Dental morphology and variation across Holocene Khoesan people of southern Africa

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THESIS ABSTRACT

Dental analyses of the Holocene Khoesan populations of southern Africa can provide insight into the biological evolution of an anthropologically important people. There have been many studies of dental variation in Holocene populations of Europe and the Americas, but few of African populations. Despite the Khoesan being the focus of much osteological research over the last two decades, their dental morphology is understudied and we know little about their dental evolution. Here, I assess the metric and non-metric dental morphology and variation of Holocene Khoesan individuals across southern Africa (N=487). Due to the fragmentary nature of many archaeological skeletons, most previous work on Khoesan osteology has focused on the second half of the Holocene, because more recent skeletons tend to be better preserved. There are, however, relatively abundant and well-preserved dental remains from the early Holocene. These are studied in detail for the first time in this dissertation, adding to our understanding of the emergence of Holocene Khoesan dentition and providing insight into phenotypic (and presumably genetic) continuity in this region. In addition to examining similarities/differences among the Khoesan through space and time, comparisons are made between the teeth of Khoesan and those of Holocene archaeological skeletons from East Africa (Kenya) to provide a broader context for interpreting the Khoesan dentition. Comparisons are also made between Holocene Khoesan and Mid-Late Pleistocene teeth from southern Africa in order to provide insights into dental relationships deeper in time. There are six aims of this thesis: (1) to construct the population's dental map and with it, (2) evaluate the significance of Khoesan Late mid-Holocene body size fluctuations and (3) assess the question of population continuity or replacement *ca.* 2000 BP with the introduction of herding in South Africa, (4) to explore possible geographic differences among Khoesan dentitions (5) to investigate temporal differences within the Holocene, and also to compare Holocene and earlier hunter-gatherers to assess population continuity/discontinuity, and (6) to evaluate the position of Khoesan dentition in a global context.

Up to 52 non-metric traits were scored using the Arizona State University Dental Anthropology System. To test for significant relationships between groups through time, chi-square statistics were employed on dichotomised data and the mean measure of divergence was assessed in order to identify phenetic similarities and dissimilarities between regions. Additionally, MANOVAs and Principal Components Analysis were used to investigate size and shape variation. Metric analyses demonstrate minor size/shape variation between temporal and regional groups. Increased metric variation is observed during the Late Holocene, coinciding with fluctuations in body size documented in previous studies. Although some differences in trait frequencies are observed during the Late Holocene, there is little variation in qualitative traits throughout the Khoesan sample. This suggests that the minor differences observed result from intrinsic factors such as geographic variation, rather than gene flow from outlying areas. Teeth from the Mid-Late Pleistocene demonstrate a degree of phenetic affinity to Holocene Khoesan dentition. Finally, the Khoesan dentition is significantly different from global dental complexes, as exemplified by a suite of twelve core Khoesan traits that distinguish Khoesan teeth from other dental patterns (including Afridonty). Taken together, these results support hypotheses of morphological and genetic continuity in southern African populations during the Holocene, with some evidence for continuity deeper in time. In addition, these results place the Khoesan dentition at the margins of the range of human dental variation and call into question the fit of this dental map into current sub-Saharan African dental models.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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This thesis, a long time in the making (perhaps a bit too long), is the culmination of an amazing (enjoyable, frustrating, illuminating) journey across continents and unexpected new cities. Now that I am at journey's end, I can see the merits of choosing the doctoral path but on and off over the last few years, I cursed my decision. However, the desire to finish the project and ultimately add to a field of enquiry made it all worthwhile. That said, desire alone was most certainly not enough! I couldn't have come this far without significant help and support from those around me.

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CHAPTER 1

INTRODUCTION

The Khoesan occupy an important place in anthropology, in many sub-fields ranging from socio-cultural to biological anthropology to studies of the origins of modern humans. The Khoesan are notably small-bodied and gracile and as such, are at one extreme of the range of variation among contemporary human populations, making their skeletal and dental morphology of great interest for understanding the range and potential limits of the human phenotype. The biological evolution of this population, particularly over the last 5000 years, is relatively well understood largely due to the increase in the number of studies of cranial and postcranial remains during approximately the last two decades (Churchill and Morris 1998; Harrington 2010; A.G. Morris 1992b; Pfeiffer 2012a; Pfeiffer and Harrington 2011; Pfeiffer and Sealy 2006; Sealy and Pfeiffer 2000; Stock 2006; Stock and Pfeiffer 2001; Stynder 2009; Stynder *et al.* 2007a, 2007b; Wilson and Lundy 1994). The nature and scope of these studies is, however, restricted by the fragmentary condition of many human remains and the fact that only a limited number of specimens have been dated – too few to fully understand this geographically, temporally and (possibly) genetically diverse population. This dissertation reports on a dental anthropological analysis of a large sample of Holocene Khoesan remains, inclusive of both dated and undated Later Stone Age dentitions from across South Africa and a small portion of Namibia. It explores metric and non-metric similarities among these teeth in order to understand how much dental variation existed within geographic and temporal boundaries and whether such variation represents a single population or one derived from genetically diverse groups. In particular, it addresses questions regarding Khoesan population history and continuity in the South African Later Stone Age. This research also has bearing on the origins of Khoesan dental morphology and its placement both in a broader African context and within previously described global dental complexes and deeper in time.

KHOESAN ORIGINS

Ancient Khoesan were once thought to have inhabited most of southern, eastern and north-eastern Africa during the Later Stone Age (Phillipson 1982). Early genetic (Nurse *et al.* 1985; Tobias 1978) and serological (Tobias 1972, 1978) research reinforced these ideas, while simultaneously identifying the unique genetic character of modern Khoesan. Genetic studies have been ongoing, placing Khoesan as genetic outliers in a sub-Saharan context (Cavalli-Sforza *et al.* 1994; Chen *et al.* 2000; Excoffier *et al.* 1987; Pickrell *et al.* 2012; Schlebusch and Soodyall 2012) with an ancient genetic lineage. A shared common ancestry between the Khoesan and earlier sub-Saharan African groups (Hayden 2013; Knight *et al.* 2003) and the Khoesan and more recent East African populations (Cruciani *et al.* 2002; Pickrell *et al.* 2012; Semino *et al.* 2002), serve as evidence of the ancestral position of the Khoesan. As convincing as this genetic evidence may seem, little osteological evidence supports an extensive and widespread Khoesan population (A.G. Morris 2002, 2003) and previous osteological studies (cranial) demonstrating Khoesan traits in East Africa (Galloway 1933; Rightmire 1970; Tobias 1978) or within an ancestral pan-African population (Tobias 1972, 1978), have been found to be, at best, ambiguous. Interestingly, some dental traits have similarities across sub-Saharan African populations (of which the Khoesan have been considered a part) (Irish 1993, 1997, 1998b). These trait similarities most likely reflect the retention of a small suite of African ancestral traits, some of which are congruent between modern African and earlier hominin specimens (Irish 1998a; Irish and Guatelli-Steinberg 2003; Irish *et al.* 2013). A.G. Morris (2002, 2003) disagrees with the idea that the Khoesan phenotype is ancestral to other sub-Saharan African phenotypes. Rather, he hypothesises a recent Khoesan morphology that emerged at about the time of the Last Glacial Maximum, *ca.* 20 000 years ago, when changing climates and shifts in population densities inland (Wadley 1993) and along the coast (Parkington 1990) may have led to the genetic isolation and ultimate variation of these groups. Studies of, and comparisons between, Pleistocene and Holocene osteological remains supports the emergence of a relatively recent southern African Khoesan phenotype (Bräuer and Rösing 1989; Churchill *et al.* 2000; Churchill *et al.* 1996; Grine *et al.* 2007; Grine *et al.* 2000; A.G. Morris 1992a; Rightmire and Deacon 1991; J.H. Schwartz and Tattersall 2003; Stynder *et al.* 2007b) that is relatively stable and continuous (Stynder *et al.* 2007a) throughout the Holocene. Small morphological changes that do emerge along the Cape coast coincide with changes in population density, climatic shifts and resource stresses (Pfeiffer and Sealy 2006; Stynder *et al.* 2007a). No dental study, until now, has evaluated Khoesan variation in light of these issues of continuity and change.

RECENT KHOESAN HISTORY

The first known European contact with the Khoesan dates back to the late 1400s when early Portuguese seafarers Bartolomeu Dias and later, Vasco Da Gama sailed around the southern tip of Africa and the Cape of Good Hope. These accounts were very brief and it is only after 1652, with the arrival of Johan Anthoniszoon “Jan” van Riebeeck, a Dutch colonial administrator for the Dutch East India Company (Vereenigde Oostindische Compagnie, or VOC), that detailed accounts of the Khoesan are recorded. Jan van Riebeeck, as first commander of the newly founded refreshment station (Cape Town, today), established the first permanent European settlements in the Cape and fortified Table Bay as a way-station for the VOC (Hunt and Campbell 2005). Jan van Riebeeck’s voluminous journal comments extensively on various Khoesan groups (hunter-gatherer and herder) in and around the colony, as well as their culture and lifeways (Thom 1958). Later expeditions to the interior (and Namaqualand) recorded contact with inland herder groups, describing these populations’ associated subsistence and culture. It is also at this time that we see the first adopted names for these indigenous groups. The Dutch settlers used a variety of exonyms to refer to the Khoesan. They called the coastal hunter-gatherers ‘Strandlopers’ (beachcombers) and the local nomadic pastoralists ‘Hottentots’ (Schapera 1926, 1930). Inland hunter-gatherers were referred to as ‘Bushmen', or ‘Soaqua’ (Barnard 1992; Boonzaier *et al.* 1996), or ‘Basarwa’ or ‘First People’ in regions further north such as Botswana (Hitchcock 2002; Hitchcock *et al.* 2006). In his diaries, Jan van Riebeeck also used the word 'Soaqua’ for hunter-gatherers living in the Western Cape (from ‘soa-‘ meaning ‘bush’ and ‘qua-‘ meaning ‘man’ or from the Nama word ‘Sa’ meaning ‘to gather or forage’) and ‘Quena’ (meaning ‘people’) to describe herder peoples living near present-day Cape Town (H.J. Deacon and Deacon 1999). The term ‘San’ (Sa’, ‘to forage’, and the suffix –n meaning ‘people’) was mostly used by other groups such as the Nama to describe their hunter-gatherer neighbours (H.J. Deacon and Deacon 1999). The Khoekhoe (‘Khoe’ is the common gender word meaning ‘people’; Khoekhoe is translated as ‘Men of men’ or ‘people of people’) would have described themselves by their clan names, e.g. Cochoqua, Attaqua, and Namaqua. Colonial accounts viewed Khoesan groups as biologically distinct, mutually exclusive populations, each with their own characteristic material culture, social structure and language. Differences between the groups were noted resulting in a typological classification of physical types for both hunter-gatherer and herder populations. Differences in stature, for example, were used to signify ethnic differences between the two lifeways; hunter-gatherers were seen as small, while herders were taller (Schapera and Farrington 1933; Thom 1958). These physical typologies, among other things, entrenched a supposed dichotomy of the Khoesan lifestyle into San hunter-gatherers and Khoekhoe herders, which has remained an element of research and discussion.

From the moment of first contact with European colonisers, Khoesan culture, land and political power was in jeopardy. A methodical and gradual process of Khoesan dispossession, and a devastating smallpox epidemic along the Cape coast in 1713, led to the population’s cultural demise and biological decline (Elphick 1985; Steyn 1990). The colonial expansion inland from the 1700s sees the rise of Khoesan resistance, particularly in frontier territories of the Northern Cape (Penn 2005) but these groups, too, ultimately succumbed to colonial rule. Surviving Khoesan groups were integrated into the socio-political structures of colonial times and their identities slowly lost.

Recent Khoesan populations living in Angola, Botswana, Namibia (Kalahari), South Africa, Zambia and Zimbabwe have played an important role in anthropological research. These investigations have focused on Khoesan lifestyles, cultural patterns, economy, language and spirituality (including studies of belief systems that have been applied to the interpretation of rock art) and have added greatly to the knowledge of hunter-gatherer systems around the world (Barnard 1992, 2008; D.F. Bleek 1929; W.H.I. Bleek 1875; W.H.I. Bleek and Lloyd 1911; Lee 1979; Lee and DeVore 1968; Lewis Williams 1981; Silberbauer 1961, 1963, 1972, 1981; Tanaka 1976; Traill 1995; Vossen 2013; Wilmsen 1989; Wilmsen and Denbow 1990). Biological investigations (skeletal and otherwise) (Broom 1923, 1941; Tobias 1972, 1978) have also been carried out on contemporary Khoesan populations including, for example, early dental analyses (J.C.M. Shaw 1927, 1928; Van Reenen 1964, 1966). Of course, studies of recent and contemporary Khoesan have limited power for evaluating questions about archaeological populations; changing environments, subsistence strategies, population movements and social systems, among others, may influence the phenotypic (and possibly genetic) patterns we see between prehistoric and recent populations. Gene flow through time is also a consideration as there is evidence of genetic contact between the Khoesan and Bantu-speaking populations in the last two thousand years (or perhaps slightly longer) (Cavalli-Sforza *et al.* 1994; Cruciani *et al.* 2002; Tobias 1972). Ideally, the evolutionary history of the Khoesan should be studied from skeletal remains predating contact (Stynder 2006).

A NOTE ON TERMINOLOGY

A standardised nomenclature is needed when discussing relationships among groups. In physical anthropology studies in South Africa, this has proven to be difficult because “[systems of] language, economy and biological make-up” have been confused (A.G. Morris 1992b: 4). Due to South Africa’s long history of institutionalised discrimination (and ethics surrounding the curation of human remains (Sealy 2003)), people are sensitive to labels that categorise or define individuals along lines of physical types or racial groups, and particularly to their connotations. To clarify the use of terminology in research, the findings of an interdisciplinary conference, held in Johannesburg in 1971, were published by Jenkins and Tobias (1977) who outlined the appropriate terms for discussing these groups. The terms ‘San’ for hunter-gatherers, ‘Khoikhoi’ (now ‘Khoekhoe’ or Khoi/Khoe) for herders and ‘Khoisan’ (‘Khoesan’) for combined populations were recommended and were adopted as standard in academic circles. Still, a substantial amount of confusion, particularly with regards to the use of linguistic terms, was evident. Terms such as ‘Bushman’ or ‘Hottentot’ were predominantly used for discussion of linguistics (alongside ‘Bantu’ referring to languages spoken by Negroid populations in South and East Africa) but were often also used to denote ethnic or physical entities (A.G. Morris 1992b).

The word ‘Khoisan’ was first coined as a collective term by Leonard Schultze (1928), and popularised by Schapera (1930), to describe both San hunter-gatherers and Khoi (later Khoe) pastoralists. Today, this term should only be used for linguistic purposes. Names such as ‘Strandloper', still used colloquially by older Afrikaans-speakers, have fallen away and no longer appear in current literature. The term ‘Bushman’ has been used extensively in southern Africa to refer to foraging and agropastoralist populations. In 1996, after the establishment of the South African San Institute (SASI), the term ‘San’ was preferred and largely replaced ‘Bushman’ (Hitchcock *et al.* 2006). At the African Human Genome Initiative conference, held in Cape Town in 2003, attending San communities (represented by the Working Group of Indigenous Minorities in Southern Africa and SASI) made it clear that ‘Khoisan’ and ‘Bushman’ were not preferred terms (Schlebusch 2010). Rather, individual communities should be referred to by name (e.g. !Xun or /Xam) and if a collective term is required, the combination of Khoe (pastoralist) and San (hunter-gatherer) is acceptable. This study follows these guidelines and uses the term Khoesan to describe the population as a whole. Only when referring to previous literature and research, are the older terms used for clarity of discussion. Additionally, the term ‘Bantu-speaking’ is used in this thesis to refer to Negroid populations from East and South Africa and Iron Age populations.

THIS STUDY

The remainder of this dissertation comprises 5 chapters. Chapter 2 reviews the history of dental anthropology and looks at how the approaches and methodologies used in dental studies have changed over the last 150 years, and outlines conclusions that have emerged as a result of these achievements. It also outlines the evidence for variation in recent dental patterns across continents. Dental anthropology is a relatively new discipline and has predominantly been used to study population relationships and illuminate modern global dental complexes. Although little research has been conducted on Khoesan dentition, this section also includes a summary of previously documented Khoesan dental diversity and its relationship to sub-Saharan African dentition as a whole. Chapter 3 provides a summary of relevant aspects of the South African archaeological record, focusing on Later Stone Age archaeology. It also reviews the Middle to Late Pleistocene[1] fossil record with specific reference to human dental remains. In addition, this chapter provides an overview of relevant Holocene archaeology in Kenya. The hypotheses that will be tested in this dissertation are presented at the end of this section. Chapter 4 outlines the geographic setting of the data studied in this thesis, and describes the materials and methods employed. Results are presented in Chapter 5. The implications of these results are discussed and concluding remarks are presented in Chapter 6.

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[1] Hereafter referred to as Mid-Late Pleistocene in this thesis. This should not to be confused with the lower case term mid-Late Pleistocene which refers to a specific time period within the Late Pleistocene archaeological depositories from the southern Cape, South Africa. Deacon, H.J. 1995. Two Late Pleistocene-Holocene archaeological depositories from the southern Cape, South Africa. *The South African Archaeological Bulletin* 50(162):121-131.

CHAPTER 2

HISTORY OF DENTAL ANTHROPOLOGY

"From the anatomist's point of view the greater part of
the world still remains in a state of dental darkness."
(Sir Arthur Keith in J.C.M. Shaw 1931: xiii-xiv).

Research into the morphological variation in human teeth started in the 1800s, but systematic studies, including quantitative ones, did not appear until the 1900s when this relatively new and growing field of interest was popularised. Although these early studies were hampered by a lack of dental metric and non-metric variation information from around the world, it is here that some of the early dental anthropological principles first emerge. Although dental studies have been a familiar resource in anthropological research since then, it is only in the last 60 years that increased interest in more analytical dental investigations appears. Today, morphometric studies of the dentition have become common, and have contributed greatly to our understanding of past peoples. This is in part because teeth are hard and resilient, and therefore minimally susceptible to post-mortem alteration, making them prime candidates for study – archaeological or otherwise. Moreover, teeth are under genetic control and the only part of the hard skeleton exposed to the environment and thus dental variation takes diverse forms (G.R. Scott and Turner 1988) that can be evaluated. Dental size, shape and morphology offer genetic information, while other processes such as tooth wear, caused by environmental factors, highlight diet (Mayhall 1992; B.H. Smith 1984) and cultural practices (Milner and Larsen 1991). Teeth also have a definite developmental path and stressors or interruptions that affect growth can be seen as defects in the enamel or dentine. Dentition can also be considered a complex system, from exhibiting structure at multiple levels (observed on individual teeth and between tooth classes within the mouth) (R.N. Smith *et al.* 2009) to the roles of genes and environment, how they interact, and how they can contribute to phenotypic variation (Hughes and Townsend

2013). What makes this system particularly interesting is that it can react to change through time, as evidenced both on an individual basis and through generational investigations (Brook and O'Donnell 2012). Taken together, morphological information from the dentition can provide important insight into the biological and cultural affinities of people who lived in the past.

A BRIEF HISTORY OF DENTAL STUDIES

The origins of dental anthropology are in palaeontology, where a number of early researchers used teeth in an attempt to categorise fossils (Bolk 1922; Gregory 1926; Osborn 1907; Owen 1845). Early human odontological studies are based in dentistry (Drennan 1929b; Gregory 1922; Hellman 1928; Sullivan 1920), where interest first arose out of pathological conditions and expanded to describing natural differences in human teeth and their relative frequencies in different populations. One of the earliest such studies was by Georg von Carabelli (1842), a prominent Hungarian dentist, who described the appearance of an additional mesiolingual cusp on the upper molars of European dentitions. This ‘Carabelli’s trait’ is still observed and recorded today in most dental evaluations and is a source of anthropological interest globally (Hassanali 1982; Hsu *et al.* 1999; Marado and Campanacho 2013; Reid *et al.* 1991; G.R. Scott 1980; Townsend and Brown 1981a). Variability in root and enamel structure were also noted (Owen 1845; Tomes 1889), and some studies dealt with racial dissimilarity (e.g. Flower 1885; Hellman 1928). Also, some early palaeopathology studies observed diet related caries rates (Mummery 1870) and developed attrition scoring techniques (Broca 1879) but overall, no systematic study of the evolution and variability of the human dentition was carried out until the 20th century. In many respects, Aleš Hrdlička was the founder of modern dental anthropology. Hrdlička (1920) was the first dental researcher to classify the degree of expression of a trait with his work on shovel-shaped incisors. His study also assessed the trait variation between human populations and described the appearance of similar traits in other species (primates, some carnivores and a variety of ungulates). He identified the similarity in the degree of shovelling frequency and expression between Asian and American Indian populations and their marked difference from African and European dentitions. He also commented on other morphological dental traits (Hrdlička 1921) but made few between-population comparisons. Hrdlička (1923) also made an attempt at standardising dental measurement techniques to improve consistency between researchers. Additionally, Hrdlička encouraged Leigh (1925) to assess dental pathological change and dental disease of various populations. He observed that different subsistence economies resulted in varied patterns of tooth wear and pathological change, noting in particular that an agricultural economy is often associated with bad dental health.

In subsequent decades dental anthropological research continued to grow. Gregory (1922) reviewed the dental evolution of many species, noting morphological similarities and identifying several morphological variants which he characterised as either “low” types (primitive) or “high” types (derived). For example, the retention of the *Dryopithecus* Y5 lower molar pattern was identified as a primitive trait (Gregory 1922: 365-368) and its occurrence indicated phylogenetic relationships between ancient apes, living apes and modern humans (G.R. Scott 1997). The potential for traits to discriminate between geographically separated populations (races) became an important research avenue (i.e. Hellman 1928), and population-specific dental observations increased, demonstrating (among other things) broad disparity in human tooth size. These included studies on the dentition of the Khoesan (Drennan 1929b), Native Americans (Goldstein 1948; Nelson 1938) and Japanese (Yamada 1932), but the most comprehensive treatises of the time were those on the Australian Aborigines (T.D. Campbell 1925) and the Bantu-speakers of South Africa (J.C.M. Shaw 1931). Having described dentitions found in various groups, studies then veered towards intensive comparative research. Comparisons of fossil hominid dentitions were also of interest (Weidenreich 1943), and later hominid dental studies, such as the descriptions of *australopithecines* by Robinson (1956) and Tobias (1967), were amplified by increased fossil finds.

An important step forward for dental anthropological research occurred when A. A. Dahlberg (1945) applied Butler’s (1937, 1939) concept of morphogenetic fields to the human dentition. He identified four (rather than Butler’s three) primary dental fields in the human dentition - incisors, canines, premolars and molars – each with a morphologically (and genetically) stable member, almost always identified as the first mesially placed tooth in the field (i.e. lower first molar (M_1) or upper first premolar

(P^3)). He also noted that the most distal field members are usually the most variable, furthering understanding of human dental evolution (e.g. third molar variability and loss). Also, his in-depth work on Native Americans (Dahlberg 1951, 1956) provided valuable comparative data for this group and would initiate a long-term population study. It was also during this time (1956) that Dahlberg developed a set a of dental reference plaques to help standardise trait observations and an improved, more detailed, method of scoring attrition emerged (Murphy 1959).

Various other human dental variation studies are worth mentioning. Pedersen (1949) and Moorrees's (1957) monographs on the Arctic peoples were not only primary comparative texts but also shed light on a previously obscure population (G.R. Scott and Turner 2000). European studies (i.e. Selmer-Olsen 1949; Thomsen 1955) were scarce, while a strong Japanese dental anthropology group emerged (K. Hanihara 1954; K. Hanihara 1955a; K. Hanihara 1955b; Suzuki and Sakai 1955, 1964), outlining what K. Hanihara (1966, 1968) would later define as the "Mongoloid dental complex". It is in the 1960s that dental anthropology took its place as an important subfield of physical anthropology. An edited volume of significant dental anthropological papers (Brothwell 1963) and the first International Symposium on Dental Morphology (Pedersen *et al.* 1967), held in Fredensborg, Denmark in 1965, paved the way.

DENTAL ANTHROPOLOGY SINCE 1965

In the last ±45 years, relatively intensive collection of dental morphological and metric data from many populations around the world has produced a comparative dental data set and, although there is still much work to be done, the world no longer remains "in a state of dental darkness". Studies of both hominin and modern human population dental difference and development have significantly increased. Hominin dental anthropological studies have, among many other things, illuminated Plio- and Pleistocene hominin dental morphology (Bailey 2004; Gómez-Robles *et al.* 2007; Gómez-Robles *et al.* 2008; Wood and Abbott 1983; Wood *et al.* 1983; Wood *et al.* 1988; Wood and Engleman 1988; Wood and Uytterschaut 1987), provided new information in the study of Neanderthals (Bailey 2002; Bailey *et al.* 2011), analysed microwear to assess hominin diet variability (R.S. Scott *et al.* 2005), identified behavioural patterns and wear-related remodelling (Dmanisi) (Margvelashvili *et al.* 2013) and most recently, have identified phylogenetic relationships between the new find, *Australopithecus sediba*, and other hominin species (Irish *et al.* 2013). Dental ontogeny investigations are substantial and although this biological subfield is an important element of dental anthropological study, it is not wholly relevant to the focus of this thesis and too wide-ranging to discuss here in detail. A number of review texts (Butler 1956, 1982; Gaunt and Miles 1967; Kovacs 1967; Kraus and Jordan 1965; Nanci 2008; Oöe 1965; Saunders and Mayhall 1982; G.T. Schwartz and Dean 2001; Townsend and Brown 1981b), outline the stages and physiological processes involved in dental development and eruption (*in utero* to adult), dental histological and morphological differentiation, and tooth chemical composition and structure. More recent studies on dental development differences between modern humans and ancestral hominoids has not only provided new insights into dental relationships between these populations but has also introduced new technical methods of visualising tooth internal and external structure (T.M. Smith and Tafforeau 2008). These studies provide assessments of enamel and dentine microstructure and hominoid dental evolution (Dean 1995, 1998; Dean *et al.* 2001; T.M. Smith 2008b; T.M. Smith *et al.* 2003; T.M. Smith *et al.* 2004; T.M. Smith *et al.* 2006; T.M. Smith *et al.* 2007; T.M. Smith *et al.* 2010).

Modern human population studies include frequency investigations of single morphological traits in a variety of populations (for example, Mihailidis *et al.* 2013; G.R. Scott 1980; Suzuki and Sakai 1973; Townsend and Brown 1981a; Townsend *et al.* 1990) and more commonly, multiple trait analyses within and between population groups (Haeussler *et al.* 1989; T. Hanihara 1990a, 1990b, 1991, 1992a, 1993, 2005, 2008; Irish 1993, 2006; Irish and Konigsberg 2007; Kaul and Prakash 1981; Kieser 1984; Kieser and Preston 1981; Matsumura *et al.* 2009; Mayhall *et al.* 1982b; G.R. Scott and Dahlberg 1982; G.R. Scott *et al.* 1983; G.R. Scott *et al.* 1986; G.R. Scott and Turner 2000; Sofaer *et al.* 1986; Turner 1983, 1984, 1986a, 1986b, 1987, 1989, 1990). To date, approximately one hundred morphological dental traits have been observed and new traits often proposed (most recently, Cunha *et al.* (2012)). A standardised method of dental morphological observation and recording was introduced in 1990, based on earlier ranking methods introduced by Hrdlička (1920) and A.A. Dahlberg after World War II (G.R. Scott and Turner 2008). A series of rank-scaled reference plaques for 36 dental non-metric traits were developed, called the Arizona State University Dental Anthropology System. These plaques were accompanied by a set of rules and guidelines for observers (Turner and Nichol 1991) that need to be followed carefully to minimise inter- and intra-observer error and ultimately maximise comparative analyses. The use of dental standardisation (including plaques) has been cautioned however (Dean *et al.* 1993; Tompkins 1996), due to population variability in dental development (e.g. molars from Africa tend to be more variable than those from Europe) and developmental timing. Metric evaluations (T. Hanihara and Ishida 2005; E.F. Harris and Bailit 1988; E.F. Harris and Lease 2005; E.F. Harris and Rathbun 1991; Kieser 1985, 1990; Matsumura 2001; Matsumura *et al.* 2009; Schnutenhaus and Rösing 1998) collectively demonstrate a great deal of morphometric variation among contemporary populations around the globe. Today, a number of “dental complexes” have been defined that are characterised by distinctive crown, root and size variation across different human populations.

Current approaches to dental studies not only compare population affinities but also ask broader questions relating to population origins, histories, movements and relationships. These questions, prominent in contemporary dental studies, are often interpreted in light of known genetic relationships between human populations. Tooth form and structure has a high genetic component (Dempsey and Townsend 2001; Garn *et al.* 1965; Hughes *et al.* 2007; Hunter *et al.* 2010; Jernvall and Jung 2000; Kelley and Larsen 1991; Maas and Bei 1997; Salazar-Ciudad and Jernvall 2010; Thesleff 2000, 2006; Townsend *et al.* 2012; Townsend and Brown 1978; Townsend *et al.* 2009; Townsend *et al.* 2003; Tucker and Sharpe 1999, among others.) largely responsible for tooth size and morphology. This, added to dental attributes such as lack of environmental plasticity and the genetic stability of numerous tooth traits allow for both synchronic and diachronic (Irish 1993) affinity and biological distance studies. These identify the relationship, difference and/or similarity between and within population groups by comparing trait expression frequencies and/or measures of size/shape. Many researchers have successfully performed such comparisons within and between geographically dispersed groups, highlighting a population’s past and in some cases, population movements. The pioneering work of Turner (1971, 1983, 1984; 1985a; 1985b; 1986a; 1986a) on the Native American dentition for example, is an important early example of how dental trait frequencies can be used to infer population histories. By surveying the frequency of three-rooted M_1 (Turner 1971), he identified three Native American population subgroups and inferred that the dental variation of these subgroups corresponds to three separate population movements into the Americas. The first wave of migration was the various Palaeoindian tribes who presented with low frequency three-rooted M_1. The second migration came from Asia and included the ancestral Na-Dene Indian populations from West and Northwest American coast. These populations presented with an intermediate frequency for the trait. The final immigrants were the Eskimo-Aleut groups from Alaska and Greenland demonstrating the highest trait frequency. By expanding his North American dental data set and assessing a suite of 29 crown and root traits, Turner (1983, 1984; 1985a; 1985b; 1986b) was able to corroborate his three-stage model for the peopling of the Americas. His analyses also demonstrated a dental relationship between Native American and Asian populations, especially North East Asians (G.R. Scott and Turner 2000). Linguistic, archaeological and genetic evidence (Greenberg *et al.* 1985, 1986; Williams *et al.* 1985) supported these findings, strengthening the hypothesis of terminal Pleistocene migrations from Asia via the Bering Strait into the Americas. The most current genetic work has shown these early ideas based on dentition and linguistics to be true (Reich *et al.* 2012).

DENTAL COMPLEXES

Contemporary studies led to what we think of today at dental complexes. There are currently a number of these including various sub-groups within each. For the purposes of this study, four major groups are outlined, providing a global dental view. They are the Sindodonts, Sundadonts (of which Australian dentition is a subgroup), the Western Eurasian group, and the sub-Saharan Africa dental complex.

SINODONTS AND SUNDADONTS

Based on observations of four traits (high frequency of shovel-shaped incisors, lower molar deflecting wrinkle, cusp 6 and the protostylid) in Japanese, Native American and Eskimo populations, K. Hanihara (1968) defined the 'Mongoloid Dental Complex. Later work by Turner focussed on populations in Asia, Australia and the Pacific (Turner 1987, 1989, 1990), and using a suite of 29 traits, showed a fundamental eight trait morphological dental division within East Asia and the Mongoloid Dental complex. The division, coined by Turner as Sinodonty (Sino- referring to China as Turner first recognised the dental pattern in Chinese skeletons from Anyang) and Sundadonty (Sunda- referring to Sundaland, a region of Southeastern Asia that encompasses the Sunda shelf) identified a subdivision between Northeast and Southeast Asians, respectively. Sinodonts are widespread comprising the major populations of China, Japan, Korea, Mongolia, Northeast Asia, and North and South America (G.R. Scott and Turner 2000) and appear to be the most derived among modern humans (Stringer *et al.* 1997). These populations present with significantly high frequencies of I^1 incisor shovelling and double shovelling, single-rooted P^3, M_1 deflecting wrinkle, 3-rooted M_1, upper first molar (M^1) enamel extensions, and reduced upper third molars (M^3). Also, Sinodont populations have intermediate sized teeth when compared globally, with the exception of Native American groups which generally have large cusp diameters (T. Hanihara and Ishida 2005). Of particular interest, are the dental studies conducted on the Neolithic hunter-gatherer populations from the Jomon period in Japan. Here, limited regional dental variation was observed between five geographically dispersed sites from similar timeframes (*ca*. 12 000 BP - 2300 BP) (Matsumura 2007). Collectively however, the population is largely homogenous and demonstrates ties to modern Southeast Asian groups, largely supporting cranial evidence (Dodo 1986). The Sundadont pattern on the other hand, is relatively confined to Southeast Asia, with most trait frequencies conservative, falling around the mid-range values of world variation. This dental division can be traced to ca. 20 – 30 ka as sinodonty has been identified in Zhoukoudien Cave fossils from China (Turner 1985b) and the sundadont pattern manifests in Minatogawa skeletons from Japan, dated to ~17 ka (Turner 1992a).

Further evidence of the Asian dental dichotomy is evident in the Pacific basin. Polynesian and Micronesian populations demonstrate the Sundadont dental pattern, supporting the hypothesis of a Southeast Asian origin for these populations (G.R. Scott and Turner 2000; Turner 1990). Polynesian and Micronesian groups join the Australian populations with some of the largest teeth (T. Hanihara and Ishida 2005) but morphologically, Australian dental groups are less defined. Although they stand out as having the largest teeth when compared globally, morphologically they demonstrate similarities to Southeast Asian dentition (Sundadont), suggestive of an ancient Southeast Asian dental evolution, not the product of admixture (Turner 1990). Surprisingly, Australian and sub-Saharan African dentitions demonstrate a close relationship (Turner 1992a). Stringer (1993) conducted cladistic analyses on Turner's (1987) work and demonstrated that the shared Australian and African dental traits were likely plesiomophic, corresponding to genetic clades (e.g. Cavalli-Sforza 1991) and cranial studies (T. Hanihara 1996; Stringer 1992). Although archaeological evidence is limited, the antiquity of Australian aboriginal populations is generally accepted and some researchers (T. Hanihara 1992b; Townsend *et al.* 1990) believed that Australian dentition was not only older than sundadont development but was also different enough to warrant its own designation. However, the unmistakeable similarities between Australian dentition and Sundadonty could not be ignored. The term proto-Sundadont (first used by Turner at the University of Tokyo symposium on the evolution and dispersal of modern humans in Asia (Trinkaus 1990)) was applied to these ancestral groups and by using genetic (Omoto 1984) and dental (Turner 1992b) evidence, T. Hanihara (1992b) developed an ancestral dental dispersal pattern for Sunda populations. According to his research, a founding proto-Sundadont population inhabited Sundaland ~100 ka and the Australian dental pattern (low frequencies of incisor shoveling and winging, and high frequencies of M_1 cusp 6, M^1 cusp 5, upper second molar (M^2) hypocone and hypoconulid) with ties to earlier proto-Sundadonts, developed in isolation later. In turn, the slightly varied (with higher frequencies) Sundadont complex developed in Sundaland during the Upper Pleistocene and thereafter spread north from Southeast Asia to Japan (G.R. Scott and Turner 2000).

WESTERN EURASIA

Alongside major Sinodont and Sundadont research, dental difference was also assessed (less fervently) in Western Eurasia which includes Western Europe, North Africa, the Middle East and the Indian sub-continent. A wide-range of skeletal research (some of which include dental) has been conducted on archaeological specimens from Mesolithic Indus civilisations to Bronze Age, Neolithic and historical populations from this region but overall, dental investigations for ancient and modern populations on the Indian subcontinent has been limited (Walimbe 2009). Available studies do however demonstrate dental affinities to teeth from Central and South Asia while indicating a large amount of regional dental dissimilarity (i.e. Hemphill 2013; Hawkey 2002; Kaul and Prakash 1981, 1984; Lukacs 1983, 1985, 1987, 1988, 1989; Lukacs and Pal 1993). Prehistoric populations here appear to have a relatively similar dental morphology structure, enough to warrant a complex of its own, often referred to as Indodont (Hawkey 1999). Ancient populations from the Iranian plateau and towards the west have also been investigated, identifying possible gene flow between these and ancient Mesopotamian groups and offer further insights to the peopling of South Asia (Hemphill 2008, 2009, 2011, 2013; Hemphill *et al.* 1998; Hemphill *et al.* 1991; Lukacs and Hemphill 1991). Also, Hawkey (2002) has found that modern farming and herding populations in the Indus Valley and Deccan plateau share dental similarities with Indian Mesolithic hunter-gatherers, suggesting a common ancestry. According to this study, early Indus civilisations are most likely descendants of aboriginal South Asian hunter-gatherer groups, rather than from genetically distinct groups from the west, suggestive of dental (and presumably genetic) continuity on the Indian sub-continent over the past ~20ka. A large part of the Indian subcontinent also demonstrates dental (and genetic) ties to Europe. The Indus civilisations not only demonstrate dental affinities to South Asia groups but are also dentally similar to Indo-European populations such as Afghanistan and Pakistan (Hawkey 2002) although further investigation is needed to strengthen these assertions. New research on the early Holocene foragers of North India compares the archaeological populations (Mesolithic Lake Culture) to prehistoric and modern South Asian dental groups, finding traits similar to both Sundadonts and Indodonts (Lukacs *et al.* 2013).

Historically, European teeth were a source of early dental investigations as is evidenced by some of the earliest dental trait analyses i.e. Carabelli's trait (Von Carabelli 1842) and comparative race dissimilarity studies (e.g. Hellman 1928) emerging there. As a dental grouping, Western Eurasians or Caucasoids (including populations of Western, Eastern and Northern Europe, the Middle East and North

Africa) exhibit simple crown morphology (Kirveskari 1978; Kirveskari *et al.* 1978; Mayhall *et al.* 1982a; G.R. Scott 1980; G.R. Scott and Turner 2000; Turner 1992b; Zubov and Khaldeeva 1979) and are separated from other dental divisions by high frequencies of four-cusped M_1 and M_2, three-cusped M^2, 2-rooted upper canines (C^1), and upper molar Carabelli's traits. Remaining traits occur at low or intermediate frequencies. Metrically, Caucasoid dentition is considered some of the smallest within a global context, on a par with only a few small South East Asian population groups (T. Hanihara and Ishida 2005). Studies of European dental ancestry and microdiffusion are limited. Although European genes are thought to emerge from the Levant during Neolithic times (Barbujani and Bertorelle 2001), dental (and cranial) research has demonstrated a lasting gene pool in Iberia during the Mesolithic and into the Neolithic (Jackes *et al.* 2001). Some studies on prehistoric European populations (predominantly central and eastern Europe) demonstrate an element of biological continuity from antiquity to early medieval times (Haussler 1995; Kaczmarek 1992; Papreckiené and Ĉesnys 1983; Piontek *et al.* 2007; Zubov 1998). Dental evidence from the Balkan Peninsula has also been used to track long-term population migrations and mixed Corinthian/Albanian ancestry across the area during the first millennium BC (Kyle McIlvaine *et al.* 2013). Overall, serological studies have shown that in Europe, European rather than Asian origins are prevalent and dental morphological studies seem to be consistent with findings (Kirveskari 1978). In addition, North Africans demonstrate a strong similarity to Europeans and they share many morphological traits (Irish 1993, 1997), while measureable homogeneity is demonstrated within North African regions.

SUB-SAHARAN AFRICA

In general, odontological investigations in sub-Saharan Africa are limited. In some regions over the last 40+ years however, there has been an increase in research providing some morphological and metric data on various populations including those populations pertinent to this thesis i.e. Bantu-speaking, Khoesan and Kenyan populations. Following the need for dental descriptions of human populations, J.C.M. Shaw (1931) provided morphological observations of the dentition of the Bantu-speaking peoples of South Africa, including those on molar cusp and root number, canines and incisors. He outlined size, morphology, tooth wear and pathological change of these populations but his study was largely descriptive in nature due to a lack of comparative data. Later, metric and morphological analyses of recent sub-Saharan Africans (Negroid samples only) by Jacobson (1968, 1982), Haeussler *et al.* (1989) and Irish (1993, 1997, 1998a, 1998b) revealed significant differences between these and other dental complexes from around the world. This research suggested that Sub-Saharan African groups were markedly homogenous in terms of their dental difference, and share several characteristic dental crown and root traits (as outlined in the sub-Saharan African dental complex). This complex also contains some ancestral traits found in earlier hominid dentitions, suggesting a remarkably long Sub-Saharan dental morphological timeframe, which could ultimately shed some light on human origins (Irish 1998a, 1998b; Stynder *et al.* 2001). In Kenya, published dental non-metric studies are limited to modern populations such as the Teso (Barnes 1968, 1969) from Western Kenya and the pastoral Masai (Barnes 1969; Hassanali 1982; Hassanali and Amwayi 1988) from the Narok and Kajiado districts. Most other publications (besides research by Irish discussed below) relate to dental health and dentistry issues. Barnes (1968; 1969) evaluated 5000 Teso individuals and recorded information on a number of traits and dental anomalies. Some trait frequencies of interest included an 11% presence of upper central incisor shoveling (I^1), 23% frequency of I^1 tuberculum dentale, and a high frequency of 2-rooted P^3. ~10% of the population presented with a M^1 Carabelli's trait and almost all (99.7%) had M_1 fifth cusps (24% on M_2) and few with cusp 7. The study also noted a difference between the sexes with regards to a few traits, namely the Carabelli's and cusp 7. The Masai teeth were reported to have dental spacing and a midline diastema frequency of 35% on a study of 206 individuals (Hassanali 1982) as well as a very high Carabelli's trait frequency (80%) but the recording methods used are possibly unreliable.

Other studies of sub-Saharan African dentition have largely grouped people geographically (by ethnic grouping) and/or linguistically. Metrically, teeth from sub-Saharan Africa are generally large, comparable to sizes found in Native Americans (T. Hanihara and Ishida 2005). In terms of non-metric information, T. Hanihara (2008) notes that sub-Saharan Africa demonstrates the most intra-regional dental phenotypic variation globally. However, sub-Saharan Africa has been grouped as a dental complex. Irish (1993) provides a large amount of valuable morphological data on a variety of northern and sub-Saharan African groups and analyses the variation between them. Beyond his work, little has been published and comparative assessments on a global scale (i.e. G.R. Scott and Turner 2000) inevitably rely on that treatise. Irish's (1993, 1998a; 1998c) work reveals a significant divergence between North African (with the exception of Chad and Mesolithic Nubia) and sub-Saharan African samples but his inter-regional comparisons (too extensive to discuss here) suggest some homogeneity between the sub-Saharan regions. Results, based on a battery of 36 dental morphological traits, reveal that Central and West African groups from, for example, Ghana, Togo/Benin, Nigeria and the Democratic Republic of Congo (DRC) have relatively close affinities to each other as well as to the Sotho (a South African Bantu-speaking population), while East African (Kenya, Tanzania), South African (Bantu-speaking populations and the Khoekhoe (Khoikhoi in his study)) and Pygmy (from DRC and Gabon) groups demonstrate some affinity. The San, and to a certain degree the Mesolithic Nubians, are noted as those with greater phenetic distance to other populations within the sub-Saharan group but still fall within the range of variation seen sub-Saharan African dentition. Based on comparisons between sub-Saharan African dentition and teeth from other world groups (North Africa, Europe, Sinodonts, Sundadonts, Australia and Melanesia) Irish (1993; 1997) proposed a suite of eleven traits that were ubiquitous in the sub-Saharan African dentition. This was termed the sub-Saharan African dental complex and most recently is referred to as "Afridonty" (Irish 2011, 2013). These terms are interchangeable in this thesis. This collection of distinctive traits identified a southern African dental complex comparable to other dental world patterns. It consists of two of the world's lowest frequency traits namely, I^1 double shoveling and M^1 enamel extension, and nine high frequency traits including, canine mesial ridge (CMR) on upper canines (Bushman canine), P_3 Tome's root, 2-rooted P^3, M_2 Y-5 groove pattern, M_1 cusp 7, 2-rooted M_2, M^1 Carabelli's trait, 3-rooted M^2, and the near highest global frequency of M^3 presence. Irish (1997) also noted relatively high frequencies of I^1 labial convexity and the midline diastema but are not included in the complex as these features are not routinely recorded around the world. Using this complex, sub-Saharan Africans are identified as least like Sinodonts and display more dental similarity to Australian and Melanesian samples than to Europeans, Sinodonts and Sundadonts (Irish 1993). On a smaller scale, the Khoesan, as part of the sub-Saharan African dental complex, have demonstrated some differences between them and other sub-Saharan groups, for example dental differences between the Khoesan and one Bantu-speaking population (Central Sotho) were identified (Haeussler *et al.* 1989), but similarities between these sub-Saharan population groups were considered to outweigh any differences.

Dental complexes are useful in terms of global patterning. Patterns known today (discussed above) emerged from meticulous and systematic inter-population dental analyses and have contributed to resolving a host of historical anthropological problems (although most work has been focused on Asian and North American populations). Examples include the dental division in Asia, the peopling of the Americas, and elucidating some Pacific basin prehistory, among others. Intra-population dental variation studies (such as this study) are not as common as fairly large sample sizes are needed to detect population continuity or distinguish regional, ethnic or otherwise segregated groups. Two of the largest studies of this type estimated both dental and genetic distance between groups in one population. A study was conducted on the Yanomama tribe of South America by Brewer-Carias *et al.* (1976), in which eight non-metric dental traits on 700 individuals from seven villages were analysed. E.F. Harris (1977) analysed 44 dental variables in >1200 Solomon Island individuals spread across 14 villages. In each study, dental traits demonstrate less divergence than genetic markers (G.R. Scott and Turner 2000). Since each trait is most likely influenced by many genes, dental traits have a “slower rate of biological differentiation and therefore smaller trait frequency differences between groups” (Sofaer *et al.* 1986 in G.R. Scott and Turner 2000: 262). Due to slow rates of differentiation, intra-population dental morphological analyses fixed in time may be limited but studies conducted on relationships among populations separated temporally are more successful (G.R. Scott and Turner 2000). Recently, such a study by Irish (2006) of 996 individuals using up to 36 dental traits illustrates moderate variation with overall population continuity from Neolithic through Roman times in Upper Egypt (sites include among others, Gebel Ramlah, Abydos and Thebes) and Lower Egypt (sites include among others, Saqqara, Giza and Hawara). Sample sizes and the batteries of traits used vary substantially in these studies and are largely dependent on specimen availability. Larger sample sizes are preferred but dental anthropological work on archaeological specimens has frequently required the development of statistical analyses that can help correct for smaller sample sizes.

Dental metric evaluations worldwide outline basic size variation (see above) but also demonstrate that odontometric patterning among major geographic populations is consistent with those seen in craniometric and genetic investigations (T. Hanihara and Ishida 2005). Geneticists have demonstrated that Africans are the most different in comparison to all human populations (Cavalli-Sforza *et al.* 1994) but craniometrically, Africans cluster with Australians and Melanesians (T. Hanihara 1996) and dentally, Africans are not the most highly differentiated group. Although some frequencies of African morphological features are distinctive and even unique, trait frequencies associated with the Sinodonts and Western Eurasian groups hold the prize for overall extreme dental difference (G.R. Scott and Turner 2000). However, sub-Saharan Africans demonstrate the greatest degree of regional dental diversity when compared globally. On a world scale, dental morphological traits demonstrate distinct patterns of geographic variation, creating the major dental complexes discussed above, each defined by a small, distinctive set of crown traits and relative size.

KHOESAN DENTAL STUDIES

The Khoesan are at one end of the spectrum of variation of human populations and have been and continue to be of great interest. While many African groups are not well-studied, there is a long history of Khoesan research, in part because of their ethnographic importance to our understanding of hunter-gatherers and in part because of their antiquity and the possibility that they represent the direct descendents of the population from which, some believe, early modern humans might have evolved.

Dental anthropological studies of the Khoesan began in the early 1900s following initial cranial investigations (i.e. Broom 1923, 1941; Drennan 1929a) and research into the paedomorphic nature of the mandible and maxilla (Galloway 1941; Schepers 1934). These limited dental studies explored metric and morphological aspects and tried to compare their findings with those for populations in other parts of the world, in as far as these were available. A number of trait frequencies were evaluated, tooth sizes assessed and pathological changes recorded. Below is a synopsis of early studies and an outline of more recent evaluations of these findings. Some of the earliest dental studies were conducted by Drennan (1929b) who analysed a group of exhumed recent Khoesan skeletons from Colesberg in the Northern Cape (Region A in this study). His study comprised a rough comparison between Khoesan and other dentitions available to him, namely those from Bantu-speaking and Australian aboriginal populations. He highlighted the population's dental index (a ratio between the length of teeth and distance from the nasion to the basion, multiplied by 100), attrition, caries, and other pathological changes, and provided mesiodistal and buccolingual tooth crown measurements. Dental measurements for Khoesan teeth were found to be generally smaller than those of Bantu-speaking populations and very small in comparison to Australian aboriginal teeth. These data were also compared with the dentition of the Peers Cave (Fish Hoek) skeleton which, at the time, was considered ancient (Middle Stone Age). Drennan (1929b) described the dental index of the Peers Cave specimen as very different from other populations but on inspection of individual dimensions, the mesiodistal and buccolingual crown measurements fall within the range of diameters of Khoesan teeth. A new radiocarbon date for the Peers Cave skeleton of 6891 ± 37 BP (OxA-17376) (Stynder *et al.* 2009) places it in the mid-Holocene and not the Upper Pleistocene, positioning it firmly within Khoesan population history. Drennan's later (1937) paper discussed recent Khoesan mandibular tori and noted a 32% frequency of the trait, contradicting previous work by J.C.M. Shaw (1931) who reported a 7% presence from a similar data set. Some dental investigations were solely aimed at describing Khoekhoen or Boskopoid (the Boskop skull was a fossil specimen thought to be the direct ancestor to modern Khoesan peoples and, for a time, was used to characterise a "physical type") dentition and its difference from San (Drennan 1946; Galloway 1959) but the little available evidence could not provide firm assertions.

A cranial study on more recent (protohistoric) Khoesan populations by A.G. Morris (1992b) (as will be discussed in greater detail in later sections), does not discuss dental morphology but briefly notes on dental pathological changes (e.g. caries) and how they relate to diet. For example, the skeletons from Riet River (Region A), present with high incidences of caries, marked occlusal attrition, low antemortem tooth loss, suggestive of, according to A.G. Morris (1992b), a hunter-gatherer lifestyle. Metric and non-metric (based on 7 traits) studies on the Griqua population (N=27) (a group of mixed descent but with substantial Khoekhoen ancestry), also compared dentitions between the Griqua and the Khoesan (N=121 to 155 and varied for each trait, depending on literature used) to evaluate correlations between related populations, and between the Griqua and other world populations to assess global standing (Kieser 1984, 1985). Little metric difference was found between the local dentitions, and small morphological differences were attributed to admixture or migration. Globally, the Griqua group showed overall differences in trait expression and size. Morphological studies on the dentition, jaws and palate of the modern Khoesan in the late 1950s (Van Reenen 1964, 1966) were largely descriptive. These studies, conducted on ~400 individuals (male and female) included dental measurements, limited trait evaluations, and information on pathological change i.e. caries and dental diseases, and dental cultural treatments and complemented earlier pathological work by Dreyer (1935) conducted on <35 archaeological specimens. Van Reenen's (1964)work identified some morphological trait characteristics of Khoesan including, for example, that 11% of the studied population displayed a midline diastema, 10% of the population presented with crowding (also identified by Sperber 1958), 11% demonstrated the Carabelli's trait, while >30% had marked spacing between teeth (Van Reenen 1966). Other morphological studies observed low frequencies of I^1 shovelling (Tobias 1972) with slightly higher frequencies in females. Irish's (1993) study demonstrates higher frequencies of shovelling (40%) on his San data and a frequency of 0% for Khoekhoe. Cleaton-Jones (1970), in a study of 189 individuals, noted that lateral incisors (I^2) were sometimes reduced (peg-shaped) or missing in ~7% of Khoesan dentition. This low frequency occurrence remained constant in later work (Irish 1993; G.R. Scott and Turner 2000). The CMR, colloquially known as the 'Bushman Canine,' was first identified by Oranje (1934) as a "premolariform" canine. Later work by D.H. Morris (1974, 1975) identified the trait in >40% of a Khoesan dental sample studied. This feature was found in conjunction with a tuberculum dentale and was strongly expressed. D.H. Morris (1975) regarded this trait as characteristic of African populations due to its low frequency in other studied populations. Evaluations by Haeussler *et al.* (1989) (N=58) also demonstrate an above 40% occurrence (43.1%) of this trait. A reassessment of the trait by Irish and Morris (1996a; 1996b) provided a clearer understanding of the trait and methods of evaluation, while other studies (Irish 1993; Irish and Turner 1990; Sakuma *et al.*

1991) highlighted the widespread African distribution of this feature as well as its rarity outside Africa.

Early enquiries described molar morphological features of the Khoesan dentition as different from other groups. The presence of a fifth cusp on lower molars was observed in over 70% of each data set and a high occurrence of the trait (nearly 100%) noted on M_1 (Drennan 1929b; Haeussler *et al.* 1989; Oranje 1934; Van Reenen 1966). According to Van Reenen (1966) and Drennan (1929b), these trait frequencies were unlike those seen in European and Australian populations and more recent work has demonstrated that four-cusped lower molars are infrequent but are most common in Western Eurasian populations (G.R. Scott and Turner 2000). Reductions in lower third molar size, resulting in a peg-shaped or largely reduced molar, were also identified (Drennan 1929b) but were rare. It was observed that upper molars usually displayed four cusps with the exception of the M^3 which, up to 50% of the time, exhibited only three (Drennan 1929b). Recently published frequencies of three-cusped upper molars demonstrate substantial hypocone variation around the globe (G.R. Scott and Turner 2000). Additional cusps on M^1 and M^2 were sometimes identified (Oranje 1934). The frequency of the Carabelli's trait in Khoesan data sets has varied due to differences in sample sizes and recording methods, i.e. lack of standardisation. Reported frequencies range from 6.5 to 42% (Haeussler *et al.* 1989; G.R. Scott 1980; Shapiro 1949; Tobias 1972; Van Reenen 1964). Also, evidence of taurodontism was demonstrated (J.C.M. Shaw 1927, 1928) and has been shown to appear predominantly on third molars (Constant and Grine 2001).

Sexual dimorphism in dental features within the Khoesan people was found to be low (Van Reenen 1970) and later studies (i.e. Irish 1993) pooled the sexes because sample sizes were small. In general, researchers consistently find low levels of metric sexual dimorphism (2-7%) in teeth globally (cf. Garn *et al.* 1966; T. Hanihara and Ishida 2005; Moorrees 1957; G.T. Schwartz and Dean 2005; G.R. Scott and Turner 2000). Canines, considered to be the most sexually dimorphic tooth in humans, have shown higher levels of dimorphism metrically - between 8-9%, depending on the population (Moreno-Gómez 2013; Staka *et al.* 2013). Dental tissue studies have also found that male canines present with more dentin, while females have more canine crown enamel (Saunders *et al.* 2007). Non-Metric sexual dimorphism also appears to be relatively low. Recent research on selected dental traits such as the Carabelli's trait and protostylid on molars, incisor shoveling, and premolar cusp formations (Moreno-Gómez 2013) have demonstrated little dimorphism and first molars are found to vary in size only, while cusp morphology is largely unrelated (Polychronis *et al.* 2013). Sexual dimorphism in Khoesan dentitions is within this range although the M^3 congenital absence trait has demonstrated significant differences between the sexes in sub-Saharan Africa (Irish 1998a) but not in this study. Metrically, Khoesan overall dental size is small, or microdont, in comparison to other human populations (Brace *et al.* 1991; Drennan 1929b; Haeussler *et al.* 1989; G.R. Scott and Turner 2000; Sperber 1958; Van Reenen 1964, 1966), and dental dimensions can be affected negatively by attrition shortly after eruption due to the nature of Khoesan diet (Van Reenen 1982).

As mentioned, Irish (1993) investigated the origins, affinities and dental morphometrics of aboriginal dentitions throughout Africa. Using techniques set out by the Arizona State University Dental Anthropology System, or ASUDAS (Turner and Nichol 1991), he examined 36 dental and osseous traits (when possible) within population geographic, cultural and/or linguistic boundaries. Furthermore, he compared the suite of dental traits between populations, identifying phenetic similarities and correlations between data sets. His study included dental observations from 20th century adult San (N=99, of which 83 were casts and 16 were skeletal specimens) and 19th century adult Khoekhoe (N=37), treating each group as a separate population. The 83 dental casts were copies made from the impressions obtained by the Nuffield Foundation Witwatersrand Kalahari Research Committee Expedition (Haeussler *et al.* 1989) from a farming region near the town of Ghanzi, in northwestern Botswana. These individuals belonged to various ethnic groups including, Gwikwe, !Kung, Mkaukau, Naron and Tshakwe (Irish 1993). The remaining specimens (16) are historical and were recovered west of Bloemfontein, near the town of Douglas. Irish (1993) does not specify how these samples were identified as San, making their ethnic identity somewhat unreliable. The majority (22) of the historic Khoekhoe data set consists of individuals from the Orange River Valley near Douglas and Upington in central South Africa and a few from the Cape, although exact provenance is unavailable. These specimens were linked to the Nama and

Korana ethnic groups who had a language which resembled that of the San, had some physical differences, and a pastoralist way of life. After being collected at the turn of the century, these specimens were curated as part of the von Luschan Collection at the American Museum of Natural History (Irish 1993). The remaining specimens, also from the Nama and Korana ethnic groups, were collected in 1816 and are housed in the Musée de l'Homme. It is important to note that today the Khoe and San cannot be separated biologically (Hausman 1982; Rightmire 1970, 1978) and are currently considered one single biological population exhibiting within-population variation i.e. cranial (Stynder 2009). Results demonstrated that the San have a highly complex dentition that includes an unusual set of trait combinations including high frequencies of I^1 shovelling, CMR, M^1 cusp 5 or metaconule, M_1 cusp 7, and five-cusped M_2. Irish (1993) also identified differences between the San and most other African dentitions. Most notable of these include the San high frequency occurrence of I^1 winging and rocker jaw and a low frequency of the upper canine (C^1) distal accessory ridge in comparison to these. He also notes that there is no evidence of the P_3 Tome's root but assessing this trait was problematic as many of the samples were casts. Furthermore, Irish (1993) identifies these trait combinations as rare in sub-Saharan Africa, placing the San (not the Khoekhoe) at "an extreme form of the dentally-complex pattern common in sub-Saharan Africans" (Irish 1993: 222). The San dental suite is unique (Haeussler *et al.* 1989) and when compared with other African samples, Irish (1993) states that only the Khoekhoe, the South African Nguni and the Pygmy populations (from the Congo) show an affinity to the San. Irish (1993) attributes the affinity between the populations as either a statistical problem due to small sample sizes (Pygmy) or an ancient relationship. Interestingly, both the Pygmy and Khoesan populations have unique dentitions and share a high frequency of African marker alleles (King and Motulsky 2002), but major morphological and genetic differences make associations unlikely. The Khoekhoe dentition presents with the highest frequency of the CMR, high frequencies of I^2 interruption groove, C^1 distal accessory ridge, M^3 congenital absence and rocker jaw, while lower frequency traits include M^1 metaconule and M_1 deflecting wrinkle, very low frequencies of the M^1 Carabelli's trait and 2-rooted P^3, and no expression of I^1 shoveling. The Khoekhoe are less extreme in their dental attributes in comparison to the San dentition and display affinities to many African groups including the Bantu-speaking (most likely the result of admixture), East African (fuelling the East African origin hypothesis popular at the time), and North African populations. Little affinity was demonstrated between Khoekhoe and West African groups from Ghana, Togo, Benin, Nigeria, Cameroon, and Gabon, attributed to a lack of gene flow in these samples. The Khoekhoe demonstrate a dental affinity to the San due to, according to Irish (1993), common ancestry and recent admixture, building on earlier skeletal, genetic and anthropometric research by Tobias (1972), Mourant (1983) and Nurse *et al.* (1985), while the dissimilarity between them he attributes to a) random genetic drift from a time when these populations lived in close proximity, b) Khoekhoe adaptation to different environments, and c) greater Khoekhoe admixture with the later arriving Bantu and European populations. Statistical results further illustrated San (and Khoekhoe) divergence but still maintain a link to sub-Saharan population groups, permitting these samples to be included in the consolidated sub-Saharan dental group. Although this complex was based on recent (i.e. 19th and 20th century) and geographically dispersed populations, it provides a preliminary characterisation of sub-Saharan dentition on a global scale.

As part of the Afridonty complex, Khoesan dental data has been included in a variety of human origins discussions and comparisons (Irish 1998a, 1998b; Irish and Guatelli-Steinberg 2003). These studies highlight the morphological variability in sub-Saharan Africa and interpret the lack of close affinity, or divergence, between these and other dental groups as evidence of either a) African origins or b) differences too great to represent an ancestral link. Traits common in the Afridonty complex are widespread and occur in high frequencies in dentitions of extinct hominins, suggestive of ancestral ties. The CMR, M^1 enamel extension, M^3 agenesis, and M_1 cusp 7 appear to be derived features, while two-rooted P^3, M^1 Carabelli's trait, three-rooted M^2, M_2 Y-groove pattern, M_2 cusp 5, P_3 Tome's root, two-rooted M_2, and low frequencies of M^3 reduction are present in early hominins and therefore represent retained archaic traits (Bailey 2002; Irish 1998a; Irish and Guatelli-Steinberg 2003). Beyond the study of Irish (1993), little morphological dental research has been directly conducted on adult Khoesan dentition. A.G. Morris (2002, 2003) suggested that Khoesan morphology developed in a geographically isolated southern African population at about the time of the Last Glacial Maximum. He argues for the existence of unique Sub-Saharan ancestral traits, but unlike Irish (1998a, 1998b) he places the distinctiveness of Khoesan morphology at its core. Genetic studies have outlined the distinctive and ancient lineage of the Khoesan (Knight *et al.* 2003; Pickrell *et al.* 2012; Schlebusch *et al.* 2012; Tishkoff *et al.* 2007) and have suggested genetic links between the Khoesan from southern Africa and East African groups such as the Hadza and Sandawe (Tishkoff *et al.* 2007) and Central African populations (Henn *et al.* 2011; Tishkoff *et al.* 2009). Stynder's (2006) recent study of Holocene Khoesan cranial material suggests long-term morphological (and presumably genetic) continuity in South African populations, also suggestive of Khoesan distinctiveness.

Many dental investigations have noted parallels between biological affinities and language families (including Irish's work on sub-Saharan Africa). Some researchers group their data according to language family groups for comparative purposes, providing notable results. For this study, linguistic groupings have not been used as a basis for dental comparisons. Khoesan languages are numerous and complex, and their histories and classification are contested. Furthermore, the use of modern Khoesan linguistic relationships and geographical locations is only peripherally applicable to the data reported in this thesis, most of which comes from regions further south than those occupied by Khoesan-speakers today. We know that there have been substantial changes in the languages spoken in southern Africa over the past several thousand years: for example, at the time of European contact, the southern and western Cape coastal regions were occupied by speakers of Khoekhoen languages. We have no records of the older San languages that these displaced, but the linguistic landscape of these regions prior to 2000 BP was certainly very different. Linguistic groupings are therefore not helpful on the time-scale addressed in this thesis.

MIDDLE AND LATE PLEISTOCENE TEETH IN SOUTHERN AFRICA

A number of investigations have focused on Middle and Late Pleistocene dental material, all >35 000 years old. Such sites have yielded more teeth than any other human skeletal elements. Sites where adult human dental remains have been recovered and are pertinent to this thesis include Blombos Cave (Grine and Henshilwood 2002; Grine *et al.* 2000), Die Kelders (Grine 2000; Grine *et al.* 1991), Sea Harvest (Grine and Klein 1993), Klasies River Mouth (Grine 2012; Grine *et al.* 1998; Rightmire and Deacon 1991, 2001; Royer *et al.* 2009; Singer and Wymer 1982), Border Cave (Beaumont 1978, 1980; De Villiers 1973, 1976), Hoedjiespunt (Berger and Parkington 1995; Stynder *et al.* 2001), Cave of Hearths (Curnoe 2009; Dart 1948; Mason 1988; Tobias 1971) and the Hofmeyr cranium (Grine *et al.* 2007). Metric and non-metric data have been collected on some of these specimens and the results have been used for limited comparisons of crown size and morphology with modern African and archaic European (Neanderthal) teeth. In general, MSA tooth dimensions from South Africa fall within the range of modern humans around the world, but many of them fall outside the range of Khoesan measurements and tend to be larger than Khoesan samples and more comparable to modern African and archaic African and European homologues. Specimens from Die Kelders (Grine 2000), Sea Harvest (Grine and Klein 1993), and Hofmeyr (Grine *et al.* 2007) for example, have crowns that tend to be large in comparison to recent African homologues and approximate or exceed archaic European measurement means. Older Middle Pleistocene specimens such as those from Cave of Hearths (Curnoe 2009; Tobias 1971) and Hoedjiespunt (Berger and Parkington 1995; Stynder *et al.* 2001) have been compared with earlier hominin species to determine size and minimal trait associations. Some crown size correlations between the Hoedjiespunt specimens and early *Homo* and *H. erectus* exist on a limited scale but results vary from tooth to tooth. The Hoedjiespunt incisors are larger than archaeological and modern African samples but comparable to dental dimensions from African, European and Asian human teeth from the early Middle Pleistocene. Other dental remains like those from Klasies River Mouth are variable with some very large molars similar to archaic European and African teeth, and others that are very small. These small teeth are comparable to Khoesan sizes and as Grine (2012) argues, in terms of modern morphometrics, have a tendency toward tooth size reduction, the degree of which is unparalleled in recent populations. Some researchers have attributed the marked size variations to sexual dimorphism (Rightmire and Deacon 1991; Royer *et al.* 2009).

Although research on permanent Mid- and Late Pleistocene teeth has focused on metric data, some non-metric traits have also been studied. The two Cave of Hearths molars for example, present with a + groove pattern and fifth cusp (Tobias 1971).

The only known non-metric evaluations of the Hoedjiespunt specimens yielded one observation of faint shoveling on HDP1-3 (Stynder *et al.* 2001), a left I^1 that was not available for this study, and a reduced hypocone on an upper second molar (HDP1-1) (Berger and Parkington 1995). Also, a number of Die Kelders specimens have been assessed for trait presence, unfortunately most of the samples are deciduous and provide little information for the purposes of this study. On available adult teeth, shoveling has been recorded as absent on one I^1 and the CMR has been recorded as absent on the only available canine. Two M_1 have a fifth and seventh cusp with Y-groove patterning, while one presents a deflecting wrinkle. One M_2 has a + groove pattern (a variant of the Y- and X-groove patterns) with a fifth and sixth cusp (Grine 2000), and none of the molars express a protostylid. Comparisons between these findings and recent sub-Saharan populations, including South African and Khoesan groups demonstrate some similarities (Grine 2000) but there are no systematic comparisons with well-described, statistically significant Khoesan samples from more recent time periods.

GENETICS IN DENTAL ANTHROPOLOGY

Starting in the 1950s, dental morphological studies were complemented by molecular genetics research. Early work by Lasker (1950) reviewed a suite of morphological crown traits, outlining dental characteristics and the possibility that discrete crown traits have simple modes of inheritance. Following this study, some of the first pedigree analyses were assessed on the presence of the Carabelli's trait in families by Kraus (1951) and Tsuji (1958). Their phenotypic studies concluded that the inheritance pattern of the trait was that of simple autosomal dominance and codominance. This was an exciting prospect because if dental morphological traits are a direct expression of gene frequencies, population genetic models can be used to identify gene flow and genetic drift (G.R. Scott and Turner 2000) through time and space. Research in the 1960s tested this. For example, by assigning genotypes to three forms of trait expression, Turner (1967, 1969) used phenotypic frequencies to estimate gene frequencies and assess admixture and drift for prehistoric and living North American populations. This research had mixed results and was heavily critiqued. Testing for simple modes of inheritance was problematic as researchers had to make certain assumptions. For instance, to test dominant-recessive modes of inheritance, workers had to assume that trait absence represented a homozygous genotype and trait presence represented a heterozygous genotype (G.R. Scott 2008). However, most dental traits are not only present or absent but exhibit a range of expression and variability. By the 1970s, many researchers agreed that dental morphological traits did not have simple modes of inheritance. Even today, studies have not found a one to one relationship between a gene and the development of specific cusp morphology, although some studies have identified gene/trait correlates i.e. Kimura *et al.* 2009. There are, however, genes that drive the amount of morphological variation seen among taxa (Salazar-Ciudad and Jernvall 2004) and over 300 genes are expressed in different parts of a tooth (Salazar-Ciudad 2012). Additionally, twin and family studies indicate high dental heritability. Dental traits analysed have heritabilities calculated between 0.40 and 0.80, while tooth size heritabilities range between 0.60 and 0.80 (i.e. K. Hanihara *et al.* 1975; Mizoguchi 1978; G.R. Scott and Potter 1984; Townsend *et al.* 1992). Heritability can however, be limited by time and environment because populations may exhibit different heritabilities in different generations and in varying environments (G.R. Scott and Turner 2000).

A practical explanation for the nature of morphological trait inheritance was based in Grüneberg's (1952) model of quasicontinuous variation. These are traits that "exhibit phenotypic discontinuity at the end of a continuous distribution" (Bailit 1975: 125) thereby facilitating a multiple gene inheritance with genes at various loci that together produce the phenotypic trait (G.R. Scott 2008). One of the best known studies on the quasicontinuous nature of tooth morphology was conducted by E.F. Harris (1977). Working with families (parents and their offspring) on the Solomon Islands in Melanesia, he tested genetic models on data collected from a suite of crown traits. He concluded that although the traits studied were quasicontinuous with complex modes of inheritance, they were not necessarily inherited in the same way. Some crown morphology traits may be largely influenced by aspects related to nutrition and health. Nutrition deficiencies and disease disrupt crown formations and leave permanent marks in the form of pits, ridges, grooves or bands i.e. enamel hypoplasia and caries. Although these events do affect crown morphology, it has not been demonstrated that these events influence trait development in any way (G.R.

Scott and Turner 2000). Mandibular and maxillary teeth demonstrate more variability between each other than to left and right teeth of the type e.g. upper and lower molars are more different to each other than LM_3 and RM_3 (Garn *et al.* 1963; Hlusko *et al.* 2004). Fluctuating asymmetry (when antimeres (i.e. RI^1 and LI^1) exhibit observable differences) is often seen in conjunction with other stress indicators including Harris lines on long bones, reduced stature, high infant mortality rates and dental malformations such as enamel hypoplasia or pitting (Perzigian 1977). This asymmetry has been used as an indicator of environmental change/stress (Barrett *et al.* 2012; DeLeon 2007) and has been evaluated in a number of populations e.g. Australian Aboriginals (Townsend 1981; Townsend and Brown 1980). It has been a useful tool because, (as demonstrated by twin studies) unlike directional asymmetry (Graham *et al.* 1993), it has little to no genetic component (P.A. Parsons 1992; Potter and Nance 1976). Although more useful in an archaeological context as less asymmetry is commonly found in modern dentitions (Doyle and Johnston 1977), various problems with this method, largely associated to sampling size and reliability issues, have been observed (B.H. Smith *et al.* 1982). It seems most crown morphology is primarily influenced by genetic factors. There has been much research on how genes are expressed during dental development (Garn *et al.* 1965; Thesleff 2000, 2006; Tompkins 1996) and interestingly, many of the *Hox* family genes are expressed during tooth growth (Tucker and Sharpe 1999). How dental morphological traits are expressed genetically is still a much understudied avenue. Early studies by Kolakowski *et al.* (1980) and Nichol (1989, 1990) demonstrated that some traits could have major genes involved in their development. Recent works have, to a degree, shown this to be true. Bianchi *et al.* (2007) demonstrated that the G-915C single nucleotide polymorphism (SNPs) in the PAX9 transcription factor were associated to third molar agenesis. Similarly, research on Southeast Asian populations by Kimura *et al.* (2009) have successfully established an association between an Ectodysplasin A receptor (EDAR) gene variant and upper incisor shoveling and double shoveling and tooth crown size, explaining nearly 20% of the heritability of the traits. Park *et al.* (2012) confirmed these findings and found further associations on another EDAR variant, including hypoconulid presence on M_2 and mesiodistal diameters of anterior teeth. Their results indicate that, to a certain extent, EDAR polymorphism is responsible for the Sinodont/Sundadont dichotomy in Asian populations.

The effects of the environment on dental plasticity are an important aspect of study when evaluating a dental population's change over time. On the whole, dentition appears to be largely unaffected by or shielded from environmental effects and changes (metric and non-metric) are likely related to other factors such as genetics. Changes in tooth size are linked to environmental and genetic influences (Dempsey and Townsend 2001; Ebeling *et al.* 1973; Garn *et al.* 1968; E.F. Harris *et al.* 2001; Kieser 1990; Kolakowski and Bailit 1981; Lavelle 1973; Perzigian 1984) and like stature, dental size plasticity has demonstrated a relatively high heritability value as evidenced by generational differences between parents and their children (Garn *et al.* 1968). Also, prenatal factors such as maternal health influence crown dimensions in humans (Garn *et al.* 1979), while altering nutritional regiments during pregnancy or lactation have been shown to influence tooth size in rats (Kruger 1966; Paynter and Grainger 1956). This may affect human tooth size as well (Bailit and Sung 1968). Non-metric traits also appear to be protected from environment-related changes, although new studies may prove otherwise. Previous work has demonstrated that limited dental trait change occurs within populations even when environments and diet change dramatically (G.R. Scott and Alexandersen 1992; G.R. Scott *et al.* 1991). In contrast, studies by Mizoguchi (1985, 1993) demonstrate that the development or increase of specific traits (I^1 shoveling and M^1 Carabelli's) are associated to food habits and environments in which milking was practiced. More recent research around twin studies has also demonstrated limited metric and non-metric environmental plasticity (Hughes and Townsend 2013; Townsend *et al.* 2012; Townsend *et al.* 2009), while Mizoguchi (2013) has shown (using allele studies and population history) that dental morphological characteristics, including molar size, the Carabelli's trait and shoveling, are somewhat adaptive to both climate shifts and subsistence strategies. Additionally, dental development appears to be less affected by environmental factors than skeletal maturation and growth (Cardoso 2007; Conceição and Cardoso 2011). In studies on modern, socio-economically stratified skeletal samples from Portugal, dental growth was found to be far less sensitive to socio-economic changes than the rest of the skeleton.

There have been great strides in genetic research focused on population origins and history and in Africa; marked genomic diversity has been demonstrated in hunter-gatherer populations (Henn *et al.* 2011). Recent work by T. Hanihara (2008) on global non-metric dental comparisons suggests that dental trait variation parallels genetic work on human diversity, supporting the African origins model. According to him, regardless of population size, increased non-metric diversity within sub-Saharan Africa and decreased diversity outside Africa is indicative of a move of early populations out of Africa. Genetic differentiation increases between populations as geographic distance increases (Ramachandran *et al.* 2005; Relethford 2004). This, as well as a rapid expansion out of Africa could generate a gradual loss of genetic diversity leading to the non-metric dental variation observed in Western Eurasian, Asian, Australian and New World groups (T. Hanihara 2008). Many studies (mtDNA and Y-chromosome) have highlighted the uniqueness of the Khoesan and demonstrated that they hold some of the oldest modern human lineages (Knight *et al.* 2003; Schuster *et al.* 2010; Tishkoff *et al.* 2007), and perhaps evidence of a southern African (instead of East African) origin for modern humans (Henn *et al.* 2011). Also, genetic links between the Khoesan and East African populations (the Hadza and Sandawe) have been suggested (Pickrell *et al.* 2012; Tishkoff *et al.* 2007) and population admixture (particularly with regards to the Khoesan and contact with Bantu-speaking groups) identified (Pickrell *et al.* 2012).

Overall, dental genetic studies have provided insight into methods of evaluating dental populations and heritability. Today it is clear that inheritance is complex and dental traits cannot be reduced to simple gene frequencies. In order to characterise the dental morphology of a population, total trait frequencies best represent genotypic variation. Phenotypic frequencies are important given the extent to which they reflect genetic relationships, particularly with regards to archaeological remains where extracting DNA is improbable. The goal of dental anthropology is to explain origins, illuminate relationships and clarify the evolution of a population at a regional, continental and global level and dental anthropological studies, including advancements in dental genetics, have thus far greatly advanced our understanding and interpretation of many of these issues. However, many questions still remain regarding the origins, interactions and movements of populations in various parts of the world, including the Khoesan in southern Africa and MSA teeth. Their relationship to wider world dental history is also in question and further systematic, comparative evaluations may help answer salient questions and clarify associations.

CHAPTER 3

THE SOUTHERN AFRICAN MID-LATE PLEISTOCENE AND HOLOCENE, AND KENYA HOLOCENE ARCHAEOLOGICAL RECORD.

INTRODUCTION

The Mid-Late Pleistocene and Holocene archaeological record pertinent to this thesis spans approximately 300 ka. Southern Africa has a rich Middle Stone Age (MSA) archaeological record. Human skeletal remains from southern Africa dating to this time fall within the range of variation of anatomically modern humans. Populations equipped with MSA toolkits were inhabiting and exploiting large parts of southern Africa (Rightmire 1984; Volman 1984). Much of the documented MSA archaeological record comes from coastal cave sites, many of which were washed out by +4-5m sea levels of the Last Interglacial, eroding any older deposits that may have been present. The surviving deposits in these sites therefore date mainly from the Late Pleistocene (Die Kelders, the archaeological layers at Hoedjiespunt, Klasies River Mouth), and what we know of the Middle Pleistocene comes from those few coastal sites that were sufficiently high above sea level that they were beyond the range of the waves (Blombos) and from inland sites (Cave of Hearths, Border Cave). This thesis is concerned with the Mid- to Late Pleistocene sites that have yielded well-preserved human dental material, suitable for collecting metric and non-metric data.

The Later Stone Age (LSA) refers to human occupation of southern Africa during the last 40 000 years. The transition from the MSA to the LSA appears to occur at different times in different sites, between about 40 – 20 ka (Villa *et al.* 2012) and is defined by changes in lithic technology. Currently, the latest known transition is at the Strathalan B cave site in the Eastern Cape (Region E) (Opperman and Heydenrych 1990). There is an ongoing debate about the extent to which there may have been changes in cognitive capacities, subsistence strategies, population sizes and other aspects (K.S. Brown *et al.* 2009; K.S. Brown *et al.* 2012; P.G. Chase 1994, 2003; Henshilwood and Marean 2003; Klein 1989, 1999, 2000, 2001, 2003; Klein and Cruz-Uribe 1996, 2000b; Mackay 2011; Mackay and Welz 2008; McBrearty and Brooks 2000; Mellars 1989; Steele and Klein 2009; Texier *et al.* 2010). Although great strides have been made in our knowledge of the MSA in the last couple of decades, we currently still have a better understanding of the LSA than of the MSA. Our most detailed knowledge is of the last 10 000 years (the Holocene) during which we can document changes in both material culture and subsistence strategies, including changes in style and composition of stone tool assemblages (a wider range of formal tools), an increasing number of rock art sites, complex burials and, in the last 2000 years, pottery and the adoption of domesticated animals (Deacon, J. 1984b). Continuities between Holocene and historic populations clearly demonstrate that the LSA represents part of the prehistory of the Khoesan and therefore, historical and ethnographic data are widely used in interpreting archaeological remains from the LSA. During the Mid- to Late Holocene we see the elaboration of material culture, population movement and expansion, and an intensification of resource exploitation in South Africa (Binneman 1996; Hall 1990; Humphreys 1969; Humphreys and Thackeray 1983; Mazel 1989b; A.I. Thackeray 1981). Additionally, the post-2000 B.P. period represents an interesting change in South African prehistory, where herding and farming is introduced, adding to population complexity.

This chapter reviews our current knowledge of the South African archaeological record with an emphasis on aspects likely to be relevant to Khoesan population history.

BACKGROUND TO THE MID-LATE PLEISTOCENE

The Middle Stone Age (MSA) was originally described by Goodwin and Van Riet Lowe (1929) as a flake industry. Later, more comprehensive classification schemes (Singer and Wymer 1982; Volman 1984) divided the MSA into chronological stages (MSA 1,2 and 3) largely based on Cape coastal sequences because this is where most research was conducted during the 1980s. In general, MSA lithics are characterised by flakes and blades struck from Levallois or prepared cores. Retouch is not common (Wurz 2002) but unifacially and bifacially retouched points occur intermittently. Most points appear to have been used as parts of spears or arrows (Brooks *et al.* 2006), while some points were hafted (Lombard 2006; J.J. Shea 2006) with various adhesives (Charrié-Duhaut *et al.* 2013; Lombard 2004, 2008; McBrearty and Brooks 2000; Wadley 2005) indicative of, according to Wadley *et al.* (2009), complex cognition. Some backed artefacts, denticulates and scrapers are also occasionally found in deposits with non-lithic cultural artefacts such as bone points, ostrich eggshell beads in various stages of production and ochre (Dusseldorp *et al.* 2013; Lombard *et al.* 2012). Today, the MSA is recognised as highly variable both geographically and temporally. Hunters targeted medium- to large-sized bovids and equids such as wildebeest, eland and zebra (J.L. Clark and Plug 2008; Klein 1977; Plug 2004), supplementing a diet of a variety of edible plants, seeds, and geophytes. Plants were also collected for use as bedding (Wadley *et al.* 2011). Many MSA point tips have impact fractures and animal residue present (Lombard 2004, 2005), confirming that they were used for hunting. Early MSA assemblages between 200 and 130 ka are rare, possibly due to a population reduction during this glacial period (Wadley and McNabb 2009). They consist of a similar generalised MSA toolkit, including Levallois flake technologies, thin blades and some retouched tools made from local raw materials. One such Early MSA industry, the Pietersburg (~200 ka), is predominantly made from hornfels, a hard metamorphic rock (Mason 1962; Sampson 1974), and occurs at various inland sites including Cave of Hearths, Wonderwerk Cave and Border Cave (Grün and Beaumont 2001), among others. However, the best-known industries (and the subject of much ongoing investigation) are the Still Bay and Howiesons Poort Industries. Known predominantly from coastal or near-coastal sites such as Blombos, Peers Cave and Sibudu (Henshilwood *et al.* 2001; Wadley 2007), the brief Still Bay tradition (72-70 ka) (Jacobs and Roberts 2008) is typified by unique thin bifacial points and (at Blombos) worked bone tools (Henshilwood and Sealy 1997; Henshilwood *et al.* 2001). Only 7 ka later, the Howiesons Poort tradition (65-60 ka) (Jacobs and Roberts 2008) emerges at well-known sites such as Border Cave (Grün *et al.* 1990a), Diepkloof (Tribolo *et al.* 2009), Klasies River Mouth (Wurz 1999, 2002), Rose Cottage Cave (Soriano *et al.* 2007) and Sibudu (Lombard 2008; Wadley 2008). It is characterised by backed tools, small blade technology and more complex hunting equipment such as segments and other backed tools hafted to wooden handles (Lombard 2008). From *ca.* 55 ka MSA assemblages demonstrate great variability, perhaps due to variations in local raw material resources, e.g. at Rose Cottage Cave. MSA tools during this time are small with residual cobble stone cortex, indicative of the small cobbles readily available (and favoured) in the area (Wadley 1997). Most notable in the Late Pleistocene is the emergence of symbolic behaviour and its trace in the archaeological record in the form of personal ornamentation and artwork (Henshilwood and Marean 2003). Shell ornaments >70 ka (d'Errico *et al.* 2005), incised ochre (Henshilwood *et al.* 2002) from Blombos, and more recently, engraved ostrich eggshell from Diepkloof (Parkington *et al.* 2005; Texier *et al.* 2010; Texier *et al.* 2013), for example, have been taken as indicators of symbolism.

