Irish, 2010; Soltysiak, 2011). The first is including as many traits as possible, especially those that

are significantly different between the groups investigated. Secondly, large sample sizes are important, especially such that each trait has more than 10 observations to prevent statistical bias. In this study, the results from the dental nonmetric and dental metric analyses (the former more so than the latter) showed some differences compared with the cranial results or the published literature. The weaker biodistance result may be due to statistical limitations because of trait availability based on the number of individuals included, or the number of traits eventually selected for the biodistance analysis after data editing. For example, when investigating the relationships between the LSA and IA peoples over time, 70 of the 100 dental nonmetric traits scored were eliminated from the biodistance analysis because they were present in less than 60% of the individuals. Similarly, when investigating the geographical relationships between the LSA and IA peoples, 60 of the 100 dental nonmetric traits scored were eliminated from the biodistance analysis. Due to reduced trait availability in the archaeological remains, substantially less dental nonmetric traits were finally selected for comparison between the groups after data editing (Tables 4.11 and 4.20). In addition to this, the dental nonmetric and dental metric data for some groups were either combined or eliminated due to their small sample sizes. This further prevented direct comparisons with the cranial results and may explain the differences with previous dental research. Future biodistance studies would therefore benefit from investigating cranial nonmetric data because it produced results with higher accuracy and were more widely available for the time period investigated. If only dental remains are available, the dental metric data showed more promising results than the nonmetrics in this study.

Future morphological research comparing other modern Khoesan populations to the Bantu-speakers would also be interesting. Only two samples were investigated in this study and very different genetic relationships were observed over time. Both groups showed admixture with the Bantu-speakers, yet expanding the analysis to include other modern Khoesan groups may further our understanding of their unique biological diversity. Finally, a significant geographical difference was identified between the SW and South coast LSA groups. Further investigation is needed to determine if their relationships were time related or due to other factors.

## 5.4. CONCLUSION

The population history of modern southern African peoples is better understood from this study. The modern Khoesan and Bantu-speakers had cranial and dental similarities with the LSA and IA peoples. More specifically, the LSA peoples were most similar to the modern Khoesan and the IA peoples were most similar to the modern Bantu-speakers. Various levels of admixture with the Bantu-speakers over time were also identified for the cranial and dental samples of modern Khoesan investigated. Their past relationships with the IA peoples in particular, were suggested to be more important than new interactions with modern Bantu-speakers. The movement of the LSA groups at the southern-most point of Africa was also apparently small-scale and gradual, according to the cranial and dental results. The similarities and differences observed between their groups possibly reflect regional environmental differences. In comparison, the Bantu-speakers migrating from the north may have assimilated with LSA groups in central Africa, prior to their migration southward towards South Africa proper. The LSA and IA groups thus showed cranial affinities prior to 2,000 BP, which implies the IA peoples may have already had admixture from Khoesan groups upon arrival in southern Africa. Once the IA farmers were settled, the cranial and dental results further indicated that they mainly interacted with those LSA groups in close geographical proximity, while the more mobile LSA groups from more distant geographical regions showed less interaction with the IA peoples. Finally, as the Bantu-speaking population increased in size over time, the LSA groups in southern Africa may have relocated to other areas more isolated from the IA farmers, like the Kalahari Desert.

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# APPENDICES

## APPENDIX A: SAMPLE LOCATIONS AND CONTEXT

Access to the following collections was granted based on successful applications submitted:

A* – Pretoria Bone Collection, Department of Anatomy, University of Pretoria (n=45)

A – Raymond A Dart Collection of Human Skeletons, School of Anatomical Sciences, University of the Witwatersrand (n=477)

NMB – Florisbad Quaternary Research Station, Bloemfontein (n=85)

UCT – Department of Human Biology, University of Cape Town (n=78)

MMK – Archaeology Department, McGregor Museum, Kimberley (n=63)

SAM – Pre-colonial Archaeology Collection, Iziko Museum of South Africa, Cape Town (n=92)

PMB – Department of Human Sciences, KwaZulu-Natal Museum, Pietermaritzburg (n=10)

D – Ditsong Museum, Pretoria (n=11)

Table A1: Archaeological samples (N=408 individuals).

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| **LSA Inland central (n=75)** | | | | | | |
| NMB1427 | 180±70 | Pta-2908 | | | Augrabies | 1 |
| UCT1 | 200±50 | Pta-1886 | | Adult | Richtersveld | 1 |
| NMB1372 | 210±40 | Pta-2901 | F | Adult | Kakamas | 1 |
| NMB1405 | 360±45 | Pta-2905 | probable M | Adult | Kakamas | 1 |
| MMK 235 | 390±50 | Pta-2894 | | Adult | Koffiefontein | 7 |
| NMB1366 | ±500 | Association† | probable M | Adult | Augrabies | 1 |
| NMB1379 | ±500 | Association† | | Adult | Augrabies | 1 |
| NMB1380 | ±500 | Association† | | | Augrabies | 1 |
| NMB1381 | ±500 | Association† | | | Augrabies | 1 |
| NMB1383 | ±500 | Association† | | Adult | Augrabies | 1 |
| NMB1420 | ±500 | Association† | F | Adult | Augrabies | 1 |
| NMB1430 | ±500 | Association† | | Adult | Augrabies | 1 |
| MMK 169 | ±500 | Association† | M | Adult | Barkley West | 1 |
| MMK 188 | ±500 | Association† | | Subadult | Barkley West | 1 |
| MMK 170 | ±500 | Association† | | Adult | Best Pan, near Riverton | 1 |
| NMB1368 | ±500 | Association† | | | Bo-Renosterkop, Kakamas | 1 |
| MMK 242 | ±500 | Association† | probable M | Adult | Douglas | 1 |
| MMK257 | ±500 | Association† | | Adult | Douglas | 1 |
| MMK286 | ±500 | Association† | | Adult | Douglas | 1 |
| NMB1 | ±500 | Association† | | Adult | Douglas | 1 |
| MMK296 | ±500 | Association† | | Adult | Driekopseiland | 1 |
| MMK 171 | ±500 | Association† | | Subadult | Dwarsvlei, Herbert | 1 |
| MMK 187 | ±500 | Association† | | Adult | Jacobsdal | 1 |
| NMB1390 | ±500 | Association† | probable M | Adult | Kakamas | 1 |
| NMB1364 | ±500 | Association† | M | Adult | Kakamas | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| NMB1370 | ±500 | Association† | | Adult | Kakamas | 1 |
| NMB1392 | ±500 | Association† | | | Kakamas | 1 |
| NMB1414 | ±500 | Association† | | | Kakamas | 1 |
| NMB1416 | ±500 | Association† | | Adult | Kakamas | 1 |
| MMK 189 | ±500 | Association† | | Adult | Koffiefontein | 1 |
| MMK 192 | ±500 | Association† | | Adult | Koffiefontein | 1 |
| MMK 200 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK 202 | ±500 | Association† | | Adult | Koffiefontein | 1 |
| MMK 203 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK 204 | ±500 | Association† | F | Adult | Koffiefontein | 1 |
| MMK 206 | ±500 | Association† | probable F | Adult | Koffiefontein | 1 |
| MMK 209 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK 212 | ±500 | Association† | | | Koffiefontein | 1 |
| MMK 213 | ±500 | Association† | F | Adult | Koffiefontein | 1 |
| MMK 217 | ±500 | Association† | F | Adult | Koffiefontein | 1 |
| MMK 222 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK 228 | ±500 | Association† | | Adult | Koffiefontein | 1 |
| MMK 229 | ±500 | Association† | M | Adult | Koffiefontein | 1 |
| MMK 230 | ±500 | Association† | | | Koffiefontein | 1 |
| MMK 230A | ±500 | Association† | | | Koffiefontein | 1 |
| MMK 231 | ±500 | Association† | M | Adult | Koffiefontein | 7 |
| MMK 236 | ±500 | Association† | F | Adult | Koffiefontein | 7 |
| MMK 237 | ±500 | Association† | F | Adult | Koffiefontein | 1 |
| MMK 239 | ±500 | Association† | | | Koffiefontein | 1 |
| MMK 245 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK248 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| MMK249 | ±500 | Association† | | | Koffiefontein | 1 |
| MMK250 | ±500 | Association† | | Adult | Koffiefontein | 1 |
| MMK272 | ±500 | Association† | | Adult | Koffiefontein | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| NMB1103 | ±500 | Association† | | Subadult | Koffiefontein | 1 |
| NMB1208 | ±500 | Association† | F | Adult | Koffiefontein | 7 |
| NMB1209 | ±500 | Association† | probable M | Adult | Koffiefontein | 1 |
| NMB1210 | ±500 | Association† | M | Adult | Koffiefontein | 1 |
| NMB1215 | ±500 | Association† | F | Adult | Koffiefontein | 1 |
| NMB1216 | ±500 | Association† | | Adult | Koffiefontein | 7 |
| MMK 194 | ±500 | Association† | | Adult | Koppieskraal, near Koffiefontein | 1 |
| MMK274 | ±500 | Association† | | Subadult | Longlands, Barkley West | 1 |
| MMK289 | ±500 | Association† | | Adult | Louisvale settlement on Orange River | 1 |
| MMK299 | ±500 | Association† | | Adult | Soutpan, Riverton | 1 |
| MMK301 | ±500 | Association† | | Subadult | Soutpan, Riverton | 1 |
| MMK308 | ±500 | Association† | | Subadult | Soutpan, Riverton | 1 |
| MMK316 | ±500 | Association† | | Subadult | St. Claire, Douglas | 1 |
| MMK321 | ±500 | Association† | M | Adult | St. Claire, Douglas | 1 |
| MMK284 | ±500 | Association† | probable M | Adult | Upington | 1 |
| NMB1332 | ±500 | Association† | probable M | Adult | Upington | 1 |
| NMB1412 | ±500 | Association† | M | Adult | Upington | 1 |
| NMB1224 | ±500 | Association† | | | Villieria, Douglas | 1 |
| MMK312 | ±500 | Association† | | Adult | Voelfontein, Campbell | 1 |
| MMK277 | 890±50 | Pta-2898 | probable F | Adult | Weltevreden, Koffiefontein | 1 |
| UCT66 (Iron Age) | 400±50 | Pta-4980 | F | Adult | Taung | 2 |
| **LSA West coast (n=17)** | | | | | | |
| SAM1446 | 740±30 | Pta-9085 | | Adult | Port Nolloth | 1 |
| UCT88 | 490±65 | Gx-13183 | | Adult | Clanwilliam | 1 |
| UCT227 | 1000±50 | Pta-4405 | | Adult | Waterbakke | 5 |
| UCT334 | 3850±80 | OxA-457 | | | Clanwilliam | 1 |
| UCT378 | 10860±180 | OxA-478 | probable M | Adult | Eland's Bay | 1 |
| UCT429 | 1870±35 | Pta-8814 | | Adult | Eland's Bay | 5 |
| UCT387 | 2055±40 | GrA-23218 | | Adult | West coast | 5 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| UCT164 | 2360±30 | Pta-8750 | F | Adult | West coast | 5 |
| UCT224 | 2400±100 | OxA-455 | | Adult | Elands Bay | 1 |
| SAM5069 | 2634±28 | OxA-V-2066-34 | probable F | Adult | Doringbaai | 1 |
| UCT427 | 2670±80 | Gx-14816 | F | Adult | Eland's Bay | 1 |
| UCT445 | 2720±60 | Pta-5617 | | Adult | West coast | 5 |
| UCT222 | 2830±85 | Gx-13184 | probable M | | Stompneusbaai | 1 |
| SAM6147 | 2920±60 | Pta-9085 | | Adult | Vredendal | 1 |
| UCT333 | 3540±60 | Pta-1642 | | Adult | Klipfonteinrand | 1 |
| SAM4931 | 3750±60 | Pta-2267 | M | Adult | Kleinsee, Namaqualand | 1 |
| UCT390 | Later Stone Age | | M | Adult | Eland's Bay | 9 |
| **LSA SW coast (n=84)** | | | | | | |
| SAM6238 | 170±50 | Pta-9075 | M | Adult | Milnerton | 4 |
| SAM4178 | 380±45 | OxA-V-2056-36 | probable F | Adult | Gouritz River (near coast) | 4 |
| SAM4867 | 590±45 | Pta-4407 | | Adult | Witklip Farm, Vredenburg | 1 |
| SAM6020 | 620±30 | Pta-4189 | M | Adult | Tikosklip, Saldanha | 1 |
| SAM5032 | 765±25 | OxA-V-2056-35 | | Adult | Milnerton Beach | 1 |
| SAM5012 | 812±26 | OxA-V-2065-36 | probable F | Adult | Langebaan | 1 |
| UCT70 | 920±40 | GrA-23074 | probable M | Adult | Ratel river, Bredasdorp | 8 |
| UCT60 | 950±50 | Pta-2005 | | Adult | Saldanha | 1 |
| SAM6332 | 980±50 | Pta-8767 | | Adult | Melkbosstrand | 1 |
| SAM1247A | 1180±50 | Pta-4281 | F | Adult | Blaauwberg, Cape | 4 |
| SAM4905 | 1210±50 | Pta-4349 | M | Adult | New Blouberg-Melkbosch Road | 4 |
| UCT94 | 1270±40 | GrA-23216 | | Adult | South-West coast | 4 |
| SAM4314 | 1319±25 | OxA-V-2066-26 | | Adult | Noordhoek | 4 |
| SAM6075 | 1330±40 | Pta-4186 | F | Adult | Saldanha | 1 |
| SAM4669 | 1333±25 | OxA-V-2056-28 | | Adult | Gordon's Bay | 4 |
| UCT75 | 1340±40 | GrA-23069 | probable M | Adult | Cape Agallas, Bredasdorp | 8 |
| SAM6074 | 1360±40 | Pta-4148 | | Subadult | Saldanha | 1 |
| SAM4920A | 1364±32 | OxA-V-2059-17 | | Adult | Blouberg Strand | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| SAM5034 | 1390±40 | Pta-4771 | probable M | Adult | Hout Bay | 1 |
| SAM6334 | 1400±50 | Pta-8790 | M | Adult | Melkbosstrand | 1 |
| SAM6149 | 1440±70 | Gx-13182 | M | Adult | Melkbosstrand | 1 |
| SAM5083 | 1490±50 | Pta-926 | F | Adult | Yzerfontein | 1 |
| UCT97 | 1560±40 | Pta-4828 | | Adult | Kommetjie | 1 |
| SAM4790 | 1610±150 | Pta-2163 | M | Adult | Hermanus | 1 |
| UCT55 | 1680±40 | GrA-23075 | probable M | Adult | South-West coast | 4 |
| SAM4659 | 1815±29 | OxA-V-2056-43 | | Adult | Melkbosstrand | 4 |
| SAM1473 | 1880±60 | Pta-8773 | F | Adult | Onrus | 1 |
| SAM4901 | 1892±28 | OxA-V-2065-40 | | Adult | Pearly Beach | 1 |
| SAM6264 | 1950±60 | Pta-9073 | M | Adult | Melkbosstrand | 1 |
| UCT120 | 1960±50 | Pta-5677 | | Adult | South-West coast | 4 |
| SAM3053 | 1990±50 | Pta-4411 | probable M | Adult | Strand, Somerset West | 1 |
| SAM5041 | 2010±50 | Pta-4376 | | Adult | Melkbosstrand | 7 |
| SAM5035B | 2011±30 | OxA-V-2055-46 | | Adult | Melkbosstrand | 4 |
| SAM1443 | 2050±50 | Pta-2309 | M | Adult | Gordon's Bay | 1 |
| SAM1142 | 2090±27 | OxA-V-2056-32 | probable F | Adult | Strand, Somerset West | 1 |
| UCT220 | 2100±21 | Pta-5678 | M | Adult | Blouberg Strand | 7 |
| SAM6260A | 2120±60 | Pta-9069 | | Adult | Melkbosstrand | 1 |
| SAM6313B | 2140±29 | OxA-V-2056-47 | | Subadult | Melkbosstrand | 1 |
| SAM4813 | 2140±45 | Pta-4202 | probable F | Adult | Bokbaai, Darling | 1 |
| SAM5082 | 2150±60 | Pta-4199 | | Adult | Hout Bay | 4 |
| SAM6313A | 2161±30 | OxA-V-2055-44 | probable F | Adult | Melkbosstrand | 1 |
| SAM1441 | 2170±60 | Pta-4201 | probable M | Adult | Melkbosstrand | 1 |
| UCT134 | 2210±40 | GrA-23226 | | Adult | South-West coast | 4 |
| SAM4942 | 2220±45 | Pta-4829 | | Adult | Kommetjie | 1 |
| UCT436 | 2240±60 | Pta-8751 | | Adult | Mykonos | 4 |
| SAM4301 | 2250±30 | OxA-V-2055-40 | | Adult | Noordhoek | 1 |
| UCT595 | 2250±40 | Beta-263613 | | Adult | Saldanha Bay | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| SAM4299 | 2294±29 | OxA-V-2065-46 | | Adult | Noordhoek | 1 |
| SAM6043 | 2295±28 | OxA-V-2056-40 | probable M | Adult | Melkbosstrand | 1 |
| SAM4300 | 2304±29 | OxA-V-2067-37 | | Adult | Noordhoek | 1 |
| UCT372 | 2360±60 | Pta-4003 | probable F | Adult | Snuifklip, near Vleesbaai | 1 |
| SAM4899 | 2440±60 | Pta-4149 | probable M | Adult | Saldanha Bay | 1 |
| SAM39 | 2448±29 | OxA-V-2055-43 | | Subadult | Gordon's Bay | 4 |
| SAM5070 | 2573±31 | OxA-V-2056-46 | probable F | Adult | Melkbosstrand | 1 |
| SAM4906A | 2635±29 | OxA-V-2065-35 | | Adult | Blouberg Strand | 1 |
| SAM5095 | 2660±70 | Pta-4674 | | Adult | Saldanha | 1 |
| SAM4627 | 2665±27 | OxA-V-2056-34 | | Adult | Darling | 4 |
| SAM4202 | 2673±29 | OxA-V-2056-25 | | Adult | Kommetjie | 4 |
| UCT167 | 2695±45 | GrA-23222 | | | South-West coast | 4 |
| NMB1827 | 2815±40 | GrA-23229 | | Adult | Gordon's Bay Beach | 4 |
| UCT162 | 2880±50 | Pta-929 | | Subadult | Yzerfontein | 1 |
| UCT421 | 2895±45 | GrA-23217 | | Adult | Darling | 1 |
| UCT157 | 587±28 | OxA-V-2055-45 | probable M | Adult | Ladismith | 1 |
| UCT148 | 600 | Assoc. With UCT157 | | | Ladismith | 1 |
| SAM6071 | 2935±32 | OxA-V-2055-42 | | Adult | Vredenberg | 1 |
| SAM6317 | 2970±60 | Pta-8807 | M | Adult | Melkbosstrand | 1 |
| SAM4906B | 2977±33 | OxA-V-2056-48 | | | Blouberg Strand | 1 |
| UCT435 | 2980±60 | Pta-5034 | | Adult | Langebaan | 1 |
| UCT343 | 2985±45 | GrA-23221 | | Adult | South-West coast | 4 |
| SAM6051 | 3190±50 | Pta-2969 | | Adult | Byneskranskop | 7 |
| SAM6319 | 3200±35 | Pta-8752 | probable F | Adult | Melkbosstrand | 1 |
| UCT229 | 3220±55 | Pta-928 | | Adult | Melkbosstrand | 1 |
| SAM6318 | 3310±60 | Pta-8741 | M | Adult | Melkbosstrand | 1 |
| SAM4974 | 3363±34 | OxA-V-2055-48 | | Subadult | Gansbaai | 1 |
| SAM4298 | 3380±33 | OxA-V-2055-41 | | Subadult | Kommetjie | 1 |
| SAM5040 | 3570±60 | Pta-4225 | | Adult | Bokbaai, Darling | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| UCT112 | 4445±50 | Pta-2003 | probable M | Adult | Darling | 1 |
| UCT248A | 4730±95 | Gx-13185 | probable F | Adult | Noordhoek | 1 |
| SAM6272 | 5830±80 | Pta-9082 | probable M | Adult | Darling | 1 |
| UCT323 | 6430±80 | Pta-8794 | F | Adult | Blombos | 1 |
| SAM6049 | Later Stone Age | | M | Adult | Byneskranskop | 7 |
| SAM4840 | Later Stone Age | | | Adult | Peer's Cave | 9 |
| SAM4844 | Later Stone Age | | | Adult | Peer's Cave | 9 |
| UCT62 (Iron Age) | 150±60 | Pta-5008 | M | Adult | Philipi, Cape Flats | 2 |
| **LSA South coast (n=109)** | | | | | | |
| SAM5051 | 184±25 | OxA-V-2056-41 | M | Adult | Robberg, Plettenberg Bay | 4 |
| SAM5053 | 370±27 | OxA-V-2065-41 | | Adult | Robberg, Plettenberg Bay | 4 |
| UCT262 | 510±40 | GrA-23221 | | Adult | Oakhurst Rock Shelter | 1 |
| UCT583 | 560±45 | Pta-8760 | | Adult | Voelvlei 2, Mossel Bay | 1 |
| NMB1207A | 560±50 | Pta-8755 | M | Adult | Hartenbos, Mossel Bay | 5 |
| NMB1338 | 650±35 | GrA-23711 | M | Adult | Wittedrif, Knysna | 1 |
| NMB1219 | 650±50 | Pta-8804 | | Adult | Groot Brak River | 1 |
| SAM1260 | 1137±27 | OxA-V-2066-28 | | Adult | Oudtshoorn | 1 |
| SAM4180 | 688±27 | OxA-V-2056-23 | probable F | Adult | Thys Bay, Humansdorp | 1 |
| UCT582 | 740±40 | Pta-7178 | | Adult | Voelvlei 1, Mossel Bay | 1 |
| NMB1704 | 760±50 | Pta-6963 | F | Adult | Plettenberg Bay | 1 |
| SAM1457 | 910±35 | Pta-2149 | F | Adult | Klein Brak River, Mossel Bay | 1 |
| SAM4898 | 1226±26 | OxA-V-2053-49 | | Adult | Robberg | 1 |
| UCT254 | 1270±50 | Pta-6820 | | Adult | Plettenberg Bay | 1 |
| UCT592 | 1370±40 | Beta-263616 | probable M | Adult | Sedgefield | 1 |
| NMB1707 | 1394±24 | OxA-V-2064-53 | | Adult | Plettenberg Bay | 1 |
| NMB5 | 1423±26 | OxA-V-2064-49 | | Adult | Plettenberg Bay | 1 |
| SAM4179 | 1528±27 | | probable F | Adult | Thys Bay, Humansdorp | 6 |
| SAM6213 | 1558±27 | OxA-V-2065-39 | probable M | Adult | Sedgefield | 1 |
| UCT109 | 1590±50 | GrA-23656 | | Adult | Humansdorp | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| SAM320G | 1707±27 | OxA-V-2056-24 | | Adult | Klein Brak River, Mossel Bay | 1 |
| SAM278G | 2158±28 | OxA-V-2065-43 | | Adult | Klein Brak River, Mossel Bay | 1 |
| SAM1878A | 2170±20 | Pta-6592 | M | Adult | Robberg (Cave E) | 1 |
| NMB1203 | 2180±50 | Pta-8783 | probable M | Adult | Groot Brak River | 4 |
| NMB1204 | 2210±35 | Pta-8744 | probable F | Adult | Groot Brak River | 1 |
| SAM1146 | 2240±20 | Pta-6646 | M | Adult | Robberg | 1 |
| SAM4312 | 2260±170 | Pta-2164 | probable F | Adult | Mossel Bay | 4 |
| A1114 | 2271±33 | OxA-V-2055-51 | | Adult | Knysna | 1 |
| UCT107 | 2290±50 | Pta-6815 | | Adult | Knysna | 1 |
| SAM34 | 2310±25 | Pta-6599 | M | Adult | Knysna Cave | 1 |
| NMB82 | 2355±40 | GrA-23228 | probable M | Adult | Groot Kommandokloof | 6 |
| SAM1893 | 2360±20 | Pta-6613 | M | Adult | Robberg | 1 |
| UCT591 | 2460±40 | Beta-263612 | | Adult | Buffel's Bay | 1 |
| SAM5050 | 2580±60 | Pta-7927 | | Subadult | Robberg | 1 |
| A1115 | 2588±28 | OxA-V-2065-48 | | Adult | Knysna | 1 |
| NMB1639A | 2590±60 | Pta-6965 | probable F | Adult | Robberg | 1 |
| SAM5049 | 2740±50 | Pta-7934 | | Adult | Robberg | 1 |
| NMB1705 | 2780±60 | Pta-6964 | | Adult | Plettenberg Bay | 1 |
| SAM5048 | 2780±60 | Pta-7924 | | Subadult | Robberg | 1 |
| NMB1241A | 2790±60 | Pta-6958 | | Adult | Matjes River Rock Shelter | 1 |
| A1172 | 2950±40 | GrA-23647 | | Adult | Whitcher's Cave | 1 |
| NMB1244A | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1244B | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1246 | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1247 | 3000 | Mytilus layer (Layer B) | | Adult | Matjes River Rock Shelter | 1 |
| NMB1248 | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1250 | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1261 | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| NMB1270A | 3000 | Mytilus layer (Layer B) | | Adult | Matjes River Rock Shelter | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| NMB1270B | 3000 | Mytilus layer (Layer B) | | | Matjes River Rock Shelter | 1 |
| A2787A | 3028±32 | OxA-V-2161-55 | | Adult | Andrieskraal | 6 |
| NMB1242 | 3030±26 | OxA-V-2064-50 | | Adult | Matjes River Rock Shelter | 4 |
| NMB1273 | 3050±60 | Pta-6942 | | Adult | Matjes River Rock Shelter | 1 |
| SAM1145 | 3120±70 | Pta-2284 | M | Adult | Robberg | 1 |
| NMB1202 | 3140±50 | Pta-8801 | | Adult | Groot Brak River | 1 |
| SAM1128 | 3156±33 | OxA-V-2055-49 | probable F | Adult | Robberg | 1 |
| NMB1241B | 3290±90 | Pta-6950 | | | Matjes River Rock Shelter | 1 |
| SAM1871 | 3310±60 | Pta-2273 | | Adult | Robberg (Cave D) | 1 |
| A1112A | 3355±45 | GrA-23232 | | Adult | South coast | 4 |
| A1112C | 3355±45 | GrA-23232 | probable M | Adult | South coast | 4 |
| SAM1879 | 3440±60 | Pta-2283 | M | Adult | Robberg | 7 |
| UCT161 | 3451±26 | OxA-V-2064-54 | probable F | Adult | Plettenberg Bay | 1 |
| SAM32 | 3754±35 | OxA-V-2055-47 | | Adult | Humansdorp | 6 |
| NMB4 | 3940±27 | OxA-V-2064-48 | | Adult | Robberg | 1 |
| UCT191 | 4100±60 | Pta-4431 | | Subadult | Oakhurst Rock Shelter | 1 |
| NMB1640 | 4120±60 | Pta-6983 | F | Adult | Robberg | 1 |
| NMB1275 | 4850±60 | Pta-6986 | M | Adult | Matjes River Rock Shelter | 1 |
| UCT186 | 4880±70 | Pta-4348 | | | Oakhurst Rock Shelter | 1 |
| NMB1274 | 5120±50 | Pta-6981 | probable M | Adult | Matjes River Rock Shelter | 1 |
| NMB1319 | 5251±29 | OxA-V-2064-51 | | Adult | Plettenberg Bay | 1 |
| UCT184 | 5330±60 | Pta-3719 | | Adult | Oakhurst Rock Shelter | 1 |
| UCT181 | 5450±70 | Pta-4367 | | Adult | Oakhurst Rock Shelter | 1 |
| UCT183A | 5990±70 | Pta-4426 | F | Adult | Oakhurst Rock Shelter | 1 |
| UCT180 | 6180±70 | Pta-3718 | | Adult | Oakhurst Rock Shelter | 1 |
| SAM4182 | 6811±36 | OxA-V-2056-26 | | Adult | Coldstream Cave (Dury's Cave) | 1 |
| SAM5055 | 6995±50 | OxA-V-2065-42 | probable M | Adult | Robberg | 1 |
| UCT182 | 7120±60 | Pta-4354 | F | Adult | Oakhurst Rock Shelter | 1 |
| NMB1448A | 7295±32 | OxA-V-2064-52 | | | Matjes River Rock Shelter | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| NMB1448B | 7295±32 | OxA-V-2064-52 | | Adult | Matjes River Rock Shelter | 1 |
| NMB1271 | 7380±120 | UCLA-1746D | | Adult | Matjes River Rock Shelter | 9 |
| NMB1264 | 8000-4000 | Layer C | | Adult | Matjes River Rock Shelter | 1 |
| NMB1265 | 8000-4000 | Layer C | | Adult | Matjes River Rock Shelter | 1 |
| NMB1278 | 8000-4000 | Layer C | | | Matjes River Rock Shelter | 1 |
| NMB1282 | 8000-4000 | Layer C | | | Matjes River Rock Shelter | 1 |
| NMB1451 | 8000-4000 | Layer C | | Adult | Matjes River Rock Shelter | 1 |
| NMB8A | 8000-4000 | Layer C | | | Matjes River Rock Shelter | 1 |
| UCT348 | 8000-4000 | Burial #5 | | | Nelson Bay Cave, Robberg | 1 |
| UCT183B | 8000-4000 | Association† | | Subadult | Oakhurst Rock Shelter | 1 |
| UCT208 | 8000-4000 | Association† | | | Oakhurst Rock Shelter | 1 |
| UCT185 | 9100±90 | Pta-3724 | probable F | | Oakhurst Rock Shelter | 1 |
| UCT192 | 9120±90 | Pta-3729 | F | | Oakhurst Rock Shelter | 1 |
| NMB1441 | 9230±160 | UCLA-1746B | | | Matjes River Rock Shelter | 1 |
| NMB1442 | 9230±160 | UCLA-1746B | | | Matjes River Rock Shelter | 1 |
| NMB1443 | 9230±160 | UCLA-1746B | | Adult | Matjes River Rock Shelter | 1 |
| UCT156 | 10110±80 | GrA-23223 | probable M | | Knysna | 1 |
| NMB1234 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1236A | 12000-8000 | Burnt layer (Layer D) | | Adult | Matjes River Rock Shelter | 1 |
| NMB1236B | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1302 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1308 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1373 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1446 | 12000-8000 | Burnt layer (Layer D) | | Adult | Matjes River Rock Shelter | 1 |
| NMB1602A | 12000-8000 | Burnt layer (Layer D) | | Adult | Matjes River Rock Shelter | 1 |
| NMB1602B | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB1603 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB6 | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |
| NMB8B | 12000-8000 | Burnt layer (Layer D) | | | Matjes River Rock Shelter | 1 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| SAM1131 | Later Stone Age | | probable F | Adult | Robberg | 9 |
| SAM3026 | Later Stone Age | | | | Robberg | 9 |
| **LSA SE coast (n=18)** | | | | | | |
| A1153 | 636±26 | OxA-V-2065-47 | | Adult | Steytlerville | 1 |
| UCT114 | 650±40 | GrA-23654 | probable M | | Cape St. Francis | 1 |
| UCT83 | 680±40 | GrA-23072 | | Adult | Cape St. Francis | 1 |
| A2226 | 800±50 | Pta-8728 | probable M | Adult | South-East coast | 5 |
| A1154 | 905±25 | OxA-V-2066-33 | | Adult | Steytlerville | 1 |
| A1117 | 1060±50 | Pta-8727 | F | Adult | Lime Bank, Loerie | 1 |
| A2227 | 1150±50 | Pta-8819 | | Adult | South-East coast | 5 |
| A1071 | 1320±50 | Pta-6997 | | Adult | Amahlongwana river, Widenham, Natal | 1 |
| SAM4874 | 1426±29 | OxA-V-2056-45 | probable F | Adult | Cape St. Francis | 6 |
| NMB83 | 1590±40 | GrA-23227 | probable M | Adult | Cape St. Francis | 6 |
| A1166 | 1818±27 | OxA-V-2056-33A | | Adult | Humewood, Port Elizabeth | 1 |
| A1152 | 1850±35 | Pta-8757 | | Adult | Amsterdam Hoek, Port Elizabeth | 1 |
| A1127 | 1891±29 | OxA-V-2066-36 | | Adult | Jeffrey's Bay | 1 |
| UCT78 | 2145±40 | GrA-23241 | | Adult | Cape St. Francis | 6 |
| NMB86 | 2275±40 | GrA-23657 | F | Adult | Cape St. Francis | 6 |
| SAM31 | 3576±30 | OxA-V-2065-34 | | Adult | Blaauwkrantz | 8 |
| A1124 | 4320±32 | OxA-V-2056-42 | | Adult | Port Elizabeth | 1 |
| A1139 | 4800±50 | Pta-8816 | | Adult | Kenkelbosch, Eastern Cape | 1 |
| **IA North East (n=80)** | | | | | | |
| PMB87/12 | 110±45 | | probable F | Adult | Thompsons Bay | 2 |
| A*1 (UP1) | 1310±50 | Pta-2692 | M | Adult | Happyrest | 2 |
| PMB91/45 | 140±40 | Pta-5780 | | Adult | Venus Substation, Estcourt | 2 |
| PMB90/11 | 20±45 | Pta-5780 | | Adult | Mhlanga Lagoon | 2 |
| A*37 | 300±35 | Pta-8944 | | | Pilanesberg | 2 |
| D-Skutwater NAS 27 | 830±40; 820±45 | Pta-3734; Pta-3716 | M | Adult | Skutwater | 2 |
| D-Skutwater NAS 28 | 830±40; 820±45 | Pta-3734; Pta-3715 | | | Skutwater | 2 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| D-Skutwater NAS 29 | 830±40; 820±45 | Pta-3734; Pta-3718 | | Adult | Skutwater | 2 |
| D-Skutwater NAS 30 | 830±40; 820±45 | Pta-3734; Pta-3717 | | Adult | Skutwater | 2 |
| D-Skutwater TSW1/1 Burial | 830±40; 820±45 | Pta-3734; Pta-3719 | | | Skutwater | 2 |
| A*103 | AD1433, AD1451, AD1487 | | | | Pilanesberg | 2 |
| A*100 | AD1485-1628 | Pta-7848 | | | Ben Alberts, Thabazimbi | 3 |
| A*99 | AD1485-1628 | Pta-7848 | | | Ben Alberts, Thabazimbi | 3 |
| A*32 | AD1519-1572 (1642) | | | | Schuinsdraai | 3 |
| A*44 | AD1519-1572 (1642) | | | | Schuinsdraai | 3 |
| A*45 | AD1519-1572 (1642) | | | | Schuinsdraai | 3 |
| A*79 | AD1692, AD1726, AD1814 | | | Adult | Pilanesberg | 2 |
| A4209 | AD1723±46 | Pta-136 | | | Klipriviersberg | 2 |
| A4221 | AD1820 | | | Adult | Olifantspoort, Rustenburg | 2, 3 |
| A4143 | AD460±50 | UCLA-1791B | | Adult | Broederstroom | 2 |
| PMB80/2 | Early Iron Age | Association | | | Mhlopeni | 2 |
| PMB86/1 Box 144 | Early Iron Age | Association | | | Nanda, Mngeni Valley | 2 |
| PMB86/1 Box 146 | Early Iron Age | Association | | | Nanda, Mngeni Valley | 2 |
| PMB86/1 Box 147 | Early Iron Age | Association | | Adult | Nanda, Mngeni Valley | 2 |
| PMB2009/11 | Early Iron Age | | | Adult | King's View | 2 |
| A*88 | Early Iron Age | | | Adult | Ha-Matshata | 2, 3 |
| A*90 | Early Iron Age | | | Adult | Ha-Matshata | 2, 3 |
| A*91 | Early Iron Age | | | | Ha-Matshata | 2, 3 |
| A*92 | Early Iron Age | | | | Ha-Matshata | 2 |
| A*94 | Early Iron Age | | | Adult | Ha-Matshata | 2 |
| A*33 | Iron Age | | | Adult | Phalaborwa | 3 |
| A*29 | Iron Age | | | Adult | Skukuza, Kruger National Park | 3 |
| A*11 | Iron Age | | | | Weltevrede, Vryheid | 3 |
| A*14 | Iron Age | | | Adult | Ashfield, Louis Trichardt | 3 |
| A*189 | Iron Age | | | Adult | Botlokwa | 3 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| A*190 | Iron Age | | | | Botlokwa | 3 |
| A*191 | Iron Age | | M | Adult | Botlokwa | 3 |
| A*183 | Iron Age | | | | De Hoop Dam | 3 |
| D-BGL 1/1 BOKS458 | Iron Age | | | | Glennel | 3 |
| D-BGL1/1 BOKS455 | Iron Age | | | | Glennel | 3 |
| D-BGL1/1 BOKS456 | Iron Age | | | Adult | Glennel | 3 |
| D-BGL1/1 BOKS457 | Iron Age | | | | Glennel | 3 |
| A*163 | Iron Age | | | | Haenertsburg, Limpopo | 3 |
| A*47 | Iron Age | | M | Adult | Makgope | 3 |
| A*48 | Iron Age | | probable M | Adult | Makgope | 3 |
| A*69 | Iron Age | | M | Adult | Malle, near Marikana | 3 |
| A*162 | Iron Age | | M | Adult | Makapanstad | 3 |
| A*155 | Iron Age | | | | Onverwacht, Mpumalanga | 3 |
| A*93 | Iron Age | | | Adult | Winteroord, Botswana | 3 |
| A*96 | Iron Age | | | | Tropic of Capricorn, Limpopo | 3 |
| A*8 | Iron Age | | | Adult | Welgegund, Pelindaba | 3 |
| A*87 | Iron Age | | | | Ha-Matshata | 3 |
| A*4 | Iron Age | | | Adult | Vrede (Witkoppen Hills) | 3 |
| A*188 | Iron Age | | | Adult | Waterpoort | 3 |
| A*67 | Iron Age | | | Subadult | Willoglen 1 | 3 |
| PMB2009/6 | Late Iron Age | Association† | | Adult | Fynnlands | 2 |
| UCT430 | Late Iron Age | Association† | probable M | Adult | Phutwane, Phalaborwa | 2 |
| UCT431 | Late Iron Age | Association† | | Adult | Phalaborwa | 2 |
| A*80 (UP88) | Late Iron Age | | | Adult | Phalaborwa | 3 |
| A*80 (UP89) | Late Iron Age | | | | Phalaborwa | 3 |
| A*6 | Late Iron Age | | | | Simunye, Swaziland | 3 |
| PMB2009/4 | Late Iron Age | Association† | F | Adult | Umdloti | 2 |
| A*83 | Late Iron Age | | F | Adult | Cyferskuil | 3 |
| UCT330 | Late Iron Age | Association† | | Subadult | Klip River Valley | 2 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| A*28 | Late Iron Age | | | Adult | Mabyanamatswana, Brits | 3 |
| UCT326 | Late Iron Age | Association† | | Adult | Makgwareng | 2 |
| UCT327 | Late Iron Age | Association† | | | Makgwareng | 2 |
| UCT328 | Late Iron Age | Association† | | Subadult | Makgwareng | 2 |
| A*22 | Late Iron Age | | | | Pilanesberg | 3 |
| A*38 (UP151) | Late Iron Age | | | | Pilanesberg | 3 |
| A*51 | Late Iron Age | | | | Pilanesberg | 3 |
| A4230 | Late Iron Age | | M | Adult | Rooikrans - RO | 2 |
| A4229 | Late Iron Age | | | Adult | Thavatshena | 2 |
| A4260 | Late Iron Age | | | | Vhunyela - VH | 2 |
| D-Asskopies 26 27 CC 1 | Late Iron Age | | | Adult | Vredefort Dome | 2, 3 |
| D-Welgegund B3/B2 | Late Iron Age | | | Adult | Welgegund | 2 |
| A*68 | Late Iron Age | | | | Willoglen 2 | 2 |
| A*7 | Late Iron Age | | | | Rooiberg | 3 |
| A4226 | mid 1600s | | M | Adult | Rooikrans - RO | 2 |
| A4227 | mid 1600s | | F | Adult | Rooikrans - RO | 2 |
| **IA South Zambia (n=23)** | | | | | | |
| A4168 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4170 | Iron Age | | | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4171 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4172 | Iron Age | | | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4175 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4177 | Iron Age | | F | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4178 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4180 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4183 | Iron Age | | probable M | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4192 | Iron Age | | | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4195 | Iron Age | | | Adult | Ingombe Ilede Mound (Zambia) | 2 |
| A4199 | Iron Age | | | Adult | Ingombe Ilede Mound (Zambia) | 2 |

Table A1: continued.

| Catalogue no. | BP | Lab number | Sex* | Age | Locality | Reference |
|---|---|---|---|---|---|---|
| A4205 | Iron Age | | | | Ingombe Ilede Mound (Zambia) | 2 |
| A4156 | Iron Age | | | | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4160 | Iron Age | | F | Adult | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4161 | Iron Age | | | | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4163 | Iron Age | | | Subadult | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4164 | Iron Age | | | | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4165 | Iron Age | | | | Isamu Patu Mound (IP) (Zambia) | 2 |
| A4140 | Iron Age | | F | Adult | Kala Ranch, Kalomo (Zambia) | 2 |
| A4272 | Late Iron Age | | probable M | Adult | Makoli (Zambia) | 2, 3 |
| A4273 | Late Iron Age | | | Adult | Makoli (Zambia) | 2, 3 |
| A4274 | Late Iron Age | | | | Makoli (Zambia) | 2, 3 |
| **Additional LSA (n=2)** | | | | | | |
| UCT106 | 2680±60 | Pta-4979 | probable F | Adult | Ladybrand | 1 |
| UCT566 | 5200 | Pta-9369 | F | Adult | Muela, Lesotho | 1 |

References: 1 - Black (2014), 2 - Warren (2013), 3 – Institution records, 4 - Stynder (2009), 5 – Stynder *et al*. (2007), 6 - Ginter (2008), 7 - Cameron and Pfeiffer (2014), 8 - Stynder (2006), 9 - Stock and Pfeiffer (2004).

† Skeletal remains assigned a specific time bracket based on archaeological association.
***** Sex determination using standard techniques for all available crania and pelvic bones (Buikstra and Ubelaker, 1994; White and Folkens, 2005).

Table A2: Modern Khoesan individuals (n=24) identified by Morris (1986).

| Catalogue no. | Sex | Age |
|---|---|---|
| MMK 142 | M | Adult |
| MMK 143 | M | Adult |
| MMK 144 | F | Adult |
| MMK 145 | M | Adult |
| MMK 150 | F | Adult |
| MMK 151 | M | Adult |
| MMK 158 | M | Adult |
| MMK 159 | M | Adult |
| MMK 161 | M | Adult |
| MMK 163 | M | Adult |
| MMK 165 | F | Adult |
| MMK 166 | M | Adult |
| MMK 167 | F | Adult |
| MMK 174 | F | Adult |
| MMK 175 | M | Subadult |
| MMK 264 | M | |
| MMK 283 | M | Adult |
| NMB1062 | F | Adult |
| UCT29 | M | Adult |
| UCT35 | M | Adult |
| UCT43 | F | |
| UCT44 | M | Adult |
| UCT50 | M | |
| UCT54 | F | Adult |

Table A3: Modern Khoesan dental casts in the Dental Cast Collection of the School of Anatomical Sciences, University of the Witwatersrand.

| Catalogue Group | Sample size | Population | Date* | Sex |
|---|---|---|---|---|
| VRB | 133 | Barakwena | 1987 | M |
| VRBF | 29 | Barakwena | 1987 | F |
| VRK | 19 | !Kung | | |
| VRVF | 23 | Vassekele | 1987 | F |
| VRE | 16 | Vassekele | 1985 | |
| VRLC | 17 | Lake Chrissie | | |
| **TOTAL** | **237** | | | |

*The year the dental casts were made from living individuals.

Table A4: Modern Bantu-speaker samples (n=176) from the Raymond A Dart Collection of Human Skeletons, School of Anatomical Sciences, University of the Witwatersrand.

| Catalogue no. | Group | Sex | Age |
|---|---|---|---|
| A1244 | NDEBELE | F | Subadult |
| A1549 | NDEBELE | F | Adult |
| A1954 | NDEBELE | F | Adult |
| A2075 | NDEBELE | F | Adult |
| A3704 | NDEBELE | F | Adult |
| A3282 | NDEBELE | F | Adult |
| A1294 | NDEBELE | M | Adult |
| A1418 | NDEBELE | M | Adult |
| A589 | NDEBELE | M | Adult |
| A702 | NDEBELE | M | Adult |
| A762 | NDEBELE | M | Adult |
| A1544 | NDEBELE | M | Adult |
| A1532 | NDEBELE | F | Adult |
| A677 | NDEBELE | M | Adult |
| A1535 | NDEBELE | M | Adult |
| A1545 | NDEBELE | M | Adult |
| A1671 | NDEBELE | M | Adult |
| A927 | NDEBELE | M | Adult |
| A1375 | NDEBELE | M | Adult |
| A196 | NDEBELE | M | Adult |
| A1274 | NDEBELE | M | Adult |
| A2483 | NDEBELE | M | Adult |
| A454 | NDEBELE | M | Adult |
| A2365 | NDEBELE | M | Adult |
| A3256 | NDEBELE | M | Adult |
| A751 | NDEBELE | M | Adult |
| A1515 | NDEBELE | M | Adult |
| A763 | NDEBELE | M | Adult |
| A1561 | NDEBELE | M | Adult |
| A3136 | NDEBELE | M | Adult |
| A964 | NDEBELE | M | Adult |
| A1278 | NDEBELE | M | Adult |
| A2735 | NDEBELE | M | Adult |
| A1801 | NDEBELE | M | Adult |
| A2214 | NDEBELE | M | Adult |
| A3141 | NDEBELE | M | Adult |
| A710 | NDEBELE | M | Adult |
| A3135 | NDEBELE | M | Adult |
| A2381 | NDEBELE | M | Adult |
| A3091 | NDEBELE | M | Adult |
| A3356 | TSONGA | M | Adult |
| A460 | TSONGA | M | Adult |
| A3426 | TSONGA | M | Adult |

| Catalogue no. | Group | Sex | Age |
|---|---|---|---|
| A591 | XHOSA | M | Adult |
| A3538 | XHOSA | M | Adult |
| A3159 | XHOSA | M | Adult |
| A462 | XHOSA | M | Adult |
| A720 | XHOSA | M | Adult |
| A1309 | XHOSA | M | Adult |
| A1283 | XHOSA | M | Adult |
| A692 | XHOSA | M | Adult |
| A832 | XHOSA | M | Adult |
| A3490 | XHOSA | M | Adult |
| A2288 | XHOSA | M | Adult |
| A959 | XHOSA | M | Adult |
| A3460 | XHOSA | M | Adult |
| A1930 | XHOSA | M | Adult |
| A3070 | XHOSA | M | Adult |
| A3350 | XHOSA | M | Adult |
| A3058 | XHOSA | M | Adult |
| A3491 | XHOSA | M | Adult |
| A1426 | XHOSA | M | Adult |
| A2768 | XHOSA | M | Adult |
| A3111 | XHOSA | M | Adult |
| A1333 | XHOSA | M | Adult |
| A1510 | XHOSA | M | Adult |
| A1313 | XHOSA | M | Adult |
| A2417 | XHOSA | M | Adult |
| A873 | XHOSA | M | Adult |
| A961 | XHOSA | M | Adult |
| A1547 | XHOSA | M | Adult |
| A2017 | XHOSA | M | Adult |
| A2128 | XHOSA | M | Adult |
| A3137 | XHOSA | M | Adult |
| A1551 | XHOSA | M | Adult |
| A3707 | XHOSA | M | Adult |
| A1786 | XHOSA | M | Adult |
| A3644 | XHOSA | M | Adult |
| A3234 | XHOSA | M | Adult |
| A1291 | XHOSA | M | Adult |
| A2134 | XHOSA | M | Adult |
| A2027 | XHOSA | M | Adult |
| A1901 | XHOSA | M | Adult |
| A746 | ZULU | F | Subadult |
| A1875 | ZULU | F | Subadult |
| A617 | ZULU | F | Subadult |

Table A4: continued.

| Catalogue no. | Group | Sex | Age |
|---|---|---|---|
| A3063 | TSONGA | M | Adult |
| A3765 | TSONGA | M | Adult |
| A3313 | TSONGA | M | Adult |
| A3555 | TSONGA | M | Adult |
| A267 | TSONGA | M | Adult |
| A1314 | TSONGA | M | Adult |
| A3713 | TSONGA | M | Adult |
| A2204 | TSONGA | M | Adult |
| A3115 | TSONGA | M | Adult |
| A3363 | TSONGA | M | Adult |
| A3591 | TSONGA | M | Adult |
| A592 | XHOSA | F | Subadult |
| A1326 | XHOSA | F | Adult |
| A278 | XHOSA | F | Adult |
| A787 | XHOSA | F | Adult |
| A2314 | XHOSA | F | Adult |
| A177 | XHOSA | F | Adult |
| A1964 | XHOSA | F | Adult |
| A758 | XHOSA | F | Adult |
| A1672 | XHOSA | F | Adult |
| A1436 | XHOSA | F | Adult |
| A3643 | XHOSA | F | Adult |
| A3590 | XHOSA | F | Adult |
| A552 | XHOSA | F | Adult |
| A1998 | XHOSA | F | Adult |
| A3480 | XHOSA | F | Adult |
| A642 | XHOSA | F | Adult |
| A2367 | XHOSA | F | Adult |
| A2863 | XHOSA | F | Adult |
| A1241 | XHOSA | F | Adult |
| A2887 | XHOSA | F | Adult |
| A439 | XHOSA | M | Subadult |
| A1893 | XHOSA | M | Adult |
| A2393 | XHOSA | M | Subadult |
| A383 | XHOSA | M | Subadult |
| A475 | XHOSA | M | Subadult |
| A801 | XHOSA | M | Adult |
| A973 | XHOSA | M | Subadult |
| A638 | XHOSA | M | Adult |
| A1865 | XHOSA | M | Adult |
| A837 | XHOSA | M | Adult |
| A640 | XHOSA | M | Adult |
| A1474 | XHOSA | M | Adult |
| A901 | XHOSA | M | Adult |
| A3416 | XHOSA | M | Adult |

| Catalogue no. | Group | Sex | Age |
|---|---|---|---|
| A3791 | ZULU | F | Adult |
| A1408 | ZULU | F | Adult |
| A2849 | ZULU | F | Adult |
| A105 | ZULU | F | Adult |
| A3805 | ZULU | F | Adult |
| A1499 | ZULU | F | Adult |
| A381 | ZULU | F | Adult |
| A2191 | ZULU | F | Adult |
| A3556 | ZULU | F | Adult |
| A1697 | ZULU | F | Adult |
| A648 | ZULU | F | Adult |
| A2404 | ZULU | F | Adult |
| A3146 | ZULU | F | Adult |
| A3157 | ZULU | F | Adult |
| A2221 | ZULU | F | Adult |
| A2156 | ZULU | F | Adult |
| A3519 | ZULU | F | Adult |
| A158 | ZULU | F | Adult |
| A527 | ZULU | F | Adult |
| A3547 | ZULU | F | Adult |
| A646 | ZULU | F | Adult |
| A1961 | ZULU | F | Adult |
| A1577 | ZULU | F | Adult |
| A2682 | ZULU | F | Adult |
| A3614 | ZULU | F | Adult |
| A508 | ZULU | M | Subadult |
| A380 | ZULU | M | Subadult |
| A800 | ZULU | M | Subadult |
| A398 | ZULU | M | Subadult |
| A794 | ZULU | M | Adult |
| A1280 | ZULU | M | Subadult |
| A1434 | ZULU | M | Subadult |
| A3784 | ZULU | M | Adult |
| A500 | ZULU | M | Adult |
| A1331 | ZULU | M | Adult |
| A3770 | ZULU | M | Adult |
| A783 | ZULU | M | Adult |
| A969 | ZULU | M | Adult |
| A14 | ZULU | M | Adult |
| A2173 | ZULU | M | Adult |
| A150 | ZULU | M | Adult |
| A848 | ZULU | M | Adult |
| A493 | ZULU | M | Adult |
| A491 | ZULU | M | Adult |
| A2653 | ZULU | M | Adult |

# APPENDIX B: DESCRIPTIVE STATISTICS FOR THE PREHISTORIC AND MODERN COMPARISONS

Table B1: Frequencies of the nonmetric cranial traits (n=73) investigated between the prehistoric and modern Khoesan and Bantu-speakers.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Incomplete (nasal part) metopic suture | 230 | 5 | 36 | 14 | 23 | 4 | 142 | 10 |
| Complete metopic suture* | 230 | 0 | 36 | 0 | 23 | 0 | 142 | 5 |
| Metopic ridge | 238 | 37 | 43 | 26 | 24 | 21 | 145 | 26 |
| Square shaped orbits* | 213 | 45 | 38 | 71 | 21 | 67 | 142 | 71 |
| Oval shaped orbits* | 213 | 53 | 38 | 29 | 21 | 29 | 142 | 27 |
| Round shaped orbits | 213 | 2 | 38 | 0 | 21 | 5 | 142 | 2 |
| Supraorbital notch (Left)* | 236 | 68 | 44 | 86 | 24 | 67 | 153 | 80 |
| Supraorbital notch (Right)* | 235 | 74 | 48 | 90 | 24 | 71 | 153 | 84 |
| Supraorbital foramen (Left)* | 234 | 47 | 45 | 13 | 24 | 50 | 152 | 25 |
| Supraorbital foramen (Right)* | 233 | 42 | 46 | 15 | 24 | 33 | 153 | 27 |
| Ethmoidal foramina (Left)* | 241 | 46 | 15 | 60 | 21 | 81 | 129 | 64 |
| Ethmoidal foramina (Right)* | 141 | 82 | 14 | 86 | 19 | 100 | 130 | 64 |
| Infraorbital foramen (Left) | 191 | 88 | 36 | 97 | 24 | 88 | 144 | 92 |
| Infraorbital foramen (Right) | 195 | 90 | 38 | 87 | 24 | 92 | 150 | 89 |
| Infraorbital form* | 215 | 5 | 44 | 16 | 24 | 17 | 144 | 6 |
| Infraorbital suture* | 124 | 24 | 22 | 23 | 14 | 0 | 127 | 9 |
| Profile curves of nasal bones | 147 | 54 | 27 | 56 | 9 | 44 | 99 | 60 |
| Superficial nasion* | 158 | 66 | 28 | 29 | 22 | 41 | 121 | 44 |
| Moderately depressed nasion* | 158 | 27 | 28 | 54 | 22 | 45 | 121 | 34 |
| Marked depression of nasion* | 158 | 7 | 28 | 18 | 22 | 14 | 121 | 22 |
| Angle of nasal bones | 198 | 91 | 37 | 100 | 22 | 95 | 149 | 95 |
| Nasal bone shape | 157 | 54 | 26 | 65 | 18 | 44 | 112 | 50 |
| Extension of nasal bones* | 145 | 14 | 22 | 41 | 8 | 63 | 86 | 41 |
| Development of anterior nasal spine | 189 | 58 | 26 | 69 | 23 | 70 | 139 | 52 |

Table B1: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Zygomaxillary tubercle (Left)* | 213 | 45 | 34 | 59 | 24 | 67 | 149 | 62 |
| Zygomaxillary tubercle (Right)* | 211 | 43 | 39 | 46 | 23 | 74 | 150 | 60 |
| Subnasal region* | 204 | 36 | 34 | 50 | 19 | 32 | 115 | 72 |
| Dental arcade shape* | 135 | 72 | 25 | 68 | 10 | 40 | 59 | 86 |
| Anterior palate form* | 229 | 85 | 45 | 98 | 22 | 91 | 151 | 99 |
| Torus palatines | 170 | 33 | 32 | 34 | 20 | 45 | 139 | 31 |
| Torus maxillaries* | 192 | 5 | 38 | 3 | 17 | 6 | 117 | 15 |
| Foramen of Huschke (Left)* | 220 | 29 | 48 | 13 | 22 | 9 | 150 | 9 |
| Foramen of Huschke (Right)* | 221 | 3 | 48 | 10 | 23 | 13 | 151 | 11 |
| Encroachment of occipital condyles* | 185 | 27 | 28 | 21 | 22 | 91 | 151 | 9 |
| Hypoglossal canal bridging (Left) | 188 | 9 | 34 | 6 | 22 | 14 | 143 | 13 |
| Hypoglossal canal bridging (Right) | 191 | 8 | 31 | 3 | 22 | 9 | 143 | 6 |
| Condylar canal (Left)* | 137 | 45 | 17 | 76 | 22 | 50 | 131 | 62 |
| Condylar canal (Right) | 142 | 54 | 14 | 64 | 22 | 55 | 134 | 65 |
| Inca bone | 224 | 1 | 38 | 0 | 24 | 0 | 146 | 68 |
| Interparietal groove | 225 | 27 | 43 | 42 | 24 | 42 | 147 | 24 |
| Parietal foramina | 201 | 94 | 30 | 97 | 23 | 100 | 137 | 91 |
| Zygomatic arch* | 200 | 29 | 29 | 7 | 24 | 8 | 145 | 43 |
| Wormian bones* | 195 | 57 | 31 | 65 | 24 | 8 | 134 | 75 |
| Ophryonic groove* | 237 | 22 | 47 | 11 | 23 | 26 | 144 | 6 |
| Sutural variations at pterion (Left)* | 114 | 76 | 21 | 48 | 10 | 90 | 81 | 68 |
| Sutural variations at pterion (Right)* | 116 | 75 | 17 | 29 | 10 | 90 | 93 | 59 |
| Inferior frontal eminence (Left) | 217 | 47 | 36 | 36 | 23 | 65 | 147 | 46 |
| Inferior frontal eminence (Right) | 216 | 47 | 37 | 38 | 24 | 63 | 150 | 47 |
| Superior temporal line (Left) | 209 | 43 | 29 | 38 | 24 | 42 | 143 | 41 |
| Superior temporal line (Right) | 196 | 42 | 28 | 43 | 24 | 42 | 140 | 45 |

Table B1: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Mons temporosphenoidalis (Left)* | 211 | 56 | 32 | 38 | 24 | 79 | 151 | 14 |
| Mons temporosphenoidalis (Right)* | 204 | 57 | 30 | 30 | 24 | 79 | 153 | 14 |
| Parietotemporal suture (Left)* | 176 | 47 | 26 | 65 | 22 | 18 | 127 | 73 |
| Parietotemporal suture (Right)* | 171 | 49 | 28 | 68 | 21 | 29 | 131 | 73 |
| Tympanic plate of temporal bone (Left)* | 227 | 41 | 49 | 57 | 24 | 46 | 152 | 60 |
| Tympanic plate of temporal bone (Right)* | 226 | 43 | 48 | 60 | 24 | 46 | 151 | 63 |
| Supra-asterionic region | 222 | 34 | 40 | 35 | 23 | 26 | 138 | 23 |
| Parietal notch bone (Left)* | 202 | 10 | 33 | 6 | 24 | 0 | 144 | 18 |
| Parietal notch bone (Right) | 204 | 12 | 31 | 10 | 24 | 0 | 145 | 12 |
| Sutura mendosa | 204 | 3 | 32 | 3 | 23 | 0 | 143 | 1 |
| Os japonicum (Left) | 219 | 1 | 33 | 0 | 24 | 0 | 150 | 1 |
| Os japonicum (Right) | 212 | 1 | 35 | 0 | 23 | 0 | 148 | 1 |
| Asterion ossicle (Left) | 207 | 3 | 39 | 3 | 24 | 4 | 147 | 8 |
| Asterion ossicle (Right) | 211 | 2 | 34 | 3 | 24 | 0 | 143 | 3 |
| Occipitomastoid wormian bone (Left)* | 196 | 8 | 28 | 21 | 23 | 4 | 141 | 17 |
| Occipitomastoid wormian bone (Right) | 195 | 8 | 24 | 13 | 24 | 13 | 146 | 16 |
| Pointed chin shape | 167 | 25 | 39 | 21 | 20 | 20 | 132 | 18 |
| Mental foramen (Left) | 180 | 86 | 43 | 91 | 21 | 86 | 142 | 87 |
| Mental foramen (Right)* | 178 | 78 | 41 | 93 | 21 | 86 | 144 | 90 |
| Genial tubercles | 127 | 43 | 38 | 50 | 20 | 60 | 117 | 39 |
| Torus mandibularis | 188 | 0 | 49 | 0 | 21 | 0 | 144 | 0 |
| Mylohyoid bridge (Left)* | 183 | 46 | 38 | 5 | 21 | 33 | 147 | 14 |
| Mylohyoid bridge (Right)* | 181 | 45 | 40 | 8 | 21 | 29 | 145 | 8 |

*Cranial nonmetric traits found significantly different between the samples ($p<0.05$).