There is substantial evidence for the presence of human populations in South Africa during the Mid-Late Pleistocene. Unfortunately, human remains from these sites are scarce and when available they are fragmentary and often consist mostly of teeth. Below is a brief description of the Mid-Late Pleistocene sites (see Fig. 4.3) pertinent to this thesis, including the South African sites of (in roughly decreasing age) Hoedjiespunt, Cave of Hearths, Border Cave, Sea Harvest, Blombos, Klasies River Mouth Mouth, Die Kelders, and Hofmeyr and the Zambian site of Mumbwa Caves, which have some of the most recent dates.

HOEDJIESPUNT

Hoedjiespunt 1 is located in Saldanha Bay on the West Coast of South Africa. The site consists of both archaeological and underlying palaeontological horizons, the latter consisting of fossil hyena dens. The archaeological layers have three occupational phases, each containing early evidence of marine exploitation, ostrich eggshell, lithics, some ground ochre and terrestrial fauna (Will *et al.* 2013). These levels are believed to date to the Mid-Late Pleistocene (between 130 ka and 100 ka) on the basis of MSA stone tools, and infrared stimulated luminescence (IRSL) and thermoluminescence (TL) dates on lower level sediments (Parkington 2003; Stynder *et al.* 2001; Will *et al.* 2013; Yoshida 1996). The dense palaeontological layers are not as successfully dated. IRSL and TL dates on surrounding sediments suggest that the receiving environment is of Middle Pleistocene age (Stynder *et al.* 2001) while the fauna, indicative of the Florisbad Faunal Span, places the deposit itself at a maximum age of *ca.* 250 ka (Stynder *et al.* 2001). Based on these dates and stratigraphic observations, Churchill *et al.* (2000) and Stynder *et al.* (2001) have suggested that the palaeontological assemblage was most likely deposited between 200 ka and 300 ka ago. Teeth examined in this study were recovered from the palaeontological levels.

CAVE OF HEARTHS

Located in the Makapan Valley, Limpopo Province, South Africa, Cave of Hearths is a landmark site providing some of the first human remains found in direct association with Middle Pleistocene hand-axes and fauna in Africa (Tobias 1971). It is also one of a very few caves in South Africa with occupation spanning the Early, Middle and Late Stone Ages. The site was well stratified with a clear archaeological sequence outlined by Mason (1962, 1988), which included Iron Age (Bed 11), LSA (Bed 10), MSA (Beds 4-9) and ESA (Beds 1-3) layers. Mason (1988) suggested ESA dates ranging from 250 ka (Bed 1) to 200 ka (Bed 3). Recent work by McNabb and Sinclair (2009) further describes the long ESA and MSA cultural sequence, concurring with Mason’s (1988) estimates. The teeth (in a partial mandible) examined for this study were recovered from Bed 3 dated by artefact association and site comparison to *ca.* 200 ka (Mason 1988). They were first attributed to the Early Late Pleistocene and *Homo rhodesiensis* (Partridge 1982; Pearson and Grine 1997; Rightmire 1975b, 1998; Tobias 1971) and later to archaic *Homo sapiens* or a transitory group between archaic and modern *Homo sapiens* (Bräuer 1992; Stringer and Bräuer 1994). More recently, McBrearty and Brooks (2000) classified the Cave of Hearths mandible as *Homo rhodesiensis*, while Stringer (2002) grouped Middle Pleistocene African specimens as a whole under *Homo heidelbergensis*. New comparisons between the Cave of Hearths mandible and various hominin samples (Curnoe 2009) demonstrate a mosaic of modern features outweighing the few archaic characteristics identified. This is strong evidence for placing the Cave of Hearths mandible among the oldest modern human specimens including those such as Herto dated to *ca.* 160 ka (J. D. Clark *et al.* 2003) and Omo-Kibish 1 at 195 ± 5 ka (McDougall *et al.* 2005) from Ethiopia.

BORDER CAVE

The archaeological site of Border Cave is located in South Africa at the boundary between Kwazulu-Natal and Swaziland, and has yielded an artefact-rich stratigraphic sequence across *ca.* 200 ka (Beaumont 1978; Grün and Beaumont 2001). The occupation is divided into four phases. The oldest phase, MSA 1, begins *ca.* 230 ka (layers 5WA, 5BS, 4WA and 4BS) followed by the Howiesons Poort *ca.* 75 ka (levels 1RGBS, 3WA and 3BS) (Grün and Beaumont 2001). The MSA 3 phase follows, concluding the MSA at Border Cave. Border Cave also offers the best example of an early microlithic industry dating to *ca.* 39 ka (Grün and Beaumont 2001; Villa *et al.* 2012), considered by some researchers to be an early expression of the LSA. Studies on excavated mammal and micromammal remains have offered palaeoenvironmental data as well as a picture of subsistence resources available in the area from *ca.* 130 – 24 ka. D.M. Avery (1982, 1992) and Klein (1977) identified moderate (warm and moist) climates with abundant small-medium bovids. A number of modern human remains have been recovered from the site, including BC2 and BC5 used in this study. However, the Border Cave human remains (other than BC3) were not recovered *in situ*, so there is uncertainty with regards to their original stratigraphic positions (and hence their ages). Beaumont *et al.* (1978a) note that BC1 and 2 were recovered in 1942 from the base of Horton's Pit, where early researchers (H.B.S. Cooke *et al.* 1945a) identified level 4WA, although this was never verified. These specimens are estimated to date between 171 ka and 71 ka (Grün and Beaumont 2001; Millard 2006; Miller *et al.* 1999). BC5 was recovered in 1974 from slumped material from the northwest edge of the excavation, and is possibly associated with level 3WA, dated to *ca.* 74 ± 5 ka (Grün *et al.* 2003).

SEA HARVEST

Located north-west of Hoedjiespunt within Saldanha Bay, the sandstone cliff site of Sea Harvest is dotted with fossiliferous outcrops. Access to the cliff was restricted in the past and investigations of fossil and archaeological deposits largely focused on material that had naturally weathered out. Later work excavated easily accessible bone-rich cavities and identified a cemented shell midden in the upper part of the stratigraphic sequence (Grine and Klein 1993). The assemblage is dominated by mammalian fauna (grazing ungulates and carnivores), some birds, reptiles and marine animals including fish, dolphins and seals, with little evidence of human occupation other than in the shell midden (Grine and Klein 1993; Hendey 1974). Hyenas (D.M. Avery *et al.* 1984), raptors and small carnivores have been implicated as the agents of accumulation due to the absence of artefacts and other archaeological markers indicative of people. The shell midden contained ostrich eggshell fragments, some animal bones and MSA artefacts (Klein 1994; Volman 1978). Dates on ostrich eggshell fragments demonstrate that the midden is older than 40 ka (UW-282 and UW 292) (Fairhall *et al.* 2006), while geological observations (Butzer 1984) bracket it within the Last Interglacial. Faunal evidence (Grine and Klein 1993) also suggests that it accumulated during this time. The fragmentary human remains studied here were recovered from deposits underlying the midden.

BLOMBOS

Blombos Cave is located in a wave-cut cliff on the southern Cape coast, slightly west of the town of Still Bay. It preserves MSA deposits dating from ca 70 to 100 ka; excavations have not yet reached the base of the sequence. The MSA levels at the site are divided into three phases each made up of a number of layers: M1, M2 and M3 (BB1 or Still Bay phase, BB2 and BB3 in earlier literature) capped by a sterile layer separating the MSA and LSA deposits (Henshilwood *et al.* 2001; Henshilwood *et al.* 2011). The phases have been dated using OSL and TL techniques; M1 has a date of around 73 ± 3 ka, M2 is dated to between 77 ± 3 ka and 85 ± 6 ka (Henshilwood *et al.* 2011), while M3 phase has been dated to 98.9 ± 4.5 ka (Jacobs *et al.* 2006), and more recently by Henshilwood *et al.* (2011) who identify a phase 3 start date of 97 ± 4 ka. Retouched tools (including Still Bay bifacial points) made from non-local raw materials are common in the upper MSA levels (Henshilwood *et al.* 2001). The site is particularly well known for evidence of symbolic material culture: engraved ochres (Henshilwood *et al.* 2009), art (Henshilwood *et al.* 2002; Henshilwood *et al.* 2011) and personal adornment (d'Errico *et al.* 2005; d'Errico *et al.* 2008), as well as the first secure evidence for bone artefacts in the MSA (Henshilwood and Sealy 1997; Henshilwood *et al.* 2001). In addition, the cave provides evidence for human subsistence during the MSA. Unlike larger sites, meat appears to have come mainly from smaller animals such as dune molerats, hyraxes, tortoises (J.C. Thompson and Henshilwood 2014) and small and small-medium bovids, as well as marine foods (Henshilwood *et al.* 2001). The human tooth studied for this thesis derives from layer AT in the MSA 3 stratigraphic levels.

KLASIES RIVER MOUTH

Klasies River Mouth cave complex is located on the Tsitsikamma coast of the Eastern Cape between Plettenberg Bay and Cape St Francis, South Africa. The site consists of a number of caves, preserving a record of human occupation that extends back to at least 110 000 years ago. Major excavations were carried out here by Singer and Wymer in the 1960s. They recognised five MSA phases within the sequence: MSA I, MSA II, Howiesons Poort, MSA III and MSA IV (Singer and Wymer 1982). Subsequent work by H.J. Deacon, and Geleijnse (1988) grouped the strata into four members, Loose Brown Soil (LBS) with a terminal Last Interglacial date (Bada and Deems 1975; H.J. Deacon *et al.* 1988; Shackleton 1982) followed by Sand and Shell (SAS) with age estimates ~90 ka (Bada and Deems 1975; H.J. Deacon *et al.* 1988; Grün *et al.* 1990b), and more recent Rockfall (RF) and Upper (U) members considered to be younger than 60 ka (H.J. Deacon 1992). Singer and Wymer’s (1982) MSA I and II phases correlate with the SAS member (A.I. Thackeray and Kelly 1988), while MSA III and Howiesons Poort phases are ascribed to the U member (H.J. Deacon 1992). The large assemblage excavated from Klasies River Mouth has enabled detailed study of Late Pleistocene faunal exploitation, dominated at this site by medium to large bovids. Shellfish and marine animals such as seals and penguins were also important (Binford 1984; Klein 1976), while fish exploitation, although relatively low and most likely periodic, is evident (Von den Driesch 2004). Most of the fragmentary human remains that have been recovered and studied (Bräuer *et al.* 1992; Churchill *et al.* 1996; Grine 2012; Grine *et al.* 1998; Lam *et al.* 1996; Rightmire and Deacon 2001; Rightmire *et al.* 2006; Royer *et al.* 2009) were excavated from Caves 1 and 1B in LBS, SAS and U members. The teeth used in this study were all recovered from the SAS member.

DIE KELDERS

The site of Die Kelders consists of two caves (DK1 and DK2) located on the southwestern coast of South Africa. Early excavations by Schweitzer (1979) exposed a rich LSA occupation at the site above substantial MSA levels alternating with sterile layers below. Of the 17 major depositional units at the site (Tankard and

Schweitzer 1974, 1976), units 4-15 contain MSA artefacts and microfauna often separated by non-occupation horizons. Luminescence dating of five of the MSA levels (4/5 complex, 7, 9, 11 and 13) yielded similar dates all between *ca.* 60 – 80 ka (Feathers and Bush 2000), largely in agreement with ESR dates from layers 4/5, 6, 10 and 12 (Schwarcz and Rink 2000). Excavations at Die Kelders have yielded large quantities of lithics and faunal remains. MSA artefacts were made predominantly from quartzite with some silcrete (G. Avery *et al.* 1997); very few were retouched (only 3% of the assemblage) (A.I. Thackeray 2000). To date, no Howiesons Poort assemblage and no MSA worked bone or shells have been identified at the site. Grine *et al.* (1991) suggest that the Late Pleistocene deposits coincided with a period of moist, temperate climate with fauna similar to that of Klasies River Mouth (medium to large grazing ungulates, tortoise, marine animals, some birds and limited fish (Klein and Cruz-Uribe 2000b)). Human remains, including the teeth used in this study, were excavated from seven of the MSA layers in DK1, with layer 6 yielding most of the skeletal remains and teeth (Grine 2000). Three single teeth used in analyses were recovered from layers 4/5, 11 and 14.

HOFMEYR

This near complete cranium was discovered in 1952, near the town of Hofmeyr in the Eastern Cape Province. It was found in a river bed with no recorded associated (archaeological or anatomical) finds and the site itself is now destroyed. We may never know the original context of the cranium. The specimen has been damaged since its recovery resulting in the loss of part of the mandible, maxilla (and some teeth including incisors, canine/s and premolars) and a significant section of the occipital, however recent work has reconstructed the cranium to provide more comprehensive morphometrics (Grine *et al.* 2010). OSL and uranium-series dating of sediments adhering to the specimen provide a depositional age of the cranium of 36.2 ± 3.3 ka. Grine *et al.* (2007) compared Hofmeyr's cranial features to archaic and modern world populations. Results demonstrate a closer relationship between Hofmeyr and Upper Pleistocene Eurasians (although the sample size was very small) than with geographically close recent Khoesan and sub-Saharan African Bantu-speakers.

MUMBWA CAVES

Mumbwa Caves are located in Central Zambia, approximately 145km north-west of Lusaka. The most recent excavations (Barham 2000a), have recognised fourteen stratigraphic units with dates across the Middle Stone Age to the present. Late Holocene strata (Units I-IV) overlie MSA levels beginning at *ca.* 40 ka (Unit V) (for date details see Barham 2000b: 41). The site contains rich deposits of lithic (Savage 1983), faunal and human remains, providing a substantial behavioural record inclusive of personal adornments such as beads (Barham and Mitchell 2008) and bone points (Barham 2000a). Additionally, occupants erected large windbreaks within the site protecting stone-circled hearths (and presumable the people) from wind. Tools include large numbers of cores and backed quartz blades as well as locally collected ochres (Barham 1995, 2000a; Barham and Mitchell 2008). Micro- (D.M. Avery 2000) and macromammalian fauna identify Late Pleistocene environments as warm wooded grasslands and although interglacial climatic fluctuations were notable, faunal change is minimal. Medium to large grazers (zebra, oribi, sable antelope and many others) and browsers (bushpig, bushbuck, eland and grey duiker) were locally numerous (Klein and Cruz-Uribe 2000a). Many human remains were recovered from the site in earlier excavations by Dart and Del Grande (1931). In addition, they discovered three beehive-shaped stone features or tombs which contained a number of artefacts and fragmentary human remains. Three of the calvaria found here were later described and paralleled to East African cranial finds (Gabel 1963; Jones 1940; Wells 1950, 1957). The human remains appeared to be in association with MSA tools in a stratigraphic level that equates to Barham's (2000b) Unit VIII, dated to the Last Interglacial. However, the chronology of these burials, and the artefacts and human remains found in close proximity to them, has been debated. Protsch (1977) reported dates of 18,000 ± 370 (UCLA 1750B) for fauna and 19,780 ±130 (UCLA 1750C) for a human fibula from outside one of the structures, but provenance discrepancies and a lack of collagen in and/or possible contamination of samples make these dates problematic and cannot be deemed reliable and are excluded from this analysis. According to Barham *et al.* (2000), specimens found inside the tombs are associated with shell, which appears only in Holocene deposits, and they are therefore likely to be of Holocene age. Also, the burials may be intrusive from a later occupation (J.D. Clark 1942). Other MSA teeth (not available for study here) were recovered in the 1994 and 1996 excavations. The uncertainty of the dating and original location of specimens from earlier excavations therefore gives the teeth used in this study a wide possible date range from the Late Holocene to Last Glacial Maximum.

HISTORICAL BACKGROUND TO THE LATER STONE AGE

From the mid-1800s, prehistoric lithic artefacts in South Africa were classified according to European terminology (Gooch 1882; Peringuey 1911). In 1929, South Africa's first professional archaeologist, A.J.H. Goodwin, in collaboration with C. van Riet Lowe, an engineer, developed a broad classification scheme for South African archaeology. They divided the South African Stone Age into Earlier (ESA), Middle (MSA) and Later (LSA) Stone Ages, each of which comprised several lithic artefact industries. Similarities between LSA artefacts and items from ethnographic collections from the Kalahari and elsewhere linked the LSA with modern Khoesan, their hunter-gatherer subsistence strategy and microlithic tool technology (Parkington 1986; A.I. Thackeray 1981).

Within the LSA, Goodwin and van Riet Lowe (1929) recognised two stone tool industries, the Smithfield and the Wilton. They believed that these lithic industries were geographically separate but contemporaneous. The Wilton, named after the type site of Wilton Large Rock Shelter in the eastern Cape (Hewitt 1921), was characterised by microlithic assemblages including small scrapers, backed blades and segments. It was widespread over coastal southern and eastern Africa and was attributed to an immigrant population due to supposed similarities with North African assemblages (Goodwin and Van Riet Lowe 1929).

The Smithfield, named after the town in the southern Free State where it was first identified, was confined to the interior of Southern Africa. It was characterised by the use of hornfels, a fine-grained and durable indurated shale found adjacent to dolerite dykes, and used for the manufacture of larger tool types. The Smithfield was considered a locally developed industry as it lacked obvious similarities with assemblages known from further north. Furthermore, Goodwin and Van Riet Lowe (1929) were of the opinion that certain elements were derived from the MSA because of the presence of heavily trimmed concavo-convex scrapers and large endscrapers that were considered more typical of the MSA than of the LSA (Goodwin and Van Riet Lowe 1929). The Smithfield was further subdivided on the basis of scraper size, shape, patination and raw material (J. Deacon 1990). Initially it was divided into three variants: Smithfield A was characterised by older, patinated, large circular scrapers, Smithfield B was dominated by long “duck-bill” shape scrapers, while Smithfield C came predominantly from cave sites and was characterised by fine-grained raw materials such as agates and jasper, small convex “thumbnail” scrapers and rare segments (J. Deacon 1984a). Later additions to the Smithfield group of assemblages included Smithfield N, describing lithics found in Kwa-Zulu Natal (Goodwin 1930) and Smithfield P for material found in Pondoland, now part of the Eastern Cape (Van Riet Lowe 1936). Both variants were characterised by notched end scrapers. A Coastal Smithfield was also recognised in the southern and western Cape (Van Riet Lowe 1946).

It is evident that, although geology and geography were recognised as factors contributing to the variability of lithic assemblages, similar assemblages were attributed to different industries (especially the Smithfield C and the Wilton). In keeping with the archaeological and anthropological views of their time, Goodwin and van Riet Lowe saw technological and typological differences as reflecting cultural boundaries, rather than temporal or other differences. They believed the origin of the LSA in South Africa to be the result of a migration of people who brought microlithic technology from North Africa. On arriving in South Africa, this cultural group split. One group was thought to be responsible for the coastal Wilton artefacts, while a combination of local MSA populations and the newly arrived Wilton people gave rise to the Smithfield industry. The Wilton and Smithfield were consequently regarded as two contemporaneous, geographically separated industries.

Physical anthropologists of the first half of the twentieth century also generally attributed biological variation in archaeological human remains in South Africa to immigrant populations. Meiring (1937), for example, seeking to identify a population physical type, studied craniofacial features of the skulls from Layer C of Matjes River Rock Shelter (as outlined in Dreyer 1933) and found that the skulls “are not comparable to those of Bushmen, Hottentots or Bantu” (Meiring 1937: 75). He attributed craniofacial differences to contact with non-local settlers from the north and therefore referred to these skulls as “Wilton”, believing that they indicated the influence of an outsider population, while the overlying layers A and B were associated with recent and pre-Bushman types respectively (Döckel 1998; Dreyer 1933). Skeletons from the oldest layer, Layer D, were attributed to the “Keurbooms People”, supposedly a Bushman/Hottentot hybrid population. Researchers believed that southward migrating anatomically modern humans and their material culture replaced or altered local inhabitants, giving rise to the ‘Bushmen’ (Goodwin and Van Riet Lowe 1929; Meiring 1937; Stynder 2006).

One of the more controversial early studies relates to an undated skullcap discovered in the North West Province in 1913, and named the type specimen of Boskop. The “Boskop physical type” or “Boskopoids” were considered to be the direct ancestors of modern Khoesan populations and were designated *Homo capensis* (Broom 1918; Broom 1923). This group grew to include composite (and not always accurately reconstructed) forms assembled from several crania (Dreyer and Meiring 1952). Galloway (1933) identified similarities between the Boskopoids and East Africa crania from various sites including Nebarara in Tanzania and Gamble’s Cave in Kenya, calling into question the aboriginal nature of the population. Later, Van Riet Lowe (1954) argued that the original Boskop skull fragment was associated with MSA archaeological assemblages, leading to the assumption that Boskopoids were the aboriginal population of the southern African MSA. Over time, more and more crania were added to the Boskopoid group, making it a problematic group with waning support.

TOWARDS A MODERN FRAMEWORK

The Goodwin and Van Riet Lowe model was questioned as research advanced but remained dominant until a new synthesis, still based in migratory theory, was proposed by J.D. Clark (1959). An increasing number of careful excavations from the mid 1960s onwards provided a wealth of information and revealed that earlier Smithfield-like LSA industries lay beneath Wilton assemblages, thereby invalidating the former division of the LSA into Smithfield and Wilton (Inskeep 1967).

Researchers also realised that a lack of typological standardisation had hampered investigations into archaeological assemblage variability (J.D. Clark *et al.* 1966; Inskeep 1967). With this recognition came a concerted effort to standardise terminology and descriptions, as suggested at the Wenner-Gren Symposium on African prehistory at Burg Wartenstein, Austria in 1965. New terms introduced at the conference helped achieve some clarity and uniformity but never eliminated misuse and misunderstanding or the association between assemblages and ethnicity (Mitchell 1988b; Parkington 1984). By this time, many researchers thought it unlikely that the origins of the South African LSA were in North Africa or elsewhere as no archaeological evidence for migration or diffusion of technology had been identified. At this stage, archaeological research still focused on the analysis of lithics. Investigations of faunal and floral remains were scarce and demographic, spatial and climatic patterns were largely ignored. Encouragingly, the increasing availability of radiocarbon dating at this time allowed for better understanding of chronology and led to the proliferation of new data.

Sampson (1974) applied the terminology and classificatory principles agreed at Burg Wartenstein to create a new model of the southern African archaeological sequence, incorporating newly available radiocarbon dates. Sampson also considered population movements and the availability of raw materials in establishing industry boundaries. He proposed four successive LSA industrial complexes, with regional variations:

1. the Oakhurst, an Early Holocene tradition with two variants, namely the Lockshoek industry in the Karoo and Free State and the Pomongwan in Zimbabwe and Botswana;
2. the mid-Holocene Wilton, divided into coastal and interior variants;
3. the Smithfield (which incorporated Van Riet Lowe's Smithfield B and C), and
4. a possible Strandloper Industry, covering Late Holocene coastal assemblages.

Sampson's approach did not, however, take into account aspects of functional choice that might lead to differences between contemporary sites, e.g. differences in subsistence strategies. Changes in assemblages were generally explained as the result of either diffusion and migration or environmental change (J. Deacon 1984a; Mitchell 1988a).

Clarity regarding regional variation in lithic assemblages emerged after further excavations by H.J. and J. Deacon in the southern Cape (region D in Fig. 4.1). In 1966/1967, J. Deacon re-excavated the key site of Wilton Large Rock Shelter and demonstrated that, contrary to Hewitt (1921), artefact frequencies, shapes and sizes varied noticeably over time even within Wilton assemblages (J. Deacon 1972b, 1984a; Parkington 1986). The heterogeneity of Wilton assemblages was also noted at Melkhoutboom, Boomplaas, Klasies River Mouth and other sites excavated at this time (H.J. Deacon 1969, 1976; J. Deacon 1972b, 1974). The presence of gradual changes, such as the replacement of segments by backed blades (J. Deacon 1972b) within the microlithic tool-kit, implies an evolutionary progression of technology, representing within-group cultural changes indicative of a dynamic culture.

In 1974, J. Deacon published a geographical and temporal assessment of all radiocarbon dates then available for the LSA. The distribution that emerged showed no dates (i.e. no evidence of occupation) in the Karoo areas from 8 000 – 4 000 years ago and no indication of Smithfield assemblages in the interior during this time. There were, however, dates throughout the Holocene from sites in the Fold Belt mountains and coastal plain. Wilton sites with large numbers of small scrapers and backed pieces tended to date to the mid-Holocene, as documented at Wilton Large Rock Shelter. This demonstrated that Van Riet Lowe's Smithfield A, B and C were discontinuous, and that the Smithfield was not contemporary with the Wilton. J. Deacon (1974) suggested that low occupational density in the interior during the mid-Holocene resulted from the dry climatic conditions of the time. The history of the LSA could reasonable be seen as a single evolving lithic tradition with regional assemblage variation driven by temporal and geographic differences in human occupation, rather than the existence of two separate and co-existing traditions (Wilton and Smithfield).

Sites such as Nelson Bay Cave in Region D and Melkhoutboom in Region E provided evidence that LSA traditions were present before the Holocene, pre-dating Sampson's (1974) Oakhurst Complex. Faunal and floral evidence at these and other sites provided an opportunity to study changes in animal and plant remains alongside stone artefact sequences from Late Pleistocene and Holocene deposits (H.J. Deacon 1972a, 1976, 1979; Klein 1972, 1974, 1976). These studies highlighted changes in subsistence strategies, for example the Terminal Pleistocene LSA was associated with limited evidence for exploitation of flora, remains of medium to large antelope and few small browsers, suggesting a link between changing stone tool technologies and the population's adaptive strategies (H.J. Deacon 1976). This study also suggested that there was a significant amount of spatial patterning in LSA artefact assemblages relating to the role of plant foods in different areas. Based on an accumulating body of anthropological descriptions of hunter-gatherers (especially from the Kalahari), it was proposed that plants with water storage abilities were important in arid regions (such as the northwest, including regions A and G in Fig. 4.1). After well documented ethnographic studies of seasonal movements and stress (Lee 1965; Lee and DeVore 1968; Silberbauer 1981) it was demonstrated that plant food choices were based on resource availability and environmental conditions. In the Eastern Cape (Region E), plants with wide seasonal availability were exploited, restricting territorial ranges (H.J. Deacon 1972a), while a reliance on above-ground plant foods such as fruit was proposed in the north and northeast. In the southern Cape, including the Fynbos biome (which is relatively treeless), the emphasis was on almost 200 edible species of geophytes (H.J. Deacon 1993).

With archaeological research now including the collection of palaeoenvironmental and economic data, it was clear that changes in artefact assemblages generally overlapped with changing subsistence strategies, such as gathering choice. This offered an alternative to the idea that migration and raw material choice were key to technological change (Mitchell 1988a). H.J. Deacon's new model, based in systems theory, explained the transitions between various industrial complexes in terms of adaptations to changing environments. He also considered variations in population distribution across the landscape based on cultural borders, subsistence ecology and behaviours, and proposed that differences between contemporary artefact assemblages might indicate cultural and/or linguistic boundaries (H.J. Deacon 1976). This gave rise to a new three-tier subdivision of the LSA into the Robberg, Oakhurst and Wilton.

Archaeological study in the interior in the 1980s led to social explanations of assemblage change that challenged previous ecological approaches. In his innovative rock art research, Lewis Williams (1981) argued that archaeologists should consider developments and changes in LSA societies through how that society procures or produces the necessities required to survive. Evidence from lithic studies alone (common pre-1980) was insufficient for differentiating aspects like site use (Wadley 1987). Therefore, a more social approach to archaeology (Barham 1992; J. Deacon 1990; Mazel 1987, 1989a, 1989b; Wadley 1987, 1989, 1992) was needed to tease apart the social context of change and provide another platform from which to study material culture variation in the LSA. Two major proponents of social archaeology, Wadley and Mazel, used a historical materialist perspective as a framework for understanding social conditions for change. After analysing the artefacts and food remains from Jubilee Shelter and Cave James in the Magaliesberg, Wadley (1989) suggested that inter-site differences were due to occupation at different stages of an annual cycle of band aggregation and dispersal, as described in the Kalahari. Aggregation sites comprised gender segregated manufacturing areas where artefacts commonly used in gift exchange (as in *hxaro* known from the Ju/'hoansi) were made. These included worked bone and shell artefacts, ostrich eggshell beads, spatulas, bone points and standardised stone tools. In contrast, dispersal sites had fewer formal tools, ornaments and finely worked bone implements. Additionally, plant remains varied seasonally between aggregation and dispersal sites, as did meat procurement strategies (Wadley 1989). It was highlighted that aggregation camps provide an outlet for social stress through extensive socialising while dispersal camps are connected to band isolation and limited ritual activity (Barham 1992). Hall (1990) also argued that Late Holocene groups used gift exchange to build ties between groups in an increasingly stressful environment. Additionally, the intensification of ritual activity, production and reciprocity (gift exchange) may reflect a means of coping with risk brought about by drier mid-Holocene climates (Wadley 1987). Mazel (1989a), on the other hand, focuses on gender and relates it to economic intensification in the Thukela Basin from 4000 BP. He argues that in response to regional population expansion, female status improved as people came to rely more on small terrestrial, marine and plant foods (seeds and geophytes) usually gathered by women. Furthermore, he argues that stylistic variations in stone tools, bone and ostrich eggshell artefacts distinguish three regional (social) units in the Thukela Basin. Although these ideas are widely used in archaeological investigations, some concerns remain. It must be stressed that ethnographic and historic evidence becomes more problematic as one goes further back into the past. Barham (1992) points out that Southern African ethnographic evidence of people living in rock shelters and caves or making stone tools is absent, and the agency, both of the researcher and the individual in prehistory is ambiguous at best, making it difficult to correlate social practices with archaeological artefacts.

CURRENT INTERPRETATIONS OF EVIDENCE FROM THE LATE PLEISTOCENE AND HOLOCENE

Dynamic change is the general theme for current interpretations of the Late Pleistocene/Holocene time span. This time period encompasses substantial climatic change (especially the Last Glacial Maximum) driving shifts in plant and animal distributions, the rise of modern human populations, technological innovations, subsistence strategies, and the changing exploitation of the southern African landscapes and resources. Archaeological evidence demonstrates much variability between sites but it is possible to identify patterns in temporal changes in material culture and lifeways throughout this time.

LATE PLEISTOCENE 40 – 12 KA

MSA/LSA TRANSITION

Assemblages dating from 50 – 20 ka vary geographically, many are unstandardised and they are therefore difficult to characterise. Dates for the MSA/LSA transition vary at different sites from around 40 ka (Border Cave (Beaumont 1978; Villa *et al.* 2012) to 20 ka (Boomplaas (H.J. Deacon 1979), Sehonghong (Mitchell 1995), Strathalan Cave B (Opperman 1987; Opperman and Heydenrych 1990), and Apollo 11, in Namibia (Vogelsang *et al.* 2010)), while the transition at other sites may be less well defined (Rose Cottage Cave (A.M.B. Clark 1997; Wadley 1997, 2004).

Early microlithic industries dating between 50 and 40 ka BP at Border Cave showed features transitional between the MSA and LSA (Villa *et al.* 2012). These levels contained ostrich eggshell beads and bone points but few formal tools. A large number of small quartz scaled pieces, often found in low frequencies in the MSA and absent from the LSA, were indicative of what Beaumont (1978) referred to as the MSA/LSA transition assemblage. This was later renamed the Early Later Stone Age (ELSA) (Wadley 1993). Similar assemblages were identified at other sites dating to this time period including Heuningsneskrans (Beaumont 1978) and Kathu Pan 5 (Beaumont and Morris 1990), however, the date ranges for ELSA assemblages vary considerably. Many sites with long occupational sequences record a period of non-occupation or hiatus between the MSA and the first visible elements of the LSA, e.g. Rose Cottage Cave at 20 600 BP (Pta-5598) (A.M.B. Clark 1997; Wadley 1993). Late dates have been obtained for MSA assemblages and there is evidence that the MSA technology continued at some sites until 26 000 – 20 000 BP. At Sehonghong in Lesotho, for example, MSA assemblages have been dated to 20 900 BP (Pta-789) and 19 860 BP (Pta-918) (Mitchell 1988a; Wadley 1993). Although Late Pleistocene microlithic assemblages are recognised in the archaeological record from 40 000 to 12 000 BP, the small assemblages and often inconsistent dates make synthesis difficult. However, the ELSA represents a distinct industry that is not part of the earliest standardised LSA, the Robberg, which by the Last Glacial Maximum is the dominant lithic industry.

ROBBERG INDUSTRY

ca. 22 000 BP – 12 000 BP.

The Robberg industry was first recognised at Nelson Bay Cave on the Robberg Peninsula (from which it derives its name), near Plettenberg Bay. Robberg assemblages are found across southern Africa from the southern Cape coast to the Caledon River Valley (Wadley 1996), the Drakensberg highlands of Lesotho (Mitchell *et al.* 2006) and possibly the southern Kalahari (Beaumont and Morris 1990). Although the industry has an approximate 10 000 year duration, there is variation in tool frequency, raw material selection, geographic location (open-air sites are rare) and time. What distinguishes Robberg assemblages from others is the mass-production of small (<25mm) standardised, unretouched bladelets, often made from quartz or cryptocrystalline silicates. These bladelets are manufactured from distinctive wedge-shaped or bipolar bladelet cores, sometimes so reduced they are referred to as scaled pieces (J. Deacon 1984a; Mitchell 2004). Usewear and trace evidence suggest that the bladelets were hafted, while the cores were sometimes used in working skins or plant matter (Binneman 1982, 1997; Binneman and Mitchell 1997; Williamson 1997). Formal tools are infrequent but when present, retouch is found as backing on bladelets, segments and small scrapers. This industry is associated with a subsistence strategy concentrating on large migratory ungulates and is found in conjunction with a wide range of non-lithic artefacts including items made from ostrich eggshell, bone points, beads and tools, perforated marine shells and ochre.

Robberg assemblages are found at many sites that fall within the focus area of this thesis. A long Robberg sequence is present at Nelson Bay Cave (Region D) where it appears at 18 660 ± 110 BP (GrN-5889) (J. Deacon 1978; Wadley 1993), Melkhoutboom in Region E with a basal date of 15 400 ± 120 BP (UW-233) (H.J. Deacon 1976) and Elands Bay Cave in Region B on the West Cape coast with a date of *ca.* 13 600 ± 140 BP (Pta-4321) (Orton 2006; Parkington 1992; Wadley 1993). Some of the earliest recorded occurrences of the Robberg Industry appear at Boomplaas Cave in Region F at 21 220 ± 195 BP (Pta-1810) (H.J. Deacon 1995; Wadley 1993) and Sehonghong in Lesotho (near Region G) at 20 900 ± 270 BP (Pta-789) and 20 200 ± 200 BP (Pta-6077) (Mitchell 1995). At Rose Cottage Cave (see Wadley 1996, 1997, 2000a), the Robberg appears later; the oldest Robberg level is firmly dated to 15 700 ± 40 BP (Pta-6195) and continues to the youngest date of 9340 ± 80 (Pta-7288) (Pienaar *et al.* 2008). Here, a hiatus during the Last Glacial Maximum is likely a site-specific cause of the later appearance of the Robberg industry and not a feature of the region as a whole.

Climates in southern Africa from 40 – 14 ka were between 3° and 6°C cooler than current temperatures with the coldest period recorded at the LGM, around 18 ka. Increased aridity in noted in south-eastern Africa during the Late Pleistocene (Castañeda *et al.* 2007). These conditions may have played a significant role in the population's isolation (Lahr and Foley 1998). Although this time is generally marked by less precipitation across most of South Africa (with the exception of the winter rainfall region, where precipitation increased (Cowling *et al.* 1999; Faith 2013) and a slightly wetter environment in the southern African tropics (Beuning *et al.* 2011)), particularly dry periods emerge after 24 ka when increased aridity drives the expansion of desert landscapes such as the Kalahari. This arid expansion constrained resources towards the coastal edges of Africa (Barham and Mitchell 2008). Sea levels were at their lowest, with shorelines located up to 200km beyond where we would find them today, exposing the Agulhas continental shelf and steep coastal cliffs (Barham and Mitchell 2008; J. Deacon 1984b; Van Andel 1989). Archaeological sites which are coastal today were not coastal 40 – 14 ka. Many of these sites reflect changes in vegetation (such as increased grasslands) and fauna relating to lower temperatures and varied rainfall. Faunal remains from southern Cape sites such as Nelson Bay Cave and Melkhoutboom, for example, indicate the presence of large social migratory grazers, indicative of a grassy environment no longer present (H.J. Deacon 1972a, 1976; Klein 1972, 1974). In contrast, faunal remains from the Holocene assemblages are dominated by smaller, solitary browsers. This phenomenon is clearly identified in the southern Cape while inland, where grasslands predominate today, the Pleistocene/Holocene faunal distinction is not as clear. Floral evidence during this time is scarce, probably due to a lack of preservation. However, plant species, both edible and inedible, and plant bedding material have been identified at a number of sites (see Beaumont 1978, 1980; H.J. Deacon 1995; J. Deacon 1984b). Warmer and wetter climates began to replace the extreme aridity and cold from around 14 ka (H.J. Deacon *et al.* (1984), continuing into the Holocene.

TERMINAL PLEISTOCENE/EARLY HOLOCENE 12 – 8 KA

OAKHURST COMPLEX

_ca. 12 000 BP – 8000 BP_

The Oakhurst (which includes Goodwin and Van Riet Lowe's Smithfield A), is a non-microlithic and informal industrial complex that replaces the Robberg. This Terminal

Pleistocene/Early Holocene complex consists of four geographic variants: the Albany Industry in the Cape Fold Belt and Cape forelands, the Kuruman Industry in the Northern Cape, Lockshoek in the Karoo and Free State and Pomongwan in the Matopo Hills in Zimbabwe. The Oakhurst Complex is limited to the region south of the Zambesi River, suggestive of a "…broad interaction network" (Barham and Mitchell 2008: 316) in southern Africa during this Pleistocene/Holocene transition. Interestingly, the number of visible archaeological sites increases compared with the Robberg, showing either population expansion or smaller, more sedentary groups leaving a stronger archaeological signature (J. Deacon 1984b; Mitchell 2004; Wadley 1986). Large groups, for example, exploited the Elands Bay Cave site extensively after 13 ka but far less at 9 ka (Parkington 1988, 1992). The pattern for archaeological sites from this transitional period is one of rapid increase in number after 13 ka, followed by a decline broadly overlapping with the Younger Dryas, ending 10.5 ka. The Oakhurst generally contains few formal tools but when present, a sizeable proportion are large (>20mm), D-shaped scrapers from coarse-grained raw materials such as hornfels and quartzite. Microlithic technology is discarded and tools such as bladelets disappear. Formal tools appear more frequently after 9 500 BP when naturally backed knives and retouched scrapers are used (Barham and Mitchell 2008) alongside sophisticated bone tools such as points, spatulas and polished double pointed shards (often called fish gorges) in some coastal site assemblages (J. Deacon 1978; 1984b). Additionally, there is a marked increase in other non-lithic artefacts, including various ostrich eggshell and marine shell equipment.

Although postglacial temperatures were increasing, evidence suggests that relatively cold conditions still prevailed until ~10 000 BP (L. Scott 1982; Tusenius 1989) and cooler and drier episodes have been recorded inland sporadically (i.e. Rose Cottage Cave *ca.* 8600 BP) (Esterhuysen and Mitchell 1996; Mitchell 2004; Plug and Engela 1992). Here, technological change coincides with a faunal shift. Species such as the Cape horse (*Equus capensis*) and giant wildebeest (*Megalotragus priscus*) are absent in levels after 12 000 BP at sites such as Rose Cottage Cave (Klein 1980; Plug and Engela 1992). Small bovids such as the grey rhebuck (*Pelea capreolus*) were not recorded at Robberg sites but their skeletal remains appear in moderate numbers by 8600 BP, during the Oakhurst (Plug and Engela 1992). Conditions after the LGM improved in a way that supported a greater diversity of, among others, bovid species and it is here that there is a gradual trend towards hunting and snaring small, territorial animals. However, it is important to note that larger bovids were still a more significant resource than in the mid- to late Holocene (H.J. Deacon 1976; Klein 1974, 1980; J.F. Thackeray 1979). Oakhurst occupations also display a noticeable increase in marine resource exploitation from 11 ka, including fish, shellfish (most commonly mussels and limpets), marine mammals and sea birds (Klein 1976; E.A. Voigt 1973, 1975, 1982) owing to sea levels rising to a few kilometres from present-day coastlines. Massive deposits of shellfish have been found in the south and south-western regions at sites such as Matjes River Rock Shelter (Döckel 1998; Louw 1960), indicative of intense marine exploitation during the early and mid-Holocene. Even sites located further inland have more marine items than in previous millennia (J. Deacon 1984b). Although plant foods are not well preserved, evidence is available for a variety of edible types such as marula nuts, bean species and various fruits. Bored stones, such as those found at Matjes River Rock Shelter, allude to a reliance on underground corms and tubers (J. Deacon 1984b).

The Late Pleistocene/Holocene shift has been a point of discussion in archaeological circles with explanations for cultural change ranging from environment, technology and subsistence economy to stress. H.J. Deacon (1976) attributed such changes to rapid population adaptations to altered environmental conditions, after which the system stabilized to homeostatic plateaux. Later, J. Deacon (1984a) proposed that social stress in difficult conditions would drive stone tool change, based on observations that the Robberg/Oakhurst transition occurred nearly 2 000 years prior to climatic improvements. This argument was valid in the southern coast sites but did not explain technological change in areas where climatic and faunal change were limited (Barham and Mitchell 2008). Shifts in population activity over time were seen as dynamic. It is during this period, as Barham and Mitchell (2008) point out, that we find increased settlement of varied and favourable environments and an increase in population density.

MID-HOLOCENE WILTON COMPLEX: CLASSIC WILTON AND PRE-CERAMIC POST-CLASSIC WILTON

ca. 8000 BP – 2000 BP

The Wilton, a Holocene microlithic tradition, replaced the Oakhurst across much of southern Africa from 8000 BP. The Wilton Complex is generally subdivided into the Classic Wilton (*ca*. 7000 BP – 4000 BP) and the Post-Classic Wilton (*ca*. 4000 BP – Historic) based on gradual variation in tool types through time but there is some diversity. Wilton assemblages are dominated by highly standardised convex scrapers, generally smaller than 20mm with near equal length and width (J. Deacon 1972b, 1984a, 1984b). Backed microliths usually also constitute a substantial part of the assemblage. Formal tools include segments, backed blades, borers, reamers, grooved and bored stones, adzes, and denticulates (J. Deacon 1972b, 1984a, 1984b) crafted from fine-grained raw materials. There is a much wider range of formal tools than in other Holocene assemblages, as well as a large percentage of utilised flakes without secondary retouch. A range of hafted tools are recognised, often with evidence of mastic (see for example J.D. Clark 1958; H.J. Deacon 1976; J. Deacon 1972b, 1984b; Lombard and Parsons 2008; Mitchell 1988b). The frequency and typology of these formal tools differentiates temporal and geographical variations within the tradition but a high degree of standardisation remains constant. In addition, a variety of bone tools complement this toolkit including new technologies such as fish hooks and needles. In sites with good preservation, perishable items such as leather (clothing), wood (bows, digging sticks etc.) and plant remains are found as well as decorative goods (beads, pendants and ornaments made from bone, stone and shell) and utility implements like ostrich eggshell water containers and tortoise shell food bowls (J. Deacon 1984b). A further increase in similar non-lithic artefacts occurs with the addition of pottery at *ca.* 2000 BP.

Formal burial sites become more abundant during this time but are fairly variable in number and more common in the western, eastern and particularly, southern Cape (Regions B, C, E and F) (Hall and Binneman 1987). A number of Early Holocene burials have been identified at Matjes River Rock Shelter (particularly Layer D) (Louw 1960; Meiring 1937) and Elands Bay Cave (Parkington 1981) but most likely due to preservation factors, it is only from the mid-Holocene that numbers of burials increase. In the southern and Eastern Cape, burials during the Wilton are often accompanied by grave goods such as shells, beads and grindstones. Painted gravestones and traces of ochre (indicating social ritual) have also been found. Caves and rock shelters with Mid- to Late Holocene deposits frequently contain rock art, much of it understood through ethnographic studies. Thousands of rock art sites are known, emphasising the Khoesan natural world and its link to ritual. Painted stones have also been found in the southern Cape (Hall and Binneman 1987), while engraved stones are commonly located inland, and are best known from the northern Cape (A.I. Thackeray 1981). In the western and south-western regions during the third millennium BP, interpersonal violence is evident, perhaps signifying within or between group struggles or increased competition for resources (A.G. Morris and Parkington 1982; A.G. Morris *et al.* 1987; Pfeiffer 2012b; Pfeiffer and Harrington 2011; Pfeiffer and Van der Merwe 2004; Pfeiffer *et al.* 1999). In contrast to the coast, burials in the interior are scarce (A.G. Morris 1992a; Stynder 2006).

Palaeoenvironmental records demonstrate that the African climate was subject to recurrent drought episodes during the Holocene. Sudden climatic changes such as the global cooling and aridifying 8.2 ka event resulted in markedly cold and dry environments in parts of Africa (Esterhuysen and Smith 2003; Hassan 2002; L.G. Thompson *et al.* 2002) which would have had an impact on African population movements and subsistence (Hassan 2002). During the Holocene altithermal, ~7000 – 4500 BP, temperatures in southern Africa increased 1-2°C (Partridge *et al.* 1999), impacting rainfall patterns. Climatic fluctuations in southernmost South Africa are particularly dynamic between 6500 – 5000 BP (B.M. Chase *et al.* 2013). Drier conditions persisted in the northern Cape and Karoo after 6500 BP, while Kalahari areas were wetter (Partridge *et al.* 1990). This dry trend continued in the summer rainfall regions of South Africa until the Late Holocene, while in the south-west winter rainfall region wetter conditions prevailed after 4500 BP (Barham and Mitchell 2008).

Mid-Holocene Wilton assemblages are infrequent areas further from the Fold Belt mountains and the coastal plain (Regions A and G). Ongoing work confirms the absence of mid-Holocene occupation in the middle of South Africa first described by Janette Deacon (1974). Occupation sites dating to *ca.* 7000 BP have been identified in the Thukela Basin of KwaZulu-Natal (Mazel 1987, 1989b), the Magaliesberg (Wadley 1989) and long, more complex LSA sequences identified at Rose Cottage Cave (although there is an occupational hiatus here between 5970 ± 70 BP (Pta-5934) and 2240 ± 60 BP (Pta-7117)) (Wadley 2000b), Sehonghong (Mitchell 1996) and Likoaeng (Mitchell 2009). Evidence of the Wilton in the Northern Cape is found at Wonderwerk Cave (Humphreys and Thackeray 1983). These sites encircle the central Karoo, where there is scant evidence of occupation.

Overall, the vast majority of mid-Holocene Wilton assemblages occur contemporaneously in the south-western and southern (C and D) regions, south of the Cape Fold Mountains. Wilton Large Rock Shelter (the Wilton Industry type site) and Melkhoutboom provide key sequences for this area. At Nelson Bay Cave, Boomplaas, Matjes River Rock Shelter (Döckel 1998; Louw 1960) and Melkhoutboom (H.J. Deacon 1976), for example, the onset of Wilton tools is dated to *ca.* 7500 BP, although at some sites (Nelson Bay Cave and Boomplaas), an increase in formal tool production is only seen between *ca.* 6000 and 6500 BP (J. Deacon 1984a). As one moves along the Atlantic coast towards the western region (Region B), the distribution of mid-Holocene Wilton occurrences becomes erratic. At Elands Bay Cave, for example, there is an occupational hiatus between *ca.* 7900 BP and 4300 BP and no Wilton is present (Parkington *et al.* 1988). This may be a site-specific feature since a few kilometres further north, Steenbokfontein cave has yielded mid-Holocene microlithic assemblages (Jerardino 1996). A detailed study by Parkington (1972, 1976, 1980, 1981) of faunal remains from Elands Bay Cave identified distinct seasonal markers in late Holocene deposits, indicating winter occupation. Faunal and floral remains from the site of De Hangen, in the Fold Belt Mountains, indicated summer occupation. In combination with climatic factors, e.g. milder winters at the coast, Parkington synthesized these observations to propose a model of seasonal transhumance in the Later Stone Age, with populations spending winters at the coast and summer in the interior (Parkington 1976, 2001; Parkington *et al.* 1988). One corollary of this is that human skeletons found at the coast and in the interior should be the remains of a single population, with stable isotope ratios reflecting a similar mix of marine and terrestrial foods. Stable isotope analyses of human skeletons in fact showed that, between 4000 BP and 2000 BP, people dying at the coast had distinctly different isotopic signatures (and therefore diets) from those dying inland (Sealy and van der Merwe 1985, 1986). Late Holocene coastal populations ate large quantities of marine food, and probably remained near the coast much or all of the year. Inland people may have visited the coast, but did not spend enough time there for marine foods to contribute a significant part of their diets. This pattern of territorial behaviour in the Late Holocene also appears to be true elsewhere in the coastal regions of southern Africa. Archaeological evidence and stable isotope analysis of skeletons along the south and southwest Cape coast in the Forest and Fynbos Biomes (Regions C and D) demonstrate that in the second half of the Holocene, populations had decreased mobility (Sealy 2006; Sealy and Pfeiffer 2000). At this time, we also see fluctuations in cranial and body size (Pfeiffer and Sealy 2006; Stynder 2006; Stynder *et al.* 2007a), although Kurki *et al.* (2012) demonstrate differences in femora, cranial centroid size and bi-illiac breadth highlighting the absence of this size reduction in skeletons from this region post-5000 BP. Regional variation becomes apparent in features of the skeleton related to habitual behaviours such as squatting and patterns of use of the upper arms, probably in relation to preferred hunting technique (Dewar and Pfeiffer 2004; Stock and Pfeiffer 2001). From 4500 BP, population sizes increase considerably as climates become more favourable and subsistence strategies shift to the increased exploitation of predictable, low risk foods such as tortoises and fish (Barham and Mitchell 2008). This is best seen in the coastal forelands, for example, in the mass collection and processing of a primary marine food source such as black mussels at open-air sites in the western region. At these sites, large megamiddens formed between 3000 BP and 2000 BP that were not only shellfish processing sites but also served as stone knapping and animal processing camps (Jerardino 1998; Jerardino and Yates 1997). Here, mussels may have been dried and stored for later consumption (Henshilwood *et al.* 1994).

Post-4000 BP, artefact assemblages show substantially greater regional diversity. In some regions, e.g. the Western region, a microlithic tradition continued, while along the southern coast there was a shift to macrolithic tools. This geographical diversity is consistent with the skeletal and isotopic evidence mentioned above, reflecting greater territoriality and differentiation of populations across the landscape. Numbers of sites and volumes of deposit increase, suggesting population growth. In addition, inland areas (i.e. the Karoo) were re-occupied, which in itself is evidence of growing numbers of people.

LATE HOLOCENE

POST-CLASSIC WILTON

ca. 2000 BP – historic times

From around 2000 BP, domesticated sheep and cattle remains and pottery appear in the archaeological record. Current debate regarding the timing and dispersal of these is split into two viewpoints: one approach suggests that pastoralism (and the Khoekhoen) arrived through a migration *ca.* 2000 years ago (Boonzaier *et al.* 1996; Ehret 1982, 1998; Elphick 1985; A.B. Smith 1992a, 2005, 2006, 2008a; B.W. Smith and Ouzman 2004), while the other suggests diffusion of domesticated animals and pottery 2000 years ago, followed by a migration *ca.* 1000 years ago (Fauvelle-Aymar 2004, 2008; Fauvelle-Aymar and Sadr 2008; Sadr 1998, 2003, 2005, 2008b). Arguments have centred on the interpretation of direct archaeological evidence and various cultural markers.

Sheep reached northern Botswana and western South Africa by 2100 BP (Robbins *et al.* 2008; Robbins *et al.* 2005; Sealy and Yates 1994) shortly after the appearance of (but not necessarily associated with) pottery (Sadr and Sampson 2006). Some western sites (i.e. Spoegrivier in Namaqualand) appear to have sheep bones slightly older than 2100 BP (Webley 2002) and there is also the earliest evidence of caprine domesticates (Leopard Cave, in central west Namibia) dated to ca. 2270 BP (Pleurdeau *et al.* 2012), all predating pottery. On the southern coast of South Africa however, sheep are slightly younger at ~2000 BP. Overall, early dates for the appearance of sheep are remarkably consistent across southern Africa, indicating the rapid spread of these domesticates which became widespread after 1600 BP (H.J. Deacon *et al.* 1978; Henshilwood 1996; Klein 1986; Sealy and Yates 1994, 1996). Early cattle remains are less common, although specimens identified as cattle have been dated to a little before 2000 BP in northern Botswana (Robbins *et al.* 2008; Robbins *et al.* 2005), and a cattle horn core from Namaqualand has recently been dated to 1625 ± 25 BP (OxA-22933) (Orton *et al.* 2013). Major excavated archaeological sites that were occupied by herders (Kasteelberg, Die Kelders, Boomplaas) date mostly to the first millennium AD. These have yielded significant quantities of sheep bones, but few cattle. Stable isotope analyses of human skeletons support the view that cattle pastoralism probably became important around 1000 AD (Sealy 2010). Sadr (2008b) suggests that there may have been a Khoekhoen migration around this time. Changes in material culture such as ostrich eggshell bead sizes, stone tool typology and the appearance of Khoekhoen thin-walled lugged pottery (Sadr and Smith 1991) at scattered second millennium AD herder sites, suggests major discontinuity within the population and according to Sadr (1998, 2003, 2008b, 2013), is indicative of immigrant Khoe-speaking pastoralists reaching southernmost Africa. Surface scatters of archaeological material and stone circles (herder kraals) are also representative of pastoralist sites in the western Cape, north of the landmark herder site, Kasteelberg (Fauvelle-Aymar *et al.* 2006) as well as in the Karoo (Sampson 1996, 2010), all appearing to date to the last 1000 years BP. Additionally, rock art, although not dated with certainty, also suggests a late migration. A Khoekhoe painting and engraving rock art tradition comprising a variety of imagery, including fat-tailed sheep and other animals, human figures, hand prints, items of material culture and highly stylised geometric images, may trace such migrations (C.K. Cooke 1965; Eastwood and Smith 2005; B.W. Smith and Ouzman 2004). One such study has used a range of finger-painted geometric images and designs to outline a (controversial) route from central to southern Africa (Eastwood and Smith 2005; B.W. Smith and Ouzman 2004). Yates *et al.* (1994) argue that handprints found in Western Cape rock shelters probably date to the second millennium AD. This non-migratory or diffusion theory of livestock introduction has considerable sway (Fauvelle-Aymar 2004, 2008; Sadr 1998, 2002, 2003, 2008b, 2013), demonstrating that first, there is no evidence for large-scale population migrations that correlate with the introduction of domesticates *ca.* 2000 BP. Secondly, there is evidence of hunter-gatherers having become herders, suggesting that the Khoekhoen and San were segments from a single homogenous population oscillating between hunting-and-gathering and herding lifestyles after 2000 BP (Elphick 1985; Schrire 1992; Schrire and Deacon 1989). Marginal biological differentiation between hunter-gatherers and herders post-2000 BP was also argued on the basis of social and cultural isolation and subsistence variability across South Africa (Hausman 1982; Rightmire 1970, 1978).

In contrast, some researchers argue for a much earlier migration *ca.* 2000 BP. Early studies argued that domestic stock may have diffused to settled local hunter gatherer populations (J. Deacon 1984b; Klein 1986) i.e. from southern Zimbabwe, northern Botswana and northern South Africa (Wadley 1987) where local hunter-gatherers came into contact with migrating north-eastern pastoralists (Walker 1983), or from Bantu-speaking pastoralists from East Africa migrating south and west (Elphick 1985). Building on these views, new work (A.B. Smith 1992a, 2006, 2008a) suggests that pastoralists from the north migrated into South Africa. Ceramics and language studies provide the best support for this early migration. Bambata pottery from Botswana (Robbins *et al.* 2005), undecorated pots from Zimbabwe (Burrett 2006), decorated sherds from Namibia (A.B. Smith and Jacobson 1995) and the Limpopo Province of South Africa (Hall and Smith 2000), among others, differ from Iron Age ceramics and can be archaeologically associated with early domestic stock and Khoekhoen rock art (Hall and Smith 2000; B.W. Smith and Ouzman 2004). Pottery from understudied areas such as Zambia and Tanzania (Chami and Chami 2001) may provide possible antecedents for thin-walled ceramics found in southern Africa alongside demonstrated linguistic connections. Linguistic evidence identifies similarities between the historic Cape Khoekhoe and the Tshu-Khwe speakers of northern Botswana (Westphal 1963). This and ethnographic evidence (Elphick 1985) profiles the dispersal of pastoralism into South Africa from Botswana to the Orange River, moving east and west from there (C.K. Cooke 1965; Stow 1905). Additionally, connections between East and South Africa have been made through language (Ehret 1973) and material culture (A.B. Smith 1992a), proposing that South African Khoekhoe pastoralists were descendents of East African pastoralist populations. Also, genetic studies (Cavalli-Sforza *et al.* 1994; Cruciani *et al.* 2002; Pickrell *et al.* 2012; Schlebusch *et al.* 2012) have found links between some modern East and South African Khoesan populations but investigations on archaeological specimens found no such link (A.G. Morris 2003, 2008).

Although there is strong linguistic, historical and ethnographic evidence for the introduction of livestock to southern Africa by immigrant Khoekhoe pastoralists, the archaeological evidence is unsupportive. The interpretations of herding societies within the archaeological record rely heavily on historical sources. Although some sites record the presence of both sheep and pottery, it is difficult to determine whether the site was inhabited by pastoralists or by hunter-gatherers who had access to domestic stock. Additionally, livestock and ceramics do not always appear contemporaneously in the archaeological record, perhaps indicating that pottery developed independently in southern Africa (Sadr 1998, 2008a; Sadr and Sampson 2006). The appearance of sheep and pottery in the Cape *ca.* 2000 years ago is attributed to Sadr's (2003) 'hunters-with-sheep' argument. Domestic stock and associated material culture (diffused through mechanisms such as *hxaro* gift giving practices used by the Ju|'hoansi), may explain domesticate bones appearing *ca.* 2000 years ago in existing, widespread hunter-gatherer sites across southern Africa (Sadr 2008b), culminating into herder populations at sites such as Kasteelberg. Another consideration was whether there were two culturally and biologically distinct populations present (one herder, one hunter-gatherer) after 2000 BP. Genetically distinct pastoralists migrating into South Africa (A.B. Smith 1983, 1986, 1990, 1992a; A.B. Smith *et al.* 1991) would be physically identifiable. A study of long bone length and cortical bone thickness from skeletons along the south-western Cape coast post-2000 BP suggests an influx of genetic material into the Khoesan population (P. Smith *et al.* 1992) as results demonstrate an increase in size/diameter of bone length/thickness. However, sample sizes in their study were limited (N=53). Recent craniometric evaluations on a much larger scale indicate only a slight increase in Khoesan cranial variation in the last 2000 years but it is not consistent with a large-scale migration of a genetically different pastoral population, or the existence of two genetically distinct populations living side by side over time (Stynder 2006, 2009; Stynder *et al.* 2007a). Rather, it is indicative of herders and hunter-gatherers being one genetic population where herding entered South Africa either via small-scale immigration or diffusion.

In some sites, the introduction of domesticated stock and pottery was accompanied by a shift in stone tool technology. The frequency and shape of some formal tools, such as scrapers, change and informal tools, such as large flakes, are manufactured on coarse-grained rock and cobbles (Sampson 1974). In general, there is a reduction in formal tool (specifically backed pieces) production across South Africa during this time (confirmed at sites such as Kasteelberg (Sadr 2008b)) with the exception of the western region. Here, formal tools such as scrapers and backed microliths become more widespread as demonstrated at sites such as Dunefield Midden (Parkington 1980; Parkington *et al.* 1992). Diets during this time appear to have changed somewhat and isotope analyses of human skeletons indicate that people were consuming less marine foods. This is reflected in the archaeological record by the abandonment of the megamiddens in the western and south-western regions from *ca.* 2000 BP (Jerardino 1998, 2003; Jerardino and Yates 1997). Populations were relying more on small terrestrial animals, including antelope and tortoises, as well as the new domesticates (Sealy and Pfeiffer 2000; Sealy and van der Merwe 1988). Plants were still a prominent food source and many sites provide evidence of abundant geophyte remains (H.J. Deacon 1976, 1993). Palaeoclimatic change in southern Africa during the Late Holocene was varied with the last 2000 years interspersed by frequent temperature and precipitation fluctuations (Barham and Mitchell 2008). These fluctuations had limited effect on established environmental biomes where grasses and shrub growth were ideal grazing grounds for resilient sheep and cattle.

THE LAST 800 YEARS INLAND

The archaeological context of the inland (Region A) geographic group (often referred to as the northern frontier in the literature) demonstrates a prehistoric Khoesan population with both a pastoralist and hunter-gatherer lifestyle. Early records depict these populations as Khoesan pastoralists with sheep and cattle (Burchell 1822; J. Campbell 1822) in contact with Bantu-speaking populations (as recorded in the journals of Hendrik Jacob Wikar (Mossop 1935) and Robert Jacob Gordon (Raper and Boucher 1988)). It is discussed briefly here because of the population’s distinctive practices, their interaction with other cultural groups and recent timeframe. People along the Riet River (Koffiefontein) and surrounds are associated with Type-R settlements (Humphreys 1972, 2009; T.M. Maggs 1971), described as circular stone-wall central enclosures surrounded by smaller enclosed spaces. Occupation dates (radiocarbon dates obtained from Type-R settlement units) for these settlements range from around AD 1100 – 1900 (Beaumont and Vogel 1984; A.G. Morris 1992b; Ouzman 2001). Faunal data from various sites confirms this activity although there is substantial evidence of a continued hunting tradition of small-medium bovids and tortoises (Humphreys 1973, 2009; T.M. Maggs 1971). Lithics (Lombard and Parsons 2008; I. Parsons 2003), material objects, including bone tools, ostrich eggshell beads and ochre, and a rock engraving tradition (D. Morris 1988, 2002b) are typical of LSA people, suggesting these groups were Khoesan hunter-gatherers who adopted a pastoral lifestyle, perhaps diffused from their Iron Age neighbours. Recovered metal objects such as beads and bangles (Maggs 1971) offer further evidence of contact between Khoesan and Iron Age groups in the area. Also, A.G. Morris (1992b) demonstrated that the Khoesan populations in the area experienced considerable gene flow from Negroid groups. The local pottery however, has no similarity to Iron Age ceramics, possibly indicating local development (A.G. Morris 1992b). Human remains, including those used in this study, were often found in stone cairn burials, associated with numerous grave goods (Humphreys 1970; Humphreys and Maggs 1970; D. Morris *et al.* 2006). Settlements further away from the Riet River, including areas such as Augrabies, Douglas and Kakamas, have similar lithic assemblages, ceramics, material culture objects and burials (Humphreys 1982, 2007; A.G. Morris 1992b; D. Morris and Beaumont 1991) but do not, as yet, include stone enclosures. Similarities between these groups are suggestive of cultural interrelationships throughout the area encompassed in Region A.

THE HOLOCENE IN KENYA

Tracing the transition from the Pleistocene to Holocene in the East African archaeological record is difficult due to a long occupational hiatus. There is however, some evidence of obsidian based stone tool industries emerging in southern Kenya at Nderit Drift from 14 ka (Bower *et al.* 1977). Additionally, in the southern Rift Valley around this time, MSA stone artefacts (predominantly obsidian and chert) are known to have been recycled to produce small bladelets (Ambrose 2002). Evidence is more forthcoming from *ca.* 12 – 10.5 ka at sites such as Gamble's Cave, near Lake Nakuru (also southern Kenya), which has yielded evidence of the Eburran industry

(Phillipson 2005). This tradition used local raw materials (obsidian) to produce large artefacts including backed blades, large retouched flakes, scrapers and crescents (Ambrose *et al.* 1980a; L.S.B. Leakey 1931). A second occupational hiatus between 10.5 and 8.5 ka limits our knowledge of the Eburran during the Kenyan Early Later Stone Age but it is recorded that by 10 ka, backed microlithic technology had spread across East Africa and successfully continued to ~2 ka (Barham and Mitchell 2008). This is well documented in central Kenya sites such as Lukenya Hill where informal microlithic assemblages, using only quartz, are dominant (Kusimba 2001).

During the mid-Holocene Kenya experienced significantly drier climates (Ambrose and Sikes 1991) and there is some evidence of abrupt drought conditions ~4500-3700 BP (L.G. Thompson *et al.* 2002). Lower water levels may have resulted in the temporary drying of Lakes Elmenteita, Nakuru and Naivasha (Barham and Mitchell 2008; Richardson 1972) from ~7500 BP (Phillipson 2005). It is during this time, when grasslands begin to expand (Marshall 1990) that east Africa is ideal for the spread of food production (herding). In the Lake Turkana basin of northern Kenya, people living at sites such as Lothagam (8400 – 6000 BP) relied heavily on a fishing economy (Robbins 1972, 1974), making use of barbed bone points, harpoons and an associated stone industry consisting of backed microliths, large retouched flakes and core tools (Phillipson 2005), and in some areas, crude ceramics. Cattle make an appearance here *ca.* 4500 – 4200 BP. There are no local wild progenitors of cattle in Kenya so these animals had to come from northeastern Africa where wild cattle (*Bos primogenius*) are indigenous (Gifford-Gonzalez 1998). Although such livestock are present, the practice is overshadowed by the fishing economy (Ambrose 1984b; Barthelme 1985). In central Kenya and parts of the eastern highlands, mixed cattle/ovicaprine pastoralism emerges ca. 4500 - 4300 BP (Lane 2004). Only ~3000 BP is there a fuller commitment to domesticated stock. Herding domestic cattle, sheep and goat is formally identified in northern Kenya around Lake Turkana during the third millennium BC (Barthelme 1985; Marshall 2000; Owen *et al.* 1982). Interestingly, camels also make an appearance during this time. It appears that here, economies based on herding and to some degree fishing, continued until at least the first millennium AD. In the south, Ambrose (1984b) argues, the drier climates facilitated a shift in subsistence strategies from hunting large game to trapping and/or snaring in the new woodland savannah environment. The southerly spread of pastoralim was slow, seemingly oscillating between herding and foraging (Lane 2004, 2013). Also, formal tools (Eburran phase 5) such as backed microliths and scrapers (obsidian) are common (Barham and Mitchell 2008), similar to those tools seen in the north, with the exception of barbed points and other fishing technologies. These are often associated with stone bowls and pottery resembling Nderit ware (Phillipson 2005). Domesticates appear in the southeastern Kenya ca. 3800 – 3500 BP (Wright 2005) and are only prominent further south during the second millennium BC (Marshall 2000; Owen *et al.* 1982), although there is some evidence of earlier cattle domestication here *ca.* 3300 BP (Ambrose 1998). A pastoral industry, known as the Elmenteitan, emerges at this time and continues into the first millennium AD (Robertshaw 1988) but is geographically restricted to the high precipitation areas of the eastern Rift Valley (e.g. Bromhead's site). Here, stone tools are characterised by large obsidian blades and are found in association with stone bowls and plain bowl-shaped pottery (Phillipson 2005). A number of other pottery traditions (called 'wares') with considerable variation are also present in southern Kenya during this time. Maringishu Ware (pots with a trellised motif) is firmly identified at Hyrax Hill (L.S.B. Leakey 1931), while later lugged, spouted and often undecorated vessels, referred to as Remnant Ware (Bower and Nelson 1978), are found further south (Ambrose 1985). At Gamble's Cave, for example, Remnant Ware persisted from c. 2400 to 1400 BP (Bower and Nelson 1978). Other recent sites such as Hyrax Hill, Wiley's Kopje II & III and Makalia I & II contain burials often found in conjunction with obsidian tools, pottery (Phillipson 1977; Rightmire 1975a), and several variants of stone bowls. Plant domestication in Africa is quite late (post-4000 BP) due to the risks of farming in arid environments and the nomadic pastoral lifestyle (Marshall and Hildebrand 2002). According to Lane (2013), in East Africa domesticating and herding livestock was prominent for over a thousand years before crops were cultivated. This is one of the few places in the world where this phenomenon occurs. In northern Kenya, there is early evidence for the exploitation of cereal crops (presumably wild) but appears to be discarded in favour of livestock farming (Gifford-Gonzalez 2003; Phillipson 2005). It is in southern Kenya that grindstones and bowls hint to crop cultivation. Although little direct evidence has been found for early cultivation, finger millet (*Eleusine sp.)* was likely to have been a primary cereal crop (J.D. Clark 1962; Fuller and Hildebrand 2013; Marshall and Hildebrand 2002). East Africa is considered the domestication centre for finger millet and some of the earliest evidence of the domestic cereal is found in Kenya *ca.* 1185 BP (Ambrose 1984a).

Studies from the first half of the 20th century proposed that Khoesan populations once extended over much of sub-Saharan Africa. Early work suggested connections between pastoralists in southern Africa and Hamitic (a language group from North Africa related to Semitic) peoples from East Africa (Vedder 1928; Von Luschan 1907). These ideas were later supported by archaeological similarities between these populations (J.D. Clark 1959; Cole 1954) and the presence of ancient Khoesan in East Africa was anthropologically accepted (Nurse *et al.* 1985; Phillipson 1982; Tobias 1978). More recently, genetic studies have highlighted the ancient origins of the Khoesan mitochondrial DNA haplotype (Cavalli-Sforza *et al.* 1994; Schlebusch *et al.* 2013; Schlebusch and Soodyall 2012; Soodyall and Jenkins 1992) as well as a Y-chromosome genetic link to populations north of the Equator (Cruciani *et al.* 2002; Semino *et al.* 2002), suggestive of an early Khoesan territory extending far north. Also, two modern east African populations, the Hadza and Sandawe, derive a fraction of their ancestry from the Khoesan (Pickrell *et al.* 2012). Osteological comparisons by Bräuer (1976, 1978, 1980); De Villiers and Fatti (1982); Gramly and Rightmire (1973); A.G. Morris (2002a, 2003); and Schepartz (1988) on the other hand, demonstrate limited affinity between East African and indigenous southern African populations such as the Khoesan. This suggests a degree of Khoesan genetic (and geographic) isolation (A.G. Morris 2002a). Additionally, Winkler (1984) shows that the Sandawe are anthropometrically dissimilar to the Khoesan but comparable to East African Bantu-speakers. Besides distinct physical dissimilarity between the Hadza and the Khoesan (Hiernaux and Hartono 1980), recent work by Knight *et al.* (2003) demonstrates distinct genetic divergence between the two populations. Also, Schlebusch *et al.* (2013) demonstrates a genetic divergence between East African and the oldest haplotypes (L0d and L0k) identified in the Khoesan diverge from East Africa at least ~83 ka years ago. Dental studies (Irish 1993; Irish and Turner 1990) have also shown a degree of dissimilarity between the two groups. Nevertheless, questions remain about the degree of relatedness of hunter-gatherer and pastoralist populations across eastern and southern Africa.

SUMMARY

Specimens from Hoedjiespunt, Cave of Hearths, Border Cave, Sea Harvest, Blombos, Klasies River Mouth, Die Kelders, Mumbwa Caves and Hofmeyr present some of the earliest dental remains falling within the range of variation of anatomically modern humans in southern Africa. These Mid-Late Pleistocene teeth are accompanied by a generalised MSA (and ESA at Cave of Hearths) toolkit. At various intervals and at various sites, these specimens are found in deposits that include specialised assemblages (i.e. Still Bay, Howiesons Poort) and a multitude of symbolic and material culture artefacts. In South Africa, the MSA/LSA transition dates between 40 000 and 20 000 years ago (A.M.B. Clark 1997; H.J. Deacon 1979; Mitchell 1995; Opperman 1996; Opperman and Heydenrych 1990; Villa *et al.* 2012; Wadley 1997, 2004). The LSA is recognised, in part, from its microlithic technology and movement away from blade-based and prepared core technologies. LSA subgroups are identified by stone tool technology shifts from around 40 000 to 12 000 BP, the first of which is the ELSA followed by the microlithic assemblage, the Robberg. Non-microlithic industries from the terminal Pleistocene and Early Holocene are succeeded by Holocene assemblages characterized by standardized, retouched microliths and a wide range of formal tool types. The final subgroup consists of societies with domestic stock and ceramics.

The distribution of the LSA assemblages provides a picture of relatively continuous and long-term settlement in most areas of southern Africa. Size differences in tortoise and shellfish remains (an easily accessible and staple food source along the coast) have been interpreted as reflections of lower population density in the Late Pleistocene compared with Holocene populations (Henshilwood *et al.* 2001; Klein 2008; Klein and Cruz-Uribe 2000b; Parkington 2003, 2008; Sealy and Galimberti 2011; Steele and Klein 2005, 2009; Teske *et al.* 2007). Larger sized shellfish and tortoises in the Late Pleistocene are often seen as reflecting lower human predation pressure and therefore smaller populations during this time, compared with smaller sized resources and larger population densities during the Holocene. Recent work (Jacobs and Roberts 2008, 2009; Powell *et al.* 2009) is proposing that there may be evidence for fluctuations in population sizes within the MSA marked by periods of innovation i.e. “complex” lithics, heat treatment of raw materials and symbolic behaviour (K.S. Brown *et al.* 2009; d'Errico *et al.* 2005; d'Errico *et al.* 2008; Henshilwood *et al.* 2009; Henshilwood *et al.* 2002; Henshilwood and Dubreuil 2011; Mackay and Welz 2008; Texier *et al.* 2010). We do not, however, have enough archaeological evidence to evaluate these claims satisfactorily. In the Holocene, however, we have much more information.

During the Holocene, not only do site distributions increase dramatically, but hunting patterns change and gathering intensifies. In the Early Holocene, changing technological (and other) strategies, the sharing of resources and/or reduction of risk, may have been a direct result of population increase, social expansion and climatic change. The number of archaeological sites dating to this time increases, suggestive of either population expansion (i.e. Elands Bay Cave) or smaller, more sedentary groups occupying smaller territories over greater ranges, thereby increasing their archaeological signature (J. Deacon 1984b; Mitchell 2004; Parkington 1986, 1988; Wadley 1986). Also, large deposits and less stylistic (i.e. blanks or uniformly mass produced) tools found at sites such as Wonderwerk Cave (Humphreys and Thackeray 1983) and Heuningneskrans (Beaumont 1981) located inland, Nelson Bay cave (J. Deacon 1984b; Inskeep 1987), Elands Bay Cave (Parkington 1980, 1992) and Matjes River Rock Shelter (Döckel 1998; Louw 1960) in the Cape Fold Mountain Belt, and Boomplaas (H.J. Deacon 1979; J. Deacon 1984b) at the coast, are indicative of population growth. During the Mid- to Late Holocene, archaeological sites in the interior of South Africa are few due to drier, harsher climates leading to population decline and movement. Coastal populations however, demonstrate generalised population increases alongside variable climates over the last 6000 years. An increase in population densities during this period is supported by the marked increase of human skeletal remains along the south and southwest coasts (Lee-Thorp *et al.* 1989; Sealy *et al.* 1992; Sealy and Pfeiffer 2000; Sealy and van der Merwe 1988). Increases in site numbers, more formalised tool production (Wilton) and the exploitation of low-risk foods in the south and south-western coasts (Regions C and D), for example, are suggestive of sporadic population increases. Although it’s difficult to reconstruct population sizes from archaeological evidence, especially for hunter-gatherers, there is a good deal of evidence for substantial population increase in the Late Holocene. For example, Rose Cottage Cave in the east (Wadley 1997, 2000b) and Elands Bay Cave in the west (Parkington *et al.* 1988) were resettled after a Mid-Holocene hiatus.

Increased pressure from population growth puts strain on local resources and disrupts mobility. Archaeological evidence from *ca.* 4000 BP suggests that in response, major changes occurred in social, economic and settlement behaviours. These groups moved toward an economy based on reduced risk and delayed return. This socio-economic system is recognised by exploitation intensification and procurement specialisation, usually requiring some form of processing and/or storage (B. Hayden 1996). This phenomenon is seen in coastal shellfish exploitation and the emergence of megamiddens (Jerardino 2010) along the west coast at sites such as Pancho's Kitchen Midden (Jerardino 1998), Elands Bay Cave (Parkington 1976; Parkington *et al.* 1988) and further south in the Vredenberg Peninsula (Kasteelberg) (A.B. Smith 2006) during this time. These middens are associated with increased sedentism and population densities, changes in burial practices, increased exchange and an amplification of material culture artefacts in the archaeological record. The voluminous deposits and less stylised tools of the Oakhurst and post-Wilton traditions, which suggest increased population sizes in moderate climates are in contrast to the mid-Holocene Wilton where tools are more formalised and population distributions sporadic in less hospitable climates. Stone tool standardisation over large distances (as seen during the Wilton) indicates a degree of inter-connectedness and contact between separated groups (Sealy In press). Wadley (1989) has suggested that the *hxaro* system (gift-giving mechanism) offered a networked structure that could have transmitted information and provided alliances. However, in contrast to the Powell *et al.* (2009) model, high population densities coincide with technological simplification rather than increased complexity. It may therefore be that cultural variations between regional (small-group) populations, migratory activity and contact (and/or diffusion) resulted in both geographic and temporal differences of knowledge accumulation (Sealy In press). Additionally, changes in demography, environment, subsistence strategy and technology features signalled in the archaeological record, may reflect episodes of biological (and dental) change within a population.

During the last 2000 years, a more temperate climate inland led to a resettling of these areas and cooler, possibly wetter climates towards the coast, made for favourable occupation and again increased population numbers. Coastal territories in the north demonstrate population decline as lower site numbers are recorded and fewer open air sites are visible (Jerardino 2003; Jerardino *et al.* 2009a; Jerardino *et al.* 2009b). It is also during this time that a new socio-economic system of herding is incorporated and populations appear more sedentary; no pattern of seasonal mobility is observed (Balasse *et al.* 2002). Population growth at herding sites is observable, particularly in the first millennium AD, at sites like Kasteelberg, where a dramatic increase in available radiocarbon dates (Sadr 2005) may represent an influx of neighbouring populations or generalised population movements.

The Terminal Pleistocene/Early Holocene in Kenya provides limited evidence of occupation between periods of hiatus. During this time, some sites such as Gamble's Cave demonstrate the rise of the Eburran Industry, a stone tool assemblage largely consisting of obsidian backed blades and large flakes (Ambrose *et al.* 1980a; L.S.B. Leakey 1931; Phillipson 2005). This was followed by a successful East African microlithic tradition, well established at sites such as Lukenya Hill (Barham and Mitchell 2008). Mid-Holocene drier climates generated ideal grassland conditions, paving the way for herding (*ca*. 4500 BP with cattle) which would later supplement an abundant fishing economy in the north (Robbins 1972, 1974). Commitment to herding livestock (i.e. cattle, sheep and goat) is only seen in northern Kenya from *ca*. 3000 BP (Barthelme 1985; Marshall 2000; Owen *et al.* 1982) alongside Eburran phase 5 formal tools (Barham and Mitchell 2008), Nderit ware pottery and some stone bowls (Phillipson 2005). In the south, domesticates appear during the second millennium BC (Marshall 2000; Owen *et al.* 1982) as does the pastoral tradition, the Elmenteitan (Robertshaw 1988). Evidence of plant domestication (only seen post-4000 BP) is limited. The identification of connections between the Khoesan and East and/or North African populations have been based on morphological (Nurse *et al.* 1985; Phillipson 1982; Tobias 1978), archaeological (J.D. Clark 1959; Cole 1954) and genetic evidence (Cruciani *et al.* 2002; Pickrell *et al.* 2012; Semino *et al.* 2002). Osteologically, this is most likely not the case (Bräuer 1976, 1978, 1980; De Villiers and Fatti 1982; Gramly and Rightmire 1973; A.G. Morris 2002a, 2003; Schepartz

1988) but questions about the relatedness between eastern and southern African hunter-gatherer and pastoralist populations remain.

Following are the hypotheses to be tested in this thesis, constructed on the basis of archaeological evidence reviewed in this chapter and Khoesan dental history thus far.

THESIS HYPOTHESES

The first hypothesis centres on the dental continuity of the Khoesan throughout South Africa and investigates possible regional variations within the group. The data set has been divided geographically to include:

A) Inland, north of the Great Escarpment
B) Western region of South Africa from the mouth of the Gariep River to Stompneusbaai.
C) South-western region (from Stompneusbaai to Mossel Bay).
D) Southern region from Mossel Bay to Cape St. Francis. This area is also known as the Forest biome (250km forest area on the south-east coast).
E) Eastern region (from Cape Padrone, eastwards).
F) Southern inland region encompassing non-coastal sites in the South-western region.
G) Eastern inland region includes all areas inland from the East coast after the Great Escarpment boundary.

Hypothesis 1: Khoesan dental homogeneity between geographically separated samples.

There are no dental metric or non-metric regional differences between Khoesan samples. Throughout the Holocene, dentitions between geographically separated Khoesan populations do not demonstrate a morphological distinction.

The second hypothesis relates to the dental antiquity of the Khoesan population. Previous studies (i.e. cranial research by Stynder (2006)) have demonstrated a degree of morphological continuity throughout the Mid- to Late Holocene but Early Holocene comparisons are limited due to a lack of adequate samples. Additionally, Stynder's (2006) study of Holocene crania highlighted craniofacial fluctuations in Khoesan populations from South Africa's western and southern coastlines. His study amplified post cranial size fluctuations defined by Pfeiffer and Sealy (2006). These studies demonstrated that cranial and post cranial sizes increased prior to 4000 BP; that sizes decrease between 4000 and 3000 BP and increase steadily thereafter. Dental studies allow for improved chronological analyses due to an increase in sample size and preservation. In order to demonstrate this morphological homogeneity, the testing of this hypothesis is divided into seven temporal sub-sections of between 1000 and 2000 years each, examining dental morphological differences and similarities within each time-frame:

Temporal sub-divisions:

A) 8000+ BP
B) 8000 – 6000 BP
C) 6000 – 4000 BP
D) 4000 – 3000 BP
E) 3000 – 2000 BP
F) 2000 – 1000 BP
G) The first millennium BP

Hypothesis 2: Khoesan dental continuity between temporal sub-divisions.

There are no dental metric or non-metric temporal differences between Khoesan samples within the Holocene. Early Holocene dental differences fall within the range of metric and morphological variation of the Late Holocene sample and no significant differences within temporal sub-divisions are present. Dentitions correspond morphologically between each temporal sub-division of the Holocene, demonstrating dental stability.

The third hypothesis focuses on the comparison between MSA and Holocene Khoesan teeth. Previous dental evaluations of Middle and Late Pleistocene teeth are limited to metric analyses with very few systematic non-metric comparisons. This hypothesis tests the relationship between MSA and Holocene teeth using a well-described, statistically significant comparative Holocene data set.

Hypothesis 3: Morphological variation between Mid- to Late Pleistocene and Holocene dentitions.

There are no significant morphological differences between teeth from the Middle Stone Age and Holocene Khoesan dentition.

The final hypothesis deals with the relationship between genetically and geographically dispersed Holocene data sets. A comparative dental subset from Kenya and the Khoesan material are compared to identify any affinities. We know that the Khoesan are at one extreme of the range of variation among contemporary human populations. However, small sample sizes have hindered previous dental study and existing views on Khoesan non-metric trait variation in comparison to other African populations are incomplete.

Hypothesis 4: Holocene Khoesan and Kenyan dental variation.

Comparisons between Khoesan dentition and a Kenya dental sub-study, identify no significant differences between these two Holocene populations.

CHAPTER 4

MATERIALS AND METHODS

DENTAL SAMPLES

Both metric and non-metric data were collected from teeth of the permanent dentitions of 595 African archaeological specimens. Dental data were collected from 487 Khoesan individuals (486 used for metric data capture) and used to test the hypotheses listed in Chapter 3. Kenya Holocene dentitions (N=81) and Mid-Late Pleistocene teeth (N=27) were also examined and data collected for comparative analyses. Additionally, previous research by Irish (1993) using dental data predominantly from casts of a 19th and 20th century Khoesan population (N=99), has been included in comparative analyses of morphological data.

KHOESAN DENTAL SAMPLE

The majority of the southern African study sample consists of 487 archaeological Khoesan dentitions of Holocene age *(*Table 4.1*)*. They are curated in seven institutions: Iziko South African Museum, Cape Town (SAM-AP; N = 192); the Department of Human Biology, University of Cape Town, Cape Town (UCT; N = 60); the Department of Anatomy, University of the Witwatersrand, Johannesburg (prefix: A) (N = 22); the Albany Museum, Grahamstown (ALB; N = 51); the Florisbad Quaternary Research Centre, National Museum, Bloemfontein (NMB; N = 104); the McGregor Museum, Kimberley (MMK; N = 57) and the Natural History Museum, London (AF; N = 1). Two recently recovered specimens are temporarily housed in the Department of Archaeology at the University of Cape Town and have not yet been accessioned into a collection.