Table B2: Frequencies of the dental nonmetric traits (n=100) investigated between the prehistoric and modern Khoesan and Bantu-speakers.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Midline diastema UI1* | 36 | 81 | 10 | 50 | 215 | 25 | 31 | 94 |
| Diminutive UI2 | 57 | 0 | 47 | 0 | 221 | 1 | 74 | 3 |
| Winging UI1s (ASU 1) | 32 | 0 | 8 | 0 | 204 | 6 | 30 | 0 |
| Winging LI1s (ASU 1) | 87 | 0 | 40 | 0 | 161 | 1 | 43 | 2 |
| Shovelling UI1 (ASU 2-6) | 32 | 72 | 24 | 54 | 118 | 62 | 17 | 41 |
| Shovelling UI2 (ASU 2-6) | 46 | 76 | 40 | 68 | 177 | 69 | 51 | 69 |
| Shovelling UC (ASU 2-6) | 52 | 83 | 40 | 93 | 187 | 79 | 70 | 81 |
| Shovelling LI1 (ASU 2-6)* | 23 | 9 | 34 | 0 | 166 | 1 | 39 | 0 |
| Shovelling LI2 (ASU 2-6)* | 34 | 18 | 42 | 2 | 191 | 5 | 63 | 2 |
| Shovelling LC (ASU 2-6)* | 58 | 84 | 48 | 67 | 209 | 51 | 84 | 38 |
| Double shovelling UI1 (ASU 2-6) | 32 | 3 | 20 | 5 | 149 | 0 | 22 | 0 |
| Double shovelling UI2 (ASU 2-6) | 39 | 3 | 37 | 3 | 177 | 2 | 51 | 0 |
| Double shovelling UC (ASU 2-6)* | 61 | 51 | 46 | 48 | 196 | 29 | 81 | 40 |
| Double shovelling UPM1 (ASU 2-6)* | 67 | 46 | 51 | 71 | 204 | 28 | 107 | 53 |
| Double shovelling LI1 (ASU 2-6) | 24 | 0 | 29 | 0 | 166 | 0 | 39 | 0 |
| Double shovelling LI2 (ASU 2-6)* | 35 | 3 | 39 | 0 | 181 | 0 | 66 | 0 |
| Interruption groove UI1 | 52 | 0 | 33 | 0 | - | - | 48 | 0 |
| Interruption groove UI2 | 60 | 0 | 41 | 2 | - | - | 57 | 0 |
| Tuberculum dentale UI1 (ASU 2-6) | 49 | 39 | 29 | 34 | 161 | 38 | 39 | 21 |
| Tuberculum dentale UI2 (ASU 2-6)* | 50 | 20 | 39 | 8 | 182 | 34 | 52 | 40 |
| Tuberculum dentale UC (ASU 2-6) | 56 | 55 | 37 | 59 | 178 | 65 | 62 | 68 |
| Peg-shaped UI2 | 65 | 2 | 47 | 0 | 225 | 3 | 82 | 0 |
| Peg-shaped UM3 | 86 | 0 | 46 | 0 | 174 | 1 | 103 | 1 |

Table B2: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Labial convexity UI1 (ASU 2-4) | 42 | 21 | 25 | 16 | 188 | 29 | 29 | 21 |
| Labial convexity UI2 (ASU 2-4) | 45 | 44 | 39 | 33 | 197 | 33 | 55 | 22 |
| Congenital absence UI2 | 111 | 0 | 55 | 0 | 233 | 2 | 119 | 1 |
| Congenital absence UPM2 | 115 | 0 | 61 | 0 | 236 | 0 | 130 | 0 |
| Congenital absence UM3 | 106 | 4 | 52 | 0 | 200 | 4 | 119 | 0 |
| Congenital absence LI1 | 87 | 0 | 50 | 0 | 227 | 0 | 118 | 0 |
| Congenital absence LPM2 | 90 | 0 | 53 | 0 | 226 | 0 | 118 | 1 |
| Congenital absence LM3 | 83 | 0 | 50 | 2 | 201 | 1 | 108 | 0 |
| Mesial ridge UC (ASU 1-3)* | 40 | 28 | 33 | 9 | 174 | 24 | 64 | 3 |
| Distal accessory ridge UC (ASU 2-5)* | 25 | 28 | 25 | 36 | 147 | 71 | 44 | 45 |
| Distal accessory ridge LC (ASU 2-5) | 23 | 57 | 26 | 65 | 146 | 58 | 40 | 48 |
| Mesial premolar accessory ridges UPM1 (ASU 1-4) | 25 | 12 | 30 | 7 | 165 | 6 | 71 | 1 |
| Distal premolar accessory ridges UPM1 (ASU 1-4)* | 26 | 12 | 28 | 7 | 172 | 26 | 74 | 19 |
| Mesial premolar accessory ridges UPM2 (ASU 1-4)* | 22 | 18 | 27 | 19 | 136 | 35 | 63 | 27 |
| Distal premolar accessory ridges UPM2 (ASU 1-4) | 23 | 35 | 26 | 23 | 134 | 40 | 64 | 33 |
| Mesial premolar accessory ridges LPM1 (ASU 1-4) | 25 | 24 | 27 | 7 | 168 | 15 | 66 | 9 |
| Distal premolar accessory ridges LPM1 (ASU 1-4) | 20 | 25 | 24 | 25 | 135 | 55 | 58 | 40 |
| Mesial premolar accessory ridges LPM2 (ASU 1-4)* | 21 | 57 | 15 | 40 | 151 | 32 | 54 | 17 |
| Distal premolar accessory ridges LPM2 (ASU 1-4) | 18 | 33 | 15 | 47 | 130 | 38 | 47 | 0 |
| Odontome UPM1 | 73 | 0 | 57 | 0 | 222 | 0 | 123 | 0 |
| Odontome UPM2 | 72 | 0 | 56 | 0 | 220 | 0 | 118 | 0 |
| Odontome LPM1 | 56 | 0 | 56 | 0 | 211 | 0 | 107 | 0 |
| Odontome LPM2 | 57 | 0 | 51 | 0 | 209 | 0 | 101 | 0 |

Table B2: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Mesial and Distal accessory cusps UPM1 | 42 | 7 | 38 | 0 | 187 | 3 | 77 | 3 |
| Mesial and Distal accessory cusps UPM2* | 33 | 9 | 30 | 3 | 166 | 7 | 59 | 20 |
| Distosagittal ridge UPM1 | 71 | 0 | 53 | 0 | 220 | 0 | 119 | 0 |
| Tricusped UPM1 | 76 | 0 | 57 | 0 | 222 | 0 | 123 | 0 |
| Tricusped UPM2 | 77 | 0 | 55 | 0 | 221 | 0 | 123 | 0 |
| Lingual cusp variation LPM1 (ASU 2-9) | 43 | 23 | 44 | 39 | 188 | 21 | 77 | 23 |
| Lingual cusp variation LPM2 (ASU 2-9)* | 31 | 84 | 30 | 90 | 171 | 61 | 59 | 85 |
| Hypocone UM1 (ASU 3-5) | 80 | 1 | 53 | 1 | 221 | 100 | 118 | 100 |
| Hypocone UM2 (ASU 3-5) | 86 | 98 | 52 | 90 | 217 | 95 | 117 | 94 |
| Hypocone UM3 (ASU 3-5)* | 75 | 84 | 45 | 80 | 82 | 55 | 88 | 82 |
| Carabelli's trait UM1 (ASU 2-7) | 30 | 63 | 23 | 48 | 161 | 46 | 85 | 41 |
| Carabelli's trait UM2 (ASU 2-7) | 62 | 10 | 46 | 4 | 194 | 8 | 104 | 7 |
| Carabelli's trait UM3 (ASU 2-7) | 55 | 15 | 40 | 8 | 95 | 5 | 85 | 6 |
| Cusp 5 UM1 (ASU 2-5) | 40 | 25 | 37 | 24 | 160 | 14 | 62 | 15 |
| Cusp 5 UM2 (ASU 2-5)* | 67 | 45 | 46 | 22 | 170 | 22 | 91 | 30 |
| Cusp 5 UM3 (ASU 2-5)* | 70 | 64 | 43 | 42 | 70 | 21 | 74 | 45 |
| Cusp 5 LM1 (ASU 2-5) | 56 | 1 | 50 | 98 | 176 | 99 | 91 | 100 |
| Cusp 5 LM2 (ASU 2-5)* | 74 | 92 | 41 | 71 | 174 | 66 | 68 | 74 |
| Cusp 5 LM3 (ASU 2-5)* | 66 | 98 | 40 | 83 | 94 | 86 | 66 | 83 |
| Groove pattern LM1 (ASU Y)* | 56 | 98 | 39 | 82 | 149 | 95 | 80 | 99 |
| Groove pattern LM2 (ASU Y) | 81 | 62 | 53 | 53 | 167 | 60 | 66 | 71 |
| Groove pattern LM3 (ASU Y)* | 59 | 24 | 45 | 22 | 69 | 51 | 27 | 56 |
| Cusp 6 LM1 (ASU 1-5) | 47 | 11 | 40 | 20 | 142 | 15 | 54 | 15 |

Table B2: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp 6 LM2 (ASU 1-5) | 59 | 29 | 40 | 15 | 167 | 14 | 51 | 14 |
| Cusp 6 LM3 (ASU 1-5) | 60 | 53 | 37 | 35 | 88 | 35 | 54 | 41 |
| Cusp 7 LM1 (ASU 2-4) | 70 | 16 | 51 | 18 | 208 | 27 | 108 | 19 |
| Cusp 7 LM2 (ASU 2-4) | 92 | 9 | 57 | 4 | 216 | 6 | 112 | 7 |
| Cusp 7 LM3 (ASU 2-4)* | 72 | 14 | 44 | 11 | 228 | 5 | 87 | 11 |
| Deflecting wrinkle LM1 (ASU 2-3) | 6 | 83 | 9 | 56 | 41 | 34 | 12 | 42 |
| Distal trigonid crest LM1 | 8 | 0 | 13 | 0 | 69 | 0 | 31 | 0 |
| Distal trigonid crest LM2 | 49 | 0 | 36 | 0 | 173 | 0 | 82 | 0 |
| Distal trigonid crest LM3 | 43 | 0 | 32 | 0 | 140 | 0 | 72 | 0 |
| Middle trigonid crest LM1 | 7 | 14 | 9 | 0 | 54 | 13 | 21 | 14 |
| Middle trigonid crest LM2* | 41 | 0 | 31 | 0 | 153 | 16 | 56 | 5 |
| Middle trigonid crest LM3 | 36 | 0 | 28 | 0 | 136 | 4 | 62 | 5 |
| Metacone UM1 (ASU 3.5-5) | 80 | 1 | 54 | 1 | 218 | 100 | 110 | 99 |
| Metacone UM2 (ASU 3.5-5)* | 96 | 99 | 57 | 1 | 222 | 96 | 123 | 100 |
| Metacone UM3 (ASU 3.5-5)* | 78 | 71 | 45 | 96 | 107 | 62 | 96 | 91 |
| Parastyle UM1 (ASU 1-5) | 77 | 0 | 51 | 2 | 202 | 1 | 98 | 0 |
| Parastyle UM2 (ASU 1-5) | 96 | 1 | 58 | 3 | 212 | 1 | 113 | 89 |
| Parastyle UM3 (ASU 1-5) | 80 | 5 | 45 | 2 | 91 | 2 | 89 | 1 |
| Anterior fovea LM1 (ASU 2-4)* | 4 | 75 | 7 | 14 | 36 | 31 | 15 | 67 |
| Cusp number LM1 (ASU 5+) | 47 | 1 | 42 | 98 | 135 | 99 | 57 | 96 |
| Cusp number LM2 (ASU 5+)* | 60 | 93 | 36 | 72 | 148 | 70 | 41 | 73 |
| Cusp number LM3 (ASU 5+) | 60 | 98 | 37 | 84 | 83 | 86 | 49 | 86 |
| Cusp number LM1 (ASU 6+) | 47 | 11 | 42 | 19 | 135 | 16 | 57 | 14 |

Table B2: continued.

| | Later Stone Age | | Iron Age | | Modern Khoesan | | Modern Bantu-speakers | |
|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp number LM2 (ASU 6+) | 60 | 28 | 36 | 17 | 148 | 16 | 41 | 17 |
| Cusp number LM3 (ASU 6+) | 60 | 53 | 37 | 35 | 83 | 39 | 49 | 45 |
| Protostylid LM1 (ASU 2-7) | 49 | 8 | 42 | 0 | 186 | 4 | 79 | 1 |
| Protostylid LM2 (ASU 2-7)* | 71 | 8 | 53 | 0 | 198 | 10 | 93 | 1 |
| Protostylid LM3 (ASU 2-7) | 59 | 5 | 41 | 2 | 121 | 7 | 70 | 4 |
| Mandibular molar pit-tubercle LM1 (P = 1-3) | 34 | 9 | 23 | 4 | 171 | 1 | 63 | 2 |
| Mandibular molar pit-tubercle LM2 (P = 1-3)* | 54 | 15 | 39 | 0 | 199 | 2 | 85 | 1 |
| Mandibular molar pit-tubercle LM3 (P = 1-3)* | 45 | 29 | 34 | 18 | 138 | 8 | 75 | 12 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73
*Dental nonmetric traits found significantly different between the samples ($p<0.05$).

Table B3: Descriptive statistics for the upper and lower dental measurements (n=44) for the prehistoric and modern Khoesan and Bantu-speakers.

| | **LATER STONE AGE** | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **UI1** | | **UI2** | | **UC** | | **UPM1** | | **UPM2** | | **UM1** | | | | **UM2** | | | | **UM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 20 | 36 | 29 | 38 | 52 | 68 | 61 | 70 | 67 | 75 | 69 | 77 | 71 | 77 | 102 | 108 | 106 | 109 | 85 | 90 | 90 | 84 |
| **Min** | 7.51 | 6.03 | 5.41 | 4.86 | 6.28 | 5.94 | 5.72 | 7.11 | 5.49 | 6.82 | 8.65 | 9.67 | 10.81 | 9.60 | 8.15 | 9.68 | 10.20 | 8.65 | 6.59 | 8.63 | 8.82 | 7.68 |
| **Max** | 9.18 | 7.80 | 7.70 | 7.12 | 8.30 | 8.81 | 7.90 | 9.83 | 7.48 | 9.93 | 12.12 | 12.43 | 13.54 | 12.63 | 11.21 | 12.57 | 13.78 | 12.09 | 10.22 | 14.05 | 13.53 | 10.81 |
| **Mean** | 8.27 | 6.76 | 6.80 | 6.10 | 7.37 | 7.67 | 6.74 | 8.60 | 6.43 | 8.56 | 10.18 | 11.00 | 12.24 | 11.04 | 9.74 | 11.02 | 11.93 | 10.57 | 8.32 | 10.42 | 10.77 | 9.40 |
| **SD** | 0.55 | 0.50 | 0.58 | 0.49 | 0.46 | 0.51 | 0.48 | 0.53 | 0.41 | 0.60 | 0.61 | 0.57 | 0.56 | 0.62 | 0.60 | 0.62 | 0.71 | 0.62 | 0.74 | 0.92 | 0.92 | 0.69 |
| | **IRON AGE** | | | | | | | | | | | | | | | | | | | | | |
| | **UI1** | | **UI2** | | **UC** | | **UPM1** | | **UPM2** | | **UM1** | | | | **UM2** | | | | **UM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 12 | 21 | 33 | 26 | 39 | 41 | 51 | 52 | 50 | 51 | 43 | 45 | 42 | 44 | 53 | 54 | 53 | 53 | 42 | 44 | 45 | 43 |
| **Min** | 7.89 | 5.83 | 6.07 | 5.82 | 6.65 | 7.60 | 6.27 | 8.36 | 5.94 | 8.20 | 9.21 | 10.15 | 11.27 | 10.24 | 8.91 | 10.13 | 10.61 | 9.02 | 7.97 | 9.65 | 10.06 | 8.93 |
| **Max** | 10.24 | 7.92 | 8.26 | 7.50 | 8.37 | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 11.35 | 12.71 | 14.28 | 12.39 | 12.03 | 13.46 | 13.89 | 13.54 | 10.32 | 12.71 | 13.03 | 12.10 |
| **Mean** | 8.87 | 7.15 | 7.14 | 6.58 | 7.67 | 8.49 | 7.18 | 9.56 | 6.84 | 9.53 | 10.58 | 11.48 | 12.63 | 11.55 | 10.12 | 11.55 | 12.28 | 11.26 | 9.07 | 11.13 | 11.46 | 10.46 |
| **SD** | 0.75 | 0.52 | 0.57 | 0.40 | 0.41 | 0.50 | 0.45 | 0.58 | 0.43 | 0.54 | 0.44 | 0.56 | 0.57 | 0.47 | 0.63 | 0.77 | 0.82 | 0.76 | 0.59 | 0.71 | 0.78 | 0.61 |
| | **MODERN KHOESAN** | | | | | | | | | | | | | | | | | | | | | |
| | **UI1** | | **UI2** | | **UC** | | **UPM1** | | **UPM2** | | **UM1** | | | | **UM2** | | | | **UM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 116 | 160 | 152 | 146 | 178 | 174 | 159 | 183 | 145 | 181 | 163 | 171 | 134 | 155 | 137 | 167 | 92 | 154 | 38 | 42 | 17 | 35 |
| **Min** | 6.45 | 5.69 | 5.01 | 4.72 | 5.66 | 6.37 | 5.88 | 7.58 | 5.57 | 7.69 | 8.71 | 9.63 | 10.76 | 9.47 | 7.83 | 9.35 | 10.22 | 8.31 | 6.82 | 9.62 | 9.25 | 8.41 |
| **Max** | 10.57 | 8.78 | 9.09 | 7.58 | 8.94 | 9.96 | 7.90 | 10.68 | 7.90 | 10.86 | 12.11 | 13.25 | 14.22 | 13.48 | 11.14 | 13.01 | 14.63 | 13.06 | 9.53 | 11.86 | 12.38 | 10.84 |
| **Mean** | 8.30 | 6.85 | 6.55 | 6.16 | 7.47 | 8.04 | 6.85 | 9.04 | 6.52 | 9.06 | 10.38 | 11.12 | 12.45 | 11.24 | 9.51 | 11.14 | 11.98 | 10.69 | 8.22 | 10.56 | 10.70 | 9.60 |
| **SD** | 0.72 | 0.57 | 0.61 | 0.59 | 0.48 | 0.67 | 0.45 | 0.65 | 0.46 | 0.66 | 0.61 | 0.64 | 0.68 | 0.73 | 0.72 | 0.77 | 0.86 | 0.83 | 0.69 | 0.59 | 0.78 | 0.64 |
| | **MODERN BANTU-SPEAKERS** | | | | | | | | | | | | | | | | | | | | | |
| | **UI1** | | **UI2** | | **UC** | | **UPM1** | | **UPM2** | | **UM1** | | | | **UM2** | | | | **UM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 11 | 36 | 46 | 54 | 83 | 92 | 87 | 103 | 77 | 95 | 91 | 92 | 94 | 85 | 95 | 99 | 87 | 98 | 74 | 76 | 76 | 78 |
| **Min** | 7.78 | 6.43 | 5.71 | 5.29 | 6.67 | 6.97 | 6.03 | 8.17 | 5.84 | 8.40 | 8.87 | 10.23 | 10.89 | 9.16 | 8.35 | 10.08 | 10.73 | 9.80 | 7.81 | 9.78 | 10.11 | 8.51 |
| **Max** | 9.75 | 8.13 | 8.44 | 7.45 | 8.83 | 10.46 | 8.11 | 11.02 | 8.02 | 11.36 | 11.91 | 12.97 | 13.76 | 13.11 | 11.30 | 13.68 | 14.41 | 13.03 | 10.62 | 13.37 | 13.86 | 12.64 |
| **Mean** | 8.80 | 7.20 | 7.00 | 6.54 | 7.66 | 8.57 | 7.19 | 9.60 | 6.71 | 9.52 | 10.45 | 11.41 | 12.57 | 11.40 | 9.92 | 11.62 | 12.33 | 11.04 | 9.06 | 11.43 | 11.61 | 10.41 |
| **SD** | 0.63 | 0.39 | 0.57 | 0.49 | 0.48 | 0.67 | 0.44 | 0.60 | 0.39 | 0.64 | 0.56 | 0.62 | 0.63 | 0.71 | 0.63 | 0.74 | 0.86 | 0.71 | 0.61 | 0.82 | 0.85 | 0.76 |

Table B3: continued.

| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **LATER STONE AGE** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 22 | 33 | 30 | 37 | 38 | 48 | 72 | 75 | 76 | 82 | 60 | 68 | 61 | 65 | 85 | 96 | 88 | 93 | 79 | 82 | 80 | 78 |
| **Min** | 4.36 | 4.66 | 4.73 | 4.86 | 5.92 | 6.03 | 5.84 | 6.45 | 5.52 | 6.54 | 10.01 | 9.29 | 10.39 | 10.03 | 9.64 | 9.33 | 10.40 | 10.22 | 7.92 | 7.94 | 8.31 | 8.04 |
| **Max** | 6.45 | 6.54 | 6.61 | 6.57 | 7.82 | 7.73 | 8.05 | 8.59 | 8.23 | 9.07 | 12.42 | 11.78 | 13.20 | 12.35 | 12.94 | 12.43 | 13.50 | 13.21 | 12.72 | 11.55 | 12.81 | 12.51 |
| **Mean** | 5.18 | 5.29 | 5.73 | 5.65 | 6.91 | 6.88 | 6.84 | 7.62 | 6.99 | 7.97 | 11.10 | 10.52 | 11.72 | 11.44 | 11.01 | 10.50 | 11.57 | 11.54 | 10.17 | 10.03 | 10.65 | 10.59 |
| **SD** | 0.49 | 0.41 | 0.45 | 0.44 | 0.53 | 0.47 | 0.49 | 0.50 | 0.52 | 0.53 | 0.55 | 0.48 | 0.53 | 0.49 | 0.67 | 0.61 | 0.60 | 0.65 | 0.86 | 0.70 | 0.74 | 0.84 |
| **IRON AGE** | **LI1** | | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | | **LM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 32 | 34 | 37 | 37 | 40 | 48 | 43 | 50 | 42 | 48 | 38 | 43 | 42 | 42 | 53 | 51 | 51 | 46 | 40 | 40 | 40 | 39 |
| **Min** | 4.73 | 5.05 | 5.25 | 5.61 | 6.34 | 6.66 | 6.13 | 7.22 | 6.28 | 7.45 | 9.63 | 9.47 | 10.85 | 10.49 | 9.37 | 9.38 | 10.39 | 10.39 | 9.66 | 8.80 | 9.76 | 9.94 |
| **Max** | 6.07 | 7.35 | 7.37 | 6.80 | 8.03 | 9.04 | 8.06 | 9.52 | 8.26 | 9.61 | 12.77 | 12.19 | 13.24 | 12.91 | 12.82 | 11.94 | 13.92 | 13.06 | 13.06 | 11.27 | 13.21 | 12.62 |
| **Mean** | 5.44 | 5.86 | 6.14 | 6.22 | 7.06 | 7.60 | 7.30 | 8.27 | 7.30 | 8.58 | 11.67 | 10.87 | 12.15 | 11.90 | 11.08 | 10.62 | 11.96 | 11.72 | 11.19 | 10.38 | 11.35 | 11.38 |
| **SD** | 0.35 | 0.43 | 0.46 | 0.33 | 0.44 | 0.52 | 0.41 | 0.57 | 0.56 | 0.58 | 0.61 | 0.56 | 0.60 | 0.60 | 0.73 | 0.63 | 0.75 | 0.69 | 0.69 | 0.60 | 0.68 | 0.63 |
| **MODERN KHOESAN** | **LI1** | | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | | **LM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 114 | 134 | 142 | 145 | 161 | 163 | 177 | 174 | 151 | 175 | 158 | 165 | 153 | 152 | 123 | 149 | 106 | 101 | 24 | 46 | 22 | 16 |
| **Min** | 4.09 | 4.24 | 4.60 | 4.72 | 5.48 | 6.06 | 5.46 | 6.49 | 5.68 | 6.61 | 8.97 | 9.30 | 10.58 | 10.06 | 8.87 | 8.13 | 9.69 | 9.85 | 8.39 | 7.97 | 9.07 | 9.45 |
| **Max** | 6.18 | 7.17 | 7.16 | 7.37 | 8.26 | 9.20 | 8.28 | 9.19 | 8.76 | 9.61 | 13.22 | 12.27 | 13.83 | 13.72 | 12.22 | 12.11 | 13.30 | 12.85 | 11.33 | 11.79 | 11.83 | 11.78 |
| **Mean** | 5.11 | 5.46 | 5.75 | 5.84 | 6.83 | 7.28 | 6.95 | 7.73 | 7.03 | 8.04 | 11.28 | 10.41 | 11.82 | 11.77 | 10.41 | 10.23 | 11.48 | 11.32 | 10.12 | 9.78 | 10.61 | 10.47 |
| **SD** | 0.41 | 0.49 | 0.49 | 0.49 | 0.50 | 0.61 | 0.49 | 0.55 | 0.57 | 0.58 | 0.71 | 0.58 | 0.64 | 0.68 | 0.73 | 0.70 | 0.73 | 0.63 | 0.73 | 0.69 | 0.68 | 0.68 |
| **MODERN BANTU-SPEAKERS** | **LI1** | | **LI2** | | **LC** | | **LPM1** | | **LPM2** | | **LM1** | | | | **LM2** | | | | **LM3** | | | |
| | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** | **M-D** | **B-L** | **MB-DL** | **ML-DB** |
| **N** | 37 | 56 | 63 | 63 | 70 | 78 | 98 | 100 | 83 | 97 | 94 | 96 | 91 | 90 | 82 | 84 | 83 | 79 | 73 | 70 | 70 | 64 |
| **Min** | 4.60 | 4.86 | 4.92 | 5.27 | 5.89 | 6.06 | 6.43 | 7.17 | 6.09 | 7.51 | 10.16 | 9.51 | 10.86 | 10.44 | 9.34 | 9.37 | 10.13 | 10.13 | 8.71 | 8.48 | 9.21 | 9.26 |
| **Max** | 6.13 | 6.54 | 6.63 | 6.85 | 7.95 | 9.04 | 8.31 | 9.50 | 8.74 | 10.00 | 13.30 | 11.89 | 13.44 | 12.72 | 13.08 | 12.43 | 14.01 | 13.66 | 13.97 | 12.87 | 13.67 | 14.17 |
| **Mean** | 5.39 | 5.68 | 6.03 | 6.14 | 7.07 | 7.78 | 7.33 | 8.32 | 7.39 | 8.69 | 11.50 | 10.75 | 12.04 | 11.68 | 11.15 | 10.55 | 11.95 | 11.67 | 11.13 | 10.44 | 11.33 | 11.41 |
| **SD** | 0.33 | 0.34 | 0.38 | 0.33 | 0.48 | 0.62 | 0.45 | 0.56 | 0.57 | 0.55 | 0.57 | 0.50 | 0.57 | 0.55 | 0.76 | 0.66 | 0.77 | 0.70 | 0.90 | 0.73 | 0.79 | 0.88 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73

# APPENDIX C: DESCRIPTIVE STATISTICS FOR THE PREHISTORIC TEMPORAL COMPARISONS

Table C1: Frequencies of the nonmetric cranial traits (n=73) investigated over time during the Holocene.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Incomplete (nasal part) metopic suture | 4 | 0 | 21 | 0 | 24 | 8 | 60 | 7 | 38 | 0 | 80 | 5 | 21 | 10 |
| Complete metopic suture | 4 | 0 | 21 | 0 | 24 | 0 | 60 | 0 | 38 | 0 | 80 | 0 | 21 | 0 |
| Metopic ridge* | 5 | 60 | 22 | 36 | 27 | 59 | 61 | 51 | 40 | 25 | 79 | 25 | 22 | 23 |
| Square shaped orbits* | 5 | 0 | 17 | 47 | 23 | 22 | 59 | 41 | 38 | 45 | 68 | 60 | 19 | 79 |
| Oval shaped orbits* | 5 | 100 | 17 | 47 | 23 | 74 | 59 | 56 | 38 | 55 | 68 | 38 | 19 | 21 |
| Round shaped orbits | 5 | 0 | 17 | 6 | 23 | 4 | 59 | 3 | 38 | 0 | 68 | 1 | 19 | 0 |
| Supraorbital notch (Left) | 6 | 67 | 21 | 67 | 23 | 52 | 63 | 70 | 40 | 73 | 79 | 71 | 23 | 91 |
| Supraorbital notch (Right)* | 6 | 67 | 22 | 77 | 22 | 73 | 63 | 67 | 39 | 67 | 80 | 85 | 26 | 92 |
| Supraorbital foramen (Left)* | 7 | 43 | 22 | 32 | 23 | 70 | 61 | 46 | 40 | 50 | 77 | 45 | 24 | 17 |
| Supraorbital foramen (Right) | 6 | 50 | 22 | 36 | 24 | 42 | 61 | 46 | 39 | 54 | 78 | 33 | 24 | 21 |
| Ethmoidal foramina (Left) | 3 | 100 | 12 | 100 | 16 | 94 | 41 | 80 | 27 | 78 | 38 | 66 | 7 | 86 |
| Ethmoidal foramina (Right) | 3 | 100 | 12 | 100 | 16 | 81 | 37 | 86 | 31 | 84 | 39 | 69 | 8 | 100 |
| Infraorbital foramen (Left) | 3 | 100 | 16 | 94 | 21 | 76 | 50 | 86 | 36 | 92 | 62 | 89 | 18 | 100 |
| Infraorbital foramen (Right) | 4 | 100 | 17 | 100 | 21 | 86 | 51 | 84 | 37 | 86 | 62 | 95 | 16 | 75 |
| Infraorbital form* | 3 | 0 | 21 | 5 | 20 | 0 | 55 | 2 | 39 | 0 | 74 | 11 | 21 | 24 |
| Infraorbital suture | 2 | 0 | 11 | 18 | 12 | 33 | 33 | 21 | 26 | 46 | 38 | 16 | 10 | 10 |
| Profile curves of nasal bones | 2 | 0 | 9 | 44 | 18 | 33 | 42 | 45 | 29 | 66 | 44 | 68 | 12 | 67 |
| Superficial nasion* | 2 | 50 | 10 | 50 | 19 | 68 | 43 | 72 | 30 | 53 | 52 | 69 | 12 | 25 |
| Moderately depressed nasion | 2 | 0 | 10 | 30 | 19 | 26 | 43 | 21 | 30 | 37 | 52 | 27 | 12 | 67 |
| Marked depression of nasion | 2 | 50 | 10 | 20 | 19 | 5 | 43 | 7 | 30 | 10 | 52 | 4 | 12 | 8 |
| Angle of nasal bones | 2 | 100 | 15 | 100 | 21 | 86 | 53 | 92 | 37 | 92 | 65 | 89 | 18 | 100 |