Geographical locations, cultural associations and archaeological data were recorded from museum catalogues and published specimen information (i.e. A.G. Morris 1992a, 1992b). The age and sex of each individual was assessed using the criteria suggested in Buikstra and Ubelaker (1994). Morphological indicators from both the cranium and pelvis were used to ascertain sex. When postcranial material was unavailable, sex was determined on the cranium alone. Sex was not determined on fragmentary samples. Sexual dimorphism for dental traits has not been adequately recorded (Irish 1993, 1998a; G.R. Scott 1980; Turner and Nichol 1991) and it is, therefore, common to pool the sexes. On average, males present slightly larger tooth crowns than females in contemporary populations as measured by tooth wet weight (G.T. Schwartz and Dean 2005) but researchers consistently find low levels of sexual dimorphism in human crown (T. Brown and Townsend 1979; Garn *et al.* 1966; E.F. Harris and Bailit 1988; Kieser 1990; G.R. Scott and Turner 2000) and cusp dimensions (Kondo *et al.* 2005) from around the world. Sexual dimorphism in Khoesan dentition is limited (Van Reenen 1966, 1970).

Three criteria were important in the selection of this data set. First, only adult dentitions were included. Juvenile crania with erupting adult dentition (approximate ages 6 years and up) were also included, but only exposed adult teeth were analysed. Because there are only a limited number of Khoesan specimens in museum collections, all individuals with adequately (if rarely perfectly) preserved dentitions were analysed. Of these, 363 have been dated. 214 individuals have radiocarbon dates, while the remainder can be assigned to time brackets by archaeological association (see Table 4.1 for details). The bulk of the sample is older than 500 BP, and therefore pre-dates European colonization in this region. Eighty-seven individuals are more recent than (or in the region of) 500 BP; they derive from areas such as the Karoo or North-Western Cape where there was, until recently, little occupation by population groups other than the Khoesan. Third, the condition of the remains dictated what data it was possible to collect. For example, for the evaluation of rocker jaw, data were collected only from unbroken, complete mandibles (with or without dentition). Bony exostoses were recorded on complete or partial mandibles and maxillae. Dental traits, too, were recorded for both complete and incomplete dentitions as each tooth was individually evaluated. This was important to obtain as large a sample size as possible, as pre- and post mortem tooth loss is common and many of the dentitions available for study are incomplete. Data on geographic origin were recorded in order to investigate possible regional differences in trait frequencies. All 487 Khoesan individuals studied have a known provenance and were placed in one of seven geographic regions (Fig. 4.1). In terms of the current geo-political layout of South Africa, specimen localities span five provinces: Northern Cape, Free State, Kwa-Zulu Natal, Eastern Cape and Western Cape Provinces. Some specimens come from the neighbouring countries of Lesotho and southernmost Namibia.

SPECIMEN	**DATE**	**LAB NUMBER**	**SEX**	**LOCALITY**
(A) Inland Region				
SAM-AP 1268	20 ± 40	Pta-1882		Orange River, Namaqualand
NMB 1427	180 ± 70	Pta-2908		Augrabies
UCT 1	200 ± 50	Pta 1886	M	Richtersveld
NMB 1372	210 ± 40	Pta-2901	F	Kakamas
NMB 1405	360 ± 45	Pta-2905	M	Kakamas
MMK 235	390 ± 50	Pta-2894	F	Koffiefontein
MMK 169	± 500	Association	M	Barkley West
MMK 170	± 500	Association	F	Best Pan, near Riverton
MMK 171	± 500	Association		Dwarsvlei, Herbert
MMK 187	± 500	Association	M	Jacobsdal
MMK 188	± 500	Association		Barkley West
MMK 189	± 500	Association		Koffiefontein
MMK 190	± 500	Association		Koffiefontein
MMK 192	± 500	Association	F	Koffiefontein
MMK 194	± 500	Association	M	Koppieskraal, near Koffiefontein
MMK 198	± 500	Association	M	Koffiefontein
MMK 200	± 500	Association		Koffiefontein
MMK 202	± 500	Association		Koffiefontein
MMK 203	± 500	Association	F	Koffiefontein
MMK 204	± 500	Association	F	Koffiefontein
MMK 206	± 500	Association	F	Koffiefontein
MMK 209	± 500	Association	F	Koffiefontein
MMK 212	± 500	Association		Koffiefontein
MMK 213	± 500	Association		Koffiefontein
MMK 217	± 500	Association	F	Koffiefontein
MMK 220	± 500	Association	M	Koffiefontein
MMK 222	± 500	Association	F	Koffiefontein
MMK 228	± 500	Association	F	Koffiefontein
MMK 229	± 500	Association	M	Koffiefontein
MMK 230	± 500	Association		Koffiefontein
MMK 230a	± 500	Association		Koffiefontein
MMK 237	± 500	Association	F	Koffiefontein
MMK 239	± 500	Association		Koffiefontein
MMK 242	± 500	Association	M	Douglas
MMK 245	± 500	Association	F	Koffiefontein
MMK 248	± 500	Association	F	Koffiefontein
MMK 249	± 500	Association	M	Koffiefontein
MMK 250	± 500	Association	M	Koffiefontein
MMK 257	± 500	Association	F	Douglas
MMK 272	± 500	Association	F	Koffiefontein
MMK 274	± 500	Association	F	Longlands, Barkley West
MMK 284	± 500	Association	M	Upington
MMK 286	± 500	Association	M	Douglas
MMK 289	± 500	Association	M	Louisvale settlement on Orange River

MMK 296	± 500	Association	M	Driekopseiland
MMK 299	± 500	Association		Soutpan, Riverton
MMK 301	± 500	Association	M	Soutpan, Riverton
MMK 308	± 500	Association	M	Soutpan, Riverton
MMK 312	± 500	Association	M	Voelfontein, Campbell
MMK 316	± 500	Association	F	St. Claire, Douglas
MMK 321	± 500	Association	M	St. Claire, Douglas
MMK 335	± 500	Association	M	Clievedon, Douglas
NMB 1	± 500	Association	F	Douglas
NMB 1103	± 500	Association	F	Koffiefontein
NMB 1209	± 500	Association		Koffiefontein
NMB 1210	± 500	Association	M	Koffiefontein
NMB 1215	± 500	Association	F	Koffiefontein
NMB 1224	± 500	Association		Villieria, Douglas
NMB 1332	± 500	Association		Upington
NMB 1364	± 500	Association	M	Kakamas
NMB 1366	± 500	Association	M	Augrabies
NMB 1368	± 500	Association	F	Bo-Renosterkop, Kakamas
NMB 1370	± 500	Association		Kakamas
NMB 1379	± 500	Association	M	Augrabies
NMB 1380	± 500	Association		Augrabies
NMB 1381	± 500	Association		Augrabies
NMB 1383	± 500	Association		Augrabies
NMB 1390	± 500	Association		Kaikaries, Kakamas
NMB 1392	± 500	Association		Kakamas
NMB 1411	± 500	Association		Upington
NMB 1412	± 500	Association	M	Upington
NMB 1414	± 500	Association		Kakamas
NMB 1416	± 500	Association		Kakamas
NMB 1420	± 500	Association		Augrabies
NMB 1430	± 500	Association		Augrabies
SAM-AP 3691	± 500	Association		Upington
SAM-AP 4895	± 500	Association	F	Douglas
SAM-AP 4915	± 500	Association		Upington
MMK 277	890 ± 50	Pta-2898	F	Weltevreden, Koffiefontein
A 240			F	Koffiefontein
A 268			M	Blaauheuwel, Riet River
A 327			M	Strydpoort, Jacobsdal
A 333			M	Strydpoort, Jacobsdal
A 334			M	Strydpoort, Jacobsdal
ALB 75			F	Olifants Kloof, Namibia border
MMK 143			M	Kuruman
MMK 150			F	Abian, southern Kalahari
MMK 151			M	Abian, southern Kalahari
MMK 155			F	Inkbos Pan, Gordonia
MMK 163			M	Karasberg, Namibia
SAM-AP 1275				Orange River, Namaqualand
SAM-AP 1455			M	Oranje River, Richtersveld
UCT 42a				Kenhardt

(B) Western Region				
SAM-AP 1269	200 ± 50	Pta-1849	M	Henkries, Bushmanland
SAM-AP 1446	740 ± 30	Pta-9085	M	Port Nolloth
SAM-AP 6331	790 ± 90	TO-8953	F	St. Helena Bay
UCT 224	2400 ± 100	OxA-455	F	Elands Bay
SAM-AP 4935	2540 ± 50	Pta-4275		Stompneusbaai
SAM-AP 5069	2634 ± 28	OxA-V-2066-34	F	Doringbaai
UCT 427	2670 ± 80	Gx-14816	F	Eland's Bay
UCT 222	2830 ± 85	Gx-13184	M	Stompneusbaai
UCT 333	3540 ± 60	Pta-1642	F	Klipfonteinrand
SAM-AP 4931	3750 ± 60	Pta-2267	M	Kleinsee, Namaqualand
UCT 373	3835 ± 50	Pta-1754	F	Elands Bay
UCT 374	9750 ± 100	Pta-3086		Elands Bay
UCT 378	10860 ± 180	OxA-478		Elands Bay
SAM-AP 4933			F	Stompneusbaai
SAM-AP 1272			F	Henkries, Bushmanland
SAM-AP 1273			F	Jackalswater, Namaqualand
SAM-AP 1274			F	Henkries, Bushmanland
ALB 52				Steinkopf, Namaqualand
ALB 53			M	Steinkopf, Namaqualand
SAM-AP 1240				Richtersveld, Namaqualand
SAM-AP 1860				Namaqualand
(C) South-western Region				
SAM-AP 4867	590 ± 45	Pta-4407	M	Witklip Farm, Vredenburg
SAM-AP 6020	620 ± 30	Pta-4189	M	Tikosklip, Saldanha
SAM-AP 5035a	620 ± 35	Pta-4401	M	Melkbosch, Cape
SAM-AP 5035d	630 ± 50	Pta-4813	M	Melkbosch, Cape
SAM-AP 5032	765 ± 25	OxA-V-2056-35	M	Milnerton Beach
SAM-AP 1863	800 ± 50	Pta-4708		Cape Point
SAM-AP 5012	812 ± 26	OxA-V-2065-36	M	Langebaan
UCT 60	950 ± 50	Pta 2005	M	Saldanha
SAM-AP 6332	980 ± 50	Pta-8767	M	Melkbosstrand
SAM-AP 1444	1290 ± 50	Pta-4398	M	Gordon's Bay
SAM-AP 4930	1130 ± 40	Pta-4827	F	Green Point, Cape Town
SAM-AP 6063	1170 ± 30	Pta-4279	F	Saldanha
UCT 437	1310 ± 50	Pta-4373		Kasteelberg, near Vredenburg
SAM-AP 6075	1330 ± 40	Pta-4186	F	Saldanha
SAM-AP 6074	1360 ± 40	Pta-4148	F	Saldanha
SAM-AP 4920a	1364 ± 32	OxA-V-2059-17	M	Blouberg Strand
SAM-AP 3737a	1370 ± 45	Pta-4219		Hout Bay
SAM-AP 5034	1390 ± 40	Pta-4771	M	Hout Bay Post Office
SAM-AP 6334	1400 ± 50	Pta-8790	F	Melkbosstrand
SAM-AP 6149	1440 ± 70	Gx-13182	M	Melkbos
SAM-AP 5083	1490 ± 50	Pta-926	F	Yzerfontein
UCT 97	1560 ± 40	Pta-4828		Kommetjie
SAM-AP 4790	1610 ± 150	Pta-2163	M	Hermanus
SAM-AP 6041a	1800 ± 50	Pta-4722	M	Milnerton
SAM-AP 1473	1880 ± 60	Pta-8773	M	Onrus

SAM-AP 4901	1892 ± 28	OxA-V-2065-40	M	Pearly Beach
SAM-AP 6264	1950 ± 60	Pta-9073	M	Melkbosstrand
SAM-AP 3053	1990 ± 50	Pta-4411	M	Strand, Somerset West
SAM-AP 4302	2000	Assoc.SAM-AP 4303/06	F	Noordhoek
SAM-AP 6041b	2010 ± 45	Pta-4768	M	Milnerton
SAM-AP 1443	2050 ± 50	Pta-2309	M	Gordon's Bay
SAM-AP 4304b	2070 ± 50	Pta-4391		Noordhoek
SAM-AP 1142	2090 ± 27	OxA-V-2056-32	F	Strand, Somerset West
SAM-AP 6260a	2120 ± 60	Pta-9069	F	Melkbosstrand
SAM-AP 6313b	2140 ± 29	OxA-V-2056-47	F	Melkbosstrand
SAM-AP 4813	2140 ± 45	Pta-4202	F	Bokbaai, Darling
SAM-AP 6313a	2161 ± 30	OxA-V-2055-44	F	Melkbosstrand
SAM-AP 1441	2170 ± 60	Pta-4201	M	Melkbosch
Not accessioned	2180 ± 60	Gx - 32517	M	Swartriet, Saldanha
SAM-AP 4964	2190 ± 60	Pta-8756	M	Die Dam (Quoin Point/Cape Agulhas)
SAM-AP 4720	2195 ± 80	Gx-13179		Kommetjie
SAM-AP 4942	2220 ± 45	Pta-4829	M	Kommetjie
SAM-AP 4304a	2220 ± 50	Pta-4656		Noordhoek
SAM-AP 4301	2250 ± 30	OxA-V-2055-40	F	Noordhoek
UCT 595	2250 ± 40	Beta 263613	F	Saldanha Bay
SAM-AP 4299	2294 ± 29	OxA-V-2065-46	F	Noordhoek
SAM-AP 6043	2295 ± 28	OxA-V-2056-40	M	Melkbosstrand
SAM-AP 4300	2304 ± 29	OxA-V-2067-37	F	Noordhoek
UCT 372	2360 ± 60	Pta 4003	M	Snuifklip, near Vleesbaai
SAM-AP 1157	2420 ± 60	Pta-4217	M	Blaauwberg
SAM-AP 4899	2440 ± 60	Pta-4149	M	Saldanha Bay
SAM-AP 6031	2560 ± 50	Pta-4814		Geelbek, Langebaan
SAM-AP 5070	2573 ± 31	OxA-V-2056-46	F	Melkbosstrand
SAM-AP 4303	2590 ± 50	Pta-4412	M	Noordhoek
SAM-AP 4943	2610 ± 50	Pta-4821		Kommetjie
SAM-AP 4906a	2635 ± 29	OxA-V-2065-35	M	Blouberg Strand
SAM-AP 5095	2660 ± 70	Pta-4674		Saldanha
SAM-AP 4203	2760 ± 50	Pta-4798	F	Kommetjie
SAM-AP 5091	2830 ± 50	Pta-4724		Yzerfontein
UCT 162	2880 ± 50	Pta-929	M	Yzerfontein
UCT 421	2895 ± 45	GrA-23217	F	Darling
SAM-AP 6071	2935 ± 32	OxA-V-2055-42		Vredenberg
SAM-AP 5036	2960 ± 60	Pta-8445		Melkbosch
SAM-AP 6317	2970 ± 60	Pta-8807	M	Melkbosstrand
SAM-AP 4906b	2977 ± 33	OxA-V-2056-48	M	Blouberg Strand
UCT 435	2980 ± 60	Pta-5034	F	Langebaan
SAM-AP 6319	3200 ± 35	Pta-8752	F	Melkbosstrand
UCT 229	3220 ± 55	Pta-928	F	Melkbosstrand
SAM-AP 6318	3310 ± 60	Pta-8741	F	Melkbosstrand
SAM-AP 4974	3363 ± 34	OxA-V-2055-48	M	Gansbaai
SAM-AP 4298	3380 ± 33	OxA-V-2055-41	F	Kommetjie
SAM-AP 5040	3570 ± 60	Pta-4225	F	Bokbaai, Darling
UCT 112b	4000	Assoc. with UCT 112		Darling
SAM-AP 4793	4110 ± 60	Pta-4694	M	Noordbaai, Saldanha

UCT 112	4445 ± 50	Pta-2003	M	Darling
UCT 248	4730 ± 95	Gx-13185	F	Noordhoek
SAM-AP 5068	5680 ± 70	Pta-4370		Yzerfontein
SAM-AP 6272	5830 ± 80	Pta 9082	M	Darling
UCT 323	6430 ± 80	Pta-8794		Blombos
SAM-AP 4692	6891 ± 37	OxA-17376	M	Peers Cave, Fish Hoek
AF 63 - 1069			M	Cape Town
MMK 183				Hawston
MMK 184			M	Hawston
NMB 1218				Strand, Somerset West
SAM-AP 3697			M	Rooi Els Cave
SAM-AP 1442				Gordon's Bay
SAM-AP 1460				Gordon's Bay
SAM-AP 3044a				Heatherton, near Blaauwberg
SAM-AP 3044b				Heatherton, near Blaauwberg
SAM-AP 3737b				Hout Bay
SAM-AP 4794				Noordbaai, Saldanha
SAM-AP 4798				Darling
SAM-AP 48			F	Hawston
SAM-AP 4802				Yzerfontein
SAM-AP 4839				Peers Cave
SAM-AP 4840			F	Peers Cave
SAM-AP 4920b			F	Bloubergstrand
SAM-AP 4928			M	Melkbosstrand
SAM-AP 4949				Simonstown
SAM-AP 4950b				Pearly Beach, Gansbaai
SAM-AP 5038			M	Belville south
SAM-AP 5084				Yzerfontein
SAM-AP 51			F	Hawston
SAM-AP 52				Hawston
SAM-AP 54a				Hawston
SAM-AP 54b			M	Hawston
SAM-AP 6022			M	Pearly Beach, Gansbaai
SAM-AP 6047a			M	Sea Harvest site, Saldanha Bay
SAM-AP 6047b			M	Sea Harvest site, Saldanha Bay
SAM-AP 6309				Melkbosstrand
SAM-AP 6332			M	Melkbosstrand
SAM-AP 6348a			F	Melkbosstrand
SAM-AP 6359			M	Die Kelders
SAM-AP 6360				Melkbosstrand
SAM-AP 6364				Melkbosch
SAM-AP 6367a			F	Uitkomst 23, Saldanha Bay
SAM-AP 6367c				Uitkomst 23, Saldanha Bay
UCT 139			M	Kalk Bay
UCT 578			M	Leentjiesklip 2, Langebaan waterfront
SAM-AP 6040			F	Wiedeland Farm, Heidelberg
SAM-AP 6044			F	Melkhoutkraal, Riversdale
SAM-AP 6048a				De Hoop Reserve
SAM-AP 6048b				De Hoop Reserve

(D) Southern Region				
ALB 316	460 ± 40	Pta-8600	F	Groot Kommandokloof Shelter
UCT 262	510 ± 40	GrA-23221	M	Oakhurst Rock Shelter, Grave 17
UCT 583	560 ± 45	Pta 8760	M	Voëlvlei 2, Mossel Bay
NMB 1338	650 ± 35	GrA-23711	M	Wittedrif, Knysna
NMB 1219	650 ± 50	Pta 8804	M	Groot Brak River
ALB 277	670 ± 50	Pta-8685	M	Humansdorp
SAM-AP 4180	688 ± 27	OxA-V-2056-23	F	Thys Bay, Humansdorp
ALB 351	725 ± 28	OxA-15140	F	Papiesfontein, Humansdorp
UCT 582	740 ± 40	Pta 7178	F	Voëlvlei 1, Mossel Bay
NMB 1704	760 ± 50	Pta-6963	F	Plettenberg Bay
SAM-AP 1457	910 ± 35	Pta-2149	F	Klein Brak River, Mossel Bay
SAM-AP 4898	1226 ± 26	OxA-V-2053-49	M	Robberg
UCT 254	1270 ± 50	Pta-6820	M	Plettenberg Bay
UCT 592	1370 ± 40	Beta-263616	M	Sedgefield
NMB 1707	1394 ± 24	OxA-V-2064-53	M	Plettenberg Bay
NMB 5	1423 ± 26	OxA-V-2064-49	F	Plettenberg Bay
SAM-AP 6213	1558 ± 27	OxA-V-2065-39	M	Sedgefield
UCT 109	1590 ± 50	GrA-23656	M	Humansdorp
SAM-AP 320g	1707 ± 27	OxA-V-2056-24	F	Klein Brak River, Mossel Bay
ALB 295	1860 ± 40	Pta-4636	F	Klasies River Mouth Cave 5
NMB 1706	2000	Late Holocene		Plettenberg Bay
SAM-AP 6102	2000 - 3000	Singer & Wymer (1982)		Klasies River Mouth
SAM-AP 4825	2060 ± 50	Pta-6607	M	Tucker's Cave
SAM-AP 278g	2158 ± 28	OxA-V-2065-43	M	Klein Brak River, Mossel Bay
SAM-AP 1878a	2170 ± 20	Pta-6592	M	Robberg (Cave E)
ALB 296	2180 ± 50	Pta-8672	M	Klasies River Mouth Cave 5
NMB 1204	2210 ± 35	Pta-8744	F	Groot Brak River
SAM-AP 1146	2240 ± 20	Pta-6646	F	Robberg
A 1114	2271 ± 33	OxA-V-2055-51	M	Knysna
UCT 107	2290 ± 50	Pta-6815	M	Knysna
SAM-AP 34	2310 ± 25	Pta-6599	M	Knysna Cave
SAM-AP 1893	2360 ± 20	Pta-6613	F	Robberg
ALB 50	2380 ± 45	Pta-8557		Plettenberg Bay
SAM-AP 5052	2416 ± 27	OxA-V-2053-46		Robberg
UCT 591	2460 ± 40	Beta 263612	M	Buffel's Bay
SAM-AP 5050	2580 ± 60	Pta-7927	F	Robberg
A 1115	2588 ± 28	OxA-V-2065-48	M	Knysna
NMB 1639	2590 ± 60	Pta-6965	F	Robberg
SAM-AP 5044	2660 ± 150	LV-217	F	Wagenaars Cave, Plettenberg Bay
SAM-AP 5049	2740 ± 50	Pta-7934	F	Robberg
NMB 1705a	2780 ± 60	Pta-6964	F	Plettenberg Bay
SAM-AP 5048	2780 ± 60	Pta-7924	F	Robberg
SAM-AP 6016	2813 ± 29	OxA-V-2053-45	F	Robberg
A 1172	2950 ± 40	GrA-23647	F	Whitcher's Cave
ALB 350	2990	TO-10243		Oyster Bay
NMB 1241	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1243a	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter

NMB 1243b	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1243c	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1244	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1245	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1246	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1247	3000	Mytilus layer (Layer B)	F	Matjes River Rock Shelter
NMB 1248	3000	Mytilus layer (Layer B)	F	Matjes River Rock Shelter
NMB 1249	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1250	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1261	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1269	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1270a	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1270b	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB MSK3	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB MSK3b	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB MSK4	3000	Mytilus layer (Layer B)		Matjes River Rock Shelter
NMB 1440	3040 ± 60	Pta-6948		Matjes River Rock Shelter
NMB 1273	3050 ± 60	Pta-6942	F	Matjes River Rock Shelter
SAM-AP 1145	3120 ± 70	Pta-2284	F	Robberg
NMB 1202	3140 ± 50	Pta-8801	F	Groot Brak River
SAM-AP 1128	3156 ± 33	OxA-V-2055-49	F	Robberg
SAM-AP 1871	3310 ± 60	Pta-2273	M	Robberg (Cave D)
A 1112	3355 ± 45	GrA-23232	F	Zitzikama Caves, near Lottering
ALB 349	3424	Unknown	M	Kromme river mouth, Humansdorp
UCT 161	3451 ± 26	OxA-V-2064-54	F	Plettenberg Bay
SAM-AP 1894	3511 ± 30	OxA-V-2053-43		Robberg (Cave F)
SAM-AP 4210	3760 ± 50	Pta-6654	F	Coldstream Cave (Drury's Cave)
NMB 4	3940 ± 27	OxA-V-2064-48	M	Robberg
SAM-AP 3026a	3980 ± 60	Pta-7925		Robberg
SAM-AP 3021	4030 ± 60	Pta-6595		Robberg
UCT 191	4100 ± 60	Pta-4431		Oakhurst Rock Shelter
NMB 1640	4120 ± 60	Pta-6983	F	Robberg
NMB 1275	4850 ± 60	Pta-6986	M	Matjes River Rock Shelter
UCT 186	4880 ± 70	Pta-4348	M	Oakhurst Rock Shelter
NMB 1274	5120 ± 50	Pta-6981	M	Matjes River Rock Shelter
NMB 1319	5251 ± 29	OxA-V-2064-51	M	Plettenberg Bay
UCT 184	5330 ± 60	Pta-3719		Oakhurst Rock Shelter
UCT 181	5450 ± 70	Pta-4367	F	Oakhurst Rock Shelter
UCT 183	5990 ± 70	Pta-4426		Oakhurst Rock Shelter
UCT 180	6180 ± 70	Pta-3718	M	Oakhurst Rock Shelter
SAM-AP 4182	6811 ± 36	OxA-V-2056-26	M	Coldstream Cave (Drury's Cave)
SAM-AP 5055	6995 ± 50	OxA-V-2065-42	M	Robberg
UCT 182	7120 ± 60	Pta-4354	F	Oakhurst Rock Shelter
SAM-AP 4728a	7210 ± 30	Pta-6627	M	Coldstream Cave (Drury's Cave)
NMB 1324	7245 ± 40	OxA-V-2055-38		Robberg
NMB 1448a	7295 ± 32	OxA-V-2064-52	M	Matjes River Rock Shelter
UCT 183b	8000 - 4000	Association		Oakhurst Rock Shelter
UCT 208	8000 - 4000	Association		Oakhurst Rock Shelter
UCT 348	8000 - 4000	Burial #5		Nelson Bay Cave, Robberg

NMB 1264	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1265	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1277	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1278	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1279	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1282	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1448	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB 1451	8000 - 4000	Layer C	F	Matjes River Rock Shelter
NMB 8a	8000 - 4000	Layer C		Matjes River Rock Shelter
NMB WSK3	8000 - 4000	Layer C	F	Matjes River Rock Shelter
NMB WSK3b	8000 - 4000	Layer C	F	Matjes River Rock Shelter
UCT 185	9100 ± 90	Pta-3724	F	Oakhurst Rock Shelter
UCT 192	9120 ± 90	Pta-3729	M	Oakhurst Rock Shelter
NMB 1441	9230 ± 160	UCLA-1746B		Matjes River Rock Shelter Cave (s4)
NMB 1442	9230 ± 160	UCLA-1746B		Matjes River Rock Shelter Cave (s4)
NMB 1443	9230 ± 160	UCLA-1746B	M	Matjes River Rock Shelter Cave (s4)
SAM-AP 4208b	9540 ± 120	Pta-6634		Coldstream Cave (Drury's Cave)
SAM-AP 4208a	9720 ± 100	Pta-6615		Coldstream Cave (Drury's Cave)
SAM-AP 4828	9830 ± 90	Pta-6605		Tucker's Cave
UCT 156	10110 ± 80	GrA-23223	M	Knysna
NMB 1234	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1236a	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1236b	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1236c	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1236d	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1236e	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1291	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1302	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1308	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1310	12000 - 8000	Burnt layer (Layer D)	F	Matjes River Rock Shelter
NMB 1373	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1445	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1446	12000 - 8000	Burnt layer (Layer D)	F	Matjes River Rock Shelter
NMB 1602	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 1603	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 6	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8b	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8c	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8d	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8e	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8f	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
NMB 8g	12000 - 8000	Burnt layer (Layer D)		Matjes River Rock Shelter
SAM-AP 4293				Van der Walt's Cave, Humansdorp
SAM-AP 4295				Van der Walt's Cave, Humansdorp
UCT 10			M	South-east Cape coast
A 1176			F	Whitcher's Cave
A 1177			M	Whitcher's Cave
A 411				Keurbooms river Cave, Plettenberg Bay
ALB 237			F	Keurbooms

MMK 128				Robberg
NMB 1223				Outenikwa
NMB 1447			M	Platbank
NMB 1449				Platbank
NMB 211				Matjes River Rock Shelter
SAM-AP 1132				Robberg
SAM-AP 1162				Coldstream Cave (Drury's Cave)
SAM-AP 1447b				Great Brak River
SAM-AP 1448				Knysna
SAM-AP 1450				Knysna
SAM-AP 1451				Knysna
SAM-AP 1452				Storm's River, Eastern Cape
SAM-AP 1458			M	Mossel Bay
SAM-AP 1459			F	Outeniqua, Brandwacht
SAM-AP 1898			F	Groot River, Knysna
SAM-AP 3024			M	Robberg
SAM-AP 3027				Robberg
SAM-AP 4178			F	Gouritz River, Mossel Bay
SAM-AP 42			F	Bergplaas Cave, George
SAM-AP 4204			F	Great Brak River
SAM-AP 4211				Coldstream Cave (Drury's Cave)
SAM-AP 43				Ezeljacht Farm, George
SAM-AP 4729				Coldstream Cave (Drury's Cave)
SAM-AP 4736b				Coldstream Cave (Drury's Cave)
SAM-AP 4844			F	Robberg
SAM-AP 5045				Plettenberg Bay, below Wagenaars Cave
SAM-AP 6082				Oakhurst Rock Shelter
SAM-AP 6153				Gouritz River, Mossel Bay
(E) Eastern Region				
ALB 179	140 ± 35	Pta-8563	M	Retreat, near Bathurst
ALB 183	220	TO-10373		Dunbrody, Sunday's River
ALB 178	240 ± 45	Pta-8599	F	Kleinpoort, Committees
ALB 184	320	TO-10374	M	Dunbrody
ALB 186	365 ± 20	Pta-8730	F	Retreat, near Bathurst
ALB 187	380 ± 50	Pta-8683		Retreat, Bushman's river, Bathurst
ALB 177	390 ± 40	Pta-8584	F	Kleinpoort, Committees
Not accessioned	540 ± 60	Gx - 32519	M	Jeffrey's Bay
A 1153	636 ± 26	OxA-V-2065-47	F	Steytlerville
UCT 114	650 ± 40	GrA-23654	M	Cape St. Francis
UCT 83	680 ± 40	GrA-23072	M	Cape St. Francis
A 1154	905 ± 25	OxA-V-2066-33	M	Steytlerville
ALB 150	1910	TO-10368	M	Kabeljaauws, Jeffrey's Bay
ALB 152	2990	TO-10369		Kabeljaauws, Jeffrey's Bay
ALB 308	5140	TO-10240	M	Welgeluk Shelter
A 1117	1060 ± 50	Pta-8727	F	Lime Bank, Loerie
A 1071	1320 ± 50	Pta-6997	M	Amahlongwana river, Widenham, Natal
ALB 303	1550 ± 20	Pta-8699	M	St. Francis Bay
ALB 323	1620 ± 35	Pta-8578	F	Sand River, Goedgeloof, St. Francis Bay

ALB 223	1650 ± 60	Pta-8631		Cape St. Francis
ALB 328	1670 ± 60	Pta-8655	M	Cape St. Francis
A 1166	1818 ± 27	OxA-V-2056-33A	M	Humewood, Port Elizabeth
A 1152	1850 ± 35	Pta-8757	M	Amsterdam Hoek, Port Elizabeth
A 1127	1891 ± 29	OxA-V-2066-36	F	Jeffrey's Bay
ALB 344	1957 ± 26	OxA-15077	F	Gonubie
ALB 314	2130 ± 50	Pta-8693	F	Kleinemonde Eiland
ALB 301	2570±50	Pta-8684	M	St. Francis Bay
ALB 222	2640 ± 60	Pta-8636	F	Cape St. Francis
ALB 151	2920 ± 45	Pta-8570		Kabeljaauws, Jeffrey's Bay
ALB 354	3340 ± 60	Pta-8680	F	Jeffrey's Bay
A 1124	4320 ± 32	OxA-V-2056-42	M	Port Elizabeth
ALB 131	4700 ± 60	Pta - 5979	M	Spitzkop
A 1139	4800 ± 50	Pta-8816	F	Kenkelbosch, Eastern Cape
ALB 139	4930 ± 70	Pta-8620		Spitzkop
ALB 199	5100	TO-10375		Middelkop Kloof, Vygeboom
ALB 200	5105 ± 20	Pta-8638	M	Middlekop Kloof, Vygeboom
ALB 198	5120 ± 70	Pta-8618	F	Middelkop Kloof, Vygeboom
ALB 119	8260 ± 720	Gak-1541		Wilton Rock Shelter
ALB 129	± 4700	Assoc. with ALB 131	M	Spitzkop
ALB 133	± 4700	Assoc. with ALB 131		Spitzkop
ALB 124	± 4700	Assoc. with ALB 121		Wilton Rock Shelter
ALB 226b			M	Spitzkop
ALB 175				Kleinpoort, Committees
ALB 181				Kleinpoort, Committees
ALB 182				Lakeside, Committees
ALB 195				Melkhoutboom
ALB 313				Welgeluk shelter
UCT 20			M	Btw Fish and Cowrie rivers E. Cape
(F) Southern Inland Region				
UCT 88	490 ± 65	Gx-13183	F	Clanwilliam
UCT 157	587 ± 28	OxA-V-2055-45	M	Ladismith
UCT 148	600	Association with UCT 157		Ladismith
SAM-AP 1260	1137 ± 27	OxA-V-2066-28	M	Oudtshoorn
SAM-AP 1449	2230 ± 100	OxA-453		Clanwilliam
SAM-AP 6147	2920 ± 60	Pta-9085	M	Vredendal
UCT 334	3850 ± 80	OxA-457	F	Clanwilliam
SAM-AP 3700			F	Welgemoed farm, Ceres
SAM-AP 4972				Nuwekloof, Tulbagh
SAM-AP 6349			M	Wolseley, (Goedgevonden Farm)
SAM-AP 1886			M	Kruidfontein, Prince Albert
SAM-AP 3058				Prince Albert
SAM-AP 3059a				Prince Albert
SAM-AP 3059b				Prince Albert
SAM-AP 3457			F	Kruidfontein, Prince Albert
SAM-AP 6252a			F	Kleinsleutelfontein, Prince Albert district
UCT 17			M	Ladismith
UCT 27				Ladismith

UCT 366			M	Waboom river, Prince Albert
(G) Eastern Inland Region				
ALB 244a	1180 ± 50	Pta-8587	F	Paardefontein, Jansenville
ALB 244b	1450 ± 50	Pta-9228	M	Paardefontein, Jansenville
ALB 244c	± 1100 - 1500	Assoc, with ALB 244a/c		Paardefontein, Jansenville
ALB 210	1580 ± 50	Pta-8734		Corn Flats, Adelaide
UCT 106	2680 ± 60	Pta-4979	F	Ladybrand
UCT 566	5200	Pta-9369	F	Muela, Lesotho
UCT 412			F	Richmond
MMK 256			M	Kuilspoort, Beaufort West
SAM-AP 6029			M	Sandgat, Victoria West
A 320			F	Eerstelling. Bedford, Eastern Cape

Table 4.1: Khoesan skeletons whose dentitions were examined for this study. Information on sex, locality and date (when know) is included.

For data analyses, samples were assigned to one of seven geographic regions. These regions were adapted from Heydorn and Flemming's (1985) division of the South African coastline. Environmental biome borders defined by A.G. Morris (1992b) were also taken into consideration. Region A (N = 93), the *inland region,* north of the Great Escarpment, includes all specimens from Koffiefontein and Riet River, (near Bloemfontein) to the Richtersveld (60 km from the coastline). Region B (N = 21), the *western region* comprises the coastal strip from the mouth of the Gariep River, north of Port Nolloth, to Stompneusbaai. Region C (N = 123) consists of all coastal samples from the *southwestern region*, extending from Stompneusbaai to Mossel Bay. The area between Mossel Bay and Cape St. Francis (D) is designated the *southern region* (N = 173) and is the only region that encompasses an entire environmental biome (forest biome; 250 km forest area on the south-east coast). The *eastern region* (E) extends from Cape St. Francis along the coast to Widenham, south of Durban, Kwa-Zulu Natal (N = 48). This region includes non-coastal sites in and around Grahamstown. Region F, or the *southern inland region*, assembles southwestern inland specimens from Clanwilliam to Oudtshoorn, including areas surrounding the Hex River Valley (N = 19). The *eastern inland region* (G) includes all specimens located more than 100 km from the eastern coast of South Africa (after the Great Escarpment boundary), extending to Maseru in Lesotho and south towards Beaufort West (N = 10). Coastal (including Regions B, C, D, E, F) and inland (including Regions A and G) groups were also created to assess data on a broader scale. Much research has been conducted on coastal regions, particularly the southern and southwestern Cape (i.e. Sealy 2006, 2010; Sealy and Pfeiffer 2000), and therefore coastal/inland assessments, in the light of current hypotheses is necessary.

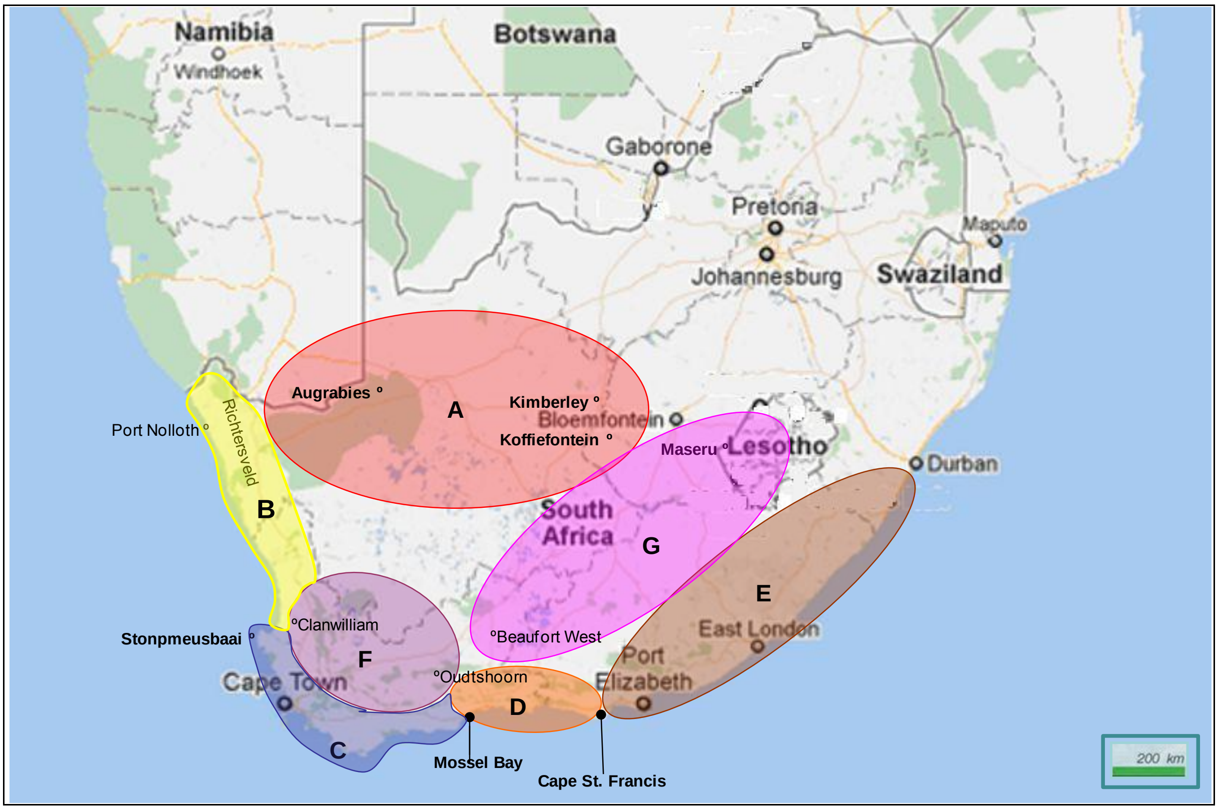

Fig. 4.1: Geographic regions to which Khoesan specimens used in this study are assigned.

KENYA DENTAL SAMPLE

Data derived from the Khoesan material are compared with data collected from a sub-Saharan African outgroup sample from Kenya. The Kenyan study sample (Table 4.2) consists of 81 dentitions, one of which is a cast (EM 770). All are currently curated in the Kenya National Museum, Nairobi, Kenya (prefix: KNM) (N= 22) and the Natural History Museum. London, United Kingdom (prefixes: BS, E, EA, EH, EM, Makalia and PA HR) (N = 59).

These specimens are grouped into those from the north of the country (Lothagam, East Rudolf (now Lake Turkana) and Koobi Fora) and those from the south, including the large sites of Bromhead's and Gamble's Cave (Fig. 4.2).

Fig. 4.2: Map of Kenyan sites in this study.

Where possible, specimens have been allocated date ranges based on associated archaeological evidence, including radiocarbon dating of sites in the Kenya highlands and Rift Valley (Sutton 1972), stratigraphy, typological analyses of stone tools and pottery found in association with skeletal remains (Ambrose *et al.* 1980b; Barham and Mitchell 2008; Phillipson 1977), climatic sequence studies (Butzer *et al.* 1972a) and environmental change (Ambrose and DeNiro 1989). However, discrepancies surrounding the dating of the East African Holocene material remain.

The bulk of the Kenyan dental sample (N=52) is Late Holocene (Table 4.2 for details). According to Rightmire (1984), pecimens from Bromhead's site (N=34) are associated with artefacts and pottery (Bower and Nelson 1978) from the Elmenteitan, a food-producing culture first identified by L.S.B. Leakey (1931), possibly dating to no older than *ca.* 2500 B.P. Other skeletons from Hyrax Hill, Makalia and Wiley's Kopje, Naishi Rock Shelter and Molo (N=18) are fragmentary but well preserved. The remaining Kenyan material is early-mid Holocene, with 19 specimens dated to between 10000 – 4000 B.P. These samples are from Lothagam and Koobi Fora, near Lake Turkana in the North. The dental preservation of this material is quite good, even though the teeth are heavily worn. This material is often collectively referred to as the 'Galana boi specimens' from the Galana boi Holocene formation, part of a series of raised Holocene sediments that surround modern Lake Turkana, principally deposited between 12 ka – 7 ka BP (F.H. Brown and Feibel 1986; Owen and Renaut 1986). Dental material dated to >8000 B.P. is found in southern Kenya (N=8) at some of the best-known and oldest of the Kenya Holocene sites. Gamble's Cave II has remarkably well preserved (albeit incomplete) dental remains, while a single complete cranium with full maxillary dentition from the Naivasha Railway site, first described by Leakey (1942), adds to this early collection. For statistical analyses, these data were divided into temporal two groups; those specimens that are dated to <4500 BP (N=54) and specimens that fit into a 4-10ka timeframe (N=27).

SPECIMEN	DATE	ASSOCIATION	SEX	LOCALITY	REFERENCE
Northern Kenya					
KNM-LT 13700	8400 - 6000	Galana Boi Formation		Lothagam	14, 15
KNM-LT 13702	8400 - 6000	Galana Boi Formation	M	Lothagam	14, 15
KNM-LT 13703	8400 - 6000	Galana Boi Formation		Lothagam	14, 15
KNM-LT 27710	8400 - 6000	Galana Boi Formation	M	Lothagam	14, 15
KNM-LT 27711	8400 - 6000	Galana Boi Formation	F	Lothagam	14, 15
KNM-LT 27717	8400 - 6000	Galana Boi Formation	F	Lothagam	14, 15
KNM-ER 7466	10000 - 4000	Galana Boi Formation		East Rudolf	2, 4, 13, 16
KNM-ER 5306	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5311	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5312	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5315	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5316	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5322	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5525	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5526	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5526b	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5548	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5549a	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
KNM-ER 5550	10000 - 4000	Galana Boi Formation		Koobi Fora	2, 4, 13, 16
Southern Kenya					
KNM-ER 1734	<4500	Nderit (Gumban B)		Hyrax Hill	1, 8, 9, 12
Makalia IB	<4500	Nderit (Gumban A)		Makalia I	1, 8, 9, 12
EM 1179	<4500	Nderit (Gumban A)		Makalia II	1, 8, 9, 12
Makalia IC	<4500	Nderit (Gumban A)	M	Makalia I	1, 8, 9, 12
EM 1046	<4500	Nderit (Gumban A)		Wiley's Kopje II	1, 8, 9, 12
EM 1081	<4500	Nderit (Gumban A)	M	Wiley's Kopje III	1, 8, 9, 12
BS NN 5	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
BS NN 6	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
E 920b	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
E920c	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EA 51 b 1	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EA 51 b 3	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EH 816	2500 - 1500	Elmenteitan	F	Bromhead's Site	1, 7, 12
EH 833	2500 - 1500	Elmenteitan	M	Bromhead's Site	1, 7, 12
EM 808	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 809	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 810	2500 - 1500	Elmenteitan	M	Bromhead's Site	1, 7, 12
EM 812	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 813	2500 - 1500	Elmenteitan	M	Bromhead's Site	1, 7, 12
EM 815	2500 - 1500	Elmenteitan	F	Bromhead's Site	1, 7, 12
EM 819	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 827	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 828	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 834	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 835	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 836	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 837	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 838	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12

EM 840	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 841	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 846	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 847	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 850	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 855	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 858	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 860	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 861	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 862	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 864	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 920a	2500 - 1500	Elmenteitan		Bromhead's Site	1, 7, 12
EM 764	9000 - 8000	Archaeological assoc.		Gambles Cave II, 2	1, 5,
EM 765	9000 - 8000	Archaeological assoc.		Gambles Cave II, 5	1, 5,
EM 765 A	9000 - 8000	Archaeological assoc.		Gambles Cave II, 2	1, 5,
EM 767	8210 ± 260	UCLA 1756		Gambles Cave II, 4	1, 5,
EM 768	8210 ± 260	UCLA 1756		Gambles Cave II, 4	1, 5,
EM 770 (cast)	9000 - 8000	Archaeological assoc.		Gambles Cave II, 1	1, 5,
EM 771	9000 - 8000	Archaeological assoc.	M	Gambles Cave II, 5	1, 5,
PA HR 11667	10850 ± 300	UCLA 1741		Naivasha Railway Site	11
KNM 43a	<4500	"Late Neolithic"		Molo	3
KNM 43b	<4500	"Late Neolithic"		Molo	3
E 920 - 1	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 2	<4500	Archaeological assoc.	M	Naishi Rock Shelter	6, 10
E 920 - 8	<4500	Archaeological assoc.	F	Naishi Rock Shelter	6, 10
E 920 - 9	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 11	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 16	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 17	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 18	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 19	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 22	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 23	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10
E 920 - 36	<4500	Archaeological assoc.		Naishi Rock Shelter	6, 10

Table. 4.2: Kenyan skeletons whose dentitions were examined for this study. Information on dates, locality, sex and references are included.

References for estimated dates: 1. Bower and Nelson (1978); 2. Butzer *et al.* (1972b); 3. Field (1949); 4. Findlater (1978); 5. Isaac (I976); 6. Kitson (1931); 7. L.S.B. Leakey (1931); 8. L.S.B. Leakey (1935); 9. M.D. Leakey (1945). (1945); 10. Parkinson (1928); 11. Protsch (1976) Although this is a recorded date for this specimen, this work is viewed with scepticism; 12. Rightmire (1975a); 13. Rightmire (1984); 14. Robbins (1972); 15. Robbins (1980), 16. J.M. Harris *et al.* (2006).

MID-LATE PLEISTOCENE DENTAL SAMPLES

Comparisons are also made between the Holocene African material and a Mid-Late Pleistocene sample from southern Africa. This sample, listed in Table 4.3, consists of 17 dentitions from three institutions: the Iziko South African Museum, Cape Town (SAM-AP; N = 11); the East London Museum, East London (EM; N = 1); and the Department of Anatomy, University of the Witwatersrand, Johannesburg (A: Mumbwa Cave; Border Cave; and SU: Cave of Hearths, N= 5). The sites from which these specimens originate are dispersed across southern Africa, from the most northerly site of Mumbwa, Zambia, to the most south-westerly site of Klasies River Mouth, South Africa (see Fig. 4.3).

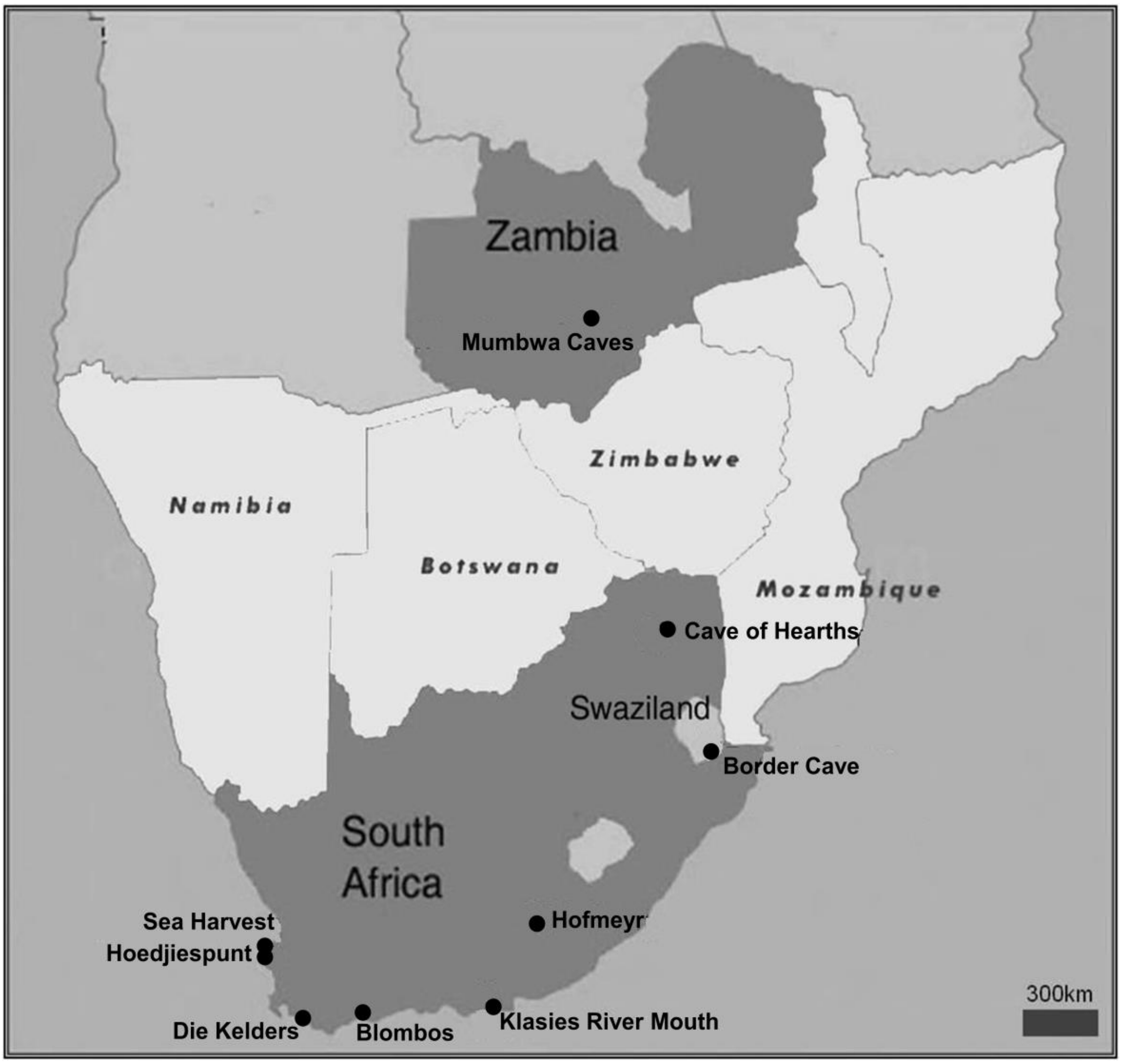

Fig. 4.3. Location of Mid-Late Pleistocene sites used in this study.

These dentitions provide a geographically diverse dataset dating between approximately 300 000 and 40 000 years ago. Most dental material from these sites is fragmentary and attrition and poor preservation has restricted data collection. Of the two Mumbwa Cave specimens studied here, one is the well-preserved, incomplete dentition of a young adult, and the other is the incomplete dental remains of an older individual. Data were recorded from two individuals from Border Cave (specimens BC2 and BC5) but unfortunately only BC2 retains complete teeth: a mandibular incisor, canine and second and third molars. Only information about root morphology could be collected from the BC5 mandible. The juvenile specimen from Bed 3 at the Cave of Hearths, which probably dates to ca. 200 ka[2], includes three teeth from which data could be collected: a lower premolar and two lower molars. The Hofmeyr cranium, recently dated and described (Grine *et al.* 2007; Grine *et al.* 2010), is the youngest Pleistocene specimen, corresponding with the appearance of the Later Stone Age. The skull has significant maxillary and mandibular damage and information could be collected on only two upper molars and one lower molar.

The largest number of Pleistocene individuals comes from Klasies River Mouth (N=9) with teeth representing both gracile and robust skeletons. The material is very fragmentary; the best-preserved teeth are mandibular molars (N=15: both fixed and loose) and mandibular premolars (N=5). Information about the roots of 5 mandibular canines was also recorded. A single, moderately worn, incomplete maxillary premolar crown from Blombos Cave and an undamaged upper premolar crown from Sea Harvest were also studied. Specimens from Die Kelders (N=8) are relatively well-preserved with minimal to moderate wear and possibly derive from young adults or juveniles. At Hoedjiespunt, data were collected from one lower central incisor (I_1) and one upper second molar[3].

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2. This estimate is based on the presence of a late Mode 2 lithic industry in Beds 1-3 at Cave of Hearths and an early Mode 3 industry in Bed 4 (Barham & Mitchell 2008). The Mode 2/3 transition in southern Africa is estimated between 280-240 ka; a late Mode 2 industry has been identified at Duinefontein, near Cape Town with a minimum age of ~160 ka. The Bed 3 mandible is therefore likely to date to ca. 200 ka.

3 The Hoedjiespunt specimens are unlikely to be older than those from Cave of Hearths.

SPECIMEN	DATE	SEX	LOCALITY	REFERENCE
Mid-Late Pleistocene				
SAM-AP 6370a	± 300 - 200ka		Hoedjiespunt Peninsula	13
SAM-AP 6370c	± 300 - 200ka		Hoedjiespunt Peninsula	13
SU 15	c. 200ka		Cave of Hearths	3,8
SAM-AP: Sea Harvest	128 - 40ka		Sea Harvest	20
A341	± 130 - 2ka		Mumbwa, Zambia	2
A343	± 130 - 2ka	M	Mumbwa, Zambia	2
Border Cave 2	171 - 71ka		Border Cave	6,9,10
Border Cave 5	74 000 ± 5000	M	Border Cave	6,7,9
SAM-AP 6292	98.9 ± 4.5ka		Blombos	16,17,18, 19
SAM-AP 6222	± 110 000 - 90 000		KRM 1b (MSA I 10) # 41815	11,12
SAM-AP 6101	90 000 - 65 000		KRM1 (MSA II 17) # 21776	1,5,11,12
SAM-AP 6223	90 000 - 65 000		KRM1 (MSA II 4) # 13400	1,5,11,12
SAM-AP 6225	90 000 - 65 000		KRM1 (MSA II 14) # 16424	1,5,11,12
SAM-AP 6226	90 000 - 65 000		KRM1 (MSA II 4) # 14696	1,5,11,12
SAM-AP 6227	90 000 - 65 000		KRM1 (MSA II 4) # 14692	1,5,11,12
SAM-AP 6228	90 000 - 65 000		KRM1 (MSA II 4) # 14691	1,5,11,12
SAM-AP 6229	90 000 - 65 000		KRM1 (MSA II 4) # 14693	1,5,11,12
SAM-AP 6230	90 000 - 65 000		KRM1 (MSA II 4) # 14694	1,5,11,12
SAM-AP 6282	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6281	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6280	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6279	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6277	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6275	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6264	75 000 - 60 000		Die Kelders	14,15
SAM-AP 6258	75 000 - 60 000		Die Kelders	14,15
ELM 24	36 200 ± 3300		Hofmeyr	4

Table 4.3: The Mid-Late Pleistocene dental sample used in this study. Information on dates, sex (where possible), locality and references are included. KRM refers to Klasies RIver Mouth.

References for estimated dates: 1. Bada and Deems (1975); 2. Barham (2000a); 3. Barham and Mitchell (2008); 4. Grine *et al.* (2007); 5. Grün *et al.* (1990b); 6. Grün and Beaumont (2001); 7. Grün *et al.* (2003); 8. Mason (1988); 9. Millard (2006); 10. Miller *et al.* (1999); 11. Rightmire and Deacon (1991); 12. Singer and Wymer (1982); 13. Stynder *et al.* (2001); 14. Feathers and Bush (2000); 15. Schwarcz and Rink (2000); 16. Henshilwood *et al.* (2001); 17. Grine *et al.* (2000); 18. Jacobs *et al.* (2006); 19. Henshilwood *et al.* (2011); 20. Grine and Klein (1993).

DATA COLLECTION

NON-METRIC DATA

A non-metric dental trait is defined as a "positive (e.g. tubercles) or negative (e.g. grooves) structure that has the potential to be present or not present at a specific location or site on one or more members of a morphological tooth class" (G.R. Scott and Turner 2000: 24). Dental traits described below are classified as present or absent (abbreviated 'P' for 'present' and 'A' for 'absent' in tables); additionally the degree to which a tooth expresses a trait is recorded (e.g. a pronounced expression or as a grade on a rank scale). Teeth of the permanent dentition are analysed and scored for a set of 52 discrete traits. All but one of these traits are found in the Arizona State University Dental Anthropology System (ASUDAS). In addition, the presence or absence of a maxillary anterior midline diastema, a non-metric trait commonly found in African populations (Irish 1998a; Jacobson 1968, 1982; J.C.M. Shaw 1931; Van Reenen 1964) but less frequent outside Africa is recorded. Tooth condition was also appraised on all dental remains, to the extent that this data was collectable. Unlike non-metric traits that form part of the genetic make-up of an individual, tooth condition is associated with tooth use and function. Dietary choices, an individual's general health and life-ways influence the development (or lack) of these conditions. Indicators of dental condition include: the presence or absence of caries; the status of occlusal and interproximal attrition as per B.H. Smith (1984); the identification of any dental pathological change such as an abscess or periodontal disease; the presence of any cultural treatment including intentional dental modification or work-related grooving; and the degree of temporo-mandibular joint damage, if any. These data however, fall outside of the scope of this thesis and are not included here.

The ASUDAS system has proven to be reliable for identifying population dental trait variation in many earlier studies (i.e. Haeussler *et al.* 1989; Haeussler *et al.* 1988; Irish 1993, 1998a, 1998b, 2006, 2013; G.R. Scott 1980; Turner 1987, 1990). Procedures used in the ASUDAS are based on fixed criteria for scoring trait variation within any given data set. A series of 23 rank-scaled reference plaques aid in recording inter-trait variation. In addition, inter-observer error between Dr. Joel Irish[4], a world-specialist on this methodology, and myself was evaluated using a cast dental set comprised of 30 individuals from varying geographic backgrounds and was found to be minimal (97% reproducibility between observers). The dental traits and methodology used in this study are illustrated in detail in Turner and Nichol (1991) and described briefly below.

Many of the traits are scored on a single, specific tooth. This is because a particular aspect of the trait is usually more well-defined on one tooth (i.e. M_1), rather than all teeth in a class (i.e. M_1, M_2 and M_3). This relates to the evolutionary developmental concept of morphogenetic fields in early development, which states that within a tooth set, teeth closer to the mid-line are subject to stronger influences from a morphogenetic field than posterior teeth (Alvesalo and Tigerstedt 1974; Dahlberg 1945). For example, a trait such as the Carabelli's is measured on all upper molars, however, the M^1 is usually larger than the others, has more defined and fully developed cusps and usually the greatest expression of the trait. An individual's Carabelli's trait score will be based solely on the score of the first tooth in the class if it has the greatest expression. For the purposes of this study, other teeth within a morphogenetic field were sometimes included in trait evaluations to assess trait degree of expression and/or reduction i.e. changes in root structure or cusp number between molars. Also, adding these traits assisted in (and increased) comparisons between data sets where small sample sizes were an issue. These additional trait assessments are included in trait descriptions.

Non-metric traits appear on crown surfaces and are therefore affected by general tooth wear, pathological change and use. Some traits need to be evaluated on relatively unworn, well-preserved teeth and dental attrition can obscure trait evaluations. These include the canine mesial and distal ridge; premolar accessory cusps and distosagittal ridge; lower molar anterior fovea, deflecting wrinkle and distal trigonid crests and the presence of the Carabelli's trait in upper molars. Remaining crown traits can be evaluated on worn teeth as long as attrition has not destroyed

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[4] Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool, John Moores University.

cusp form entirely. Also, teeth still fixed in the jaw could not be evaluated for root traits. Depending on their location, traits can disappear in older individuals or in populations whose diets consist of heavy grains or ground foods. Tooth deterioration is reliant on both attrition and abrasion. Attrition is caused by general tooth facet wear due to mastication while abrasion relates to types of foods consumed and the unintentional addition of abrasive materials in food preparation or food choice. Abrasive foods include, among others, gritty shellfish and plants containing silica phytoliths (Fiorenza *et al.* 2011).

These 52 traits were selected in order to provide a collective expression of Khoesan dentition and to enable a comprehensive dental comparison to other major world populations. Additionally, the traits aid in the comparisons of sets of dental features among the groups from different geographic locations within South Africa. Decisions regarding which antimere to score as suggested by Haeussler *et al.* (1988) have been disregarded. Here, the individual counting procedure method was applied where both sides in an individual are scored, allowing for possible asymmetry as well as an evaluation of the greatest genetic possibility for that trait, per individual (Turner 1985b). The side that displayed the highest expression of the trait was used for analysis. Thus, if a grade 3 Carabelli's trait appeared on the upper left second molar and had a grade of 0 on the right, grade 3 was used for analysis of that individual in this study.

Non-metric dental traits used in this study

Incisor traits

Shoveling I^1

The upper incisors, canines and lower incisors may show the presence of mesial and distal marginal ridges on the lingual surface, giving the tooth a shovel-shape appearance. This trait is scored within seven grades as seen on an ASU reference plaque:

0. No expression of the trait
1. Faint mesial and distal ridging

2. Trace ridge elevations
3. Semi-shovel
4. Semi-shovel with strong ridging
5. Shovel shape is well-developed
6. Marked shovel
7. Barrel-shape. This expression is only reflected on upper lateral incisors.

Winging I^1

The upper central incisors may be rotated mesiolingually, giving a V-shaped appearance when viewed from the occlusal surface. There are four ASU ranks:

1. Bilateral winging
2. Unilateral winging
3. No expression of the trait
4. Counter winging

Double Shovelling I^1

The upper incisors, canine, first premolar and lower incisors present with labial marginal ridges both mesially and distally. An ASU plaque is available. Scoring:

0. None
1. Faint ridging
2. Trace ridging
3. Semi-double shovel
4. Double shovel
5. Pronounced double shovel
6. Extreme expression of the trait

Peg-shaped Incisor I^2

The upper lateral incisor/s are markedly reduced in size and lacks the expected crown morphology. The tooth appears peg-shaped and rounded. Scoring:

0. Normal sized incisor
1. Incisor has normal crown form but is reduced in size
2. Peg-shaped

Labial Convexity I^1

The labial surface of the upper incisors range from appearing flat, to demonstrating a degree of convexity when viewed occlusally. Reference plaque available. Ranking:

0. Flat labial surface
1. Trace convexity
2. Weak convexity
3. Moderate convexity
4. Pronounced convexity

Interruption Groove I^2

These are grooves that appear lingually on the upper incisors. The groove usually crosses the cingulum and may continue down to the root. Scoring:

1. No groove

M. An interruption groove occurs mesially

D. An interruption groove occurs distally

MD. Grooves occur on both the mesio- and distolingual borders

Med. An interruption groove occurs in medially

Tuberculum dentale I^2

This feature occurs on the upper incisors and canines. It presents lingually on the cingular region of the tooth as ridging or cusp formation in various degrees of expression. ASU reference plaques identify the following scoring:

0. No expression of the trait
1. Faint ridging
2. Trace ridging
3. Strong ridging
4. Pronounced ridging

5-. Weakly developed cuspule without a free apex

5. Weak cuspule with a free apex
6. Strong, fully-developed cusp

Canine traits

Canine Mesial Ridge C^1

This trait presents on the upper canines and is identified when the mesiolingual ridge is larger than the distal ridge. This ridge can incorporate the Tuberculum Dentale and envelop most of the lingual surface of the tooth. This trait is also colloquially known as the "Bushman Canine" (Morris, 1975). ASU plaque present. Scoring:

0. Trait does not occur
1. The larger mesiolingual ridge is weakly attached to the tuberculum dentale.
2. The larger mesiolingual ridge is moderately attached to the tuberculum dentale.
3. Mesiolingual ridge is much larger and is fully incorporated into the tuberculum dentale.

Canine Distal Accessory Ridge C^1

A distolingual ridge appears on the upper and lower canines between the tooth apex and the distal tooth margin. This ridge can be very pronounced and is very susceptible to wear. Reference plaque present. Scoring:

0. Trait is absent
1. Very faint ridge
2. Weakly developed ridge
3. Moderately developed ridge
4. Strongly developed ridge
5. Very pronounced ridge is present

Canine Root Number C_1

The mandibular canines can have one or two roots. The second root, if present, is usually small and narrowed. Ranking:

1. One root
2. Two roots

Premolar traits

Premolar Mesial and Distal Accessory Cusps P^3

Small cusps are sometimes present on the upper premolars. They appear on the mesial and/or distal ends of the upper premolar sagittal grooves but are completely separate from the buccal and lingual cusps. Scoring:

0. No accessory cusps occur
1. Accessory cusp/s are present

Tricusped Premolars P^3

Upper premolars with three cusps (very rare). Scoring:

0. Extra distal cusp is absent
1. Extra distal cusp is present

Premolar Root Number P^3

Upper premolars are usually single-rooted but on occasion, two or three roots occur. Scoring:

1. One root
2. Two roots
3. Three roots

Distosagittal Ridge P^3

This is a rare upper first premolar trait. A pronounced ridge from the buccal cusp extends to the distal occulsal border. This trait, also called the Uto-Aztecan premolar due to the ASU plaque example, is geographically restricted and has not been, as yet, identified in Africa. Scoring:

0. Normal premolar form occurs
1. Distosagittal ridge is present

Odontome P3-P4

This trait occurs on both upper and lower premolars and is recognised as a small rounded enamel and dentin projection on the occlusal surface. They are very rare. Scoring:

0. Odontome is absent
1. Odontome is present

Premolar Lingual Cusp Variation P^4

The lingual cusps on lower premolars vary in both size and frequency. Reference plaque is available. Ranking:

0. One lingual cusp
1. One or two cusps may be present.
2. Two lingual cusps are present. Mesial cusp is much larger than the distal cusp.
3. Two lingual cusps are present. Mesial cusp is slightly larger than the distal cusp.
4. Two equal sized lingual cusps are present.
5. Two lingual cusps are present. Distal cusp is slightly larger than the mesial cusp.
6. Two lingual cusps are present. Distal cusp is much larger than the mesial cusp.
7. Two lingual cusps are present. Distal cusp is very much larger than the mesial cusp.
8. Three equal sized lingual cusps are present.
9. Three lingual cusps are present. Mesial cusp is much larger than the medial and/or distal cusp.

Tome's Root P_3

This presents on the root surface of lower first premolars. Developmental grooving displays at various frequencies from a very shallow, V-shaped indentation to a deep V-shaped cross-section. At its highest grade, the root can separate, forming mesial and distal roots. Reference plaque present. Ranking:

0. Developmental grooving is absent or very shallow and rounded.
1. Developmental groove is present and V-shaped.
2. Groove is moderately deep and V-shaped.
3. Groove is V-shaped and deep, extending one-third of the total root length.
4. Grooving is deeply invaginated.

5. Two free roots are present.

Lower molar traits

Anterior Fovea M_1

This trait appears on the lower first molar. It is recognised as a ridge that connects the mesial aspects of cusps 1 and 2, producing a visible groove. Reference plaque present. Scoring:

0. Trait is absent
1. A weak ridge is present, producing a faint groove.
2. A larger connecting ridge and deeper groove is present.
3. Groove is larger than seen in grade 2.
4. Groove is long and mesial ridge is robust.

Distal Trigonid Crest M_1

A ridge forms that bridges cusps 1 and 2 on lower molars. Scoring:

0. Trait is absent
1. Trait is present

Groove Pattern M_1 and M_2

One of three distinct groove patterns is recognisable on lower molars. Scoring:

Y. Cusps 2 and 3 are in contact.
X. Cusps 1 and 4 are in contact.
+. All four cusps are in contact.

The degree of expression of both X- and Y-groove patterns are, in this study, assessed on lower first and second molars.

Cusp Number M_1 and M_2

Lower molars are classified as having cusps 4, 5 or 6 present. Scoring:

4. Cusps 1 to 4 are present.
5. Cusp 5 (the hypoconulid) is also present.
6. Cusp 5 (the entoconulid) is also present.

Cusp 5 M_1 and M_2

The hypoconulid, or 5th cusp, occurs distally between cusps 3 and 4 and usually presents towards the buccal side. ASU reference plaque is present. Scoring:

1. Cusp 5 is present and very small
2. Cusp 5 is small
3. Cusp 5 is medium-sized
4. Cusp 5 is large
5. Cusp 5 is very large

Cusp 6 M_1 and M_2

The entoconulid, presents distally on the lower molar and is always lingual to cusp 5. Its size is scored relative to cusp 5. Reference plaque is available. Scoring:

0. Cusp 6 is absent
1. Cusp 6 is much smaller than cusp 5
2. Cusp 6 is smaller than cusp 5
3. Cusp 6 is equal in size to cusp 5
4. Cusp 6 is larger than cusp 5
5. Cusp 6 is much larger than cusp 5

Cusp 7 M_1 and M_2

The metaconulid, or 7th cusp, occurs in the lingual groove between cusps 2 and 4 of the lower molars. Reference plaque is present. Scoring:

0. Cusp 7 is not present
1. Two lingual grooves present
1A. Faint tipless cusp 7 occurs
2. Cusp 7 is small
3. Cusp 7 is medium sized
4. Cusp 7 is large

Deflecting Wrinkle M_1

This occurs on lower first molars and is recognised by variation of the mesial ridge on cusp 2. The mesial ridge can deflect distally and in some cases makes contact with cusp 4, forming an L-shaped ridge. This variation can be seen on the available reference plaque. Scoring:

0. Trait is absent
1. A midpoint constriction occurs on the medial ridge of cusp 2.
2. Cusp 2 medial ridge is deflected distally but does not make contact with cusp 4.
3. Medial ridge is deflected distally, creating an L-shape and makes contact with cusp 4.

Protostylid M_1

This trait is usually associated with the groove separating the protoconid and hypoconid (cusps 1 and 3) and presents as a second groove. At its highest score, a paramolar cusp can be found on the buccal surface of cusp 1. Reference plaque present. Scoring:

0. No expression of trait.
1. A pit occurs in the buccal groove.
2. Buccal groove is curved distally.
3. Faint secondary buccal groove extends mesially.
4. Secondary groove is pronounced.
5. Secondary groove is very pronounced and easily seen.
6. Faint cusp. The secondary groove extends across cusp 1.
7. Separate cusp present.

Lower Molar Root Number M_1 and M_2

Lower molars can have one to three roots. Scoring:

1. One root
2. Two roots
3. Three roots

Torsomolar Angle M_3

The lower third molar can be rotated lingually or buccally relative to a central line drawn through the first and second molars. This condition can be measured with a protractor and is scored in degrees of rotation and directionality.

<u>Upper molar traits</u>

Enamel Extensions M^1

Projections of the enamel border toward the root can be identified in upper premolars and molars. These extensions can be very long, extending to the root bifurcation on molars. Scoring:

0. Enamel border is straight
1. Faint, ±1mm extension
2. Medium sized, ±2mm extension
3. Long, >4mm extension

Peg-shaped Molar M^3

When the upper third molar is smaller than 7mm buccolingually and lacking in normal crown morphology, it is considered a peg-shaped molar. Scoring:

0. Full-sized, normal crown.
1. Reduced molar with a 7mm-10mm buccolingual diameter.
2. Molar is <7mm in buccolingual diameter.

Upper Molar Root Number M^2

There is variation in the number of roots present in upper molars. First molars usually have three roots, while third molars often have one or two. Second molars have the greatest variation and present with anything from one to four roots, although four is rare. This study includes a fifth root rank as one individual in the data set presents with five roots. Scoring:

1. One root
2. Two roots
3. Three roots
4. Four roots
5. Five roots

Metacone M^3

Cusp 3 (distobuccal) is expressed with minimal variation in molars one and two. Some weaker forms of cusp expression can occasionally be seen on the third molar. Reference plaque available. Scoring:

0. Metacone is absent
1. A ridge is present

2. Faint cuspule is present
3. Weak cusp
3.5 Medium sized cusp
4. Metacone is large
5. Metacone is very large

Small metacone M^3 is also assessed. Present = scoring of 3 and lower.

Hypocone M^2

Cusp 4 (distolingual) can be reduced or absent on the first and second upper molars. Variation on the third molars is less commonly seen. Reference plaque is available. Scoring:

0. Hypocone is absent
1. Ridging is present
2. Faint cuspule
3. Small cusp present
3.5 Medium sized cusp
4. Large hypocone
5. Very large hypocone

Large hypocone M^2 is also assessed. Present = scoring of 3 and higher.

Metaconule M^1

The 5th cusp, may be present in the distal fovea between the metacone and the hypocone. This cusp is usually small and can present as only a faint cusp or grooving, as seen in the ASU reference plaque. Metaconule data collected for this study, however, demonstrates the presence of a large fifth cusp and additional ranking was required. Scoring:

0. No expression of the cusp
1. Faint cuspule
2. Trace cuspule
3. Small cuspule
4. Small cusp
5. Medium sized cusp
6. Large cusp
7. Very large cusp

Large metaconule M^1 is also assessed. Present = scoring of 4 and higher.

Carabelli's Trait M^1

This trait occurs on the lingual surface of the mesiolingual cusp, or cusp 1 of the upper molars. The molars may display a large range of variation from a pit or groove to a large cusp with a free apex. Reference plaque available. Scoring:

0. No trait expression
1. A groove is present
2. A pit is present
3. Small Y-shaped depression
4. Large Y-shaped depression
5. Small cusp without a free apex
6. Medium sized cusp
7. Large cusp with a free apex

Parastyle M^3

A paramolar cusp occurs on the buccal surface of cusp 2, or mesiobuccal cusp. It may present as a pit between cusps 2 and 3 or a more defined, protruding cusp. Reference plaque present. Scoring:

0. No expression of the trait
1. A pit is present
2. Small cusp with attached apex
3. Medium sized cusp is present
4. Large cusp
5. Very large cusp
6. Free peg-shaped crown is present

Other features

Midline Diastema (not in the ASUDAS)

A noticeable gap or space between the upper central incisors.

0. Trait is not present
1. Diastema occurs (space >0.5mm)

Congenital absence M^3

The tooth may not form in adult individuals.

0. Tooth is present
1. Tooth is congenitally absent

Palatine Torus

A linear exostosis that develops on the palate. Variation is identified height and width of the bony protrusion. Scoring:

0. Palate is smooth
1. Torus elevated ± 1-2mm
2. Torus elevated ± 2-5mm
3. Torus elevated >5mm
4. Very marked. Torus elevated up to 10mm and very wide.

Mandibular Torus

Bony exostosis can develop on the lingual aspect of the mandible. The elevation is nobular, rarely larger than 5mm and occurs in the canine and premolar regions. Scoring:

0. Mandible is smooth
1. Trace
2. Medium elevation of 2-5mm
3. Marked elevation >5mm

Rocker Jaw

This scores the curvature of the mandibular ramus. A jaw rocks when the horizontal ramus is very convexly curved. Scoring:

0. Absent
1. Almost rocker.
2. Rocker. Jaw will rock for several seconds.

METRIC DATA

Careful and repeatable measurements of teeth are taken with specialized electronic dental callipers (readouts to 0.001mm), and subsequent statistical analyses focus on identifying size and shape variation between geographically and temporally dispersed specimens. Unfortunately, teeth can often be poorly preserved, with signatures of heavy wear and attrition, both of which can make measurement demanding and can influence quantitative results. In order to overcome some of these problems, both conventional and contemporary measurement techniques are adopted, following Hillson *et al.* (2005). Measurements are taken on both the cervical (mostly unaffected by heavy wear) and, where possible, crown sections of all available maxillary and mandibular teeth, as follows:

Incisors, canines and premolars

- Mesiodistal cervical diameter
- Buccolingual cervical diameter
- Mesiodistal crown diameter
- Buccolingual crown diameter

Molars

- Mesiodistal cervical diameter
- Buccolingual cervical diameter
- Mesiolingual-distobuccal cervical diameter
- Mesiobuccal-distolingual cervical diameter
- Mesiodistal crown diameter
- Buccolingual crown diameter
- Mesiolingual-distobuccal crown diameter
- Mesiobuccal-distolingual crown diameter

Measurements are abbreviated in this thesis as follows:

MDCD	Mesiodistal cervical diameter
BLCD	Buccolingual cervical diameter
MDcrD	Mesiodistal crown diameter
BLcrD	buccolingual crown diameter
MLDBcrD	Mesiolingual-distobuccal crown diameter (diagonal)
MBDLcrD	Mesiobuccal-distolingual crown diameter (diagonal)
MLDBCD	Mesiolingual-distobuccal cervical diameter (diagonal)
MBDLCD	Mesiobuccal-distolingual cervical diameter (diagonal)

Table 4.4: Measurement abbreviations used in this study.

Crown height measurements were not included in this study as many individuals in the data set had some wear, making crown height measurements imprecise. Tooth crowns are usually measured by mesiodistal and buccolingual crown diameters and although this method has been reassessed often (i.e. Goose 1963; Kieser 1990), most researchers still use the method of Moorrees and Reed (1954), as does this study. Moorrees and Reed (1954) define the mesiodistal crown diameter as the largest mesial to distal measurement taken parallel to the occlusal surface, while the buccolingual crown diameter is the largest distance between the buccal and lingual surface, perpendicular to the mesiodistal diameter. Problems with this measurement technique can arise when small occlusal variations or malocclusions appear.

Incisor, canine and premolar measurements

Incisors, canines and premolars were measured by locating: (a) the maximum mesiodistal crown diameter; (b) the mesiodistal cervical diameter, located directly below the enamel crown or cemento-enamel junction (Fig. 4.4a) (c) the maximum buccal to lingual crown surface; (d) the buccolingual cervical diameter, located at the base of the enamel crown; and (e) the maximum root length from the most occlusal point of the mesial cemento-enamel junction to the root tip (see Fig. 4.4b).

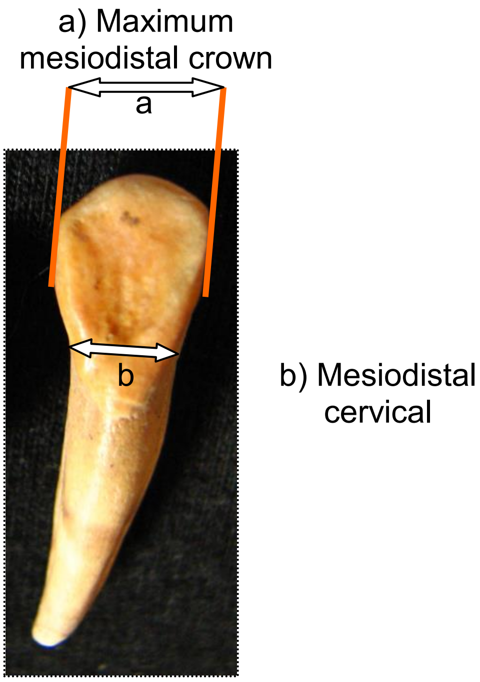


Figure 4.4a: Lingual view of incisor

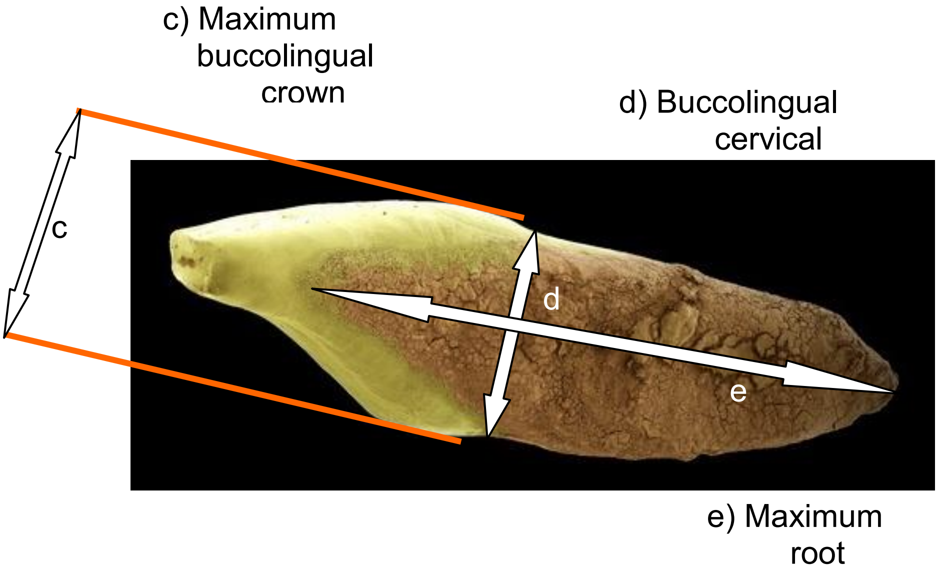


Fig. 4.4b: Mesial view of canine.

Molar measurements

Teeth fixed in the jaw fit closely together and make it difficult to take mesiodistal crown measurements. The needle points of dental callipers assist in overcoming this problem. Interproximal attrition is also a concern and samples with excess dental wear, i.e. wear beyond the crown's maximum diameter, were excluded for various measurements. Often, if an individual presents with heavy occlusal wear, only cervical measurements can be taken, while interproximal caries or wear make cervical measurements problematic. In these instances, if possible, only crown data is recorded. Also, cervical measurements on teeth not fully erupted are not possible and only crown measurements were recorded for these samples.

When available, mesiodistal crown diameters (see (f) in Fig. 4.5) are simple to take. Buccolingual crown diameter measurements on upper and lower molars, on the other hand, are more problematic because teeth are comparably wide in more than one place. First and second molars usually present with one bulge on their lingual side and two on the buccal. Adhering to Hillson *et al.* (2005), in order to achieve maximum buccolingual distance (see (g) in Fig. 4.5) in this study (when possible) I rotated the molar slightly during measurement to record the distance between the lingual bulge and the larger of the two buccal bulges (this bulge is usually mesially placed). The perpendicular measurement rule followed when measuring buccolingual distances for incisors, canines and premolars (Tobias 1967) no longer applies. Also, lingual and buccal bulges occur at different heights on the crown and therefore maximum measurements are not achieved in parallel to the occlusal surface as is required in other measurements.