Table C1: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Nasal bone shape | 2 | 50 | 8 | 63 | 18 | 28 | 45 | 51 | 29 | 62 | 52 | 60 | 12 | 58 |
| Extension of nasal bones | 2 | 0 | 10 | 10 | 20 | 0 | 46 | 4 | 24 | 17 | 41 | 32 | 9 | 44 |
| Development of anterior nasal spine* | 3 | 67 | 16 | 63 | 21 | 52 | 44 | 61 | 34 | 50 | 67 | 61 | 12 | 83 |
| Zygomaxillary tubercle (Left) | 4 | 50 | 19 | 53 | 22 | 55 | 59 | 37 | 35 | 43 | 71 | 49 | 17 | 59 |
| Zygomaxillary tubercle (Right) | 4 | 50 | 18 | 50 | 21 | 38 | 53 | 42 | 39 | 41 | 72 | 44 | 18 | 56 |
| Subnasal region | 4 | 50 | 17 | 47 | 22 | 55 | 52 | 31 | 34 | 29 | 71 | 35 | 17 | 59 |
| Dental arcade shape | 2 | 100 | 10 | 50 | 12 | 67 | 36 | 69 | 22 | 77 | 49 | 76 | 11 | 82 |
| Anterior palate form* | 5 | 100 | 22 | 86 | 23 | 65 | 55 | 82 | 40 | 93 | 81 | 85 | 24 | 100 |
| Torus palatinus | 3 | 0 | 13 | 31 | 17 | 18 | 46 | 33 | 31 | 35 | 57 | 39 | 17 | 35 |
| Torus maxillaris | 3 | 0 | 16 | 6 | 17 | 12 | 50 | 8 | 35 | 3 | 67 | 3 | 21 | 5 |
| Foramen of Huschke (Left)* | 3 | 0 | 14 | 14 | 23 | 61 | 61 | 33 | 36 | 33 | 80 | 20 | 26 | 4 |
| Foramen of Huschke (Right)* | 4 | 0 | 16 | 25 | 19 | 53 | 60 | 28 | 39 | 31 | 78 | 28 | 26 | 8 |
| Encroachment of occipital condyles | 2 | 50 | 16 | 25 | 18 | 17 | 50 | 26 | 32 | 34 | 63 | 29 | 14 | 29 |
| Hypoglossal canal bridging (Left) | 1 | 0 | 15 | 7 | 17 | 0 | 55 | 11 | 36 | 11 | 61 | 8 | 16 | 0 |
| Hypoglossal canal bridging (Right) | 2 | 0 | 15 | 7 | 17 | 6 | 55 | 5 | 37 | 8 | 61 | 10 | 15 | 0 |
| Condylar canal (Left) | 0 | 0 | 7 | 57 | 11 | 45 | 42 | 40 | 24 | 42 | 50 | 48 | 9 | 78 |
| Condylar canal (Right) | 1 | 100 | 10 | 60 | 12 | 42 | 37 | 57 | 24 | 58 | 54 | 54 | 8 | 38 |
| Inca bone | 1 | 0 | 18 | 6 | 24 | 4 | 61 | 0 | 38 | 0 | 79 | 1 | 19 | 0 |
| Interparietal groove | 4 | 0 | 17 | 41 | 27 | 33 | 59 | 25 | 38 | 18 | 77 | 27 | 22 | 41 |
| Parietal foramina | 4 | 100 | 15 | 87 | 23 | 87 | 52 | 94 | 31 | 97 | 73 | 99 | 15 | 93 |
| Zygomatic arch* | 2 | 50 | 16 | 38 | 20 | 35 | 54 | 46 | 38 | 18 | 68 | 15 | 15 | 13 |
| Wormian bones | 2 | 100 | 17 | 65 | 19 | 63 | 54 | 61 | 34 | 59 | 66 | 48 | 16 | 63 |
| Ophryonic groove | 5 | 40 | 23 | 39 | 24 | 21 | 62 | 11 | 39 | 21 | 81 | 26 | 26 | 12 |
| Sutural variations at pterion (Left) | 1 | 100 | 7 | 86 | 13 | 62 | 27 | 81 | 14 | 79 | 50 | 78 | 11 | 45 |

Table C1: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Sutural variations at pterion (Right)* | 1 | 100 | 5 | 100 | 15 | 60 | 28 | 75 | 15 | 93 | 50 | 74 | 11 | 36 |
| Inferior frontal eminence (Left) | 2 | 50 | 17 | 47 | 23 | 39 | 56 | 46 | 40 | 45 | 76 | 53 | 17 | 47 |
| Inferior frontal eminence (Right) | 3 | 33 | 16 | 56 | 22 | 36 | 57 | 47 | 39 | 41 | 76 | 51 | 20 | 50 |
| Superior temporal line (Left) | 2 | 50 | 14 | 50 | 24 | 50 | 56 | 45 | 36 | 42 | 74 | 39 | 15 | 47 |
| Superior temporal line (Right) | 2 | 50 | 13 | 54 | 23 | 48 | 53 | 45 | 33 | 42 | 70 | 37 | 17 | 47 |
| Mons temporosphenoidalis (Left) | 2 | 100 | 17 | 59 | 22 | 50 | 57 | 49 | 38 | 61 | 72 | 63 | 17 | 53 |
| Mons temporosphenoidalis (Right) | 3 | 100 | 15 | 67 | 20 | 50 | 54 | 54 | 38 | 58 | 70 | 61 | 18 | 33 |
| Parietotemporal suture (Left) | 1 | 100 | 11 | 9 | 21 | 43 | 48 | 54 | 28 | 54 | 65 | 43 | 13 | 62 |
| Parietotemporal suture (Right) | 3 | 67 | 13 | 31 | 23 | 57 | 42 | 52 | 27 | 52 | 61 | 44 | 17 | 71 |
| Tympanic plate of temporal bone (Left) | 4 | 75 | 18 | 39 | 23 | 43 | 61 | 43 | 36 | 33 | 82 | 40 | 27 | 70 |
| Tympanic plate of temporal bone (Right) | 4 | 50 | 18 | 50 | 22 | 41 | 60 | 45 | 39 | 36 | 80 | 43 | 25 | 72 |
| Supra-asterionic region | 3 | 33 | 18 | 39 | 26 | 15 | 60 | 27 | 38 | 34 | 74 | 46 | 20 | 35 |
| Parietal notch bone (Left) | 2 | 0 | 13 | 8 | 23 | 22 | 56 | 9 | 35 | 9 | 70 | 6 | 16 | 0 |
| Parietal notch bone (Right) | 2 | 0 | 18 | 11 | 23 | 22 | 56 | 11 | 34 | 9 | 68 | 9 | 18 | 11 |
| Sutura mendosa | 2 | 0 | 13 | 8 | 22 | 9 | 58 | 2 | 36 | 0 | 70 | 3 | 18 | 0 |
| Os japonicum (Left) | 6 | 0 | 20 | 0 | 23 | 4 | 61 | 2 | 36 | 3 | 71 | 0 | 16 | 0 |
| Os japonicum (Right) | 5 | 0 | 16 | 0 | 22 | 0 | 58 | 2 | 36 | 3 | 71 | 1 | 17 | 0 |
| Asterion ossicle (Left) | 1 | 0 | 13 | 8 | 24 | 0 | 60 | 2 | 35 | 3 | 71 | 4 | 20 | 0 |
| Asterion ossicle (Right) | 2 | 0 | 16 | 6 | 24 | 0 | 60 | 3 | 37 | 0 | 69 | 3 | 22 | 0 |
| Occipitomastoid wormian bone (Left)* | 2 | 0 | 12 | 0 | 22 | 9 | 55 | 15 | 34 | 9 | 67 | 3 | 14 | 36 |
| Occipitomastoid wormian bone (Right) | 3 | 0 | 15 | 0 | 21 | 10 | 51 | 14 | 34 | 9 | 67 | 4 | 14 | 14 |
| Pointed chin shape | 6 | 50 | 16 | 25 | 16 | 19 | 43 | 33 | 30 | 27 | 53 | 17 | 17 | 18 |
| Mental foramen (Left) | 7 | 100 | 15 | 73 | 18 | 78 | 48 | 92 | 32 | 88 | 57 | 84 | 21 | 90 |
| Mental foramen (Right) | 8 | 88 | 14 | 79 | 18 | 72 | 47 | 74 | 33 | 79 | 54 | 80 | 22 | 86 |

Table C1: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Genial tubercles | 6 | 0 | 7 | 14 | 10 | 30 | 30 | 33 | 25 | 48 | 44 | 57 | 18 | 56 |
| Torus mandibularis | 7 | 0 | 17 | 0 | 19 | 0 | 47 | 0 | 33 | 0 | 61 | 0 | 26 | 0 |
| Mylohyoid bridge (Left)* | 6 | 83 | 16 | 31 | 18 | 67 | 48 | 63 | 32 | 47 | 59 | 27 | 17 | 12 |
| Mylohyoid bridge (Right)* | 5 | 40 | 16 | 38 | 18 | 72 | 47 | 66 | 32 | 34 | 59 | 25 | 19 | 16 |

*Cranial nonmetric traits found significantly different between the samples ($p<0.05$).

Table C2: Frequencies of the dental nonmetric traits (n=100) investigated over time during the Holocene.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Midline diastema UI1 | 1 | 0 | 3 | 0 | 1 | 0 | 10 | 0 | 2 | 0 | 14 | 0 | 4 | 0 |
| Diminutive UI2 | 1 | 100 | 3 | 67 | 1 | 100 | 10 | 90 | 2 | 100 | 18 | 72 | 6 | 50 |
| Winging UI1s (ASU 1)* | 1 | 100 | 5 | 100 | 2 | 50 | 6 | 17 | 0 | 0 | 17 | 82 | 17 | 65 |
| Winging LI1s (ASU 1) | 0 | 0 | 4 | 100 | 3 | 67 | 9 | 56 | 3 | 67 | 26 | 85 | 25 | 76 |
| Shovelling UI1 (ASU 2-6) | 4 | 100 | 7 | 100 | 6 | 67 | 7 | 71 | 0 | 0 | 26 | 81 | 25 | 92 |
| Shovelling UI2 (ASU 2-6) | 1 | 0 | 5 | 0 | 2 | 0 | 7 | 0 | 0 | 0 | 17 | 6 | 15 | 7 |
| Shovelling UC (ASU 2-6) | 0 | 0 | 4 | 0 | 2 | 0 | 11 | 0 | 1 | 0 | 21 | 5 | 23 | 4 |
| Shovelling LI1 (ASU 2-6) | 3 | 33 | 6 | 67 | 6 | 50 | 13 | 31 | 0 | 0 | 32 | 56 | 27 | 59 |
| Shovelling LI2 (ASU 2-6) | 3 | 0 | 6 | 17 | 6 | 83 | 13 | 38 | 4 | 100 | 33 | 45 | 30 | 70 |
| Shovelling LC (ASU 2-6) | 2 | 0 | 7 | 0 | 2 | 0 | 12 | 0 | 2 | 0 | 25 | 0 | 20 | 0 |
| Double shovelling UI1 (ASU 2-6) | 2 | 0 | 8 | 0 | 3 | 0 | 15 | 0 | 3 | 0 | 26 | 0 | 27 | 4 |
| Double shovelling UI2 (ASU 2-6) | 2 | 50 | 6 | 50 | 2 | 50 | 10 | 40 | 1 | 0 | 27 | 37 | 18 | 33 |
| Double shovelling UC (ASU 2-6) | 2 | 0 | 6 | 0 | 3 | 33 | 11 | 9 | 0 | 0 | 26 | 31 | 25 | 28 |
| Double shovelling UPM1 (ASU 2-6) | 4 | 75 | 8 | 100 | 7 | 29 | 8 | 25 | 3 | 67 | 24 | 50 | 26 | 58 |
| Double shovelling LI1 (ASU 2-6) | 2 | 0 | 5 | 40 | 2 | 50 | 9 | 33 | 0 | 0 | 24 | 13 | 18 | 17 |
| Double shovelling LI2 (ASU 2-6) | 2 | 50 | 6 | 67 | 3 | 0 | 12 | 33 | 0 | 0 | 22 | 50 | 23 | 35 |
| Interruption groove UI1 | 2 | 0 | 6 | 0 | 3 | 0 | 15 | 0 | 4 | 0 | 32 | 3 | 27 | 0 |
| Interruption groove UI2 | 2 | 0 | 8 | 0 | 5 | 0 | 16 | 0 | 8 | 0 | 44 | 0 | 25 | 0 |
| Tuberculum dentale UI1 (ASU 2-6) | 2 | 0 | 6 | 0 | 3 | 0 | 13 | 0 | 3 | 0 | 28 | 0 | 27 | 0 |
| Tuberculum dentale UI2 (ASU 2-6) | 2 | 0 | 12 | 0 | 10 | 0 | 21 | 0 | 9 | 0 | 53 | 0 | 32 | 0 |
| Tuberculum dentale UC (ASU 2-6) | 4 | 0 | 12 | 0 | 10 | 0 | 21 | 0 | 10 | 0 | 55 | 0 | 38 | 0 |
| Peg-shaped UI2 | 3 | 0 | 11 | 9 | 7 | 0 | 20 | 5 | 10 | 0 | 52 | 4 | 30 | 0 |
| Peg-shaped UM3 | 3 | 67 | 7 | 43 | 4 | 0 | 4 | 0 | 0 | 0 | 20 | 25 | 22 | 5 |

Table C2: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Labial convexity UI1 (ASU 2-4) | 1 | 100 | 2 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 15 | 40 | 16 | 38 |
| Labial convexity UI2 (ASU 2-4) | 4 | 0 | 8 | 0 | 7 | 0 | 16 | 0 | 5 | 0 | 30 | 0 | 36 | 0 |
| Congenital absence UI2 | 4 | 0 | 9 | 0 | 5 | 0 | 16 | 0 | 6 | 0 | 30 | 0 | 36 | 0 |
| Congenital absence UPM2 | 3 | 0 | 3 | 0 | 7 | 0 | 6 | 17 | 1 | 0 | 21 | 10 | 25 | 0 |
| Congenital absence UM3 | 3 | 33 | 3 | 0 | 4 | 0 | 6 | 17 | 0 | 0 | 17 | 6 | 21 | 5 |
| Congenital absence LI1 | 4 | 0 | 8 | 0 | 7 | 0 | 15 | 0 | 5 | 0 | 29 | 0 | 32 | 0 |
| Congenital absence LPM2 | 4 | 0 | 8 | 0 | 7 | 0 | 16 | 0 | 6 | 0 | 32 | 0 | 36 | 0 |
| Congenital absence LM3 | 4 | 0 | 9 | 0 | 6 | 0 | 18 | 0 | 6 | 0 | 32 | 0 | 36 | 0 |
| Mesial ridge UC (ASU 1-3) | 0 | 0 | 1 | 100 | 2 | 0 | 3 | 0 | 1 | 0 | 17 | 12 | 18 | 11 |
| Distal accessory ridge UC (ASU 2-5) | 0 | 0 | 2 | 0 | 2 | 0 | 4 | 0 | 1 | 0 | 16 | 19 | 16 | 6 |
| Distal accessory ridge LC (ASU 2-5) | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 15 | 27 | 18 | 22 |
| Mesial premolar accessory ridges UPM1 (ASU 1-4) | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 15 | 53 | 18 | 22 |
| Distal premolar accessory ridges UPM1 (ASU 1-4) | 5 | 100 | 8 | 100 | 8 | 100 | 16 | 100 | 7 | 100 | 35 | 100 | 32 | 100 |
| Mesial premolar accessory ridges UPM2 (ASU 1-4) | 3 | 100 | 7 | 100 | 5 | 100 | 16 | 94 | 6 | 100 | 47 | 98 | 32 | 88 |
| Distal premolar accessory ridges UPM2 (ASU 1-4) | 1 | 0 | 7 | 100 | 4 | 75 | 17 | 76 | 7 | 100 | 36 | 83 | 24 | 71 |
| Mesial premolar accessory ridges LPM1 (ASU 1-4) | 3 | 67 | 4 | 50 | 3 | 100 | 2 | 100 | 1 | 0 | 16 | 56 | 18 | 56 |
| Distal premolar accessory ridges LPM1 (ASU 1-4) | 1 | 0 | 7 | 14 | 3 | 33 | 10 | 10 | 4 | 25 | 37 | 5 | 27 | 7 |
| Mesial premolar accessory ridges LPM2 (ASU 1-4) | 0 | 0 | 5 | 0 | 2 | 0 | 12 | 17 | 5 | 20 | 28 | 18 | 23 | 13 |
| Distal premolar accessory ridges LPM2 (ASU 1-4) | 2 | 0 | 4 | 50 | 5 | 40 | 3 | 0 | 1 | 0 | 25 | 24 | 28 | 29 |
| Odontome UPM1 | 2 | 100 | 6 | 50 | 4 | 50 | 14 | 50 | 3 | 33 | 38 | 39 | 29 | 28 |
| Odontome UPM2 | 1 | 0 | 6 | 67 | 3 | 67 | 12 | 67 | 7 | 100 | 38 | 58 | 24 | 38 |
| Odontome LPM1 | 5 | 100 | 8 | 100 | 8 | 100 | 16 | 100 | 7 | 100 | 35 | 100 | 32 | 100 |
| Odontome LPM2 | 4 | 100 | 8 | 100 | 5 | 100 | 19 | 100 | 8 | 100 | 50 | 98 | 34 | 100 |

Table C2: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Mesial and Distal accessory cusps UPM1* | 1 | 100 | 7 | 86 | 4 | 50 | 14 | 71 | 8 | 63 | 41 | 68 | 25 | 96 |
| Mesial and Distal accessory cusps UPM2 | 4 | 0 | 8 | 0 | 6 | 0 | 13 | 0 | 5 | 0 | 40 | 0 | 32 | 3 |
| Distosagittal ridge UPM1 | 4 | 0 | 8 | 0 | 4 | 0 | 17 | 0 | 8 | 0 | 53 | 2 | 35 | 3 |
| Tricusped UPM1 | 1 | 0 | 8 | 0 | 4 | 0 | 15 | 0 | 8 | 13 | 41 | 7 | 25 | 0 |
| Tricusped UPM2 | 1 | 0 | 4 | 0 | 3 | 0 | 5 | 0 | 0 | 0 | 18 | 0 | 18 | 0 |
| Lingual cusp variation LPM1 (ASU 2-9) | 2 | 0 | 3 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 15 | 13 | 20 | 0 |
| Lingual cusp variation LPM2 (ASU 2-9) | 4 | 25 | 7 | 14 | 2 | 0 | 3 | 0 | 1 | 0 | 17 | 24 | 25 | 0 |
| Hypocone UM1 (ASU 3-5) | 6 | 100 | 6 | 100 | 9 | 67 | 10 | 100 | 3 | 67 | 22 | 86 | 30 | 77 |
| Hypocone UM2 (ASU 3-5) | 2 | 0 | 3 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 15 | 0 | 20 | 0 |
| Hypocone UM3 (ASU 3-5) | 4 | 0 | 7 | 14 | 2 | 0 | 4 | 0 | 1 | 0 | 17 | 0 | 25 | 0 |
| Carabelli's trait UM1 (ASU 2-7) | 7 | 0 | 8 | 0 | 10 | 0 | 17 | 0 | 5 | 0 | 37 | 0 | 30 | 0 |
| Carabelli's trait UM2 (ASU 2-7) | 8 | 0 | 7 | 0 | 10 | 0 | 17 | 0 | 6 | 0 | 39 | 0 | 32 | 0 |
| Carabelli's trait UM3 (ASU 2-7) | 6 | 0 | 6 | 0 | 8 | 0 | 18 | 0 | 7 | 0 | 35 | 0 | 27 | 4 |
| Cusp 5 UM1 (ASU 2-5) | 4 | 50 | 3 | 33 | 3 | 0 | 2 | 50 | 0 | 0 | 11 | 82 | 15 | 67 |
| Cusp 5 UM2 (ASU 2-5) | 5 | 0 | 4 | 0 | 8 | 0 | 9 | 0 | 2 | 0 | 26 | 0 | 34 | 0 |
| Cusp 5 UM3 (ASU 2-5) | 6 | 0 | 5 | 0 | 7 | 0 | 11 | 0 | 2 | 0 | 24 | 0 | 31 | 0 |
| Cusp 5 LM1 (ASU 2-5) | 2 | 50 | 1 | 0 | 3 | 33 | 2 | 0 | 1 | 100 | 15 | 20 | 17 | 6 |
| Cusp 5 LM2 (ASU 2-5) | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 100 | 0 | 0 | 13 | 31 | 16 | 25 |
| Cusp 5 LM3 (ASU 2-5) | 4 | 75 | 1 | 0 | 3 | 0 | 3 | 67 | 1 | 100 | 9 | 67 | 10 | 40 |
| Groove pattern LM1 (ASU Y) | 2 | 50 | 1 | 0 | 3 | 0 | 1 | 100 | 1 | 0 | 10 | 40 | 11 | 45 |
| Groove pattern LM2 (ASU Y) | 2 | 0 | 3 | 33 | 7 | 29 | 7 | 29 | 3 | 0 | 21 | 24 | 28 | 46 |
| Groove pattern LM3 (ASU Y) | 3 | 67 | 3 | 100 | 7 | 100 | 4 | 100 | 1 | 0 | 12 | 75 | 21 | 90 |
| Cusp 6 LM1 (ASU 1-5) | 8 | 100 | 6 | 100 | 6 | 100 | 8 | 100 | 3 | 100 | 23 | 100 | 33 | 97 |

Table C2: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp 6 LM2 (ASU 1-5) | 8 | 100 | 6 | 100 | 9 | 89 | 12 | 92 | 4 | 100 | 33 | 88 | 25 | 76 |
| Cusp 6 LM3 (ASU 1-5)* | 5 | 100 | 7 | 86 | 5 | 100 | 14 | 100 | 6 | 100 | 26 | 100 | 23 | 74 |
| Cusp 7 LM1 (ASU 2-4) | 6 | 17 | 5 | 0 | 7 | 0 | 5 | 0 | 3 | 33 | 21 | 14 | 27 | 11 |
| Cusp 7 LM2 (ASU 2-4) | 5 | 40 | 6 | 33 | 8 | 0 | 8 | 50 | 3 | 67 | 28 | 25 | 26 | 12 |
| Cusp 7 LM3 (ASU 2-4) | 5 | 40 | 7 | 57 | 4 | 50 | 10 | 60 | 6 | 17 | 26 | 62 | 21 | 33 |
| Deflecting wrinkle LM1 (ASU 2-3) | 8 | 38 | 8 | 13 | 8 | 0 | 11 | 18 | 6 | 33 | 27 | 11 | 33 | 21 |
| Distal trigonid crest LM1 | 9 | 11 | 8 | 13 | 9 | 0 | 18 | 6 | 6 | 0 | 39 | 10 | 34 | 6 |
| Distal trigonid crest LM2 | 7 | 29 | 7 | 14 | 4 | 50 | 15 | 7 | 7 | 29 | 29 | 3 | 24 | 8 |
| Distal trigonid crest LM3 | 7 | 100 | 5 | 100 | 6 | 100 | 5 | 100 | 3 | 100 | 20 | 100 | 28 | 96 |
| Middle trigonid crest LM1 | 6 | 100 | 6 | 100 | 8 | 88 | 8 | 88 | 4 | 100 | 26 | 92 | 21 | 76 |
| Middle trigonid crest LM2* | 5 | 100 | 7 | 86 | 3 | 100 | 10 | 100 | 6 | 100 | 27 | 100 | 21 | 76 |
| Middle trigonid crest LM3 | 7 | 14 | 5 | 0 | 6 | 0 | 5 | 0 | 3 | 33 | 20 | 15 | 28 | 11 |
| Metacone UM1 (ASU 3.5-5) | 6 | 33 | 6 | 33 | 8 | 0 | 8 | 50 | 4 | 50 | 26 | 27 | 21 | 14 |
| Metacone UM2 (ASU 3.5-5) | 5 | 40 | 7 | 57 | 3 | 67 | 10 | 60 | 6 | 17 | 27 | 59 | 21 | 33 |
| Metacone UM3 (ASU 3.5-5)* | 8 | 100 | 5 | 100 | 7 | 100 | 9 | 100 | 1 | 100 | 23 | 96 | 28 | 79 |
| Parastyle UM1 (ASU 1-5) | 7 | 86 | 7 | 14 | 8 | 13 | 14 | 64 | 4 | 100 | 38 | 68 | 32 | 56 |
| Parastyle UM2 (ASU 1-5) | 5 | 40 | 5 | 0 | 2 | 0 | 12 | 33 | 4 | 25 | 28 | 21 | 26 | 23 |
| Parastyle UM3 (ASU 1-5) | 0 | 0 | 2 | 50 | 0 | 0 | 1 | 100 | 0 | 0 | 3 | 100 | 7 | 57 |
| Anterior fovea LM1 (ASU 2-4) | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 5 | 0 | 9 | 0 |
| Cusp number LM1 (ASU 5+) | 5 | 0 | 5 | 0 | 5 | 0 | 7 | 0 | 4 | 0 | 21 | 0 | 20 | 0 |
| Cusp number LM2 (ASU 5+) | 4 | 0 | 4 | 0 | 0 | 0 | 10 | 0 | 4 | 0 | 18 | 0 | 19 | 0 |
| Cusp number LM3 (ASU 5+) | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 25 | 5 | 0 |
| Cusp number LM1 (ASU 6+) | 4 | 0 | 3 | 0 | 5 | 0 | 6 | 0 | 2 | 0 | 20 | 0 | 18 | 0 |

Table C2: continued.

| | LSA (12ka - 8ka) | | LSA (8ka - 4ka) | | LSA (4ka - 3ka) | | LSA (3ka - 2ka) | | LSA (2ka - 1ka) | | LSA (1ka - 0ka) | | IA (2ka - 0ka) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp number LM2 (ASU 6+) | 3 | 0 | 3 | 0 | 0 | 0 | 9 | 0 | 3 | 0 | 15 | 0 | 16 | 0 |
| Cusp number LM3 (ASU 6+) | 0 | 0 | 2 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 50 | 5 | 20 |
| Protostylid LM1 (ASU 2-7) | 5 | 0 | 4 | 0 | 6 | 0 | 5 | 0 | 3 | 0 | 21 | 0 | 29 | 0 |
| Protostylid LM2 (ASU 2-7) | 8 | 0 | 6 | 17 | 8 | 0 | 10 | 0 | 5 | 0 | 28 | 0 | 31 | 0 |
| Protostylid LM3 (ASU 2-7) | 6 | 0 | 5 | 0 | 3 | 0 | 9 | 0 | 5 | 0 | 26 | 0 | 24 | 0 |
| Mandibular molar pit-tubercle LM1 (P = 1-3)* | 3 | 0 | 4 | 25 | 5 | 20 | 3 | 100 | 2 | 50 | 17 | 12 | 16 | 6 |
| Mandibular molar pit-tubercle LM2 (P = 1-3)* | 7 | 0 | 3 | 67 | 5 | 0 | 8 | 25 | 2 | 50 | 29 | 14 | 24 | 0 |
| Mandibular molar pit-tubercle LM3 (P = 1-3)* | 2 | 100 | 3 | 100 | 1 | 100 | 11 | 64 | 5 | 60 | 20 | 25 | 19 | 32 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73
*Dental nonmetric traits found significantly different between the samples ($p<0.05$).

Table C3: Descriptive statistics for the upper and lower dental measurements (n=44) investigated over time during the Holocene.

| | LSA (12ka – 8ka) | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | | | 1 | | 2 | | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 2 |
| **Min** | | | | 5.40 | | 7.04 | | 8.17 | 5.75 | 7.86 | 9.73 | 10.74 | 11.63 | 10.76 | 8.36 | 10.36 | 10.72 | 9.96 | 7.89 | 8.63 | 9.36 | 8.31 |
| **Max** | | | | 5.40 | | 7.33 | | 8.17 | 6.54 | 8.27 | 9.82 | 11.18 | 12.73 | 11.43 | 9.68 | 11.04 | 11.15 | 10.33 | 7.89 | 9.60 | 9.36 | 8.62 |
| **Mean** | | | | 5.40 | | 7.19 | | 8.17 | 6.15 | 8.07 | 9.77 | 10.97 | 12.21 | 11.13 | 9.02 | 10.70 | 10.94 | 10.15 | 7.89 | 9.12 | 9.36 | 8.47 |
| **SD** | | | | 0.00 | | 0.21 | | 0.00 | 0.56 | 0.29 | 0.05 | 0.22 | 0.55 | 0.34 | 0.93 | 0.48 | 0.30 | 0.26 | 0.00 | 0.69 | 0.00 | 0.22 |

| | LSA (8ka – 4ka) | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 3 | 5 | 4 | 6 | 7 | 7 | 8 | 8 | 9 | 8 | 9 | 9 | 8 | 9 | 9 | 10 | 9 | 10 | 7 | 7 | 7 | 7 |
| **Min** | 7.99 | 6.54 | 5.44 | 5.80 | 6.78 | 7.04 | 6.32 | 7.81 | 6.16 | 7.90 | 10.03 | 10.46 | 11.74 | 10.63 | 9.45 | 10.68 | 11.47 | 10.24 | 8.07 | 8.71 | 8.82 | 8.74 |
| **Max** | 9.18 | 7.15 | 7.70 | 7.10 | 8.30 | 8.52 | 7.72 | 9.51 | 7.48 | 8.93 | 11.28 | 11.97 | 12.96 | 11.86 | 11.21 | 12.22 | 12.84 | 12.09 | 10.22 | 12.01 | 12.61 | 10.02 |
| **Mean** | 8.41 | 6.90 | 6.87 | 6.37 | 7.50 | 7.76 | 7.08 | 8.56 | 6.72 | 8.48 | 10.29 | 11.01 | 12.26 | 11.06 | 10.19 | 11.34 | 12.27 | 11.02 | 8.71 | 10.31 | 10.70 | 9.34 |
| **SD** | 0.67 | 0.23 | 1.04 | 0.57 | 0.48 | 0.45 | 0.45 | 0.56 | 0.42 | 0.36 | 0.39 | 0.46 | 0.38 | 0.36 | 0.56 | 0.61 | 0.51 | 0.67 | 0.82 | 1.13 | 1.27 | 0.41 |

| | LSA (4ka – 3ka) | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 2 | 2 | 1 | 2 | 5 | 7 | 10 | 10 | 9 | 9 | 5 | 8 | 8 | 8 | 8 | 10 | 10 | 10 | 6 | 7 | 7 | 7 |
| **Min** | 7.92 | 6.03 | 6.26 | 6.03 | 6.71 | 6.68 | 5.72 | 7.11 | 5.52 | 7.70 | 8.65 | 9.81 | 10.81 | 9.78 | 8.15 | 9.85 | 10.20 | 9.03 | 6.94 | 9.03 | 9.21 | 8.23 |
| **Max** | 8.63 | 6.67 | 6.26 | 6.22 | 7.40 | 8.08 | 6.90 | 8.95 | 6.86 | 9.16 | 9.84 | 11.85 | 13.07 | 12.10 | 10.18 | 12.30 | 13.40 | 11.45 | 9.60 | 12.06 | 12.16 | 10.71 |
| **Mean** | 8.28 | 6.35 | 6.26 | 6.13 | 7.04 | 7.54 | 6.52 | 8.33 | 6.32 | 8.43 | 9.43 | 10.89 | 12.12 | 10.78 | 9.26 | 11.14 | 12.01 | 10.41 | 8.01 | 10.37 | 10.60 | 9.01 |
| **SD** | 0.50 | 0.45 | 0.00 | 0.13 | 0.30 | 0.48 | 0.37 | 0.53 | 0.45 | 0.50 | 0.50 | 0.73 | 0.78 | 0.75 | 0.66 | 0.77 | 0.90 | 0.74 | 0.94 | 1.03 | 1.25 | 1.00 |

| | LSA (3ka – 2ka) | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 7 | 11 | 11 | 13 | 12 | 14 | 15 | 16 | 16 | 19 | 16 | 19 | 17 | 20 | 23 | 25 | 25 | 24 | 20 | 20 | 19 | 20 |
| **Min** | 7.51 | 6.10 | 5.41 | 5.60 | 6.75 | 6.59 | 6.04 | 7.80 | 5.84 | 6.82 | 9.41 | 9.92 | 11.27 | 10.00 | 8.47 | 9.85 | 10.88 | 9.43 | 6.59 | 9.54 | 9.59 | 8.00 |
| **Max** | 8.81 | 7.24 | 7.30 | 7.04 | 7.89 | 8.81 | 7.69 | 9.40 | 7.02 | 9.45 | 10.98 | 12.43 | 13.54 | 12.63 | 10.84 | 12.20 | 13.22 | 11.38 | 9.16 | 11.97 | 12.00 | 10.69 |
| **Mean** | 7.90 | 6.43 | 6.64 | 6.01 | 7.27 | 7.46 | 6.67 | 8.51 | 6.36 | 8.23 | 10.13 | 10.84 | 12.19 | 10.81 | 9.66 | 10.81 | 11.82 | 10.35 | 8.13 | 10.62 | 10.73 | 9.21 |
| **SD** | 0.42 | 0.38 | 0.53 | 0.40 | 0.33 | 0.53 | 0.53 | 0.45 | 0.30 | 0.64 | 0.47 | 0.62 | 0.63 | 0.64 | 0.66 | 0.59 | 0.60 | 0.49 | 0.75 | 0.68 | 0.86 | 0.69 |

Table C3: continued.

| | LSA (2ka - 1ka) | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | | | | 1 | 3 | 4 | 5 | 2 | 6 | 3 | 5 | 5 | 5 | 14 | 15 | 16 | 16 | 15 | 16 | 17 | 15 |
| **Min** | | | | | 7.59 | 7.48 | 6.42 | 8.06 | 6.08 | 8.18 | 9.40 | 10.20 | 11.56 | 10.30 | 8.33 | 10.14 | 10.36 | 8.65 | 7.38 | 9.09 | 8.99 | 7.68 |
| **Max** | | | | | 7.59 | 8.69 | 7.20 | 9.47 | 6.49 | 9.50 | 10.29 | 11.42 | 12.49 | 11.61 | 10.25 | 12.57 | 13.78 | 11.45 | 9.77 | 12.26 | 12.45 | 10.81 |
| **Mean** | | | | | 7.59 | 8.00 | 6.85 | 8.93 | 6.29 | 8.88 | 9.80 | 10.85 | 12.07 | 10.90 | 9.48 | 11.11 | 12.00 | 10.45 | 8.53 | 10.33 | 10.76 | 9.64 |
| **SD** | | | | | 0.00 | 0.62 | 0.33 | 0.63 | 0.29 | 0.55 | 0.45 | 0.46 | 0.36 | 0.53 | 0.54 | 0.75 | 0.98 | 0.80 | 0.60 | 1.03 | 0.79 | 0.74 |
| | LSA (1ka -0ka) | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 7 | 17 | 13 | 15 | 24 | 31 | 21 | 26 | 27 | 28 | 31 | 32 | 29 | 31 | 44 | 44 | 42 | 45 | 34 | 36 | 37 | 31 |
| **Min** | 7.89 | 6.18 | 6.34 | 5.40 | 6.28 | 5.94 | 5.81 | 7.78 | 5.55 | 7.68 | 9.06 | 9.67 | 11.22 | 9.60 | 8.63 | 9.68 | 10.36 | 9.54 | 7.04 | 9.26 | 9.15 | 8.15 |
| **Max** | 9.17 | 7.80 | 7.57 | 7.12 | 8.26 | 8.76 | 7.90 | 9.83 | 7.45 | 9.93 | 12.12 | 12.24 | 13.35 | 12.45 | 10.72 | 11.88 | 13.01 | 11.77 | 9.59 | 14.05 | 13.53 | 10.61 |
| **Mean** | 8.63 | 7.00 | 6.96 | 6.21 | 7.46 | 7.78 | 6.76 | 8.74 | 6.47 | 8.83 | 10.40 | 11.12 | 12.31 | 11.23 | 9.87 | 11.03 | 11.92 | 10.68 | 8.29 | 10.45 | 10.86 | 9.53 |
| **SD** | 0.49 | 0.50 | 0.44 | 0.44 | 0.51 | 0.52 | 0.47 | 0.52 | 0.42 | 0.57 | 0.65 | 0.57 | 0.55 | 0.59 | 0.47 | 0.54 | 0.61 | 0.52 | 0.72 | 0.94 | 0.91 | 0.59 |
| | IA (2ka - 0ka) | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 8 | 13 | 18 | 16 | 19 | 21 | 29 | 28 | 27 | 28 | 24 | 26 | 24 | 25 | 29 | 31 | 30 | 30 | 23 | 25 | 25 | 24 |
| **Min** | 7.89 | 5.83 | 6.14 | 5.82 | 6.65 | 7.60 | 6.27 | 8.36 | 6.28 | 8.49 | 9.21 | 10.15 | 11.27 | 10.24 | 8.91 | 10.35 | 10.61 | 9.02 | 8.03 | 9.65 | 10.10 | 9.25 |
| **Max** | 9.65 | 7.92 | 8.10 | 7.50 | 8.37 | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 11.35 | 12.71 | 14.28 | 12.21 | 11.40 | 13.46 | 13.89 | 13.54 | 9.89 | 12.69 | 12.62 | 11.35 |
| **Mean** | 8.68 | 7.14 | 7.04 | 6.68 | 7.71 | 8.52 | 7.21 | 9.59 | 6.94 | 9.59 | 10.61 | 11.57 | 12.62 | 11.53 | 10.12 | 11.64 | 12.23 | 11.26 | 8.86 | 11.01 | 11.27 | 10.32 |
| **SD** | 0.26 | 0.17 | 0.13 | 0.10 | 0.11 | 0.12 | 0.09 | 0.12 | 0.09 | 0.11 | 0.10 | 0.13 | 0.13 | 0.10 | 0.12 | 0.15 | 0.16 | 0.15 | 0.10 | 0.15 | 0.15 | 0.10 |

Table C3: continued.

| | LSA (12ka – 8ka) | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 1 | 2 | 2 | 3 | 1 | 2 | 4 | 4 | 7 | 7 | 5 | 6 | 5 | 5 | 7 | 10 | 8 | 9 | 4 | 5 | 5 | 5 |
| **Min** | 5.05 | 5.01 | 5.29 | 5.57 | 7.70 | 6.81 | 6.74 | 7.35 | 5.52 | 7.18 | 10.69 | 10.26 | 10.94 | 10.80 | 9.95 | 9.53 | 10.56 | 10.41 | 8.08 | 8.97 | 9.63 | 8.04 |
| **Max** | 5.05 | 5.23 | 6.32 | 5.98 | 7.70 | 6.84 | 6.98 | 7.95 | 7.77 | 8.82 | 11.98 | 10.94 | 12.11 | 11.69 | 12.03 | 11.05 | 12.27 | 12.43 | 11.52 | 10.93 | 11.80 | 12.44 |
| **Mean** | 5.05 | 5.12 | 5.81 | 5.76 | 7.70 | 6.83 | 6.85 | 7.51 | 6.81 | 7.79 | 11.05 | 10.50 | 11.48 | 11.28 | 10.98 | 10.33 | 11.45 | 11.34 | 9.74 | 9.61 | 10.47 | 10.13 |
| **SD** | 0.00 | 0.16 | 0.73 | 0.21 | 0.00 | 0.02 | 0.11 | 0.29 | 0.70 | 0.53 | 0.53 | 0.26 | 0.54 | 0.33 | 0.66 | 0.51 | 0.60 | 0.56 | 1.52 | 0.79 | 0.89 | 1.70 |
| | LSA (8ka – 4ka) | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 4 | 5 | 5 | 6 | 6 | 7 | 8 | 9 | 6 | 9 | 9 | 10 | 9 | 9 | 6 | 8 | 8 | 8 | 7 | 8 | 8 | 8 |
| **Min** | 4.55 | 4.96 | 4.73 | 5.34 | 6.10 | 6.36 | 6.40 | 7.05 | 6.52 | 7.53 | 10.40 | 9.61 | 11.11 | 10.92 | 10.70 | 10.23 | 11.32 | 11.17 | 9.48 | 9.12 | 9.65 | 10.15 |
| **Max** | 5.53 | 5.77 | 6.37 | 6.21 | 7.82 | 7.63 | 7.55 | 8.39 | 8.23 | 8.97 | 11.86 | 11.32 | 12.46 | 11.92 | 12.94 | 11.90 | 13.34 | 13.19 | 11.10 | 10.62 | 11.30 | 11.47 |
| **Mean** | 5.12 | 5.32 | 5.79 | 5.78 | 6.83 | 7.03 | 6.90 | 7.80 | 7.33 | 8.23 | 11.14 | 10.62 | 11.72 | 11.50 | 11.60 | 10.96 | 11.92 | 11.96 | 10.01 | 10.01 | 10.57 | 10.65 |
| **SD** | 0.45 | 0.32 | 0.69 | 0.29 | 0.66 | 0.45 | 0.43 | 0.51 | 0.56 | 0.53 | 0.52 | 0.46 | 0.43 | 0.41 | 0.75 | 0.53 | 0.68 | 0.69 | 0.62 | 0.53 | 0.56 | 0.48 |
| | LSA (4ka – 3ka) | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 1 | 3 | 2 | 4 | 4 | 7 | 8 | 9 | 10 | 11 | 10 | 11 | 10 | 10 | 13 | 13 | 13 | 13 | 7 | 6 | 6 | 6 |
| **Min** | 4.36 | 4.77 | 5.09 | 4.90 | 6.14 | 6.15 | 5.85 | 6.59 | 5.93 | 7.19 | 10.01 | 9.29 | 10.39 | 10.03 | 9.94 | 9.38 | 10.40 | 10.32 | 7.92 | 9.21 | 9.08 | 9.21 |
| **Max** | 4.36 | 5.22 | 5.38 | 5.51 | 7.46 | 7.47 | 7.29 | 7.80 | 7.65 | 8.67 | 11.57 | 11.06 | 12.67 | 12.15 | 12.63 | 11.73 | 13.04 | 13.12 | 11.09 | 10.89 | 11.11 | 11.39 |
| **Mean** | 4.36 | 5.01 | 5.24 | 5.29 | 6.70 | 6.73 | 6.66 | 7.19 | 6.89 | 7.87 | 10.78 | 10.38 | 11.44 | 11.26 | 10.97 | 10.46 | 11.44 | 11.54 | 9.73 | 9.77 | 10.12 | 10.13 |
| **SD** | 0.00 | 0.23 | 0.21 | 0.27 | 0.55 | 0.52 | 0.56 | 0.43 | 0.48 | 0.52 | 0.50 | 0.64 | 0.63 | 0.61 | 0.70 | 0.72 | 0.74 | 0.79 | 0.98 | 0.59 | 0.73 | 0.76 |
| | LSA (3ka – 2ka) | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 1 | 5 | 5 | 8 | 8 | 12 | 13 | 15 | 15 | 14 | 10 | 13 | 10 | 12 | 12 | 17 | 16 | 16 | 13 | 14 | 12 | 14 |
| **Min** | 4.87 | 4.91 | 5.34 | 5.00 | 5.92 | 6.03 | 6.03 | 6.87 | 6.41 | 7.38 | 10.08 | 9.58 | 10.96 | 10.36 | 9.65 | 9.61 | 10.74 | 10.47 | 8.56 | 7.94 | 9.12 | 8.51 |
| **Max** | 4.87 | 5.16 | 6.06 | 6.57 | 7.25 | 7.39 | 7.86 | 8.33 | 7.38 | 8.58 | 11.91 | 11.46 | 12.46 | 12.35 | 12.37 | 11.55 | 12.68 | 12.89 | 12.72 | 11.55 | 12.81 | 12.51 |
| **Mean** | 4.87 | 5.02 | 5.58 | 5.58 | 6.53 | 6.57 | 6.66 | 7.49 | 6.88 | 7.84 | 10.81 | 10.33 | 11.53 | 11.26 | 10.99 | 10.44 | 11.37 | 11.39 | 10.03 | 9.85 | 10.67 | 10.27 |
| **SD** | 0.00 | 0.09 | 0.29 | 0.50 | 0.45 | 0.47 | 0.51 | 0.49 | 0.32 | 0.38 | 0.58 | 0.47 | 0.48 | 0.57 | 0.78 | 0.58 | 0.55 | 0.67 | 1.12 | 0.97 | 0.94 | 0.99 |

Table C3: continued.

| | LSA (2ka - 1ka) | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | | | | | 1 | 5 | 6 | 9 | 10 | 4 | 3 | 4 | 4 | 11 | 12 | 9 | 11 | 13 | 14 | 14 | 12 |
| **Min** | | | | | | 6.87 | 6.01 | 7.05 | 6.28 | 6.54 | 10.92 | 10.49 | 11.82 | 11.36 | 10.28 | 9.64 | 10.91 | 10.51 | 9.17 | 9.19 | 8.31 | 9.72 |
| **Max** | | | | | | 6.87 | 7.25 | 8.52 | 7.08 | 8.68 | 11.90 | 11.02 | 12.64 | 12.04 | 11.89 | 11.58 | 12.52 | 12.62 | 11.32 | 11.34 | 11.66 | 11.65 |
| **Mean** | | | | | | 6.87 | 6.57 | 7.56 | 6.69 | 7.94 | 11.44 | 10.73 | 12.18 | 11.84 | 10.94 | 10.42 | 11.68 | 11.59 | 10.26 | 10.30 | 10.68 | 10.77 |
| **SD** | | | | | | 0.00 | 0.46 | 0.52 | 0.32 | 0.64 | 0.41 | 0.27 | 0.34 | 0.32 | 0.49 | 0.63 | 0.54 | 0.62 | 0.67 | 0.67 | 0.90 | 0.68 |
| | LSA (1ka -0ka) | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 15 | 17 | 15 | 15 | 18 | 18 | 30 | 29 | 26 | 27 | 20 | 22 | 20 | 22 | 33 | 33 | 31 | 33 | 30 | 30 | 30 | 28 |
| **Min** | 4.49 | 4.66 | 5.41 | 4.86 | 6.03 | 6.30 | 5.84 | 6.45 | 5.71 | 7.01 | 10.13 | 9.83 | 11.01 | 10.54 | 9.64 | 9.33 | 10.48 | 10.22 | 8.79 | 8.69 | 9.35 | 9.54 |
| **Max** | 6.45 | 6.54 | 6.61 | 6.53 | 7.62 | 7.73 | 8.05 | 8.59 | 8.16 | 9.07 | 12.42 | 11.78 | 13.20 | 12.29 | 12.73 | 12.43 | 13.50 | 13.21 | 12.01 | 11.18 | 12.14 | 12.41 |
| **Mean** | 5.29 | 5.46 | 5.87 | 5.72 | 7.14 | 7.09 | 6.99 | 7.80 | 7.18 | 8.09 | 11.29 | 10.61 | 11.90 | 11.50 | 10.97 | 10.50 | 11.63 | 11.53 | 10.38 | 10.16 | 10.80 | 10.87 |
| **SD** | 0.50 | 0.46 | 0.33 | 0.52 | 0.40 | 0.41 | 0.49 | 0.48 | 0.57 | 0.55 | 0.52 | 0.49 | 0.52 | 0.45 | 0.66 | 0.63 | 0.56 | 0.58 | 0.77 | 0.61 | 0.64 | 0.70 |
| | IA (2ka - 0ka) | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 22 | 22 | 23 | 21 | 26 | 30 | 26 | 31 | 24 | 27 | 22 | 26 | 26 | 26 | 29 | 28 | 28 | 25 | 22 | 22 | 21 | 21 |
| **Min** | 4.73 | 5.05 | 5.25 | 5.61 | 6.34 | 6.66 | 6.13 | 7.22 | 6.33 | 7.45 | 10.58 | 10.00 | 11.11 | 10.96 | 9.37 | 9.58 | 10.39 | 10.39 | 10.04 | 8.80 | 9.76 | 10.33 |
| **Max** | 6.07 | 7.35 | 7.37 | 6.80 | 8.03 | 8.78 | 8.06 | 9.52 | 8.09 | 9.61 | 12.59 | 12.19 | 13.24 | 12.91 | 12.82 | 11.66 | 13.47 | 12.94 | 12.03 | 11.25 | 12.18 | 12.34 |
| **Mean** | 5.44 | 5.85 | 6.18 | 6.26 | 7.04 | 7.49 | 7.35 | 8.30 | 7.32 | 8.57 | 11.68 | 10.96 | 12.23 | 11.93 | 11.11 | 10.69 | 11.95 | 11.69 | 11.08 | 10.32 | 11.27 | 11.25 |
| **SD** | 0.08 | 0.10 | 0.11 | 0.07 | 0.09 | 0.09 | 0.08 | 0.12 | 0.12 | 0.12 | 0.11 | 0.12 | 0.13 | 0.11 | 0.14 | 0.12 | 0.14 | 0.15 | 0.13 | 0.14 | 0.13 | 0.12 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73

# APPENDIX D: DESCRIPTIVE STATISTICS FOR THE PREHISTORIC GEOGRAPHICAL COMPARISONS

Table D1: Frequencies of the nonmetric cranial traits (n=73) investigated in the geographical regions of southern Africa.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Incomplete (nasal part) metopic suture | 53 | 8 | 11 | 0 | 76 | 3 | 68 | 6 | 17 | 0 | 29 | 14 | 5 | 20 |
| Complete metopic suture | 53 | 0 | 11 | 0 | 76 | 0 | 68 | 0 | 17 | 0 | 29 | 0 | 5 | 0 |
| Metopic ridge | 52 | 29 | 12 | 42 | 77 | 38 | 74 | 49 | 18 | 17 | 33 | 24 | 8 | 25 |
| Square shaped orbits* | 43 | 60 | 13 | 31 | 74 | 49 | 62 | 35 | 17 | 35 | 27 | 74 | 9 | 56 |
| Oval shaped orbits* | 43 | 37 | 13 | 54 | 74 | 49 | 62 | 65 | 17 | 65 | 27 | 26 | 9 | 44 |
| Round shaped orbits* | 43 | 2 | 13 | 15 | 74 | 3 | 62 | 0 | 17 | 0 | 27 | 0 | 9 | 0 |
| Supraorbital notch (Left) | 52 | 67 | 12 | 67 | 77 | 69 | 73 | 67 | 17 | 82 | 33 | 88 | 9 | 78 |
| Supraorbital notch (Right) | 53 | 83 | 12 | 67 | 77 | 66 | 73 | 75 | 17 | 88 | 36 | 89 | 9 | 89 |
| Supraorbital foramen (Left)* | 50 | 44 | 11 | 73 | 76 | 49 | 74 | 50 | 18 | 17 | 34 | 12 | 9 | 22 |
| Supraorbital foramen (Right)* | 52 | 37 | 11 | 73 | 77 | 43 | 73 | 42 | 17 | 29 | 34 | 21 | 9 | 0 |
| Ethmoidal foramina (Left)* | 23 | 65 | 8 | 63 | 47 | 77 | 49 | 86 | 10 | 100 | 13 | 62 | 1 | 0 |
| Ethmoidal foramina (Right) | 21 | 76 | 7 | 86 | 45 | 76 | 50 | 86 | 14 | 93 | 13 | 85 | 0 | 0 |
| Infraorbital foramen (Left) | 42 | 90 | 10 | 90 | 59 | 90 | 60 | 87 | 17 | 82 | 26 | 96 | 8 | 100 |
| Infraorbital foramen (Right) | 40 | 95 | 10 | 100 | 61 | 87 | 65 | 88 | 17 | 88 | 25 | 88 | 10 | 100 |
| Infraorbital form* | 49 | 12 | 11 | 0 | 71 | 0 | 64 | 5 | 17 | 6 | 30 | 17 | 11 | 18 |
| Infraorbital suture | 26 | 15 | 4 | 25 | 43 | 26 | 37 | 22 | 13 | 54 | 15 | 13 | 6 | 33 |
| Profile curves of nasal bones | 31 | 65 | 10 | 40 | 49 | 55 | 45 | 44 | 9 | 78 | 18 | 56 | 8 | 50 |
| Superficial nasion* | 36 | 78 | 9 | 67 | 54 | 74 | 46 | 54 | 10 | 30 | 19 | 26 | 8 | 38 |
| Moderately depressed nasion* | 36 | 17 | 9 | 11 | 54 | 24 | 46 | 30 | 10 | 70 | 19 | 58 | 8 | 50 |
| Marked depression of nasion | 36 | 6 | 9 | 22 | 54 | 2 | 46 | 15 | 10 | 0 | 19 | 16 | 8 | 13 |
| Angle of nasal bones | 41 | 88 | 11 | 91 | 69 | 94 | 56 | 89 | 16 | 94 | 27 | 100 | 9 | 100 |
| Nasal bone shape | 37 | 62 | 10 | 50 | 54 | 44 | 43 | 49 | 9 | 67 | 19 | 63 | 6 | 83 |

Table D1: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Extension of nasal bones | 29 | 34 | 10 | 20 | 47 | 4 | 47 | 6 | 9 | 11 | 13 | 54 | 7 | 29 |
| Development of anterior nasal spine* | 45 | 62 | 11 | 73 | 53 | 49 | 59 | 61 | 18 | 61 | 16 | 75 | 9 | 56 |
| Zygomaxillary tubercle (Left) | 47 | 51 | 11 | 18 | 74 | 49 | 61 | 43 | 16 | 50 | 23 | 52 | 9 | 67 |
| Zygomaxillary tubercle (Right) | 48 | 48 | 10 | 20 | 69 | 49 | 62 | 34 | 18 | 50 | 27 | 44 | 11 | 45 |
| Subnasal region* | 47 | 32 | 12 | 17 | 63 | 27 | 61 | 49 | 16 | 38 | 25 | 56 | 7 | 43 |
| Dental arcade shape | 32 | 72 | 9 | 67 | 46 | 83 | 37 | 59 | 8 | 88 | 17 | 71 | 7 | 57 |
| Anterior palate form | 53 | 83 | 14 | 71 | 70 | 86 | 69 | 84 | 18 | 94 | 32 | 100 | 11 | 100 |
| Torus palatines | 37 | 24 | 9 | 33 | 54 | 46 | 54 | 24 | 11 | 45 | 24 | 42 | 7 | 14 |
| Torus maxillaries | 43 | 0 | 9 | 0 | 65 | 6 | 57 | 7 | 13 | 8 | 27 | 0 | 10 | 10 |
| Foramen of Huschke (Left)* | 52 | 17 | 12 | 33 | 74 | 23 | 62 | 42 | 16 | 44 | 36 | 11 | 9 | 11 |
| Foramen of Huschke (Right) | 53 | 26 | 13 | 23 | 70 | 24 | 63 | 40 | 16 | 31 | 39 | 10 | 8 | 13 |
| Encroachment of occipital condyles | 39 | 31 | 11 | 27 | 68 | 21 | 48 | 33 | 15 | 27 | 20 | 15 | 6 | 17 |
| Hypoglossal canal bridging (Left) | 35 | 0 | 11 | 0 | 69 | 14 | 52 | 10 | 18 | 6 | 25 | 4 | 6 | 17 |
| Hypoglossal canal bridging (Right) | 35 | 14 | 12 | 8 | 71 | 10 | 52 | 4 | 17 | 0 | 23 | 4 | 6 | 0 |
| Condylar canal (Left) | 29 | 41 | 7 | 43 | 46 | 37 | 40 | 55 | 10 | 40 | 16 | 81 | 0 | 0 |
| Condylar canal (Right) | 34 | 50 | 7 | 57 | 46 | 54 | 41 | 54 | 9 | 56 | 13 | 69 | 0 | 0 |
| Inca bone | 51 | 0 | 11 | 0 | 76 | 0 | 64 | 5 | 17 | 0 | 25 | 0 | 10 | 0 |
| Interparietal groove | 51 | 24 | 12 | 17 | 73 | 25 | 67 | 31 | 17 | 29 | 32 | 47 | 9 | 22 |
| Parietal foramina | 47 | 98 | 10 | 90 | 65 | 91 | 64 | 95 | 12 | 92 | 24 | 96 | 4 | 100 |
| Zygomatic arch | 43 | 19 | 9 | 33 | 67 | 31 | 60 | 33 | 17 | 24 | 21 | 10 | 6 | 0 |
| Wormian bones | 40 | 45 | 11 | 36 | 66 | 61 | 61 | 66 | 13 | 69 | 26 | 62 | 3 | 100 |
| Ophryonic groove | 54 | 24 | 11 | 18 | 77 | 17 | 73 | 26 | 17 | 18 | 36 | 14 | 9 | 0 |
| Sutural variations at pterion (Left)* | 33 | 82 | 5 | 80 | 32 | 69 | 31 | 87 | 10 | 50 | 18 | 50 | 2 | 0 |
| Sutural variations at pterion (Right)* | 34 | 74 | 4 | 75 | 31 | 65 | 34 | 88 | 11 | 73 | 13 | 23 | 3 | 33 |

Table D1: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Inferior frontal eminence (Left) | 49 | 55 | 8 | 38 | 75 | 39 | 63 | 49 | 17 | 53 | 26 | 46 | 8 | 13 |
| Inferior frontal eminence (Right) | 49 | 51 | 7 | 14 | 75 | 41 | 63 | 51 | 18 | 56 | 28 | 46 | 7 | 14 |
| Superior temporal line (Left) | 49 | 41 | 11 | 27 | 72 | 38 | 58 | 53 | 15 | 53 | 24 | 33 | 3 | 33 |
| Superior temporal line (Right) | 45 | 38 | 9 | 22 | 66 | 38 | 60 | 55 | 13 | 46 | 21 | 43 | 5 | 20 |
| Mons temporosphenoidalis (Left) | 44 | 66 | 10 | 80 | 75 | 51 | 61 | 56 | 18 | 44 | 22 | 32 | 7 | 29 |
| Mons temporosphenoidalis (Right)* | 44 | 70 | 10 | 70 | 71 | 46 | 61 | 61 | 15 | 47 | 20 | 20 | 7 | 29 |
| Parietotemporal suture (Left) | 39 | 44 | 11 | 55 | 59 | 56 | 49 | 37 | 14 | 64 | 20 | 60 | 3 | 67 |
| Parietotemporal suture (Right) | 38 | 42 | 8 | 50 | 53 | 58 | 56 | 46 | 13 | 54 | 21 | 71 | 4 | 50 |
| Tympanic plate of temporal bone (Left)* | 54 | 43 | 12 | 50 | 73 | 52 | 67 | 27 | 17 | 29 | 37 | 54 | 9 | 67 |
| Tympanic plate of temporal bone (Right)* | 55 | 47 | 12 | 50 | 70 | 54 | 67 | 27 | 17 | 29 | 37 | 57 | 9 | 78 |
| Supra-asterionic region* | 47 | 57 | 13 | 46 | 73 | 23 | 67 | 21 | 18 | 44 | 30 | 43 | 8 | 13 |
| Parietal notch bone (Left) | 43 | 5 | 11 | 0 | 69 | 12 | 57 | 16 | 17 | 6 | 25 | 4 | 6 | 17 |
| Parietal notch bone (Right) | 44 | 7 | 12 | 0 | 67 | 9 | 63 | 21 | 13 | 15 | 23 | 13 | 6 | 0 |
| Sutura mendosa | 43 | 2 | 9 | 0 | 74 | 4 | 58 | 2 | 16 | 6 | 25 | 4 | 5 | 0 |
| Os japonicum (Left)* | 46 | 0 | 13 | 15 | 75 | 1 | 67 | 0 | 16 | 0 | 24 | 0 | 7 | 0 |
| Os japonicum (Right) | 46 | 2 | 13 | 8 | 70 | 1 | 62 | 0 | 17 | 0 | 25 | 0 | 9 | 0 |
| Asterion ossicle (Left) | 43 | 5 | 11 | 0 | 71 | 3 | 61 | 2 | 16 | 6 | 30 | 3 | 7 | 0 |
| Asterion ossicle (Right) | 44 | 5 | 12 | 0 | 70 | 3 | 64 | 2 | 16 | 0 | 27 | 4 | 5 | 0 |
| Occipitomastoid wormian bone (Left) | 40 | 5 | 12 | 0 | 65 | 11 | 57 | 11 | 17 | 6 | 22 | 18 | 5 | 20 |
| Occipitomastoid wormian bone (Right) | 42 | 2 | 12 | 8 | 64 | 9 | 57 | 11 | 15 | 7 | 20 | 15 | 3 | 0 |
| Pointed chin shape | 39 | 18 | 11 | 9 | 55 | 33 | 46 | 30 | 11 | 18 | 29 | 28 | 9 | 0 |
| Mental foramen (Left) | 45 | 84 | 12 | 92 | 57 | 88 | 51 | 86 | 11 | 82 | 32 | 88 | 9 | 100 |
| Mental foramen (Right) | 40 | 83 | 12 | 75 | 59 | 73 | 51 | 78 | 12 | 75 | 30 | 90 | 9 | 100 |
| Genial tubercles | 33 | 48 | 9 | 44 | 40 | 38 | 35 | 40 | 6 | 67 | 29 | 48 | 8 | 50 |
| Torus mandibularis | 47 | 0 | 11 | 0 | 61 | 0 | 54 | 0 | 11 | 0 | 36 | 0 | 11 | 0 |

Table D1: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cranial Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Mylohyoid bridge (Left)* | 45 | 31 | 12 | 25 | 58 | 52 | 53 | 57 | 10 | 70 | 27 | 7 | 10 | 0 |
| Mylohyoid bridge (Right)* | 45 | 31 | 11 | 27 | 58 | 47 | 50 | 60 | 12 | 50 | 29 | 10 | 10 | 0 |

*Cranial nonmetric traits found significantly different between the samples ($p<0.05$).