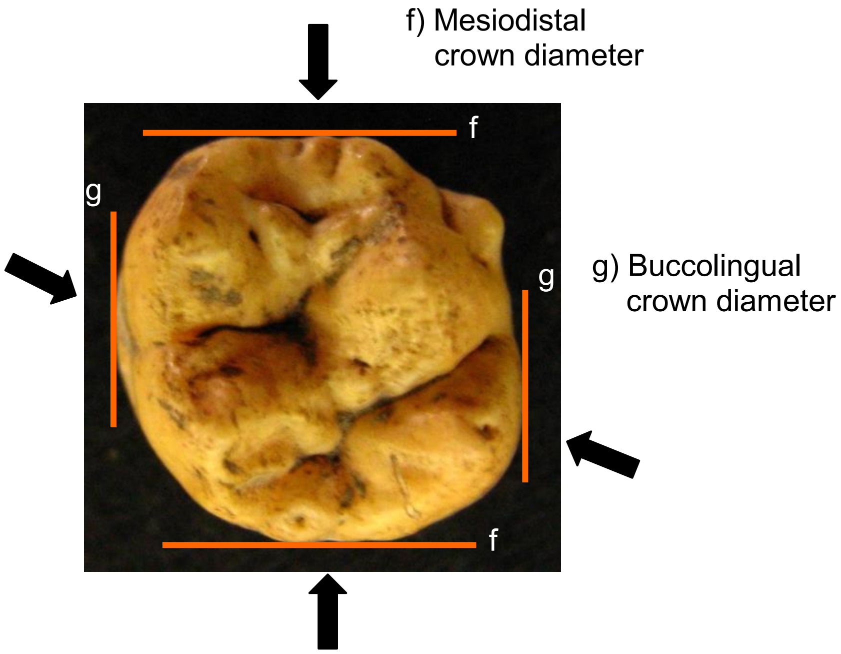
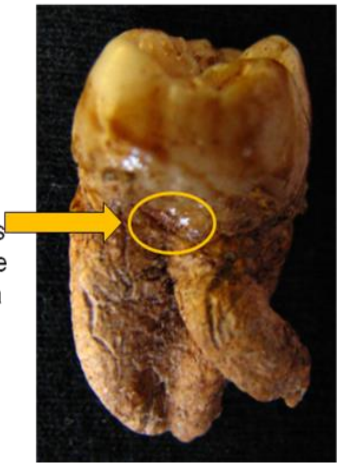


Fig. 4.5: Crown measurements on an upper left first molar.

Crown measurements, usually defined at the widest points of a tooth, are not useful on heavily worn teeth. To increase quantitative information, circumvent problems due to attrition, and allow for a larger data set, alternative measurements, particularly measurements at the cervix of the tooth, and measurements along a diagonal axis in molars were taken in this study.

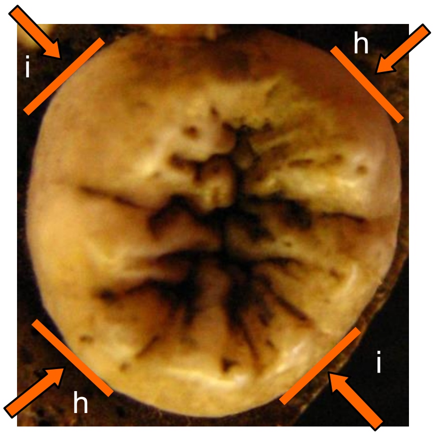
Cervical measurements are taken at the base of the crown, along the cemento-enamel junction of the cervix. Previous investigations using this method (Azoulay and Regnault 1893; Colby 1996; Falk and Corruccini 1982; Fitzgerald and Hillson 2008; Goose 1963; Kieser 1990; Pilloud and Hillson 2012; Pilloud and Larsen 2011) demonstrate this measurement's application and, with the exception of Stojanowski (2007), it's effectiveness. The buccolingual cervical measurement of the crown is simply the greatest distance between the buccal and lingual sides of the tooth; however a concave area may exist below the cemento-enamel junction where the roots begin to bifurcate. Measurements were taken above this, at the base of the crown. The mesiodistal cervical measurement is important for archaeological specimens as this measurement is often not possible on the crown due to wear. However, fixed teeth can be problematic as the mesial and distal sides are often concave at the cemento-enamel junction (see (j) in Fig. 4.6). Also, the mesiodistal cervical measurement Hillson *et al.* (2005) formulated on loose teeth is often not possible on *in situ* teeth (typical of archaeological collections) and access to their outlined measurement points can be problematic (see Aubry 2014 for details). To overcome mesiodistal measurement errors associated to *in situ* teeth, this study took mesiodistal measurements from the buccal (or labial) side only and included only the buccal portion of the tooth in mesiodistal molar measurements to ensure consistency and repeatability. Aubry (2014) has recently proposed a similar methodology to combat these issues. Hillson *et al.* (2005) also do not mention the angle at which the callipers should be held for these cervical measurements and it was found that varying degrees could produced different results. In order to be consistent in these measurements, here I adopt methods used by Tobias (1967). The calliper points are held in parallel lines, perpendicular to the mesiodistal axis at the cemento-enamel junction. This technique has been successful and is generally only hindered by severe calculus deposits.



(j) Cement-enamel Junction (CEJ). Note the concave nature of the CEJ at the base of the crown and beginning of the root. Measurements are taken at the arrow, superior to the start of the root, as the concave area begins.

Fig. 4.6: Cemento-enamel Junction.

Diagonal diameters of molars are also advantageous as they are much less affected by wear. Attrition is minimal on the diagonals as there is no corner contact between teeth. The mesiobuccal to distolingual diameter, and mesiolingual to distobuccal diameter, at both crown and cervix, are a simple maximum measurement where the tooth is rotated to give the highest diagonal value (see (h and i) in Fig. 4.7). The degree of molar rounding is all that hinders this measurement and has been overcome by consistent, repeated measurement in this study.



h) Mesiolingual distobuccal crown diameter

i) Mesiobuccal distolingual crown diameter

Fig. 4.7: Diagonal crown measurements on a lower left third molar.

The use of cervical measurements and their ability to successfully supplement crown data has only recently been popularised with some success on adult Holocene dentitions (Aubry 2009; Bernal *et al.* 2009; Pilloud 2009; Pilloud and Larsen 2011; Stojanowski 2007), Late Pleistocene/Early Holocene material (Fitzgerald and Hillson

2008) and deciduous teeth (Pilloud and Hillson 2012). These alternatives have been successfully evaluated (Benazzi *et al.* 2011; Fitzgerald and Hillson 2008; Stojanowski 2007) and demonstrate confidence regarding the repeatability with which they can be measured and used as supplements to crown metrics. Stojanowski (2007) however, finds that mesiodistal cervical diameters are not always good proxies for mesiodistal crown metrics and are therefore not used in isolation in this study.

STATISTICAL ANALYSES OF DATA

Statistical analyses were performed on the data set using the Statistica (StatSoft 2011), SPSS (IBM Corp 2012) and R (R Development Core Team 2012) programs. Descriptive, univariate and multivariate techniques were used to differentiate and evaluate degrees of phenetic similarity and numerically evaluate the affinity (Sokal and Sneath 1963) between and within the Khoesan dental sample and between this sample and other geographically or temporally distant African populations.

Metric

To evaluate intra-observer accuracy, a repeatability study on 30 individuals was conducted showing that measurements were suitably reproduced with a 95% confidence. Repeatability was assessed by measuring cervical and crown mesiodistal and buccolingual diameters of each individual three times, and through analysis of variance (ANOVA) (IBM Corp 2012), evaluated the error associated with repeat measurement relative to intra-individual variation. Correlations between crown and cervical measurements were also assessed using Pearson product moment correlations (StatSoft 2011). All measurements from left upper and lower teeth were evaluated for correlations (r), demonstrating comparable r-values between crown and cervical diameters.

Multivariate analyses of variance (MANOVAs) (IBM Corp 2012), using the Wilks' Lambda distribution, were used to test for overall significant differences between populations across all dental measurements. To perform MANOVAs, it was necessary to modify missing data. Means were therefore added to measurement variables, where necessary. Pairwise tests (t-tests for independent samples by group) were then used (including the Bonferroni Correction) to identify specific variable differences between populations.

Principal Components Analyses (PCA) (StatSoft 2011) were employed in order to identify and visualise patterns in the metric data. PCA is a useful transformational statistical technique, commonly used to find patterns in complex data by reducing the number of variables and allowing the user to display variation graphically. PCA allows for the analysis of a series of measures described by several dependent variables. Its goal is to reduce a large interrelated data set, and at the same time, retain most of the variation present in that data set. For this study, PCA variables included tooth measurements (discussed earlier in this chapter) from both geographical and temporal subdivisions. The PCA expresses the dental data as a new set of orthogonal variables (eigenvectors and eigenvalues) relating to the maximum variance in the original data, called principal components (Abdi and Williams 2010). A correlation matrix was utilised for the extraction of the components. These data are projected onto an x-y axis of two factors formed by a sub-set of the highest variance. The eigenvector with the largest eigenvalue demonstrates the direction of the most variation (x-axis) and the second largest eigenvalue demonstrates the next highest variation and is displayed on the y-axis. Using associated eigenvalues, the principal components reflect variation in both size and shape. In this study, the first factor, principal component 1, is largely a tooth size variable, and accounts for the highest percentage of the total variance. Principal component 2 relates to tooth shape and accounts for the largest portion of the remaining variance. Other components account for the residual variance but percentages are generally smaller. Although size is taken to account for PC1 and shape appears to be associated to PC2, it is possible that these are interchangeable and that susequent components also relate to size and shape variability. Component loadings or variable contributions are the weight by which each of the original variables are to be multiplied to get factor scores (P. Shaw 2003). These loadings complement PCA plots and are used in conjunction with discussion relating to component or factor scores. Component loading for subsequent factors (PC3, PC4 etc.) can be found in Appendix 14 on the CD.

Non-metric

Data was first dichotomised into present and absent. Certain low grade ASUDAS scores were excluded in order to fully characterise the population's trait expression (morphological threshold or breakpoint) and to correspond to current standardised methods of trait evaluation. For example, I^1 shoveling that has been scored between grades 2 and 6 using the ASUDAS are used in these assessments, while those scored with a 1 or 7 represent very faint or extreme expressions of the trait and are largely excluded (palatine and mandibular tori are scored for all expressions in between-Khoesan evaluations). Thereafter, frequencies for each dental trait, within each population, were calculated. Once traits were dichotomised, trait frequencies within geographical and temporal groups were calculated. The number of individuals displaying a trait is calculated along with the total number of individuals scored for the trait (N). From this, the present trait occurrence is calculated, permitting an overview of the population's dental characteristics based on a suite of traits, and a dental phenetic comparison between groups. To evaluate Khoesan regional non-metric variation, frequency data is assessed within individual geographic regions A, B, C, D, E, F and G, as well as combined regions of the coastal group (Regions B to F), an inland group (Regions A+G), and an all-inclusive group evaluating the population as a whole (sum of frequencies in regions A to G). Temporal data were assessed in sets of samples dated to 8000 ka+, 8-6 ka, 6-4 ka, 4-3 ka, 3-2 ka, 2-1 ka, the first millennium BP (1-0 ka), and a collective grouping of all data (dated or not) from all time periods. Additionally, frequencies for Khoesan dental data through time, inclusive of all regional samples, are also assessed.

To assess whether there are temporal and geographic differences in non-metric dental variation between Khoesan populations, data were compared using a chi-square statistic (Goodness-of-fit) for the individual traits. Chi-squares were calculated between all outlined geographic regions and temporal subsets. Chi-square (X^2) statistics are used to investigate whether distributions of categorical variables differ from one another. This study uses the Pearson's chi-square test and employs the Yates Correction to correct for small sample sizes (<5) when necessary. Here, the chi-square statistic facilitates the comparison of morphological (or phenetic) similarity of particular traits between groups by evaluating the relationship between two of the dichotomous variables discussed above. Significance levels are demonstrated at 95% (p = 0.05; df = 1).

The Mean Measure of Divergence (MMD) is a statistic for comparing non-metric trait frequencies between two populations in order to measure biological distance. This formula converts a series of trait frequencies into a numerical value, which can then be used to evaluate how similar two samples are to each other. MMD values that are greater than 2 x the standard deviation, differ from each other at the 0.025 significance level (Sjøvold (1977). The greater the MMD value, the more dissimilar the two samples are, while a lower number indicates greater affinity. This formula, developed by C.A.B. Smith and first popularised in human biological studies by the non-metric skeletal variation studies of Berry (1974, 1976); Berry and Berry (1967), and Sjøvold (1977), is an accepted mechanism among dental anthropologists for approximating the variation among groups with the aim of reconstructing population histories through time.

The MMD equation has been a popular method of assessing inter-sample distance. First used extensively by Turner (1984, 1985a, 1985b, 1986b, 1987) to estimate dental affinities between the New World and Asian populations, this method has continued prominence in dental research (Edgar 2004; E.F. Harris 2008; E.F. Harris and Sjøvold 2004; Irish 1993, 1998b, 2005, 2006; Irish and Konigsberg 2007). The MMD has been misrepresented in the past (Berry and Berry 1967) and much criticism surrounding the appropriate and correct use of the statistic has been a topic of discussion (E.F. Harris 2008; Konigsberg 2006) but recent discussions about the formula have corrected any confusion surrounding its incorrect use (E.F. Harris and Sjøvold 2004) and validity (Irish 2010). The MMD equation for this study has been taken from E.F. Harris and Sjøvold (2004) and (Irish 2010), as follows. First, the difference between samples *i* and *j* for the frequencies of trait *k* is calculated and then this difference is squared.

$$MMD = \sum_{k=1}^{r} \left(\theta_{ik} - \theta_{jk}\right)^{2}$$

This enables the measurement of the phenetic difference ($(\theta ik - \theta jk)^2$) between samples. Sample size can become an issue at this stage, especially small sample sizes, and an adjustment is necessary. Many researchers such as Green and Suchey (1976) and Berry and Berry (1967), confirm that using the Freeman and Tukey (1950) angular transformation to correct for small sample sizes stabilises the sampling fluctuation. This correction is:

$$\left(\frac{1}{n_{ik} + \frac{1}{2}} + \frac{1}{n_{jk} + \frac{1}{2}} \right)$$

The sum of the differences is then divided by *r*, the number of traits used in the equation, in order to generate the average difference between samples i and j.

$$MMD = \frac{\sum_{k=1}^{r} \left(\theta_{ik} - \theta_{jk} \right)^2 - \left(\frac{1}{n_{ik} + \frac{1}{2}} + \frac{1}{n_{jk} + \frac{1}{2}} \right)}{r}$$

Using these equations, Sołtysiak (2011) developed R-script for the MMD statistic. This script (using the R statistical program (R Development Core Team 2012)) was used in analysis for all MMD calculations. In determining the MMD, Sjøvold (1977) suggests that as many discrete and uncorrelated traits as possible should be used in the analysis in order to avoid false weighting of the samples and errors. Previous studies on sub-Saharan African populations, including the Khoesan, by (Irish 1993, 1998a, 1998b) have consistently shown little to no undesired correlations between traits. Overall, the greatest correlation found in African dental populations occurred between I^1 double shovelling and labial curvature and was negligible (Irish 1993). Also, low correlations, generally found in anthropological data sets, will largely, not distort MMD results (E.F. Harris and Sjøvold 2004). In order to test for unwanted correlation, the Spearman R rank-order correlation coefficient statistic was employed on all ordinal data. The only significant correlation demonstrated was between M_1 anterior fovea and M_1 deflecting wrinkle (p = 0.0194). Samples that produced errors in correlation analyses are those that incorporated traits evaluating degrees of expression, including M_1 and M_2 X-groove pattern, M^3 metacone, M^2 Hypocone and M^{1}'s expression of the large metaconule. These and the M_1 deflecting wrinkle were removed from MMD analyses. Due to high sexual dimorphism previously recorded with regards to congenital absence M^3, this trait was also removed.

SUMMARY OF STATISTICS USED TO EVALUATE HYPOTHESES

Evaluation of hypothesis 1

MANOVAs and principle components analysis were used to investigate metric regional size and shape variation within the Khoesan dental data set. Additionally, trait frequency analyses were assessed on dichotomised non-metric data for regional percentages. Thereafter, chi-square statistics were employed to test for significant regional relationships. Lastly, the mean measure of divergence was assessed on regional data in order to identify phenetic similarities and dissimilarities between geographical regions.

Evaluation of hypothesis 2

Metric evaluations consisted of MANOVAs and principle components analyses on maxillary and mandibular dental dimensions. Non-metric temporal data, divided into sub-groups, were dichotomised into present and absent and trait frequencies assessed. Chi-square analyses were used to identify significant temporal affinities and patterns (if any) within the data set.

Evaluation of hypothesis 3

PCAs and pairwise tests were employed to highlight metric dental patterns between Mid-Late Pleistocene and Khoesan Holocene diameters. Thereafter, non-metric trait frequencies were used to assess similarities and differences between Mid-Late Pleistocene and Khoesan Holocene populations. Chi-square statistics were then applied to these data to evaluate possible significant affinities and/or differences between them.

Evaluation of hypothesis 4

Metric analyses consist of MANOVAs and PCAs between Holocene Kenya and Khoesan dental data in order to evaluate dimensional similarities or differences. Trait frequency and chi-square assessments were also employed using non-metric data to identify disparities or associations between the Holocene Kenya and Khoesan populations. Lastly, mean measure of divergence statistics were utilised to investigate phenetic distances between these two populations.

CHAPTER 5

DATA ANALYSES AND RESULTS

THE KHOESAN DENTAL MAP AND DATA ANALYSIS

METRICS

REPEATABILITY

The repeatability of individual measurements is presented in Appendix 1. To determine the accuracy of data capture (i.e. intra-observer measurement error), variable repeatabilities were calculated on all cervical and crown measurements from thirty (30) randomly selected Khoesan skeletons (left side only). Repeatability (t) is the proportion of the total variance attributable to individual differences, rather than the variation due to measurement error (Ackermann 1998, 2002; Cheverud 1995). To calculate repeatability, the equation $t = Vb/(Vb+Vw)$ was used, where Vb is the individual variance between samples and Vw is the variance within samples. Vb is calculated as $Vb=(MSb-MSw)/n$, where MSb is the mean square between samples, MSw the mean square within samples (obtained from one-way ANOVAs, where individuals were identified as the factor) and n the number of repeats. Vw is equal to MSw. To be cautious and to minimise technical errors of measurement (TEM) as outlined by E.F. Harris and Smith (2009), in this study each tooth was measured three times, thus $n= 3$. The repeatabilities for all measurements are high, and all are above 90%, with the exceptions of 86% in I_2 mesiodistal cervical diameter and 80% in P^4 buccolingual crown diameter. Because of these higher measurement errors, these two variables were removed from statistical analyses.[5] The high repeatability of cervical measurements in this study also demonstrates that these alternative

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[5] The reasons for these errors are unknown but are most likely due to technical errors of measurement.

diameters can be measured just as reliably as crown diameters and therefore may be better measures for worn teeth, as is commonly found archaeologically.

CROWN AND CERVICAL CORRELATIONS

Using Pearson product-moment correlations, results indicate that alternative dental measurements (cervical) can be used as a proxy for certain crown measurements. When relative size and shape are compared, measurements yield similar results between cervical and crown data sets. The Pearson correlation coefficient determines the degree to which values of two variables are linearly related (proportional) to each other where the closer r=1, the stronger the correlation. Here, all correlations are positive with varying degrees of strength. Detailed correlations are given in Appendix 2, while ranges of correlations (r) between crown and cervical measurements on all teeth are given below (Table 5.1).

Table 5.1: Correlation (r) range between crown and cervical measurements on all teeth.

	Mesiodistal	Buccolingual	Mesiolingual-distobuccal	Mesiobuccal-distolingual
r	Range 0.162 - 0.763	Range 0.630 -0.852	Range 0.607 - 0.863	Range 0.703 - 0.853

The correlations between crown and their equivalent cervical measurements do not show consistently strong relationships. In general, mesiodistal diameters demonstrate moderate correlations with an average value of 0.550 but present the greatest correlation range of all measurements. The highest mesiodistal correlations are observed in upper incisor diameters (similarly demonstrated in Hillson *et al.* (2005)), lower canines and upper and lower third molars. The weakest (and by far the lowest correlation in the entire data set) is observed in mesiodistal diameters of LP^4 (r = 0.162). Buccolingual cervical and crown measurements are strongly correlated (an average of 0.745) with higher correlation values noted for upper and lower lateral incisors and canines and slightly lower values for all molars. Diagonal cervical and crown molar measurements reveal consistently strong correlations with the exception of the mesiolingual-distobuccal diameter of LM_1 which demonstrates a slightly lower correlation value of 0.607. In analyses, mesiodistal cervical measurements (lowest correlated to crown measurements) were not used in isolation to avoid any possible biases in outputs and were always used in conjunction with either crown or buccolingual diameters.

A general comparison between crown and cervical measurements is demonstrated on two principal components analyses (PCA), illustrated in Fig. 5.1 below. The PCA on the left consists of upper first and second molar mesiodistal and buccolingual cervical diameters (categorised by date range), while the same teeth are used to reflect corresponding crown measurements in the PCA on the right.

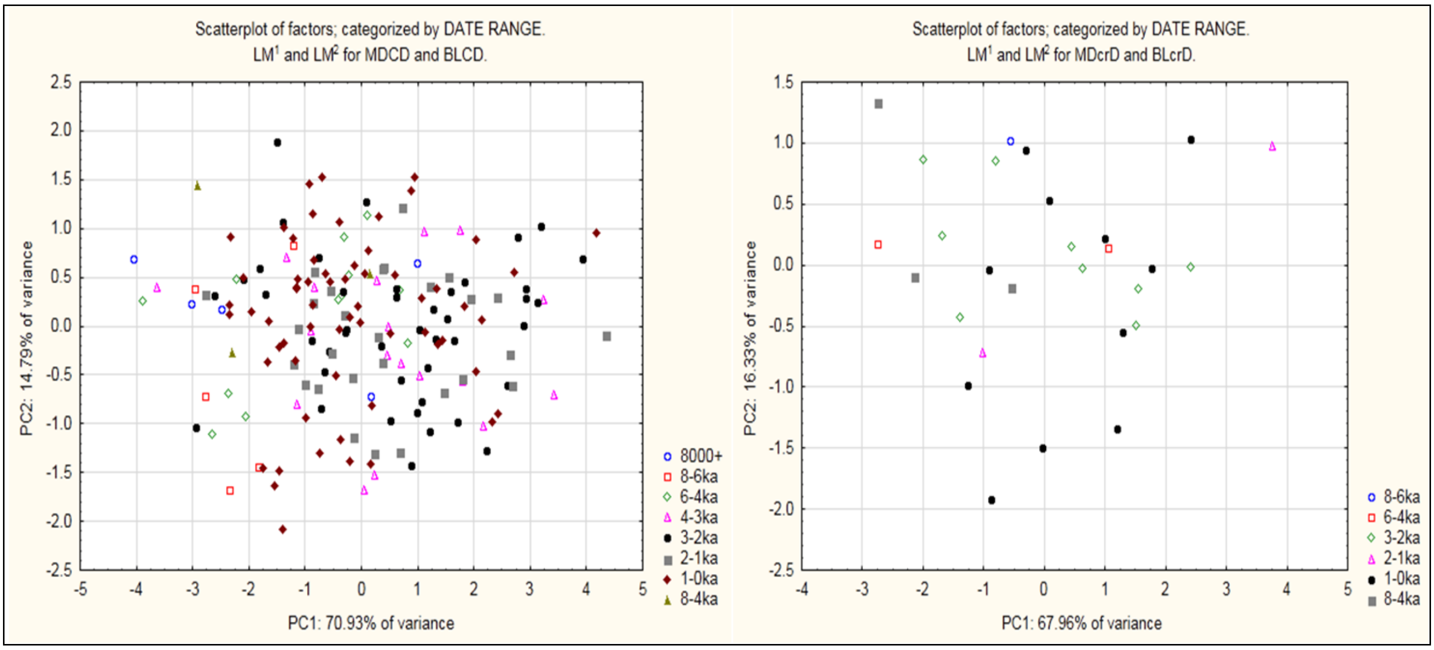


Fig 5.1: PCAs depicting cervical mesiodistal and buccolingual measurements on upper first and second molars (graph on left) and crown mesiodistal and buccolingual measurements (graph on right).

SEXUAL DIMORPHISM

To examine whether sexual dimorphism exists in the dental variables examined here, a t-test combined with principal components analyses (PCA) were used on crown and cervical measurements of maxillary and mandibular teeth. Results of t-tests with a p-value of 0.05 indicate that 37.5% of the 88 (33/88) measurements (left side; traditional and cervical measurements) differ significantly between sexes. After the application of the Bonferroni Correction (p-value is reduced to 0.00058), 2/88 (2%) differ significantly. Buccolingual cervical and crown measurements and mesiobuccal-distolingual diagonal measurements demonstrate most of the differences 31/88 (35%). Seven PCAs were performed and the variables and percentage of variance values for each factor (PC1 and PC2) can be found in Table 5.2 below. Results were consistent across all the analyses so only 1 PCA plot is illustrated here. The PCA of male (M) and female (F) mandibular first and second molar cervical measurements (4 variables) is illustrated in Fig. 5.2. While there are some significant differences for the univariate tests, there is no clear pattern when examining the PCA data. Since the differences are only prevalent in some measurements and general practice in dental anthropological studies has been to pool the sexes, this thesis applies this methodology. Sexual dimorphism is not a central theme to this thesis and variability here does not effect thesis hypotheses. Later studies should attempt to identify sexual dimorphic differences in more detail.

Table 5.2: List of variables and percentage of variance explained for the first two principal components. Abbreviations can be found in Table 4.4.

Variables		**% of variance**	
Teeth	**Measurements taken on each tooth**	**PC1**	**PC2**
LP^3, LP^4	MDCD / BLCD	69.88	17.64
LM_1, LM_2	MDCD / BLCD	70.93	15.45
LM^1, LM^2	MDCD / BLCD	71.82	14.46
LM_1, LM_2, LM^1, LM^2	MDCD / BLCD	66.12	8.83
LP_3, LP_4	MDcrD / BLcrD	68.42	18.35
LM_1, LM_2	MDcrD / BLcrD	70.37	15.59
LM^1, LM^2	MDcrD / BLcrD	71.68	16.21

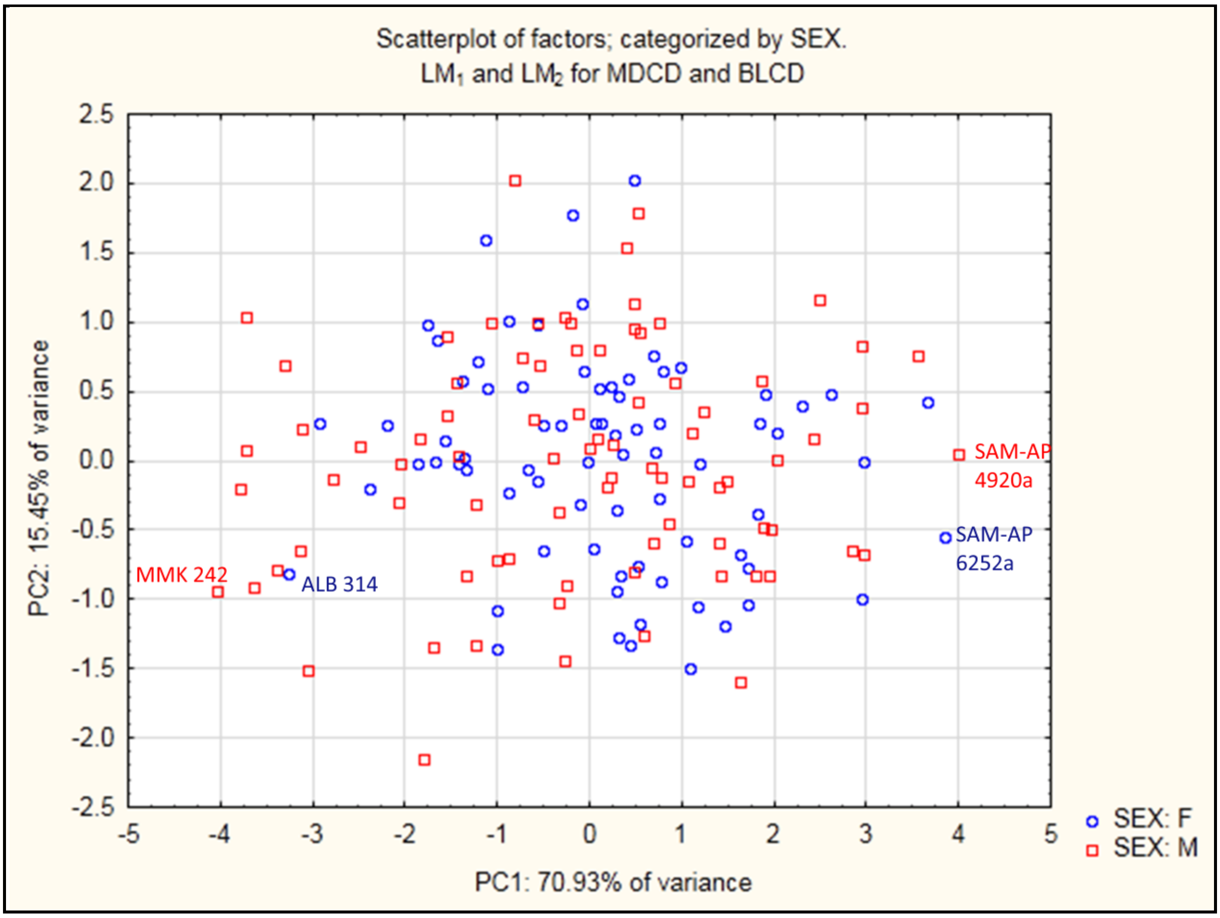


Fig. 5.2: Principal components plot of PC1 versus PC2. PCA based on LM_1 and LM_2 mesiodistal cervical diameters (MDCD) and buccolingual cervical diameters (BLCD) categorized by sex.

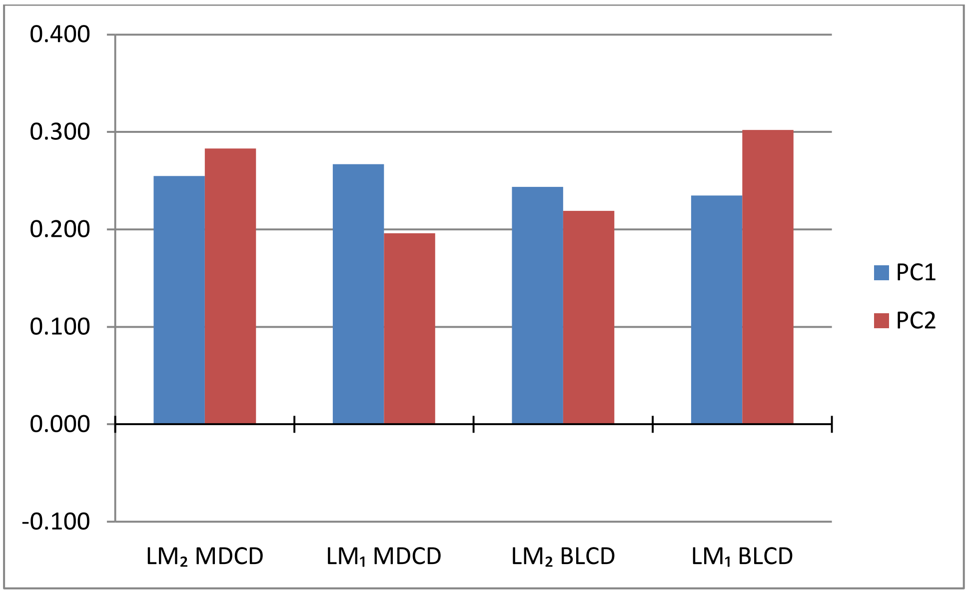


Fig. 5.3: Principal component loadings of PC1 and. PC2 for lower first and second molar cervical dental measurements categorized by sex.

The PCA plot (Fig. 5.2) shows that male and female specimens largely overlap in both PC1 (size; x-axis) and PC2 (shape; y-axis) and present some large individuals located on the left of the graph (i.e. MMK 242 (M) and ALB 314 (F)) and very small individuals towards the right (i.e. SAM-AP 4920a (M) and SAM-AP 6252a (F)). The component loadings (Fig. 5.3) are all positive and comparable in magnitude, with PC2 LM_1 BLCD weighted the highest (0.302) and the lowest for LM_1 MDCD (0.196). As is shown here, although a handful of individuals are at the extreme of ranges of size and shape variation, there is no definitive pattern that clearly separates males and females dentally and therefore the sexes for this study are pooled in further analyses.

NON-METRICS

The Khoesan have often been considered separately in anthropological (and dental) studies because they exhibit more genetic variation. A close examination of Khoesan dentition further highlights the uniqueness of this population. Although Khoesan dental trait frequencies vary somewhat across space and through time, as will be discussed in following sections, overall the pattern of variation is fairly consistent (a bar graph summarising trait frequencies can be seen in Fig. 5.14). As a result, first Khoesan dental variation as a whole is presented, followed by a more detailed look at regional and temporal variation, where it exists, within the sample. For presentation and discussion purposes, the dentition is divided into five groups: incisors and canines, premolars, lower molars, upper molars, and a group of other features (including intra-oral osseous traits, the midline diastema, and M^3 congenital absence).

Incisors and canines

Globally, an important incisor trait is the I^1 shovel. On average, this trait occurs with a frequency of ~20% within the Khoesan population (see Fig. 5.4). I^1 winging also occurs at approximately the same frequency. I^1 labial convexity, I^1 interruption groove and I^1 tuberculum dentale occur at intermediate frequencies throughout the data set. The I^2 peg-shaped incisor (Fig 5.5) and C^1 accessory ridge both occur in relatively low frequencies (10.6% and 8.2%, respectively), while I^1 double shoveling and the presence of lower canines (C_1) with more than one root is rare (>1%). Another important trait for African populations is the upper canine CMR, commonly known as the Bushman canine (see Fig. 5.6). This trait, occurring in varying degrees in populations across sub-Saharan Africa, occurs here in 61.5% of the total population.

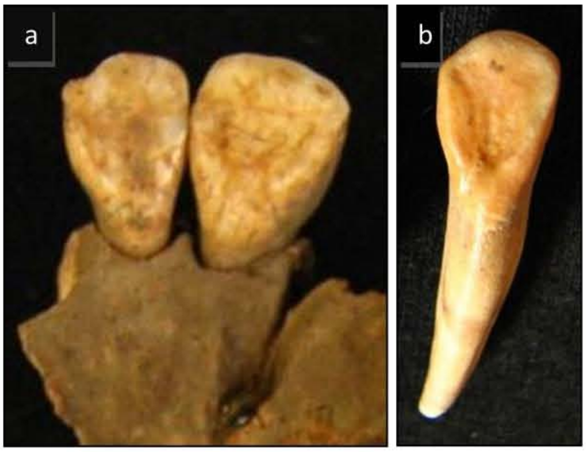


Fig. 5.4: Examples of Khoesan shovel-shaped incisors: a) RI^1 and I^2 with grade 2 shoveling (SAM-AP 3738); b) RI^1 with grade 2 shoveling (SAM-AP 4211). Low grade shoveling is common in the dental data set with no scores exceeding ASU grade 3.

Fig. 5.5: Example of a pair of peg-shaped upper lateral incisors (SAM-AP 3737a).

Fig. 5.6: Examples of the Khoesan canine mesial ridge. On the left is a grade 2 CMR on RC^1 (UCT 162) and on the right is a grade 3 CMR on RC^1 (NMB 1412).

Premolars

Intermediate trait occurrences of P^3 root and P_4 cusp variation are identified within the population. The P_3 Tome's root (see Fig. 5.7), previously not assessed due to the use of cast material for analyses (Irish 1993), occurs at 23.2% overall. Low frequencies of P^3 accessory cusps are present. Odontomes are generally scarce in sub-Saharan Africa and the appearance of this trait, albeit negligible (0.5%), is of note. The remaining premolar traits, the P^3 disto-sagittal ridge and P^3 tricuspid, are absent. The disto-sagittal ridge, thus far known only from the south-western United States, unsurprisingly is not present in this Khoesan data set.

Fig. 5.7: Example of P_3 Tome's root, ASU grade 3 (SAM-AP 1272).

Lower Molars

Lower molar traits that occur at the highest frequencies include M_1 Y-groove pattern (88.6%; see Fig. 5.8), M_1 cusp 5 (98.8%; see Fig. 5.9), M_1 cusp number (98.8%; 5+ cusps must be present), and M_2 root number (93.8%; tooth has 2+ roots). Although some of these traits occur at higher frequencies than their sub-Saharan African counterparts outlined in Irish (1993, 1997; 1998b), their frequencies are on a par with high rates of occurrence found in Africa. M_2 cusp 5 (84.8%), M_2 cusp number (83.3%) and M_2 Y-groove patterns (72.4%) also present with high frequencies, slightly lower than their M_1 equivalents. The M_2 cusp 6 (20.5%) occurs at a higher frequency than it does in M_1 (15.7%). The presence of the M_1 7th cusp is a trait often associated to sub-Saharan African dentition. Here, the trait was evaluated on both M_1 and M_2 demonstrating slightly higher occurrences of the trait in M_1 (18.1% versus 11.5%). Similarly, the M_2 X-groove pattern (see Fig. 5.8) exceeds X-groove M_1 frequencies (17.6% and 12.7%, respectively). The M_3 torsomolar angle, M_1 deflecting wrinkle and M_1 protostylid traits occur at fairly low frequencies (≤20%) throughout the population. M_1 with 3 or more roots and M_1 distal trigonid crest (also called C1-C2 crest) are not present in the data set.

Upper Molars

Four of the upper molar traits occur at very high frequencies. These include the M^2 hypocone (100%), the M^2 large hypocone (those that have an ASU score of 3+; 93.4%), M^2 root number (those that have an ASU score of 3+ roots; 94.1%) (see Figs 5.10 and 5.11) and the M^3 metacone (100%). The metacone is usually large in dental samples (Turner and Nichol 1991) therefore identifying M^3 small metacone (ASU score of 3) is worthwhile. This trait occurs at 36% within the population. M^1 metaconule incidence occurs in 51.7% of the sample, while the M^1 large metaconule (a metaconule with an ASU score of 5+) appears at relatively low occurrence rates of 7%. Interestingly, the metaconule is periodically (~32%) accompanied by a distal accessory tubercle (see Fig. 5.12). The M^3 peg and M^1 enamel extensions present at low to mid-range frequencies throughout the population (22.8% and 18.7%, respectively). The M^1 Carabelli's trait, common in Europe, has a moderate incidence rate in the Khoesan data set. Presenting here at 25.4%, the Carabelli's trait occurs at a relatively low rate in comparison to many sub-Saharan African groups (see Fig. 5.13). The last of the upper molar traits, the M^3 parastyle, occurs at very low frequencies (2.8%) in the data set.

Other Features

The midline diastema, identified as a trait fairly common (44%) in South African Bantu-speaking populations (Irish 1993), exists in approximately 20% of the Khoesan sample. The congenital absence of the M^3 is rare (3.7%), aligning with published high frequencies (Irish 1993) of M^3 presence. Generally, intra-oral osseous traits have a low to intermediate frequency within the Khoesan data set. Palatine tori (57.8%) are far more common than mandibular tori (29.6%), and the frequency of rocker jaws is 37.8%.

Fig. 5.8: RM_1 and RM_2 (MMK 230a). The RM_1 has a Y-groove pattern (top tooth), while RM_2 presents with a X-groove pattern (bottom tooth).

Fig 5.9: LM_1 and LM_2 expressing a cusp 5 (small), cusp 6 (very large) and cusp 7 (also very large) (SAM-AP 3691).

Fig. 5.10: LM^2 root with an ASU score of 3, identifying three roots present (SAM-AP 3738). Three-rooted upper molars are common in the Khoesan dental map.

Fig. 5.11: RM^3 root with an ASU score of 5 (UCT 366). This is very unusual for Khoesan dentition and is the only example of excessive roots found by the researcher. The tooth also has an enamel pearl half way down the length of the root (middle left of the image).

Fig. 5.12. An example of a distal accessory tubercle on an LM^2 with an ASU grade 3 metaconule alongside (SAM-AP 2920b).

Fig. 5.13: Example of an RM^1 Carabelli's trait, ASU grade 6 (SAM-AP 3691).

The following table (Table 5.3) summarises the frequencies of Khoesan dental traits according to low, intermediate and high frequencies. The majority of the traits have low frequencies, with high frequency traits limited to upper and lower molar traits and the CMR.

Table 5.3: List of low, intermediate and high trait frequencies in Khoesan dental data.

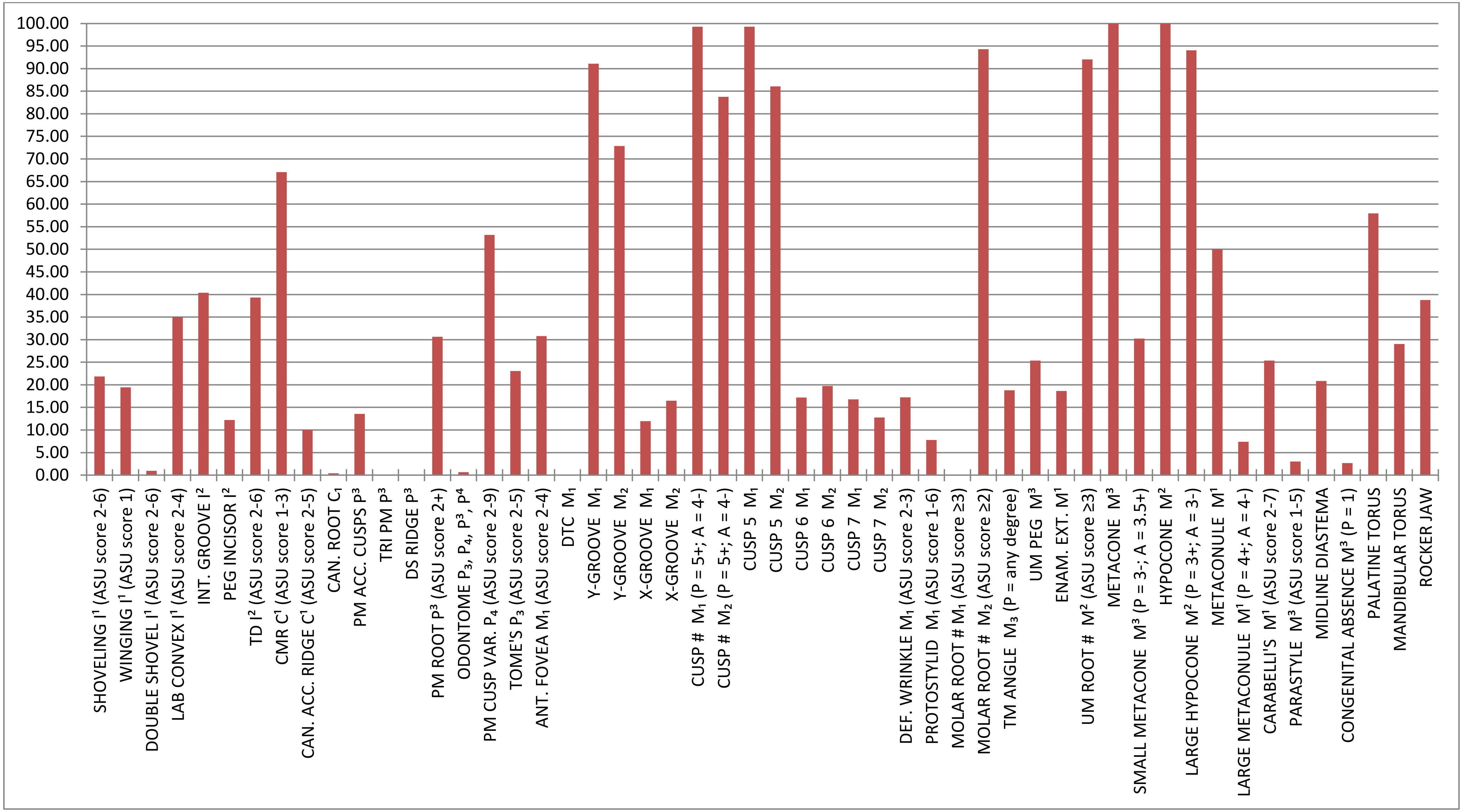
LOW 0-30%	**INTERMEDIATE 30-60%**	**HIGH 60-100%**
SHOVEING I^1	LAB CONVEX I^1	CMR C^1
WINGING I^1	INT. GROOVE I^2	Y-GROOVE M$_2$
DOUBLE SHOVEL I^1	TD I^2	Y-GROOVE M$_1$
PEG INCISOR I^2	PM ROOT P^3	CUSP # M$_2$
CAN. ACC. RIDGE C^1	PM CUSP VAR. P$_4$	CUSP # M$_1$
CAN. ROOT C$_1$	ANT. FOVEA M$_1$	CUSP 5 M$_1$
PM ACC. CUSPS P^3	SMALL METACONE M^3	CUSP 5 M$_2$
TRI PM P^3	METACONULE M^1	M ROOT # M$_2$
DS RIDGE P^3	PALATINE TORUS	M ROOT # M^2
ODONTOME P^3, P^4, P$_3$, P$_4$	ROCKER JAW	METACONE M^3
TOME'S P$_3$		HYPOCONE M^2
DTC M$_1$		LARGE HYPOCONE M^2
X-GROOVE M$_2$		
X-GROOVE M$_1$		
CUSP 6 M$_1$		
CUSP 6 M$_2$		
CUSP 7 M$_1$		
CUSP 7 M$_2$		
DEF. WRINKLE M$_1$		
PROTOSTYID M$_1$		
M ROOT # M$_1$		
TM ANGLE M$_3$		
M PEG M^3		
ENAM. EXT. M^1		
LARGE METACONULE M^1		
CARABELI'S M^1		
PARASTYLE M^3		
MIDINE DIASTEMA		
CONGENITAL ABSENCE M^3		
MANDIBULAR TORUS		

Trait reductions/increases between molars have also been assessed. Trait frequencies between M_1 and M_2 were largely similar for Y-groove/X-groove, cusp #, cusp 5, cusp 6 and cusp 7. Frequencies are listed in Table 5.4 below (N values can be found in Appendix 3 under the heading "All Regions"). Lower molar root # could not be included here as breakpoints used were different for each tooth within the morphogenic field. Frequencies for M_3 were recorded but are not used in this study because third molars have a tendency to be highly variable with regards to both size and morphology. Trait frequencies between M_1 and M_2 vary no more than 16%.

Table 5.4: Trait reductions/increases between molars.

TRAIT	TOOTH	FREQUENCY
Y-groove	M_1	88.65
	M_2	72.43
X-groove	M_1	12.68
	M_2	17.60
Cusp #	M_1	98.77
	M_2	83.33
Cusp 5	M_1	98.77
	M_2	84.82
Cusp 6	M_1	15.66
	M_2	20.54
Cusp 7	M_1	18.10
	M_2	11.54

Fig. 5.14: Khoesan dental trait frequencies.



REGIONAL AND TEMPORAL VARIATION WITHIN THE KHOESAN DENTITION

CONTINUITY BETWEEN GEOGRAPHICALLY SEPARATED SAMPLES: THE EVALUATION OF HYPOTHESIS 1.

This section evaluates hypothesis 1, which tests for significant dental metric or non-metric geographical differences between Holocene Khoesan samples. These data are assessed by geographic regions A,B,C,D,E,F and G (see page 109 for a map of regions).

METRIC EVALUATIONS

Crown and cervical measurements of maxillary and mandibular teeth for the entire Khoesan sample are presented in Appendix 10 on the CD at the back of this thesis (Mid-Late Pleistocene and Kenya data are available here, too). To explore regional metric variation within the population, MANOVAs and principal components analyses (PCA) were performed on crown and cervical measurements of maxillary and mandibular teeth from all study regions. To perform MANOVAs, it was necessary to modify missing data and therefore means were added to measurement variables, where necessary (inclusive of all measurements, 63% of the data had to be modified). Significant differences were not detected between regions (MANOVA; Wilks' Lambda; p=0.871). Unfortunately, due to wear and/or poor preservation, not all measurements could be obtained on all teeth and therefore missing data limited the number of variables analysed for any one PCA. Seventeen PCAs were performed. Variables and percentage of variance values for each factor (PC1 and PC2) can be found in Table 5.5 below. Although 17 PCA analyses were performed, the results were consistent across all the analyses so only 3 PCA plots are illustrated here. The PCA of mandibular first and second molar cervical measurements (4 variables) from all of the geographic regions is shown in Fig. 5.15.

Table 5.5: List of variables and percentage of variance explained for the first two principal components. Abbreviations are explained in the text box below.

Variables		**% of variance**	
Teeth	**Measurements taken on each tooth**	**PC1**	**PC2**
LM_1, LM_2	MDCD / BLCD	68.80	13.20
LM^1, LM^2	MDCD / BLCD	69.36	15.58
LP_3, LP_4	MDCD / BLCD	67.00	18.98
LI_1, LI_2, LC_1	MDCD / BLCD	58.60	12.18
LI^1, LI^2, LC^1	MDCD / BLCD	57.27	10.24
LM_1, LM_2	MDcrD / BLcrD	70.60	16.71
LM^1, LM^2	MDcrD / BLcrD	66.64	18.73
LP_3, LP_4	MDcrD / BLcrD	60.65	17.86
LP^3, LP^4, LP_3, LP_4	MDcrD / BLcrD	74.37	13.54
LI_1, LI_2	MDcrD / BLcrD	81.64	8.09
LI^1, LI^2	MDcrD / BLcrD	71.66	15.39
LM_1, LM_2	MLDBcrD / MBDLcrD	71.83	12.74
LM^1, LM^2	MLDBcrD / MBDLcrD	71.99	13.77
LM_1, LM_2, LM^1, LM^2	MLDBcrD / MBDLcrD	73.84	11.71
LM_1, LM_2	MLDBCD / MBDLCD	84.66	10.32
LM^1, LM^2	MLDBCD / MBDLCD	77.28	11.22
LM_1, LM_2, LM^1, LM^2	MLDBCD / MBDLCD	73.81	9.50

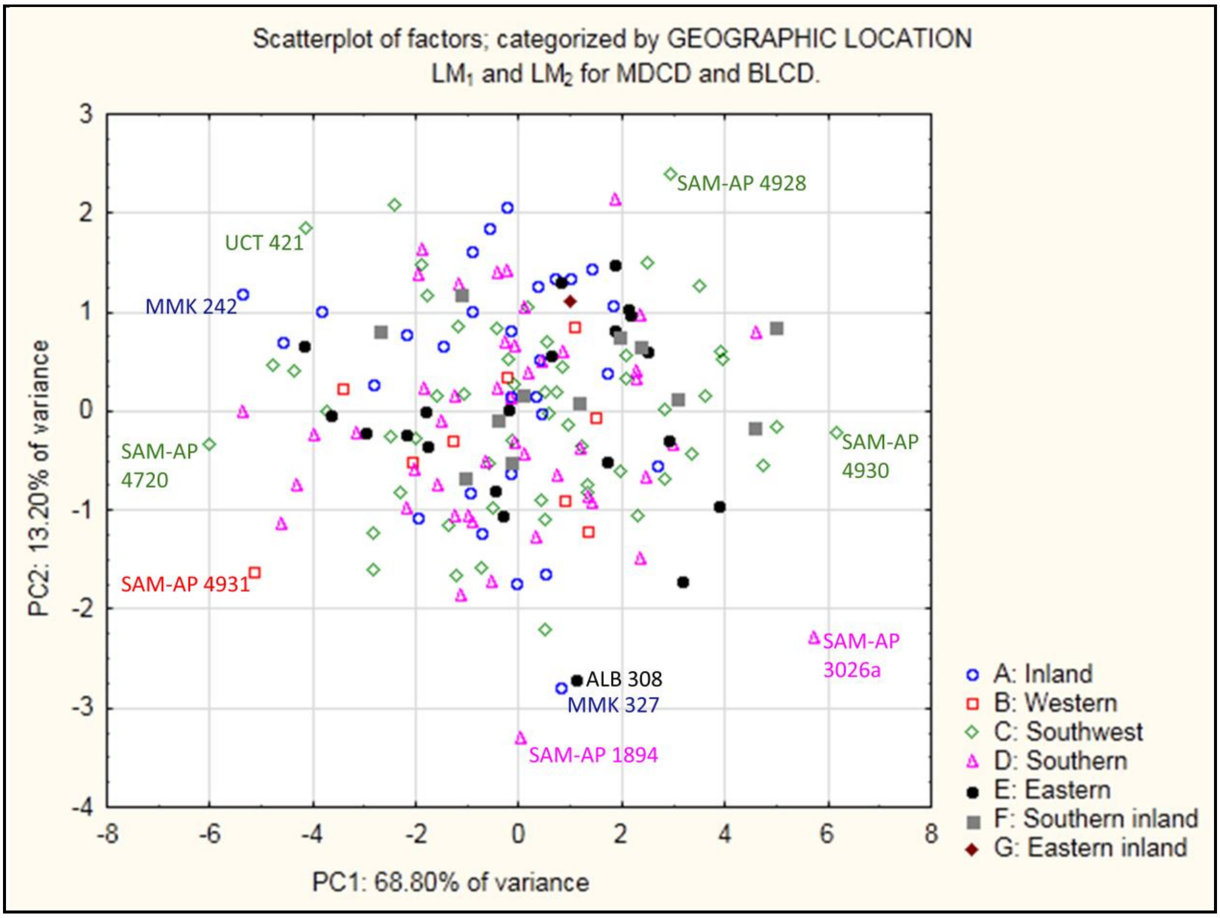


Fig. 5.15: Principal components plot of PC1 versus PC2. PCA based on LM_1 and LM_2 mesiodistal cervical diameters (MDCD) and buccolingual cervical diameters (BLCD) from Regions A to G.

Individuals from various regions are dispersed similarly across the PCA plot, demonstrating no specific geographic pattern with regards to dental size and shape variation. A few outlying specimens on the left hand side of the graph identify large specimens such as SAM-AP 4720, while small individuals are on the right (i.e. SAM-AP 4930). The outliers are predominantly from Regions A (MMK 242 and MMK 327), C (SAM-AP 4928, SAM-AP 4930, SAM-AP 4720 and UCT 421), and D (SAM-AP 3026a and SAM-AP 1894) and although these few individuals stand out, the overall dispersal of specimens is uniform. Component loadings (Fig. 5.16) for this plot are positive. Three of the four variables are evenly weighted for PC1, suggesting that this is largely a size variable reflecting overall molar size. However, the variation in size/shape for LM2 BLCD appears to be captured primarily by PC2.

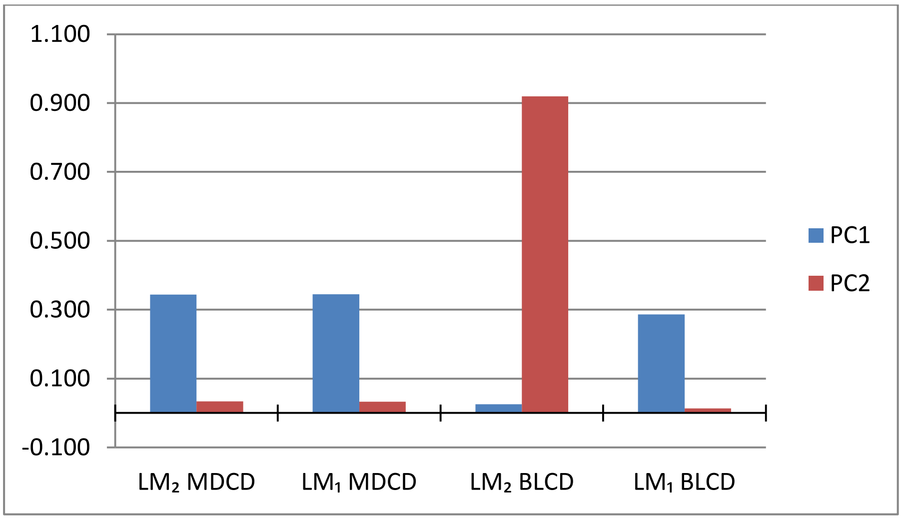


Fig. 5.16: Principal component loadings of PC1 and. PC2 for lower first and second molar cervical dental measurements associated to Fig. 5.15.

The PCA of first and second upper molar diagonal cervical measurements (4 variables) from all of the geographic regions is shown in Fig. 5.17.

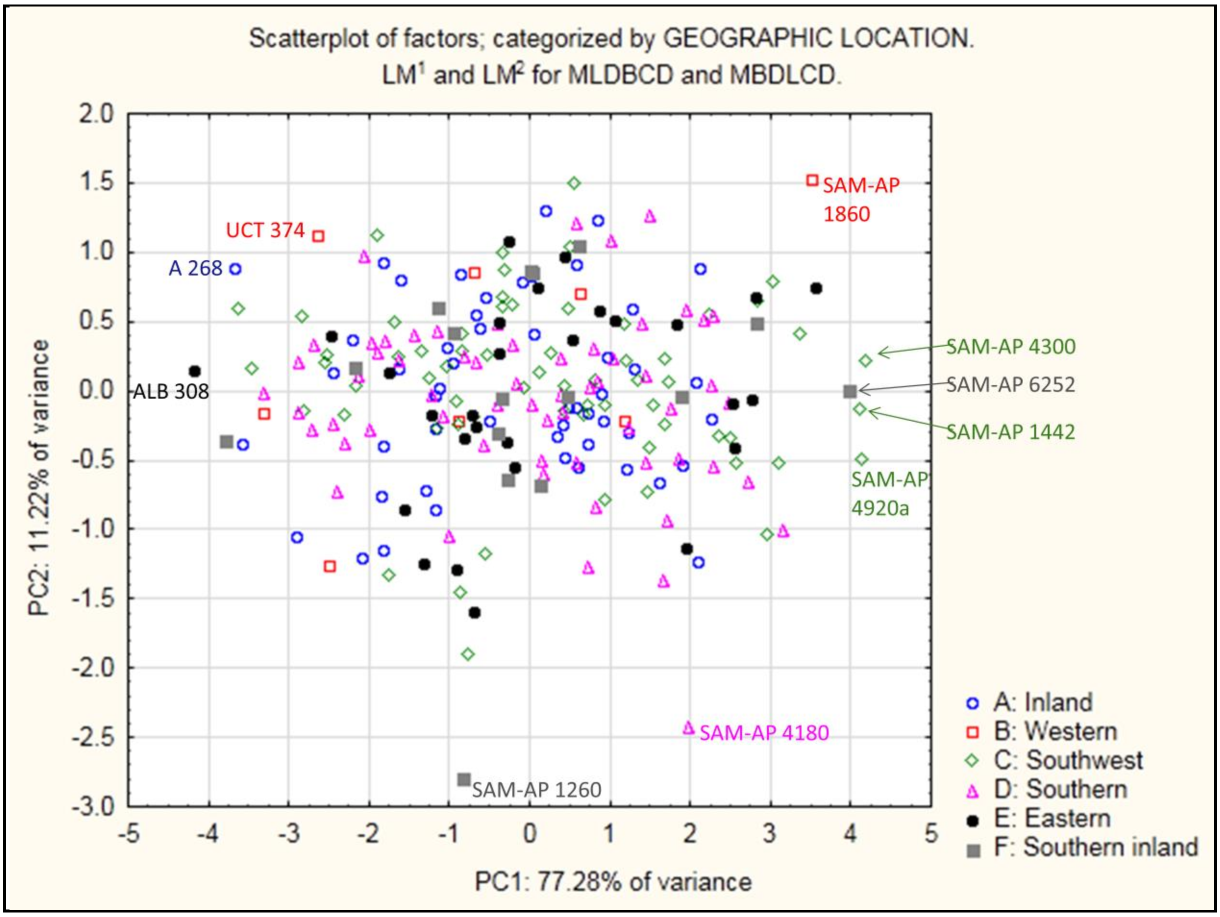


Fig. 5.17: Principal components plot of PC1 versus PC2. PCA based on LM^1 and LM^2 mesiolingual-distobuccal cervical diameters (MLDBCD) and mesiobuccal-distolingual cervical diameters (MBDLCD) from Regions A to F (insufficient data for Region G).

The PCA using alternative diagonal cervical measurements displays results similar to the previous analysis (Fig. 5.15), demonstrating a geographic overlap between samples. Large individuals are identified to the left of the graph (UCT 374, A 268, ALB 308), while small individuals are towards the right (SAM-AP 4300, SAM-AP 6252, SAM-AP 1442 and SAM-AP 4920a). The outlier from Region F (SAM-AP 1260) has an unusually short LM^1/LM^2 MLDBCD and elongated MBDLCD, as reflected in the heavily weighted PC2 component loadings illustrated in Fig. 5.18 (LM^2 MLDBCD (0.643) and LM^1 MBDLCD (0.342)). Here, loadings clearly demonstrate a size measure for PC1, and a shape measure for PC2. Other outliers include specimens from Region D (SAM-AP 4180) and the small individual from the Western Region (SAM-AP 1860).

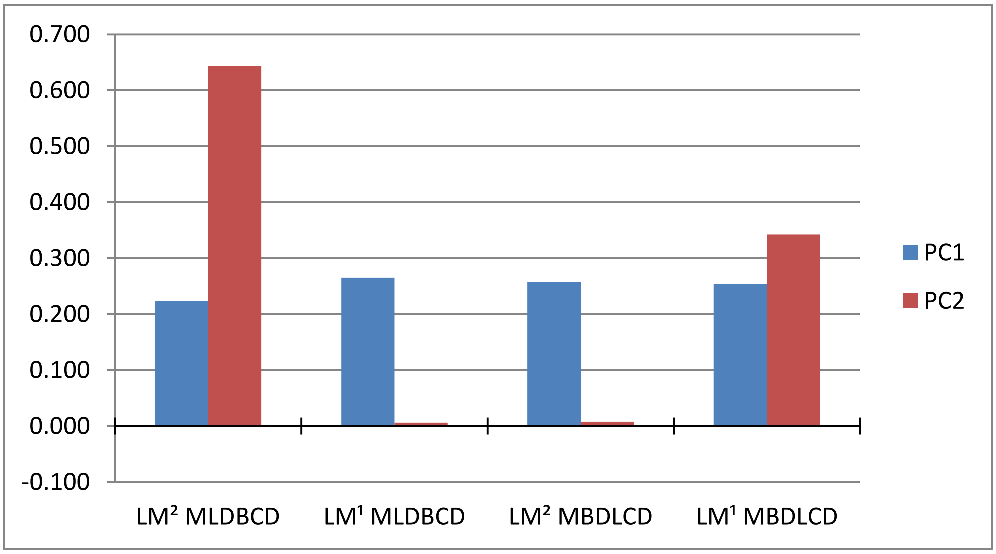


Fig. 5.18: Principal component loadings of PC1 and. PC2 for upper first and second molar diagonal cervical dental measurements associated to Fig. 5.17.

The PCA of upper first and second molar crown measurements (4 variables) from all of the geographic regions is shown in Fig. 5.19.

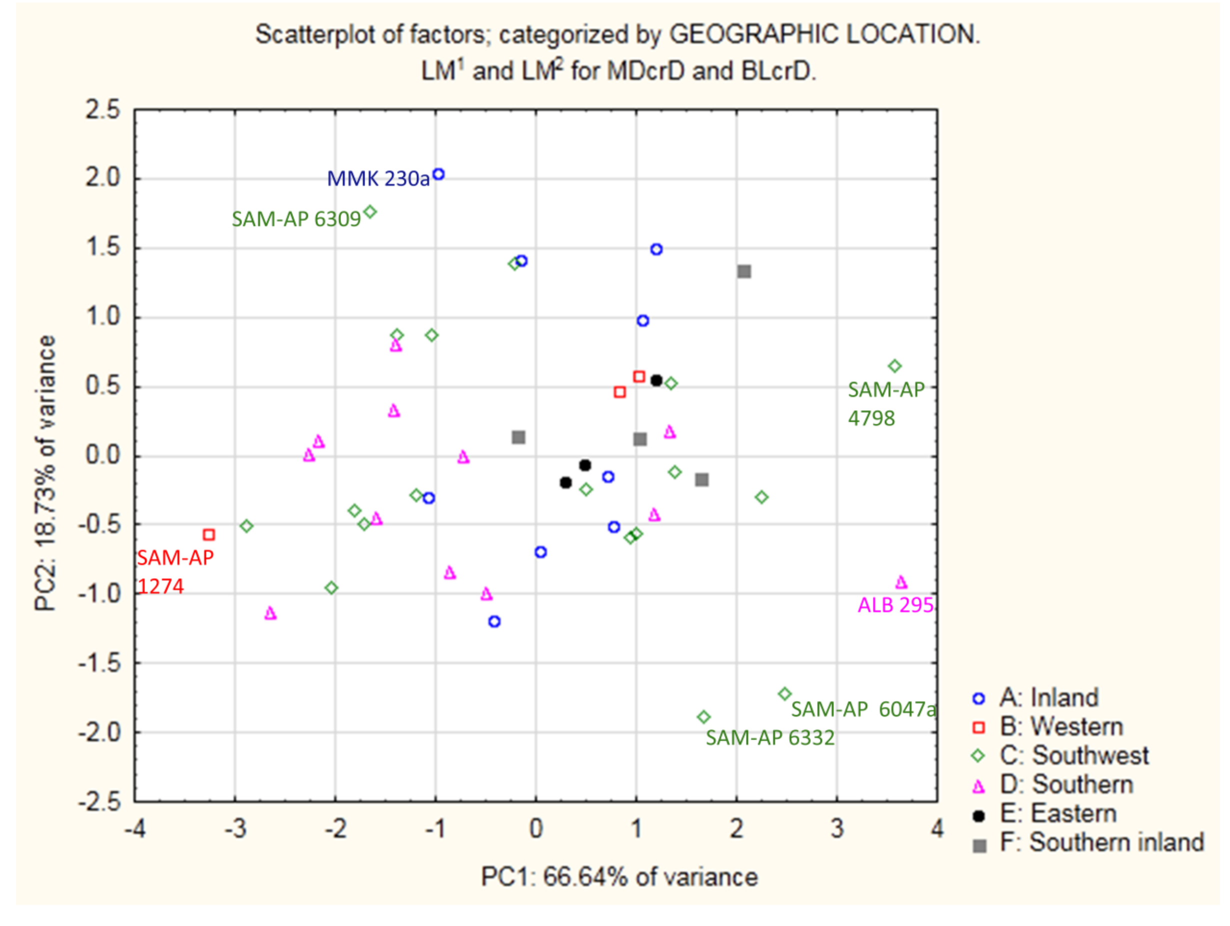


Fig. 5.19: Principal components plot of PC1 versus PC2. PCA is based on LM^1 and LM^2 mesiodistal crown diameters (MDcrD) and buccolingual crown diameters (BLcrD) from Regions A to F (insufficient data for Region G).

Although crown measurements are not as numerous as cervical measurements, the results from this PCA plot correspond with those analyses conducted on cervical diameters. Large specimens are located towards the left of the plot (SAM-AP 1274) and small specimens on the right (SAM-AP 4798, ALB 295). Outliers are predominantly individuals from Regions A, C and D, similar to results seen in the previous lower molar MDCD/BLCD analysis. PC1 loadings are positive and similar in magnitude, suggesting that this is a size variable. For PC2, component loadings are weighted the highest for LM^1 MDcrD (0.387) and lowest for LM^1 BLcrD (0.148), although the difference in the variable weighting is not much more than seen for PC1, suggesting that this is a size/shape variable. As is shown here, although a handful of individuals are at the extreme of size and shape variation, there is no consistent pattern that indicates regional differences in size/shape variation.

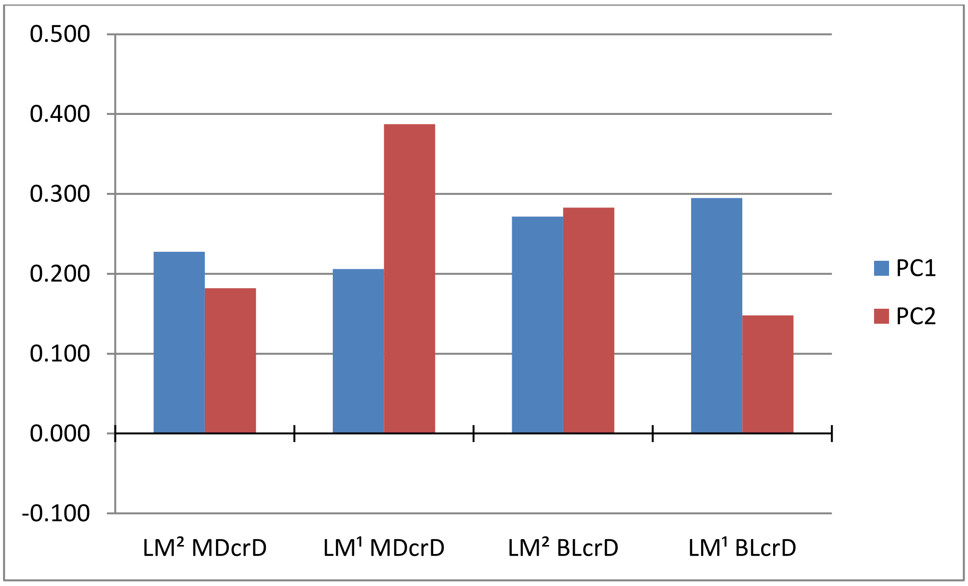


Fig. 5.20: Principal component loadings of PC1 and. PC2 for upper first and second molar crown dental measurements associated to Fig. 5.19.

NON-METRIC EVALUATIONS

Non-metric raw data is available in Appendix 11 (on the CD; includes Mid-Late Pleistocene and Kenya data). Trait frequencies were calculated for each region (A-G) and are presented in Appendix 3. Bar graphs summarising these frequencies across the different regions are shown in Figures 5.21 - 5.25. A summary of inland (Regions A+G) and coastal (Regions B to F) frequencies, as well as dental frequencies for all regions combined, is included for comparison. Chi-square tests, using the Yates correction for sample sizes <5, were used to assess relationships between all regional Khoesan samples for all 52 traits. Summary tables of chi-square results can be found in Appendix 4.1 - 4.9 and chi-square results for regional comparisons within each temporal interval are located in Appendix 12a-12g on the CD. Although trait frequencies for the regions are generally similar, these univariate comparisons identify some significant differences ($p \leq 0.05$, df 1) between samples on a trait-by-trait basis.

Table 5.6 summarises Khoesan regional chi-square results. Chi-square analyses of 47-52 dental traits (depending on available samples) between geographical regions were performed. Only traits demonstrating statistically significant differences are discussed here. Of the incisor traits, I^1 winging and I^1 labial convexity are markedly different between Region A and other areas. I^1 shovelling, a commonly observed trait globally, appears at a very high frequency (100%) in Region B, and is significantly different from frequencies found in Regions A, C, D and E. Some traits, such as I^1 shoveling and I^1 double shoveling in Region B, have very high frequencies (as illustrated in Fig. 5.21) that are significantly different from regions A, C, D, and E. However, this might be due to small sample sizes ($N \leq 5$), and therefore poor frequency estimates, for region B. The I^2 interruption groove frequency in Region E differs from frequencies observed in Regions A, C, D and F, while the I^2 peg-shaped incisor only shows a significant difference between Regions E and A. Additionally, the frequency of I^2 tuberculum dentale in Region E differs from the frequencies observed in Regions C and D; differences between these regions also exist for CMR values. An intermediate CMR frequency (38.9%) is observed in Region A, while much greater rates (>50%) are found everywhere else, highlighting significant differences between this area and others, particularly Regions C, D and E.

As illustrated in Fig. 5.22, trait frequencies of P^3 roots range from 19.64 to 81.82% across the entire sample. Significant differences are evident between Region A and all other regions, as well as between Region E, and Regions C and D. Differences in premolar root number and premolar accessory cusps also exist between Region F and Regions B and D.

Lower molar trait frequencies, shown in Fig. 5.23, are largely similar between regions with only a few exceptions. The M_2 Y-groove demonstrates a significant difference between Regions A and all other regions except Region F, while the Y-groove pattern for M_1 differs between Regions C, D and G. Similarly, X-groove pattern differences on M_1 and M_2 are evident between Regions A, C, D, F and G. M_1 anterior fovea and M_1 cusp 6 differ between Regions A, D and E. Further cusp 6 differences (M_2) exist solely between western and southern coasts (Regions A, B, C and D), while M_1/M_2 cusp 7 differs between Regions A - E and Region F, signifying a notable difference in this southern inland region. It is interesting to observe that lower molar cusp numbers (M_2 cusp # and M_1 cusp 5 presence) are comparable across regions, except between neighbouring Regions E and G (perhaps due to small sample sizes in Region G). As with many other traits, the M_1 deflecting wrinkle differs between Region A, and Regions C and D as well as between Regions C and D, and Region

E. Lastly, M_1 protostylid occurrence differs between Regions C and E, while M_3 torsomolar angles differ between Regions D and E.

Figure 5.24 demonstrates that upper molar trait frequencies (i.e. M^2 root, M^3 metacone, M^2 hypocone and M^2 large hypocone) are generally similar across regions, but as seen with lower molar traits, Regions A and E appear to differ markedly compared to other geographic areas. M^1 enamel extensions, for example, are significantly different between Region A and all other areas, with the exception of Region F, as well as between Regions B, C and D, and Region E. M^2 hypocone differences (M^2 large hypocone and M^2 hypocone presence) occur between Region A, and Regions D and G as well as between Regions C and D, and Region G, while the predominant metaconule differences (M^1 metaconule presence and M^1 large metaconule) occur between Region D, and Regions A, E and G as well as between Region F, and Regions A, B and E. The remaining upper molar traits demonstrating significant differences only occur between Region A and most other regions, particularly Regions C and D. These traits include M^3 peg, M^2 root #, M^3 small metacone, M^1 Carabelli's and M^3 parastyle.

Of the intra-oral osseous trait frequencies (bar graph in Fig. 5.25) palatine tori differ significantly in two Regions, A and F, where trait frequencies are at their lowest (33.3% and 38.6%, respectively). Differences are noticed between both of these regions and coastal Regions B, C and G. The midline diastema occurs at a high frequency (45.56%) in Region A, while Regions E and G have <8% occurrence. Significant differences are evident between these regions as well as between Region A and the southern coasts (Regions C and D). Rocker jaw demonstrates an overall difference in Region A where the trait does not occur. Additional difference is observed between Regions B and C, where frequencies are quite dissimilar (66.6% and 34.1%, respectively).

Based on the total number of significant p-values (≤0.05), Region A demonstrates the largest amount of statistically significant differences among traits relative to all other regions (see Table 5.6 for details). It is the least similar to Regions C and D, where approximately half the p-values are significant. Region A is more similar to Regions B, E and G, and shares the most similarity with Region F, where only 8 traits are significantly different. Region B is statistically indistinguishable from Region G (with no significant trait differences); indeed, differences between Region B and all of the other regions are minimal. Another pattern emerges when evaluating Regions B, C and D. These regions consistently have traits that are significantly different from Region E. Additionally, Regions C and D are more similar to Regions F and G. Interestingly, people in Regions C and D (who are geographically close) appear to be less similar dentally than people in the geographically (and environmentally) distant Regions F and G. Regions E and F appear to be as similar to each other as Regions B, C and D are to each other. Very few significant p-values were identified when comparing Region G to Regions E and F, suggesting morphological homogeneity. Comparisons between inland and coastal groups demonstrate some dissimilarity (9/47 traits analysed were significantly different) but overall, these larger geographic areas are very similar dentally. Sample size could be an issue when assessing frequency traits and their patterns. Sample sizes for Regions B, F and G are smaller than those in other regions. For incisor and canine traits in particular, sample sizes are often <10. Region A, however, has no sample size concerns, and consistent trait frequency differences separate this group from the rest of the studied populations. What is interesting to note is that many of the significant p-values are concerned with mass-additive traits (i.e. traits in which there is an increase in tooth mass).

Fig. 5.21: Regional frequencies of incisor and canine dental traits.

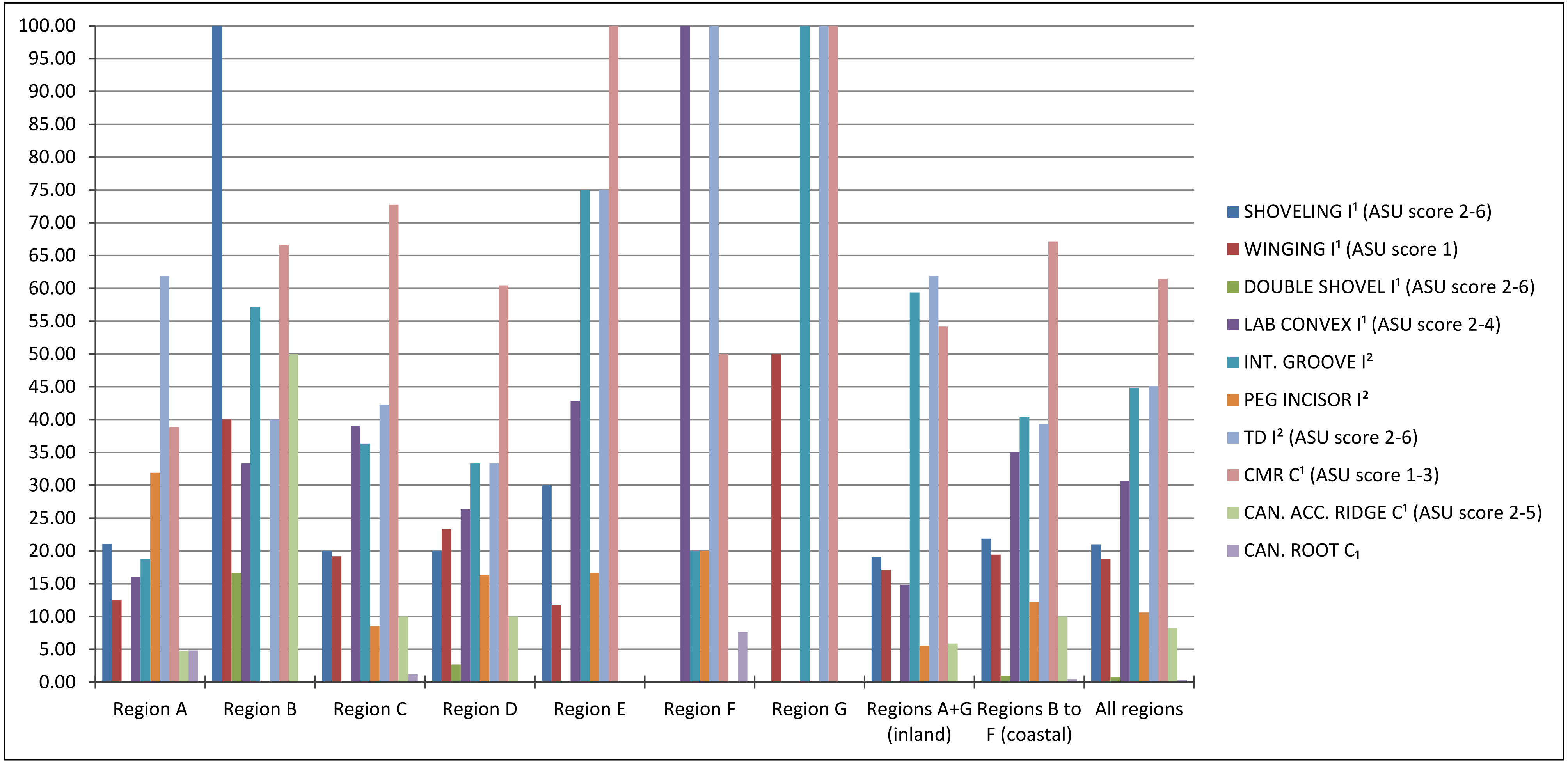


Fig. 5.22: Regional frequencies of premolar dental traits.

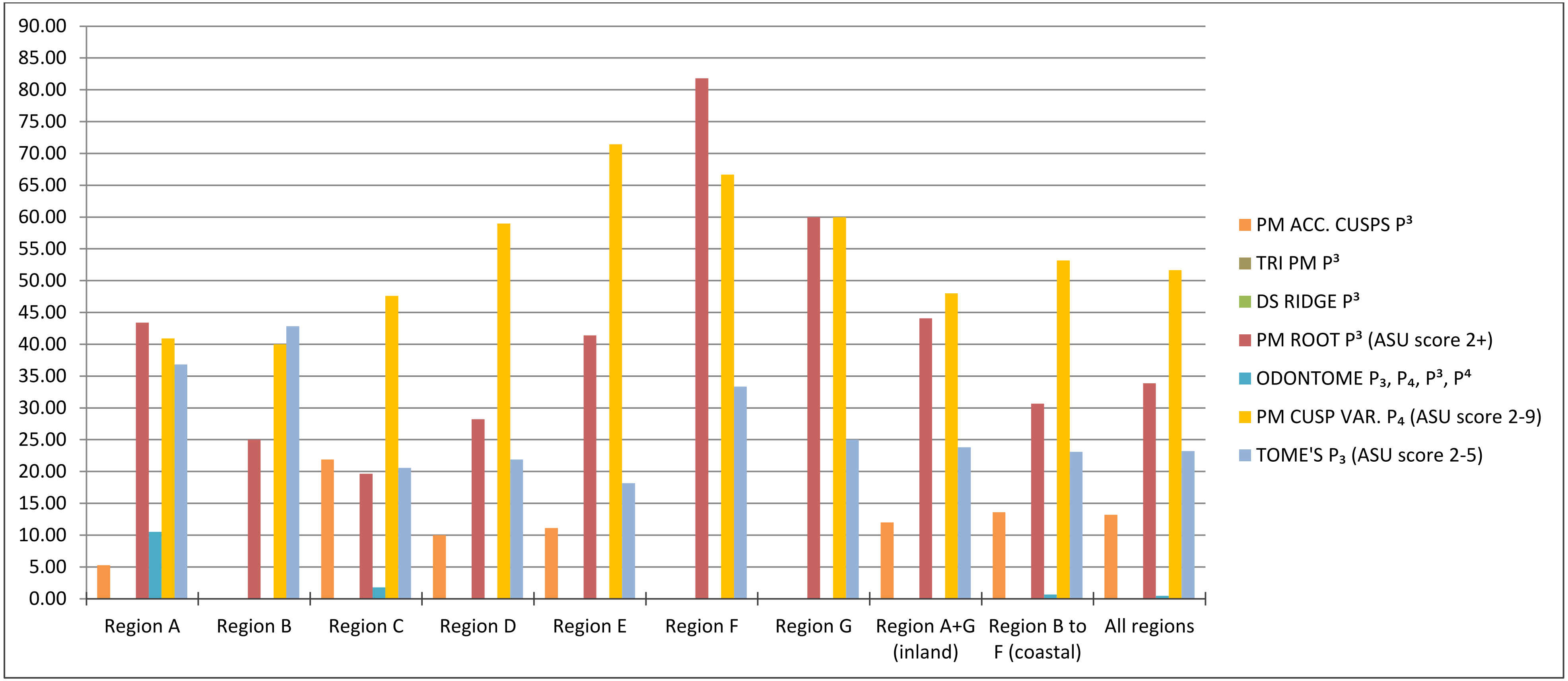


Fig. 5.23: Regional frequencies of lower molar dental traits.

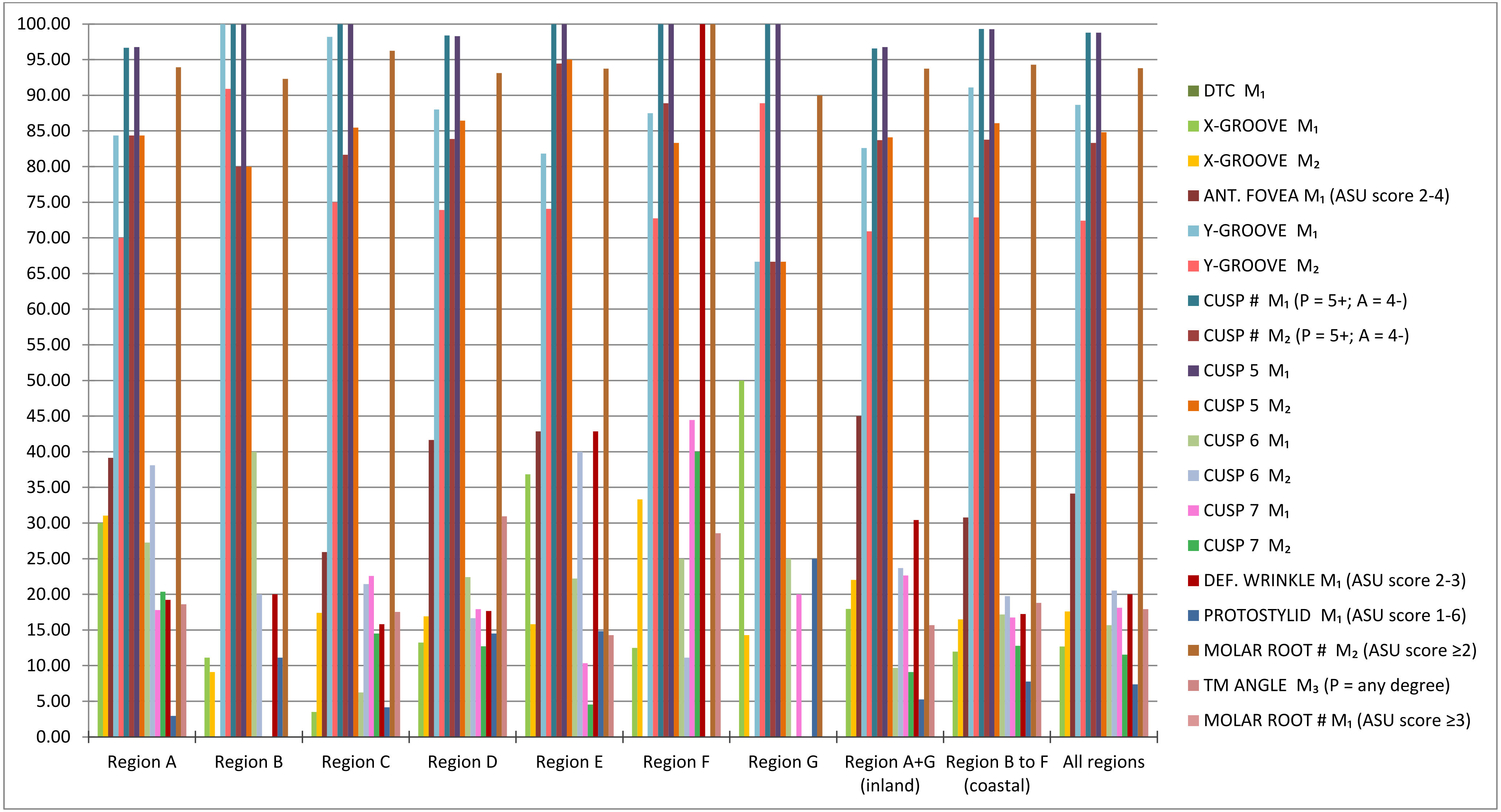


Fig. 5.24: Regional frequencies of upper molar dental traits.

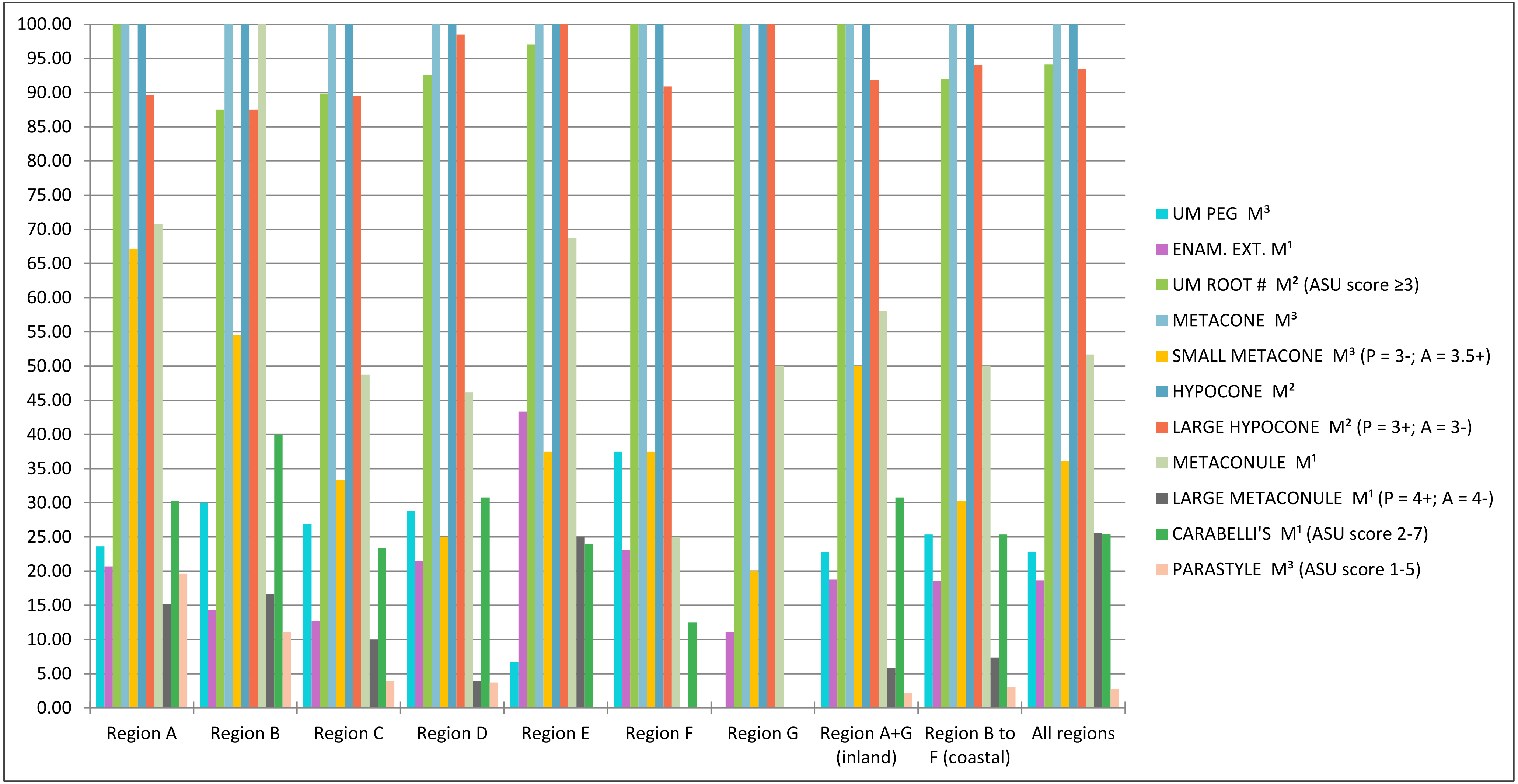


Fig. 5.25: Regional trait frequencies of other features, including intra-oral osseous traits, midline diastema, and M^3 congenital absence.

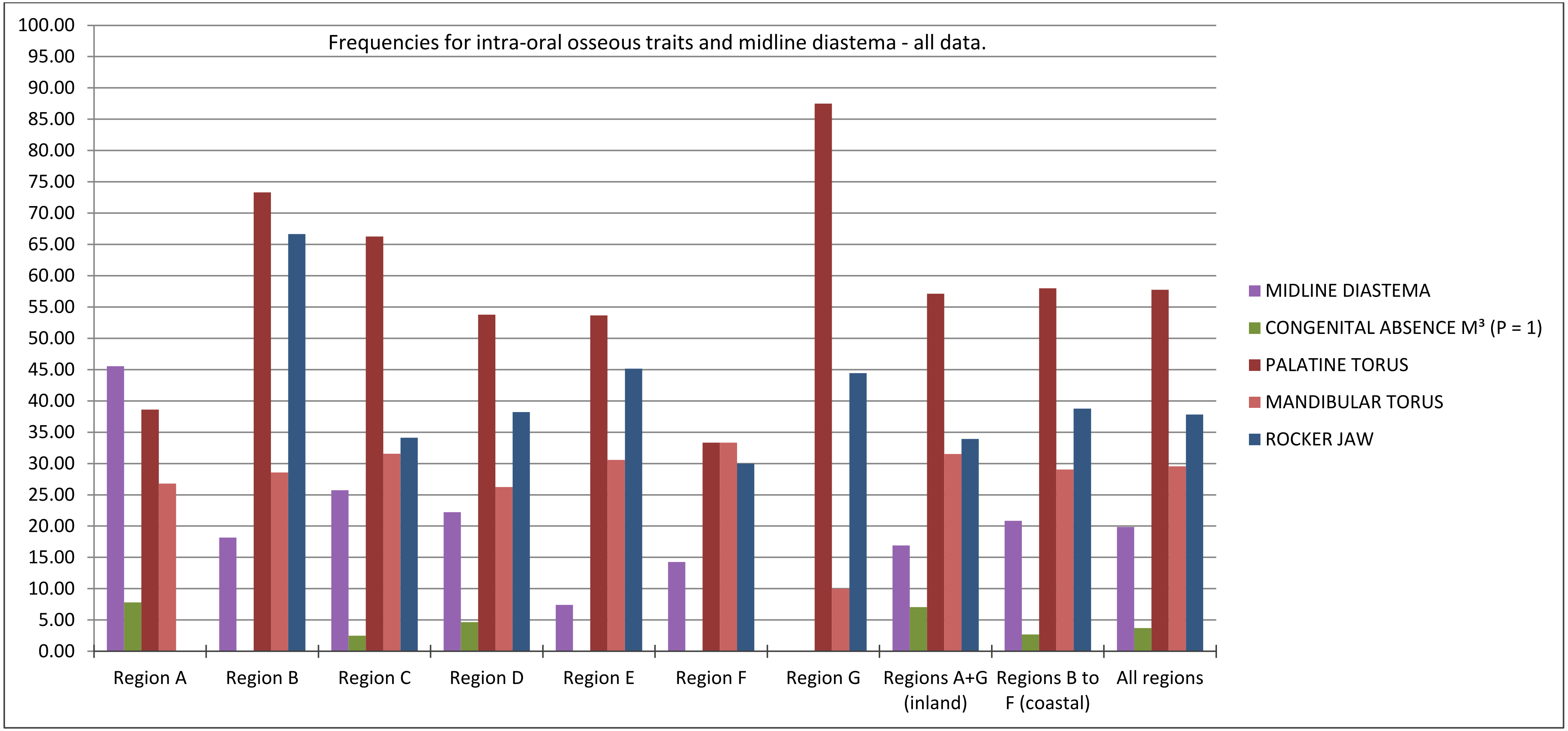


Table 5.6: Summary of traits that are significantly different between regions ($p \leq 0.05$, df 1).

	Region B	Region C	Region D	Region E	Region F	Region G
Region A	Shoveling I^1, Winging I^1, Double shovel I^1, M_2 Y-groove, M^1 enam ext., M^2 root #, M^3 metacone, M^1 Carabelli's, palatine torus, rocker jaw.	Winging I^1, labial convex I^1, Peg incisor I^2, CMR, PM acc cusp P^3, PM root P^3, M_2 Y-groove, M_1 Y-groove, M_2 X-groove, M_1 X-groove, M_1 cusp #, M_2 cusp 6, M_1 Def. wrinkle, M^3 peg, M^1 enam ext., M^2 root #, M^3 small metacone, M^1 metaconule, M^1 Carabelli's, M^3 parastyle, midline diastema, palatine torus, rocker jaw.	Winging I^1, CMR, PM root P^3, M_1 anterior fovea, M_2 Y-groove, M_1 X-groove, M_1 cusp 6, M_2 cusp 6, M_1 Def. wrinkle, M^3 peg, M^1 enam ext., M^2 root #, M^3 small metacone, M^2 large hypocone, M^1 metaconule, M^1 large metaconule, M^1 Carabelli's, M^3 parastyle, midline diastema, rocker jaw.	Labial convex I^1, Int. groove I^2, I^2 peg, TD I^2, CMR, PM root P^3, M_1 anterior fovea, M_2 Y-groove, M_1 X-groove, M_1 cusp 6, M^1 enam ext., M^3 small metacone, M^1 Carabelli's, midline diastema, rocker jaw.	PM root P3, M_2 X-groove, M_1 cusp 7, M_2 cusp 7, M^3 peg, M^3 small metacone, M^1 metaconule, rocker jaw.	Int. groove I^1, PM acc cusp P^3, PM root P^3, M_2 Y-groove, M_1 X-groove, M^1 enam ext., M^2 root #, M^3 small metacone, M^2 hypocone, midline diastema, palatine torus, rocker jaw.
Region B		Shoveling I^1, Double shovel I^1, M_2 cusp 6, rocker jaw.	Shoveling I^1, Double shovel I^1, M_2 cusp 6, M^3 small metacone.	Shoveling I^1, M^1 enam ext., M^2 large hypocone.	PM root P^3, M_1 cusp 7, M_2 cusp 7, M^1 metaconule, palatine torus.	

Region C			M_1 Y-groove, M_1 X-groove, M_2 cusp 6, M_2 cusp 7, M_1 protostylid, M^2 large hypocone	Int. groove I^2, TD I^2, CMR, PM root P^3, M_1 Y-groove, M_1 X-groove, M_1 def. wrinkle, M_1 protostylid, M^1 enam ext., midline diastema.	PM root P^3, M_1 cusp 7, palatine torus.	PM root P^3, M_1 Y-groove, M_1 X-groove, M_1 protostylid, M^2 hypocone.
Region D				Int. groove I^2, TD I^2, CMR, PM root P^3, M_1 Y-groove, M_1 X-groove, M_1 cusp 6, M_1 def. wrinkle, M_3 TM angle, M^1 enam ext., M^1 large metaconule.	Can. Acc. Ridge C^1, Can. Root C_1, PM root P^3, M_1 cusp 7, M_2 cusp 7,	Double shovel I^1, PM acc. Cusps P^3, M_1 Y-groove, M_1 X-groove, M^2 hypocone, M^1 large metaconule.
Region E					Int. groove I^2, PM root P^3, M_1 cusp 7, M_2 cusp 7, M^1 metaconule.	M_2 cusp #, M_1 cusp 5, M^1 enam ext.,
Region F						Palatine torus.
Region G						

The mean measure of divergence statistical procedure (MMD) (Berry and Berry 1967; Green and Suchey 1976; E.F. Harris and Sjøvold 2004; Irish 2010; Sjøvold 1977) was employed here as an estimate of morphological distance between Khoesan regional populations; results are presented in Table 5.7. MMD analyses include the entire Holocene timeframe. Negative values were adjusted to 0.00 as outlined in E.F. Harris and Sjøvold (2004) and Irish (2010).

All regional data sets were analysed using 45 discrete traits. Seven traits were excluded from the analysis for a number of reasons. First, LM_1 deflecting wrinkle was removed because it was significantly correlated with LM_1 anterior fovea ($p = 0.0194$). Traits that evaluate degrees of expression were also significantly correlated and were removed. These include LM_1 and LM_2 X-groove pattern, LM^3 metacone, LM^2 Hypocone and $LM^{1'}$s expression of the large metaconule. Due to high sexual dimorphism previously recorded with regards to congenital absence of LM^3, this trait was also removed.

Using the standardised method established by Sjøvold (1977) to assess significance, if the MMD is greater than two times the standard deviation, samples (or populations) differ from each other at the 0.025 significance level. Red and underlined MMD's in Table 5.7 indicate those samples which differ in this manner. Insignificant MMD's denote samples that are morphologically indistinguishable from each other; in some cases this may be because sample sizes are too small. Small sample sizes are found in Region F where 8 out of the 45 traits included in the MMD had less than 10 observations (i.e. $N < 10$). Percentages based on such sample sizes can be flawed, as they may be poor estimates of population ranges of values, which consequently affect MMD results. Where small sample sizes were unavoidable (like Region F), a correction was applied to minimise errors. These possible issues should be considered when viewing MMD results. Region G was removed entirely from the analysis due to an extremely small sample size.

The mean measure of divergence results support the results of the frequency comparisons by: 1) indicating substantial dental homogeneity within the Holocene

Khoesan sample, while 2) nonetheless highlighting significant phenetic differences between select regions. Only 4 of the 15 MMD values produced are significantly different and all are associated with Region A. These significant values suggest a degree of phenetic distance between Region A and individual Regions B, C, D and E. All other MMD values are insignificant, suggesting that regions B, C, D, E and F are dentally indistinguishable from each other. The mean measure of divergence inter-regional analysis identifies an overall degree of morphological similarity within the Khoesan population for the selected suite of dental and osseous traits.

This section has evaluated hypothesis 1 and has demonstrated that there are some statistically significant geographical differences in trait frequencies between Holocene Khoesan samples. However, the bulk of the differences served to distinguish Region A from everything else. No clear metric differences were found among the regions. Importantly, geographic comparisons did not factor in the element of time, which may alter dental results thus far, and is addressed below.

Table 5.7: Mean measure of divergence values between Khoesan regional data. Red and underlined values indicate those samples which differ from each other at the 0.025 significance level.

MMD						
	Region A	**Region B**	**Region C**	**Region D**	**Region E**	**Region F**
Region A		0.1449	0.0940	0.0819	0.1243	0.0000
Region B			0.0594	0.0697	0.0581	0.0660
Region C				0.0000	0.0372	0.0000
Region D					0.0237	0.0000
Region E						0.0000
Region F						

THE CONTINUITY OF KHOESAN DENTITION THROUGH TIME: EVALUATION OF HYPOTHESIS 2.

This section evaluates hypothesis 2 by assessing whether dental metric or non-metric temporal differences exist between Khoesan samples within the Holocene (i.e. whether dental variation remains constant through time). The Holocene has been separated into temporal sub-groups as follows:

A. Samples dated to 8000+ BP
B. Samples dated to between 8000-6000 BP (8-6ka)
C. Samples dated to between 6000-4000 BP (6-4ka)
D. Samples dated to between 4000-3000 BP (4-3ka)
E. Samples dated to between 3000-2000 BP (3-2ka)
F. Samples dated to between 2000-1000 BP (2-1ka)
G. Samples dated to the first millennium BP (1-0ka).

METRIC EVALUATIONS

To explore temporal metric variation within the population, MANOVAs and principal components analyses (PCA) were performed on crown and cervical measurements of maxillary and mandibular teeth from all temporal subdivisions. To perform MANOVAs, missing data were adjusted (inclusive of all temporal measurements, 64% of the data had to be modified). Significant differences were not detected between timeframes (MANOVA; Wilks' Lambda; p=0.059). Due to a close significance p-value, T-tests were conducted to evaluate differences between individual timeframes. T-tests only demonstrate differences between the 3-2 ka timeframe and all other time periods (42.8% of 175 variables; 75/175). After the application of the Bonferroni Correction (p-value is reduced to 0.00029), 4/175 (2%) differ significantly. There are fewer dated specimens and this, coupled with dental wear and/or poor preservation, led to a sizeable amount of missing data and therefore limited the number of variables analysed for any one PCA. Fifteen PCAs were performed and variables and percentage of variance values for each factor (PC1 and PC2) can be found in Table 5.8 below.

Table 5.8: List of variables and percentage of variance values for the first two principle components in temporal PCAs.

Variables		**% of variance**	
Teeth	**Measurements taken on each tooth**	**PC1**	**PC2**
LI^1, LI^2, LC^1	MDCD / BLCD	53.02	14.34
LP_3, LP_4	MDCD / BLCD	69.78	19.4
LP^3, LP^4	MDCD / BLCD	63.02	21.52
LM_1, LM_2	MDCD / BLCD	70.92	14.89
LM^1, LM^2	MDCD / BLCD	70.93	14.79
LM_1, LM_2, LM^1, LM^2	MDCD / BLCD	67.66	8.14
LI^1, LI^2, LC^1	MDcrD / BLcrD	49.43	26.55
LP_3, LP_4	MDcrD / BLcrD	81.24	10.18
LP^3, LP^4	MDcrD / BLcrD	59.99	23.86
LM_1, LM_2	MDcrD / BLcrD	70.98	18.4
LM^1, LM^2	MDcrD / BLcrD	67.96	16.33
LM_1, LM_2	MLDBCD / MBDLCD	87.27	6.59
LM^1, LM^2	MLDBCD / MBDLCD	77.93	10.74
LM_1, LM_2	MLDBcrD / MBDLcrD	80.46	10.92
LM^1, LM^2	MLDBcrD / MBDLcrD	68.18	16.21

Results were consistent between dental evaluations, so only 4 PCA plots are illustrated here, three on molar measurements and one upper premolar analysis. Fig. 5.26 is a PCA plot of PC1 versus PC2, based on analyses conducted on LM_1, LM_2, LM^1 and LM^2 cervical measurements (8 variables). Small individuals, such as one of the specimens from Blouberg Strand, near Cape Town (SAM-AP 4920a dated to 1364 ± 32 BP (OxA-V-2059-17)), appear at the extreme right, while large specimens, such as the Elands Bay individual (UCT 374, 9750 ± 100 BP (Pta-3086)) appear on the left edge. Although individuals from the 8000+ BP group (marked in blue circles on the plot), and 8-6 ka BP individuals (marked in red squares on the plot) show a fair degree of size variation (Axis 1) and limited shape variation (Axis 2), this might be an artefact of small sample sizes. A further possible increase in variation is arguably demonstrated at the 6-4 ka boundary (marked in green diamonds on the plot), where outliers (ALB 200, 5105 ± 20 (Pta-8638); ALB 129, ± 4700 by association) identify noticeable shape deviation *ca*. 5000 BP. Thereafter, variation increases substantially (as does sample size) and remains considerable over the next 3000 years, presumably coinciding with a population increase. Importantly, the groups continue to overlap; only the amount of variation increases, demonstrated by the widespread dispersal of specimen plots (pink, black, grey and olive). Increased variation is most notable during 3-2 ka and 2-1 ka time periods. Outlying specimens (SAM-AP 4920a, 1364 ± 32 BP (OxA-V-2059-17) and SAM-AP 6147, 2920 ± 60 BP (Pta-9085)) and those appearing on the edge of the range of variation are predominantly associated to these timeframes (black circles and grey squares). Interestingly, variation across most of the sample appears to somewhat decrease to earlier levels during the first millennium BP (marked by dark red filled diamonds), though this might be an artifact of sample size. It is during this time that herder populations can be evaluated. Although known herder specimens are scarce, these are identified here (marked as H on the plot), and their positions on the plot indicate that two individuals, one from Oakhurst Rock Shelter (UCT 262 dated to 510 ± 40 BP (GrA-23221)) and the other from Mossel Bay (UCT 582, 740 ± 40 BP (Pta-7178)) are at the edges of the range of variation (and in opposite directions) relative to other first millennium BP individuals. The Knysna (NMB 1338, 650 ± 35 BP (GrA-23711)) specimen fell firmly at the middle of the range of variation for all other Khoesan specimens. Component loadings are illustrated in Fig. 5.27. All loadings are positive and comparable in magnitude, with LM_2 BLCD PC2 weighted the highest (0.193) and LM_2 MDCD, the lowest (0.089). Here, lower second molars have the greatest amount of shape variation, while size variation remains relatively constant across all samples.

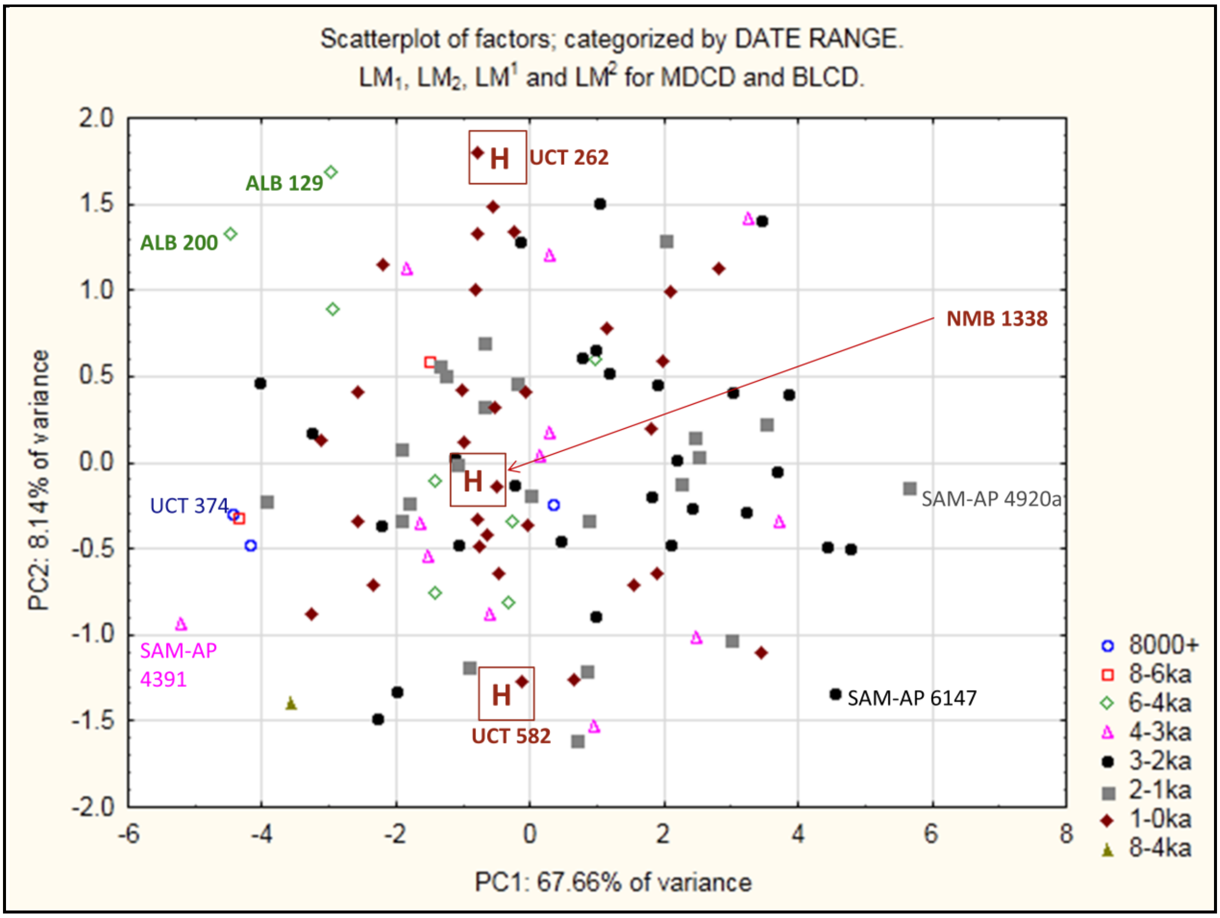


Fig. 5.26: Principal components plot of PC1 versus PC2. PCA is based on LM_1, LM_2 LM^1 and LM^2 mesiodistal cervical diameters (MDCD) and buccolingual cervical diameters (BLCD) from all timeframes.

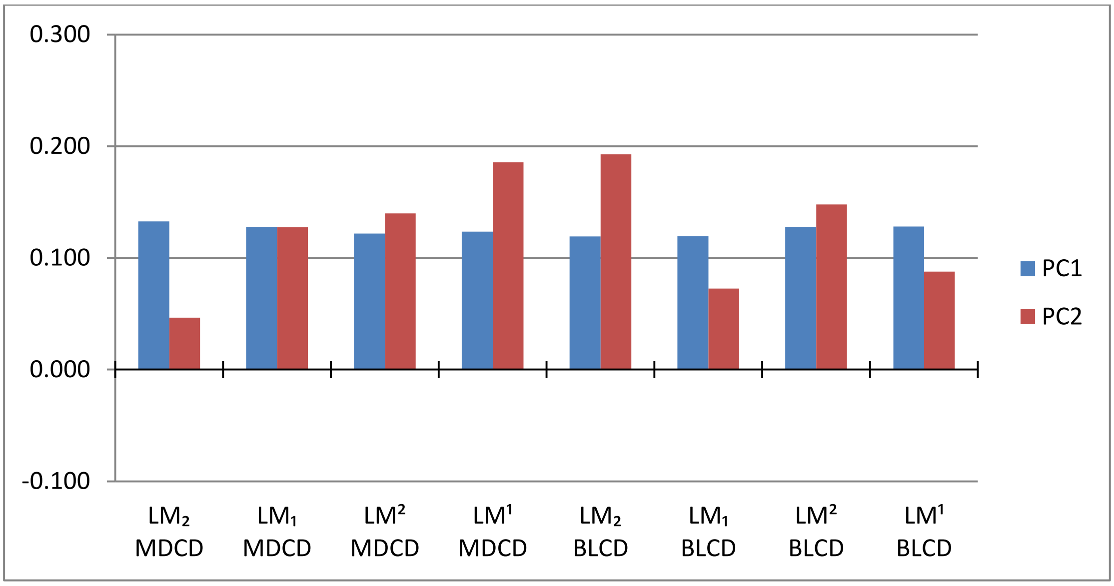


Fig. 5.27: Principal component loadings of PC1 and PC2 for upper first and second molar cervical dental measurements associated to Fig. 5.26.

A second temporal PCA plot, this time using LM^1 and LM^2 and alternative dental measurements (diagonal cervical diameters) (4 variables), is depicted in Fig. 5.28. A similar pattern of variation is demonstrated with the large individuals such as the Elands Bay specimen (UCT 374 dated to 9750 ± 100 BP (Pta-3086)) towards the left, and smaller individuals such as SAM-AP 4813 (2140 ± 45 BP (Pta-4202)) from Darling in the southwestern Cape on the right, suggesting that PC1 is a size variable, but no clear temporal trend is evident. Although limited variation is seen in the 8000+ BP, 8-6 ka and 6-4 ka temporal groups, sample plots are largely within the range of variation observed throughout the Holocene. Slight increased variation over the next 3000 years is demonstrated by outliers (SAM-AP 4813, 2140 ± 45 BP (Pta-4202); SAM-AP 1260, 1137 ± 27 BP (OxA-V-2066-28) and SAM-AP 4180, 688 ± 27 BP (OxA-V-2056-23)). Variation during the first millennium BP does not decrease as expected, but rather remains constant (including an outlier, specimen SAM-AP 1260 from Oudtshoorn dated to 1137 ± 27 BP (OxA-V-2066-28), with notable shape variation) in comparison to earlier time periods. Also, herders are not widely dispersed as previously observed. PC1 component loadings (Fig. 5.29) are relatively equal in magnitude (0.224 – 0.259) but vary substantially for PC2 where LM^2 MLDBCD is weighted the highest (0.650) and LM^2 MBDLCD the lowest (0.054).

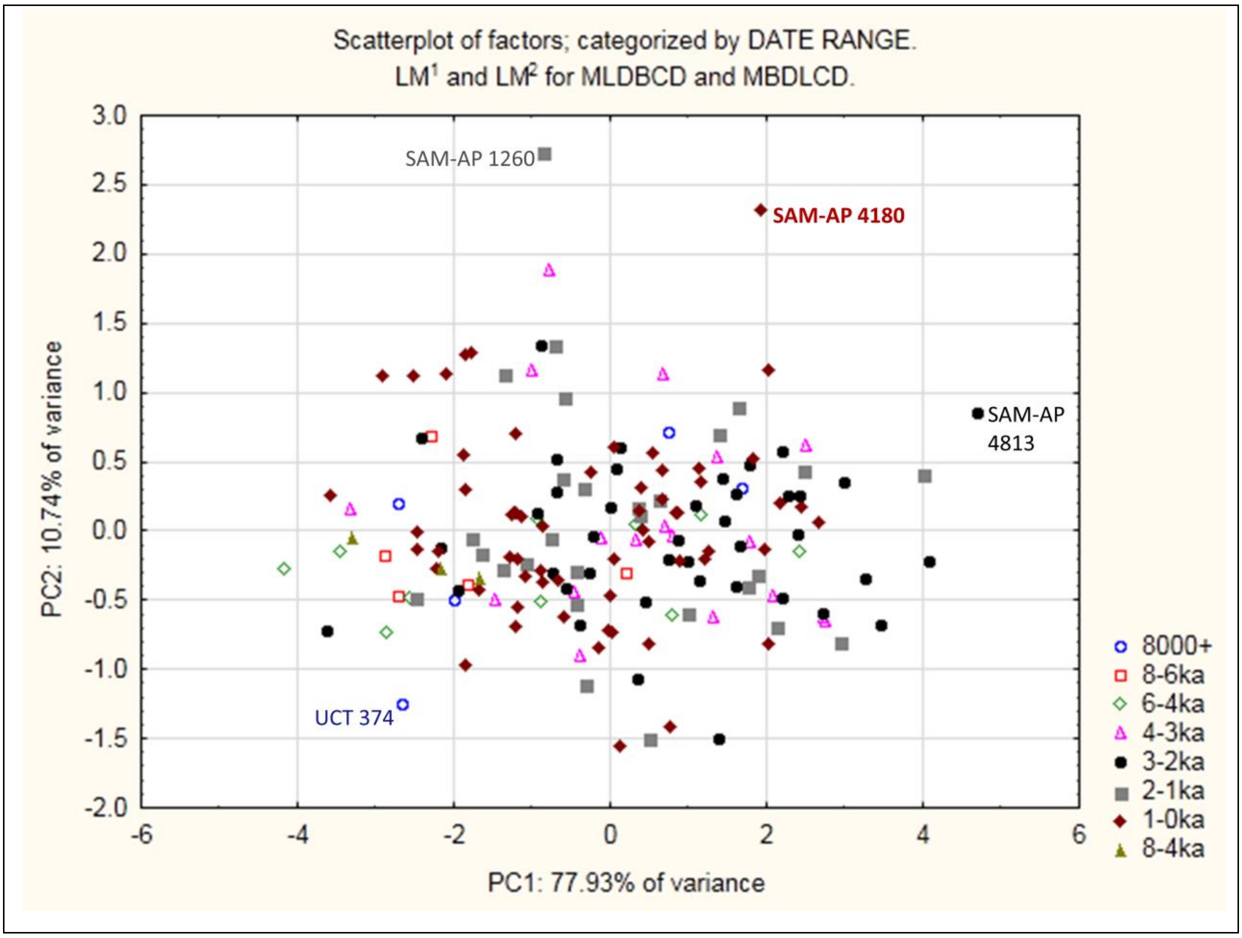


Fig. 5.28: Principal components plot of PC1 versus PC2. PCA is based on LM^1 and LM^2 mesiolingual-distobuccal (MLDBCD) and mesiobuccal-distolingual cervical diameters (MBDLCD) from all timeframes.

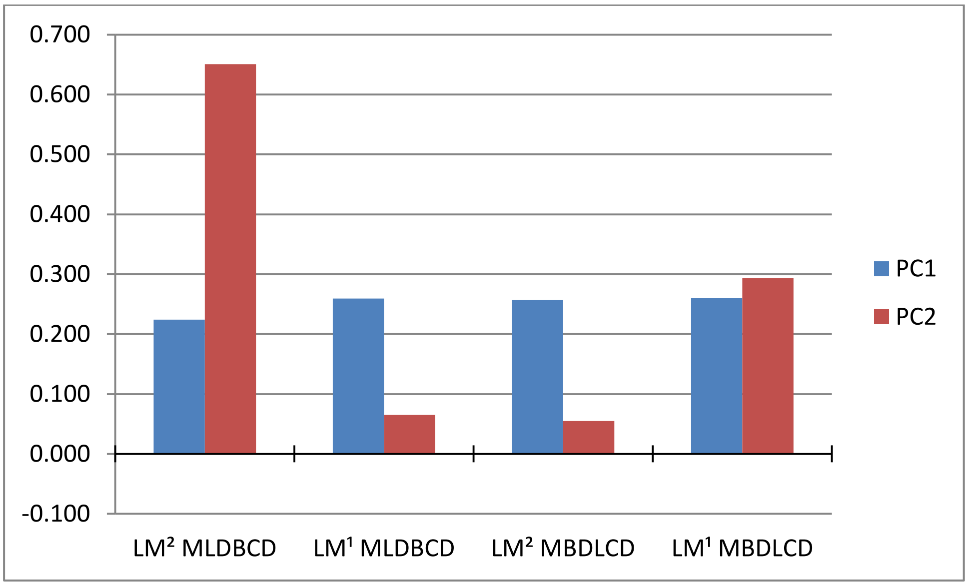


Fig. 5.29: Principal component loadings of PC1 and PC2 for upper first and second molar diagonal cervical dental measurements associated to Fig. 5.28.

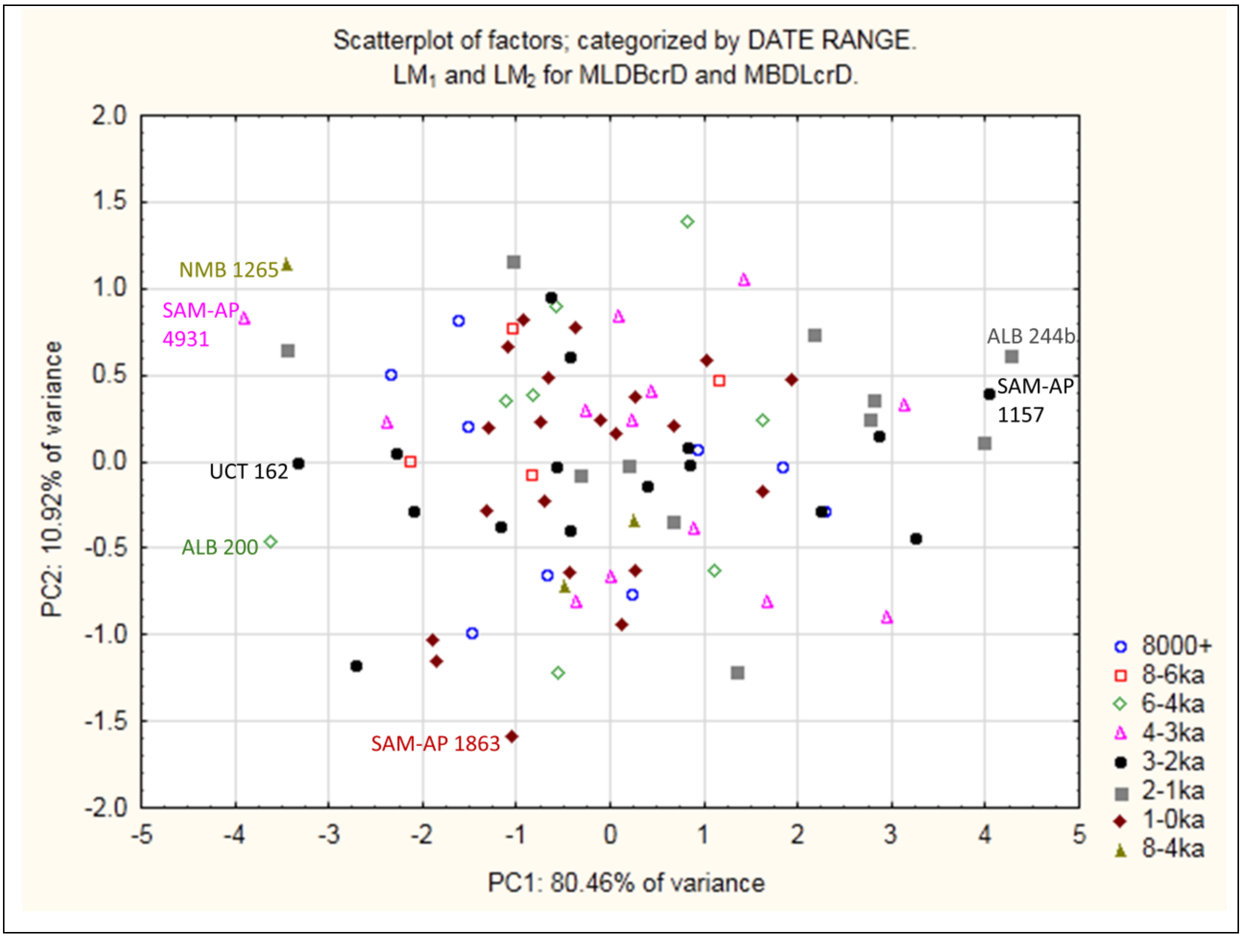


Fig. 5.30: Principal components plot of PC1 versus PC2. PCA is based on LM_1 and LM_2 mesiolingual-distobuccal (MLDBcrD) and mesiobuccal-distolingual cervical diameters (MBDLcrD) from all timeframes.

The PCA plot based on the analysis of lower first and second molar diagonal crown measurements (4 variables) from all of the temporal subdivisions is shown in Fig 5.30, illustrating a similar pattern of variation to the other plots presented above. Large specimens such as those from Matjes River Rock Shelter (NMB 1265, 8000 – 4000 BP (Layer C)) and Yzerfontein (UCT 162, 2880 ± 50 BP (Pta-929)) appear on the left of the plot, while small specimens (i.e. ALB 344, 1957 ± 26 BP (OxA-15077)) are on the right, suggesting that PC1 is related to size. Size and shape variation is limited during the Early Holocene, possibly due to small sample sizes, while increased variation is noted during the 6-4 ka time period. Even further increases are shown during the Mid-Late Holocene and are demonstrated by the number of specimens appearing on the outskirts of the range of variation associated to the 4-3 ka (SAM-AP 4931, 3750 ± 60 BP (Pta-2267)), 3-2 ka groups (UCT 162, 2880 ± 50

BP (Pta-929) and SAM-AP 1157, 2420 ± 60 BP (Pta-4217)) and 2-1 ka (ALB 244b, 1450 ± 50 BP (Pta-9228)) periods. A slight decrease in size variation during the last 1000 years is also observed but largely overlaps with previous timeframes, while one specimen at the edge of variation demonstrates some difference in shape (SAM-AP 1863, 800 ± 50 BP (Pta-4708)). Once again, second molar component loadings for PC2 demonstrate the highest (0.432) and lowest (0.102) magnitude for LM_2 MBDLcrD and LM_2 MLDBcrD, respectively, while PC1 presents with equal magnitude across all samples (see Fig. 5.31).

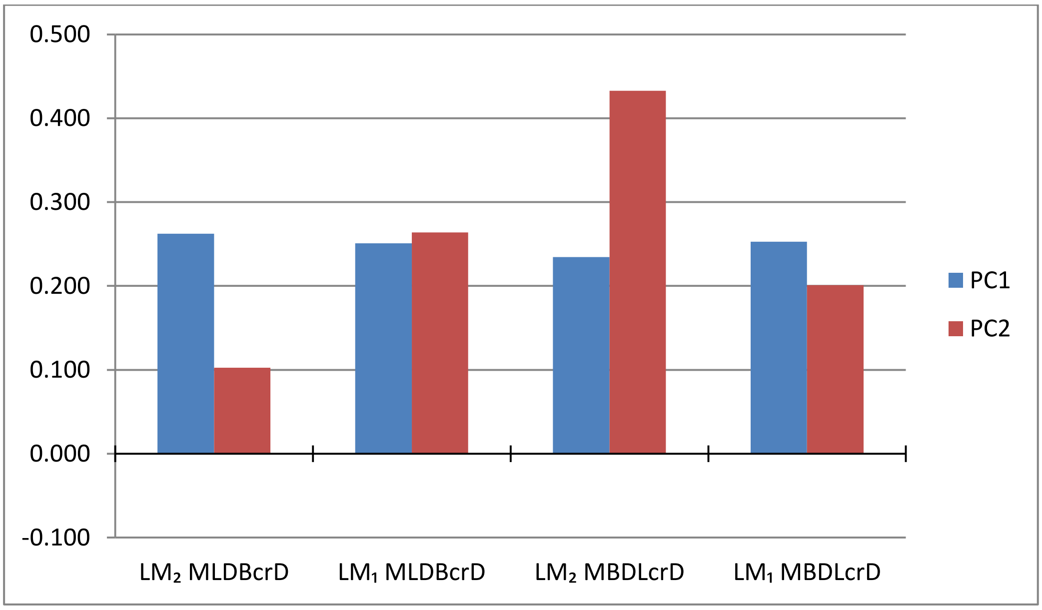


Fig. 5.31 Principal component loadings of PC1 and PC2 for lower first and second molar diagonal crown dental measurements associated to Fig. 5.30.

The PCA of lower premolar cervical measurements (4 variables) from all of the temporal subdivisions is shown in Fig 5.32. There is no clear temporal trend demonstrating no time-specific variation increase. Larger premolars such as ALB 308 from Welgeluk Shelter (5140 BP (TO-10240)) and MMK 312 from Voëlfontein (± 500 by association) appear on the left and small specimens such as an individual from Darling (SAM-AP 4813, 2140 ± 45 BP (Pta-4202)) on the right. Component loadings are illustrated in Fig. 5.33 and demonstrate relatively equivalent PC1 loadings but comparatively high (0.551) LP^4 MDCD and low (0.103) LP^3 MDCD loadings for PC2.

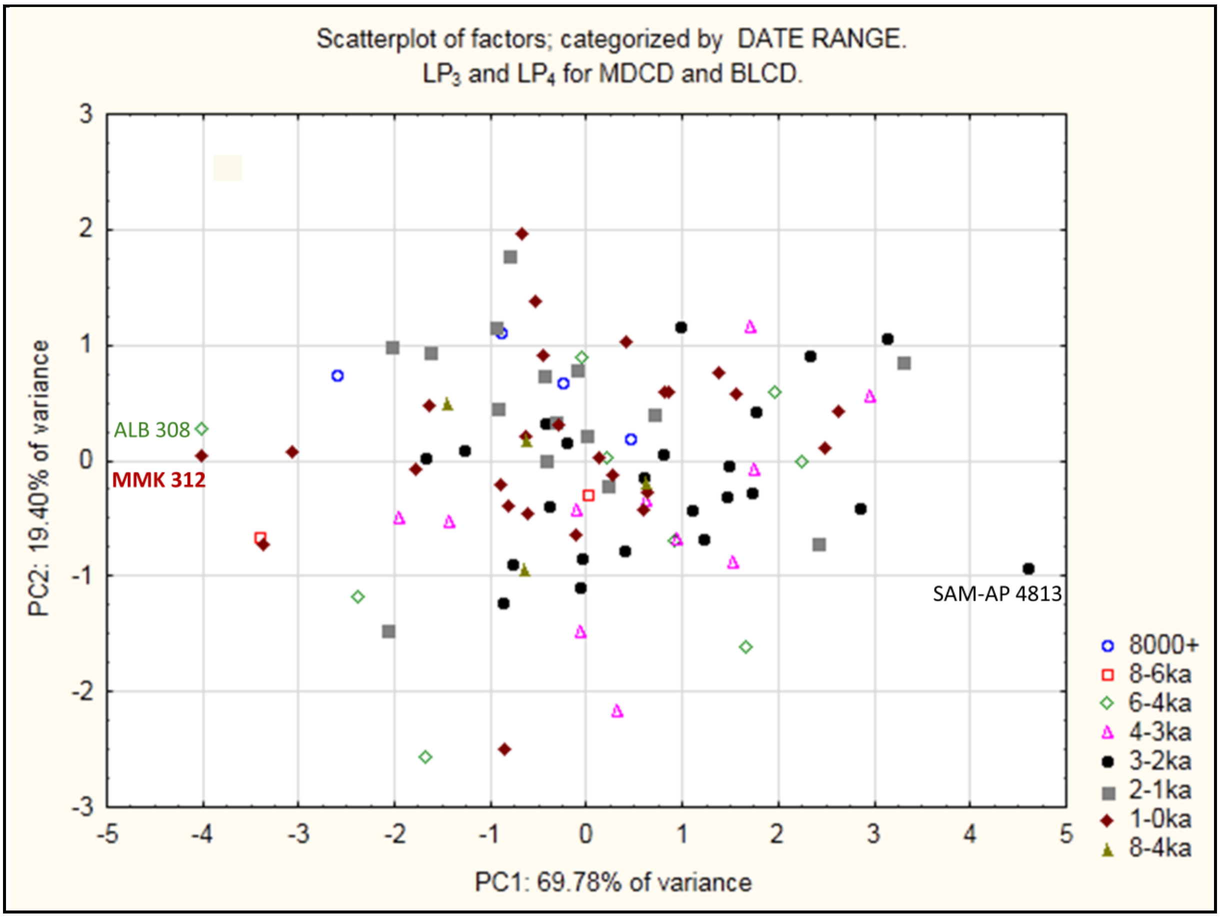


Fig. 5.32: Principal components plot of PC1 versus PC2. The PCA is based on LP_3 and LP_4 mesiodistal (MDCD) and buccolingual (BLCD) cervical diameters (MBDLcrD) through time.

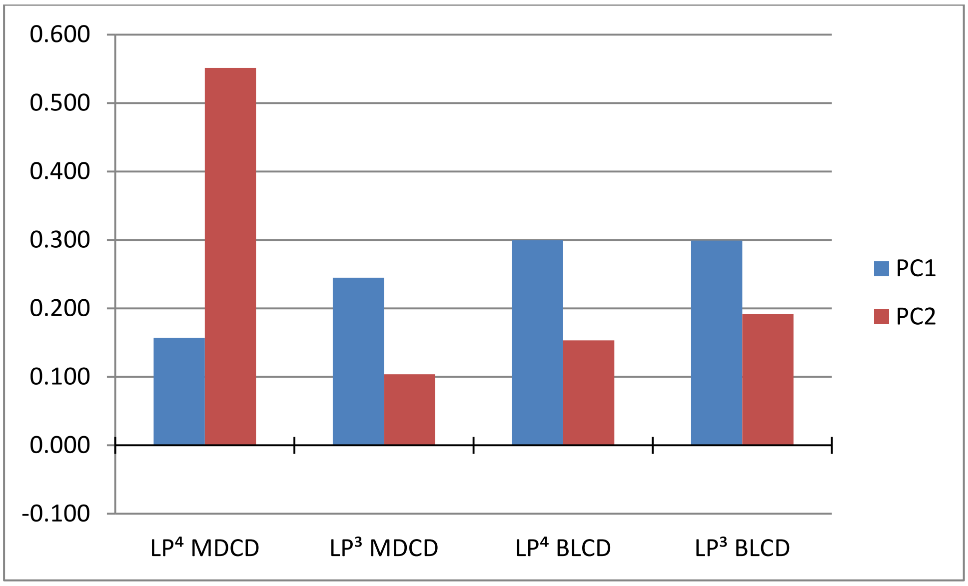


Fig. 5.33: Principal component loadings of PC1 and PC2 for upper first and second premolar cervical dental measurements associated to Fig. 5.32.

Although size and shape variation through time is demonstrated, temporal variations appear to be minor and largely a reflection of increased or decreased intra-population variation rather than shifts in size/shape over time. Some of these effects may be artefacts of sample size (i.e. increasing variation due to increasing sample sizes).

NON-METRIC EVALUATIONS

Trait frequencies were calculated for each temporal subgroup (8000+; 8-6 ka; 6-4 ka; 4-3 ka; 3-2 ka; 2-1 ka and 1-0 ka) and are presented in Appendix 5. Bar graphs summarising these frequencies across the different timeframes are shown in Figures 5.34 – 5.38. A summary of frequencies from all time periods combined is included for comparison. Additionally, trait frequencies were calculated on a region by region basis through time, outlining the trait presence of each region within each time interval and, where possible, traits are linked to specific regions. This frequency data can be found in Appendix 13 (CD). Overall, a visual assessment of these bar graphs suggests that the temporal subgroups are similar in terms of the presence of traits and their frequencies; this was tested using Chi-square tests. Table 5.9 summarises Khoesan temporal chi-square results. Chi-square analyses were performed to assess relationships between temporal subdivisions for 46-52 traits (depending on available samples). These summary tables can be found in Appendices 6.1 – 6.7.

Although trait frequencies appear to be somewhat variable between regions, only those demonstrating statistical significance are discussed. Incisor and canine trait frequencies (Fig. 5.34) only begin to demonstrate between-region significant differences from 3000 – 2000 BP and even then, differences are few. The earliest timeframes (8000+ and 8-6 ka) differ for only two traits when compared to the 3-2 ka period: the I^2 peg and the CMR. These differences remain relatively stable well into the Late Holocene (post-2000 BP). It is interesting to note that the CMR has a lower frequency at 8000+ than at any other timeframe. It also only emerges in Region D during this time with a frequency (57.1%) slightly lower than the average seen throughout the samples (61.5%). The trait's occurrence increases substantially at 8-6 ka and remains above 77% until a slight decline with the onset of the first millennium BP. Incisor trait differences between the Mid-Holocene (6-4 ka) and 3-2 ka include only I^2 interruption groove and I^2 tuberculum dentale, while I^1 shoveling, I^1 labial convexity and the CMR are also different post-2000 BP when compared to the Mid-Holocene. Incisor trait dissimilarities between 4-3 ka and 3-2 ka increase compared to earlier timeframes to include I^1 winging in conjunction with those mentioned above. Interestingly, many of these trait differences are no longer significant later (i.e. I^2 peg and I^2 tuberculum dentale) possibly indicating a small dental shift during the first and second millennium BP. Incisor and canine differences between 3-2 ka and 2-1 ka groups include I^1 shoveling, I^2 peg, I^2 tuberculum dentale and the CMR, while differences in the first and second millennium BP are fewer and include only I^1 interruption groove and the CMR. Incisor and canine trait frequencies found in the 3-2 ka and 2-1 ka groups are the most different from the others.

There are few significant premolar trait differences through time (frequencies illustrated in Fig. 5.35). Only the P_3 Tome's root demonstrates a difference at 3000 BP when compared to Early Holocene time periods. When compared to Early and Mid-Holocene time periods, P^3 root dissimilarity is only evident from 2000 BP and remains constant well into the first millennium BP. No other notable premolar changes are observed.

Although there are numerous lower molar traits, few demonstrate a large amount of frequency fluctuation (Fig. 5.36). The traits displaying consistently high frequencies (with no significant differences through time) include the M_1 cusp number, M_2 cusp 5, and M_2 root number. Unlike incisors, canines and premolars, few molar trait differences are observed during the Early – Mid Holocene, while a sizeable amount of difference exists between terminal Pleistocene/Early Holocene and Late Holocene samples. The 8000 BP and 3000 BP groups are most similar to each other. Lower molar traits such as M_2 cusp #, M2 X-groove, M_2 cusp 6 and M_1 cusp 5 differ significantly between 8000+ BP and other time periods (8-6 ka, 6-4 ka and 4-3 ka). M_2 X-groove has its highest frequency in the Early Holocene and only occurs in Region D at 8000+ BP. As illustrated with incisor and canine traits, marked differences only begin to emerge at 3-2 ka. Similarly, an increase in lower molar trait differences also appears during this time, including traits such as M_2/M_1 Y-groove, M_2 root # and M_2 cusp numbers when compared to Early - Mid Holocene frequencies. Between 4-3 ka and 3-2 ka dissimilarities between M_2 Y-groove, M_2 cusp 7 and M_1 cusp 6 appear, while other differences from earlier comparisons no longer feature. Interestingly, cusps 6 and 7 in the Early to Mid- Holocene appear to be associated with Regions C and D more so than other time intervals. Analyses between the first and second millennium and 4-3 ka, 6-4 ka, 8-6 ka and 8000+ BP trait frequencies demonstrate comparable and significant differences solely related to lower second molars, including M_2 Y- and X-groove, M_2 root #, M_2 cusp # and M_2 cusp 6. Differences are particularly pronounced between the 4-3 ka and 2-1 ka time periods. When assessing Late Holocene frequencies, a different pattern emerges. No differences between 3-2 ka and 2-1 ka are observed but some significant differences exist between the 3-2 ka and 1-0 ka temporal groups (more so than any other analysis). For the first time M_1 anterior fovea demonstrates a significant difference, as do other traits such as M_2 Y-groove, M_1 Y- and X-groove and M_2 root #, similar to what was seen in previous comparisons. Analyses between the first and second millennium demonstrate only two significantly different traits, the related M_2 Y- and X-grooves.

Upper molar trait frequencies (Fig. 5.37) are more uniform, and like lower molars, a number of traits present with similarly high frequencies. For example, the M^3 metacone, M^2 hypocone and the M^2 large hypocone (ASU score of 3+) all express with very high frequencies >83%. Upper molars differ less between time periods than lower molars do. Few significant differences are observed in the upper molars during the Early – Mid Holocene; only M^2 root # and M^1metaconule differences exist between these early groups. Again, when compared to Early and Mid-Holocene frequencies, increased differences appear at 3-2 ka. Upper molar trait frequency differences between the 8000+ BP and 3-2 ka groups include M^2 root #, M^1 metaconule and M^1 Carabelli's trait. These traits differences recur between earlier time periods and post-2000 BP groups. Conversely, no upper molar differences are observed between 8-6 ka and 3-2 ka groups and no differences are seen between this Early Holocene period and the first and second millennium BP. Only one trait differs between the 6-4 ka and 3-2 ka, and the 4-3 ka and 3-2 ka time periods, namely M^1 Carabelli's trait and M^2 root #, respectively. Only one trait differs between 6-4 ka/4-3 ka and the 1-0 ka time period (M^3 metaconule) and between the 3-2 ka and 2-1 ka groups (M^1 enamel extension). The highest number of upper molar differences are observed post-3000 BP. Traits that differ between 3-2 ka and 1-0 ka groups include M^3 peg, M^3 small metacone, M^1 Carabelli's trait and M^3 parastyle, while differences between 2-1 ka and the first millennium BP change and include M^2 root #, M^3 small metacone and M^2 small hypocone.

Intra-oral osseous trait frequencies (Fig. 5.38) vary little through time. The only differences occur between the first and second millennium BP and the Early Holocene, and between the Late Holocene groups, and include only the midline diastema and rocker jaw. The midline diastema, a predominantly African trait, is most widespread in the Early Holocene with frequencies decreasing slightly over the next few thousand years.

Based on the total number of significant p-values ($p \leq 0.05$, df 1), it appears that samples 8000 BP and older demonstrate some statistically significant differences to Late Holocene material from 3-2 ka to 1-0 ka. Here, between 3 and 9/47 traits (19%) differ between the Early and Late Holocene. Moreover, the 8000+ BP group has a close affinity to the 8-6 ka, 6-4 ka and 4-3 ka time intervals, as do the later groups to each other, demonstrating dental continuity over these time periods. The 8-6 ka group is statistically indistinguishable from the 6-4 ka and 4-3 ka groups. However, the 4-3 ka time period differs from all groups post-3000BP, but most significantly with the 3-2 ka group. This difference is comparable to that seen between 8000+ and 3-2 ka/2-1 ka/1-0 ka, and is expected since the 8000+ and 4-3 ka groups are similar. Thirty percent of traits (14/46) differ between the 3-2 ka group and the first millennium BP group, while 14% (6/43) differ between the former and the second millennium BP group; indeed, the 3-2 ka group has demonstrated some differences with every temporal subgroup. Although this indicates the highest magnitude of difference within the dataset, overall the groups are still statistically very similar. Finally, a very close affinity exists between 2-1 and 1-0 ka. Overall, these evaluations demonstrate little dental change from the Early Holocene to 3000 BP where an increase in trait difference thereafter is clear.

This section has evaluated hypothesis 2 and has demonstrated that there are some statistically significant trait differences between temporal subdivisions. These dissimilarities are small relative to overall similarity, and therefore the data do not suggest that these are heterogeneous dental populations, but they do highlight a certain degree of differentiation across time. Also, metric variation largely overlaps through time and although some evidence does demonstrate various temporal fluctuations (which may be driven by sample size), these data suggest overall similarity between time periods rather than distinctive dental size and shape changes at temporal intervals.

Fig. 5.34: Temporal frequencies of incisor and canine dental traits.

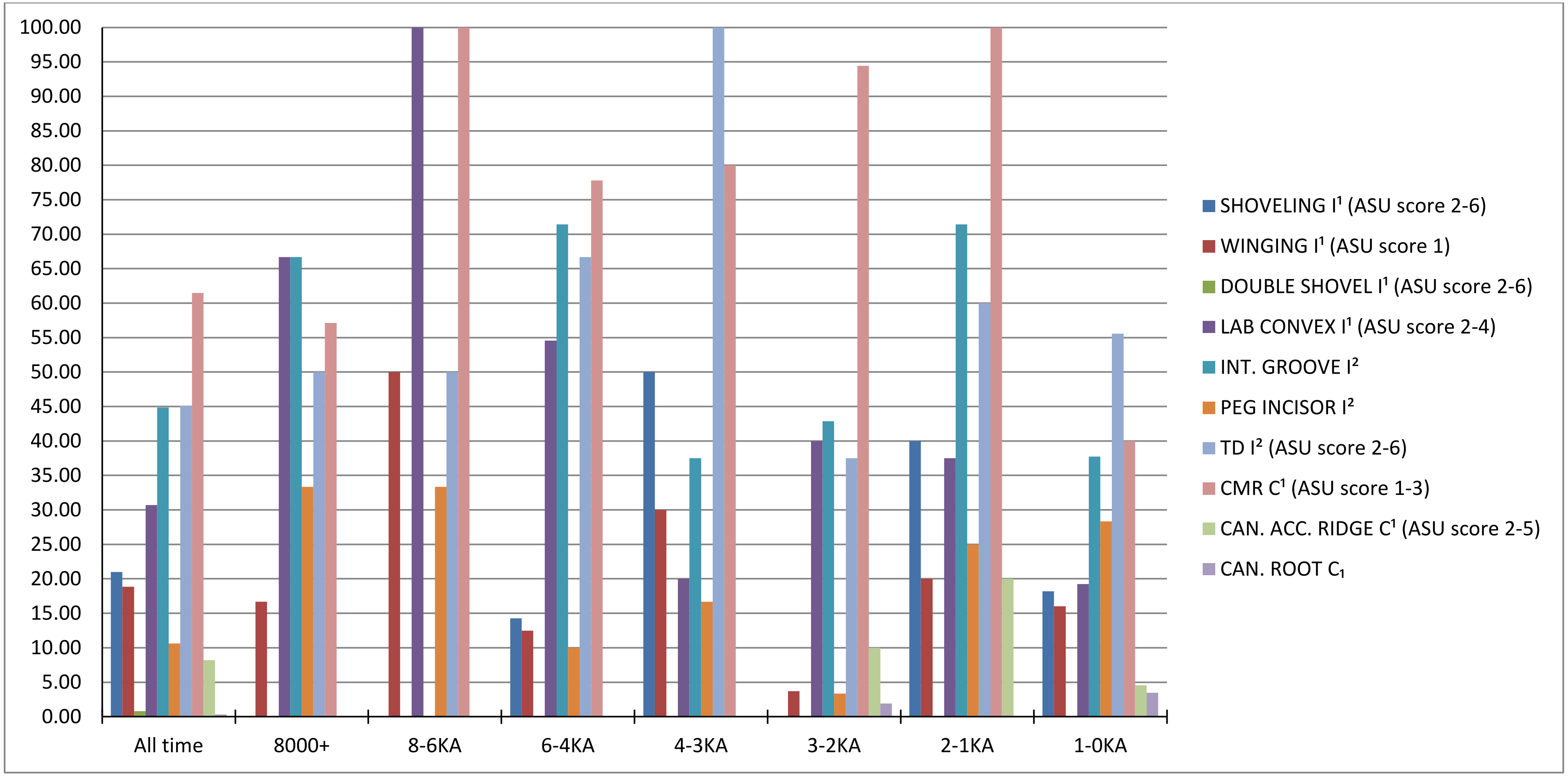


Fig. 5.35: Temporal frequencies of premolar dental traits.

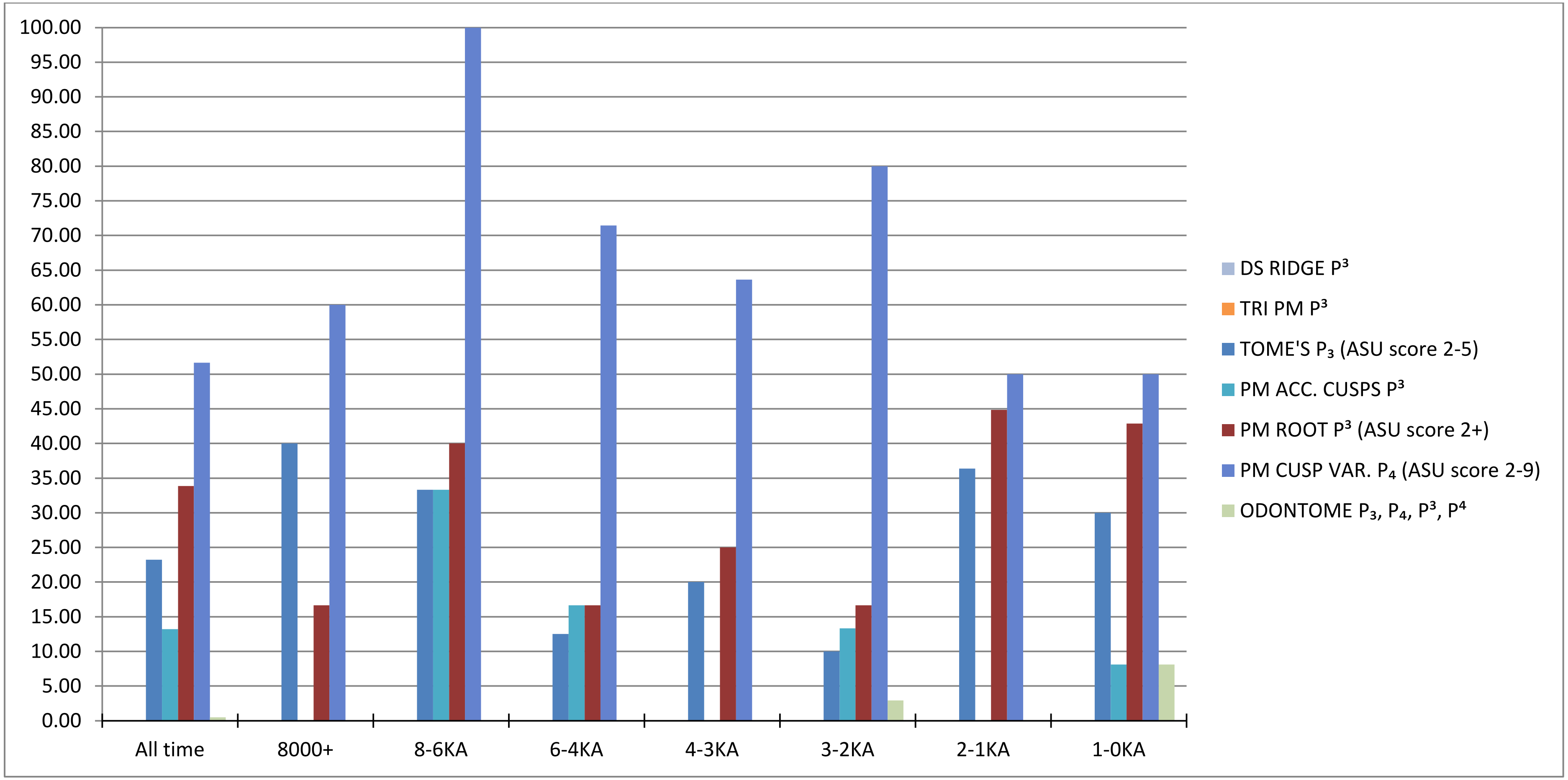


Fig. 5.36: Temporal frequencies of lower molar dental traits.

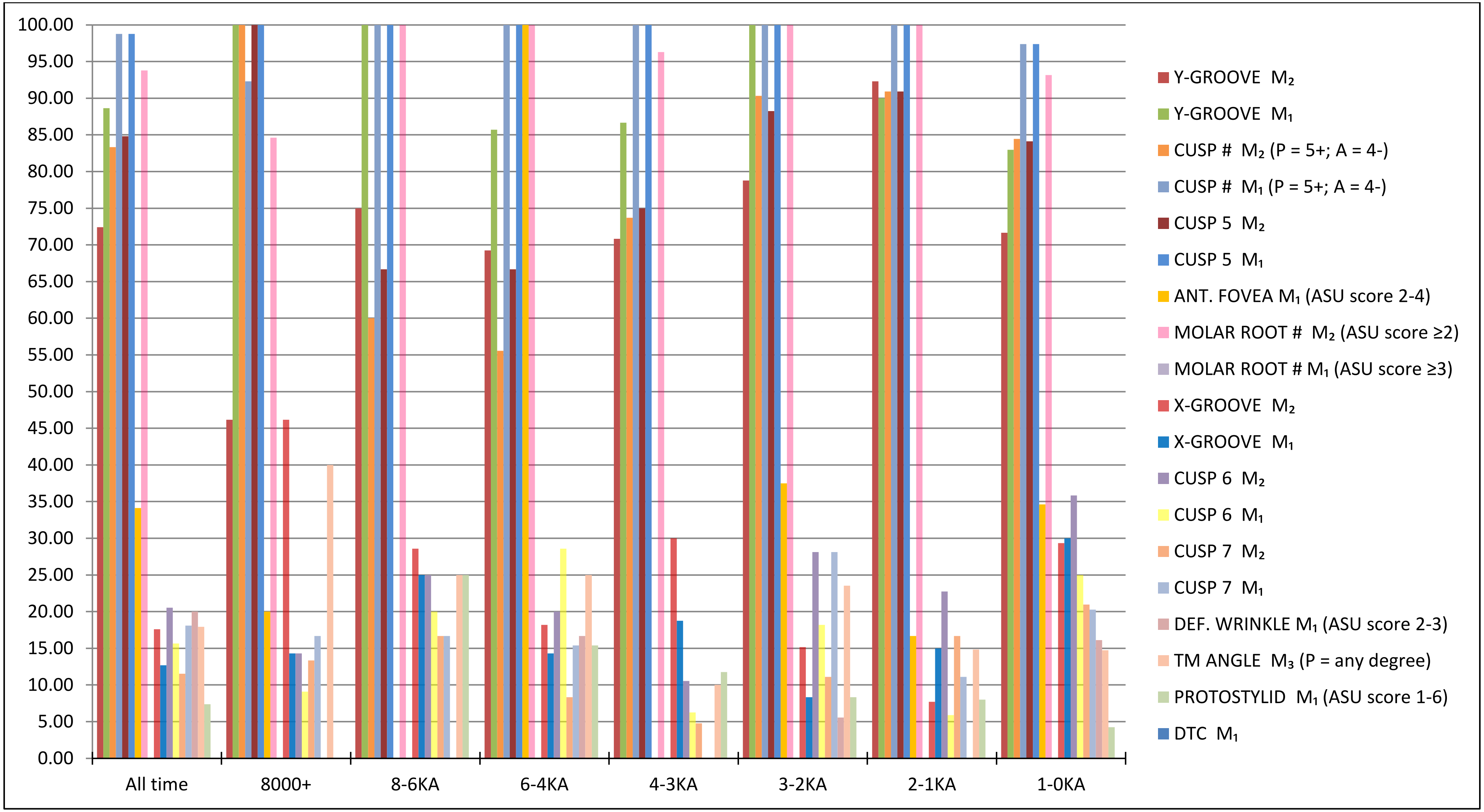


Fig. 5.37: Temporal frequencies of upper molar dental traits.

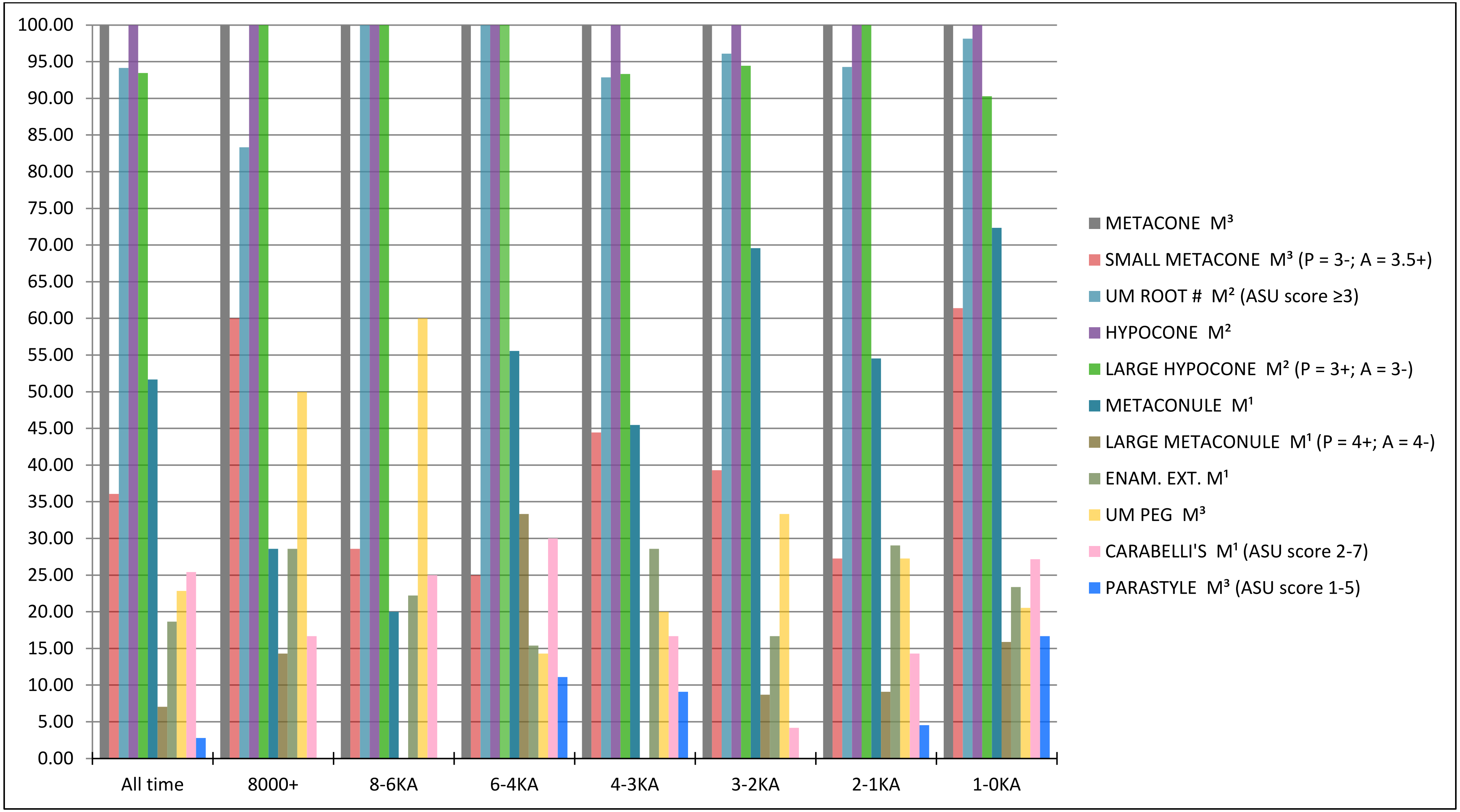


Fig. 5.38: Temporal frequencies of other features including intra-oral osseous traits, midline diastema and M^3 congenital absence

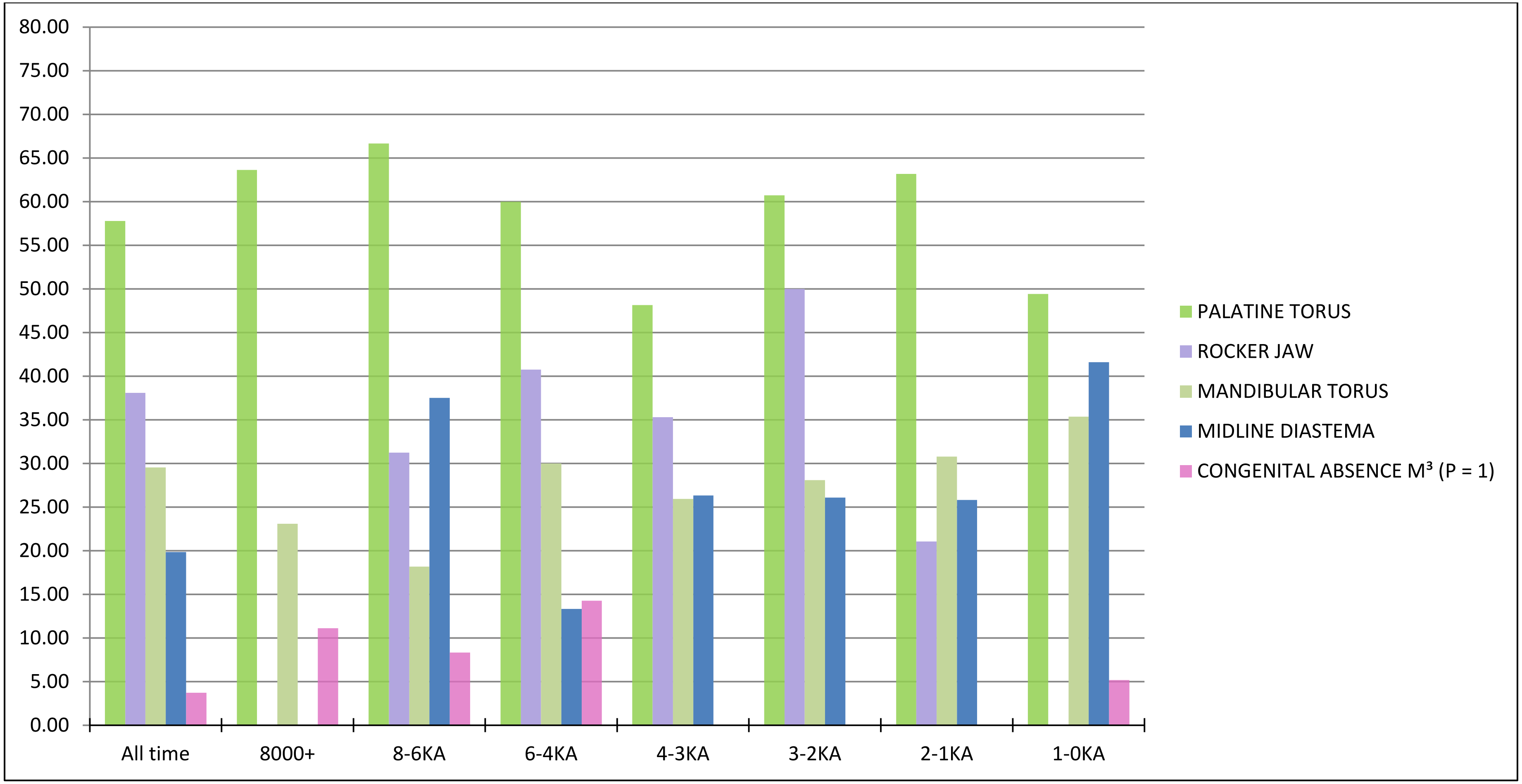


Table 5.9: Summary of traits that are significantly different between time periods ($p \leq 0.05$, df 1).

	8-6ka	6-4ka	4-3ka	3-2ka	2-1ka	1-0ka
8000+	M_2 cusp #, M_1 cusp 5, M^2 root #.	M_2 X-groove, M_2 cusp #, M1 cusp 5, M^1 metaconule.	M_2 X-groove, M_1 cusp 5, M^1 metaconule.	I^2 peg, CMR, Tome's root P_3, M_2 Y-groove, M_2 X-groove, M_2 root #, M^2 root #, M^1 metaconule, M^1 Carabelli's.	CMR, PM root P^3, M_2 Y-groove, M_2 X-groove, M_2 root #, M^2 root #, M^1 metaconule.	M_2 cusp 6, M^1 enam. Ext., M^2 root #, M^1 metaconule, midline diastema.
8-6ka				I2 peg incisor, CMR, Tome's root P_3, M^1 Y-groove, M_2 cusp #.	Int. groove I^2, M_2 Y-groove, M_2 cusp #, rocker jaw.	M^3 peg.
6-4ka			M_2 cusp 6, M^1 large metaconule.	Int. groove I^2, TD I^2, M_1 Y-groove, M_2 cusp 5, M^1 Carabelli's.	Shoveling I^1, PM root P^3, M_2 Y-groove, M_2 cusp #,	I^1 labial convexity, Int. groove I^2, CMR, M_2 cusp #, M^3 metacone, midline diastema.
4-3ka				Winging I^1, Peg incisor I^2, TD I^2, M_2 Y-groove, M_1 cusp 6, M_2 cusp 7, M^2 root #.	CMR, PM root P^3, M_2 Y-groove, M_2 X-groove.	I^1 winging, PM root P^3, M_1 cusp 6, M_2 cusp 6, M^1 enam. Ext.

3-2ka					Shoveling I^1, Peg incisor I^2, TD I^2, CMR, PM root P^3, M^1 enam. Ext.	I^1 labial convexity, I^2 peg, CMR, PM root P^3, PM cusp var. P_4, M_1 anterior fovea, M_2 Y-groove, M_1 Y-groove, M_1 X-groove, M_2 root #, M^3 peg, M^3 small metacone, M^1 Carabelli's, M^3 parastyle.
2-1ka						Int. groove I^2, CMR, M_2 Y-groove, M_2 X-groove, M^2 root #, M^3 small metacone, M^2 small hypocone, rocker jaw.
1-0ka						

RELATIONSHIP BETWEEN KHOESAN AND OTHER GROUPS

This section evaluates hypothesis 3 by assessing whether or not significant dental metric or non-metric differences exist between Holocene Khoesan and Mid-Late Pleistocene dentitions, and between Khoesan and another African Holocene sample from Kenya. In this context, it is extending the previous analyses to evaluate whether the Khoesan dentition has deep roots (i.e. is consistent across a broader timescale) and is regionally distinct (i.e. relative to other Holocene African groups).

COMPARING MID-LATE PLEISTOCENE AND HOLOCENE DENTITIONS: EVALUATION OF HYPOTHESIS 3A.

METRIC EVALUATIONS

To assess metric dental variation between the Khoesan and the Mid-Late Pleistocene sample, pairwise tests and PCAs were conducted on crown and cervical measurements of all available molar teeth. T-tests indicate that there are some differences between Khoesan and Mid-Late Pleistocene dentitions. These differences are predominantly between the Mid-Late Pleistocene and <5000 BP populations (51% of 118 variables; 60/118). Less difference is observed between Mid-Late Pleistocene and >5000 BP groups (29% of 118 variables; 34/118). After the application of the Bonferroni Correction (p-value is reduced to 0.00043), and no variables differ significantly. Due to the Mid-Late Pleistocene sample size, crown and cervical measurements from all teeth were included in these analyses, resulting in some measurement repetition i.e. both left and right lower molar measurements (mesiodistal, buccolingual etc) per individual.

For PCA analyses, Khoesan data divisions were used. Those that were dated to >5000 BP (marked in blue circles on the PCA plot); those that were dated to <5000 BP (marked in red squares); and undated Khoesan samples (marked in green diamonds). Mid-Late Pleistocene samples appear in pink. Limited Mid-Late Pleistocene data limit the number of variables analysed for any one PCA, restricting the analyses to a few recurring lower molar specimens. Due to wear and sample size, only 7 PCA analyses could be performed and analysed variables and percentage of variance explained for each factor (PC1 and PC2) can be found in Table 5.10 below. The results were consistent across all the analyses and 4 PCA plots are illustrated here.

Table 5.10: List of variables and percentage of variance explained by PC1 and PC2 for analysis of Mid-Late Pleistocene and Holocene metric data.

Variables		**% of variance**	
Teeth	**Measurements taken on each tooth**	**PC1**	**PC2**
RM_2, RM_3	MDCD / BLCD	64.28	21.40
LM_1, LM_2	MDCD / BLCD	67.84	16.22
RM_2, RM_3	BLcrD / MLDBcrD	70.89	19.64
RM_2, RM_3	MLDBCD / MBDLCD	74.00	15.96
RM_3	MLDBCD / MBDLCD / MBDLcrD	86.12	10.08
LM_1	MDCD / BLCD / MLDBCD / MBDLCD	79.45	10.85
RM_3	MDCD / BLCD / BLcrD / MLDBCD / MLDBcrD	71.87	14.56

The PCA of lower second and third molar cervical measurements (4 variables) from all of the temporal subdivisions is shown in Fig. 5.39. Component loadings (Fig. 5.40) are all positive and equal in magnitude for PC1, suggesting that this is a size variable. Component loadings for shape (PC2) however, are varied. RM_3 MDCD is weighted the highest (0.676), while RM_2 MDCD is lowest (0.046). Although within-period variation does appear to increase over time, this is possibly an artefact of increasing sample size. More importantly, there is no clear difference between Mid-Late Pleistocene individuals and the Khoesan sample, with the Mid-Late Pleistocene teeth falling well within the range of Khoesan variation. Some Mid-Late Pleistocene samples are well-known to vary substantially in size, i.e. those from Klasies River Mouth (H.J. Deacon 1992, 1995; Rightmire and Deacon 1991, 2001), possibly due to sexual dimorphism. A number of the teeth excavated from the site are extremely small (i.e. SAM-AP 6222, SAM-AP 6225). This makes the placement of the small-toothed Klasies River Mouth specimen (SAM-AP 6225) especially interesting, as its size is not exceptional relative to other Khoesan individuals. Large teeth from Klasies River Mouth (i.e. SAM-AP 6223) are comparable in size to modern African homologues (Grine 2012; Rightmire and Deacon 2001) and although they are included in this study, they are not represented in these PCAs due to measurement limitations. A number of identified Early Holocene specimens are similar to Mid-Late Pleistocene specimens in terms of size/shape. For example, the large specimens (appearing on the left of the graph) such as those from Elands Bay (UCT 378), Coldstream Cave (SAM-AP 4208a) and Matjes River Rock Shelter (NMB 1264) resemble the Cave of Hearths (SU 15) individual, while smaller Matjes River Rock Shelter specimens such as NMB 8a, located to the right of the plot, have measurements resembling material from Klasies River Mouth (SAM-AP 6225) and Border Cave (BC 2), respectively. It is interesting to note that Late Pleistocene specimens still fall within the range of post-5000 BP variation, suggesting sustained size/shape continuity from the Mid-Late Pleistocene well into the Holocene. There appears to be some increase in variation post-5000 BP, as demonstrated by the outliers SAM-AP 4964, SAM-AP 6147 and ALB 303.