Table D2: Frequencies of the dental nonmetric traits (n=100) investigated in the geographical regions of southern Africa.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Midline diastema UI1 | 11 | 0 | 0 | 0 | 7 | 0 | 11 | 0 | 2 | 0 | 5 | 0 | 3 | 0 |
| Diminutive UI2 | 15 | 73 | 0 | 0 | 7 | 86 | 12 | 92 | 1 | 100 | 7 | 43 | 3 | 67 |
| Winging UI1s (ASU 1) | 16 | 81 | 0 | 0 | 6 | 67 | 12 | 67 | 0 | 0 | 20 | 55 | 2 | 0 |
| Winging LI1s (ASU 1) | 21 | 86 | 0 | 0 | 12 | 67 | 11 | 73 | 3 | 100 | 34 | 65 | 4 | 75 |
| Shovelling UI1 (ASU 2-6)* | 23 | 78 | 2 | 100 | 6 | 33 | 20 | 95 | 1 | 100 | 32 | 100 | 6 | 83 |
| Shovelling UI2 (ASU 2-6) | 17 | 6 | 0 | 0 | 7 | 0 | 9 | 0 | 1 | 0 | 17 | 6 | 1 | 0 |
| Shovelling UC (ASU 2-6) | 19 | 5 | 0 | 0 | 11 | 0 | 8 | 0 | 2 | 0 | 31 | 3 | 4 | 0 |
| Shovelling LI1 (ASU 2-6) | 28 | 61 | 1 | 100 | 11 | 18 | 19 | 47 | 1 | 100 | 36 | 56 | 9 | 11 |
| Shovelling LI2 (ASU 2-6) | 28 | 43 | 1 | 100 | 13 | 46 | 21 | 43 | 3 | 100 | 40 | 73 | 10 | 60 |
| Shovelling LC (ASU 2-6) | 22 | 0 | 2 | 0 | 11 | 0 | 15 | 0 | 3 | 0 | 26 | 0 | 5 | 0 |
| Double shovelling UI1 (ASU 2-6) | 20 | 0 | 2 | 0 | 16 | 0 | 18 | 0 | 4 | 0 | 34 | 3 | 5 | 0 |
| Double shovelling UI2 (ASU 2-6) | 24 | 33 | 1 | 0 | 10 | 40 | 14 | 57 | 1 | 0 | 24 | 33 | 3 | 33 |
| Double shovelling UC (ASU 2-6) | 22 | 32 | 1 | 0 | 10 | 20 | 15 | 7 | 2 | 50 | 33 | 24 | 4 | 0 |
| Double shovelling UPM1 (ASU 2-6) | 24 | 46 | 2 | 50 | 8 | 50 | 22 | 64 | 1 | 100 | 31 | 65 | 4 | 50 |
| Double shovelling LI1 (ASU 2-6) | 23 | 9 | 1 | 0 | 7 | 43 | 12 | 33 | 1 | 100 | 21 | 14 | 2 | 0 |
| Double shovelling LI2 (ASU 2-6) | 21 | 48 | 1 | 100 | 8 | 50 | 14 | 43 | 2 | 0 | 32 | 38 | 5 | 0 |
| Interruption groove UI1 | 26 | 4 | 1 | 0 | 17 | 0 | 16 | 0 | 4 | 0 | 36 | 0 | 9 | 0 |
| Interruption groove UI2 | 35 | 0 | 3 | 0 | 19 | 0 | 20 | 0 | 3 | 0 | 34 | 0 | 11 | 0 |
| Tuberculum dentale UI1 (ASU 2-6) | 24 | 0 | 1 | 0 | 14 | 0 | 16 | 0 | 3 | 0 | 36 | 0 | 9 | 0 |
| Tuberculum dentale UI2 (ASU 2-6) | 42 | 0 | 4 | 0 | 25 | 0 | 29 | 0 | 6 | 0 | 43 | 0 | 10 | 0 |
| Tuberculum dentale UC (ASU 2-6) | 44 | 0 | 4 | 0 | 25 | 0 | 31 | 0 | 6 | 0 | 48 | 0 | 11 | 0 |
| Peg-shaped UI2 | 40 | 3 | 4 | 0 | 24 | 4 | 26 | 4 | 6 | 17 | 39 | 0 | 12 | 0 |
| Peg-shaped UM3* | 20 | 20 | 2 | 0 | 2 | 0 | 15 | 47 | 1 | 0 | 29 | 7 | 3 | 33 |

Table D2: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Labial convexity UI1 (ASU 2-4) | 14 | 43 | 1 | 0 | 3 | 0 | 7 | 14 | 0 | 0 | 20 | 35 | 4 | 50 |
| Labial convexity UI2 (ASU 2-4) | 26 | 0 | 2 | 0 | 17 | 0 | 24 | 0 | 4 | 0 | 45 | 0 | 10 | 0 |
| Congenital absence UI2 | 25 | 0 | 3 | 0 | 17 | 0 | 23 | 0 | 4 | 0 | 44 | 0 | 10 | 0 |
| Congenital absence UPM2 | 19 | 11 | 0 | 0 | 8 | 13 | 14 | 0 | 1 | 0 | 31 | 0 | 6 | 0 |
| Congenital absence UM3 | 16 | 6 | 0 | 0 | 7 | 14 | 9 | 11 | 1 | 0 | 27 | 4 | 2 | 0 |
| Congenital absence LI1 | 25 | 0 | 2 | 0 | 17 | 0 | 23 | 0 | 4 | 0 | 42 | 0 | 10 | 0 |
| Congenital absence LPM2 | 28 | 0 | 2 | 0 | 18 | 0 | 24 | 0 | 4 | 0 | 45 | 0 | 10 | 0 |
| Congenital absence LM3 | 27 | 0 | 3 | 0 | 20 | 0 | 23 | 0 | 4 | 0 | 43 | 0 | 10 | 0 |
| Mesial ridge UC (ASU 1-3) | 15 | 13 | 0 | 0 | 3 | 0 | 4 | 25 | 2 | 0 | 27 | 7 | 3 | 0 |
| Distal accessory ridge UC (ASU 2-5) | 15 | 20 | 0 | 0 | 3 | 0 | 5 | 0 | 2 | 0 | 25 | 8 | 3 | 0 |
| Distal accessory ridge LC (ASU 2-5) | 13 | 23 | 0 | 0 | 1 | 0 | 5 | 20 | 2 | 0 | 24 | 17 | 3 | 33 |
| Mesial premolar accessory ridges UPM1 (ASU 1-4) | 14 | 50 | 0 | 0 | 1 | 0 | 5 | 0 | 2 | 50 | 24 | 21 | 2 | 50 |
| Distal premolar accessory ridges UPM1 (ASU 1-4) | 29 | 100 | 1 | 100 | 19 | 100 | 27 | 100 | 3 | 100 | 41 | 100 | 11 | 100 |
| Mesial premolar accessory ridges UPM2 (ASU 1-4) | 39 | 97 | 2 | 100 | 18 | 94 | 21 | 100 | 4 | 100 | 43 | 88 | 8 | 100 |
| Distal premolar accessory ridges UPM2 (ASU 1-4) | 30 | 80 | 2 | 100 | 16 | 81 | 18 | 83 | 3 | 100 | 33 | 79 | 11 | 91 |
| Mesial premolar accessory ridges LPM1 (ASU 1-4) | 14 | 57 | 0 | 0 | 5 | 100 | 11 | 55 | 0 | 0 | 22 | 45 | 1 | 100 |
| Distal premolar accessory ridges LPM1 (ASU 1-4) | 31 | 6 | 1 | 0 | 11 | 18 | 11 | 18 | 5 | 0 | 38 | 5 | 8 | 0 |
| Mesial premolar accessory ridges LPM2 (ASU 1-4) | 23 | 17 | 2 | 0 | 12 | 17 | 10 | 20 | 3 | 0 | 30 | 10 | 9 | 0 |
| Distal premolar accessory ridges LPM2 (ASU 1-4) | 22 | 27 | 0 | 0 | 7 | 0 | 11 | 36 | 1 | 0 | 32 | 25 | 4 | 25 |
| Odontome UPM1* | 34 | 38 | 1 | 0 | 12 | 50 | 15 | 60 | 2 | 50 | 37 | 24 | 8 | 0 |
| Odontome UPM2 | 30 | 60 | 2 | 50 | 14 | 64 | 15 | 80 | 3 | 67 | 31 | 35 | 11 | 55 |
| Odontome LPM1 | 30 | 100 | 1 | 100 | 19 | 100 | 25 | 100 | 4 | 100 | 43 | 100 | 10 | 100 |
| Odontome LPM2 | 41 | 98 | 3 | 100 | 22 | 100 | 22 | 100 | 5 | 100 | 45 | 100 | 11 | 100 |

Table D2: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Mesial and Distal accessory cusps UPM1* | 32 | 66 | 2 | 50 | 19 | 74 | 16 | 75 | 3 | 67 | 33 | 100 | 11 | 82 |
| Mesial and Distal accessory cusps UPM2 | 36 | 0 | 0 | 0 | 13 | 0 | 24 | 0 | 3 | 0 | 41 | 2 | 8 | 0 |
| Distosagittal ridge UPM1 | 44 | 2 | 3 | 0 | 18 | 0 | 22 | 0 | 5 | 0 | 46 | 4 | 11 | 0 |
| Tricusped UPM1 | 32 | 6 | 2 | 0 | 18 | 6 | 19 | 5 | 3 | 0 | 33 | 3 | 11 | 0 |
| Tricusped UPM2 | 18 | 0 | 2 | 0 | 4 | 0 | 8 | 0 | 1 | 0 | 21 | 0 | 5 | 0 |
| Lingual cusp variation LPM1 (ASU 2-9) | 15 | 13 | 0 | 0 | 2 | 0 | 6 | 0 | 0 | 0 | 27 | 0 | 7 | 0 |
| Lingual cusp variation LPM2 (ASU 2-9)* | 18 | 22 | 0 | 0 | 3 | 0 | 12 | 17 | 1 | 0 | 31 | 0 | 10 | 10 |
| Hypocone UM1 (ASU 3-5)* | 23 | 87 | 2 | 100 | 8 | 63 | 24 | 92 | 1 | 100 | 38 | 76 | 9 | 22 |
| Hypocone UM2 (ASU 3-5) | 15 | 0 | 0 | 0 | 2 | 0 | 7 | 0 | 0 | 0 | 24 | 0 | 5 | 0 |
| Hypocone UM3 (ASU 3-5) | 18 | 0 | 0 | 0 | 3 | 0 | 13 | 8 | 1 | 0 | 30 | 0 | 8 | 0 |
| Carabelli's trait UM1 (ASU 2-7) | 31 | 0 | 4 | 0 | 17 | 0 | 27 | 0 | 3 | 0 | 40 | 0 | 9 | 0 |
| Carabelli's trait UM2 (ASU 2-7) | 33 | 0 | 4 | 0 | 18 | 0 | 28 | 0 | 3 | 0 | 40 | 0 | 11 | 0 |
| Carabelli's trait UM3 (ASU 2-7) | 29 | 0 | 5 | 0 | 17 | 0 | 25 | 0 | 4 | 0 | 37 | 3 | 11 | 0 |
| Cusp 5 UM1 (ASU 2-5) | 11 | 82 | 0 | 0 | 1 | 100 | 10 | 30 | 0 | 0 | 21 | 62 | 5 | 80 |
| Cusp 5 UM2 (ASU 2-5) | 24 | 0 | 2 | 0 | 11 | 0 | 18 | 0 | 0 | 0 | 43 | 0 | 11 | 0 |
| Cusp 5 UM3 (ASU 2-5) | 22 | 0 | 1 | 0 | 12 | 0 | 20 | 0 | 1 | 0 | 39 | 0 | 11 | 0 |
| Cusp 5 LM1 (ASU 2-5) | 15 | 20 | 0 | 0 | 3 | 33 | 6 | 33 | 0 | 0 | 23 | 9 | 4 | 0 |
| Cusp 5 LM2 (ASU 2-5) | 13 | 31 | 0 | 0 | 1 | 100 | 4 | 0 | 0 | 0 | 22 | 23 | 2 | 50 |
| Cusp 5 LM3 (ASU 2-5) | 9 | 67 | 0 | 0 | 2 | 100 | 8 | 50 | 0 | 0 | 14 | 36 | 1 | 100 |
| Groove pattern LM1 (ASU Y) | 10 | 40 | 0 | 0 | 2 | 50 | 4 | 25 | 0 | 0 | 14 | 43 | 1 | 100 |
| Groove pattern LM2 (ASU Y) | 21 | 29 | 1 | 0 | 9 | 22 | 11 | 27 | 0 | 0 | 35 | 40 | 8 | 25 |
| Groove pattern LM3 (ASU Y) | 13 | 77 | 0 | 0 | 4 | 75 | 12 | 92 | 0 | 0 | 26 | 92 | 3 | 67 |
| Cusp 6 LM1 (ASU 1-5) | 22 | 100 | 2 | 100 | 10 | 100 | 20 | 100 | 1 | 100 | 42 | 98 | 7 | 100 |

Table D2: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp 6 LM2 (ASU 1-5)* | 29 | 86 | 4 | 100 | 13 | 92 | 22 | 100 | 2 | 100 | 34 | 74 | 6 | 50 |
| Cusp 6 LM3 (ASU 1-5)* | 22 | 100 | 5 | 100 | 13 | 100 | 21 | 95 | 4 | 100 | 30 | 77 | 9 | 100 |
| Cusp 7 LM1 (ASU 2-4) | 20 | 15 | 2 | 0 | 9 | 11 | 15 | 7 | 0 | 0 | 34 | 18 | 5 | 40 |
| Cusp 7 LM2 (ASU 2-4) | 25 | 24 | 3 | 33 | 8 | 13 | 17 | 35 | 2 | 100 | 35 | 14 | 4 | 25 |
| Cusp 7 LM3 (ASU 2-4) | 22 | 64 | 4 | 50 | 12 | 25 | 17 | 59 | 4 | 50 | 27 | 33 | 9 | 33 |
| Deflecting wrinkle LM1 (ASU 2-3) | 25 | 8 | 1 | 0 | 13 | 15 | 25 | 24 | 2 | 0 | 42 | 19 | 8 | 0 |
| Distal trigonid crest LM1 | 36 | 11 | 4 | 25 | 18 | 0 | 29 | 10 | 2 | 0 | 45 | 2 | 10 | 0 |
| Distal trigonid crest LM2 | 25 | 8 | 4 | 25 | 13 | 8 | 24 | 29 | 4 | 0 | 33 | 6 | 10 | 20 |
| Distal trigonid crest LM3 | 19 | 100 | 2 | 100 | 10 | 100 | 15 | 100 | 0 | 0 | 36 | 97 | 5 | 100 |
| Middle trigonid crest LM1* | 23 | 91 | 3 | 100 | 10 | 90 | 18 | 100 | 2 | 100 | 30 | 77 | 6 | 50 |
| Middle trigonid crest LM2* | 23 | 100 | 3 | 100 | 12 | 100 | 17 | 94 | 4 | 100 | 27 | 78 | 9 | 100 |
| Middle trigonid crest LM3 | 19 | 16 | 2 | 0 | 10 | 10 | 15 | 7 | 0 | 0 | 36 | 17 | 5 | 40 |
| Metacone UM1 (ASU 3.5-5) | 23 | 26 | 3 | 33 | 10 | 10 | 18 | 33 | 2 | 100 | 30 | 17 | 6 | 17 |
| Metacone UM2 (ASU 3.5-5) | 23 | 61 | 3 | 67 | 12 | 25 | 17 | 59 | 4 | 50 | 27 | 33 | 9 | 33 |
| Metacone UM3 (ASU 3.5-5) | 21 | 95 | 3 | 100 | 10 | 100 | 19 | 100 | 0 | 0 | 35 | 80 | 4 | 100 |
| Parastyle UM1 (ASU 1-5) | 33 | 73 | 4 | 100 | 17 | 71 | 21 | 43 | 2 | 50 | 42 | 52 | 9 | 56 |
| Parastyle UM2 (ASU 1-5) | 23 | 13 | 3 | 0 | 13 | 23 | 17 | 35 | 2 | 50 | 34 | 24 | 9 | 22 |
| Parastyle UM3 (ASU 1-5) | 3 | 100 | 0 | 0 | 1 | 100 | 2 | 50 | 0 | 0 | 9 | 56 | 0 | 0 |
| Anterior fovea LM1 (ASU 2-4) | 5 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 12 | 0 | 1 | 0 |
| Cusp number LM1 (ASU 5+) | 18 | 0 | 0 | 0 | 10 | 0 | 16 | 0 | 2 | 0 | 28 | 0 | 8 | 0 |
| Cusp number LM2 (ASU 5+) | 12 | 0 | 3 | 0 | 11 | 0 | 14 | 0 | 1 | 0 | 24 | 0 | 8 | 0 |
| Cusp number LM3 (ASU 5+) | 4 | 25 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 1 | 0 |
| Cusp number LM1 (ASU 6+) | 19 | 0 | 0 | 0 | 7 | 0 | 12 | 0 | 0 | 0 | 26 | 0 | 5 | 20 |

Table D2: continued.

| | LSA Inland central | | LSA West coast | | LSA SW coast | | LSA South coast | | LSA SE coast | | IA North East | | IA South Zambia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dental Trait** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** | **N** | **Freq (%)** |
| Cusp number LM2 (ASU 6+) | 11 | 0 | 3 | 0 | 9 | 0 | 11 | 0 | 0 | 0 | 22 | 0 | 6 | 0 |
| Cusp number LM3 (ASU 6+) | 2 | 50 | 0 | 0 | 0 | 0 | 2 | 100 | 0 | 0 | 6 | 17 | 1 | 0 |
| Protostylid LM1 (ASU 2-7) | 22 | 0 | 2 | 0 | 5 | 0 | 14 | 0 | 1 | 0 | 36 | 0 | 5 | 0 |
| Protostylid LM2 (ASU 2-7) | 25 | 0 | 2 | 0 | 14 | 0 | 20 | 5 | 3 | 0 | 43 | 0 | 8 | 0 |
| Protostylid LM3 (ASU 2-7) | 21 | 0 | 2 | 0 | 12 | 0 | 17 | 0 | 3 | 0 | 31 | 0 | 7 | 0 |
| Mandibular molar pit-tubercle LM1 (P = 1-3) | 16 | 13 | 0 | 0 | 4 | 50 | 12 | 33 | 0 | 0 | 22 | 5 | 1 | 0 |
| Mandibular molar pit-tubercle LM2 (P = 1-3)* | 25 | 16 | 2 | 50 | 10 | 10 | 13 | 23 | 0 | 0 | 32 | 0 | 6 | 0 |
| Mandibular molar pit-tubercle LM3 (P = 1-3)* | 17 | 29 | 2 | 100 | 13 | 38 | 12 | 92 | 0 | 0 | 27 | 26 | 6 | 33 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73
*Dental nonmetric traits found significantly different between the samples ($p<0.05$)

Table D3: Descriptive statistics for the upper and lower dental measurements (n=44) for the geographical regions of southern Africa.

| | LSA INLAND CENTRAL | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 7 | 16 | 13 | 14 | 20 | 25 | 18 | 23 | 23 | 25 | 26 | 28 | 24 | 27 | 34 | 35 | 34 | 34 | 24 | 27 | 28 | 21 |
| **Min** | 7.89 | 6.18 | 6.34 | 5.40 | 6.86 | 7.24 | 5.93 | 7.78 | 5.55 | 7.91 | 9.06 | 9.67 | 11.47 | 10.28 | 9.02 | 9.68 | 10.36 | 9.54 | 7.04 | 9.26 | 9.15 | 8.15 |
| **Max** | 9.17 | 7.80 | 7.57 | 7.12 | 8.26 | 8.76 | 7.90 | 9.83 | 7.45 | 9.93 | 12.12 | 12.24 | 13.35 | 12.45 | 10.72 | 11.88 | 13.01 | 11.70 | 9.59 | 14.05 | 13.53 | 10.47 |
| **Mean** | 8.63 | 7.00 | 7.01 | 6.27 | 7.60 | 7.93 | 6.80 | 8.77 | 6.51 | 8.89 | 10.53 | 11.21 | 12.44 | 11.36 | 9.95 | 11.04 | 11.93 | 10.70 | 8.24 | 10.46 | 10.91 | 9.48 |
| **SD** | 0.49 | 0.51 | 0.45 | 0.49 | 0.38 | 0.40 | 0.45 | 0.52 | 0.40 | 0.52 | 0.62 | 0.56 | 0.48 | 0.50 | 0.42 | 0.54 | 0.57 | 0.50 | 0.77 | 1.06 | 0.97 | 0.59 |
| | LSA WEST COAST | | | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | | | | | 3 | 1 | 3 | 1 | 4 | 1 | 3 | 2 | 3 | 3 | 3 | 3 | 3 | 2 | 4 | 3 | 4 |
| **Min** | | | | | | 7.04 | 6.86 | 8.17 | 6.86 | 7.86 | 9.82 | 10.71 | 12.73 | 10.87 | 8.47 | 10.23 | 11.22 | 9.88 | 7.24 | 9.54 | 10.27 | 8.00 |
| **Max** | | | | | | 8.08 | 6.86 | 8.66 | 6.86 | 9.16 | 9.82 | 11.85 | 13.07 | 11.43 | 9.95 | 12.30 | 12.33 | 10.77 | 8.78 | 12.06 | 11.81 | 9.95 |
| **Mean** | | | | | | 7.61 | 6.86 | 8.44 | 6.86 | 8.57 | 9.82 | 11.25 | 12.90 | 11.21 | 9.35 | 11.07 | 11.86 | 10.41 | 8.01 | 10.33 | 10.92 | 9.13 |
| **SD** | | | | | | 0.53 | 0.00 | 0.25 | 0.00 | 0.54 | 0.00 | 0.57 | 0.24 | 0.30 | 0.78 | 1.09 | 0.57 | 0.47 | 1.09 | 1.18 | 0.80 | 0.98 |
| | LSA SW COAST | | | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 5 | 7 | 5 | 8 | 13 | 17 | 18 | 19 | 18 | 19 | 20 | 20 | 19 | 21 | 31 | 30 | 30 | 33 | 27 | 27 | 27 | 26 |
| **Min** | 7.51 | 6.11 | 6.36 | 4.86 | 6.28 | 5.94 | 5.72 | 7.11 | 5.49 | 7.68 | 8.65 | 9.81 | 10.81 | 9.60 | 8.15 | 9.85 | 10.36 | 8.65 | 6.59 | 9.16 | 8.99 | 7.68 |
| **Max** | 8.81 | 7.24 | 7.12 | 7.04 | 7.89 | 8.81 | 7.69 | 9.40 | 7.02 | 9.55 | 10.98 | 12.43 | 13.54 | 12.63 | 10.80 | 12.53 | 13.30 | 11.86 | 9.77 | 12.26 | 12.45 | 10.81 |
| **Mean** | 7.95 | 6.44 | 6.85 | 5.98 | 7.14 | 7.42 | 6.63 | 8.51 | 6.26 | 8.43 | 9.90 | 10.81 | 12.09 | 10.79 | 9.60 | 10.99 | 11.76 | 10.34 | 8.35 | 10.40 | 10.72 | 9.40 |
| **SD** | 0.51 | 0.40 | 0.30 | 0.63 | 0.52 | 0.61 | 0.59 | 0.59 | 0.41 | 0.57 | 0.60 | 0.67 | 0.69 | 0.77 | 0.67 | 0.70 | 0.76 | 0.70 | 0.69 | 0.85 | 0.91 | 0.63 |
| | LSA SOUTH COAST | | | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 8 | 12 | 10 | 15 | 18 | 20 | 18 | 20 | 20 | 20 | 16 | 20 | 19 | 20 | 24 | 28 | 27 | 28 | 25 | 25 | 25 | 25 |
| **Min** | 7.72 | 6.03 | 5.41 | 5.40 | 6.71 | 6.68 | 6.04 | 7.80 | 5.75 | 6.82 | 9.41 | 10.13 | 11.55 | 10.19 | 8.36 | 10.25 | 10.72 | 9.75 | 6.76 | 8.63 | 8.82 | 8.23 |
| **Max** | 9.18 | 7.15 | 7.56 | 6.99 | 7.62 | 8.69 | 7.72 | 9.51 | 7.18 | 9.19 | 11.28 | 11.97 | 13.05 | 12.10 | 11.21 | 12.04 | 13.40 | 12.09 | 10.22 | 11.97 | 12.61 | 10.71 |
| **Mean** | 8.16 | 6.62 | 6.48 | 6.00 | 7.22 | 7.56 | 6.76 | 8.54 | 6.46 | 8.29 | 10.11 | 10.96 | 12.19 | 10.99 | 9.70 | 11.00 | 11.98 | 10.66 | 8.34 | 10.36 | 10.63 | 9.23 |
| **SD** | 0.49 | 0.41 | 0.70 | 0.39 | 0.30 | 0.44 | 0.46 | 0.46 | 0.32 | 0.56 | 0.40 | 0.46 | 0.44 | 0.52 | 0.69 | 0.52 | 0.66 | 0.57 | 0.83 | 0.89 | 0.97 | 0.73 |

Table D3: continued.

| | LSA SE COAST | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | 1 | 2 | 2 | 2 | 2 | 5 | 5 | 3 | 5 | 3 | 4 | 4 | 4 | 6 | 7 | 7 | 7 | 1 | 2 | 2 | 2 |
| **Min** | | 7.01 | 6.75 | 6.12 | 7.81 | 7.80 | 6.63 | 7.81 | 6.30 | 8.04 | 9.95 | 10.46 | 11.34 | 10.62 | 9.54 | 10.64 | 11.28 | 10.43 | 8.40 | 10.45 | 10.96 | 9.82 |
| **Max** | | 7.01 | 7.70 | 7.10 | 8.30 | 8.52 | 7.20 | 9.47 | 7.48 | 9.50 | 10.14 | 11.07 | 12.31 | 11.11 | 10.25 | 12.57 | 13.78 | 11.45 | 8.40 | 11.73 | 11.48 | 10.47 |
| **Mean** | | 7.01 | 7.23 | 6.61 | 8.06 | 8.16 | 6.90 | 8.75 | 6.85 | 8.73 | 10.04 | 10.71 | 11.89 | 10.85 | 9.89 | 11.40 | 12.40 | 10.89 | 8.40 | 11.09 | 11.22 | 10.15 |
| **SD** | | 0.00 | 0.67 | 0.69 | 0.35 | 0.51 | 0.25 | 0.67 | 0.59 | 0.68 | 0.10 | 0.28 | 0.44 | 0.21 | 0.29 | 0.74 | 1.06 | 0.43 | 0.00 | 0.91 | 0.37 | 0.46 |
| | IA NORTH EAST | | | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 11 | 18 | 26 | 21 | 27 | 28 | 40 | 39 | 37 | 36 | 34 | 35 | 33 | 34 | 39 | 40 | 39 | 40 | 29 | 30 | 31 | 30 |
| **Min** | 7.89 | 5.83 | 6.14 | 5.82 | 6.65 | 7.60 | 6.27 | 8.36 | 5.94 | 8.49 | 9.21 | 10.15 | 11.27 | 10.24 | 8.91 | 10.13 | 10.61 | 9.02 | 8.03 | 9.65 | 10.10 | 8.93 |
| **Max** | 10.24 | 7.92 | 8.26 | 7.50 | 8.37 | 9.56 | 8.17 | 10.87 | 8.07 | 11.11 | 11.35 | 12.45 | 13.50 | 12.39 | 12.03 | 13.46 | 13.85 | 13.54 | 10.32 | 12.71 | 13.03 | 12.10 |
| **Mean** | 8.90 | 7.13 | 7.15 | 6.65 | 7.68 | 8.49 | 7.21 | 9.62 | 6.87 | 9.57 | 10.62 | 11.55 | 12.61 | 11.59 | 10.21 | 11.65 | 12.32 | 11.33 | 9.04 | 11.12 | 11.44 | 10.42 |
| **SD** | 0.24 | 0.13 | 0.12 | 0.08 | 0.09 | 0.10 | 0.07 | 0.09 | 0.07 | 0.08 | 0.08 | 0.09 | 0.09 | 0.08 | 0.11 | 0.12 | 0.12 | 0.13 | 0.12 | 0.14 | 0.14 | 0.12 |
| | IA SOUTH ZAMBIA | | | | | | | | | | | | | | | | | | | | | |
| | UI1 | | UI2 | | UC | | UPM1 | | UPM2 | | UM1 | | | | UM2 | | | | UM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 1 | 3 | 6 | 4 | 11 | 12 | 11 | 12 | 13 | 14 | 9 | 9 | 9 | 9 | 13 | 13 | 13 | 12 | 13 | 13 | 13 | 13 |
| **Min** | 8.51 | 6.90 | 6.07 | 6.01 | 7.25 | 7.82 | 6.47 | 8.45 | 6.09 | 8.20 | 9.97 | 10.66 | 11.87 | 10.74 | 9.16 | 10.19 | 10.79 | 10.03 | 7.97 | 10.45 | 10.06 | 9.57 |
| **Max** | 8.51 | 7.81 | 7.54 | 6.31 | 8.15 | 9.27 | 7.66 | 10.80 | 7.32 | 10.57 | 10.87 | 12.71 | 14.28 | 12.18 | 10.50 | 12.78 | 13.89 | 12.51 | 10.12 | 12.23 | 12.77 | 11.43 |
| **Mean** | 8.51 | 7.29 | 7.07 | 6.14 | 7.64 | 8.48 | 7.07 | 9.39 | 6.75 | 9.44 | 10.42 | 11.23 | 12.71 | 11.39 | 9.88 | 11.31 | 12.21 | 11.08 | 9.15 | 11.14 | 11.51 | 10.56 |
| **SD** | 0.00 | 0.47 | 0.56 | 0.13 | 0.34 | 0.50 | 0.39 | 0.68 | 0.37 | 0.65 | 0.34 | 0.62 | 0.70 | 0.51 | 0.48 | 0.78 | 0.99 | 0.67 | 0.52 | 0.65 | 0.86 | 0.53 |

Table D3: continued.

| | LSA INLAND CENTRAL | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 15 | 17 | 15 | 15 | 18 | 18 | 27 | 27 | 25 | 26 | 19 | 22 | 20 | 22 | 30 | 29 | 27 | 30 | 24 | 25 | 24 | 23 |
| **Min** | 4.49 | 4.66 | 5.41 | 4.86 | 6.03 | 6.30 | 6.27 | 7.09 | 6.32 | 7.01 | 10.60 | 9.99 | 11.01 | 10.85 | 9.64 | 9.49 | 10.48 | 10.22 | 8.79 | 8.69 | 9.35 | 9.76 |
| **Max** | 6.45 | 6.54 | 6.61 | 6.53 | 7.62 | 7.73 | 8.05 | 8.59 | 8.16 | 9.07 | 12.42 | 11.78 | 13.20 | 12.29 | 12.73 | 12.43 | 13.50 | 13.21 | 12.01 | 11.12 | 11.67 | 12.37 |
| **Mean** | 5.29 | 5.47 | 5.87 | 5.72 | 7.14 | 7.11 | 7.05 | 7.83 | 7.21 | 8.10 | 11.35 | 10.68 | 11.93 | 11.55 | 10.97 | 10.50 | 11.64 | 11.53 | 10.41 | 10.12 | 10.77 | 10.83 |
| **SD** | 0.50 | 0.47 | 0.33 | 0.52 | 0.40 | 0.41 | 0.44 | 0.41 | 0.53 | 0.49 | 0.46 | 0.47 | 0.50 | 0.40 | 0.69 | 0.61 | 0.56 | 0.56 | 0.76 | 0.51 | 0.60 | 0.62 |
| | LSA WEST COAST | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | | | | | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 2 | 3 | 4 | 5 | 5 | 5 | 5 | 4 | 5 | 5 |
| **Min** | | | | | | 7.47 | 7.19 | 7.80 | 5.52 | 7.18 | 10.44 | 10.39 | 11.99 | 11.03 | 9.95 | 10.35 | 10.93 | 11.05 | 9.12 | 10.24 | 9.90 | 9.96 |
| **Max** | | | | | | 7.47 | 7.19 | 7.80 | 7.29 | 8.64 | 11.57 | 11.06 | 12.67 | 12.15 | 12.63 | 11.73 | 13.04 | 13.12 | 11.09 | 10.89 | 11.11 | 11.39 |
| **Mean** | | | | | | 7.47 | 7.19 | 7.80 | 6.41 | 7.91 | 10.90 | 10.62 | 12.33 | 11.54 | 11.09 | 10.93 | 11.81 | 11.69 | 10.24 | 10.46 | 10.73 | 10.65 |
| **SD** | | | | | | 0.00 | 0.00 | 0.00 | 1.25 | 1.03 | 0.59 | 0.38 | 0.48 | 0.57 | 1.14 | 0.52 | 0.78 | 0.83 | 0.78 | 0.30 | 0.48 | 0.57 |
| | LSA SW COAST | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | | 2 | 3 | 3 | 6 | 8 | 19 | 21 | 24 | 25 | 11 | 15 | 13 | 14 | 23 | 27 | 24 | 26 | 24 | 23 | 23 | 21 |
| **Min** | | 4.99 | 4.91 | 5.52 | 6.17 | 6.10 | 5.84 | 6.45 | 5.71 | 6.54 | 10.01 | 9.29 | 10.39 | 10.03 | 9.65 | 9.33 | 10.74 | 10.47 | 8.79 | 8.85 | 8.31 | 9.54 |
| **Max** | | 5.59 | 6.06 | 6.57 | 7.25 | 7.63 | 7.86 | 8.52 | 8.23 | 8.97 | 11.91 | 11.46 | 12.46 | 12.35 | 12.37 | 11.55 | 12.68 | 12.89 | 12.72 | 11.55 | 12.81 | 12.51 |
| **Mean** | | 5.29 | 5.48 | 5.94 | 6.58 | 6.85 | 6.73 | 7.43 | 6.82 | 7.96 | 10.73 | 10.37 | 11.55 | 11.32 | 10.98 | 10.38 | 11.49 | 11.45 | 10.35 | 10.09 | 10.74 | 10.70 |
| **SD** | | 0.42 | 0.58 | 0.56 | 0.45 | 0.53 | 0.54 | 0.51 | 0.51 | 0.63 | 0.67 | 0.53 | 0.53 | 0.65 | 0.67 | 0.59 | 0.52 | 0.69 | 0.78 | 0.72 | 0.85 | 0.79 |
| | LSA SOUTH COAST | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 5 | 12 | 10 | 16 | 10 | 18 | 21 | 23 | 24 | 28 | 23 | 26 | 23 | 24 | 24 | 30 | 28 | 28 | 22 | 24 | 23 | 23 |
| **Min** | 4.55 | 4.90 | 4.73 | 4.90 | 5.92 | 6.03 | 6.01 | 6.83 | 6.39 | 7.19 | 10.33 | 9.58 | 10.90 | 10.36 | 10.19 | 9.38 | 10.40 | 10.41 | 7.92 | 7.94 | 9.08 | 8.04 |
| **Max** | 5.53 | 5.52 | 6.37 | 6.21 | 7.70 | 7.44 | 7.55 | 8.39 | 7.77 | 8.82 | 11.98 | 11.32 | 12.46 | 12.03 | 12.94 | 11.90 | 13.34 | 13.19 | 11.52 | 10.93 | 11.80 | 12.44 |
| **Mean** | 4.99 | 5.12 | 5.63 | 5.54 | 6.73 | 6.66 | 6.74 | 7.53 | 6.95 | 7.87 | 11.07 | 10.55 | 11.57 | 11.37 | 11.05 | 10.51 | 11.51 | 11.55 | 9.75 | 9.67 | 10.34 | 10.13 |
| **SD** | 0.36 | 0.17 | 0.54 | 0.36 | 0.56 | 0.43 | 0.41 | 0.48 | 0.40 | 0.42 | 0.42 | 0.41 | 0.43 | 0.45 | 0.61 | 0.60 | 0.63 | 0.65 | 0.99 | 0.78 | 0.76 | 1.02 |