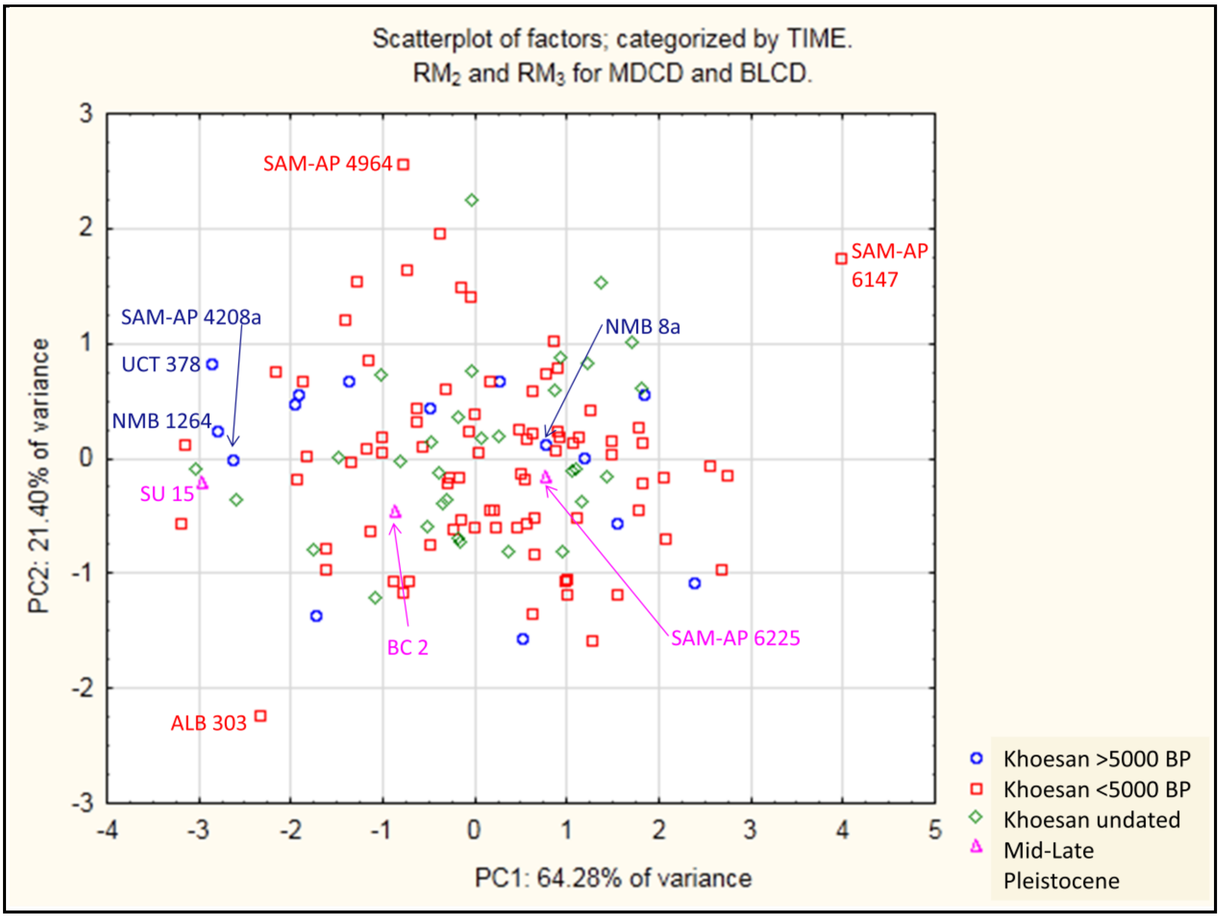


Fig. 5.39: Principal components plot of PC1 versus PC2. The PCA is based on RM_2 and RM_3 mesiodistal (MDCD) and buccolingual (BLCD) cervical diameters through time.

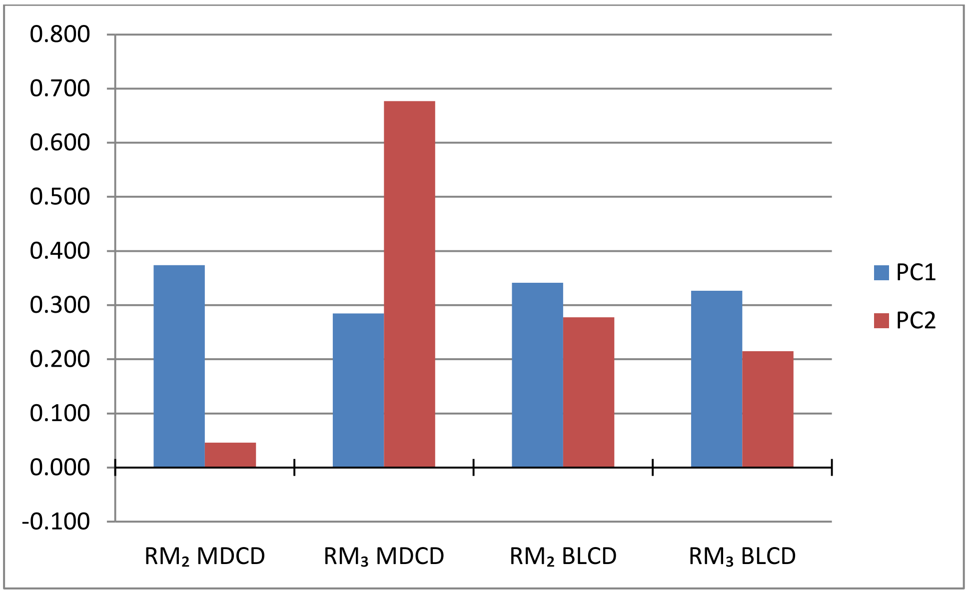


Fig. 5.40: Principal component loadings of PC1and PC2 for lower second and third molar cervical dental measurements associated to Fig. 5.39.

The PCA of lower second and third molar crown measurements (4 variables) from all temporal subdivisions is shown in Fig. 5.41. Component loadings (Fig. 5.42) are all similar in magnitude for PC1, suggesting that this is a size variable; for PC2 RM3 MLDBcrD PC2 has a relatively high loading (0.337), capturing shape variation. Again, pre- and post-5000 BP Khoesan and Mid-Late Pleistocene specimens overlap in size and shape variation. Small (towards the right of the plot) Mid-Late Pleistocene teeth from Klasies River Mouth (SAM-AP 6225) are comparable to small Early Holocene samples including NMB 1441 from Matjes River Rock Shelter, although SAM-AP 6225 in this case does appear to be very small relative to the entire sample. Larger (towards the left of the graph) Mid-Late Pleistocene individuals (SU 15 from Cave of Hearths) are similar to large-toothed Early Holocene specimens such as UCT 182 from Oakhurst Rock Shelter and NMB 1442 from Matjes River Rock Shelter, as well as more recent individuals such as ALB 150 from Jeffrey's Bay. Mid-range samples comparable to material from Border Cave (BC 2) include intermediate sized Early Holocene specimens such as NMB 1443 from Matjes River Rock Shelter, as well as Late Holocene specimens including SAM-AP 5070 from Melkbosstrand.

Late Holocene outliers (NMB 1273, ALB 314 and ALB 308) may, once again, be indicative of increased shape variation at this time.

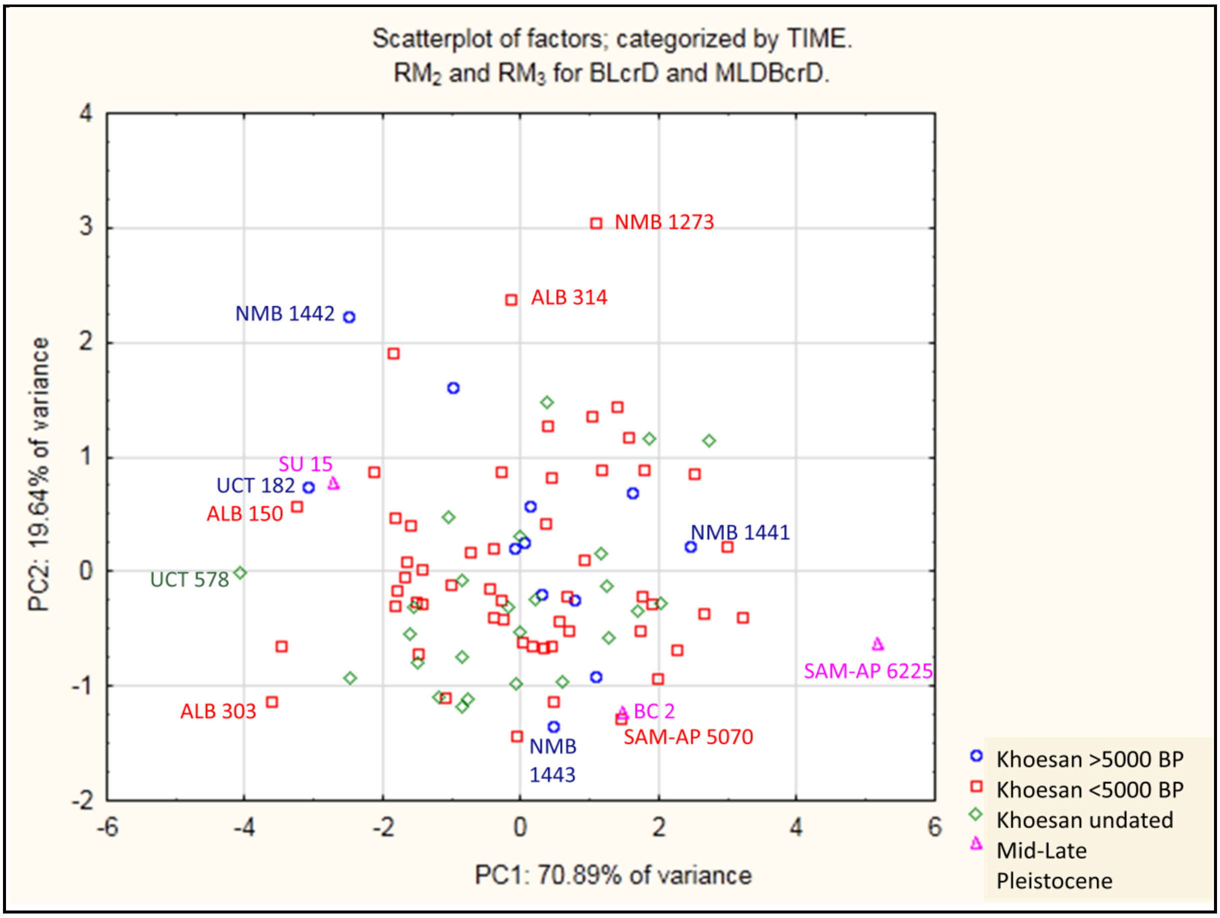


Fig. 5.41: Principal components plot of PC1 versus PC2. The PCA is based on RM_2 and RM_3 buccolingual (BLcrD) and diagonal mesiolingual-distobuccal (MLDBcrD) crown diameters for all time periods.

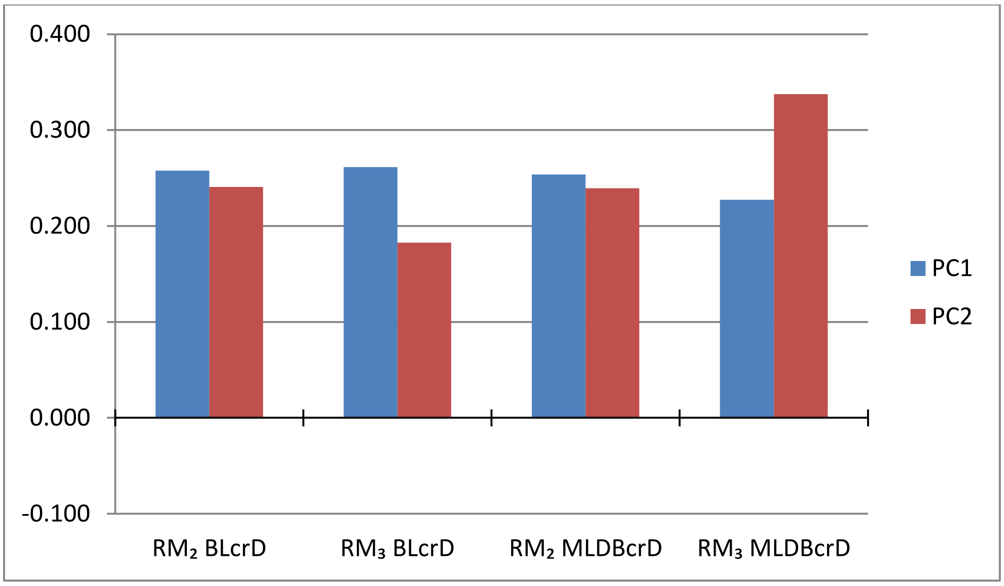


Fig. 5.42: Principal component loadings of PC1 and PC2 for lower second and third molar crown dental measurements associated to Fig. 5.41.

The PCA of lower third molar cervical and crown measurements (6 variables) from all time periods is shown in Fig. 5.43. The component loadings for PC1 are similar in magnitude, suggesting that this is a size component. PC2 has a very high loading for RM3 BLCD (0.710) relative to the other traits (Fig. 5.44). A similar pattern to what is seen in previous PCAs is seen here, including the increased shape variation for <5000 BP specimens, identified by numerous outliers. Small Early Holocene specimens such as NMB 1441 from Matjes River Rock Shelter, are comparable in size to small Late Pleistocene samples (SAM-AP 6225), while mid-range Late Pleistocene individuals (BC 2) are found alongside intermediate Early Holocene samples including Blombos (UCT 323) and Matjes River Rock Shelter (NMB 1373), among others. Larger specimens from the Mid-Late Pleistocene (i.e. SU 15) are similar to large Early Holocene individuals (Oakhurst Rock Shelter – UCT 182), while the large Hofmeyr molar (ELM 24) falls at the extreme edge of Mid-Late Pleistocene (and Holocene) variation. Importantly, the range of variation is comparable from the Mid-Late Pleistocene to the present, despite very small sample sizes in the Mid-Late Pleistocene.

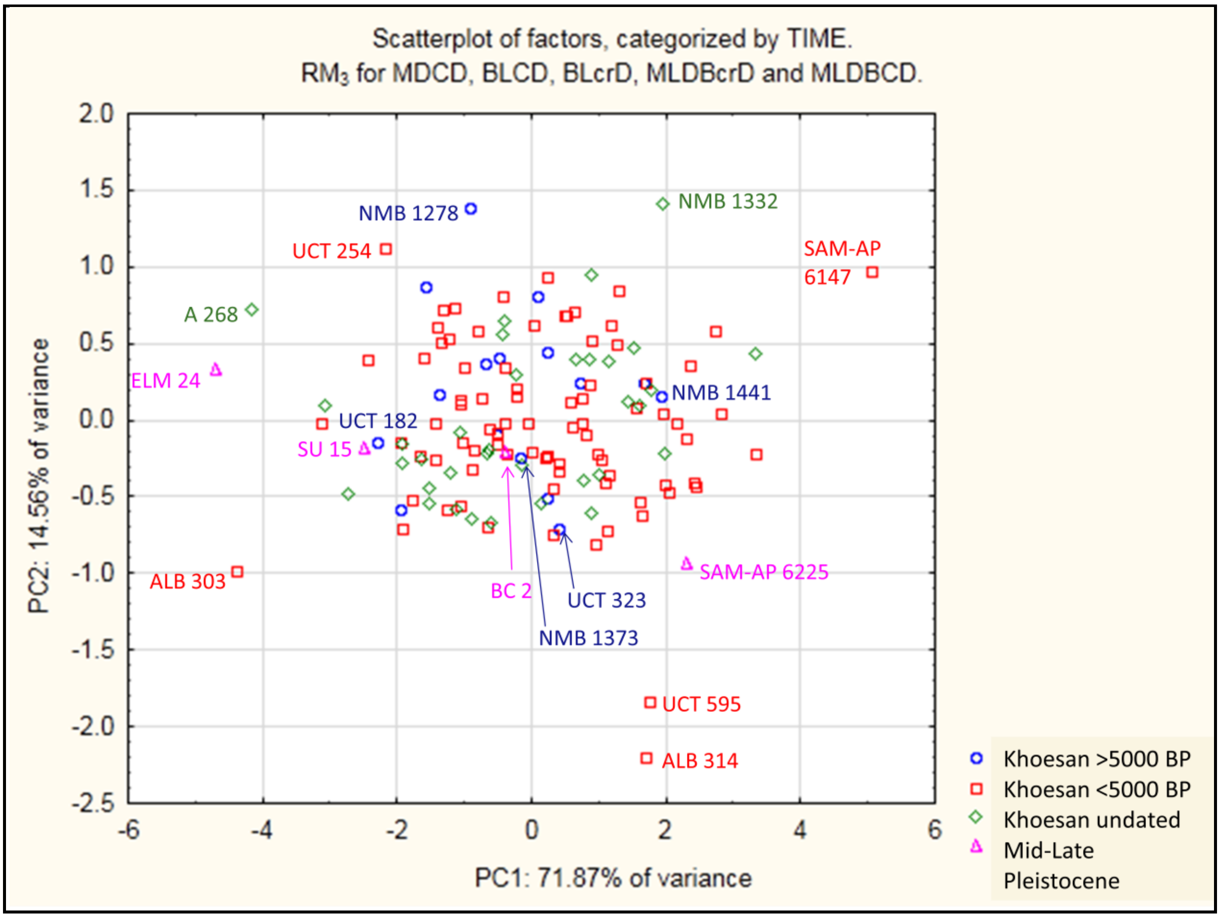


Fig. 5.43: Principal components plot of PC1 versus PC2. The PCA is based on RM$_3$ mesiodistal (MDCD), buccolingual (BLCD) and mesiolingual-distobuccal cervical diameters (MLDBCD), and buccolingual (BLcrD) and mesiolingual-distobuccal (MLDBcrD) crown diameters for all time periods.

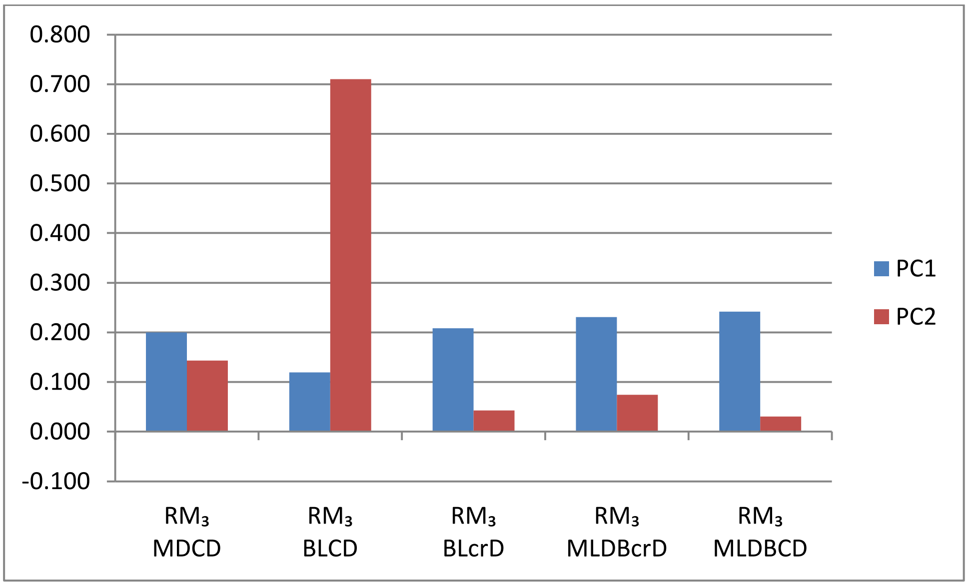


Fig. 5.44: Principal component loadings of PC1 and PC2 for lower third molar crown and cervical dental measurements associated to Fig. 5.43.

NON-METRIC EVALUATIONS

Trait frequencies were calculated for Mid-Late Pleistocene and Khoesan samples and are presented in Table 5.11. The frequencies of 44 traits (missing teeth resulted in elimination of other traits) were assessed for each population inclusive of all available data from all regions and time periods. It is important to note that the Mid-Late Pleistocene frequencies are unlikely to represent the true frequencies of the populations from which they were drawn, given the small sample size, so comparisons with the Khoesan data must be interpreted with caution. For example, the extremely high frequencies of some Mid-Late Pleistocene traits are certainly the result of very small sample sizes (e.g. N=1). Such traits should be regarded as present within the sample but, as mentioned above, interpreted with caution. Of the 44 trait frequency comparisons between the Khoesan and the Mid-Late Pleistocene population, 52.27% (23) are similar and 9.09% (4) demonstrate moderately higher Mid-Late Pleistocene frequencies (I^1 labial convexity, P_3 cusp variation, M^3 metacone and rocker jaw). 11.36% (5) of the traits depict extremely high Mid-Late Pleistocene percentages with low Khoesan rates (I^1 double shovel, M_2 cusp 7, M1 deflecting wrinkle, M_1 protostylid and M^1 large metaconule). Each of these five traits in the Mid-Late Pleistocene group is represented by a sample size of one (N-=1). The remaining 12 (27.27%) traits are not present in the available Mid-Late Pleistocene dataset.

Mid-Late Pleistocene and Khoesan data as a whole, i.e. from all regions and time periods, were also evaluated to identify overall differences and similarities between both populations. Chi-square analyses were employed on 17 dental traits and p-values (≤ 0.05, 1 df) can be found in Table 5.12. Thereafter, Mid-Late Pleistocene and Khoesan regional and temporal data are compared (see Appendix 4.1 – 4.9 for regional and 6.1 – 6.6 for time). Chi-square analyses demonstrate a closer affinity between the Mid-Late Pleistocene and Khoesan populations than identified in trait frequency assessments. This is not surprising, as Chi-square tests take sample size into account. None of the seventeen traits assessed display statistically significant p-values, suggesting phenetic similarity between the two groups.

Although frequencies for 44 traits were evaluated, only traits where Mid-Late Pleistocene N>1 were used in chi-square analyses and are discussed here. Unfortunately no Mid-Late Pleistocene incisor traits could be evaluated statistically. Very low grade (ASU score of 1) incisor shoveling has been recorded in 2 individuals from Hoedjiespunt (Stynder *et al.* 2001)) and Die Kelders (Grine 2000), as well as in this study. However, in order to accurately characterise the population and to promote uniformity in this study, low grades are excluded. The Khoesan generally express low I^1 shoveling trait frequencies but further data collection is required before comparisons to Mid-Late Pleistocene incisor traits can be performed at global standards. For the purposes of this analysis, the Mid-Late Pleistocene collection does not express these traits.

Only one canine trait (lower canine root number) was evaluated and no significant differences were detected between the Khoesan and Mid-Late Pleistocene frequencies for this trait (no tooth presented with more than one root). Unfortunately no Mid-Late Pleistocene upper canines were available for assessment of the CMR, usually a high frequency Khoesan trait. Few premolar trait frequency evaluations were possible. Mid-Late Pleistocene P_3 cusp variation presents with high frequency compared to Khoesan data and no P^3 root presents with two or more roots but this could not be assessed for significance. No difference between Mid-Late Pleistocene (0%) and Khoesan (23.2%) frequencies of P_3 Tome's root was observed.

Of the lower molars, only the M_1 root #, M_1 Y- and X-groove and M_1 distal trigonid crest traits do not feature in Mid-Late Pleistocene samples, while they exist at variable frequencies in the Khoesan. The M_2 Y-groove, M_2 cusp number, M_1 cusp 5, and the M_2 root number all occur at similarly high frequencies in both the Khoesan and Mid-Late Pleistocene populations and no significant difference is observed between them. Additionally, the M_2 X-groove, and M_1 cusp 6 and cusp 7 (see Fig. 5.45 for cusp 5, 6 and 7 expression) express at similarly low frequencies for both groups and are not significantly different. Other notable lower molar traits such as M_1 deflecting wrinkle and M_1 protostylid appear in both populations but due to sample size could not be tested for significance.

Fig. 5.45: LM_1 from Die Kelders (SAM-AP 6277). This molar includes a cusp 5, cusp 6, cusp 7 and Y-groove pattern.

Fig. 5.46: LM^2 from Hoedjiespunt Peninsula (SAM-AP 6370a). This upper molar includes ASU grade 3 metacone, hypocone and metaconule.

Upper molar trait frequencies between the two groups follow a similar pattern seen in lower molars. Some prominent traits, including M^1 Carabelli's and M^3 parastyle, are not expressed in the Mid-Late Pleistocene collection and are only present in the Khoesan data set. However, a number of high upper molar trait frequencies, namely M^2 root number, M^2 hypocone and M^2 large hypocone, show no significant differences between the two samples. No statistically significant difference is found between M^3 peg values. Other traits, including M^3 small metacone, demonstrate comparable low to intermediate frequencies in both populations but due to low sample sizes, significance could not be tested. Similarly, the M^1 metacone and M^1 large metacone are present in both groups but occur at higher frequencies in the Mid-Late Pleistocene (see Fig. 5.46) and again, cannot be assessed due to sample size limitations. Lastly, the only two intra-oral osseous traits available for comparison were the mandibular torus and rocker jaw. Mid-Late Pleistocene samples concur with Khoesan intermediate frequencies and no difference between the populations is observed.

To assess whether a closer relationship exists between Early Holocene Khoesan and Mid-Late Pleistocene teeth, frequencies between the Khoesan 8000+ group and the Mid-Late Pleistocene were also compared (chi-square comparisons can be found in Appendix 6.1). Results remained similar: of the 17 trait frequencies that could be tested for significance (N>1), none were different. Lower molar traits including P_3 Tomes root, M_2 Y- and X-grooves, M_1 cusps 5, 6 and 7, M_2 root # and M_3 torsomolar angle make up the bulk of significance testing and demonstrate no differences between the two populations. Upper molar traits such as M^3 peg and M^2 root # are also different as are two intra-oral osseous traits, the mandibular torus and rocker jaw. Despite sample size concerns, Early Holocene Khoesan and Mid-Late Pleistocene dental frequency similarities is suggestive of a degree of continuity between the two populations.

All dental traits that appear in the Mid-Late Pleistocene samples appear in the Khoesan data set. Chi-square analyses on up to 17 traits suggest that for those traits, Khoesan temporal groups 8000+, 8-6 ka and 6-4 ka are phenetically indistinguishable from the Mid-Late Pleistocene (i.e. no significant p-values) suggestive of dental continuity between Mid- to Early Holocene Khoesan and Mid-Late Pleistocene populations (see Appendix 6.1-6.7). Additionally, only one significant trait difference emerges between the Mid-Late Pleistocene and the Khoesan 4-3 ka (M_1 protostylid) and 3-2 ka (M^2 hypocone) groups, in line with increasing Khoesan variation during this time. At 2000 BP, the total significant differences between the Khoesan and Mid-Late Pleistocene return to zero. No increased variation is seen between the Mid-Late Pleistocene and 1-0 ka Khoesan group as would be expected given the close relationship between the Mid-Late Pleistocene and Early Holocene. Chi-square analyses were also conducted on Klasies River Mouth and Khoesan specimens for up to 9 traits (only available data) to not only assess dental similarities and differences between these two groups but to evaluate whether the variation present in Klasies River Mouth specimens is consistent with the degree of Holocene variation. Results were similar to those seen in previous overall Mid-Late Pleistocene evaluations. Klasies River Mouth and all Holocene samples demonstrate no difference overall, while the 8000+ Khoesan temporal group has only one difference (1/9 significant p-values). P-values can be found in Appendix 6.8.

Although few Mid-Late Pleistocene specimens were available and missing data was thought to be a considerable problem, results were consistent. Metric analyses suggest an increase in size/shape variation within time intervals but this is likely the result of an increase in sample size over time. Importantly, metric analyses demonstrate that there are no clear differences between the Mid-Late Pleistocene samples and the Khoesan data set as a whole and Mid-Late Pleistocene teeth fall within the range of Khoesan dental variation throughout the Holocene. While size differences are clearly depicted during the Mid-Late Pleistocene (i.e. differences between smaller Klasies River Mouth material versus the large Cave of Hearths specimen), shape variation appears limited, though it is seemingly a factor in Khoesan dental variation, particularly post-5000 BP. Non-metric investigations largely complimented metric analyses in evaluating hypothesis 3a. These analyses have demonstrated that there are no statistically significant differences between Mid-Late Pleistocene and Early Holocene Khoesan populations, and although some disparity exists, and total significant values vary slightly between other temporal evaluations, differences are limited. This demonstrates a degree of phenetic affinity between Mid-Late Pleistocene and Khoesan dentition throughout the Holocene, suggestive of population connections deeper in time.

Table 5.11: Khoesan and Mid-Late Pleistocene trait frequencies.

Trait	Khoesan		Mid-Late Pleistocene	
	N	Frequency	N	Frequency
SHOVELING I^1 (ASU score 2-6)	83	20.99	1	0.00
DOUBLE SHOVEL I^1 (ASU score 2-6)	138	0.76	1	100.00
LAB CONVEX I^1 (ASU score 2-4)	127	30.71	1	100.00
INT. GROOVE I^2	141	44.85	1	0.00
PEG INCISOR I^2	160	10.63	1	0.00
TD I^2 (ASU score 2-6)	82	45.12	1	0.00
CAN. ROOT C_1	300	0.33	6	0.00
PM ACC. CUSPS P^3	106	13.21	1	0.00
TRI PM P^3	194	0.00	2	0.00
DS RIDGE P^3	102	0.00	1	0.00
PM ROOT P^3 (ASU score 2+)	245	33.88	1	0.00
ODONTOME P^3, P^4, P_3, P_4	209	0.48	4	0.00
PM CUSP VAR. P_4 (ASU score 2-9)	122	51.64	1	100.00
TOME'S P_3 (ASU score 2-5)	112	23.21	4	0.00
ANT. FOVEA M_1 (ASU score 2-4)	92	34.12	4	0.00
DTC M_1	74	0.00	1	0.00
Y-GROOVE M_2	243	72.43	5	80.00
X-GROOVE M_2	243	17.60	5	20.00
CUSP # M_1 (P = 5+; A = 4-)	174	98.77	5	100.00
CUSP # M_2 (P = 5+; A = 4-)	206	83.33	1	100.00
CUSP 5 M_1	168	98.77	4	100.00
CUSP 5 M_2	206	84.82	1	100.00
CUSP 6 M_1	166	15.66	4	33.00
CUSP 6 M_2	201	20.54	1	0.00
CUSP 7 M_1	232	18.10	5	25.00
CUSP 7 M_2	234	11.54	1	100.00
DEF. WRINKLE M_1 (ASU score 2-3)	110	20.00	1	100.00
PROTOSTYLID M_1 (ASU score 1-6)	231	7.36	1	100.00
ROOT # M_1 (ASU score >=3)	333	0.00	5	0.00
ROOT # M_2 (ASU score >=2)	290	93.79	6	100.00
TM ANGLE M_3 (P = any degree)	185	17.93	3	33.00
PEG M^3	194	22.83	2	0.00
ROOT # M^2 (ASU score >=3)	290	94.14	2	100.00
METACONE M^3	191	100.00	1	100.00
SMALL METACONE M^3 (P = 3-; A = 3.5+)	191	36.07	1	50.00
HYPOCONE M^2	229	100.00	2	100.00
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	229	93.45	2	100.00
METACONULE M^1	156	51.68	1	100.00
LARGE METACONULE M^1 (P = 5+; A = 4+)	156	7.05	1	100.00

CARABELLI'S M^1 (ASU score 2-7)	179	25.42	1	0.00
PARASTYLE M^3 (ASU score 1-5)	180	2.78	1	0.00
CONGENITAL ABSENCE M^3 (P = 1)	296	3.72	1	0.00
MANDIBULAR TORUS	352	29.55	4	25.00
ROCKER JAW	296	37.84	3	66.67

Table 5.12: Chi-square p-values (≤ 0.05, 1 df) for 17 traits between all Khoesan and Mid-Late Pleistocene data.

TRAITS	**P-VALUES**
CAN. ROOT C_1	0.4532
TOME'S P_3 (ASU score 2-5)	0.6285
ANT. FOVEA M_1 (ASU score 2-4)	0.5284
Y-GROOVE M_2	0.6010
X-GROOVE M_2	0.8891
CUSP # M_2 (P = 5+; A = 4-)	0.3185
CUSP 5 M_1	0.8928
CUSP 6 M_1	0.6845
CUSP 7 M_1	0.9633
ROOT # M_2 (ASU score >=2)	0.5211
TM ANGLE M_3 (P = any degree)	0.9453
PEG M^3	0.9344
UM ROOT # M^2 (ASU score >=3)	0.0866
HYPOCONE M^2	0.0502
HYPOCONE M^2 (P = 3+; A = 3-)	0.1445
MANDIBULAR TORUS	0.7240
ROCKER JAW	0.6704

COMPARING KENYA AND KHOESAN HOLOCENE DENTITIONS: EVALUATION OF HYPOTHESIS 3B.

Hypothesis 3b looks at the differences between Khoesan dentition and a Kenyan sample to determine whether significant regional differences exist more broadly in the Holocene across Africa. Comparisons with the Mid-Late Pleistocene sample looked at continuity across time. This hypothesis aims to evaluate continuity (or a lack thereof) across the broader sub-Saharan African region.

METRIC EVALUATIONS

To assess metric dental variation between the Khoesan and Kenyan sample, a MANOVA and PCAs were conducted on crown and cervical measurements of all available teeth. The Kenyan sample was divided into pre- and post-4500 BP and these were analysed against Khoesan pre- and post-2000 BP specimens (due to economic similarity and to identify overall similarity, if any, due to migrations from East Africa to South Africa). To perform MANOVAs, some missing data was modified by adding means to measurement variables, where necessary (inclusive of all measurements, 75% of the data had to be modified). Significant differences were detected between populations (MANOVA; Wilks' Lambda; p=0.000). Pairwise tests indicate that these differences are predominantly between >2000 BP and >4500 BP populations (89.1% of 175 variables; 156/175). The least amount of difference is observed between the more recent material; <2000 BP and <4500 BP (59.8% of 169 variables; 101/169).

Khoesan data in the following PCA analyses (blue circles on the plot) include data from all regions and timeframes. The Kenyan dataset (red squares on the plot) is not very large and this led to some missing data, limiting the amount of variables used in each PCA. Some of the Kenyan specimens have been dated and this allows for a temporal assessment between the Khoesan and Kenyan data. Overall, twenty PCA's were conducted. Variables used and percentage of variance explained values for each principal component are depicted in Table 5.13 below.

Table 5.13: List of variables and percentage of variance explained for PC1 and PC2 for Kenya/Khoesan PCAs.

Variables		**% of variance**	
Teeth	**Measurements taken on each tooth**	**PC1**	**PC2**
Inclusive of all time periods (pre- and post 4500 BP)			
LM$_1$, LM$_2$	MDCD / BLCD	67.51	15.63
LM^1, LM^2	MDCD / BLCD	71.62	14.32
LM$_1$, LM$_2$	MDcrD / BLcrD	70.79	13.21
LM^1, LM^2	MDcrD / BLcrD	74.33	13.21
RM^1, RM^2	MDBLCD / MLDBCD	82.73	8.36
Khoesan pre-2000 BP and Kenya pre-4500 BP			
LM$_1$, LM$_2$	MDCD / BLCD	76.01	11.92
LM^1, LM^2	MDCD / BLCD	78.94	11.95
RM$_1$, RM$_2$	MDCD / BLCD	77.59	12.47
LM^1, LM^2	MDcrD / BLcrD	84.03	9.87
RM$_1$, RM$_2$	MDcrD / BLcrD	74.89	12.58
RM^1, RM^2	MDcrD / BLcrD	84.58	7.84
RM$_1$, RM$_2$	MDBLCD / MLDBCD	83.59	9.28
LM$_1$, LM$_2$	MDBLcrD / MLDBcrD	88.35	6.92
LM^1, LM^2	MDBLcrD / MLDBcrD	89.73	5.18
LM$_2$	MDCD / BLCD / MDBLCD / MLDBCD	87.43	6.05
Khoesan post-2000 BP and Kenya post-4500 BP			
LM$_1$, LM$_2$	MDCD / BLCD	67.94	14.82
LM^1, LM^2	MDCD / BLCD	69.89	16.63
LM$_2$	MDcrD / BLcrD / MDBLcrD / MLDBcrD	84.61	8.73
LM^1	MDcrD / BLcrD / MDBLcrD / MLDBcrD	88.13	6.13
LM$_1$, LM$_2$	MDBLCD / MLDBCD	81.77	9.75
LM^1, LM^2	MDBLCD / MLDBCD	74.33	15.12

Although 21 PCA's were performed (five inclusive of the entire Holocene, 10 analysing data from Khoesan dentition pre-2000 BP and Kenyan dentition pre-4500 BP, and 6 from the Late Holocene), results were remarkably similar across all evaluations and therefore only 5 are illustrated here. In all PCA plots, Kenyan samples are clearly grouped together, demonstrating size and shape variation ranges comparable to that seen in Khoesan dentition, but teeth are substantially larger overall. There is limited overlap between Khoesan and Kenyan samples in size and shape variation demonstrating some similarity between the two samples. This could be attributed to sexual dimorphism in the Kenya data set (which has been demonstrated in some traits in earlier dental studies on modern Kenyan populations

(Barnes 1968)), with smaller female Kenyan specimens comparable to some Khoesan. This hypothesis could not be tested here as sex determination of the Kenyan samples was not possible.

The PCA of upper molar crown measurements (4 variables) from Kenyan and Khoesan datasets spanning the Holocene is shown in Fig. 5.47. Large individuals from Kenya such as KNM-LT 13702 from Lothagam and EM 815 from Bromhead's Site are situated towards the left, while the smallest Khoesan individuals (i.e. SAM-AP 4798 and SAM-AP 6332) are on the right, suggesting PC1 is related to size. Component loadings are illustrated in Fig. 5.48. Loadings for both PC1 and PC2 are all positive and equal in magnitude with PC2 LM^2 BLcrD being weighted the highest (0.285) and LM^1 BLcrD, the lowest (0.208).

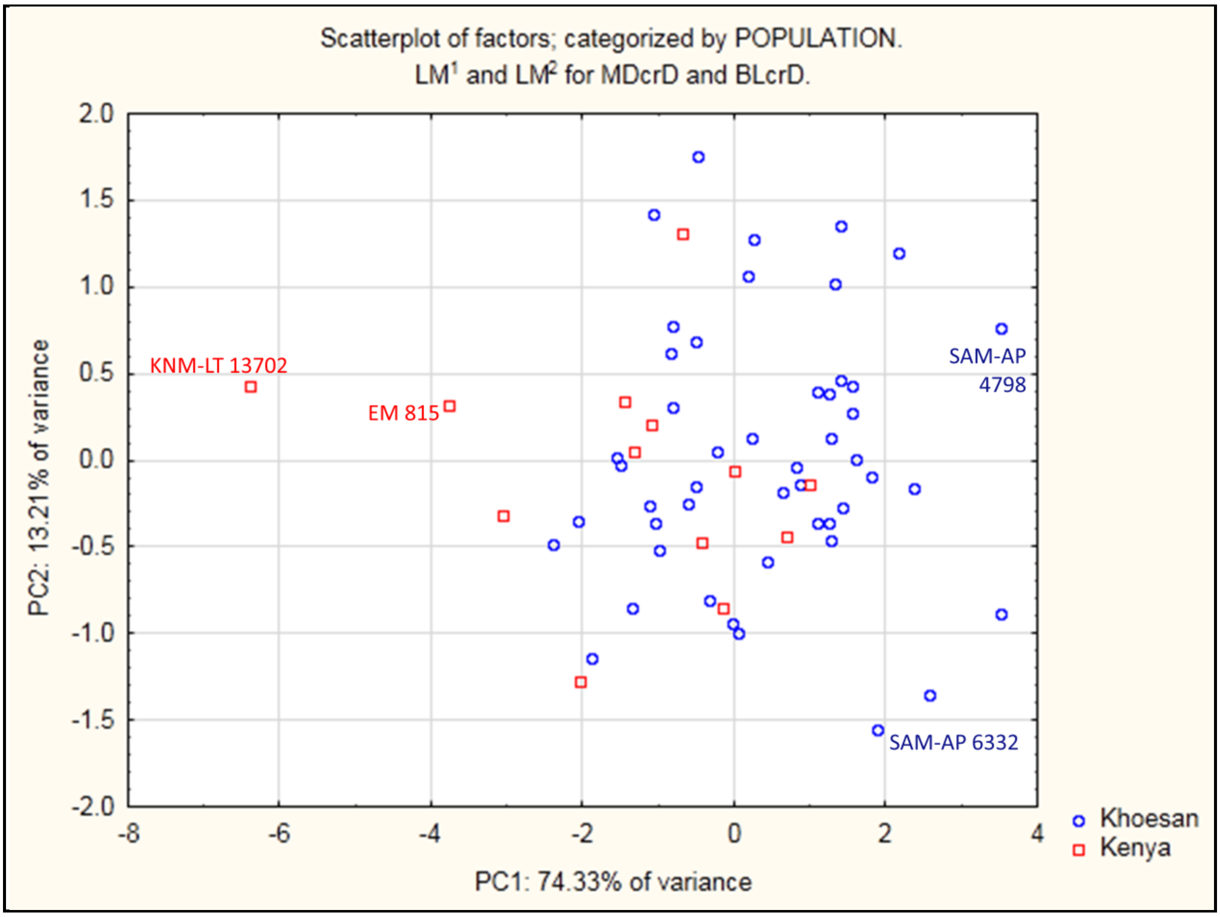


Fig. 5.47: Principal components plot of PC1 versus PC2. The PCA is based on LM^1 and LM^2 mesiodistal (MDcrD) and buccolingual (BLcrD) crown diameters throughout the Holocene.

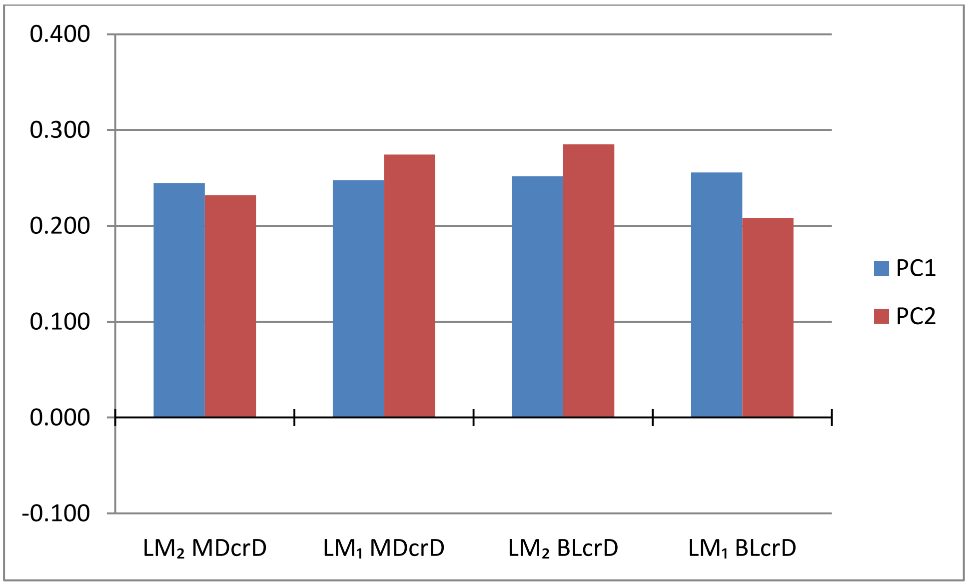


Fig. 5.48: Principal component loadings of PC1 and PC2 for upper first and second molar crown dental measurements associated to Fig. 5.47.

The PCA of lower molar cervical measurements (4 variables) from Kenya pre-4500 BP and Khoesan pre-2000 BP data sets is shown in Fig. 5.49. Here, PC1 (presumably size) and PC2 (most likely shape) variation of the Kenyan sample is somewhat increased with the use of lower molar cervical measurements. The two groups are also slightly more differentiated, with some large Kenyan individuals and small Khoesan specimens at the extreme size range of variation. However, some overlap between samples is still evident. A closer size relationship among large individuals (left of plot) is shown i.e. between the Kenyan individual KNM-LT 13700 from Lothagam dated to ca. 8400 – 6000 BP and Khoesan specimen UCT 162 from Yzerfontein dated to 2880 ± 50 BP (Pta-929), while Khoesan specimens such as SAM-AP 1894 from Robberg dated to 3511 ± 30 BP (OxA-V-2053-43) demonstrate much smaller diameters and some shape variation (seen in the outlier SAM-AP 1871 from Robberg dated to 3310 ± 60 BP (Pta-2273)). Component loadings (Fig. 5.50) for PC1 are relatively equal in magnitude (0.236 – 0.271) but vary with regard to PC2, where the loadings are weighted the highest for RM_2 BLCD (0.443) and the lowest for RM_1 BLCD (0.074).

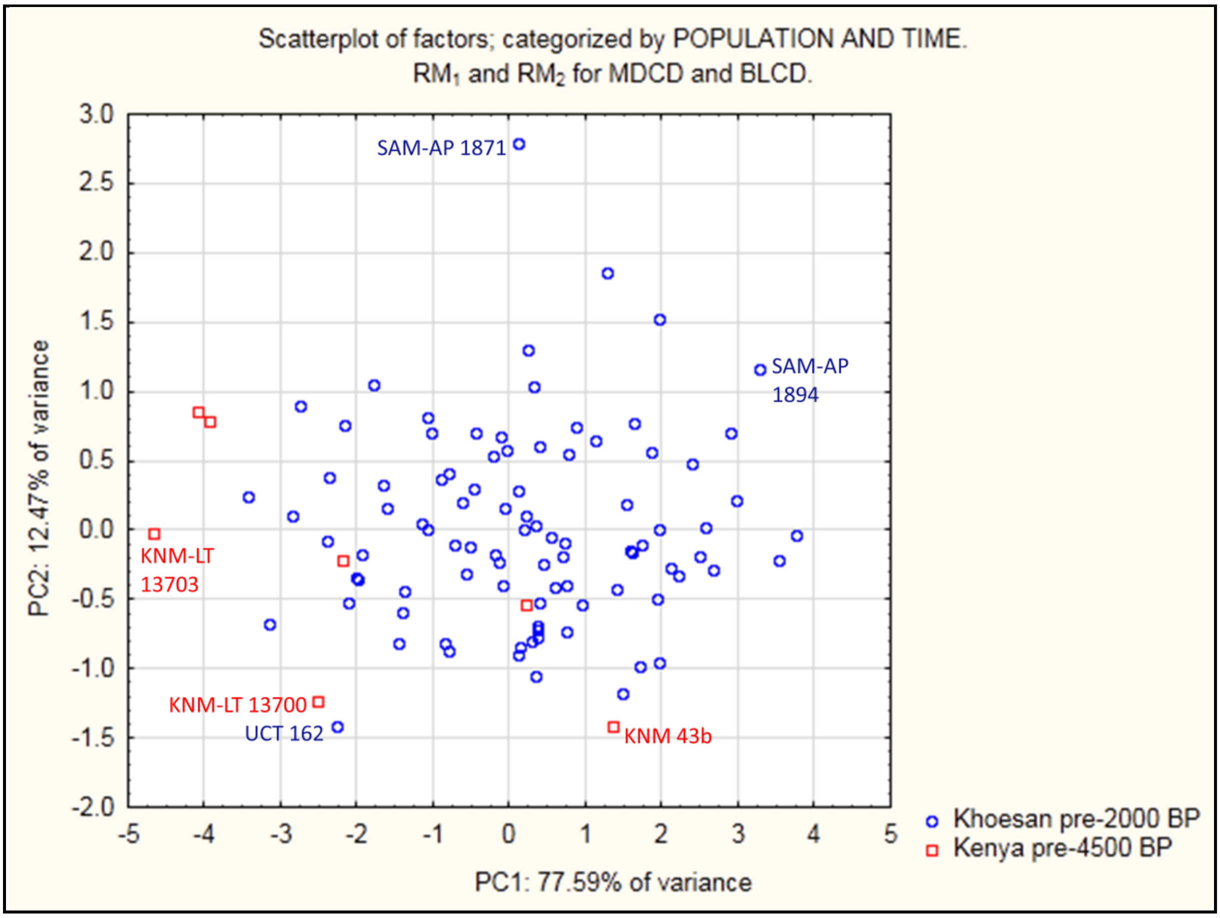


Fig. 5.49: Principal components plot of PC1 versus PC2. The PCA is based on RM_1 and RM_2 mesiodistal (MDCD) and buccolingual (BLCD) cervical diameters of pre-2000 BP and pre-4500 BP Khoesan and Kenyan populations respectively.

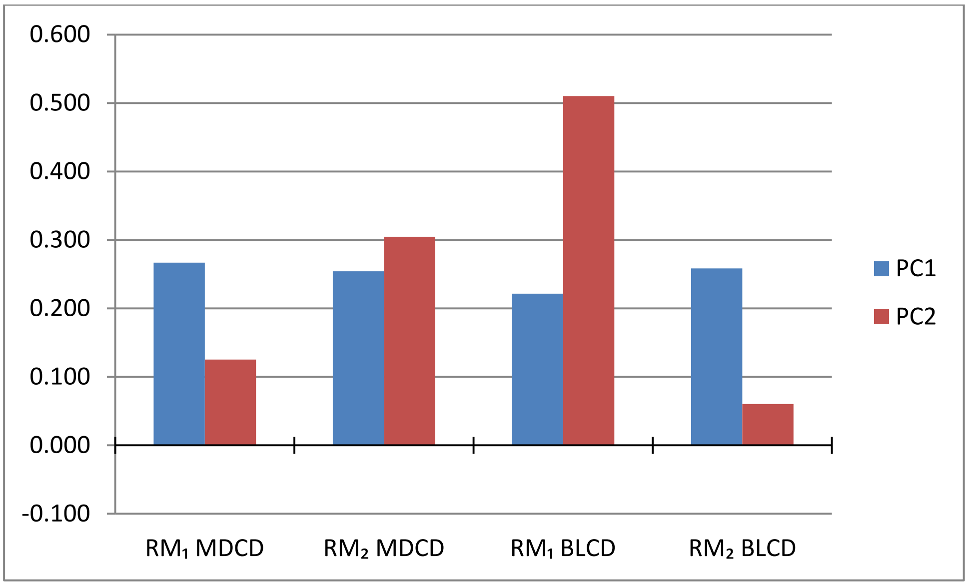


Fig. 5.50: Principal component loadings of PC1 and PC2 for lower first and second molar cervical dental measurements associated to Fig. 5.49.

The PCA of upper molar alternative diagonal cervical measurements (4 variables) from Kenya and Khoesan data sets is shown in Fig. 5.51. Here, the two groups are slightly less differentiated with comparable size/shape variation. However, some individuals such as the large Kenyan individual KNM-LT 13702 and small Khoesan individuals, including SAM-AP 4813 and UCT 180, appear at the extreme range of variation. As before, large Kenyan specimens (i.e. KNM-LT 27710 dated to *ca.* 8400 – 6000 BP) are comparable in cervical size to large Khoesan samples (i.e. UCT 374 dated to 9750 ± 100 (Pta-3086)). Component loadings (Fig. 5.52) for PC1 are similar in magnitude, suggestive of a size measure. PC2 loadings are somewhat comparable where LM^2 MBDLCD (0.351) is weighted the highest and LM^1 MBDLCD (0.152) the lowest, likely indicative of a size/shape variable.

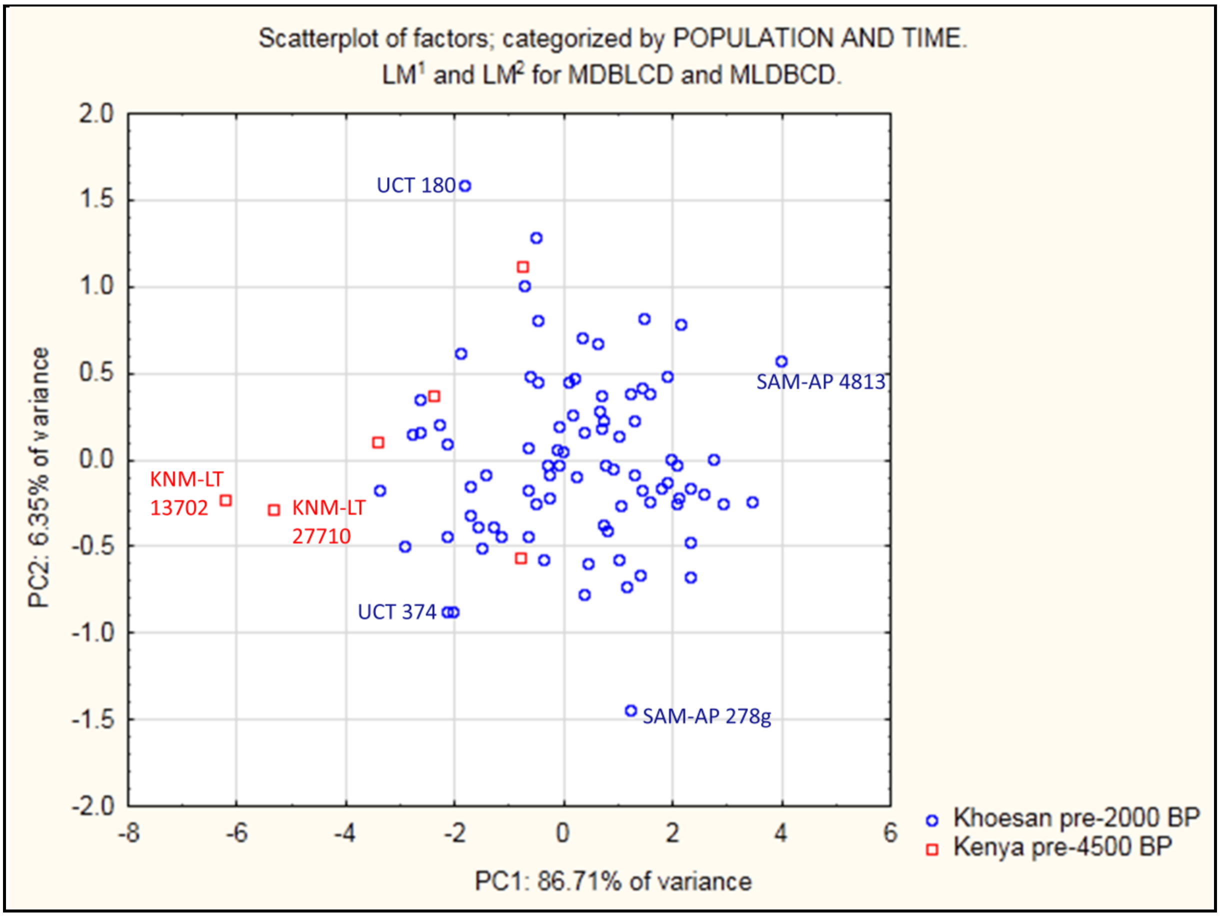


Fig. 5.51: Principal components plot of PC1 versus PC2. The PCA is based on LM^1 and LM^2 mesiodistal buccolingual (MDBLCD) and mesiolingual-distobuccal (MLDBCD) cervical diameters of pre-2000 BP and pre-4500 BP Khoesan and Kenyan populations, respectively.

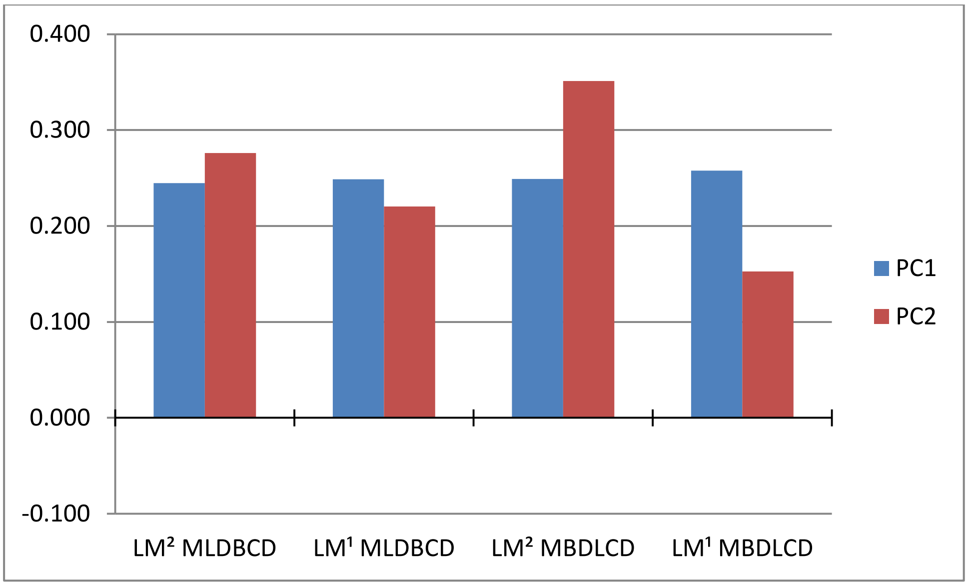


Fig. 5.52: Component loadings of PC1 and PC2 for lower first and second molar diagonal cervical dental measurements associated to Fig. 5.51.

The PCA of lower molar cervical measurements (4 variables) from Kenya (post-4500 BP) and Khoesan (post-2000 BP) temporal datasets is shown in Fig. 5.53. A similar pattern to previous analyses is shown with increased size and shape variation and more differentiation between the two groups. Large Kenyan individuals (EH 815, EM 343) and small Khoesan specimens (SAM-AP 4920a) appear at the extreme ranges of variation (PC1 = size). The two populations are clearly separated but some overlap between sample plots is observed. Interestingly, an outlying herder specimen (marked H on the plot), UCT 582 from Voëlvlei 1, Mossel Bay dated to 740 ± 40 (Pta-7178) is comparable to both Bromhead's site (i.e. EM 834 dated to *ca*. 2500 – 1500 BP) and Naishi Rock Shelter (i.e. E920-8 dated to <4500 BP) individuals. The only other identified Khoesan herder specimen (UCT 262) is located in the middle of the range of variation. Component loadings (Fig. 5.54) for PC1 are very similar in magnitude but PC2 loadings vary substantially; LM_2 MDCD and LM_1 BLCD PC2 loadings are weighted the highest (0.053 and 0.041, respectively), while LM_1 MDCD and LM_2 BLCD are weighted the lowest (0.011 and 0.005).

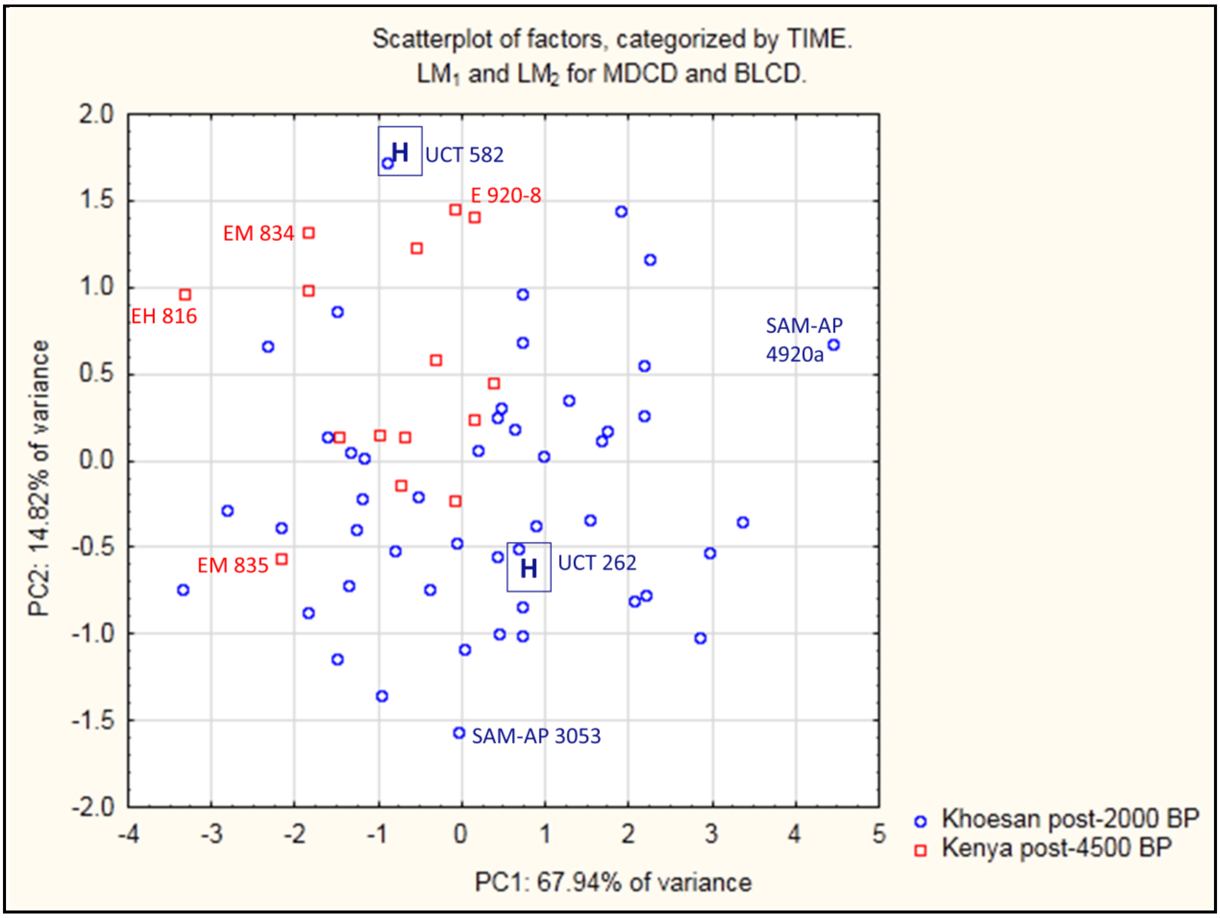


Fig. 5.53: Principal components plot of PC1 versus PC2. The PCA is based on LM_1 and LM_2 mesiodistal (MDCD) and buccolingual (BLCD) cervical diameters of post-2000 BP and post-4500 BP Khoesan and Kenyan populations, respectively.

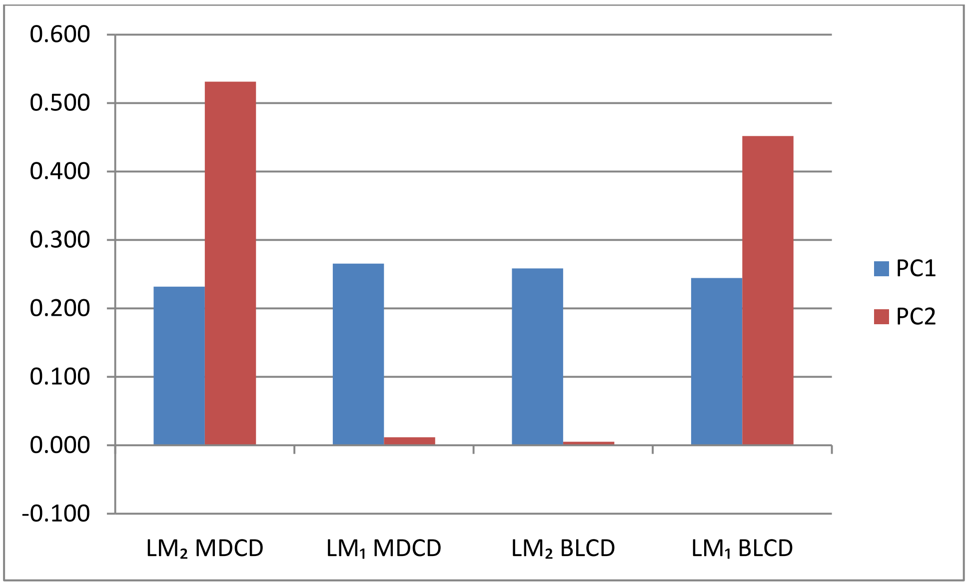


Fig. 5.54: Component loadings of PC1 and PC2 for lower first and second molar cervical dental measurements associated to Fig. 5.53.

The PCA of upper molar diagonal cervical measurements (4 variables) from Kenyan and Khoesan datasets illustrating pre- and post-4500 BP temporal separations for both populations is shown in Fig. 5.55. Large individuals from Kenya such as KNM-LT 13702 and KNM-LT 27710 from Lothagam are situated towards the left, while the smaller Khoesan individuals (i.e. SAM-AP 4813) are on the right, suggesting PC1 is related to size. Again, a closer relationship between Kenyan pre-4500 BP and Khoesan pre-4500 BP samples is observed, while more recent Kenyan material are comparable to recent Khoesan size/shape. There is little overlap between Khoesan post-4500 BP and earlier Kenyan (pre-4500 BP) samples. Component loadings are illustrated in Fig. 5.56. Loadings for both PC1 and PC2 are all positive but vary substantially. RM^2 MLDBCD PC2 loadings are weighted the highest (0.542), while RM^1 MLDBCD PC2 (0.058), the lowest.

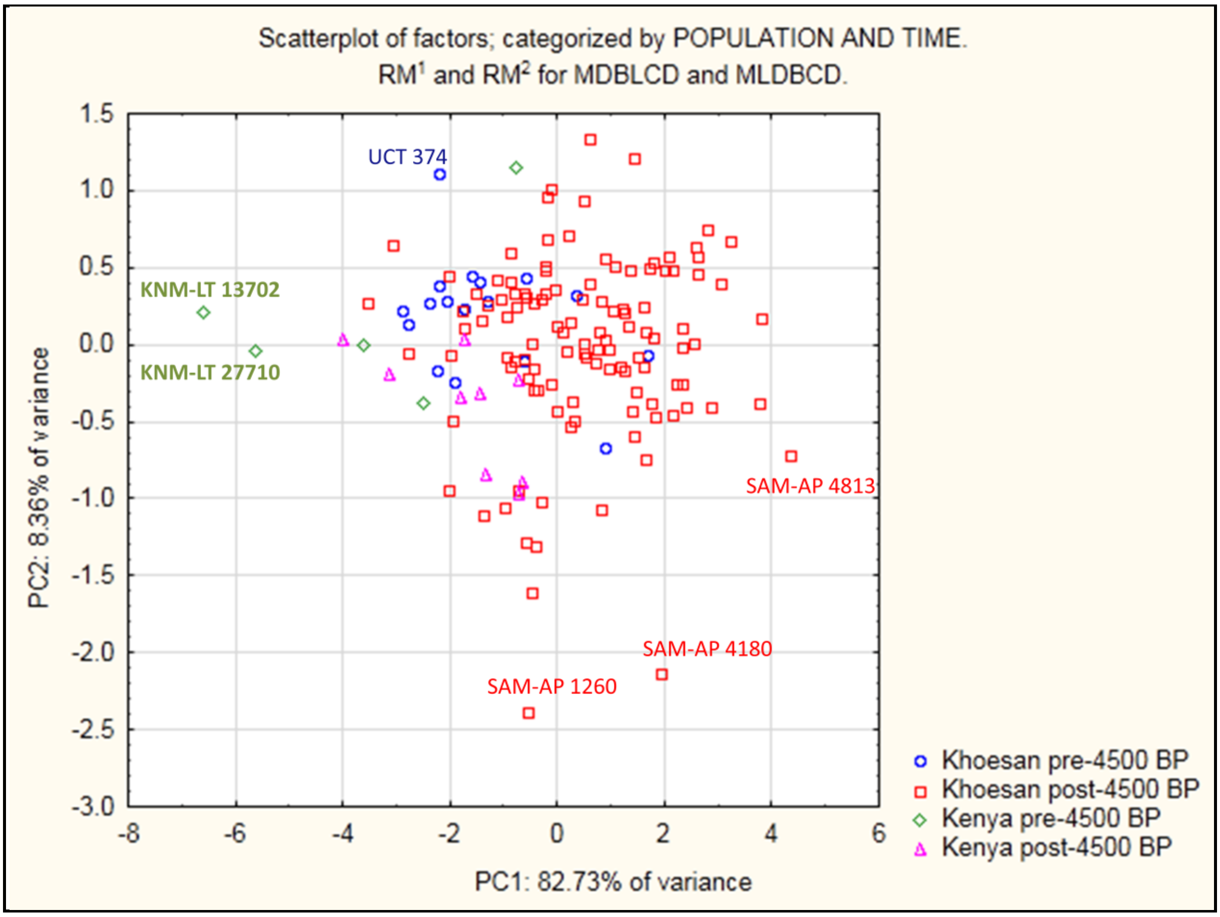


Fig. 5.55: Principal components plot of PC1 versus PC2. The PCA is based on RM_1 and RM^2 mesiodistal-buccolingual (MDBLCD) and mesiolingual- distobuccal

(MLDBCD) cervical diameters of both Khoesan and Kenyan pre- and post-4500 BP populations

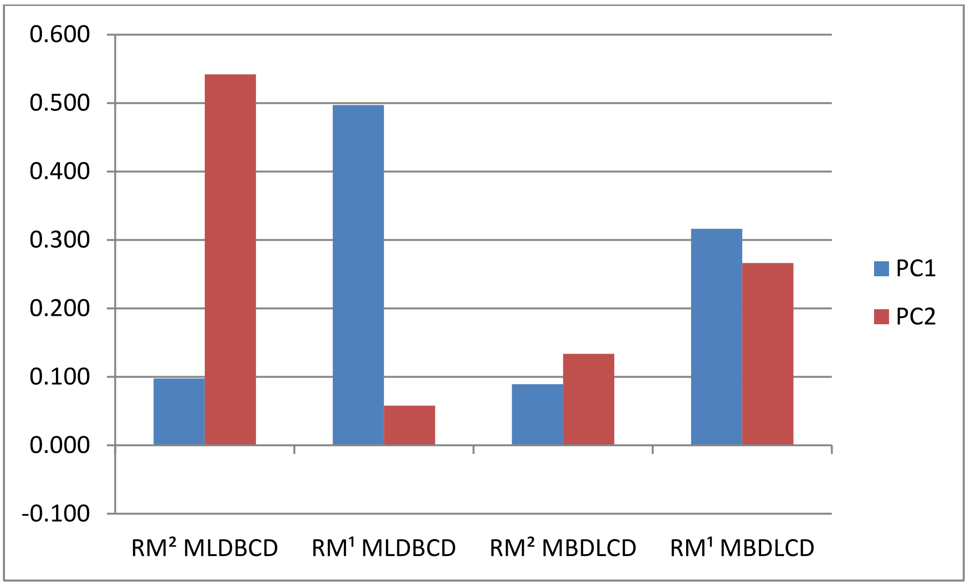


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Fig. 5.56: Component loadings of PC1 and PC2 for upper first and second molar diagonal cervical dental measurements associated to Fig. 5.55.

On the whole, Holocene Kenyan dental metric variation differs from Khoesan variation, with a number of individuals being considerably larger than Khoesan individuals.

NON-METRIC EVALUATIONS

Frequencies of up to 52 traits (depending on available data) were calculated for Holocene Kenyan and Khoesan samples and are presented as a bar graph in Fig. 5.57 (trait frequencies are available in Appendix 7). Trait frequencies were then tested for significance (using chi-square analyses) to identify overall differences and similarities between both populations. Only significant differences between populations will be discussed here. Further evaluations were then performed between temporally divided sub-groups. The first group consists of dentition from Kenyan post-4500 BP and Khoesan post-2000 BP populations, while the second group includes Kenyan pre-4500 BP and Khoesan pre-2000 BP individuals. Chi-square analyses were employed on up to 52 dental traits and p-values (≤ 0.05, 1 df) can be found in Table 5.14.

In general, I^1 shoveling, I^1 labial convexity and I^2 tuberculum dentale occur at much higher frequencies in the Kenyan data set. Significant differences between the Kenyan and Khoesan groups for these traits are observed in the two populations as a whole, except I^1 shoveling which only occurs between the Kenyan pre-4500 BP and Khoesan pre-2000 BP groups. The Bushman canine (CMR) occurs at a very high frequency in the Kenyan dentition (77.78%), higher than seen in the Khoesan (61.46%) but this difference is not significant. No canine traits present with notable differences but some premolar traits are dissimilar. P^3 accessory cusps and P_3 cusp variation demonstrate some difference during different time intervals. Additionally, the Tome's root, occurring in 23.21% of Khoesan, has a much stronger expression in the Kenyan dentition (75%). This trait's frequency is higher than most rates found in sub-Saharan Africa (Irish 1993, 1998a, 2013). Many lower molar traits are comparable between the two populations with only slight frequency variations between some traits; M_2 Y-groove, M_1 cusp number, M_2 cusp 6, M_1/M_2 cusp 7, M_2 root number, and M_3 torsomolar angle frequencies are similar. Differences are limited to mass-additive and groove traits including M_1 X and Y-grooves, M_1 distal trigonid crest and M_2 cusp # (these are not observed in during individual temporal groups), as well as M_1/M_2 cusp 5 and 6 (most notable in the group including Kenyan post-4500 BP and Khoesan post-2000 BP). Similarly, some Kenyan upper molar trait frequencies are comparable to Khoesan, including M^2 root number, M^1 large metaconule and M^3 parastyle. The Kenya M^1 enamel extension and M^1 metaconule are expressed at much lower frequencies than in the Khoesan, while peg-shaped upper third molars appear far more frequently in the Kenyan dataset; 64.3% compared to 22.8%. The M^1 Carabelli's trait occurs at a higher frequency in the Kenyan sample at a frequency of 30.4%, still lower than the reported frequency for sub-Saharan Africa (51.5% as reported by Irish (2013)). The trait only reflects a significant difference between Kenya post-4500 BP and Khoesan post-2000 BP groups. Intra-oral osseous traits such as the mandibular torus and rocker jaw demonstrate significant differences between the two populations where each trait appears at much higher frequencies in Kenyan dentition. Palatine torus only demonstrates a difference between pre-4500 BP Kenyan and pre-2000 BP Khoesan populations.

Based on the total number of significant p-values, analyses between the Khoesan and Kenyan groups as a whole demonstrate a number of differences. As a whole (i.e. inclusive of all time frames throughout the Holocene), 34.04% (16/47) of the traits are significantly different, including many of the high frequency traits identified in earlier analyses. Evaluating the two Kenyan/Khoesan temporal sub-groups separately yielded contrasting results to a merged approach, demonstrating more similarity between the Kenyan and Khoesan dentition (9/44 significant differences; 20.45%) within outlined time intervals. More incisor and premolar traits are significantly different in the pre-4500 BP Kenyan and pre-2000 BP Khoesan temporal sub-group, while lower molar traits predominantly drive difference in the Kenyan post-4500 BP and Khoesan post-2000 BP group. It is important to note that the difference between temporal sub-groups may also relate to regional variation as the Kenyan post-4500 BP dataset is predominantly from southern Kenya, while much of the pre-4500 BP data is from northern Kenya.

Fig 5.57: Khoesan and Holocene Kenyan trait frequencies.

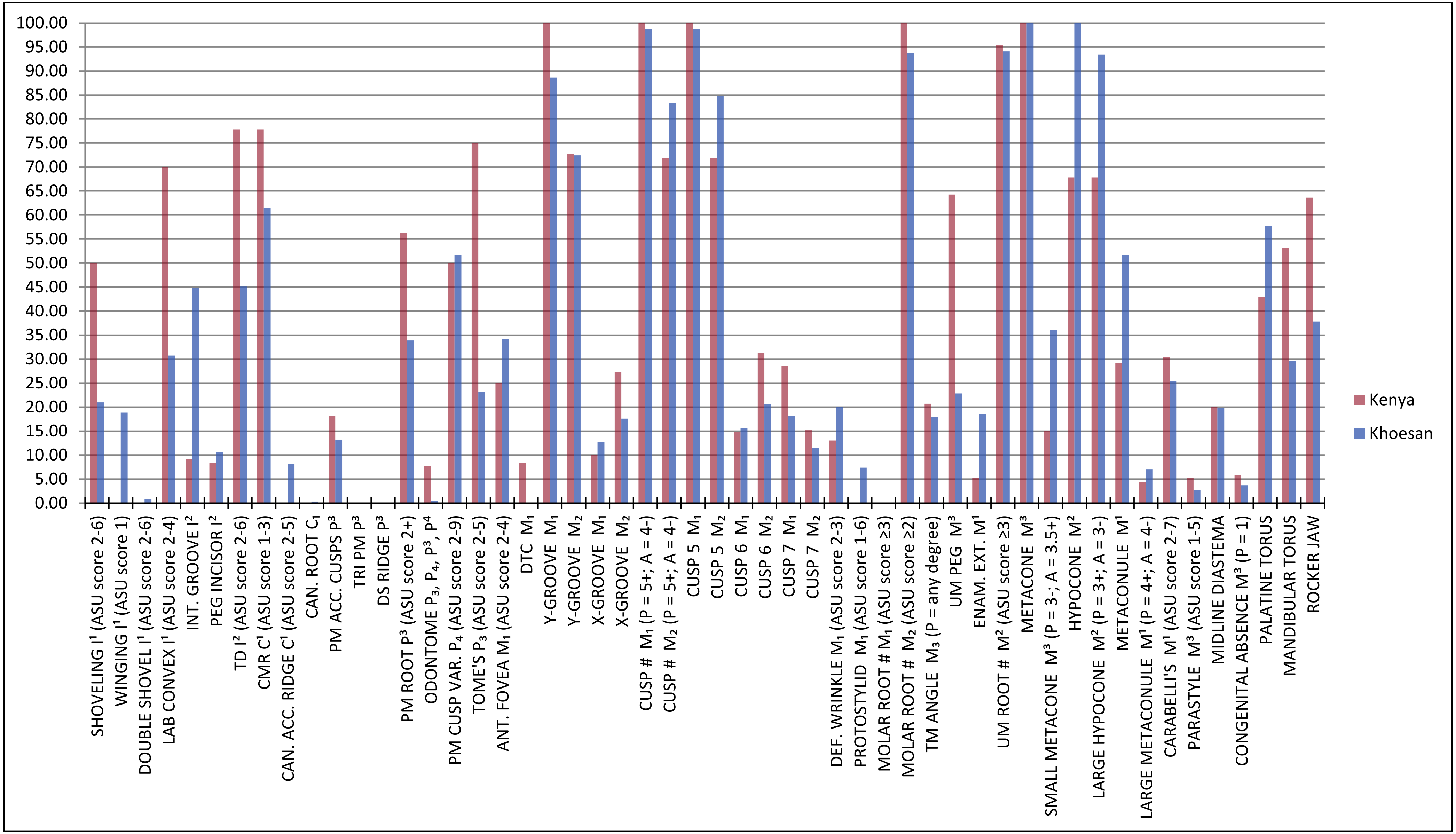


Table 5.14: Chi-square p-values (≤ 0.05, 1 df) between Kenya and Khoesan populations at various time intervals for 52 traits. Red and underlined values indicate significant differences.

TRAITS	Kenya and Khoesan (All Holocene)	KENYA post-4500 BP & Khoesan post-2000 BP	KENYA pre-4500 BP & Khoesan pre-2000 BP
SHOVELING I^1 (ASU score 2-6)	0.1032	0.6455	0.0000
WINGING I^1 (ASU score 1)	0.1512	0.4193	0.2519
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.7824	*	*
LAB CONVEX I^1 (ASU score 2-4)	0.0021	0.8965	0.1498
INT. GROOVE I^2	0.3120	0.5060	0.4372
PEG INCISOR I^2	0.7180	0.7408	0.2439
TD I^2 (ASU score 2-6)	0.0167	0.2104	0.0376
CMR C^1 (ASU score 1-3)	0.1140	0.5234	0.1572
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.3521	0.3774	0.5251
CAN. ROOT C_1	0.5612	*	*
PM ACC. CUSPS P^3	0.3599	0.0431	0.9027
TRI PM P^3	*	*	*
DS RIDGE P^3	*	*	*
PM ROOT P^3 (ASU score 2+)	0.0695	0.0559	0.1357
ODONTOME P^3, P^4, P_3, P_4	*	*	*
PM CUSP VAR. P_4 (ASU score 2-9)	0.2590	0.6777	0.0175
TOME'S P_3 (ASU score 2-5)	0.0387	0.4429	0.3275
ANT. FOVEA M_1 (ASU score 2-4)	0.3843	0.8792	0.1428
DTC M_1	0.0125	0.3961	*
Y-GROOVE M_2	0.3275	0.2329	0.6139
Y-GROOVE M_1	0.0334	0.0248	0.2376
X-GROOVE M_2	0.1272	0.0558	0.2048
X-GROOVE M_1	0.0456	0.6104	0.2922
CUSP # M_2 (P = 5+; A = 4-)	0.0002	0.2560	0.4288
CUSP # M_1 (P = 5+; A = 4-)	0.4918	*	0.7503
CUSP 5 M_1	0.0000	0.0020	0.0000
CUSP 5 M_2	0.4761	0.0182	0.1787
CUSP 6 M_1	0.1088	0.0402	0.2159
CUSP 6 M_2	0.9100	0.9190	0.6989
CUSP 7 M_1	0.3512	0.1580	0.8859
CUSP 7 M_2	0.1843	0.1989	0.5148
DEF. WRINKLE M_1 (ASU score 2-3)	0.3585	0.1681	0.4821
PROTOSTYLID M_1 (ASU score 1-6)	0.1103	0.1839	0.3333
ROOT # M_1 (ASU score >=3)	*	*	*
ROOT # M_2 (ASU score >=2)	0.1335	0.2143	0.5296
TM ANGLE M_3 (P = any degree)	0.7214	0.2796	0.8360
PEG M^3	0.0006	0.1764	0.6321

ENAM. EXT. M^1	0.0201	0.1063	0.3566
ROOT # M^2 (ASU score >=3)	0.7886	0.9659	0.3480
METACONE M^3	*	*	*
METACONE M^3 (P = 3-; A = 3.5+)	0.0434	0.3547	0.0171
HYPOCONE M^2	0.0000	0.0002	0.0000
HYPOCONE M^2 (P = 3+; A = 3-)	0.0000	0.0009	0.0023
METACONULE M^1	0.0145	0.1792	0.1507
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.6284	0.8010	0.4620
CARABELLI'S M^1 (ASU score 2-7)	0.6063	0.0318	0.9461
PARASTYLE M^3 (ASU score 1-5)	0.2959	0.5192	0.3952
MIDLINE DIASTEMA	0.9902	0.5782	0.3976
CONGENITAL ABSENCE M^3 (P = 1)	0.5218	0.4897	0.5442
PALATINE TORUS	0.1804	0.9746	0.0055
MANDIBULAR TORUS	0.0060	0.0132	0.3116
ROCKER JAW	0.0170	0.4729	0.2617
Total significant values	16	9	9

MEAN MEASURE OF DIVERGENCE ANALYSIS

The mean measure of divergence statistical procedure (MMD) was employed here as an estimate of morphological distance between Khoesan and Kenyan populations. Results are presented in Table 5.15. Significantly correlated traits (LM_1 anterior fovea and LM_1 deflecting wrinkle; p = 0.0255) and samples associated with trait degrees of expression produce errors, and were therefore removed; both data sets were analysed using 45 discrete traits.

Red and underlined MMD's indicate those samples which differ from each other at the 0.025 significance level. Insignificant MMD's denote samples that are morphologically indistinguishable from each other. The mean measure of divergence results highlight the phenetic differences between Khoesan and Kenya dental data, supporting chi-square and frequency evaluations. A degree of morphological similarity within the Kenya population for the selected suite of dental and osseous traits is also demonstrated through time.

Hypothesis 3b considered the differences between Khoesan dentition and a Kenyan sample to assess broader regional differences in the Holocene across Africa.

Overall, Kenyan and Khoesan dental samples demonstrate a number of differences in morphology, size and shape. Metric evaluations have highlighted consistent size differences between the two populations; Kenyan dentition generally presents with much larger teeth. Some Early Holocene Kenyan teeth, although larger, are comparable in size, shape and to a degree morphology, to Khoesan Early Holocene dentition and larger Mid-Late Holocene Khoesan teeth also demonstrate some similarity to Kenyan post 4500 BP dentitions. However, although there is some size/shape overlap, a clear distinction between the two groups is discernible. Morphological variation between the two populations is also varied. Many trait frequencies differ only slightly, while there are those (i.e. I^2 tuberculum dentale, P_3 Tome's root, M_1 Y-groove and M^3 hypocone) that differ substantially. The MMD analysis also demonstrates a degree of phenetic distance between the Kenyan and Khoesan populations. While comparisons with the Mid-Late Pleistocene sample looked at continuity across time, Hypothesis 3b evaluated the possible continuity between dental populations over broader geographic regions and has demonstrated that there are statistically significant differences in morphological and metric variation between Holocene Khoesan and Holocene Kenyan teeth.

Table 5.15: Mean measure of divergence values between Khoesan and Kenya samples. Red and underlined values indicate those samples which differ from each other at the 0.025 significance level.

	Khoesan	**Kenya**	**Kenya pre-4500 BP**	**Kenya post-4500 BP**
Khoesan		0.4300	0.2605	0.3130
Kenya			0.0620	0.0624
Kenya pre-4500 BP				0.0496
Kenya post-4500 BP				

As an interesting addition, PCAs were also performed to evaluate the relationship between Holocene Khoesan and Kenyan, and Mid-Late Pleistocene specimens. Unfortunately, the Mid-Late Pleistocene, and to a certain degree the Kenyan, samples are few and led to missing data driving the minimal variables used and only two PCAs yielded results with all three population groups reflected. Results (depicted in Figs. 5.58 and 5.59), were obtained from lower second molar measurements and included all Holocene and Mid-Late Pleistocene timeframes. Component loadings for PC1 are positive and similar in magnitude, indicating that this is likely a size variable, but vary substantially for PC2 with LM_2 BLCD being weighted the highest (0.689) and LM_2 MBDLCD, the lowest (0.0004). In Fig. 5.57, the larger Mid-Late Pleistocene samples on the left (SAM-AP 6222; SAM-AP 6226 and SAM-AP 6229, all from Klasies River Mouth) fall within the range of Khoesan variation (albeit at the edge of this range) but do not overlap with Kenyan variation. There is a significant overlap between the Khoesan and Kenyan data, although a few Kenyan individuals are at the extreme of Khoesan variation. The Mid-Late Pleistocene specimen from Mumbwa in Zambia (A 343) falls firmly in the middle of the range of variation of both Kenyan and Khoesan teeth.

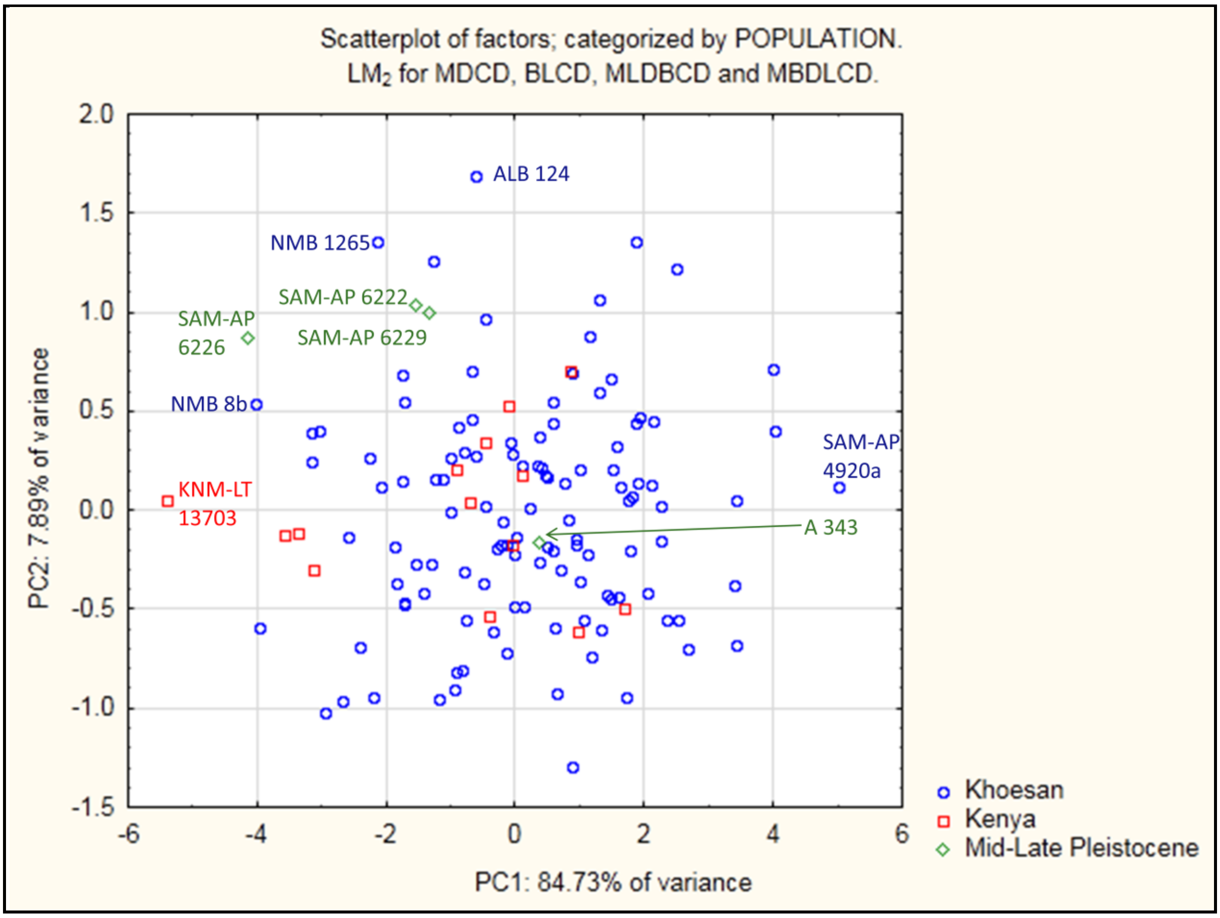


Fig. 5.58: Principal components plot of PC1 versus PC2. The PCA is based on LM_2 mesiodistal (MDCD), buccolingual (BLCD), mesiolingual-distobuccal (MLDBCD) and mesiodistal buccolingual (MDBLCD) cervical diameters (5 variables) of Khoesan, Kenyan and Mid-Late Pleistocene samples from all time periods.

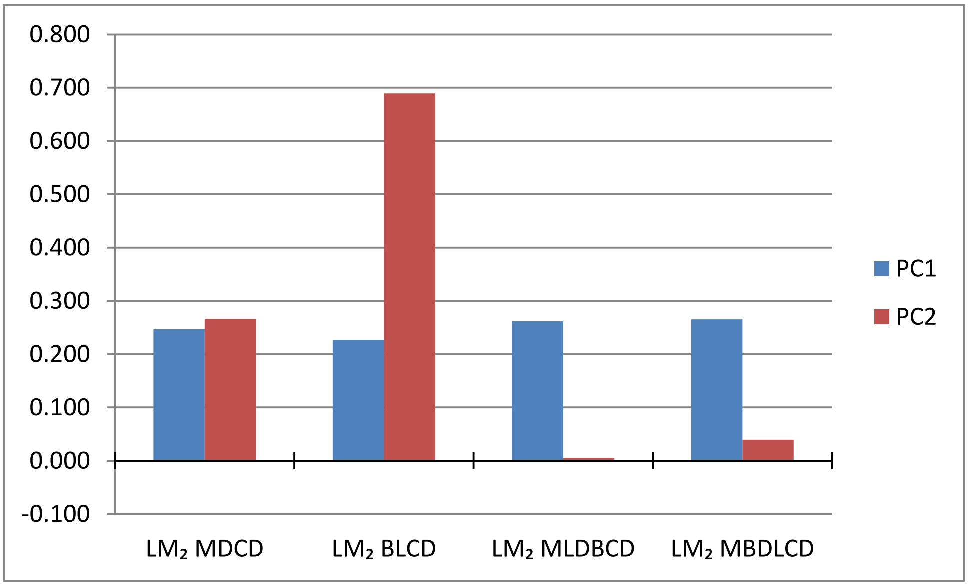


Fig. 5.59: Component loadings of PC1 and PC2 for LM_2 cervical dental measurements associated to Fig. 5.58.

Results depicted in the PCA in Fig. 5.60 are comparable. All Mid-Late Pleistocene samples (SAM-AP 6223, BC 2 and SAM-AP 6225) fall within the range of Khoesan variation, while some are outside of the Kenyan range of variation. There is considerable overlap between Kenyan and Khoesan variation, although a number of Kenyan individuals are outside of the Khoesan range. One Mid-Late Pleistocene specimen (SAM-AP 6282 from Die Kelders) falls mid-range between Kenyan and Khoesan dentition, while a final specimen (SU 15 from Cave of Hearths) appears at the edge of Khoesan variation but well within the range of Kenyan variation. SU 15 is a larger individual and often appears at the extreme range of Khoesan variation (as seen in Mid-Late Pleistocene evaluation earlier in this chapter). Component loadings (Fig. 5.61) indicate that PC1 loadings are positive and of a comparable magnitude, suggesting this is a size component. PC2 loadings vary; RM2 MDCD (0.658) is weighted the highest, while RM2 BLcrD (0.092), the lowest, suggestive of a size/shape variable. The PCA plot in conjunction with PC2 component loadings suggest that Mid-Late Pleistocene size/shape may be more variable than the previous PCA demonstrates but further data is needed to answer this question.

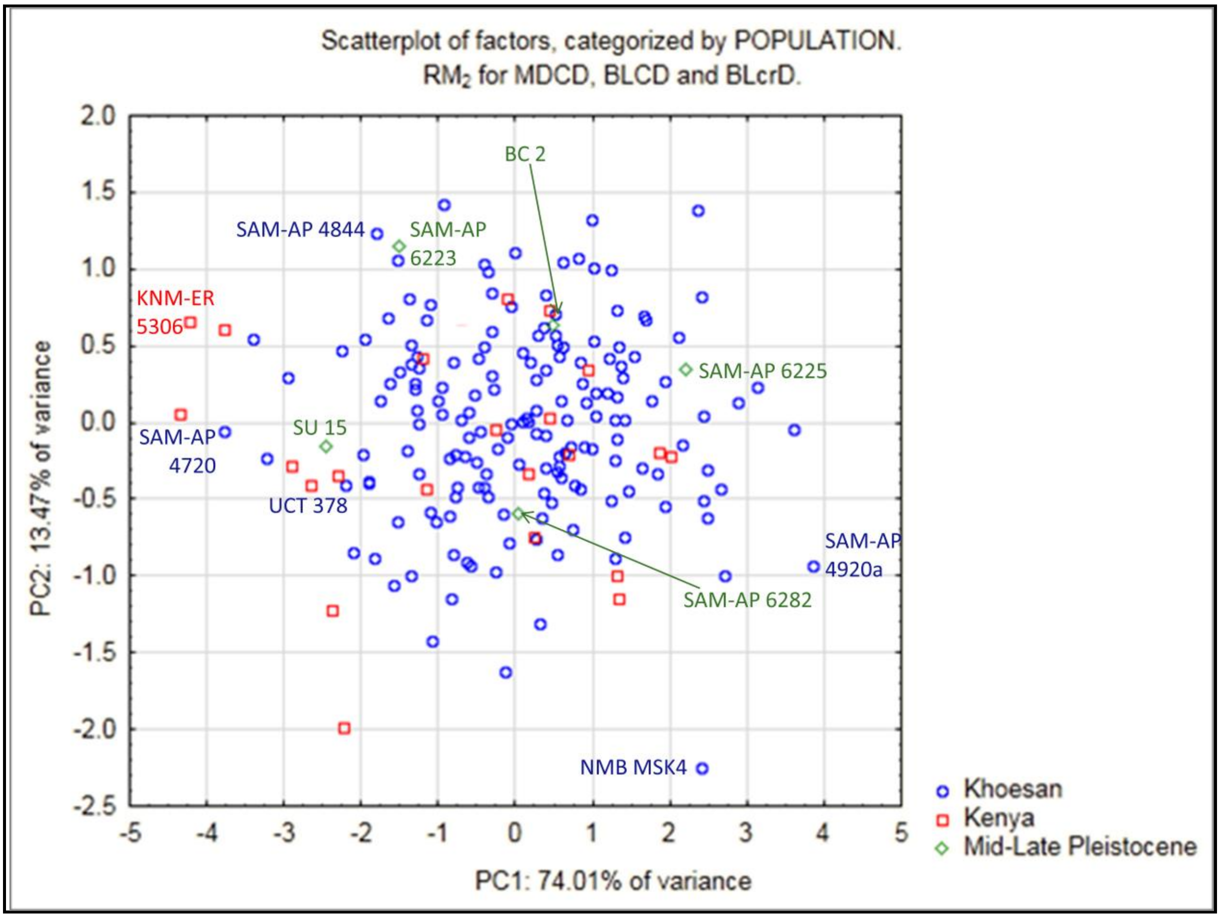


Fig. 5.60: Principal components plot of PC1 versus PC2. The PCA is based on RM_2 mesiodistal (MDCD) and buccolingual (BLCD) cervical diameters and buccolingual (BLcrD) crown diameters (4 variables) of Khoesan, Kenyan and Mid-Late Pleistocene samples from all time periods.

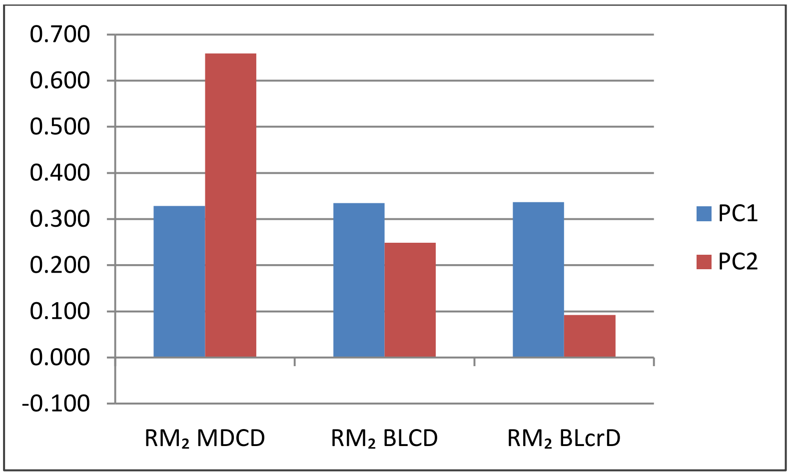


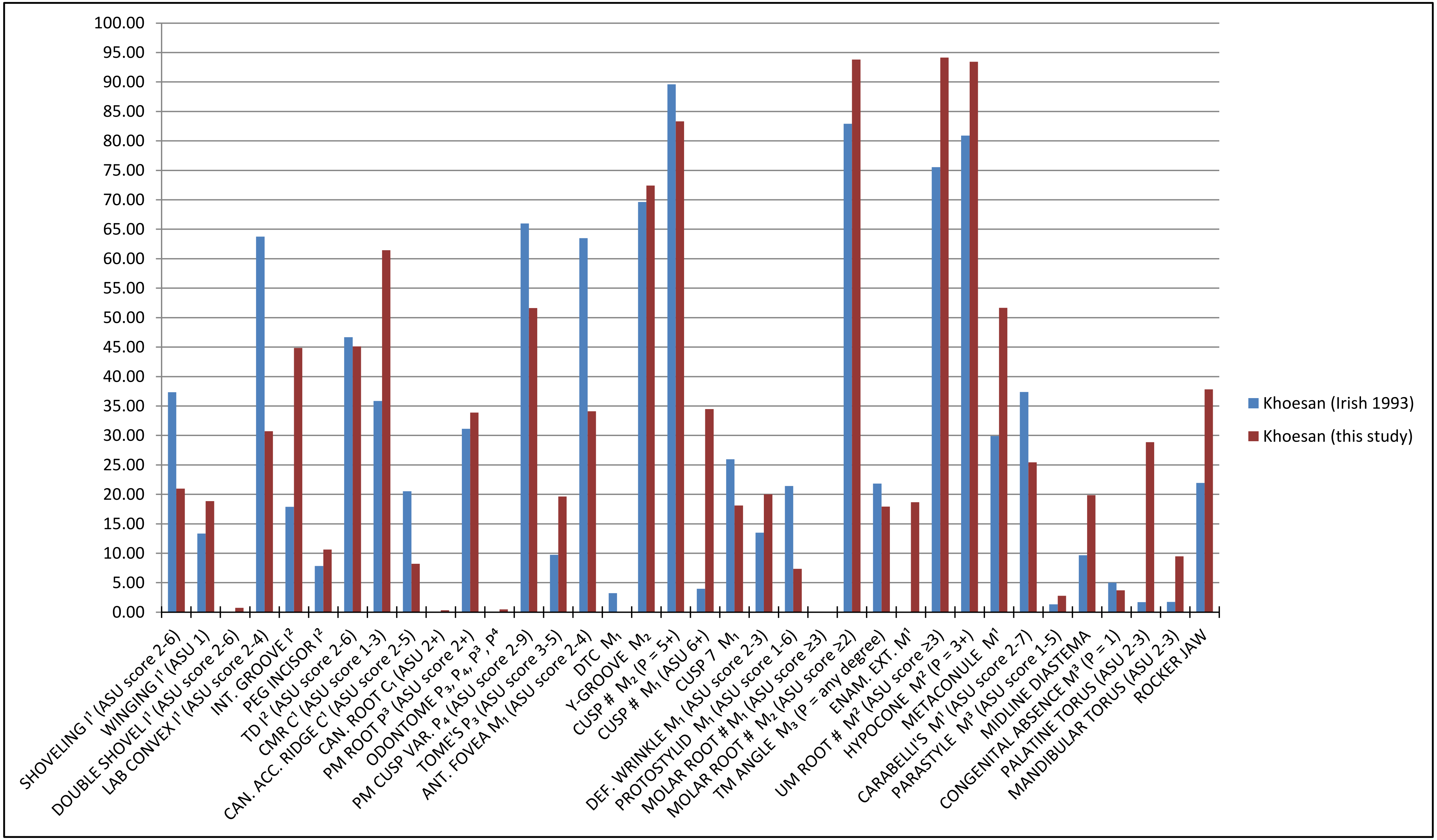
Fig. 5.61: Component loadings of PC1 and PC2 for RM_2 cervical and crown dental measurements associated to Fig. 5.60.

BROADER DENTAL COMPARISONS

In this final section, Irish's (1993) Khoesan morphological dental appraisal is compared to the dental map obtained in this study. Also, the Khoesan dental map obtained here is compared to the well-known sub-Saharan African dental complex (Irish 1993, 1997), or Afridonty (Irish 2013). This is itself, however, a comparative analysis and therefore, a Khoesan/sub-Saharan comparison cannot be complete without an evaluation of Khoesan dental relationships relative to other world populations. Comparisons between the Holocene Khoesan dentition and other global dental complexes are necessary for understanding the placement of this dental group.

Early research by Irish (1993) outlined Khoesan dentition for a suite of 36 traits and comparisons between that study and the Khoesan trait frequency data obtained here are illustrated in the bar graph in Fig. 5.62, while chi-square p-values can be found in Table 5.16. Although Irish (1993) separates Khoekhoe and San samples in his study, the frequencies from both populations have been combined here for overall comparative purposes. Breakpoints (ASU scores) used by Irish (1993) vary for four traits used to identify the Khoesan dental map in this chapter. To conform to Irish's (1993) breakpoints and allow for accurate comparisons, the breakpoints for those traits have been amended. These include M_1 cusp #, P_3 Tome's root, palatine torus and mandibular torus. A number of significant differences between Irish's (1993) research and data from this study are demonstrated. With regards to incisor traits, Irish (1993) identifies much higher frequencies of I^1 shoveling and I^1 labial convexity than is found here, while the I^2 interruption groove in this study displays significantly higher frequencies in comparison to Irish's data. Some incisor traits are, however, similar – i.e. I^2 tuberculum dentale in Irish (1993) data presents at 46.67%, while they occur at 45.12% in this study. The CMR (Bushman canine) is far more prevalent than previously thought, occurring at a significantly higher frequency (61.46%) in this study, compared to previous research (35.87%). Additionally, the prevalence of the upper canine accessory ridge between the two studies is significantly different. Premolar traits are largely similar, including P^3 root number and P_3 Tome's root, with the exception of a difference between P_4 cusp variation. It is surprising that the frequencies for P_3 Tome's root correspond considering Irish (1993) was limited to a large amount of cast material which does not necessarily record root traits. Of the eleven lower molar trait frequencies compared, four demonstrate marked differences; in this study M_1 anterior fovea, and M_1 protostylid present with considerably lower frequencies than previously assessed, while 6+ cusped M_1's and ≥2-rooted M_2's occur at a significantly higher frequency in this study. Remaining lower molar traits are similar, with only minor frequency variations between the two datasets. The most frequency fluctuations are observed in upper molar traits; marked differences are demonstrated in all but one (M^3 parastyle is similar). Interestingly, previously unidentified M^1 enamel extensions, are present (18.66%) in this study. Significant increases are identified in the intra-oral osseous traits palatine torus and rocker jaw and other features such as the appearance of the midline diastema. Overall, 18 of the 36 traits assessed show significant differences in frequency between the two datasets, while the remaining trait frequencies are statistically indistinguishable (see Table 5.16).

Fig. 5.62: Frequency comparisons for 36 traits between Khoesan data (this study) and Irish's (1993, 1997) combined Khoekhoe and San data.



As outlined in Chapter 2, Irish's (1993) work on Khoekhoe and San populations was based on 19th and 20th century dentitions. A comparison between trait frequencies of the most recent Khoesan data groups from this study (located in Region A) and Irish (1993) Khoekhoe and San data from largely from the same region (see Appendix 8.2 for bar graph), reveals a somewhat different pattern to earlier comparisons (see Table 5.16). Less trait difference is observed (9/36 traits are significant) between the two groups in contrast to the differences observed between the collective Khoesan data from Irish (1993) and this study. This is suggestive of a closer affinity between Region A and Irish's (1993) Khoekhoe populations. Interestingly, upper molar traits remain the most variable, while most other trait frequencies are comparable. Testing trait frequency significance between Irish's (1993) Khoesan data and this study's first millennium BP Khoesan data also indicates more similarity (11/36 significant differences) than seen in the analyses that includes the entire Holocene sample. These results suggest that although 19th and 20th century Khoesan dentition changed (due to admixture, genetic drift, geographical separation, etc.), there was retention of some earlier Holocene Khoesan dental morphology (i.e. I^2 tuberculum dentale and M_1 cusp 7) in recent Khoesan populations. Although Irish's (1993) data suggests a degree of population difference between the Khoekhoe and San populations, this difference is most likely due to sample selection. If this is true, the disparity Irish (1993) shows between his Khoekhoe and San data sets may relate to the disparity identified in this study between Region A and other regions within the Khoesan data set.

Table 5.16: Chi-square p-values (≤ 0.05, 1 df) for 36 traits evaluated between Khoesan data from this study and Irish (1993) data. All breakpoints are identical.

TRAITS	**Khoesan data from this study and Irish (1993) Khoekhoe and San combined data**	**1-0 ka Khoesan data from this study and Irish (1993) Khoekhoe and San combined data**	**Region A from this study and Irish (1993) Khoekhoe and San combined data**
SHOVELING I^1 (ASU score 2-6)	**0.0260**	0.1495	0.5568
WINGING I^1 (ASU score 1)	0.6013	0.9570	0.3909
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.4079	*	*
LAB CONVEX I^1 (ASU score 2-4)	**0.0000**	**0.0000**	0.0578
INT. GROOVE I^2	**0.0128**	0.0839	0.3703
PEG INCISOR I^2	0.7619	**0.0005**	**0.0416**
TD I^2 (ASU score 2-6)	0.8391	0.4177	0.9234
CMR C^1 (ASU score 1-3)	**0.0010**	0.9359	0.9481
CAN. ACC. RIDGE C^1 (ASU score 2-5)	**0.0324**	0.0783	0.1441
CAN. ROOT C_1	0.7112	0.2289	0.2449
PM ROOT P^3 (ASU score 2+)	0.6208	0.2842	0.5492
ODONTOME P^3, P^4, P_3, P_4	*	*	0.0859
PM CUSP VAR. P_4 (ASU score 2-9)	**0.0309**	0.1329	0.2670
TOME'S P_3 (ASU score 2-5)	0.1274	0.1034	0.0981
ANT. FOVEA M_1 (ASU score 2-4)	**0.0004**	**0.0128**	0.3997
DTC M_1	0.1196	0.4161	*
Y-GROOVE M_2	0.5889	0.9431	0.4405
CUSP # M_2 (P = 5+; A = 4-)	0.0787	0.1523	0.2896
CUSP # M_1 (P = 6+; A = 4-)	**0.0000**	**0.0000**	**0.0269**
CUSP 7 M_1	0.0993	0.3903	0.7808
DEF. WRINKLE M_1 (ASU score 2-3)	0.2550	0.7268	0.0794
PROTOSTYLID M_1 (ASU score 1-6)	**0.0003**	**0.0064**	0.0546
ROOT # M_1 (ASU score >=3)	*	*	*
ROOT # M_2 (ASU score >=2)	**0.0137**	0.1800	0.4020
TM ANGLE M_3 (P = any degree)	0.4460	0.2243	0.6121
ENAM. EXT. M^1	**0.0016**	**0.0004**	**0.0073**
ROOT # M^2 (ASU score >=3)	**0.0002**	**0.0000**	**0.0000**
HYPOCONE M^2 (P = 3+; A = 3-)	**0.0005**	0.1468	**0.0442**
METACONULE M^1 (ASU 2-5)	**0.0011**	**0.0000**	**0.0000**
CARABELLI'S M^1 (ASU score 2-7)	**0.0372**	0.1388	0.3575
PARASTYLE M^3 (ASU score 1-5)	0.4964	**0.0022**	**0.0365**
MIDLINE DIASTEMA	**0.0154**	**0.0000**	**0.0003**
CONGENITAL ABSENCE M^3 (P = 1)	0.5266	0.1326	0.8200
PALATINE TORUS (ASU 2-3)	**0.0000**	**0.0001**	0.3979
MANDIBULAR TORUS (ASU 2-3)	0.5890	0.7381	0.0741
ROCKER JAW	**0.0469**	0.9148	**0.0095**
Total significant values	**18**	**11**	**9**

*no evaluation possible

The Khoesan, when compared to sub-Saharan African dental morphology as a whole, differ significantly. Fig. 5.63 illustrates a bar graph comparing Khoesan data from this study to the pooled sub-Saharan dental data from Irish (1993, 1997; 1998b). These pooled data include the Sub-Saharan African Dental Complex (SSACD), more recently termed Afridonty (Irish 2013), which will be discussed when global comparisons are made below. For the sake of convenience, Irish's (1993, 1997) frequency data are reproduced in Appendix 8.1. Table 5.17 provides significant p-values for comparisons between these data. Out of 36 traits assessed, 21 (58.33%) demonstrate very different frequencies across all teeth (incisors, canines, premolars and molars) and other features (intra-oral osseous traits and the midline diastema). Those traits that correspond to Afridonty include many incisor traits such as I^1 shovelling, I^2 tuberculum dental and I^2 interruption groove, as well as one canine trait (the lower canine root) and two premolar traits including the P_3 Tome’s root. Of the eleven lower molar traits, six are significantly different, while upper molar traits demonstrate the most difference with all but one trait significantly different between the groups. The midline diastema and all three intra-oral osseous traits differ. When comparing the SSADC (those marked with ★ on the bar graph in Fig. 5.63 and Table 5.17) to the Khoesan dental map, trait frequencies are significantly different for 9/14 SSADC traits. These include the two traits seldom recorded globally (I^1 labial convexity and midline diastema). The traits that are similar between the Khoesan data from this study and the SSADC include the low frequencies of I^1 double shovel and M^3 congenital absence, the prevalence of the P_3 Tome’s root, and the high frequency of M_2 cusp and root #. Remaining traits all show marked differences, demonstrating that the data from this study does not adequately fit the complex, while SSADC traits are not ubiquitous within the sample.

Fig. 5.63: Sub-Saharan African and Khoesan frequencies for 36 traits. Traits included in the Sub-Saharan African Dental Complex are marked with ★ on the bar graph.

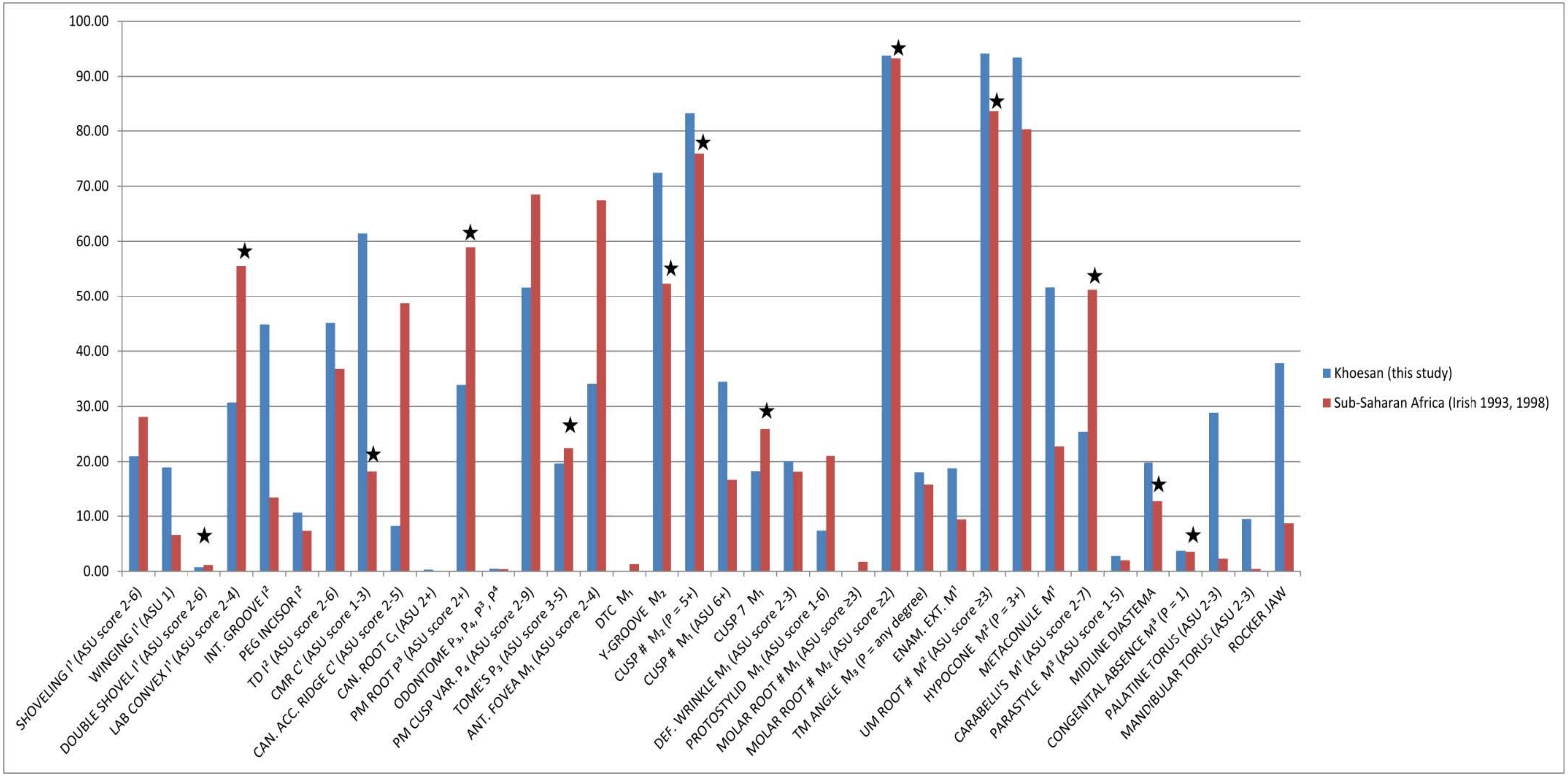


Table 5.17: Chi-square p-values (≤ 0.05, 1 df) for 36 traits between pooled sub-Saharan African dentitions, which includes the SSADC* (Irish 1993, 1998) and Khoesan data from this study. Breakpoints are identical.

TRAITS	**P-VALUES**
SHOVELING I^1 (ASU score 2-6)	0.1965
WINGING I^1 (ASU score 1)	**0.0002**
*DOUBLE SHOVEL I^1 (ASU score 2-6)	0.7032
*LAB CONVEX I^1 (ASU score 2-4)	**0.0000**
INT. GROOVE I^2	0.0505
PEG INCISOR I^2	0.5090
TD I^2 (ASU score 2-6)	0.1524
*CMR C^1 (ASU score 1-3)	**0.0000**
CAN. ACC. RIDGE C^1 (ASU score 2-5)	**0.0000**
CAN. ROOT C_1	0.2917
*PM ROOT P^3 (ASU score 2+)	**0.0000**
ODONTOME P^3, P^4, P_3, P_4	0.3870
PM CUSP VAR. P_4 (ASU score 2-9)	**0.0004**
*TOME'S P_3 (ASU score 2-5)	0.6489
ANT. FOVEA M_1 (ASU score 2-4)	**0.0000**
DTC M_1	0.3161
*Y-GROOVE M_2	**0.0000**
CUSP # M_2 (P = 5+; A = 4-)	0.0695
CUSP # M_1 (P = 6+; A = 4-)	**0.0000**
*CUSP 7 M_1	**0.0175**
DEF. WRINKLE M_1 (ASU score 2-3)	0.6388
PROTOSTYLID M_1 (ASU score 1-6)	**0.0000**
ROOT # M_1 (ASU score >=3)	**0.0165**
*ROOT # M_2 (ASU score >=2)	0.7961
TM ANGLE M_3 (P = any degree)	0.4975
*ENAM. EXT. M^1	**0.0001**
*ROOT # M^2 (ASU score >=3)	**0.0002**
HYPOCONE M^2 (P = 3+; A = 3-)	**0.0000**
METACONULE M^1 (ASU 2-5)	**0.0000**
*CARABELLI'S M^1 (ASU score 2-7)	**0.0000**
PARASTYLE M^3 (ASU score 1-5)	0.5362
*MIDLINE DIASTEMA	**0.0057**

CONGENITAL ABSENCE M^3 (P = 1)	0.9672
PALATINE TORUS (ASU 2-3)	**0.0000**
MANDIBULAR TORUS (ASU 2-3)	**0.0022**
ROCKER JAW	**0.0000**
Total significant values	**21**

Based on Irish's (1993) evaluations and a comparison between sub-Saharan and other world dental complexes, he proposed that a set of derived and archaic dental traits (the sub-Saharan African dental complex) differentiate these people from others around the globe. These traits have been discussed in detail but in summary include high frequencies of the UC mesial ridge, two-rooted P^3, P$_3$ Tome's root, M$_2$ Y-5 pattern, M$_1$ cusp 7, two-rooted M$_2$, three-rooted M^2, M^1 Carabelli's trait and low frequencies of I^1 double shovel, M^1 enamel extension and M^3 agenesis[6]. I^1 labial convexity and the midline diastema are considered part of the SSADC but this trait is seldom scored globally and therefore world variation is unknown. To evaluate the 'fit' of this study's Khoesan data to the SSADC, the same comparisons need to be made. Using mean frequencies from published data (T. Hanihara 2008; Irish 1997, 2013; G.R. Scott and Turner 2000) that use similar scoring breakpoints (morphological thresholds), Table 5.18 presents frequencies for 31 traits from four generalised world dental complexes and one subgroup (Australia, Melanesia and New Guinnea, abbreviated Aus.), as well as Khoesan frequencies from this study for comparison. Congruent to Irish (1997), sub-Saharan Africa demonstrates the most similarity to Western Eurasia (and particularly North Africa, *cf*. Irish 1998c). Sub-Saharan Africa exhibits a large amount of divergence from the Sundadonts but less so than the Sinodonts, who are most dissimilar (also noted by Irish (1997) who provides an MMD statistic of 0.671, indicative of a large amount of phenetic difference). Some trait similarities between the Aus. group and sub-Saharan Africa are apparent – i.e. I^1 shovelling, M$_2$ root number and M$_1$ deflecting wrinkle – but marked frequency fluctuations identify more dissimilarity than affinity. High frequency traits such as M$_2$ Y- groove pattern, M$_2$ cusp number (and by extension, low frequencies of the 4-cusped M$_2$ in Table 5.18), M$_2$ and M^2 root number, and very low frequencies of I^1 double shovelling are extreme in comparison to world rates (Table

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[6] High frequencies of I^1 labial convexity and I^1 midline diastema are also demonstrated but due to inadequate world scoring and recording of these traits, they are not included.

5.18). Khoesan traits that present with low frequencies instead of the expected higher frequencies outlined by the SSADC include: i) the 2-rooted P^3 with a 33.88% frequency, lower than what is seen in all compared complexes except the Sinodonts; ii) M_1 cusp 7 with a 11.54% frequency, comparable to all compared dental complexes except sub-Saharan Africa; iii) M_1 Carabelli's trait that occurs at 25.42% in the Khoesan data set, similar to rates found in Western Eurasia and Sundadonts. SSADC expected very low frequencies for M^1 enamel extension and M^3 agenesis (although M^3 congenital absence is minimal) are not found in the Khoesan. Rather, both these traits appear at frequencies similar to those found in other complexes such as the Western Eurasian and Sundadont populations. Overall, 7 traits of the SSADC correspond to Khoesan data, while 5 traits are very different and further highlight the extreme range of variation of the Khoesan dentition. Additionally, according to Irish (1997), sub-Saharan Africans have notable frequencies of I^1 labial convexity (56%) and midline diastema (13%). Khoesan frequencies for these traits in this study are 30.71% and 19.84%, respectively.

Table 5.18: Mean frequencies for 31 traits from around the world. Mean frequencies calculated from published data in Hanihara (2008), Scott and Turner (2000) and Irish (1993, 1998 and 2013)[7]. Traits part of the SSADC* are italicised.

TRAITS	**Khoesan - this study**	**Sub-Saharan Africa**	**Western Eurasia**	**Sinodont**	**Sundadont**	**Aus.**
SHOVELING I^1 (ASU score 2-6)	20.99	28.10	10.00	70.24	48.00	28.00
WINGING I^1 (ASU 1)	18.84	6.60	9.95	30.00	26.60	11.90
*DOUBLE SHOVEL I^1 (ASU score 2-6)	0.76	8.60	5.72	35.30	9.78	*
INT. GROOVE I^2	44.85	13.40	34.80	53.55	31.82	17.70
*LABIAL CONVEX. ^{I1} (ASU score 2-4)	30.71	56.80	*	*	*	*
TD I^2 (ASU score 2-6)	45.12	61.20	48.40	64.20	58.10	*
*CMR C^1 (ASU score 1-3)	61.46	20.60	4.26	2.41	4.40	2.20
CAN. ACC. RIDGE C^1 (ASU score 2-5)	8.22	71.80	43.30	73.90	65.00	*
CAN. ROOT C_1 (ASU 2+)	0.33	0.00	4.25	0.74	0.60	0.00
PM ACC. CUSPS P^1	13.21	4.80	3.17	9.30	13.80	11.05
*PM ROOT P^3 (ASU score 2+)	33.88	60.50	46.96	15.29	42.36	39.60
ODONTOME P^3, P^4, P_3, P_4	0.48	0.40	0.48	3.88	2.04	2.00
PM CUSP VAR. P_4 (ASU score 2-9)	51.64	68.50	67.75	47.20	79.10	*
*TOME'S P_3 (ASU score 3-5)	19.64	17.10	7.42	10.61	17.46	17.10
DTC M_1	0.00	1.30	3.67	10.43	5.74	2.10
*Y-GROOVE M_2	72.43	63.30	26.46	16.23	19.10	26.23
*CUSP # M_2 (ASU 4)	17.96	24.10	70.68	16.65	31.32	40.00
CUSP # M_1 (ASU 6+)	34.48	16.60	7.80	47.80	35.50	*
CUSP 6 M_1	15.66	20.45	9.50	42.15	39.43	45.98
CUSP 6 M_2	20.54	13.65	1.43	15.40	12.17	24.82
*CUSP 7 M_1	18.10	38.50	10.26	6.87	7.02	7.73
DEF. WRINKLE M_1 (ASU score 2-3)	20.00	30.10	16.83	35.32	26.86	26.85
PROTOSTYLID M_1 (ASU score 1-6)	7.36	21.00	10.21	15.00	16.17	5.60
ROOT # M_1 (ASU score ≥3)	0.00	1.70	0.76	16.51	8.62	3.40
*ROOT # M_2 (ASU score ≥2)	93.79	91.70	79.85	65.50	81.50	93.05
*PEG M^3	22.83	5.40	19.50	22.50	44.00	9.50
*ENAM. EXT. M^1	18.66	4.80	12.66	44.57	28.80	6.04
*ROOT # M^2 (ASU score ≥3)	94.14	78.50	65.92	51.70	69.44	73.46
HYPOCONE M^2	100.00	99.00	87.55	86.80	91.50	97.50
METACONULE M^1	51.68	32.80	17.78	20.52	32.86	56.44
*CARABELLI'S M^1 (ASU score 2-7)	25.42	51.30	28.30	10.68	20.32	16.08
PARASTYLE M^3 (ASU score 1-5)	2.78	2.00	2.85	4.80	1.30	*
*MIDLINE DIASTEMA	19.84	10.50	*	*	*	* [8]

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[7] Only data obtained from similar breakpoints were used and regional averages were calculated. Sub-Saharan African samples include frequencies obtained by Irish (1993, 1998, and 2013) for various population groups, including those from South Africa and the Khoesan. Western Eurasia samples include those from Western Europe, Northern Europe, southernmost Europe, India, Western Asia and North Africa. Sinodont data includes samples from China-Mongolia, Jomon and recent Japan, Northeast and southern Siberia, American Arctic, Northwest North America and North and South American Indian. Sundadont data was obtained from archaic and recent Southeast Asia populations, Polynesia and Micronesia. The final group, Aus., includes data from Australia, Melanesia and New Guinea (Scott & Turner 2000; Irish 1998 and Hanihara 2008).

[8] These frequencies are as yet, unavailable or breakpoints were too dissimilar to use.

On the whole, Afridonty does not directly correlate to Khoesan dentition and on the basis of that comparison, the Khoesan dentition does not conform to the sub-Saharan African dental complex; although some traits can be placed under the SSA dental umbrella, it appears that overall differences outweigh similarities. Khoesan dentition displays some extreme morphology in comparison to all other dental complexes and a series of core traits differentiate this population from other world groups. These core traits consist of five low and seven high frequency traits, illustrated in Table 5.19 below. Six of these traits appear at similarly high or low frequencies in the Afridonty complex. These include high frequency CMR, M_2 Y-groove, 2-rooted M_2, 3-rooted M^3 and low frequency I^1 double shovel. The midline diastema, although not wholly included in the SSADC due to a lack of global frequencies, is included in the core Khoesan traits because of its higher prevalence relative to sub-Saharan African averages. These core traits, coupled with a general reduction in tooth size, place Khoesan dentition at the extreme range of sub-Saharan dental morphology.

Table 5.19: Core Khoesan high and low frequency traits.

CORE KHOESAN DENTAL TRAITS	
Low frequency traits	**High frequency traits**
I^1 double shovel	I^2 interruption groove
C^1 distal accessory ridge	CMR
M_1 protostylid	M_2 Y-groove
M_1 distal trigonid crest	2-rooted M_2
M_2 cusp #	3-rooted M^2
	M^1 metaconule
	Midline diastema

SUMMARY OF RESULTS

The Khoesan dental map has been described here, and although trait frequencies vary somewhat regionally and through time, overall the pattern of within-group variation is relatively consistent. Additionally, the Khoesan dental map consists of a number of morphological trait frequencies that highlight this population's extreme range of variation in comparison to dental complexes in Africa and around the world. Hypothesis 1 was set up to investigate the regional continuity of the Khoesan dentition. This was assessed both metrically and non-metrically, using Khoesan dental data that was divided into regional groups consisting of both coastal and inland specimens. Principal components analysis (PCA) evaluated metric observations obtained from crown and cervical molar measurements and identified some size and shape variation inter-regionally. Geographic analyses (hypothesis 1) are inclusive of all Khoesan data (dated or not) and therefore also provide an overall picture of Khoesan dental continuity. This is however, further tested in hypothesis 2. Non-metric evaluations included trait frequency, chi-square and mean measure of divergence assessments, all of which identified regional similarities and some inter-regional variation. Trait frequencies highlighted that Region A demonstrates the most frequency variation when compared to other groups and is the most different to trait frequencies in Regions C and D. Chi-square analysis supports trait frequency findings and demonstrates that Region A is phenetically the least similar to the rest of Southern Africa, most notably Regions C and D along the southern and south-west coast. Other regions display slight variability. No differences are enough to isolate a region as phenetically distinct. Overall, chi-square analyses demonstrate dental homogeneity throughout the geographic focus of the thesis. The mean measure of divergence analysis supports the above-mentioned results. MMD's highlight phenetic differences between Region A and a number of coastal groups and identify a disparity between the first millennium BP inland population and the rest of the Khoesan population. Other than Region A, the MMD's suggest substantial dental homogeneity within the Holocene. Regardless of Region A's phenetic difference (up to 51% of traits), Khoesan dental continuity across Southern Africa is apparent.

To test dental metric and non-metric temporal variation between Holocene Khoesan samples, hypothesis 2 was evaluated, which asserts that dental features remain constant through time. Dated Holocene Khoesan data were separated into temporal sub-groups to examine patterns of variation. Using PCA's, metric evaluations demonstrated minor size and shape variation that largely overlaps. Variation during the last 4000 years BP appears to increase, perhaps a product of increased sample size. On the whole, temporal variations appear to be a reflection of within-population variation, rather than distinct changes in size and/or shape over time. Temporal chi-square analyses demonstrate a generalised dental continuity throughout the Holocene. Early Holocene teeth remain morphologically similar into the Mid-Holocene where some differences are observed. Small trait frequency shifts are also seen well into the Late Holocene, with marked differences observed at the 3-2 ka boundary. Although some significant differences between time intervals are demonstrated, these differences are overshadowed by the similarities, suggestive of dental homogeneity through time.

Hypothesis 3 evaluates Khoesan dentition in comparison to a broader geographic region (Kenya) and with deep time (Mid-Late Pleistocene). Hypothesis 3a states that dental metrics and non-metrics are similar between Holocene Khoesan and Mid-Late Pleistocene dentition. To evaluate this, PCA's were used on metric data, while trait frequency and chi-square analysis evaluated non-metric data. Mid-Late Pleistocene samples display limited metric variation (due to limited sample size) and when plotted against Khoesan material >5000 BP, the Mid-Late Pleistocene variation falls well within the range of Khoesan variation over time. Also, there is overlap between Early Holocene and Mid-Late Pleistocene material. For example, the large Early Holocene Elands Bay specimen (UCT 374) has a close relationship to the larger Mid-Late Pleistocene Cave of Hearths specimen (SU 15). Additionally, material post-5000 BP demonstrates increased variability but is still comparable to the range of Mid-Late Pleistocene material. Comparisons between the Khoesan and Mid-Late Pleistocene populations demonstrate a >60% trait frequency similarity. This similarity is further supported by chi-square analysis which suggests a close phenetic affinity between the two groups. The Khoesan Region A is identified as phenetically less similar to the Mid-Late Pleistocene group but on the whole, there appears to be dental continuity between the Mid-Late Pleistocene and Holocene Khoesan populations. Hypothesis 3b tests the relationship between metric and non-metric evaluations from a sub-Saharan African Holocene sub-group from Kenya and the Khoesan. Metric investigations (using PCAs) demonstrate some size/shape overlap but in general, the teeth differ metrically and Kenyan teeth are usually much larger. Both as a population as a whole or at time-specific intervals, size and shape results are similar. Also, MMD results show a degree of phenetic distance between the Khoesan and Kenyan dentitions. Non-metric evaluations (chi-square) concur and also demonstrate a fair amount of difference between the two populations through time. Interestingly, metric comparisons between the Khoesan, Mid-Late Pleistocene and Kenyan samples highlight the disparity between Kenyan and Khoesan material and shows that Mid-Late Pleistocene tooth variation falls outside of or on the edge of Kenyan, and typically within the range of Khoesan, dental variation.

Lastly, the placement of Khoesan dentition in an African and global context is evaluated. Comparisons are made between Khoesan data from this study and previous Khoesan investigations, as well as the Sub-Saharan African Dental Complex (SSADC), of which the Khoesan are a part. Both morphological similarity and difference is found between this study and the previous (and more temporally recent) Khoesan data set (Irish 1993), indicative of a degree of homogeneity between Holocene and 19th/20th century Khoesan dentition. A substantial difference is noted between this study and the SSADC, demonstrating that SSADC traits are not ubiquitous within the Khoesan sample. Furthermore, although some Khoesan trait frequencies correspond to those in the SSADC, Khoesan dentitions do not adequately fit the complex. When compared to world frequencies, a set of core traits place the Khoesan dentition at the periphery of sub-Saharan African dentition and separate it from global patterns.

CHAPTER 6

DISCUSSION AND CONCLUSION

Population history around the world has been investigated using numerous biological, archaeological, linguistic, cultural, geographic and genetic approaches. In terms of dental research, various dental complexes have been identified and the patterns of similarity and difference between them used to investigate possible links, movements and micro-evolutionary changes within and between populations. In Africa, examinations of population continuity and history have led to the proposal of a sub-Saharan/North African dental dichotomy, since samples from each geographic region exhibit distinctly different trait frequencies, while demonstrating a degree of within-population homogeneity (Irish 1998b, 1998c). Closer inspection of sub-Saharan populations has demonstrated that, in terms of dentition, this group has the greatest phenotypic variation (T. Hanihara 2008) calling into question the validity of a collective sub-Saharan African dental complex (SSADC or Afridonty). This study, focusing on the Khoesan as one of the populations within the complex that exhibit variation at one extreme of the documented range of variation, highlights the variability found within this dental group and not only provides the most detailed description to date of Holocene Khoesan dentition but affirms its place within the global dental community.

The question of population continuity or replacement during the Later Stone Age of South Africa has been a focus of much archaeological/anthropological research. Early investigations invariably interpreted material cultural change in terms of population migrations but more recent studies have suggested population continuity within the Khoesan (Stynder *et al.* 2007a). Using both new metric techniques (recording alternative cervical and diagonal measurements) to alleviate some constraints surrounding specimen limits, and established non-metric techniques, the dental research here supports these findings and offers new insights into population history. Although the Khoesan dental map described in this study includes slightly varying frequencies of traits through space and time, overall there is relatively little within-group variation. Also, this map has highlighted the population's extreme position in the overall range of human dental variation through comparison to various dental complexes both in Africa (Kenyan) and around the world (European and North African, Australian and Melanesian, Sinodont and Sundadont).

KHOESAN DENTAL ANTIQUITY AND CONTINUITY

Genetic evidence indicates that the Khoesan (and other sub-Saharan African indigenous populations) hold some of the most ancient genetic markers of recent humans (Chen *et al.* 2000; Pickrell *et al.* 2012; Soodyall *et al.* 2008). Some early studies, predominantly of ancient calvaria and teeth and their likeness to modern humans (Beaumont 1980; Beaumont *et al.* 1978b; J.D. Clark 1942; H.B.S. Cooke *et al.* 1945b; Dart 1948; Dart and Del Grande 1931; De Villiers 1973; Gabel 1963; Jones 1940; Klein 1974; Rightmire *et al.* 1979; Singer and Wymer 1982; Wells 1950, 1957) led researchers to suggest possible Khoesan morphological continuity over at least the last 100 ka (including ancestral ties to the Broken Hill fossil) (Tobias 1978, 1985), but much of the Mid-Late Pleistocene fossil record (including specimens from Hofmeyr, Klasies River Mouth, Cave of Hearths and Border Cave) has, in the past, demonstrated otherwise. Metrically, Mid-Late Pleistocene teeth are comparable to both modern African and archaic European dentitions (Grine 2000; Grine *et al.* 2007; Grine *et al.* 2000; Grine and Klein 1993; Stynder *et al.* 2001). Non-metrically some Mid-Late Pleistocene dental morphological traits, including for example M^3 peg (or reduction), M_1 cusp 7 and M^1Carabelli's trait, have been aligned with those observed in early *Homo* (Curnoe 2009; Grine 2000; Stynder *et al.* 2001) but these comparisons have been limited. Many Mid-Late Pleistocene teeth (i.e. Die Kelders) have demonstrated similarities to modern sub-Saharan African non-metric traits (for example, M_2 Y-groove pattern and M_1 cusps 5 and 7 (Grine 2000), and, in this study, the Khoesan). The oldest typically Khoesan dentition (those demonstrating core Khoesan traits as outlined in Chapter 5, Table 5.18) is seen in terminal Pleistocene individuals from Matjes River Rock Shelter, Oakhurst Rock Shelter, Coldstream Cave and Elands Bay. Craniofacial studies (Rightmire 1978; Stynder *et al.* 2007b) also indicate a terminal Pleistocene appearance of morphology akin to recent Khoesan populations although many terminal Pleistocene crania are more robust (Bräuer and Rösing 1989; Stynder 2006). Although conducted on a limited sample size, Stynder *et al.* (2007b) demonstrated that facial shape of Early to Mid-Holocene specimens resembles that of Late Holocene Khoesan. Analyses here have shown that terminal Pleistocene/Early Holocene dentitions fall well within the range of variation of recent Khoesan dentition, and although early specimens such as UCT 374 and UCT 378 from Elands Bay and NMB 6 from Matjes River Rock Shelter are generally robust, early Holocene dentitions resemble later populations in terms of dental size, shape and trait frequency.

During the Early to Mid-Holocene dental metric variation is minimal. Tooth dimensions exhibit only slight fluctuations across all regions. Overall size and shape is largely homogeneous for southern Africa but increased size and shape variation post-6000BP is seen. Although statistical corrections were used to combat sample size issues, nonetheless this increase may be a function of an increase in sample size. Khoesan non-metric variation (i.e. the differences between trait frequencies) displays limited statistical difference (a maximum of 4/41 traits (9.8%) are statistically different) during the Early to Mid-Holocene, demonstrating that teeth from the terminal Pleistocene to Mid-Holocene show less variation than more recent material. Since dental morphological plasticity is generally minimal, these variations might be as a result of demographic changes such as population decreases during known climatic changes post-7000 BP. These early teeth (pre-4000 BP) are homogeneous, displaying similar trait frequencies and dimensions, consistent with dentition originating from one distinct biological population. This corresponds to earlier work that demonstrate Khoesan craniofacial traits remain constant pre- and post-5000 BP (Stynder *et al.* 2007b).

The high level of morphological similarity and homogeneity between geographically dispersed Early Holocene dental specimens (as well as those closer to the Mid-Holocene) is consistent with Morris' (2002a, 2003) hypothesis that Khoesan morphology developed in southern Africa in geographic isolation during the LGM. Changing climatic conditions, especially increased aridity in south-eastern Africa during the Late Pleistocene (Castañeda *et al.* 2007) may have played a significant role in the population's isolation (Lahr and Foley 1998). Under these conditions gene flow between Khoesan peoples and other populations would have been restricted. However, recent pollen studies do not indicate significant aridity in the southern

African tropics at this time (Beuning *et al.* 2011) and therefore the effect of climate/environment on population adaptation may not be clearly defined. According to Relethford (2004), in isolated populations, a lack of gene flow coupled with increased genetic drift would reduce population homogeneity and increase population differentiation. This could explain the extreme frequencies of some Khoesan dental traits (such as the high frequency of the C^1 mesial ridge or CMR) as well as the disparity between Khoesan and other sub-Saharan African (i.e. Kenyan) Holocene dentitions. Relethford's (2004) hypothesis also appears to account for the morphology of South African Late Pleistocene (prior to the LGM) specimens (Die Kelders, Hofmeyr, Klasies River Mouth) which are generally characterised as having either African features (craniofacial), or equated with large African or European homologues (dental) with little or no Khoesan similarity, suggestive of marked population differentiation.

MID-HOLOCENE DENTAL FLUCTUATIONS

From *ca.* 4000 BP, notable stature (Pfeiffer and Sealy 2006) and cranial (Stynder 2006; Stynder *et al.* 2007a) reductions are exhibited on the Cape coasts and coastal forelands of South Africa. This is almost immediately followed by a linear recovery beginning *ca.* 3000 BP to previous stature and cranial sizes (Pfeiffer and Sealy 2006; Stynder *et al.* 2007a). Craniofacial variation observed from *ca.* 4000 BP to 2000 BP demonstrates marked variability. In terms of size, most crania are smaller between 4000 BP and 2000 BP in comparison to Early Holocene specimens and post-2000 BP crania. Short/narrow faces with high frontal bones are characteristic of individuals between 4000 BP and 2000 BP in contrast to low/broad faces and long/low frontal bones pre-4000 BP (Stynder *et al.* 2007a). In contrast, Kurki *et al.* (2012) demonstrate no size reduction or subsequent recovery in femoral head diameter, femoral length, cranial centroid size or bi-illiac breadth in skeletons from this region post-5000 BP. Rather, femoral head diameter and length increase through time, while there is no change in cranial centroid size or bi-illiac breadth. Like teeth, bi-illiac breadth appears to be less plastic (Kurki *et al.* 2012) and while bi-illiac breadth may be constrained by a thermoregulatory principle between body size/mass and climate (Ruff 1991, 1994), the reasons for body size and craniofacial (and dental) fluctuations are not clear. According to Pfeiffer and Sealy (2006) a lack of nutrient-rich resources at a constant or seasonal rate is most likely the cause of the reduction, while the recovery may be attributed to solving problems around food insufficiency. These constraints can also be observed archaeologically. There is a dramatic increase in archaeological sites in both coastal and inland South Africa after *ca.* 4000 BP, during the post-Classic Wilton. This suggests a marked increase in population growth, which in turn may have restricted population mobility and strained available resources (Hall 1990; Jerardino 1996; Sealy 2006). Archaeological evidence demonstrates that resource intensification and the exploitation of a wider range of foods enabled these populations to adapt to changing circumstances (Hall 1990; Jerardino 1996, 1998, 2010; Jerardino *et al.* 2009a; Sealy 2006). A change in dietary resources is noted, for example, along the Fish River basin where people started to eat freshwater fish and molluscs, which were both previously underutilised food sources (Hall 1990). Also, as populations became more sedentary they intensely exploited certain resources e.g. the focus on shellfish exploitation that led to the accumulation of very large shell middens, in some areas termed 'megamiddens' (Jerardino 1998, 2010; Jerardino and Yates 1997; Parkington 1981, 1984; Parkington and Hall 1987; Parkington *et al.* 1988). Higher population densities across the landscape are also evident through diet. At Matjes River Rock Shelter, for example, stable isotope research has demonstrated that people buried at the site ate a mixture of terrestrial foods and low trophic-level marine foods such as shellfish in contrast to those buried on the Robberg Peninsula who ate predominantly high trophic-level marine foods, and lived only a short distance away (Sealy 2006). These differences in diet indicate sedentary settlement patterns in which groups claimed territories, suggestive of higher population densities. Regional differences in stone artefact assemblages and burial styles during this time also coincide with increased population densities over large areas and demonstrate regional cultural differences (Sealy In press). Such changes in demography, environment, economic strategy and technology correspond with periods of biological change, as observed post-4000 BP.

Dental trait frequencies between 4000 – 3000 BP are very similar to that observed during the Early Holocene (a maximum of 3/40 (7.5%) traits demonstrate significant difference between 4-3 ka and earlier temporal groups), however increased changes in tooth morphology commence *ca.* 3000 BP and are observed into the first millennium BP. A handful of traits, including five associated with the sub-Saharan African dental complex (P_3 Tomes root, CMR, M_2 cusp 6, M^1metaconule and M^1Carabelli's cusp), are present at significantly different frequencies in pre-3000 BP and post-3000 BP dentitions. This pattern occurs in all regions, suggesting that morphological change occurs throughout the population during the last 3000 years BP. 5/51 (10%) traits are significantly different if one compares 8-6 ka and 3-2 ka groups and 5/44 (11.4%) in 6-4 ka and 3-2 ka groups. Not surprisingly, comparisons with older groups indicate a greater degree of difference: 9/44 traits (20.5%) in 8000+ compared with 3-2 ka groups. The timing of these changes in dental traits does not precisely coincide with Mid-Late Holocene fluctuations in dimensions of crania and postcrania. Dental morphological change appears to have a late onset, beginning only *ca.* 3000 BP, a time when subsistence stresses had been addressed and reductions in cranial and postcranial dimensions had begun to recover to pre-4000 BP levels. The dental evidence demonstrates a slow change that begins at *ca.* 3000 BP, followed by a reduction in the amount of change. Thereafter, some of the post-2000 BP trait frequencies return to similar levels previously observed *ca.* 4000 BP. It is possible that these dental changes might reflect one (or more) of a number of genetic influences including random changes in gene frequency over time or the influx of new genetic material. However, since stature and cranial size recovery is detected in the Khoesan from *ca.* 3000 BP (Pfeiffer and Sealy 2006; Stynder 2006; Stynder *et al.* 2007a), a millennium prior to any possible addition of genetic material from immigrants or changes due to the introduction of livestock, gene flow from a biologically distinct population is unlikely. Also, the introduction of a distinct population's dentition would likely have dramatically altered the dental morphological pattern. Rather, it seems more likely that the morphological changes can be attributed to random gene frequency changes, perhaps a delayed response to environmental/resource stress during the previous millennium.

The reasons for this difference in timing of the onset of dental changes are unclear and may be attributed to a number of factors. Relative to skeletal development, dentition, to a degree, appears to be fairly shielded from environmental effects so the observed changes are likely related to other factors (i.e. genetic). Tooth size exhibits a degree of plasticity (Dempsey and Townsend 2001; Ebeling *et al.* 1973; E.F. Harris *et al.* 2001; Kieser 1990; Kolakowski and Bailit 1981; Lavelle 1973; Perzigian 1984) and although it has a mid-high range heritability value (between *c*. 0.50 and 0.70, depending on the measurement, but consistently lower than values seen in stature (*c*. 0.80) (Alvesalo and Tigerstedt 1974; Garn *et al.* 1968; Sofaer *et al.* 1972; Townsend and Brown 1978)) it is flexible, as evidenced by generational differences between parents and offspring (Garn *et al.* 1968). In this study, size variation appears to be associated with known environmental changes such as the Holocene altithermal *ca.* 7000 BP/6000 BP (climate) and post-4000 BP (resource stress and climate). Also, prenatal factors (Garn *et al.* 1979) and maternal influences such as differing nutritional regiments during pregnancy or lactation have been shown to influence tooth size in rats (Kruger 1966; Paynter and Grainger 1956) and as Bailit and Sung (1968) suggest, may affect human tooth size as well. Extended breastfeeding and late weaning practices of the Khoesan during the mid-Holocene (Clayton *et al.* 2006) may well have had an effect on dental size. It is probable that gradual genetic changes steer gradual dental changes as a few traits (i.e. I^1shovelling and M^3/M_3 agenesis) have been strongly correlated with specific genes (EDAR and PAX9, respectively) (Bianchi *et al.* 2007; Kimura *et al.* 2009). However, research has not conclusively demonstrated environmental plasticity of non-metric dental traits and they appear to remain remarkably similar within populations, even in the face of changing environments. There also seems to be little change associated with selective pressures acting on the teeth over time. For example, G.R. Scott and Alexandersen (1992) demonstrate that when medieval Norse populations colonised northern territories (Iceland) and were subjected to new, harsher environments with variable climates and food resources, tooth morphology remained largely similar to that observed in ancestral populations. The morphological deviations were only significant with regards to some intra-oral osseous traits and craniofacial features (G.R. Scott *et al.* 1991). The Khoesan appear to exhibit a similar tendency. However, recent twin (Townsend *et al.* 2012; Townsend *et al.* 2009) and allele (Mizoguchi 2013) studies have demonstrated some connections between environmental and dental metric and non-metric change. Research by Mizoguchi (2013) quantitatively assessed metric (mesiodistal and buccolingual crown diameters on upper molars) and non-metric traits (I^1 shovelling and M^1 Carabelli's) in relation to their associations with various alleles (blood group systems) and fluctuations in climate and/or differences in subsistence strategies. Dental metrics were significantly correlated with temperature and rainfall shifts, while non-metrics were predominantly associated with subsistence (i.e. Carabelli's and shovelling are associated with populations where milking in dry areas is practiced (Mizoguchi 1985, 1993). This work demonstrated that dental morphological characteristics were adaptive and that there exists a measurable relationship between within-population dental characteristics and their environments (Mizoguchi 2013). It all provides a preliminary link between teeth and the environment and although the findings are suggestive, they are not conclusive and much further research is needed on a larger suite of dental traits to determine the full scope of environmental effects on dental morphological development.

Other environmental effects are related to stress and can manifest in teeth as dental development abnormalities, defects and pathological changes, which can have an effect on dental crown morphology. Khoesan body size reductions and cranial changes *ca.* 4000 BP suggest that these populations may have been under nutritional stress from food shortages or lack of resource access. Malnutrition or nutritional stresses inhibit normal body growth and affect stature, but in teeth the effects are manifested differently. For example, delayed tooth eruption and/or development can occur (Cardoso 2007; Conceição and Cardoso 2011), as well as tooth formation defects. Also, increased dental caries later in life have been observed as a result of poor nutritional status in children (Alvarez 1995; Alvarez *et al.* 1990; Garn *et al.* 1965; Rami Reddy *et al.* 1986) although some recent work has shown that tooth formation is not affected by malnutrition (Elamin and Liversidge 2013). Since tooth sizes are affected by maternal health status during pregnancy and birth (Garn *et al.* 1979), it is possible that dental trait development is as well. Malnutrition and disease insults (i.e. caries, enamel pitting and enamel hypoplasia) affect not only crown gross morphology but also provide some evidence of stress. There appears to be an indirect relationship between the increased appearance of dental caries and tooth growth interruptions such as linear enamel hypoplasia (particularly incisal) in undernourished children from modern populations (Infante and Gillespie 1977; Jelliffe and Jelliffe 1971; Sweeney *et al.* 1971). Also, fluctuating asymmetry (observable differences in size and morphology between antimeres), is often observed in conjunction with other stress indicators such as Harris lines, reduced stature and enamel hypoplasia (Perzigian 1977). This asymmetry has little to no genetic component (P.A. Parsons 1992; Potter and Nance 1976) and can be an indicator of environmental change/stress, although some problems with this method (sampling size and reliability) are known (B.H. Smith *et al.* 1982). Although no quantitative assessments have been performed, a general impression from looking at the material is that the current data set between 4000 BP and 2000 BP demonstrates evidence of enamel hypoplasia, pitting and fluctuating asymmetry (particularly on incisors and molars). Also, the prevalence of dental caries at this time appears to be slightly increased in comparison to Early Holocene dentitions but no firm conclusions can be drawn as dental health investigations are still ongoing and not included in this study. Although most populations display some overall within-population dental morphological variation and demonstrate dimensional fluctuations, the differences observed in the Khoesan dentition at 3000 BP are pronounced in comparison to earlier teeth, denoting change that may have been affected by a variety of the above-mentioned factors. However, the predominant cause of morphological change appears to be genetic and *in situ* factors such as genetic drift, genetic isolation, random changes in gene frequency, mutation and natural selection are most likely to account for (with the exception of pathological effects) morphological change.

THE INTRODUCTION OF DOMESTICATION AND KHOESAN DENTAL CONTINUITY

Archaeological and biological research has aimed to determine whether the introduction of domestic stock was facilitated by the migration of biologically (and presumably genetically) distinct herding populations from the north or whether herding was adopted locally through acculturation *ca.* 2000 BP. Results obtained in this thesis are consistent with the views of Sadr (1998, 2005, 2008b) and recent studies by Stynder (2009) which found that although there were some morphological differences between pre- and post-2000 BP coastal Khoesan crania, this was not due to an influx of morphologically distinct individuals. Dental morphology from 2000 - 1000 BP is somewhat variable but less so in comparison to dentitions from 3000 – 2000 BP. Dental morphology post-2000 BP is similar to that observed pre-4000 BP (i.e. fewer significant trait differences are observed between these two temporal groups in comparison to the 3-2 ka group) across most of this thesis' geographic focus. Sizes of dentitions from 2000 – 1000 BP are comparable to those *ca.* 4000 BP. This is in contrast to size fluctuations demonstrated in the crania (Stynder *et al.* 2007a); crania display a general increase in size post-2000 BP (Stynder 2009). Also, craniofacial form does not change suddenly at 2000 BP, rather the changes observed are allometric in nature, reflecting the ongoing effects of cranial size recovery that began *ca.* 3000 BP. Craniofacial results are consistent with the Khoesan remaining a single biological population after 2000 BP and after the introduction of livestock (Stynder 2009). The same is true with regards to dentition post-2000 BP. The introduction of new genetic material would be expected to alter dental morphology resulting in greater differences between the 2000 BP and earlier populations than is indicated here. The reduction in morphological change during this time (2-1 ka), although not consistent with cranial and post-cranial size recovery time-frames outlined by Pfeiffer and Sealy (2006) as it occurs 1000 years later, may also be the result of random changes in gene frequency rather than selective pressures acting on the teeth over time. Since dental anthropological studies focus more on modern populations, further research on archaeological dental populations may clarify how and why these types of changes occur.

During the first millennium BP, both metric and non-metric dental variation demonstrate further fluctuations. A marked decrease in size and shape differences (perhaps not a function of sample size as this dataset is relatively substantial in comparison to others; N=115) coincides with the emergence of cattle pastoralism and possible Khoekhoen migrations (Sadr 2008b; Sealy 2010). Although results indicate a reduction in dental dimensions, some individuals believed (from their $\delta^{13}C$ and $\delta^{15}N$ values) to be cattle herders (NMB 1338; NMB 1704; UCT 262; UCT 582; UCT 583) (A.G. Morris *et al.* 2004/2005; Sealy 2010) have unusually large molars, at the upper limits of the range of overall Khoesan dental variation. Observed differences between hunter-gatherers and herders might be explained by differential access to resources, altered economic strategies and political/social constraints. Along the southern and south-western coasts of South Africa for example, groups without livestock were marginalised and forced out of the coastal forelands into mountainous regions where subsistence was based on hunting and gathering (Parkington and Hall 1987). The divergence of herder individuals may suggest a difference amongst them and while this may be environmental, it may indicate a substantial genetic difference.

Dental similarities between temporal subdivisions far outweigh differences, once again indicating a general pattern of Khoesan dental homogeneity. Differences (albeit minor) are likely due to random change (e.g. genetic drift) in a growing, isolated population. The largest amount of difference is demonstrated between the terminal Pleistocene/Early Holocene and samples from post-3000 BP. The last 1000 years, however, sees a decrease in variation (metric and non-metric) to pre-4000 BP levels and there appears to be a correlation between Early Holocene trait frequencies and those of the first and second millennium BP. However, the inland regional group (Region A) exhibits significantly increased morphological change but still falls within the Khoesan range (to be discussed later in this chapter). Interestingly, more than others, the most significant overall trait differences within the Khoesan dental data set through time appear to occur among incisor and lower molar traits. This may suggest that incisors and lower molars are more susceptible to morphological change or more affected by change.

REGIONAL VARIATION

There is very little regional variation in the Khoesan dental sample. Inter-regional comparisons of dental size and shape are statistically indistinguishable, with one exception: Region A (the inland region, north of the Great Escarpment, which includes all specimens from Koffiefontein and Riet River (located near Bloemfontein) to the Richtersveld. Trait frequency differences are significant between Region A and all other regional groups (between 17% and 50%). Nevertheless, this group's low MMD values (0.0000 - 0.1449) suggest a small amount of phenetic distance from other regions, particularly the southern and south-western coast (Regions C and D). The distance between Region A and other groups is more than any distance among other groups in this study but is, however, considerably less than that observed between the Khoesan and Kenyan samples (MMD = 0.4300), demonstrating Regions A's retained close association to the Khoesan dental map.

It is useful to explore the background information relating to Region A to understand the cause of the variation. Most of the Region A skeletons date to within the last few hundred years (A.G. Morris 1992b) and although most of them may not have been in direct contact with the Cape colony, they were certainly affected by the waves of disturbance and influx of indigenous populations, including Iron Age communities, Colony refugees and criminals (e.g. stock thieves and raiders), that preceded the expansion of the frontier (Klein 1986; Penn 1986, 2005). The most recent of these Region A communities were within the Colonial contact era as evidenced by Burchell (1822) who visited groups living there in the early 19thcentury. According to A.G. Morris (1992b), the cranial morphology of populations in Region A could be separated into two groups, those with distinctly Khoesan cranial morphology along the Riet River (Koffiefontein) and the admixed Khoesan/Bantu-speaking populations in Kakamas and Augrabies areas, further west. Maggs (1971) and Humphreys (1970, 1982, 1988) suggest that many individuals at Riet River/Koffiefontein were relatively isolated San hunter-gatherers who adopted stock-keeping after prolonged contact with Iron Age Bantu-speaking neighbours and only benefited materially from trade of material culture objects and game/ostrich products (Maggs 1976), thereby limiting contact (and by extension, admixture). Although this population's cultural context indicates Iron Age contact, their cranial morphology remains strictly Khoesan. In contrast, populations in Kakamas and Augrabies were not uniquely Khoesan or Bantu-speaking in their morphology but rather a mixture from both groups (A.G. Morris 1992b). The Kakamas and Augrabies skeletons have Khoi (Khoe) associations based on burial practices that mirror known herder graves but although investigations here are limited, cultural diffusion between both groups is evident archaeologically (Humphreys 1982, 2007; A.G. Morris 1992b; D. Morris and Beaumont 1991). Specimens from the Augrabies/Kakamas area are also likely more recent as many trade goods (e.g. glass beads) associated with some of these remains have been dated to within the 18th century and according to early journals (i.e. Wikar (Mossop 1935) and Gordon (Raper and Boucher 1988)) from the late 1700s, genetic intermixture between the Khoi (Khoe) and Iron Age groups was abundant here at the time. Using many of the same crania incorporated into this study's Region A, A.G. Morris (1992b) concluded that although crania from this study's Region A are morphologically Khoesan-like, there is a large amount of intra-population variation pointing to a degree of biological distinctiveness. This distinctiveness suggests that the population as a whole was most likely subject to a degree of genetic admixture into the group. Early studies demonstrated that gene flow was unidirectional from the Khoesan to the Bantu-speakers (Tobias 1974).Gene markers (Gm ^{1,13} allele), common only in Khoesan were found in Sotho-Tswana populations; gene flow was not matched in the opposite direction. Cranial evidence also identified possible admixture between Sotho and San groups and in general, Sotho-Tswana groups exhibit a number of Khoesan osteological features (De Villiers 1968). Many hunter-gatherer objects, including lithics and other LSA artefacts are associated with the population in Region A and although Iron Age goods (e.g. jewellery) and stock herding appears to have been a part of the groups' economic strategy, they remained Khoesan (A.G. Morris 1992b), supporting the idea of a unidirectional gene flow pattern and explaining the observed Khoesan cranial morphology.

Depending on trait frequency ranges and overlap, admixture should be identifiable as Iron Age populations (Early and Late) are found to be significantly different dentally (both in morphology and size) to the Khoesan (Warren 2013). This would also account for the observed dental morphological variation. More recent genetic work, however, provides evidence of far more significant genetic contact between the Khoesan and Bantu-speaking populations in the last two thousand years (Cavalli-Sforza *et al.* 1994; Chen *et al.* 2000; Cruciani *et al.* 2002), contradicting earlier unidirectional gene flow hypotheses and temporal limitations to genetic exchange. In terms of the dentition, although tooth dimensions fall within the range of Khoesan dental variation, the dental morphological differences here are significant when compared to all other regions and therefore suggest a degree of admixture from Bantu-speaking groups. However, since Khoesan dentition from Region A fits the current dental map and, with the exception of the I^2 interruption groove (which occurs at only 18.8% during the first millennium BP here, in comparison to 44.9% in the Khoesan as a whole), clearly mirrors high and low frequencies comprised in core Khoesan traits, identifying this group as essentially Khoesan.

BROADER TEMPORAL AND GEOGRAPHIC CONTEXTS

MID-LATE PLEISTOCENE DENTITION AND ITS RELATIONSHIP TO HOLOCENE KHOESAN TEETH.

The dental evidence from this study suggests that the origins of the Khoesan dentition may be deeper in time. Metric analyses demonstrate that Mid-Late Pleistocene samples consistently fall within the range of metric variability observed in Early Holocene Khoesan teeth, while Mid-Late Pleistocene teeth are phenetically similar to those observed in the Early Holocene. A number of authors have suggested that Southern African Mid-Late Pleistocene humans may have been ancestral to Holocene populations (Khoesan) (H.J. Deacon 1992; Grine 2012; Grine *et al.* 2007; Rightmire and Deacon 1991; 2001; among others). Additionally, some researchers have argued that there is cultural and cognitive similarity between the MSA and LSA (Beaumont 1978; H.J. Deacon 1995; Henshilwood and Sealy 1997; Parkington 1988; Singer and Wymer 1982; Wurz 1999), particularly from sites that have long occupational sequences, some of which have yielded Mid-Late Pleistocene human remains (i.e. Klasies River Mouth, Die Kelders, Blombos and Border Cave). According to H.J. Deacon (1992), fossils from sites such as these are products of selection that produced more gracile and less sexually dimorphic individuals in isolated regional populations. These teeth (and other maxillary, mandibular, cranial and postcranial finds) have been compared to archaic specimens from both Eurasia and Africa as well as to modern African homologues; measurements generally fall within the upper limits of modern African samples (G. Avery *et al.* 1997; Bräuer *et al.* 1992; Grine 1981, 2000; Grine *et al.* 2007; Grine and Henshilwood 2002; Grine *et al.* 2000; Grine and Klein 1993; Grine *et al.* 1998). Some teeth from Klasies River Mouth are, however, relatively small compared to both modern and archaic specimens (Grine 2012). It has been suggested that due to their diverse sizes, the teeth from Klasies River Mouth display high sexual dimorphism where (supposedly) male specimens have large crown and mandibular corpus dimensions comparable to archaic and modern specimens (Rightmire and Deacon 1991), while possible females exhibit small dimensions (Bräuer *et al.* 1992; Rightmire and Deacon 1991, 2001), smaller than archaic and modern homologues but similar to those observed in the Khoesan(Rightmire and Deacon 2001). Marked sexual dimorphism is also observed in Klasies River Mouth mandibular and molar specimens relative to both modern and archaic Eurasian populations (Royer *et al.* 2009). Both small and large specimens from Klasies River Mouth were expected to appear as outliers in the metric analyses (PCA) presented here, however, the small Klasies River Mouth specimens fall within the range of the Holocene Khoesan sample. Some Khoesan teeth are smaller than those found at Klasies River Mouth. The large Klasies River Mouth specimens could unfortunately not be included in these analyses due to limited samples and caries/post-mortem damage. However, the large Late Pleistocene individual from Hofmeyr, one of the largest Mid-Late Pleistocene specimens, also falls within the range of variation seen in Holocene Khoesan dentition. Both cranial (Grine *et al.* 1998; Lam *et al.* 1996; F.H. Smith 1992b) and postcranial (Churchill *et al.* 1996; Rightmire *et al.* 2006) skeletal evidence demonstrate a degree of sexual dimorphism at Klasies River Mouth (and within the South African Middle Stone Age), but perhaps sexual dimorphism does not account for all the differences seen. As evidenced by this study and others (Van Reenen 1966, 1970), sexual dimorphism is relatively low (and size variation small) in Khoesan dentition. Khoesan teeth, in comparison to other sub-Saharan African dentitions, are generally diminutive and both male and female teeth exhibit different sizes (large and small) across the full range of Khoesan metric variation. This may also be true for Mid-Late Pleistocene specimens but more samples from this time period are needed to fully evaluate this possibility.

The variability observed in Mid-Late Pleistocene teeth may reflect demographic factors, especially fluctuations in population sizes (Jacobs and Roberts 2008, 2009; Powell *et al.* 2009). Regional differences in population densities, mobility and contact may have led to various innovations and symbolic material culture (K.S. Brown *et al.* 2009; d'Errico *et al.* 2005, 2008; Henshilwood *et al.* 2009, 2002; Henshilwood and Dubreuil 2011; Mackay and Welz 2008; Texier *et al.* 2010), possibly driving elements of biological (and perhaps dental) change. Rapid population increases of regionally isolated groups may have increased genetic drift and therefore population variability (Relethford 2004) and could explain the size/shape variability identified in the Mid-Late Pleistocene teeth -i.e. dental size variations seen at Klasies River Mouth.

The small Klasies River Mouth teeth and associated mandible fragments (Lam *et al.* 1996) (considered female) exhibit notably modern characteristics, while larger, more robust remains (considered male) appear more archaic (H.J. Deacon 1992).

However, Grine *et al.* (1998) note that overall, Klasies River Mouth postcranial remains display both archaic and modern features. The same combinations of archaic and modern features are observed in other Mid-Late Pleistocene specimens such as Hofmeyr (Grine *et al.* 2007) and Die Kelders (Grine 2000). Limited dental morphological study has been conducted on these early teeth (in terms of the ASUDAS) as most studies focus on metric variability and comparisons to other ancient populations around the world. In this study, morphological comparisons of Mid-Late Pleistocene and Holocene teeth confirm the presence of archaic/modern combinations in a sub-Saharan African context. Relative to other modern populations, sub-Saharan Africans appear to be the least derived dentally from ancestral hominins, exhibiting the highest incidents of ancestral dental traits (Irish 1998a; Irish and Guatelli-Steinberg 2003). These traits include: low frequencies of I^1 double shovelling and M^1 enamel extension, high frequencies of P_3 Tome's root, M_1 cusp 7, M_2 Y-groove, two-rooted M_2, M^1Carabelli's trait and M^3 presence(also recorded as low frequencies of M^3 agenesis in the literature), while traits such as the CMR are apparent derived features. This is suggestive of an ancient dental population which, in broader contexts, supports the out-of-Africa hypothesis. Many retained traits appear in the South African Mid-Late Pleistocene fossils but few studies have highlighted them. Ancestral traits on teeth from Die Kelders includeM_1 cusp 7 and M^1Carabelli's, but small sample sizes did not allow for frequency evaluations (Grine 2000). Unfortunately some of these teeth are now missing and therefore could not be included in this thesis. Other traits, not considered ancestral, are also present, i.e. the presence of shovelling on the Hoedjiespunt mandibular incisor (SAM-AP 6370c) (Stynder *et al.* 2001) and the presence of M_1 Y-groove, M_1 cusp 6 and M_1 distal trigonid crest on Die Kelders material (Grine 2000). In the Mid-Late Pleistocene data set reported here, five of the eight ancestral traits outlined by Irish and Guatelli-Steinberg (2003) are observed, including four high frequency traits, namely theM_1 cusp 7 (which also appears on M_2), M_2 Y-groove pattern, two-rooted M_2 and M^3 presence, and one low frequency trait, the absence or low occurrence of I^1 double shovel. Other ancestral traits could not be assessed because of missing teeth. Also of interest are the ancestral trait frequencies similar to those observed in the Holocene Khoesan data set, i.e. high frequencies of M_2Y-groove pattern (80% in the Mid-Late Pleistocene data set and 72.4% in the Khoesan) and relatively high frequencies of M_1 cusp 7 (25% in Mid-Late Pleistocene data and 18.1% in Khoesan), among others, suggesting a degree of morphological similarity between Mid-Late Pleistocene and Holocene Khoesan individuals. Furthermore, comparisons between other Holocene Khoesan and Mid-Late Pleistocene trait frequencies revealed additional similarities. Frequencies of 17 morphological traits that could be compared were indistinguishable between Early-Mid Holocene (8000+, 8-6 ka and 6-4 ka) and Mid-Late Pleistocene specimens, suggestive of continuity between the two groups. A close phenetic affinity akin to the relationship between 8000+ and 8-6 ka Khoesan samples exists between them. Much of the Khoesan dental morphology observed during the Early Holocene remains consistent across a broader timescale and suggests that Khoesan dental origins are much deeper in time. The first differences between the Mid-Late Pleistocene and Holocene specimens appear at 4000 BP and increase at 3000 BP, continuing into the first millennium BP. Again, this suggests that it is the *ca.* 3000 BP sample that differs.