Table D3: continued.

| | LSA SE COAST | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |
| **Min** | 0.00 | 0.33 | 0.00 | 0.17 | 0.24 | 0.36 | 0.12 | 0.44 | 0.00 | 0.00 | 0.61 | 0.58 | 0.62 | 0.38 | 0.01 | 0.71 | 0.64 | 0.64 | 0.93 | 0.60 | 0.68 | 0.84 |
| **Max** | 5.43 | 5.77 | 6.06 | 5.93 | 7.82 | 7.21 | 6.89 | 8.36 | 7.19 | 8.64 | 11.90 | 10.69 | 12.64 | 12.04 | 11.48 | 11.58 | 12.52 | 12.62 | 11.61 | 11.34 | 12.14 | 12.41 |
| **Mean** | 2.88 | 3.17 | 3.20 | 3.25 | 4.19 | 3.89 | 3.73 | 4.46 | 3.76 | 4.49 | 6.37 | 5.63 | 6.69 | 6.43 | 6.06 | 6.12 | 6.55 | 6.60 | 6.21 | 6.32 | 6.65 | 6.74 |
| **SD** | 2.82 | 2.49 | 3.16 | 2.69 | 3.65 | 3.24 | 3.26 | 3.80 | 3.77 | 4.56 | 5.46 | 4.98 | 5.80 | 5.67 | 5.91 | 5.13 | 5.95 | 6.00 | 4.83 | 4.89 | 5.19 | 5.19 |
| | IA NORTH EAST | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 25 | 25 | 27 | 26 | 31 | 34 | 34 | 38 | 34 | 36 | 29 | 33 | 32 | 33 | 39 | 38 | 38 | 34 | 27 | 27 | 27 | 26 |
| **Min** | 4.73 | 5.05 | 5.25 | 5.61 | 6.34 | 6.66 | 6.13 | 7.22 | 6.33 | 7.45 | 9.63 | 9.47 | 10.85 | 10.49 | 9.37 | 9.38 | 10.39 | 10.39 | 10.04 | 8.80 | 9.76 | 10.33 |
| **Max** | 6.07 | 7.35 | 7.37 | 6.80 | 8.03 | 8.38 | 8.06 | 9.25 | 8.26 | 9.60 | 12.77 | 12.19 | 13.24 | 12.91 | 12.82 | 11.94 | 13.92 | 13.06 | 13.06 | 11.23 | 13.21 | 12.34 |
| **Mean** | 5.47 | 5.86 | 6.16 | 6.25 | 7.06 | 7.55 | 7.34 | 8.29 | 7.34 | 8.62 | 11.68 | 10.86 | 12.15 | 11.93 | 11.17 | 10.69 | 12.02 | 11.77 | 11.13 | 10.34 | 11.33 | 11.28 |
| **SD** | 0.07 | 0.10 | 0.10 | 0.07 | 0.08 | 0.08 | 0.07 | 0.09 | 0.10 | 0.10 | 0.12 | 0.11 | 0.11 | 0.11 | 0.12 | 0.11 | 0.13 | 0.13 | 0.13 | 0.11 | 0.14 | 0.11 |
| | IA SOUTH ZAMBIA | | | | | | | | | | | | | | | | | | | | | |
| | LI1 | | LI2 | | LC | | LPM1 | | LPM2 | | LM1 | | | | LM2 | | | | LM3 | | | |
| | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB | M-D | B-L | MB-DL | ML-DB |
| **N** | 7 | 8 | 10 | 11 | 9 | 13 | 9 | 11 | 7 | 11 | 9 | 9 | 9 | 8 | 13 | 12 | 12 | 11 | 11 | 11 | 11 | 11 |
| **Min** | 5.02 | 5.52 | 5.49 | 5.69 | 6.46 | 7.10 | 6.55 | 7.36 | 6.28 | 7.49 | 10.93 | 10.33 | 11.43 | 10.86 | 9.39 | 9.66 | 11.09 | 10.92 | 9.66 | 9.16 | 9.78 | 9.94 |
| **Max** | 5.78 | 6.32 | 6.61 | 6.55 | 7.73 | 9.04 | 7.58 | 9.52 | 7.79 | 9.61 | 12.39 | 11.52 | 13.18 | 12.68 | 11.95 | 11.51 | 13.13 | 12.90 | 12.24 | 11.27 | 12.04 | 12.62 |
| **Mean** | 5.34 | 5.88 | 6.08 | 6.14 | 7.08 | 7.78 | 7.15 | 8.28 | 7.24 | 8.52 | 11.63 | 10.86 | 12.18 | 11.86 | 10.86 | 10.42 | 11.80 | 11.61 | 11.37 | 10.46 | 11.39 | 11.58 |
| **SD** | 0.26 | 0.28 | 0.34 | 0.31 | 0.45 | 0.65 | 0.33 | 0.62 | 0.53 | 0.59 | 0.49 | 0.39 | 0.51 | 0.62 | 0.66 | 0.57 | 0.62 | 0.55 | 0.73 | 0.64 | 0.65 | 0.73 |

Dental abbreviations follow the terminology outlined in the Methods section, p. 71-73

# APPENDIX E: ARTICLE FOR PUBLICATION

(To be submitted to the South African Archaeological Bulletin)

**POPULATION HISTORIES IN SOUTHERN AFRICA: A BIODISTANCE ANALYSIS USING CRANIAL NONMETRIC TRAITS OF KHOESAN AND BANTU-SPEAKERS**

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**ABSTRACT**

The southern African population of today consists of small, diverse groups of Khoesan peoples living in and among the larger, widespread Bantu-speaking population, amongst others. Current genetic research, as well as previous archaeological and bioanthropological studies, have highlighted admixture within the Khoesan groups and the possible genetic exchanges with Bantu-speakers during the last 2000 years. Their relationships however, have not been fully investigated. Using cranial nonmetric traits and the application of the Mean Measure of Divergence statistic, Later Stone Age (n=303), Iron Age (n=105), modern Khoesan (n=24) and modern Bantu-speaker (n=176) samples were compared through time and geography. The population histories of the Khoesan and Bantu-speaking peoples showed a long history of genetic admixture, as reflected by their changes in biodistance. Genetic exchanges between the migrating IA farmers and LSA foragers/herders in central Africa were proposed prior to 2000 BP. This possibly resulted in an already admixed IA population with Khoesan characteristics upon arrival in southern Africa post-2000 BP. Increased gene flow was therefore suggested between the LSA and IA groups over time from approx. 4000 to 0 BP. The rather sedentary IA groups of southern Africa subsequently interacted with those Khoesan groups (from a more widespread, mobile population) geographically closest to them. Lastly, early gene flow with Bantu-speakers was also suggested for the modern Khoesan individuals, after which genetic drift or isolation of these Khoesan groups may have occurred with time. Further morphological research on other modern Khoesan groups may further our understanding of their unique biological diversity, when compared with the Bantu-speakers.

Keywords: Bioarchaeology, Later Stone Age, Iron Age, prehistoric populations

## INTRODUCTION

The population history of southern Africa is still not fully understood. Current genetic research on the modern population reveals a complex history, especially with regard to the interactions between the indigenous Khoesan and migrating Bantu-speaking peoples. Present-day Bantu-speakers show genetic links with both living and prehistoric Khoesan individuals (Coelho *et al*. 2009, Barbieri *et al*. 2013a, Barbieri *et al*. 2013b, Barbieri *et al*. 2014), while all present-day Khoesan groups are estimated to have between 9 to 30% genetic admixture from other populations, like the Bantu-speakers (Schlebusch *et al*. 2013, Schlebusch *et al*. 2016, Schlebusch *et al*. 2017). Previous bioanthropological research also suggested genetic exchanges between the Khoesan and Bantu-speaking peoples (Hausman 1980, Morris 1992a, Black 2014, Irish *et al*. 2014), but more large-scale research is needed to evaluate the patterns of those population changes. Using cranial nonmetric traits, these poorly understood relationships are explored. Using the geographical distribution of their population groups over time, a framework derived from our current understanding of their prehistoric population movements in southern Africa, are also used to contextualise the study design and analysis.

Later Stone Age (LSA) foragers were identified mainly along the coastal and adjacent coastal forelands of the southern Cape, showing continuous occupation of these areas from the Late Pleistocene to the Late Holocene (Stynder 2006, Stynder *et al*. 2007b, Black 2014, Irish *et al*. 2014). Herders were also identified in those areas post-2000 BP, but there is still considerable debate with regards to the origin of pastoralism in southern Africa (Sadr 2015, Cameron 2019). According to cranial, postcranial and dental analyses (Stynder *et al*. 2007b, Ginter, 2008, Stynder 2009, Pfeiffer & Harrington 2011, Black 2014, Irish *et al*. 2014), however, the co-existing foragers and herders are a single homogenous population that show morphological continuity, extending back for over 12 000 years with the earlier foragers. In comparison, the Iron Age (IA) Bantu-speaking farmers migrated into southern Africa from East Africa during the 1$^{st}$ and 2$^{nd}$ millennium AD. They began occupying the more arable eastern half of South Africa in the Early Iron Age (EIA), eventually reaching their southern limit of expansion in the Eastern Cape Province during the Late Iron Age (LIA) (Mitchell & Whitelaw 2005, Barham & Mitchell 2008, Russell & Steele 2009, Hall 2010, Ribot *et al*. 2010, Bostoen 2018). Recent bioanthropological research on the farmers found morphological continuity throughout the IA to their present-day populations (Warren *et al*. 2014, Warren *et al*. 2015).

With new genetic insights, this paper expands on previous work by exploring Khoesan and Bantu-speaking groups over time and geographical space. Biodistance methods are used based on the premise that the similarity of the phenotypic characteristics of the skull reflect genetic similarities (Relethford & Harpending 1994, Relethford 2002, 2004). Firstly, crania from the LSA and IA were compared with those of modern/historic Khoesan and Bantu-speaking groups, to determine how biologically similar they are to one another. Secondly, the LSA and IA groups were investigated in more detail over time and in terms of geography. This further enhances our understanding of the population histories of southern Africa, especially with regard to the interactions between the Khoesan

and Bantu-speaking peoples. The collective term 'Khoesan' represents the prehistoric and historic foragers and herders, as well as their remnant communities today.

## MATERIALS AND METHODS

### SAMPLES

This study included 608 crania from archaeological and modern contexts. The LSA (n=303) and IA (n=105) specimens had known localities and were dated by radiocarbon or through archaeological association. The archaeological remains were separated into seven geographical regions in southern Africa: LSA Inland central (n=75), LSA West coast (n=17), LSA SW coast (n=84), LSA South coast (n=109), LSA SE coast (n=18), IA North East (n=80) and IA South Zambia (n=23) (Fig. 1). The geographical regions varied in terms of the temporal range that was represented. The LSA South coast sample had the most time depth, consisting of sites dated from 12 000 to 150 BP. The LSA West coast and LSA SW coast regions consisted mostly of sites dated to later than 3000 BP, while the LSA SE coast sites were primarily dated to later than 2000 BP. The LSA Inland central sites were predominantly dated to ±500 BP. Lastly, the IA North East group consisted mainly of LIA sites whereas the IA South Zambia group included mostly the IA sites of Ingombe Ilede and Isamu Patu Mounds dated to the LIA (Gibbon *et al*. 2014). In addition to this, the archaeological remains were also assigned to six temporal groups: 8000 to 4000 BP (LSA, n=32), 4000 to 3000 BP (LSA, n=34), 3000 to 2000 BP (LSA, n=67), 2000 to 1000 BP (LSA, n=42), 1000 to 0 BP (LSA, n=103) and 2000 to 0 BP (IA, n=59). The modern samples consisted of 24 19$^{th}$ to 20$^{th}$ century Khoesan individuals (Morris 1986; 1987), as well as 176 20$^{th}$ century Bantu-speakers from the Raymond A Dart Collection of Human Skeletons (Ref: W-CJ-140604-1). Individuals identified as Zulu and Xhosa were included because they have a high degree of Khoesan admixture (Jenkins *et al*. 1970, Hitzeroth 1986, Mitchell 2010, Barbieri *et al*. 2014) and Ndebele and Tsonga were selected because they have a low degree of Khoesan admixture (Hitzeroth 1986, Esterhuysen *et al*. 2009).

### METHODS

Cranial nonmetric traits are viable proxies for genetic data (Hefner *et al*. 2016, Pink *et al*. 2016) and may even be superior to metric studies when investigating population affinities (Berry & Berry 1967, Rightmire 1972, Buikstra 1974). Forty-eight discrete cranial and mandibular traits (see Supplimentary material, Table S1) were observed on all adult crania, following stipulations by De Villiers (1968) and Hauser and De Stefano (1989). The frequencies of the nonmetric traits are population specific and the traits employed here have high heritability in the South African Bantu-speaking groups (De Villiers, 1968). Each trait was scored according to its level of expression as either a categorical value or as present/absent. Additional categories were also used to retain as much information as possible about the expression of certain complex traits, their variations scored as separate traits. To maximise the genetic information collected, some traits were only scored if they were bilaterally expressed, whereas other traits were scored independently for both sides of the skull. Both the left and right scores for

each trait were analysed separately. The categorical traits were given breakpoints by assessing the range of expression for each trait, after which all the traits were dichotomised as present/absent for input into the biodistance statistic. Table 1 lists only the final traits selected after data editing for the biodistance analysis (discussed below), with their scoring procedures. Initial calibration of the scoring protocol resulted in 90% accuracy and the repeatability had excellent agreement (Cohen's k=0.85) for intraobserver scoring and good agreement (Cohen's k=0.63) for interobserver scoring.

Descriptive statistics were calculated for the samples and the Mean Measure of Divergence (MMD) statistic was used to calculate the biodistance between the groups investigated. For the MMD trait selection, the following steps were taken, as recommended by Sjøvold (1977), Harris and Sjøvold (2004), Irish (2010) and Soltysiak (2011). As many traits as possible were included, especially those of significance between the groups according to chi-squared test results. Highly correlated traits were addressed to prevent redundancies. Tetrachoric correlations were calculated using TetMat v.1.0.3 (Uebersax 2006) with $r>0.5$, $r<-0.5$, in conjunction with $p<0.05$ (Pawn 2012). Both traits found to be correlated were not necessarily removed, but rather assessed independently to determine which trait to select. Lastly, to correct for small sample size and to prevent statistical bias, variables totalling less than 60% of the maximum number of observations for any trait in the total sample were eliminated, and traits with fewer than 10 observations removed (Pawn 2012). This left a total of 49 traits (Table 1). To calculate the MMD statistic, the AnthropMMD package (Soltysiak 2011, Santos 2016) was used in R (R Core Team 2018), with the Freeman and Tukey angular transformation (Green & Suchey 1976, Green *et al*. 1979, Irish 2010). Negative MMD values were set to zero (Konigsberg *et al*. 1994, Relethford *et al*. 1997, Harris & Sjøvold 2004). The biodistances were inserted into a matrix and significance ($p<0.025$) was set at MMD greater than two times the standard deviation [the square root of the variance of the MMD] (Sjøvold 1977).

## RESULTS

### PREHISTORIC VS MODERN COMPARISONS

When comparing the LSA, IA, modern Khoesan and modern Bantu-speaking groups, thirty-six cranial nonmetric traits were selected for the biodistance analysis, of which 26 were significantly different at the $p<0.05$ level (see Supplimentary material, Table S2). All the groups were significantly different when comparing their biodistances (Table 2). When comparing the LSA sample to the modern groups, greater similarity was observed with the modern Khoesan sample. Likewise, when comparing the IA sample to the modern groups, the modern Bantu-speaking sample was more similar than the modern Khoesan. Lastly, the modern Khoesan group was as similar to the LSA sample (MMD=0.155) as the IA sample (MMD=0.165), showing dissimilarity with the modern Bantu-speaking group (Table 2).

### PREHISTORIC RELATIONSHIPS OVER TIME

When comparing the temporally different LSA groups with the IA sample, eighteen cranial nonmetric traits were selected, of which eight were significantly different at the $p<0.05$ level of significance (see

Supplimentary material, Table S2). All the LSA groups were significantly different from the IA group and their biodistances decreased over time from 4000 BP (Table 3). The IA sample was therefore least similar to the LSA (4000 to 3000 BP) group and most similar to the LSA (1000 to 0 BP) group. The LSA (8000 to 4000 BP) group was also as similar to the IA sample as the LSA (2000 to 1000 BP) group (Table 3).

PREHISTORIC GEOGRAPHICAL RELATIONSHIPS

When comparing the geographical groups, eighteen cranial nonmetric traits were selected, of which 10 were significantly different at $p<0.05$ (see Supplimentary material, Table S2). Significant differences were observed between all the groups, except when comparing the IA samples with one another (Table 4). The North East and South Zambia IA samples were biologically identical and most similar to the LSA Inland central group, whilst being least similar to the LSA South coast group. In general, the geographical distance between the LSA and IA groups appeared to be associated with the degree of biological relationship over time (Fig. 1). The IA North East sample was more similar to the LSA groups from the Inland central and SE coast areas, showing less similarity to those slightly more distant in the West and SW coast areas. Similarly, the IA South Zambia sample was more similar to the LSA Inland central group, followed by the LSA individuals on the West and SW coasts, showing even less similarity with the LSA SE coast group (Table 4, Fig. 1).

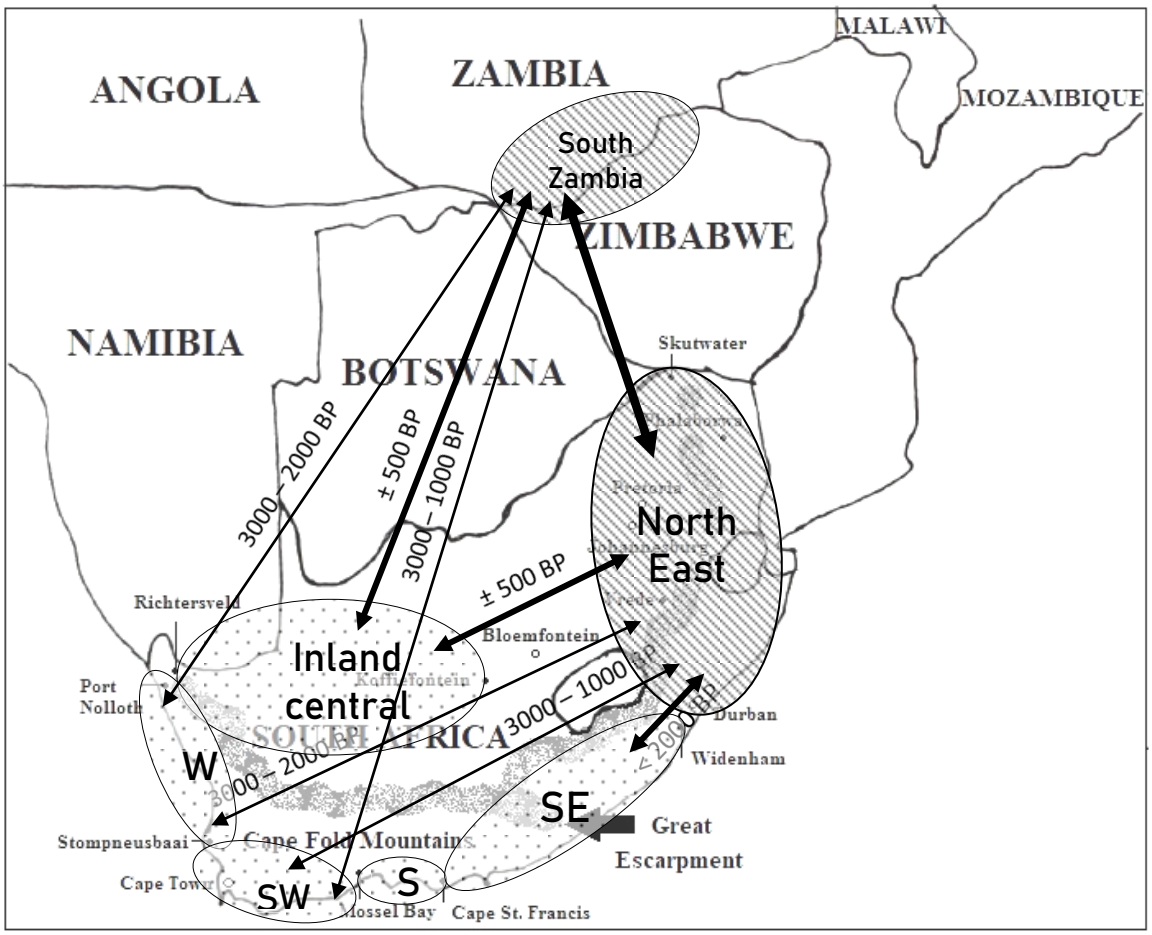


**FIG. 1.** *Geographical divisions of the archaeological samples illustrating the relationships between the Later Stone Age (dots) and Iron Age (stripes) groups over time. Arrow thickness correlates with degree of genetic similarity.*

## DISCUSSION

When comparing the prehistoric and modern samples of Khoesan and Bantu-speaking peoples, the results from this study supported previous morphological and genetic research. Like this study, cranial and dental similarity was identified between similar IA and modern Bantu-speaking groups (Rightmire 1970, L'Abbé *et al*. 2006, Warren 2013, Warren *et al*. 2014), and dental similarity was identified between a similar LSA sample and another modern Khoesan group (Black, 2014). This was indicative of biological continuity over time for these particular individuals, which was supported by current genetic research that suggested present-day Khoesan and Bantu-speaking groups were descendants of the LSA and IA peoples respectively (Schlebusch *et al.* 2017, Bodiba *et al.* 2019, Steyn *et al.* 2019). In addition to this, the modern Khoesan sample also appeared to have some Bantu admixture present, possibly reflecting their past relationships with the IA peoples, rather than new interactions with the modern Bantu-speakers. Morris (1987) previously described these particular Khoesan individuals as poor representatives of prehistoric Khoesan groups because possible genetic interactions may have occurred with other populations. The results from this study support this.

Genetic, archaeological and bioanthropological research suggests the interactions between the indigenous Khoesan and the migrating Bantu-speakers of southern Africa began approx. 2000 years ago. The genetic exchanges between their groups was previously reconstructed for specific living Khoesan groups and interactions with Bantu-speakers was suggested from 1500 years ago or thereafter (Pickrell *et al.* 2012, Uren *et al.* 2016, Montinaro *et al.* 2017, Schlebusch *et al.* 2017). Extant Khoesan populations may have also been absorbed into the Bantu-speaking population however (Barbieri *et al.* 2013a, Barbieri *et al.* 2013b, Barbieri *et al.* 2014), possibly suggesting genetic exchanges prior to this. Nonetheless, the archaeological record suggests initial contact between the LSA peoples and the EIA communities of southern Africa during the latter part of the 1st millennium AD (Hall & Smith 2000, Robertson & Bradley 2000, Parkington & Hall 2010, Ribot *et al.* 2010) and morphological studies have further indicated that the Khoesan peoples were less similar to Bantu-speakers pre-2000 BP compared with post-2000 BP (Irish, 1997, 2013; Ginter, 2008; Black, 2014). This supports the genetic research by further suggesting increased gene flow between the Khoesan and Bantu-speakers during the last 2000 years.

The results from this study were in line with previous morphological research that showed the LSA individuals gradually became more similar to the IA peoples over time, but more specifically from 4000 to 0 BP. Cranial variation within the LSA population through time is beyond the scope of this paper, but the morphological pattern of variation identified is briefly summarised here to better understand the relationships between the LSA and IA groups over time. The pattern reflects the genetic responses to environmental pressures and supports previous cranial, postcranial and dental research (Pfeiffer & Sealy 2006, Neuweger 2007, Stynder *et al*. 2007, Ginter 2008, Black 2014). There was a distinct cranial change from 4000 BP that appeared to recover from 2000 BP to previously observed morphology (pre-4000 BP) (Lander 2020). The LSA individuals from 4000 to 2000 BP were thus biologically indistinguishable. This may explain the similar biodistances observed between the IA group and the LSA (8000 to 4000 BP) and the LSA (2000 to 1000 BP) samples respectively, but not why the LSA (3000 to 2000 BP) group was more similar to the IA sample than the LSA (4000 to 3000 BP) group.

Gene flow was thus proposed between the Khoesan and Bantu-speaking groups prior to 2000 BP. This may be due to Bantu-speakers coming into contact with other indigenous groups of LSA individuals (possibly living in Angola, Zambia or Malawi), especially during their southward migration towards South Africa. Gene flow may have occurred between their groups, as suggested by genetic research (Wood *et al.* 2005, Schlebusch *et al.* 2017, Bajić *et al.* 2018), which may have resulted in prehistoric Khoesan lineages introduced into the IA population. A morphological study on Middle Holocene Malawians supported this, but larger sample sizes are needed to confirm the suggestions made (Morris & Ribot 2006). Nonetheless, the results suggested these particular LSA individuals had cranial similarity with both Khoesan and Bantu-speaking peoples. If the migrating Bantu-speakers assimilated with these LSA individuals (or others like them), the resulting IA

population may have already been admixed with Khoesan characteristics upon arrival in southern Africa. This may explain why the LSA population in the southern Cape regions from 4000 to 2000 BP remained morphologically indistinguishable, because there is little evidence of their population movement from the coastal edges of the southern Cape prior to 2000 BP (Parkington 1976, 2001, Parkington *et al*. 1988, Morris 1992, Stynder 2006). This also supports Warren (2013), whom suggested the Khoesan admixture identified in modern Bantu-speakers may have already been present in the IA peoples of southern Africa.

Finally, when comparing the regional variation between the prehistoric Khoesan and Bantu-speaking groups, time and their geographical distance from one another appeared to establish their biological relationships. Similar to previous dental research (Warren *et al*. 2015), the North East and South Zambia IA samples were biologically identical to one another and both were most similar to the LSA Inland central sample and least similar to the LSA South coast sample. Considering that the Inland central sample consisted of more recent LSA individuals (±500 BP), their increased similarity to the IA peoples was expected due to the relationships described previously. The LSA groups became more similar to the IA sample over time and the LSA individuals dated from 1000 to 0 BP in particular, were most similar to the IA peoples. This was in line with previous cranial (Hausman 1980, Morris 1992) and dental (Black 2014, Irish *et al*. 2014) research that suggested recent inland LSA individuals had significant gene flow from Bantu-speakers. The LSA South coast group on the other hand, had the largest time span compared with the other geographical regions occupied by the LSA peoples. It encompassed LSA individuals dated from 12 000 to 150 BP, whereas the other LSA groups (West, SW and SE coast – excluding the Inland central group) had very few individuals older than 3000 BP. The high biological variability present within the LSA South coast sample may have resulted in their dissimilarity to the IA peoples, but further investigation is needed.

Besides time, the geographical pattern identified between the LSA and IA groups was consistent with the isolation-by-distance model (Wright 1943, Relethford *et al*. 1981, Konigsberg 1990). This model predicts that genetic similarity between populations decreases exponentially as their geographical distance increases (Relethford 2002). The IA North East group in particular, was therefore most similar to those LSA individuals closest (Inland central and SE coast), while those further away (West and SW coast) were least similar (Fig. 1). The conclusion made by Stynder (2006) was therefore supported because the SW and South coast areas of South Africa were considered relatively free from outside gene flow. This was because Bantu-speaking farmers were thought to have avoided these less suitable areas during the Holocene period.

The isolation-by-distance model did not however apply when comparing the LSA South coast group with the IA North East sample (possibly due to previously mentioned factors), and comparing some of the LSA groups with the IA South Zambia sample. The latter however, needed a larger South Zambian sample to explore this further. Nonetheless, the results suggested different relationships between the LSA groups and the IA South Zambia sample, compared with the IA North East sample

and the LSA groups (Table 4, Fig. 1). The Kalahari Desert (spread mostly over Namibia and Botswana) separated the IA South Zambians from the LSA groups in South Africa and was uninhabitable for the IA farmers. Archaeological evidence in KwaZulu-Natal during the EIA (East of South Africa) also suggested that the Bantu-speakers were rather sedentary, interacting with a more widely dispersed and mobile Khoesan population (Ribot *et al*. 2010). If this was the case, this study's results suggest the LSA groups may have already expanded into the Kalahari region during the LIA or prior to this, genetic exchanges possibly occurring with the South Zambian IA farmers as well as those LSA groups in the south-western areas of southern Africa.

The population histories of the Khoesan and Bantu-speaking peoples of southern Africa showed a long history of genetic admixture, as reflected by the changes in biodistance between their population groups. Future morphological research comparing other modern Khoesan groups to the IA peoples may further our understanding of their unique biological diversity. Clarification is also needed for the 'Khoesan' specimens currently housed in osteological collections.

## CONCLUSION

Early gene flow was suggested between the Khoesan and Bantu-speaking peoples. Prior to 2000 BP, the IA farmers possibly had genetic exchanges with LSA foragers/herders in central Africa, which may have continued thereafter with other population groups, as they migrated southwards and eventually settled in southern Africa post-2000 BP. Once settled, further gene flow was suggested between the rather sedentary Bantu-speaking peoples and those Khoesan groups geographically closest during the IA period. The LSA population at this time may have been more widespread and mobile throughout the south-western areas of southern Africa, over and above their continued occupation in the southern Cape regions of South Africa. The Bantu-speaking peoples may have therefore already been admixed with Khoesan characteristics upon arrival in southern Africa. Genetic drift or isolation of the Khoesan groups may have also resulted over time, as their population size decreased or they felt threatened by the ever increasing Bantu-speaking population.

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## TABLES

**TABLE 1.** *Discrete cranial traits (n=49) following De Villiers (1968) and Hauser & De Stefano (1989) with their breakpoints.*

| Trait | Absent | Present |
|---|---|---|
| Incomplete (nasal part) metopic suture | Absence of metopic suture<br>Complete metopic suture | Present |
| Metopic ridge | Absent | A low vertical elevation located along a fused metopic suture |
| Oval shaped orbits | Round shaped orbits<br>Square shaped orbits | Present |
| Round shaped orbits | Oval shaped orbits<br>Square shaped orbits | Present |
| Supraorbital notch (Left & Right) | Absent | Present |
| Supraorbital foramen (Left & Right) | Absent | Present |
| Ethmoidal foramina (Left & Right) | 1 Foramen | 2 or 3 Foramina |
| Infraorbital foramen (Left & Right) | 1 Foramen | 2, 3 or 4 Foramina |
| Infraorbital form | No excavation, the maxilla is slightly convex but the frontal curve is present<br>Slight degree of excavation and is curved in the horizontal, sagittal and frontal planes | Moderate degree of excavation and the horizontal, sagittal and frontal curves are more pronounced<br>Marked degree of excavation with 3 pronounced curves |
| Infraorbital suture | Absent | Blending with the zygomaxillary suture for some distance<br>Touching the zygomaxillary suture at the infraorbital margin<br>Running medial to the zygomaxillary suture |
| Superficial nasion | Moderately depressed nasion and a moderately curved glabella<br>Depressed nasion and marked curvature of the glabella | Superficial nasion and a flat/slightly curved glabella |
| Moderately depressed nasion | Superficial nasion and a flat/slightly curved glabella<br>Depressed nasion and marked curvature of the glabella | Moderately depressed nasion and a moderately curved glabella |
| Marked depression of nasion | Superficial nasion and a flat/slightly curved glabella<br>Moderately depressed nasion and a moderately curved glabella | Depressed nasion and marked curvature of the glabella |
| Angle of nasal bones | Acute: an angle of 90 degrees or less | Obtuse minus: an angle substantially greater than 90 degrees but the resulting ridge is still pronounced<br>Obtuse: angle between the nasal bones is wide<br>Obtuse plus: Nasal bones lie in the same transverse plane, the angle between them approximating 180 degrees |

**TABLE 1.** *continued.*

| Trait | Absent | Present |
|---|---|---|
| Nasal bone shape | Short, wide nasal bones | Long, narrow nasal bones with the midsection extremely narrow due to distinct lateral concavity |
| | Short, extremely wide nasal bones | Long, narrow nasal bones with the lateral border distinctly concaved |
| | Long nasal bones, narrow superiorly becoming gradually wider inferiorly | Long, wide nasal bones with the lateral border only slightly concaved |
| | Long nasal bones, narrow superiorly becoming extremely wide inferiorly | |
| | Long nasal bones, superiorly and inferiorly extremely wide with a moderate width midsection due to lateral border concavity | |
| Zygomaxillary tubercle (Left & Right) | Absence of zygomaxillary tubercle | Medium expression of zygomaxillary tubercle |
| | Weak expression of zygomaxillary tubercle | Strong expression of zygomaxillary tubercle |
| Subnasal region | Smooth subnasal region associated with orthognathic jaws | Strong delineated subnasal corrugations associated with prognathic jaws |
| | Slight vertical subnasal corrugations associated with mesognathic jaws | |
| Anterior palate form | Flat anterior region of the palate | Curved anterior region of the palate |
| Foramen of Huschke (Left & Right) | Absence of tympanic dehiscence (complete closure of tympanic floor) | Medium expression of tympanic dehiscence (foramen present) |
| | Trace expression of tympanic dehiscence (thin translucent area on tympanic floor) | |
| Encroachment of occipital condyles | Condyles do not encroach (obscure/extend over) the outline of the foramen | Condyles encroach (obscure/extend over) the outline of the foramen |
| Left condylar canal | Absent | Condylar canal is present and undivided |
| | | Condylar canal is divided by a thin bony bridge |
| | | Multiple condylar canals occur |
| Inca bone | Absent | Present |
| Interparietal groove | Interparietal region is evenly rounded/flat, groove is absent | Postcoronal grooving associated with narrow interparietal grooving |
| | | Wide interparietal groove encroaching on the parietal bone on either side of sagittal suture |
| Parietal foramina | Absence of parietal foramina | A median parietal foramen |
| | Numerous minute foramina in the posterior part of the parietal bones | A single foramen on one side |
| | Three parietal foramina, two on one side and one on the other | Two parietal foramina, one on each side |

**TABLE 1.** *continued.*

| Trait | Absent | Present |
|---|---|---|
| Zygomatic arch | Phaenozygous arch associated with a relatively narrow cranial vault | Cryptozygous arch associated with a somewhat broader cranial vault |
| Left inferior frontal eminence | Absent | An oval projection of the frontal bone, immediately posterior to the anterior extremity of the superior temporal line |
| Left mons temporosphenoidalis | Absent | A marked temporosphenoidal swelling resulting from the temporal fossa being diminished posteroinferiorly |
| Parietotemporal suture (Left & Right) | Superior limb is horizontal and does not rise above the level of pterion, posterior limb is low and oblique<br>Superior limb is horizontal and does not rise above the level of pterion, posterior limb is low and curved<br>Superior limb is convex, rising above the level of pterion, while the posterior limb descends as an oblique line | Superior limb of the parietotemporal suture is convex, rising above pterion and the posterior limb continues the even curvature |
| Tympanic plate of temporal bone (Left & Right) | Delicate or foetal type of tympanic plate | Moderate development of the tympanic plate<br>Massive tympanic plate |
| Parietal notch bone (Left & Right) | Absent | Present |
| Left occipitomastoid wormian bone | Absent | Present |
| Genial tubercles | One tubercle<br>Superior pit and two inferior tubercles<br>Absent: mandible showing neither tubercles nor pit<br>Common median spine<br>Superior and an inferior pit<br>Single pit<br>Superior pit and an inferior tubercle | Two superior tubercles only<br>Two superior and one inferior tubercle<br>Two superior and two inferior genial tubercles |
| Mylohyoid bridge (Left & Right) | Absent | Present |
| Ophryonic groove | Absent | A groove found on the forehead just above the orbit and glabella, generally associated with marked development of the superciliary ridges |
| Left hypoglossal canal bridging | Completely undivided hypoglossal canal<br>One small spine protrudes from the margin of the aperture<br>One spine (from above) and one spine from below protrude into the internal aperture of the hypoglossal canal | A thick osseous septum divides symmetrically the internal aperture of the hypoglossal canal<br>A thick osseous septum divides asymmetrically the internal aperture of the hypoglossal canal<br>The hypoglossal canal is divided by a thick osseous septum for some distance |

**TABLE 1.** *continued.*

| Trait | Absent | Present |
|---|---|---|
| Profile curves of nasal bones | Deeply curved profile recurving slightly before rhinion<br>Shallow curves produced by short nasal bones recurving slightly before rhinion<br>A short, relatively deep profile curve<br>Shallow curves produced by long nasal bones<br>Shallow curves produced by short nasal bones | Moderately curved profiles recurving slightly before rhinion<br>Moderately curved profiles ending abruptly at rhinion |
| Supra-asterionic region | An evenly rounded supra-asterionic region | Slight flattening of the supra-asterionic region associated with moderate bossing of the parietal bones<br>Moderate flattening of the supra-asterionic region associated with marked bossing of the parietal bones |
| Left os japonicum | Absent | Present |
| Right mental foramen | One mental foramen | Multiple mental foramina |

**TABLE 2**. *Biodistances between the prehistoric and modern groups.*

| Population groups | MMD value* |
|---|---|
| Modern Bantu/Modern Khoesan | 0.372 |
| Modern Bantu/LSA | 0.242 |
| Modern Bantu/IA | 0.136 |
| Modern Khoesan/LSA | 0.155 |
| Modern Khoesan/IA | 0.165 |

**All MMD values are significant at p<0.025*

**TABLE 3.** *Biodistances of the prehistoric relationships over time.*

| Population groups | MMD value* |
|---|---|
| LSA(8ka–4ka)/IA(2ka–0ka) | 0.154 |
| LSA(4ka–3ka)/IA(2ka–0ka) | 0.423 |
| LSA(3ka–2ka)/IA(2ka–0ka) | 0.306 |
| LSA(2ka–1ka)/IA(2ka–0ka) | 0.189 |
| LSA(1ka–0ka)/IA(2ka–0ka) | 0.098 |

**All MMD values are significant at p<0.025*

**TABLE 4.** *Biodistances of the prehistoric geographical relationships.*

| Population groups | MMD value* |
|---|---|
| IA(North East)/LSA Inland central | 0.137 |
| IA(North East)/LSA West coast | 0.236 |
| IA(North East)/LSA SW coast | 0.231 |
| IA(North East)/LSA South coast | 0.314 |
| IA(North East)/LSA SE coast | 0.173 |
| IA(North East)/IA(South Zambia) | **0.000** |
| IA(South Zambia)/LSA Inland central | 0.164 |
| IA(South Zambia)/LSA West coast | 0.198 |
| IA(South Zambia)/LSA SW coast | 0.216 |
| IA(South Zambia)/LSA South coast | 0.347 |
| IA(South Zambia)/LSA SE coast | 0.284 |

**All MMD values are significant at p<0.025 except the Iron Age comparisons*

**FIGURE CAPTIONS**

**FIG. 1.** *Geographical divisions of the archaeological samples, illustrating the relationships between the Later Stone Age (dots) and Iron Age (stripes) groups over time. Arrow thickness correlates with degree of genetic similarity.*

**SUPPLIMENTARY MATERIAL**

**TABLE S1.** *Discrete cranial traits (n=48) scored following De Villiers (1968) and Hauser & De Stefano (1989)*

| Location | Trait |
|---|---|
| Facial | Metopic suture |
| | Metopic ridge |
| | Orbital shape |
| | Supraorbital notch (Left & Right) |
| | Supraorbital foramen (Left & Right) |
| | Ethmoidal foramina (Left & Right) |
| | Infraorbital foramen (Left & Right) |
| | Infraorbital form |
| | Infraorbital suture |
| | Profile curves of nasal bones |
| | Position of nasion |
| | Angle of nasal bones |
| | Nasal bone shape |
| | Extension of nasal bones |
| | Development of anterior nasal spine |
| | Zygomaxillary tubercle (Left & Right) |
| | Subnasal region |
| Basilar | Dental arcade shape |
| | Anterior palate form |
| | Torus palatinus |
| | Torus maxillaris |
| | Foramen of Huschke (Left & Right) |
| | Encroachment of occipital condyles |
| | Hypoglossal canal bridging (Left & Right) |
| | Condylar canal (Left & Right) |
| Posterior | Inca bone |
| Superior | Interparietal groove |
| | Parietal foramina |
| | Zygomatic arch |
| | Wormian bones |
| | Ophryonic groove |
| Lateral | Sutural variations at pterion (Left & Right) |
| | Inferior frontal eminence (Left & Right) |
| | Superior temporal line (Left & Right) |
| | Mons temporosphenoidalis (Left & Right) |
| | Parietotemporal suture (Left & Right) |
| | Tympanic plate of temporal bone (Left & Right) |
| | Supra-asterionic region |
| | Parietal notch bone (Left & Right) |
| | Sutura mendosa (biasterionic suture) |
| | Os japonicum (left & Right) |
| | Asterion ossicle (Left & Right) |
| | Occipitomastoid wormian bone (Left & Right) |
| Mandible | Chin shape |
| | Mental foramen (Left & Right) |
| | Genial tubercles |
| | Torus mandibularis |
| | Mylohyoid bridge (Left & Right) |

**TABLE S2.** *Descriptive statistics for the groups investigated (p=0.05).*

| Cranial Trait | | LSA | IA | Modern Khoesan | Modern Bantu | p | LSA (8ka–4ka) | LSA (4ka–3ka) | LSA (3ka–2ka) | IA (2ka–0ka) | LSA (2ka–1ka) | LSA (1ka–0ka) | p | LSA Inland central | LSA West coast | LSA SW coast | LSA South coast | LSA SE coast | IA North East | IA South Zambia | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Incomplete (nasal part) metopic suture | N | – | – | – | – | – | 21 | 24 | 60 | 21 | 38 | 80 | 0.42 | 53 | 11 | 76 | 68 | 17 | 29 | 5 | 0.19 |
| | % | – | – | – | – | | 0 | 8 | 7 | 10 | 0 | 5 | | 8 | 0 | 3 | 6 | 0 | 14 | 20 | |
| Metopic ridge | N | 238 | 43 | 24 | 145 | 0.05 | 22 | 27 | 61 | 22 | 40 | 79 | **0.00** | 52 | 12 | 77 | 74 | 18 | 33 | 8 | 0.06 |
| | % | 37 | 26 | 21 | 26 | | 36 | 59 | 51 | 23 | 25 | 25 | | 29 | 42 | 38 | 49 | 17 | 24 | 25 | |
| Oval shaped orbits | N | 213 | 38 | 21 | 142 | **0.00** | – | – | – | – | – | – | – | 43 | 13 | 74 | 62 | 17 | 27 | 9 | **0.01** |
| | % | 53 | 29 | 29 | 27 | | – | – | – | – | – | – | | 37 | 54 | 49 | 65 | 65 | 26 | 44 | |
| Round shaped orbits | N | – | – | – | – | – | – | – | – | – | – | – | – | 43 | 13 | 74 | 62 | 17 | 27 | 9 | **0.03** |
| | % | – | – | – | – | | – | – | – | – | – | – | | 2 | 15 | 3 | 0 | 0 | 0 | 0 | |
| Supraorbital notch (L) | N | 236 | 44 | 24 | 153 | **0.01** | 21 | 23 | 63 | 23 | 40 | 79 | 0.12 | – | – | – | – | – | – | – | – |
| | % | 68 | 86 | 67 | 80 | | 67 | 52 | 70 | 91 | 73 | 71 | | – | – | – | – | – | – | – | |
| Supraorbital notch (R) | N | – | – | – | – | – | 22 | 22 | 63 | 26 | 39 | 80 | **0.03** | 53 | 12 | 77 | 73 | 17 | 36 | 9 | 0.07 |
| | % | – | – | – | – | | 77 | 73 | 67 | 92 | 67 | 85 | | 83 | 67 | 66 | 75 | 88 | 89 | 89 | |
| Supraorbital foramen (L) | N | – | – | – | – | – | – | – | – | – | – | – | – | 50 | 11 | 76 | 74 | 18 | 34 | 9 | **0.00** |
| | % | – | – | – | – | | – | – | – | – | – | – | | 44 | 73 | 49 | 50 | 17 | 12 | 22 | |
| Supraorbital foramen (R) | N | 233 | 46 | 24 | 153 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 42 | 15 | 33 | 27 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Ethmoidal foramina (L) | N | 241 | 15 | 21 | 129 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 46 | 60 | 81 | 64 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Ethmoidal foramina (R) | N | 141 | 14 | 19 | 130 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 82 | 86 | 100 | 64 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Infraorbital foramen (L) | N | 191 | 36 | 24 | 144 | 0.25 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 88 | 97 | 88 | 92 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Infraorbital foramen (R) | N | – | – | – | – | – | 17 | 21 | 51 | 16 | 37 | 62 | 0.10 | – | – | – | – | – | – | – | – |
| | % | – | – | – | – | | 100 | 86 | 84 | 75 | 86 | 95 | | – | – | – | – | – | – | – | |
| Infraorbital form | N | 215 | 44 | 24 | 144 | **0.01** | 21 | 20 | 55 | 21 | 39 | 74 | **0.00** | – | – | – | – | – | – | – | – |
| | % | 5 | 16 | 17 | 6 | | 5 | 0 | 2 | 24 | 0 | 11 | | – | – | – | – | – | – | – | |
| Infraorbital suture | N | 124 | 22 | 14 | 127 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 24 | 23 | 0 | 9 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |

**TABLE S2.** *continued.*

| Cranial Trait | | LSA | IA | Modern Khoesan | Modern Bantu | p | LSA (8ka–4ka) | LSA (4ka–3ka) | LSA (3ka–2ka) | IA (2ka–0ka) | LSA (2ka–1ka) | LSA (1ka–0ka) | p | LSA Inland central | LSA West coast | LSA SW coast | LSA South coast | LSA SE coast | IA North East | IA South Zambia | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Superficial nasion | N | 158 | 28 | 22 | 121 | **0.00** | – | – | – | – | – | – | – | 36 | 9 | 54 | 46 | 10 | 19 | 8 | **0.00** |
| | % | 66 | 29 | 41 | 44 | | – | – | – | – | – | – | | 78 | 67 | 74 | 54 | 30 | 26 | 38 | |
| Moderately depressed nasion | N | 158 | 28 | 22 | 121 | **0.03** | 10 | 19 | 43 | 12 | 30 | 52 | 0.07 | – | – | – | – | – | – | – | – |
| | % | 27 | 54 | 45 | 34 | | 30 | 26 | 21 | 67 | 37 | 27 | | – | – | – | – | – | – | – | |
| Marked depression of nasion | N | 158 | 28 | 22 | 121 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 7 | 18 | 14 | 22 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Angle of nasal bones | N | 198 | 37 | 22 | 149 | 0.12 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 91 | 100 | 95 | 95 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Nasal bone shape | N | 157 | 26 | 18 | 112 | 0.47 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 54 | 65 | 44 | 50 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Zygomaxillary tubercle (L) | N | 213 | 34 | 24 | 149 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 45 | 59 | 67 | 62 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Zygomaxillary tubercle (R) | N | 211 | 39 | 23 | 150 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 43 | 46 | 74 | 60 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Subnasal region | N | 204 | 34 | 19 | 115 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 36 | 50 | 32 | 72 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Anterior palate form | N | 229 | 45 | 22 | 151 | **0.00** | – | – | – | – | – | – | – | 53 | 14 | 70 | 69 | 18 | 32 | 11 | 0.07 |
| | % | 85 | 98 | 91 | 99 | | – | – | – | – | – | – | | 83 | 71 | 86 | 84 | 94 | 100 | 100 | |
| Foramen of Huschke (L) | N | 220 | 48 | 22 | 150 | **0.00** | 14 | 23 | 61 | 26 | 36 | 80 | **0.00** | – | – | – | – | – | – | – | – |
| | % | 29 | 13 | 9 | 9 | | 14 | 61 | 33 | 4 | 33 | 20 | | – | – | – | – | – | – | – | |
| Foramen of Huschke (R) | N | 221 | 48 | 23 | 151 | **0.00** | 16 | 19 | 60 | 26 | 39 | 78 | **0.05** | 53 | 13 | 70 | 63 | 16 | 39 | 8 | 0.06 |
| | % | 30 | 10 | 13 | 11 | | 25 | 53 | 28 | 8 | 31 | 28 | | 26 | 23 | 24 | 40 | 31 | 10 | 13 | |
| Encroachment of occipital condyles | N | 185 | 28 | 22 | 151 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 27 | 21 | 91 | 9 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Condylar canal (L) | N | 137 | 17 | 22 | 131 | **0.01** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 45 | 76 | 50 | 62 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |

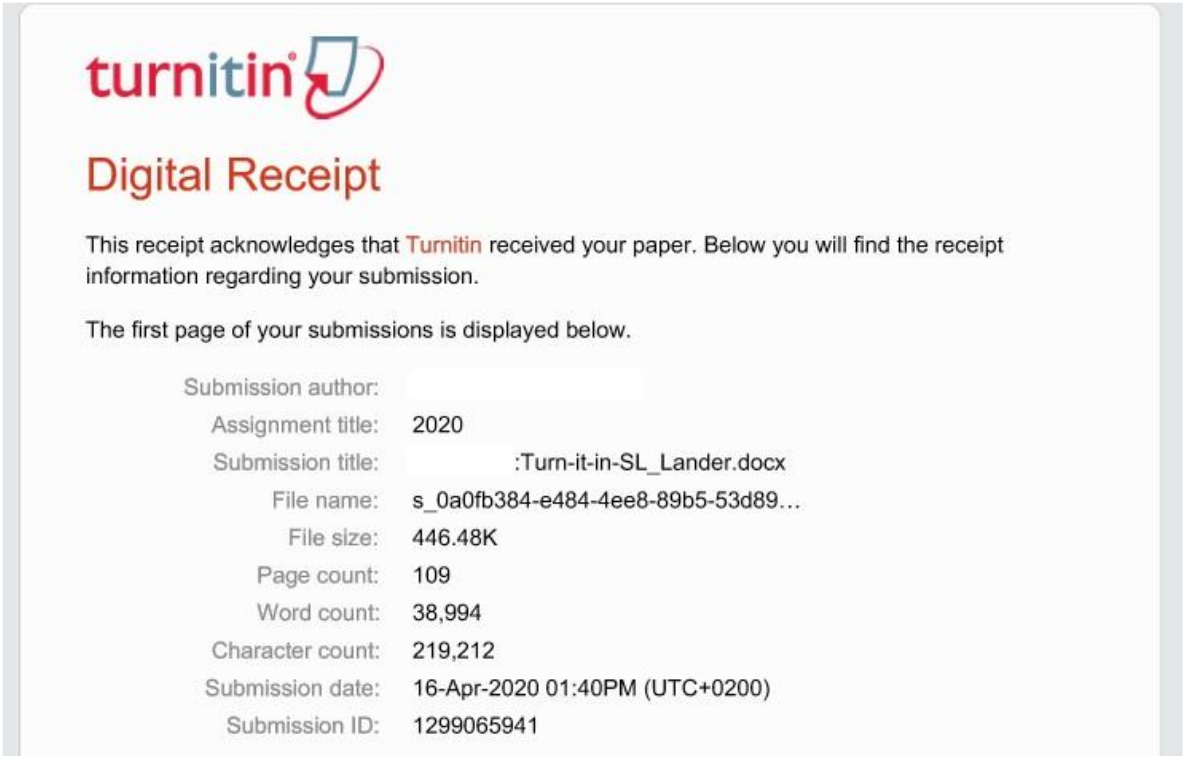
**TABLE S2.** *continued.*

| Cranial Trait | | LSA | IA | Modern Khoesan | Modern Bantu | p | LSA (8ka–4ka) | LSA (4ka–3ka) | LSA (3ka–2ka) | IA (2ka–0ka) | LSA (2ka–1ka) | LSA (1ka–0ka) | p | LSA Inland central | LSA West coast | LSA SW coast | LSA South coast | LSA SE coast | IA North East | IA South Zambia | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Inca bone | N | 224 | 38 | 24 | 146 | 0.78 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 1 | 0 | 0 | 68 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Interparietal groove | N | 225 | 43 | 24 | 147 | 0.06 | 17 | 27 | 59 | 22 | 38 | 77 | 0.35 | – | – | – | – | – | – | – | – |
| | % | 27 | 42 | 42 | 24 | | 41 | 33 | 25 | 41 | 18 | 27 | | – | – | – | – | – | – | – | |
| Parietal foramina | N | 201 | 30 | 23 | 137 | 0.34 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 94 | 97 | 100 | 91 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Zygomatic arch | N | 200 | 29 | 24 | 145 | **0.00** | 16 | 20 | 54 | 15 | 38 | 68 | **0.00** | – | – | – | – | – | – | – | – |
| | % | 29 | 7 | 8 | 43 | | 38 | 35 | 46 | 13 | 18 | 15 | | – | – | – | – | – | – | – | |
| Inferior frontal eminence (L) | N | 217 | 36 | 23 | 147 | 0.18 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 47 | 36 | 65 | 46 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Mons temporosphenoidalis (L) | N | 211 | 32 | 24 | 151 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 56 | 38 | 79 | 14 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Parietotemporal suture (L) | N | 176 | 26 | 22 | 127 | **0.00** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 47 | 65 | 18 | 73 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Tympanic plate of temporal bone (L) | N | – | – | – | – | – | – | – | – | – | – | – | – | 54 | 12 | 73 | 67 | 17 | 37 | 9 | **0.02** |
| | % | – | – | – | – | | – | – | – | – | – | – | | 43 | 50 | 52 | 27 | 29 | 54 | 67 | |
| Tympanic plate of temporal bone (R) | N | 226 | 48 | 24 | 151 | **0.00** | 18 | 22 | 60 | 25 | 39 | 80 | 0.10 | 55 | 12 | 70 | 67 | 17 | 37 | 9 | **0.00** |
| | % | 43 | 60 | 46 | 63 | | 50 | 41 | 45 | 72 | 36 | 43 | | 47 | 50 | 54 | 27 | 29 | 57 | 78 | |
| Parietal notch bone (L) | N | 202 | 33 | 24 | 144 | **0.02** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 10 | 6 | 0 | 18 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Parietal notch bone (R) | N | 204 | 31 | 24 | 145 | 0.34 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 12 | 10 | 0 | 12 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Occipitomastoid wormian bone (L) | N | 196 | 28 | 23 | 141 | **0.01** | – | – | – | – | – | – | – | 40 | 12 | 65 | 57 | 17 | 22 | 5 | 0.52 |
| | % | 8 | 21 | 4 | 17 | | – | – | – | – | – | – | | 5 | 0 | 11 | 11 | 6 | 18 | 20 | |
| Genial tubercles | N | 127 | 38 | 20 | 117 | 0.29 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | % | 43 | 50 | 60 | 39 | | – | – | – | – | – | – | | – | – | – | – | – | – | – | |
| Mylohyoid bridge (L) | N | 183 | 38 | 21 | 147 | **0.00** | 16 | 18 | 48 | 17 | 32 | 59 | **0.00** | 45 | 12 | 58 | 53 | 10 | 27 | 10 | **0.00** |
| | % | 46 | 5 | 33 | 14 | | 31 | 67 | 63 | 12 | 47 | 27 | | 31 | 25 | 52 | 57 | 70 | 7 | 0 | |

**TABLE S2.** *continued.*

| Cranial Trait | | LSA | IA | Modern Khoesan | Modern Bantu | p | LSA (8ka–4ka) | LSA (4ka–3ka) | LSA (3ka–2ka) | IA (2ka–0ka) | LSA (2ka–1ka) | LSA (1ka–0ka) | p | LSA Inland central | LSA West coast | LSA SW coast | LSA South coast | LSA SE coast | IA North East | IA South Zambia | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mylohyoid bridge (R) | N | 181 | 40 | 21 | 145 | **0.00** | 16 | 18 | 47 | 19 | 32 | 59 | **0.00** | 45 | 11 | 58 | 50 | 12 | 29 | 10 | **0.00** |
| | % | 45 | 8 | 29 | 8 | | 38 | 72 | 66 | 16 | 34 | 25 | | 31 | 27 | 47 | 60 | 50 | 10 | 0 | |
| Parietotemporal suture (R) | N | – | – | – | – | – | 13 | 23 | 42 | 17 | 27 | 61 | 0.29 | – | – | – | – | – | – | – | – |
| | % | – | – | – | – | | 31 | 57 | 52 | 71 | 52 | 44 | | – | – | – | – | – | – | – | |
| Ophryonic groove | N | – | – | – | – | – | 23 | 24 | 62 | 26 | 39 | 81 | 0.06 | 54 | 11 | 77 | 73 | 17 | 36 | 9 | 0.44 |
| | % | – | – | – | – | | 39 | 21 | 11 | 12 | 21 | 26 | | 24 | 18 | 17 | 26 | 18 | 14 | 0 | |
| Hypoglossal canal bridging (L) | N | – | – | – | – | – | 15 | 17 | 55 | 16 | 36 | 61 | 0.55 | – | – | – | – | – | – | – | – |
| | % | – | – | – | – | | 7 | 0 | 11 | 0 | 11 | 8 | | – | – | – | – | – | – | – | |
| Profile curves of nasal bones | N | – | – | – | – | – | 9 | 18 | 42 | 12 | 29 | 44 | 0.06 | – | – | – | – | – | – | – | – |
| | % | – | – | – | – | | 44 | 33 | 45 | 67 | 66 | 68 | | – | – | – | – | – | – | – | |
| Supra-asterionic region | N | – | – | – | – | – | – | – | – | – | – | – | – | 47 | 13 | 73 | 67 | 18 | 30 | 8 | **0.00** |
| | % | – | – | – | – | | – | – | – | – | – | – | | 57 | 46 | 23 | 21 | 44 | 43 | 13 | |
| Os japonicum (L) | N | – | – | – | – | – | – | – | – | – | – | – | – | 46 | 13 | 75 | 67 | 16 | 24 | 7 | **0.00** |
| | % | – | – | – | – | | – | – | – | – | – | – | | 0 | 15 | 1 | 0 | 0 | 0 | 0 | |
| Mental foramen (R) | N | – | – | – | – | – | – | – | – | – | – | – | – | 40 | 12 | 59 | 51 | 12 | 30 | 9 | 0.36 |
| | % | – | – | – | – | | – | – | – | – | – | – | | 83 | 75 | 73 | 78 | 75 | 90 | 100 | |
| **Total sample size** | | **303** | **105** | **24** | **176** | | **32** | **34** | **67** | **59** | **42** | **103** | | **75** | **17** | **84** | **109** | **18** | **80** | **23** | |

APPENDIX F: TURN-IT-IN REPORT



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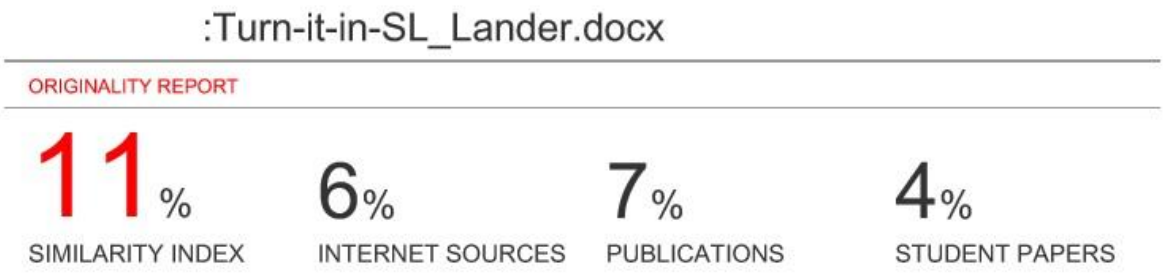

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