Trait frequencies observed here for Mid-Late Pleistocene teeth differ from those reported in the Afridonty complex. Of 11 traits that characterize the Afridonty complex, the frequencies of five (P_3 Tomes root, M_2 Y-groove, M_1 cusp 7, two-rooted M_2 and three-rooted M^2) are statistically indistinguishable from frequencies in the Mid-Late Pleistocene. However, some caution is required when interpreting this evidence as Mid-Late Pleistocene sample sizes are small ($N \geq 4$).The remaining six traits could not be evaluated due to missing or inadequate data. With the exception of the 3-rooted M^2, these similarities are not unexpected as the remaining traits are considered ancestral and appear in high frequencies across Africa. A number of other traits (7), not included in the Afridonty complex, could be compared between the Mid-Late Pleistocene and sub-Saharan African teeth. All but one (M_1 anterior fovea) are statistically similar. Overall, of the 12 traits compared, 11 are indistinguishable. This suggests that Mid-Late Pleistocene teeth may share more traits with sub-Saharan Africans in general than with the Khoesan specifically, but more data are required to test this. On the basis of the data presented here, dental trait frequencies in the Mid-Late Pleistocene sample resembles 6 of the core Khoesan traits, including low frequency M_1 distal trigonid crest, and high frequencyM_2 (and M_1) Y-groove pattern, M_2 cusp #,2-rooted M_2, 3-rooted M^2, and M^1metaconule. Three of these traits also appear in the Afridonty complex (with comparable frequencies), thereby linking Mid-Late Pleistocene teeth from this study to elements of both the Afridonty complex and the Khoesan dental map.

HOLOCENE KENYAN DENTITION AND ITS RELATIONSHIP TO HOLOCENE KHOESAN TEETH.

The dental similarities and differences between the Khoesan and the Holocene Kenyans offer dental insights in a broader geographical framework. The Khoesan differ somewhat from the general picture of sub-Saharan dentition put forward by Irish (1997, 2013); comparisons between Khoesan and the Kenyan sample reveal comparable differences. Kenyan teeth tend to be larger than those of the Khoesan, as expected given that tooth sizes are relatively large for much of sub-Saharan Africa (T. Hanihara and Ishida 2005). Khoesan post-2000 BP overlap in size/shape with the Kenyan Late Holocene sample (post-4500 BP), but pre-2000 BP Khoesan and pre-4500 BP Kenyan material does not overlap, suggesting that they do not share ancestry. When comparing pre- and post-4500 BP metric variation within each population, the same results are observed. Interestingly, the metric variation shared between Khoesan post-2000 BP (excluding Region A specimens for reasons discussed above) and post-4500 BP Kenyan samples relates to Khoesan herders and Elmenteitan pastoralists (Bromhead’s site). Interpretation of these results should be cautious as sample sizes are very small (N=4) due to the scarcity of identified Khoesan herder individuals. The archaeology demonstrates very little material likeness between the two groups barring their mutual subsistence strategy. The Elmenteita populations do not share cultural, stone tool technology and raw material procurement, pottery traditions or settlement patterns (although there is evidence of the use of rock shelters) (Robertshaw 1988) with known herder or hunter-gatherer sites in South Africa during the LSA.

34% (16/47) of traits show significant differences in frequency between the Kenyan and Khoesan samples. A large amount of phenetic distance between them is evident from the MMD value of 0.4300. Early Holocene Kenyan dentition is morphologically more similar to Khoesan Holocene dentition as a whole (as evidenced by lower MMD values of 0.2605) than the Late Holocene Kenya material (MMD value of 0.3130). Some dental similarity however is apparent, particularly between Early Holocene

Kenyan and Early to Mid-Holocene Khoesan, sharing high frequencies of I^1 labial convexity, I^2 tuberculum dentale, M_1 Y-groove pattern, M_1 and M_2 cusp 5 presence. Significant differences between Kenyan and Khoesan dentitions relate to mass-additive traits, i.e. I^2 tuberculum dentale, M^1metaconule and M^2large hypocone, while others are demonstrated in cusp differences (e.g. M_1 Y-groove pattern) and intra-oral osseous traits (mandibular torus and rocker jaw), further highlighting between-population differences. This is indicative of substantial population separation.

The Kenyan dataset also shows marked differences from the Afridonty complex, with significant differences between a number of the highlighted “uniquely African” traits and the Kenya subset. This is suggestive of significant regional dental differences among archaeological populations across Africa, rather than overall similarity. Three of the Kenya traits associated with the sub-Saharan African dental complex (P_3 Tome’s root, M_2 cusp number and M^1 enamel extension) are significantly different from the Khoesan, while many of the other observed trait frequencies are comparable to the core Khoesan trait frequencies. Of particular note is the presence of the CMR. This trait, considered uniquely Khoesan (Irish and Morris 1996b; D.H. Morris 1975), occurs at a higher frequency in the Kenyan population than it does in the Khoesan dataset (77.78% versus 61.46, respectively). This suggests that the Khoesan and Kenyan dentitions, although similar to the SSADC for a number of traits, both diverge somewhat from it. As discussed earlier, shared dental traits (and frequencies) may reflect an ancestral condition in sub-Saharan Africa and the shared Kenya/Khoesan traits should therefore be ancestral to other sub-Saharan African dentitions and to a degree, they are. They do not however, present at the same frequencies, calling into question the validity of the all-encompassing SSADC. However, the Kenya dataset in this study is relatively small, and research on a larger Kenyan dataset may demonstrate closer ties to the Afridonty complex, but it ultimately may not. As mentioned by Irish (2013), early[9] Kenyan teeth exhibit lower dental complexity (i.e. more mass-additive traits) and may therefore also not align to what is observed in the Afridonty complex. Also, these comparisons are predominantly between modern and ancient populations and a degree of difference is expected.

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[9] Date range not specified.

COMBINED COMPARISONS: HOLOCENE KHOESAN, HOLOCENE KENYA AND MID-LATE PLEISTOCENE.

Metric comparisons between Holocene Khoesan, Mid-Late Pleistocene (or Upper Palaeolithic) and modern African homologues (Bantu-speaking groups) have been useful in identifying relationships between archaic and modern teeth (Grine 2000; Grine *et al.* 2007; Grine and Klein 1993; Grine *et al.* 1991; Grine *et al.* 1998; among others). These relationships have been based solely on traditional crown diameters which limited the scope of study because these measurements require almost complete teeth with minimal wear/damage. Using alternative measurements (cervical and diagonal) further illuminates our understanding of the relationships between the Mid-Late Pleistocene and the Holocene. Metrically, the Klasies River Mouth material falls within Holocene Khoesan variation but outside the variation demonstrated by the Kenyan sample. This provides some evidence that specimens from Klasies River Mouth have closer ties to the Khoesan than to other populations in sub-Saharan Africa. Larger Mid-Late Pleistocene specimens such as SU15 (Cave of Hearths) are comparable to some of the larger Kenyan individuals but still fall within the range of variation seen in the Khoesan. Specimens from Border Cave, Die Kelders and Mumbwa Cave in Zambia all share similar size/shape variation to both the Khoesan and Kenyan dentitions, further suggestive of ancestral ties to sub-Saharan African dentitions deeper in time. Non-metric investigations (based on small sample sizes) reveal that although the Mid-Late Pleistocene material demonstrates connections to Kenyan examples from this study and Irish (1993), the reduced degree of similarity between Mid-Late Pleistocene and the SSADC (see Appendix 7 and 8 for frequencies and Appendix 9 for chi-square comparisons), suggests a closer relationship between the Khoesan and Mid-Late Pleistocene dentitions than other sub-Saharan African populations.

Overall, results obtained in this thesis favour population continuity of the Khoesan throughout the Holocene across all geographic regions in South Africa (and a small portion of Namibia) and trace dental antiquity to at least the terminal Pleistocene. With the exception of Bantu-speaking farming populations migrating into eastern South Africa during the last 2000 years, there is no biological evidence to support gene flow into the coastal areas at any point during the Holocene. This is consistent with the conclusions of previous studies of cranial morphology (Stynder 2009;

Stynder *et al.* 2007b) but in contrast to long bone studies by P. Smith *et al.* (1992). In their study, cortical bone thickness and humeri and femora length from the south-western Cape coast post-2000 BP increased, suggestive of a population replacement and/or genetic admixture (P. Smith *et al.* 1992). Sample sizes in their study were however limited (N=53) in comparison to Stynder's (2009; 2007b) work and this thesis, making their argument less convincing. It is likely that cultural, demographic and subsistence changes during the Holocene are the product of social and/or political reorganization within the population, perhaps partly in response to environmental changes. These processes of population reconfiguration, rather than the introduction of new genetic material are likely behind metric variation during the Holocene and perhaps the Mid-Late Pleistocene, while a certain degree of population isolation within southern Africa as a whole may drive morphological distinctiveness.

AFRIDONTY

With half of the trait frequencies in this study similar to those reported by Irish (1993), the relationship between the Holocene Khoesan and Irish's (1993) historical (Khoekhoe and San) material cannot be overlooked. The 20th century San data from his 1993 study were collected from dental casts obtained from people belonging to various ethnic groups (e.g. !Kung) living in farming communities in north-western Botswana (N=83), or from skeletal samples (N-16) recovered west of Bloemfontein (Region A). His Khoekhoe data (N=37), associated with pastoral Nama and Korana (Khoesan linguistic groups) communities, were largely collected from central South Africa (near the towns of Douglas and Upington, also in Region A). These data are problematic because 1) the Khoe and the San are not mutually exclusive and are considered one biological population, 2) the influx of genetic admixture over the last few hundred years would likely affect dentition, and 3) cast material does not capture all the relevant dental data (i.e. root morphology). Irish (1993) finds marked dental morphological disparity between the Khoekhoe and San, and attributes differences in morphology to random genetic drift in the San, and greater Khoekhoe admixture with the Bantu-speaking populations and Europeans. Nonetheless he associates both Khoekhoe and San populations to one early ancestral group. Overall, 18/34 traits

(53%) are statistically different between Irish's (1993) Khoekhoe and San combined data and this study's Khoesan data. This can only be attributed to differences in material (Irish examined a number of casts, whereas this study was based only on skeletal remains) or temporal differences. The latter is more likely, given the much longer time span in this study compared with Irish's historic sample.

Interestingly, Khoekhoe material described by Irish (1993) is most similar to the data set from Region A in this thesis, a set which includes many samples from the first millennium BP, and which is likely to have a least some genetic admixture from Negroid farmers. This region's sample is far more similar to Irish's (1993) work than to the Khoesan data set as a whole (73% similarity versus 47%, respectively). It should be noted that recent peoples often have poorly understood signatures of recent admixture; in an African context, even more so if these samples are from the very recent Colonial past, such as with Irish's (1993) dataset. These data are therefore poor models for the ancestral dental condition.

Assuming that dental phenetic expression is a reflection of genetic variability, Irish's (1993, 1998) work suggests that in terms of dentition, sub-Saharan Africans are not closely related to other world populations as they "have a pattern of several morphologically complex crown and, particularly, root traits" (Irish 1993: 264). Irish (2013) has recently added new (both recent and archaic) data from sub-Saharan Africa to his well-established SSADC. These new specimens are said to range from a Late Palaeolithic to Iron Age timeframe but dates are not specified. Although he mentions having included Early Holocene data from southern Africa (i.e. pre-Bantu), the exact provenance, number of individuals and dates of these specimens are unpublished. Nonetheless, there are only minor fluctuations in trait frequencies between the original and the revised sub-Saharan complex. In relation to the SSADC (high frequencies of the CMR, two-rooted P^3, P_3 Tome's root, M_1 cusp 7, M_2 Y-groove pattern, 2-rootedM_2, M^1 Carabelli's trait, 3-rooted M^2, M^3 presence, and very low incidences of I^1 double shovel and M^1enamel extension), "all aboriginal sub-Saharan African peoples collectively share similar percentages of the 11 traits" (Irish 2013: 288). He also notes, however, that in his study there is extensive interregional variability, providing an example of P_3 Tome's root occurrence in eastern Africa; the trait presence varies between 0 and 36% for groups in the region.

Currently modern sub-Saharan African teeth appear to be positioned within the SSADC but Khoesan dentition throughout the Holocene is not. Khoesan dentition (sampled from deeper time) does not wholly correspond with trait frequencies observed in the Afridonty complex; 58% of the traits used to assess sub-Saharan African teeth as a whole are different from this study's Khoesan dental data and the Afridonty traits and trait frequencies (high frequencies CMR, two-rooted P^3, P_3 Tome's root, M_2 Y-5 pattern, M_1 cusp 7, two-rooted M_2, three-rooted M^2, M^1Carabelli's trait, and low frequencies of I^1 double shovel, M^1 enamel extension) as well as two recurring sub-Saharan African traits not commonly associated with the central 11 SSADC traits (high frequencies of the I^1 labial convexity and midline diastema). These two traits are not routinely recorded in other dental studies and therefore global comparison can't be made, making it difficult to determine if they are representative of the SSADC diagnostic set (Irish 1997). The frequencies for these traits do not align with what is observed in the Holocene Khoesan. Additionally, sub-Saharan dentitions are generally larger than Khoesan and are known to be amongst the largest in size of all human populations (T. Hanihara and Ishida 2005).

KHOESAN DENTITION IN GLOBAL CONTEXT

The relationship between Afridonty and the Khoesan dentition should also be discussed relative to a modern global context as high and low frequencies are evaluated in terms of other dental complexes around the world. Based on 31 traits, the Khoesan display a pattern of trait frequency that is remarkably similar to all of the world complexes, with the exception of the Sinodonts (see Table 5.18). A number of high and low frequency traits correspond – a likely reflection of common ancestry. Interestingly, there exists a pattern of similarity (i.e. the number of traits with frequencies that demonstrate <10% difference between populations) between the Khoesan and Western Eurasia. Dental traits such as low frequencies of M^3 parastyle and higher frequencies of I^2 interruption groove are characteristic of the Khoesan dentition and appear at similar frequencies in Western Eurasia. The Khoesan dentition is least like the Sinodont complex. As with the sub-Saharan dentition in general, these two samples appear to be at opposite ends of the morphological spectrum (e.g. the Khoesan have high frequencies of P_3 Tome's root and lower frequencies of M_1 cusp 6, in contrast to the Sinodonts). The Khoesan and Sinodonts are geographically quite distant which could account, in part, for the high degree of dissimilarity seen between them. The Sundadonts appear to have intermediate trait frequencies in comparison to some of the extremes seen in the Khoesan and sub-Saharan African dentitions. When compared, the Sundadonts and Khoesan demonstrate a number of trait frequencies that appear within 10% of each other (e.g. M^1 Carabelli's). Metrically, Sundadont dentition is also intermediate in size, comparable to some larger Khoesan individuals. The Khoesan display more dental similarity to the Australia/Melanesia/New Guinea (Aus.) groups than to Western Eurasian groups. A number of similar frequencies between the Khoesan and Aus. populations are seen (including among others, M_1 deflecting wrinkle and M_1 protostylid), but size differs greatly. There has been much study on possible skeletal and genetic links between Africa and Australia (Cavalli-Sforza *et al.* 1994; Nurse *et al.* 1985) and although there appears to be a close relationship between sub-Saharan African and Australian dentitions (Turner 1992a), in general, similarities are attributed to parallel adaptations rather than genetic affinity (King and Motulsky 2002; McEvoy *et al.* 2010; Nurse *et al.* 1985).

The similarities and differences observed between the Khoesan and world populations are somewhat congruent (with some notable exceptions, e.g. CMR and C^1 canine accessory ridge) with Irish's (1993) findings comparing sub-Saharan African and world dental complexes. The Khoesan/world population relationship is also consistent with distance analyses in both Irish (1993, 1997) and G.R. Scott and Turner (2000). However, G.R. Scott and Turner (2000: 289) demonstrate in a tree based distance analysis of 23 crown and root traits that the San do not generally cluster with the sub-Saharan African dentition, although the smallest pairwise distances for the San are between West and South Africa indicating some relationship. The Khoesan dataset studied here also has higher frequencies of mass-additive traits (i.e. traits in which there are an increase in tooth mass), commonly observed in sub-Saharan Africa (Irish 1993). In general, sub-Saharan African samples have higher frequencies of such traits, including CMR and extra lower molar cusps (5th, 6th and 7th), which are similarly observed in the Khoesan. This differs from other world complexes such as Western Eurasia and North Africa (that have mass-reductive trait differences such as M^3 agenesis) (Irish 1993) but is also seen to some degree in Southeast Asia and the Pacific. Therefore the Khoesan data set studied here is consistent with the pattern seen in sub-Saharan Africa. Why there are regional differences in these traits is less clear, though it might simply be due to the fact that traits that occur at a higher frequency can vary more.

CORE KHOESAN DENTAL TRAITS AND INTERESTING FEATURES

Since Khoesan dentition in the Holocene does not wholly conform to the Afridonty complex, it is useful to identify core traits that are signatures of Khoesan dental morphology. Twelve traits broadly define the overall Khoesan dental map: low frequencies of I^1 double shovel, C^1 distal accessory ridge, M_1protostylid, M_1 distal trigonid crest, M_2 cusp # (ASU score of 4), and high frequencies of I^2 interruption groove, CMR, M_2 Y-groove, M_2 root #, 3-rooted M^2, M^1metaconule and the presence of the midline diastema. These core Khoesan traits identify this group within a global context, and allow for quick differentiation between this group and other world populations.

Arguably the most interesting aspects of Khoesan dental morphology relate to a few of the key traits that form part of the core Khoesan dental map and, according to current data, are relatively distinctive in their expression worldwide. The CMR (C^1 CMR; discussed briefly in chapter 5; see Fig. 5.3), as expected for this population, has a very high frequency (61.5%). Although CMR has been reported elsewhere in Africa (Irish 1993; Sakuma *et al.* 1991), it is much less common in other populations, making this trait, and especially its high frequency, a key feature of the Khoesan. However, this trait has been identified at an even higher frequency (77.8%) in the Holocene Kenyan population (this study), suggesting that such a high frequency might be a reflection of time depth (e.g. archaeological material).

The M^1 metaconule also occurs at a very high frequency (51.7%). Indeed, this is one of the highest frequencies worldwide, surpassed only by its occurrence in Australian Aborigines (56.5%). The metaconule (also referred to as a fifth cusp or distal accessory tubercle) is located between the hypocone and metacone and is considered an ancestral trait due to its presence in hominin dentitions, i.e. Dmanisi

(Martinón-Torres *et al.* 2008) and South African Plio-Pleistocene teeth (G.T. Schwartz *et al.* 1998). Metaconules are consistently large in size among the Khoesan. The ASUDAS scores this trait only up to a “medium” size and the associated dental plaques demonstrate relatively small metaconules compared with those found on Khoesan teeth. The importance of the trait in southern African populations has been noted by Macho and Moggi-Cecchi (1992) who demonstrate that the development of the fifth cusp is not related to crown area or the development of other cusps such as the hypocone. If this is the case, the trait expression is one unique to Khoesan dental morphology as it is not formed as a response to the diminutive size of Khoesan teeth. Interestingly, the metaconule often occurs as multiple cusps (in 23.7% of cases) but this is not restricted to the first molar. Multiple metaconules (or additional distal accessory cusps) are often observed on second and third molars (see Fig. 6.1). Multiple metaconules have been noted in Australian Aboriginal populations (Townsend *et al.* 1986), while other irregular cusps such as protoconules (mesial accessory cusps) have also been observed in human dentitions (Kanazawa *et al.* 1990).

Fig. 6.1: SAM-AP 6313B. Left M^1 with a metaconule, M^2 with two metaconules (one large and one cuspule size) and M^3 with two distinct metaconules.

The C^1 distal accessory ridge, a polymorphic feature that presents distally as an extra marginal ridge, also differs in the Khoesan data set, presenting at a very low frequency (8.22%). This highly sexually dimorphic trait (Noss *et al.* 1983; G.R. Scott 1977) is generally more robust in upper canines than lower (D.H. Morris 1975) and is therefore evaluated in this study on upper canines only. This trait is particularly susceptible to under-recording as a result of attrition. In this study, it was evaluated only on unworn teeth, but attrition rates in hunter-gatherer populations are high and begin in youth. This may provide an explanation for the exceptionally low frequency of this trait in this study relative to world rates.

The maxillary midline diastema has been included as one of the core Khoesan traits due to its high frequency (19.84%) relative to the average demonstrated in the SSADC (10.5%) and Irish's (1993) Khoesan data set (9.65%). Many studies outside Africa do not include this trait as it is most commonly observed in Negroid populations (Lavelle 1970). It is frequently identified in Bantu-speaking groups of eastern and southern Africa (Jacobson 1968). Irish's (1993) work indicates that it is more prevalent in eastern Africa and parts of central and southern Africa (among non-Khoesan populations) than it is in West Africa. The trait is present from *ca.* 8000 BP in Khoesan groups from this study, maintaining relatively similar frequencies throughout the Holocene at higher rates of occurrence than indicated in previous research. Interestingly, recent research has suggested a genetic basis for, and prevalence of, this trait in black populations (African ancestry). It has also been linked to possible environmental factors (Gass *et al.* 2003). Future work on the occurrence of this trait elsewhere may help define its significance globally.

Although not part of the core Khoesan traits, as frequencies are similar to those found in other populations, the M^3 peg and M_1 cusp 7 traits deserve a note. Khoesan teeth are generally very small in comparison to dental sizes elsewhere; only the Sundadonts demonstrate comparably sized teeth. Both upper and lower third molars are also generally smaller (and more variable) than other molars. From a visual assessment, Khoesan M^3's are often much reduced in comparison to M^1 and M^2. They do not always reduce to the size of a peg molar (<7mm buccolingual diameter) but are frequently undersized. A tendency towards tooth size reduction has been observed in many Mid-Late Pleistocene teeth such as those seen at Klasies River Mouth (Grine 2012). M^3 reduction in particular has been observed in Mid-Late Pleistocene data from this thesis, comparable to reductions seen in Holocene Khoesan material. M_1 cusp 7 is an ancestral trait found in many hominin and extant African populations and occurs in 25% of the Mid-Late Pleistocene dental remains studied here. It is observed at 38.5% in the SSADC but occurs in the Khoesan at a lower frequency (18.1%). This frequency aligns more with what we see in Western Eurasia (10.3%) but is still higher in frequency than observed outside Africa as is expected due to the ancestral nature of its appearance. Interestingly, the trait occurs at 15.2% in the Kenyan group from this study, comparable to what we see in the Khoesan.

Trait reductions/increases between molars within morphogenic fields (Butler 1937, 1939) have also been of interest. Lower molar trait frequencies (between $M_1$and M_2) were largely similar for Y-groove/X-groove, cusp #, cusp 5, cusp 6 and cusp 7, with differences between them ≤16%. This is of interest because it means that, where traits cannot be recorded on first molars due to advanced wear (a particular problem in hunter-gatherer populations), and where archaeological excavations have not yielded first molars, it is possible to use second molars as a reasonable substitute in assessing the presence/absence of traits in the Khoesan dental map. Further investigations are needed to see if this pattern holds in other populations.

IMPLICATIONS FOR DENTAL ANTHROPOLOGY

The implications of this study for dental anthropology in general, and in Africa specifically, are three-fold. By using alternative dental measurements (cervical and diagonal), this study was able to collect more dimensional data on more individuals in comparison to previous studies based only on crown measurements and therefore limited by tooth wear. As outlined in Chapter 4, Hillson *et al.* (2005) proposed a set of alternative dental measures to combat recording problems associated with dental attrition, in-jaw measurement difficulties and factors (genetic, environmental, cultural) affecting tooth crowns (Hillson 1998). They compared cervical and diagonal diameters with standardised crown measurements on unworn teeth and observed that they were highly correlated and repeatable. This study applied these techniques to archaeological teeth and results concur with previous work (Fitzgerald and Hillson 2008; Hillson *et al.* 2005; Pilloud and Hillson 2012) demonstrating that alternative dental measurements record similar information to, and can be performed as reliably as, commonly recorded occlusal crown diameters. Some studies however, have demonstrated some problems with this method in terms of the degree of measurement correlation between fixed and loose teeth (mesiodistal diameters, in particular) (Stojanowski 2007) and recording strategies (Aubry 2014). Adopting this method here has, however, proven beneficial in an archaeological context as more dental information could be drawn from samples. The use of these measurements has been successful in providing new and relevant Khoesan dental measurement data, previously hampered by the high levels of dental attrition common amongst hunter-gatherer populations. These new measurements will allow for the inclusion of Khoesan dental dimensions in large-scale studies such as T. Hanihara (2005) in the future.

In terms of Khoesan dental metrics, in comparison to world measurements, the Khoesan dentition is small. Comparable in size only to some Sundadont populations e.g. Jomon in Japan (Brace and Nagai 1982; T. Hanihara and Ishida 2005), the Khoesan display diminutive dentition with limited variation in size over the last 12 000 years. Teeth from sub-Saharan Africa in general are much larger than most other global dental populations (T. Hanihara and Ishida 2005), including the Khoesan (although dimensions for all sub-Saharan African populations have not, as yet, been recorded), and even African Pygmy populations appear to exhibit larger dentitions as there is a lack of allometry between body size and tooth size (B.T. Shea and Gomez 1988) in these groups. Khoesan teeth are also not very sexually dimorphic (Van Reenen 1970) and both male and female teeth present with similar size ranges. Therefore, Khoesan teeth appear to stand apart metrically from other dental populations in sub-Saharan Africa.

Morphologically, this study has confirmed the unique nature of Khoesan dentition and its extreme position in the range of variation of populations across the world. The Khoesan have always been considered an outlying biological group but have, on occasion, been incorporated into combined studies of southern African or sub-Saharan populations (for example: Irish (1993) and Scott and Turner (2000)). These evaluations have been successful in identifying the generalised placement of historical southern African and Khoesan populations in the dental world but lacked specificity with regards to Holocene Khoesan dentition. The differences between Khoesan dentition and Irish's (1998, 2013) sub-Saharan complex, as well as between Holocene Khoesan and Holocene Kenyan samples, has implications for the overall Afridonty complex, as the Khoesan dentition does not fit neatly into the Afridonty box. Granted, as Irish (1998) mentions, some traits could not be assessed due to sample constraints (e.g. root traits cannot be evaluated accurately when using cast material) and although his Khoe and San trait frequencies exhibit similarities to the overall complex, this study has identified some discrepancies previously unknown to researchers. It may be that grouping all sub-Saharan African populations into one dental complex is problematic, but further research into African dentition is needed to assess significant differences between and within both archaeological and modern populations. However, it is important to remember that the Khoesan dental map does maintain some important links with the Afridonty complex, relative to other worldwide complexes, and therefore the complex should not be disregarded when discussing Khoesan dentition. Rather, the additional core traits that distinguish Khoesan dentition from other world populations should be considered in conjunction with the SSADC.

IMPLICATIONS FOR THE UNDERSTANDING OF THE EMERGENCE OF KHOESAN DENTITION

No previous study has attempted to use dental analyses as a platform to evaluate Khoesan population dynamics. This study, apart from providing a dental perspective on prehistoric human occupation in southern Africa, confirms population continuity. It also implies that certain processes of change (demographic, genetic, and/or possibly environmental) or lack thereof played a role in the emergence of the Holocene Khoesan dental map. Mid-Late Pleistocene teeth share many dental traits with the Holocene including to some degree, dental size. In addition, variation such as that seen in the Klasies River Mouth material is typical when viewed in light of overall Khoesan variation. The dental evidence is consistent with a degree of population continuity from the MSA to the LSA. Moreover, there have been no detectable population migrations into the regions over time. Significant changes in dental morphology would have been identified if new, substantially different genetic material had been introduced. Rather, the Khoesan remain a single, geographically restricted, dentally distinct population throughout the Holocene and a degree of admixture is observed only during the Colonial contact period. This places the emergence of the

Khoesan phenotype no later than the terminal Pleistocene/Early Holocene, supporting previous hypotheses (Bräuer and Rösing 1989; Churchill *et al.* 2000; Churchill *et al.* 1996; Grine *et al.* 2007; Grine *et al.* 2000; A.G. Morris 1992a; Rightmire and Deacon 1991; J.H. Schwartz and Tattersall 2003; Stynder *et al.* 2007b) and extending our knowledge of Khoesan population history deeper in time.

This study also highlights the value of analysing intra-population similarities/differences across both time and space. Assessing regional variability has identified overall dental homogeneity and pinpointed small-scale regional and temporal variation. Having a large set of dated skeletons enabled investigation of changes through time, finding changes in dental morphology delayed by approximately 1000 years relative to changes in crania and postcrania; reasons for these changes are not clear. Assessing samples through time also showed that nutritional or dietary constraints may have influenced dental size, while changes in population dynamics may have resulted in random gene frequency changes which ultimately influenced tooth morphology.

FUTURE RESEARCH

In terms of non-metric dental information, CT scanning to reveal the internal structure of dentin would be beneficial. Currently, incremental enamel (i.e. perikymata) and dentine microstructures are assessed using CT scan and transmitted light microscopy techniques (T.M. Smith and Tafforeau 2008) to identify rates of dental development within and between modern and hominin populations (Dean *et al.* 2001; T.M. Smith *et al.* 2010). These include, for example, assessing enamel thickness (T.M. Smith *et al.* 2003), dentine striations and features corresponding to enamel observations (Dean 1995, 1998), specimen developmental age (at death) (T.M. Smith *et al.* 2006) and the application of new methods in understanding overall dental development (T.M. Smith 2008b; T.M. Smith *et al.* 2004; T.M. Smith and Tafforeau 2008). The technology to observe internal tooth structure is available but no study thus far has assessed the prevalence of non-metric traits on dentine. Crown features are more susceptible to wear than dentine and only substantial enamel attrition will affect dentine morphology. By using CT scanning technologies, the shape, form and structure of cusp/crown morphology can be observed on relatively worn teeth by looking at the dentine morphology. A new scoring methodology would need to be applied as the traits would not present at the same sizes (scores) as seen on the current standardised ASUDAS dental plaques but many of the traits (particularly cusp and mass-additive traits) should be visible in varying degrees on the dentine. This type of study may provide new insights into non-metric trait variation in populations where dental attrition is problematic (e.g. archaeological specimens).

Further comparisons between the Khoesan data set and other African populations would also be of great interest. In particular, comparisons with Bantu-speaking groups from Southern Africa are needed in order to evaluate the relationship between these two groups and better understand gene flow and population history over the last two thousand years. No morphological study has compared the dentitions of these two populations in the context of geographic spread and time. Assessing metric and non-metric data from Holocene individuals from areas like Botswana, for example, may help answer questions relating to possible population migrations from this region into South Africa. Further research on African dentition, in general, is needed as information for African populations is scarce. More research into various sub-Saharan African groups may offer new insights into the veracity of Afridonty as an umbrella complex.

Dental anthropological studies have predominantly focused on modern populations. Archaeological dentitions are often assessed metrically but non-metric evaluations are rare. Future work on dental non-metric traits on other archaeological populations will allow for richer, time-appropriate comparisons between ancient groups. In addition, further research on the effects of environment on teeth would be beneficial. Although these effects are currently deemed limited, this study has demonstrated delayed temporal variations that may be attributable to environmental change over time. The continued study of archaeological dental populations may shed light on such questions. Archaeology offers a time dimension that dental anthropological studies of modern populations do not have, and examining changes over time allows for a long-term perspective on dental variation that can make an important contribution to the discipline.

REFERENCES

Abdi, H., and Williams, L.J. 2010. Principal component analysis. *Wiley Interdisciplinary Reviews: Computational Statistics* 2:1-47.

Ackermann, R.R. 1998. A quantitative assessment of the variability in the Australopithecine, human, chimpanzee and gorilla face. Ph.D. dissertation. St. Louis, Missouri.

Ackermann, R.R. 2002. Patterns of covariation in the hominoid craniofacial skeleton: implications for paleoanthropological models. *Journal of Human Evolution* 43(2):167-187.

Alvarez, J.O. 1995. Nutrition, tooth development, and dental caries. *The American journal of clinical nutrition* 61(2):410S-416S.

Alvarez, J.O., Eguren, J.C., Caceda, J., and Navia, J.M. 1990. The effect of nutritional status on the age distribution of dental caries in the primary teeth. *Journal of dental research* 69(9):1564-1566.

Alvesalo, L., and Tigerstedt, P.M.A. 1974. Heritabilities of human tooth dimensions. *Hereditas* 77(2):311-318.

Ambrose, S.H. 1984a. Excavations at Deloraine, Rongai. *Azania* 20:29-67.

Ambrose, S.H. 1984b. The introduction of pastoral adaptations to the highlands of East Africa. In: J.D. Clark, and S.A. Brandt, editors. From hunters to farmers: The causes and consequences of food production in Africa Berkeley: University of California Press. p 212-239.

Ambrose, S.H. 1985. Excavations at Masai Gorge Rockshelter, Naivasha. *Azania* 20(1):29-67.

Ambrose, S.H. 1998. Chronology of the Later Stone Age and food production in East Africa. *Journal of Archaeological Science* 25(4):377-392.

Ambrose, S.H. 2002. Small Things Remembered: Origins of Early Microlithic Industries in Sub-Saharan Africa. *Archeological papers of the American Anthropological Association* 12(1):9-29.

Ambrose, S.H., and DeNiro, M.J. 1989. Climate and habitat reconstruction using stable carbon and nitrogen isotope ratios of collagen in prehistoric herbivore teeth from Kenya. *Quaternary research* 31(3):407-422.

Ambrose, S.H., Hivernel, F., and Nelson, C.M. 1980a. The taxonomic status of the Kenya Capsian. In: R.E. Leakey, and B.A. Ogot, editors. Proceedings of the

VIIIth Panafrican Congress of Prehistory and Quaternary Studies, Nairobi: International Louis Leakey Memorial Institute for African Prehistory. p 248-252.

Ambrose, S.H., Hivernel, F., and Nelson, C.M. 1980b. The taxonomic status of the Kenya Capsian. In: R.E.L.a.B.A. Ogot, editor. Proceedings of the 8th Panafrican Congress of

Prehistory and Quaternary Studies. Nairobi: International Louis Leakey Memorial Institute for African Prehistory. p 248-252.

Ambrose, S.H., and Sikes, N.E. 1991. Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. *Science* 253(5026):1402-1405.

Aubry, B.S. 2009. Population structure and interregional interaction in pre-Hispanic Mesoamerica: a biodistance study. Columbus: Ohio State University.

Aubry, B.S. 2014. Cervical dimensions for in situ and loose teeth: A critique of the Hillson et al.(2005) method. *American Journal of Physical Anthropology* Article first published online: 23 Jan. 2014. DOI: 10.1002/ajpa.22475.

Avery, D.M. 1982. The micromammalian fauna from Border Cave, Kwazulu, South Africa. *Journal of Archaeological Science* 9(2):187-204.

Avery, D.M. 1992. The environment of early modern humans at Border Cave, South Africa: micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 91(1):71-87.

Avery, D.M. 2000. Past and present ecological and environmental information from micromammals. In: L. Barham, editor. The Middle Stone age of Zambia, South Central Africa. University of Bristol: Western Academic and Specialist Press. p 63-72.

Avery, D.M., Braine, S., and Loutit, R. 1984. Bone accumulation by hyenas and jackals: a taphonomic study. *South African Journal of Science* 80:186-187.

Avery, G., Cruz-Uribe, K., Goldberg, P., Grine, F.E., Klein, R.G., Lenardi, M.J., Marean, C.W., Rink, W.J., Schwarcz, H.P., Thackeray, A.I., and Wilson, M.L. 1997. The 1992-1993 excavations at the Die Kelders Middle and Later Stone Age cave site, South Africa. *Journal of Field Archaeology* 24(3):263-291.

Azoulay, L., and Regnault, F. 1893. Des diverses formes des dents incisives supérieures. *Bulletins de la Société d'anthropologie de Paris* 4(1):266-269.

Bada, J., and Deems, L. 1975. Accuracy of dates beyond the C-14 dating limit using the aspartic acid racemization reaction. *Nature* 255:218-219.

Bailey, S.E. 2002. Neandertal dental morphology: implications for modern human origins: Arizona State.

Bailey, S.E. 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. *Journal of Human Evolution* 47(3):183-198.

Bailey, S.E., Skinner, M.M., and Hublin, J.J. 2011. What lies beneath? An evaluation of lower molar trigonid crest patterns based on both dentine and enamel expression. *American Journal of Physical Anthropology* 145(4):505-518.

Bailit, H.L. 1975. Dental variation among populations. an anthropologic view. *Dental Clinics of North America* 19(1):125-139.

Bailit, H.L., and Sung, B. 1968. Maternal effects on the developing dentition. *Archives of Oral Biology* 13(2):155-161.

Balasse, M., Ambrose, S.H., Smith, A.B., and Price, T.D. 2002. The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. *Journal of Archaeological Science* 29(9):917-932.

Barbujani, G., and Bertorelle, G. 2001. Genetics and the population history of Europe. *Proceedings of the National Academy of Sciences* 98(1):22-25.

Barham, L. 1992. Let's walk before we run: An appraisal of historical materialist approaches to the Later Stone Age. *The South African Archaeological Bulletin* 47(155):44-51.

Barham, L. 1995. The Mumbwa Caves project, Zambia, 1993-94. *Nyame Akuma* 43:66-72.

Barham, L. 2000a. The Middle Stone Age of Zambia, south central Africa. University of Bristol: Western Academic & Specialist Press.

Barham, L. 2000b. The Mumbwa Caves 1993 - 1996. In: L. Barham, editor. The Middle Stone age of Zambia, South Central Africa. University of Bristol: Western Academic and Specialist Press. p 11-49.

Barham, L., and Mitchell, P. 2008. The first Africans: African archaeology from the earliest tool makers to most recent foragers. New York: Cambridge University Press.

Barham, L., Pinto, A.C., and Andrews, P. 2000. The Mumbwa Caves behavioural record. In: L. Barham, editor. The Middle Stone age of Zambia, South Central Africa. University of Bristol: Western Academic and Specialist Press. p 81-148.

Barnard, A. 1992. Hunters and herders of southern Africa. Cambridge: Cambridge University Press.

Barnard, A. 2008. Ethnographic analogy and the reconstruction of early Khoekhoe society. *Southern African Humanities* 20(1):61-75.

Barnes, D.S. 1968. Variations in tooth morphology between males and females in the Iteso. *Journal of dental research* 47:971-972.

Barnes, D.S. 1969. Tooth morphology and other aspects of the Teso dentition. *American Journal of Physical Anthropology* 30(2):183-193.

Barrett, C.K., Guatelli-Steinberg, D., and Sciulli, P.W. 2012. Revisiting dental fluctuating asymmetry in neandertals and modern humans. *American Journal of Physical Anthropology* 149(2):193-204.

Barthelme, J.W. 1985. Fisher-hunters and neolithic pastoralists in East Turkana, Kenya. Oxford: Archaeopress.

Beaumont, P.B. 1978. Border Cave. Unpublished MA thesis: University of Cape Town.

Beaumont, P.B. 1980. On the age of Border Cave homonids 1-5. *Palaeontologia Africana* (23):21-33.

Beaumont, P.B. 1981. The Heuningneskrans Shelter. In: E.A. Voigt, editor. Guide to archaeological sites in the Northern and Eastern Transvaal. Pretoria: South African Association of Archaeologists. p 133-145.

Beaumont, P.B., De Villiers, H., and Vogel, J. 1978a. Modern man in sub-Saharan Africa prior to 49 000 years BP: a review and evaluation with particular reference to Border Cave. *South African Journal of Science* 74(1978):409-419.

Beaumont, P.B., De Villiers, H., and Vogel, J.C. 1978b. Modern man in sub-Saharan Africa prior to 49,000 years BP: a review and evaluation with particular reference to Border Cave. *South African Journal of Science* 74:409-419.

Beaumont, P.B., and Morris, D. 1990. Guide to archaeological sites in the Northern Cape: Prepared for the Southern African Association of Archaeologists post-conference excursion, 9th-13th September 1990: McGregor Museum.

Beaumont, P.B., and Vogel, J.C. 1984. Spatial patterning of the ceramic Later Stone Age in the Northern Cape Province, South Africa. In: M. Hall, G. Avery, D.M. Avery, M.L. Wilson, and A.J.B. Humphreys, editors. Frontiers: southern

African archaeology today. Oxford: British Archaeological Reports International Series. p 80-95.

Benazzi, S., Coquerelle, M., Fiorenza, L., Bookstein, F., Katina, S., and Kullmer, O. 2011. Comparison of dental measurement systems for taxonomic assignment of first molars. *American Journal of Physical Anthropology* 144(3):342-354.

Berger, L.R., and Parkington, J.E. 1995. A new pleistocene hominid-bearing locality at Hoedjiespunt, South Africa. *American Journal of Physical Anthropology* 98(4):601-609.

Bernal, V., Perez, S.I., Gonzalez, P.N., and Diniz-Filho, J.A.F. 2009. Ecological and evolutionary factors in dental morphological diversification among modern human populations from southern South America. *Proceedings of the Royal Society B: Biological Sciences*. DOI: 10.1098/rspb.2009.1823.

Berry, A.C. 1974. The use of non-metrical variations of the cranium in the study of Scandinavian population movements. *American Journal of Physical Anthropology* 40(3):345-358.

Berry, A.C. 1976. The anthropological value of minor variants of the dental crown. *American Journal of Physical Anthropology* 45(2):257-267.

Berry, A.C., and Berry, R.J. 1967. Epigenetic variation in the human cranium. *Journal of Anatomy* 101(2):361-379.

Beuning, K.R., Zimmerman, K.A., Ivory, S.J., and Cohen, A.S. 2011. Vegetation response to glacial–interglacial climate variability near Lake Malawi in the southern African tropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 303(1):81-92.

Bianchi, F.J., Oliveira, T.F.d., Saito, C.B.P., Peres, R.C.R., and Line, S.R.P. 2007. Association between polymorphism in the promoter region (G/C-915) of PAX9 gene and third molar agenesis. *Journal of Applied Oral Science* 15(5):382-386.

Binford, L.R. 1984. Faunal remains from Klasies River Mouth. Florida: Academic Press

Binneman, J. 1982. Mikrogebruikstekens op steenwerktuie: eksperimentele waarnemeings en 'n studie van werktuie afkomstig van Boomplaasgrot. MA Thesis.: University of Stellenbosch.

Binneman, J. 1996. Symbolic construction of communities during the Holocene Later Stone Age in the south-eastern Cape. Johannesburg: University of the Witwatersrand.

Binneman, J. 1997. Usewear traces on robberg bladelets from Rose Cottage Cave. *South African Journal of Science* 93:479-481.

Binneman, J., and Mitchell, P. 1997. Microwear analysis of Robberg bladelets from Sehonghong Shelter, Lesotho. *Southern African Field Archaeology* 6:42-49.

Bleek, D.F. 1929. Comparative vocabularies and Bushman languages. Cambridge: Cambridge University Press.

Bleek, W.H.I. 1875. A brief account of bushman folklore and other texts. London: Trübner and Brockhaus.

Bleek, W.H.I., and Lloyd, L. 1911. Specimens of Bushman folklore. London: George Allen.

Bolk, L. 1922. On the relationship between reptialian and mammalian teeth. Odontological Essays IV. *Journal of Anatomy* 56:107-136.

Boonzaier, E., Malherbe, C., Smith, A.B., and Behrens, P. 1996. The Cape herders: a history of the Khoikhoi of southern Africa. Cape Town: David Philip.

Bower, J.R.F., and Nelson, C.M. 1978. Early pottery and pastoral cultures of the Central Rift Valley, Kenya. *Man* 13(4):554-566.

Bower, J.R.F., Nelson, C.M., Waibel, A.F., and Wandibba, S. 1977. The University of Massachusetts' Later Stone Age/Pastoral 'Neolithic' comparative study in Central Kenya: an overview. *Azania* 12(1):119-146.

Brace, C.L., and Nagai, M. 1982. Japanese tooth size: past and present. *American Journal of Physical Anthropology* 59(4):399-411.

Brace, C.L., Smith, S.L., and Hunt, K.D. 1991. What big teeth you had grandma! Human tooth size, past and present. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. New York: Wiley-Liss. p 33-57.

Bräuer, G. 1976. Morphological and multivariate analysis of human skeletons from Iron Age graves northeast of Lake Eyasi (Tanzania). *Homo* 27:185-196.

Bräuer, G. 1978. The morphological differentiation of anatomically modern man in Africa, with special regard to recent finds from East Africa. *Zeitschrift für Morphologie und Anthropologie* 69(3):266-292.

Bräuer, G. 1980. Human skeletal remains from Mumba rock shelter, northern Tanzania. *American Journal of Physical Anthropology* 52:71-84.

Bräuer, G. 1992. Africa’s place in the evolution of *Homo sapiens*. In: G. Bräuer, and F. Smith, editors. Continuity or replacement: controversies in Homo sapiens evolution. Rotterdam: Balkema. p 83-98.

Bräuer, G., Deacon, H.J., and Zipfel, F. 1992. Comment on the new maxillary finds from Klasies River Mouth, South Africa. 23(5).

Bräuer, G., and Rösing, F.W. 1989. Human biological history in southern Africa. *Rassengeschichte der Menschheit* 13:6-137.

Brewer-Carias, C.A., le Blanc, S., and Neel, J.V. 1976. Genetic structure of a tribal population, the Yanomama Indians. XIII. Dental microdifferentiation. *American Journal of Physical Anthropology* 44(1):5-14.

Broca, P. 1879. Instructions relatives à l'étude anthropologique du système dentaire. *Bulletins de la Société d'anthropologie de Paris* 2:128-163.

Brook, A.H., and O'Donnell, M.B. 2012. Modelling the complexity of the dentition. In: G. Townsend, E. Kanazawa, and H. Takayama, editors. New directions in dental anthropology. Adelaide: University of Adelaide Press. p 1-9.

Brooks, A.S., Nevell, L., Yellen, J.E., and Hartman, G. 2006. Projectile technologies of the African MSA: Implications for Modern Human origins. In: E. Hovers, and S.L. Kuhn, editors. Transitions before the Transition. New York: Springer. p 233-255.

Broom, R. 1918. The evidence afforded by the Boskop skull of a new species of primitive man (*Homo capensis*). *Anthropological Papers of the American Museum of Natural History* 23:63-79.

Broom, R. 1923. A contribution to the craniology of the yellow-skinned races of South Africa. *The Journal of the Royal Anthropological Institute of Great Britain and Ireland* 53:132-149.

Broom, R. 1941. Bushmen, Koranas and Hottentots: University Press.

Brothwell, D.R. 1963. Dental anthropology. New York: Pergamon Press.

Brown, F.H., and Feibel, C.S. 1986. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geological Society* 143(2):297-310.

Brown, K.S., Marean, C.W., Herries, A.I.R., Jacobs, Z., Tribolo, C., Braun, D., Roberts, D.L., Meyer, M.C., and Bernatchez, J. 2009. Fire as an engineering tool of early modern humans. *Science* 325(5942):859-862.

Brown, K.S., Marean, C.W., Jacobs, Z., Schoville, B.J., Oestmo, S., Fisher, E.C., Bernatchez, J., Karkanas, P., and Matthews, T. 2012. An early and enduring advanced technology originating 71,000 years ago in South Africa. *Nature* 491(7425):590-593.

Brown, T., and Townsend, G. 1979. Sex determination by single and multiple tooth measurements: Australian Institute of Aboriginal Studies.

Buikstra, J.E., and Ubelaker, D.H. 1994. Standards for data collection from human skeletal remains. *Arkansas Archeological Survey Research Series* 44:16-19.

Burchell, W. 1822. Travels in the interior of southern Africa. Vol. 1. London: Batchworth.

Burrett, R.S. 2006. Forager ceramics in Mashonaland? *Zimbabwean Prehistory* 26:39-41.

Butler, P.M. 1937. Studies of the Mammalian Dentition I. The Teeth of Centetes ecaudatus and its allies. Proceedings of the Zoological Society of London. p 103-132.

Butler, P.M. 1939. Studies of the mammalian dentition – differentiation of the post-canine dentition. Proceedings of the Zoological Society of London: Wiley Online Library. p 1-36.

Butler, P.M. 1956. The ontogeny of molar pattern. *Biological Reviews* 31(1):30-69.

Butler, P.M. 1982. Some problems of the ontogeny of tooth patterns. In: B. Kurtén, editor. Teeth: form, function and evolution. New York: Columbia University Press. p 44-51.

Butzer, K.W. 1984. Late Quaternary environments in South Africa. In: J.C. Vogel, editor. Late Cainozoic palaeoclimates of the southern hemisphere. Rotterdam: Balkema. p 235-264.

Butzer, K.W., Isaac, G.L., Richardson, J.L., and Washbourn-Kamau, C. 1972a. Radiocarbon dating of East african lake levels. *Science* 175(4026):1069-1076.

Butzer, K.W., Isaac, G.L., Richardson, J.L., and Washbourn-Kamau, C. 1972b. Radiocarbon dating of East African lake levels. *Science* 175(4026):1069-1076.

Campbell, J. 1822. Travels in South Africa. Being a narrative of a second journey in the interior of that country. London: Westley.

Campbell, T.D. 1925. The dentition and palate of the Australian Aboriginal. Adelaide: Hassell Press.

Cardoso, H.F. 2007. Environmental effects on skeletal versus dental development: Using a documented subadult skeletal sample to test a basic assumption in human osteological research. *American Journal of Physical Anthropology* 132(2):223-233.

Castañeda, I.S., Werne, J.P., and Johnson, T.C. 2007. Wet and arid phases in the southeast African tropics since the Last Glacial Maximum. *Geology* 35(9):823-826.

Cavalli-Sforza, L.L. 1991. Genes, people and languages. *Scientific American* 265:72-78.

Cavalli-Sforza, L.L., Menozzi, P., and Piazza, A. 1994. The history and geography of human genes. Princeton: Princeton University Press.

Chami, F., and Chami, R. 2001. Narosura pottery from the southern coast of Tanzania: first incontrovertible coastal Later Stone Age pottery. *Nyame Akuma* 56:29-35.

Charrié-Duhaut, A., Porraz, G., Cartwright, C.R., Igreja, M., Connan, J., Poggenpoel, C., and Texier, P.J. 2013. First molecular identification of a hafting adhesive in the Late Howiesons Poort at Diepkloof Rock Shelter (Western Cape, South Africa). *Journal of Archaeological Science* 40(9):3506-3518.

Chase, B.M., Boom, A., Carr, A.S., Meadows, M.E., and Reimer, P.J. 2013. Holocene climate change in southernmost South Africa: rock hyrax middens record shifts in the southern westerlies. *Quaternary Science Reviews* 82:199-205.

Chase, P.G. 1994. On symbols and the Palaeolithic. *Current Anthropology* 35:627-629.

Chase, P.G. 2003. Comment on Hensilwood and Marean on article: the origin of modern human behavior: a review and critique of models and test implications. *Current Anthropology* 44:627-651.

Chen, Y.S., Olckers, A., Schurr, T.G., Kogelnik, A.M., Huoponen, K., and Wallace, D.C. 2000. mtDNA variation in the South African Kung and Khwe-and their genetic relationships to other African populations. *Am J Hum Genet* 66(4):1362-1383.

Cheverud, J.M. 1995. Morphological integration in the saddle-back tamarin (*Saguinus fuscicollis*) cranium. *American Naturalist*:63-89.

Churchill, S.E., Berger, L.R., and Parkington, J. 2000. A Middle Pleistocene human tibia from Hoedjiespunt, Western Cape, South Africa. *South African Journal of Science* 96:367-368.

Churchill, S.E., and Morris, A.G. 1998. Muscle marking morphology and labour intensity in prehistoric Khoisan foragers. *International Journal of Osteoarchaeology* 8(5):390-411.

Churchill, S.E., Pearson, O.M., Grine, F.E., Trinkaus, E., and Holliday, T.W. 1996. Morphological affinities of the proximal ulna from Klasies River Mouth Main Site: archaic or modern? *Journal of Human Evolution* 31:213-237.

Clark, A.M.B. 1997. The MSA/LSA transition in southern Africa: new technological evidence from Rose Cottage Cave. *The South African Archaeological Bulletin* 52(166):113-121.

Clark, J.D. 1942. Further excavations (1939) at the Mumbwa Caves, Northern Rhodesia. *Transactions of the Royal Society of South Africa* 29:133-201.

Clark, J.D. 1958. Some Stone Age woodworking tools in southern Africa. *The South African Archaeological Bulletin* 13(52):144-152.

Clark, J.D. 1959. The prehistory of southern Africa. Harmondsworth: Penguin.

Clark, J.D. 1962. The spread of food production in sub-Saharan Africa. *The Journal of African History* 3(2):211-228.

Clark, J.D., Beyene, Y., Wolde Gabriel, G., Hart, W.K., Renne, P.R., Gilbert, H., Defleur, A., Suwa, G., Katoh, S., and Ludwig, K.R. 2003. Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423(6941):747-752.

Clark, J.D., Cole, G.H., Isaac, G.L., and Kleindienst, M.R. 1966. Precision and definition in African archaeology. *The South African Archaeological Bulletin* 21(83):114-121.

Clark, J.L., and Plug, I. 2008. Animal exploitation strategies during the South African Middle Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. *Journal of Human Evolution* 54(6):886-898.

Clayton, F., Sealy, J., and Pfeiffer, S. 2006. Weaning age among foragers at Matjes River Rock Shelter, South Africa, from stable nitrogen and carbon isotope analyses. *American Journal of Physical Anthropology* 129(2):311-317.

Cleaton-Jones, P. 1970. Agenesis and peg-shaped permanent maxillary lateral incisors in Kalahari Bushmen. *Journal of dental research* 49(2):457.

Colby, G.R. 1996. Analysis of dental sexual dimorphism in two western Gulf of Mexico precontact population utilizing cervical measurement. *American Journal of Physical Anthropology* 22:87.

Cole, S. 1954. The Prehistory of East Africa. *American Anthropologist* 56(6):1026-1050.

Conceição, E.L.N., and Cardoso, H.F. 2011. Environmental effects on skeletal versus dental development II: further testing of a basic assumption in human osteological research. *American Journal of Physical Anthropology* 144(3):463-470.

Constant, D.A., and Grine, F.E. 2001. A review of taurodontism with new data on indigenous southern African populations. *Archives of Oral Biology* 46(11):1021-1029.

Cooke, C.K. 1965. Evidence of human migrations from the rock art of Southern Rhodesia. *Africa: Journal of the International African Institute* 35:263-285.

Cooke, H.B.S., Malan, B.D., and Wells, L.H. 1945a. Fossil Man in the Lebombo Mountains, South Africa: The 'Border Cave,' Ingwavuma District, Zululand. *Man* 45:6-13.

Cooke, H.B.S., Malan, B.D., and Wells, L.H. 1945b. Fossil man in the Lebombo Mountains, South Africa: the 'Border Cave,' Ingwavuma District, Zululand. *Man* 45 (ArticleType: research-article/Full publication date: Jan. - Feb., 1945/Copyright © 1945 Royal Anthropological Institute of Great Britain and Ireland):6-13.

Cowling, R.M., Esler, K.J., and Rundel, P.W. 1999. Namaqualand, South Africa: an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology* 142(1/2):3-21.

Cruciani, F., Santolamazza, P., Shen, P., Macaulay, V., Moral, P., Olckers, A., Modiano, D., Holmes, S., Destro-Bisol, G., Coia, V., Wallace, D.C., Oefner, P.J., Torroni, A., Cavalli-Sforza, L.L., Scozzari, R., and Underhill, P.A. 2002. A back migration from Asia to sub-Saharan Africa Is supported by high-resolution analysis of human Y-chromosome haplotypes. *American Journal of Human Genetics* 70(5):1197-1214.

Cunha, C., Silva, A.M., Irish, J.D., Scott, G.R., Tomé, T., and Marquéz, J. 2012. Hypotrophic roots of the upper central incisors - a proposed new discrete dental trait. *Dental Anthropology* 25(1):8-14.

Curnoe, D. 2009. The mandible from bed 3, Cave of Hearths. In: J. McNabb, and A. Sinclair, editors. The Cave of Hearths: Makapan middle pleistocene research project Field research by Anthony Sinclair and Patrick Quinney, 1996-2001. Oxford: Archaeopress.

d'Errico, F., Henshilwood, C.S., Vanhaeren, M., and Van Niekerk, K. 2005. *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *Journal of Human Evolution* 48(1):3-24.

d'Errico, F., Vanhaeren, M., and Wadley, L. 2008. Possible shell beads from the Middle Stone Age layers of Sibudu Cave, South Africa. *Journal of Archaeological Science* 35(10):2675-2685.

Dahlberg, A.A. 1945. The changing dentition of man. *Journal of the American Dental Association* 32:676-690.

Dahlberg, A.A. 1951. The dentition of the American Indian. In: W.S. Laughlin, editor. The physical anthropology of the American Indian. New York: The Viking Fund. p 138-176.

Dahlberg, A.A. 1956. Analysis of the American Indian dentition. In: D.R. Brothwell, editor. Dental Anthropology. New York: Pergamon Press. p 149-177.

Dart, R.A. 1948. The first human mandible from the Cave of Hearths, Makapansgat. *The South African Archaeological Bulletin* 3(12):96-98.

Dart, R.A., and Del Grande, N. 1931. The ancient iron-smelting cavern at Mumbwa. *Transactions of the Royal Society of South Africa* 19:379-427.

De Villiers, H. 1968. The skull of the South African Negro. Johannesburg: Witwatersrand University Press.

De Villiers, H. 1973. Human skeletal remains from Border Cave, Ingwavuma District, Kwa Zulu, South Africa. *Annals of the Transvaal Museum* 28:229-256.

De Villiers, H. 1976. A second adult human mandible from Border Cave, Ingwavuma District, Kwa Zulu, South Africa. *South African Journal of Science* 72:212-215.

De Villiers, H., and Fatti, L.P. 1982. The antiquity of the Negro. *South African Journal of Science* 78:321-332.

Deacon, H.J. 1969. Re-excavation and description of the Wilton type-site, Albany District, eastern Cape. Unpublished M.A. thesis: University of Cape Town.

Deacon, H.J. 1972a. A review of the post-Pleistocene in South Africa. *South African Archaeological Society Goodwin Series*(1):26-45.

Deacon, H.J. 1976. Where hunters gathered: a study of Holocene Stone Age people in the Eastern Cape. Claremont: South African Archaeological Society.

Deacon, H.J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. *World Archaeology* 10(3):241-257.

Deacon, H.J. 1992. Southern Africa and modern human origins. *Philosophical Transactions: Biological Sciences* 337(1280):177-183.

Deacon, H.J. 1993. Planting an idea: an archaeology of Stone Age gatherers in South Africa. *The South African Archaeological Bulletin* 48(158):86-93.

Deacon, H.J. 1995. Two Late Pleistocene-Holocene archaeological depositories from the southern Cape, South Africa. *The South African Archaeological Bulletin* 50(162):121-131.

Deacon, H.J., and Deacon, J. 1999. Human beginnings in South Africa: uncovering the secrets of the Stone Age. Cape Town: David Philips.

Deacon, H.J., Deacon, J., Brooker, M., and Wilson, M.L. 1978. The evidence for herding at Boomplaas Cave in the southern Cape, South Africa. *The South African Archaeological Bulletin* 33(127):39-65.

Deacon, H.J., Deacon, J., Scholtz, J., Thackeray, J.F., Brink, J.S., and Vogel, J.C. 1984. Correlation of palaeoenvironmental data from the Late Pleistocene and Holocene deposits at Boomplaas Cave, southern Cape. In: J.C. Vogel, editor. Late Cainozoic palaeoclimates of the Southern Hemisphere. Rotterdam: Balkema. p 339-351.

Deacon, H.J., and Geleijnse, V.B. 1988. The stratigraphy and sedimentology of the main site sequence, Klasies River Mouth, South Africa. *The South African Archaeological Bulletin* 43(147):5-14.

Deacon, H.J., Talma, A.S., and Vogel, J.C. 1988. Biological and cultural development of the Pleistocene people in an Old World southern continent. In: J.R. Prescott, editor. Early man in the Southern Hemisphere: supplement to archaeometry, Australian studies: Dept. of Physics and Mathematical Physics, University of Adelaide. p 523-531.

Deacon, J. 1972b. Wilton: an assessment after fifty years. *The South African Archaeological Bulletin* 27(105/106):10-48.

Deacon, J. 1974. Patterning in the radiocarbon dates for the Wilton/Smithfield complex in southern Africa. *The South African Archaeological Bulletin* 29(113/114):3-18.

Deacon, J. 1978. Changing patterns in the late Pleistocene/early Holocene prehistory of southern Africa as seen from the Nelson Bay Cave stone artifact sequence. *Quaternary research* 10(1):84-111.

Deacon, J. 1984a. The Later Stone Age of southernmost Africa. Oxford: Archaeopress.

Deacon, J. 1984b. Later Stone Age people and their descendants in southern Africa. In: R.G. Klein, editor. Southern African prehistory and paleoenvironments. Rotterdam: Taylor & Francis. p 221-328.

Deacon, J. 1990. Weaving the fabric of Stone Age research in southern Africa. In: P. Robertshaw, editor. A history of African archaeology. Oxford: James Currey Publishers. p 39-58.

Dean, C.M. 1995. The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 *(Homo habilis)*. In: J. Moggi-Cecchi, editor. Aspects of dental Biology: paleontology, anthropology and evolution. Florence: International Institute for the Study of Man. p 239-265.

Dean, C.M. 1998. Comparative observations on the spacing of short-period (von Ebner's) lines in dentine. *Archices of Oral Biology* 43:1009-1021.

Dean, C.M., Beynon, A.D., Reid, D., and Whittaker, D.K. 1993. A longitudinal study of tooth growth in a single individual based on long- and short-period incremental markings in dentine and enamel. *International Journal of Osteoarchaeology* 3:249-264.

Dean, C.M., Leakey, M.G., Reid, D., Schrenk, F., Schwartz, G.T., Stringer, C., and Walker, A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature Communications* 414:628-631.

DeLeon, V.B. 2007. Fluctuating asymmetry and stress in a medieval Nubian population. *American Journal of Physical Anthropology* 132(4):520-534.

Dempsey, P.J., and Townsend, G. 2001. Genetic and environmental contributions to variation in human tooth size. *Heredity* 86(6):685-693.

Dewar, G., and Pfeiffer, S. 2004. Postural behaviour of Later Stone Age people in South Africa. *The South African Archaeological Bulletin* 59(180):52-58.

Döckel, W. 1998. Re-investigation of the Matjes River Rock Shelter. MA thesis.: University of Stellenbosch.

Dodo, Y. 1986. Metrical and non-metrical analyses of Jomon crania from eastern Japan. In: T. Akazawa, and A. C.M., editors. Prehistoric Hunter-gatherers in Japan: Bulletin of the University Museum of the University of Tokyo. p 137-161.

Doyle, W.J., and Johnston, O. 1977. On the meaning of increased fluctuating dental asymmetry: a cross populational study. *American Journal of Physical Anthropology* 46(1):127-134.

Drennan, M.R. 1929a. An Australoid skull from the Cape Flats. *The Journal of the Royal Anthropological Institute of Great Britain and Ireland* 59:417-427.

Drennan, M.R. 1929b. The dentition of a Bushman tribe. *Annals of the South African Museum* 24:61-88.

Drennan, M.R. 1937. The torus mandibularis in the Bushman. *Journal of Anatomy* 72(1):66-70.

Drennan, M.R. 1946. A macrodontic Bushman skull in relationship to a Boskopoid skull with a similar dentition and large jaws. *British dental journal* 80:224-227.

Dreyer, T.F. 1933. The archaeology of the Matjes River Rock Shelter. *Transactions of the Royal Society of South Africa* 21(2):187-209.

Dreyer, T.F. 1935. Dental caries in prehistoric South Africans. *Nature136*:302-303.

Dreyer, T.F., and Meiring, A.J.D. 1952. The Hottentot. *Researches of the National Museum, Bloemfontein* 1:19-22.

Dusseldorp, G., Lombard, M., and Wurz, S. 2013. Pleistocene *Homo* and the updated Stone Age sequence of South Africa. *South African Journal of Science* 109(5/6):1-7.

Eastwood, E.B., and Smith, B.W. 2005. Fingerprints of the Khoekhoen: geometric and handprinted rock art in the central Limpopo basin, southern Africa. *South African Archaeological Society Goodwin Series* 9:63-76.

Ebeling, C.F., Ingervall, B., Hede-gård, B., and Lewin, T. 1973. Secular changes in tooth size in Swedish men. *Acta Odontologica* 31(3):141-147.

Edgar, H.J.H. 2004. Dentitions, distances, and difficulty: a comparison of two statistical techniques for dental morphological data. *Dental Anthropology* 17:55-62.

Ehret, C. 1973. Patterns of Bantu and Central Sudanic settlement in central and southern Africa. (ca. 1000 BC – 500 AD). *Transafrican Journal of History* 3:1-71.

Ehret, C. 1982. The first spread of food production to southern Africa. In: C. Ehret, and M. Posnansky, editors. The archaeological and linguistic reconstruction of African history. Berkeley: University of California Press. p 158-181.

Ehret, C. 1998. An African classical age: eastern and southern Africa in world history, 1000 B.C. to A.D. 400. Oxford: James Currey.

Elamin, F., and Liversidge, H.M. 2013. Malnutrition has no effect on the timing of human tooth formation. *PLoS ONE* 8(8):e72274.

Elphick, R. 1985. Khoikhoi and the founding of white South Africa. Johannesburg: Ravan Press.

Esterhuysen, A.B., and Mitchell, P. 1996. Palaeoenvironmental and archaeological implications of charcoal assemblages from Holocene sites in western Lesotho, southern Africa. *Palaeoecology of Africa* 24:233-240.

Esterhuysen, A.B., and Smith, J.M. 2003. A comparison of charcoal and stable carbon isotope results for the Caledon River Valley, southern Africa, for the period 13 500-5000 yr BP. *The South African Archaeological Bulletin* 58(177):1-5.

Excoffier, L., Pellegrini, B., Sanchez-Mazas, A., Simon, C., and Langaney, A. 1987. Genetics and history of sub-Saharan Africa. *Yearbook of Physical Anthropology* 30:151-194.

Fairhall, A.W., Young, A.W., and Erickson, J.L. 2006. University of Washington dates IV. *Radiocarbon* 18(2):221-239.

Faith, J.T. 2013. Ungulate diversity and precipitation history since the Last Glacial Maximum in the Western Cape, South Africa. *Quaternary Science Reviews* 68:191-199.

Falk, D., and Corruccini, R. 1982. Efficacy of cranial versus dental measurements for separating human populations. *American Journal of Physical Anthropology* 57(1):123-127.

Fauvelle-Aymar, F.X. 2004. Between the first herders and the last herders: are the Khoekhoe descendants of the Neolithic 'hunters-with-sheep'? *Before farming* 2004/4, article 5.

Fauvelle-Aymar, F.X. 2008. Against the 'Khoisan paradigm' in the interpretation of Khoekhoe origins and history: a re-evaluation of Khoekhoe pastoral traditions. *Southern African Humanities* 20:77-92.

Fauvelle-Aymar, F.X., and Sadr, K. 2008. Introduction: trends and traps in the reconstruction of early herding societies in southern Africa. *Southern African Humanities* 20:1-6.

Fauvelle-Aymar, F.X., Sadr, K., Bon, F., and Gronenborn, D. 2006. The visibility and invisibility of herders' kraals in southern Africa, with reference to a possible early contact period Khoekhoe kraal at KFS5, Western Cape. *Journal of African Archaeology* 4(2):253-271.

Feathers, J.K., and Bush, D.A. 2000. Luminescence dating of middle stone age deposits at Die Kelders. *Journal of Human Evolution* 38(1):91-119.

Field, H. 1949. The University of California African Expedition II, Sudan and Kenya. *American Anthropologist* 51(1):72-84.

Findlater, I.C. 1978. Stratigraphy. In: M.G. Leakey, and R.E. Leakey, editors. Koobi Fora research project, vol I ; The fossil hominids and an introduction to their context, 1968-1974. Oxford: Clarendon Press. p 14-31.

Fiorenza, L., Benazzi, S., Tausch, J., Kullmer, O., Bromage, T.G., and Schrenk, F. 2011. Molar macrowear reveals Neanderthal eco-geographic dietary variation. *PLoS ONE* 6(3):e14769.

Fitzgerald, C., and Hillson, S. 2008. Dental reduction in Late Pleistocene and Early Holocene hominids: alternative approaches to assessing tooth size. In: J.D. Irish, and G.C. Nelson, editors. Technique and application in dental anthropology Cambridge: Cambridge University Press. p 364-388.

Flower, W.H. 1885. On the size of teeth as a character of race. *Journal of the Anthropological Insititute of Great Britain and Ireland* 14:183-186.

Freeman, M.F., and Tukey, J.W. 1950. Transformations related to the angular and the square root. *The Annals of Mathematical Statistics* 21(4):607-611.

Fuller, D., and Hildebrand, E. 2013. Domesticating plants in Africa. In: M. Bollig, M. Schnegg, and H.-P. Wotzka, editors. Pastoralism in Africa: past, present, and future. New York: Berghahn Books. p 507-525.

Gabel, C. 1963. Further Human Remains from the Central African Later Stone Age. *Man* 63(2):38-43.

Galloway, A. 1933. The Nebarara Skull. *South African Journal of Science* 30:585-596.

Galloway, A. 1941. Palatal measurements of Negro and other crania. *South African Journal of Science* 37:285-292.

Galloway, A. 1959. The skeletal remains of Bambandyanalo. Johannesburg: Witwatersrand University Press.

Garn, S.M., Lewis, A.B., and Kerewsky, R.S. 1965. Genetic, nutritional, and maturational correlates of dental development. *Journal of dental research* 44(1):228-242.

Garn, S.M., Lewis, A.B., and Kerewsky, R.S. 1966. Sexual dimorphism in the buccolingual tooth diameter. *Journal of dental research* 45(6):1819-1819.

Garn, S.M., Lewis, A.B., and Vicinus, J.H. 1963. Third molar polymorphism and its significance to dental genetics. *Journal of dental research* 42:1344-1363.

Garn, S.M., Lewis, A.B., and Walenga, A. 1968. Evidence for a secular trend in tooth size over two generations. *Journal of dental research* 47(3):503-503.

Garn, S.M., Osborne, R.H., and McCabe, K.D. 1979. The effect of prenatal factors on crown dimensions. *American Journal of Physical Anthropology* 51(4):665-677.

Gass, J.R., Valiathan, M., Tiwari, H.K., Hans, M.G., and Elston, R.C. 2003. Familial correlations and heritability of maxillary midline diastema. *American Journal of Orthodontics and Dentofacial Orthopedics* 123(1):35-39.

Gaunt, W.A., and Miles, A. 1967. Fundamental aspects of tooth morphogenesis. In: A. Mills, editor. Structural and chemical organization of teeth. New York: Academic Press. p 151-197.

Gifford-Gonzalez, D. 1998. Early pastoralists in East Africa: ecological and social dimensions. *Journal of Anthropological Archaeology* 17(2):166-200.

Gifford-Gonzalez, D. 2003. The fauna from Ele Bor: evidence for the persistence of foragers into the later Holocene of arid north Kenya. *African Archaeological Review* 20(2):81-119.

Goldstein, M.S. 1948. Dentition of Indian crania from Texas. *American Journal of Physical Anthropology* 6:63-84.

Gómez-Robles, A., Martinón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A., Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., and Martínez, L.M. 2007. A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution* 53(3):272-285.

Gómez-Robles, A., Martinón-Torres, M., Bermúdez de Castro, J.M., Prado, L., Sarmiento, S., and Arsuaga, J.L. 2008. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *Homo*. *Journal of Human Evolution* 55(4):627-638.

Gooch, W.D. 1882. The Stone Age of South Africa. *The Journal of the Anthropological Institute of Great Britain and Ireland* 11:124-183.

Goodwin, A.J.H. 1930. A new variation of the Smithfield culture from Natal. *Transactions of the Royal Society of South Africa* 19:7-14.

Goodwin, A.J.H., and Van Riet Lowe, C. 1929. The Stone Age cultures of South Africa. *Annals of the South African Museum* 27:1-289.

Goose, D.H. 1963. Dental measurement: an assessment of its value in anthropological studies. *Dental Anthropology* 125:148.

Graham, J.H., Freeman, D.C., and Emlen, J.M. 1993. Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* 89(1-3):121-137.

Gramly, R.M., and Rightmire, P.G. 1973. A fragmentary cranium and dated Later Stone Age assemblage from Lukenya Hill, Kenya. *Man* 8(4):571-579.

Green, R.F., and Suchey, J.M. 1976. The use of inverse sine transformations in the analysis of non-metric cranial data. *American Journal of Physical Anthropology* 45(1):61-68.

Greenberg, J., Turner, C.G.I., and Zegura, S. 1985. Convergence of evidence for the peopling of the Americas. *Collegium Antropologicum* 9:33-42.

Greenberg, J., Turner, C.G.I., and Zegura, S. 1986. The settlement of the Americas: a comparison of the linguistic, dental, and genetic evidence *Current Anthropology* 24:477-497.

Gregory, W.K. 1922. The origin and evolution of the human dentition. Baltimore: Williams and Wilkins.

Gregory, W.K. 1926. Paleontology of the human dentition. *American Journal of Physical Anthropology* 9:401-426.

Grine, F.E. 1981. Occlusal morphology of the mandibular permanent molars of the South African Negro and the Kalahari San (Bushman). *Annals of the South African Museum* 86:157-215.

Grine, F.E. 2000. Middle Stone Age human fossils from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* 38(1):129-145.

Grine, F.E. 2012. Observations on Middle Stone Age human teeth from Klasies River Mouth Main Site, South Africa. *Journal of Human Evolution* 63(5):750-758.

Grine, F.E., Bailey, R.M., Harvati, K., Nathan, R.P., Morris, A.G., Henderson, G.M., Ribot, I., and Pike, A.W. 2007. Late Pleistocene human skull from Hofmeyr, South Africa, and modern human origins. *Science* 315(5809):226-229.

Grine, F.E., Gunz, P., Betti-Nash, L., Neubauer, S., and Morris, A.G. 2010. Reconstruction of the late Pleistocene human skull from Hofmeyr, South Africa. *Journal of Human Evolution* 59(1):1-15.

Grine, F.E., and Henshilwood, C.S. 2002. Additional human remains from Blombos Cave, South Africa: (1999-2000 excavations). *Journal of Human Evolution* 42(3):293-302.

Grine, F.E., Henshilwood, C.S., and Sealy, J. 2000. Human remains from Blombos Cave, South Africa: (1997–1998 excavations). *Journal of Human Evolution* 38:755-765.

Grine, F.E., and Klein, R.G. 1993. Late Pleistocene human remains from the Sea Harvest site, Saldanha Bay, South Africa. *South African Journal of Science* 89:145-152.

Grine, F.E., Klein, R.G., and Volman, T.P. 1991. Dating, archaeology and human fossils from the Middle Stone Age levels of Die Kelders, South Africa. *Journal of Human Evolution* 21(5):363-395.

Grine, F.E., Pearson, O.M., Klein, R.G., and Rightmire, P.G. 1998. Additional human fossils from Klasies River Mouth, South Africa. *Journal of Human Evolution* 35(1):95-107.

Grün, R., and Beaumont, P.B. 2001. Border Cave revisited: a revised ESR chronology. *Journal of Human Evolution* 40(6):467-482.

Grün, R., Beaumont, P.B., Tobias, P.V., and Eggins, S. 2003. On the age of Border Cave 5 human mandible. *Journal of Human Evolution* 45(2):155-167.

Grüneberg, H. 1952. Genetical studies on the skeleton of the mouse. *Journal of Genetics* 51(1):95-114.

Grün, R., Beaumont, P.B., and Stringer, C. 1990a. ESR dating evidence for early modern humans at Border Cave in South Africa. *Nature* 344(6266):537-539.

Grün, R., Shackleton, N.J., and Deacon, H.J. 1990b. Electron-spin-resonance dating of tooth enamel from Klasies River Mouth Cave. *Current Anthropology* 31(4):427-432.

Haeussler, A.M., Irish, J.D., Morris, D.H., and Turner, C.G. 1989. Morphological and metrical comparison of San and Central Sotho dentitions from southern Africa. *American Journal of Physical Anthropology* 78(1):115-122.

Haeussler, A.M., Turner, C.G.I., and Irish, J.D. 1988. Concordance of American and Soviet methods in dental anthropology. Abstract. *American Journal of Physical Anthropology* 75:218.

Hall, S. 1990. Hunter-gatherer-fishers of the Fish River Basin: a contribution to the Holocene prehistory of the Eastern Cape. Stellenbosch: University of Stellenbosch.

Hall, S., and Binneman, J. 1987. Later Stone Age burial variability in the Cape: a social interpretation. *The South African Archaeological Bulletin* 42(146):140-152.

Hall, S., and Smith, B.W. 2000. Empowering places: rock shelter and ritual control in farmer-forager interactions in the Northern Province. *South African Archaeological Society Goodwin Series* 8:30-46.

Hanihara, K. 1954. Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids. III. Deciduous lower molars. *Journal of the anthropological society of Nippon* 64:95-116.

Hanihara, K. 1955a. Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids. I. Deciduous incisors. *Journal of the anthropological society of Nippon* 63:168-185.

Hanihara, K. 1955b. Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids. II. Deciduous canines. *Journal of the anthropological society of Nippon* 64:63-82.

Hanihara, K. 1966. Mongoloid dental complex in the deciduous dentition. *Journal of the anthropological society of Nippon* 74:61-71.

Hanihara, K. 1968. Mongoloid dental complex in the permanent dentition. Proceedings of the VIIIth International Symposium of Anthropological and Ethnological Sciences. Tokyo: Science Council of Japan. p 298-300.

Hanihara, K., Masuda, T., and Tanaka, T. 1975. Family studies of the shovel trait in the maxillary central incisor. *Journal of the anthropological society of Nippon* 83:107-112.

Hanihara, T. 1990a. Dental anthropological evidence of affinities among the Oceania and the Pan-Pacific populations: The basic populations in East Asia, II. *Journal of the anthropological society of Nippon* 98:233-246.

Hanihara, T. 1990b. Studies on the affinities of Sakhalin Ainu based on dental characters: The basic populations in East Asia, III. *Journal of the anthropological society of Nippon* 98(4):425-437.

Hanihara, T. 1991. Dentition of Nansei Islanders and peopling of the Japanese archipelago: the basic populations in East Asia, IX. *Journal of the anthropological society of Nippon* 99:399-409.

Hanihara, T. 1992a. Biological relationships among Southeast Asians, Jomonese, and the Pacific populations as viewed from dental characters: the basic populations in East Asia, X. *Journal of the anthropological society of Nippon* 100:53-67.

Hanihara, T. 1992b. Negritos, Australian Aborigines, and the “proto-sundadont” dental pattern: The basic populations in East Asia, V. *American Journal of Physical Anthropology* 88(2):183-196.

Hanihara, T. 1993. Dental affinities among Polynesian and circum-Polynesian populations. *Nichibunken Japan Review*:59-82.

Hanihara, T. 1996. Comparison of craniofacial features of major human groups. *American Journal of Physical Anthropology* 99(3):389-412.

Hanihara, T. 2005. Dental and cranial affinities among populations of East Asia and the Pacific: the basic populations in East Asia, IV. *American Journal of Physical Anthropology* 88(2):163-182.

Hanihara, T. 2008. Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology* 136(2):169-182.

Hanihara, T., and Ishida, H. 2005. Metric dental variation of major human populations. *American Journal of Physical Anthropology* 128(2):287-298.

Harrington, L. 2010. Ontogeny of postcranial robusticity among Holocene hunter-gatherers of southernmost Africa. PhD dissertation.: University of Toronto.

Harris, E.F. 1977. Anthropologic and genetic aspects of the dental morphology of Solomon Islanders, Melanesia. Tempe: Arizona State University.

Harris, E.F. 2008. Statistical applications in dental anthropology. In: J.D. Irish, and G.C. Nelson, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 35-67.

Harris, E.F., and Bailit, H.L. 1988. A principal components analysis of human odontometrics. *American Journal of Physical Anthropology* 75(1):87-99.

Harris, E.F., and Lease, L.R. 2005. Mesiodistal tooth crown dimensions of the primary dentition: a worldwide survey. *American Journal of Physical Anthropology* 128(3):593-607.

Harris, E.F., Potter, R.H., and Lin, J. 2001. Secular trend in tooth size in urban Chinese assessed from two-generation family data. *American Journal of Physical Anthropology* 115(4):312-318.

Harris, E.F., and Rathbun, T.A. 1991. Ethnic differences in the apportionment of tooth sizes. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. New York: Wiley-Liss. p 121-142.

Harris, E.F., and Sjøvold, T. 2004. Calculation of Smith's mean measure of divergence for intergroup comparisons using nonmetric data. *Dental Anthropology Journal* 17(3):83-93.

Harris, E.F., and Smith, R.N. 2009. Accounting for measurement error: a critical but often overlooked process. *Archives of Oral Biology* 54 (Suppl 1):107-117.

Harris, J.M., Leakey, M.G., and Brown, F.H. 2006. A brief history of research at Koobi Fora, northern Kenya. *Ethnohistory* 53(1):35-69.

Hassan, F.A. 2002. Droughts, food and culture: ecological change and food security in Africa's later prehistory: Springer.

Hassanali, J. 1982. Incidence of Carabelli's trait in Kenyan Africans and Asians. *American Journal of Physical Anthropology* 59(3):317-319.

Hassanali, J., and Amwayi, P. 1988. Report on two aspects of the Maasai dentition. *East African medical journal* 65(11):798.

Hausman, A.J. 1982. The biocultural evolution of Khoisan populations of southern Africa. *American Journal of Physical Anthropology* 58(3):315-330.

Haeussler, A.M. 1995. Origins and relationships of people buried in large Ukrainian Mesolithic cemeteries: the evidence from dental morphology. *American Journal of Physical Anthropology: Supplement* 20:103.

Hawkey, D. 1999. The Indodont dental pattern of prehistoric South Asia and early world affinities. *American Journal of Physical Anthropology* (Suppl. 28):146-147.

Hawkey, D. 2002. The peopling of south Asia: evidence for affinities and microevolution of prehistoric populations of India and Sri Lanka. *Spolia Zeylanica* 39:1-314.

Hayden, B. 1996. Competition, labour and complex hunter-gatherers. In: E.S. Burch, and L.J. Ellanna, editors. Key issues in hunter-gatherer research. Oxford: Berg Publishers. p 223-239.

Hayden, E. 2013. African genes tracked back. *Nature* 500 (7464):514.

Hellman, M. 1928. Racial characters in human dentition part I. A racial distribution of the *Dryopithecus* pattern and its modifications in the lower molar teeth of man. *Proceedings of the American Philosophical Society* 67(2):157-174.

Hemphill, B.E. 2008. Are the inhabitants of Madaklasht an emigrant Persian population in Northern Pakistan? A dental mor-phometric investigation. *American Journal of Physical Anthropology* 135 (Suppl. 46):115.

Hemphill, B.E. 2009. The Swatis of Northern Pakistan-emigrants from Central Asia or colonists from peninsular India? A dentalmorphometric investigation. *American Journal of Physical Anthropology* 138 (Suppl. 48):147.

Hemphill, B.E. 2011. To the West! A dental morphology investigation of gene flow between populations of the Iranian Plateauand the macro-Mesopotamian interaction sphere during the last three millennia B.C. *American Journal of Physical Anthropology* 144 (Suppl.52):160.

Hemphill, B.E. 2013. Grades, gradients and geography: a dental morphometric approach to the population history of South Asia. In: G.R. Scott, and J.D. Irish, editors. Anthropological perspectives on tooth morphology. Cambridge: Cambridge University Press. p 341-387.

Hemphill, B.E., Christensen, A.F., Mustafakulov, S.I. 1998. Biological adaptations and affinities of Bronze Age Bactrians: II dentalmorphology. In: J.R. Lukacs, editor. Human dental development, morphology, and pathology: a tribute to Albert A Dahlberg,University of Oregon Anthropology Papers, vol 54. Eugene: University of Oregon. p 51-77.

Hemphill, B.E., Lukacs, J.R., Kennedy, K.A.R. 1991. Biological adaptations and affinities of Bronze Age Harappans. In: R. Meadow, and J.M. Kenoyer, editors. Harappa excavations 1986-1990: a multidisciplinary approach to third millennium urbanism. Madison: Prehistory Press. p 137-182.

Hendey, Q.B. 1974. The Late Cenozoic carnivora of the south-western Cape Province. *Annals of the South African Museum* 63:1-369.

Henn, B.M., Gignoux, C.R., Jobin, M., Granka, J.M., Macpherson, J., Kidd, J.M., Rodríguez-Botigué, L., Ramachandran, S., Hon, L., and Brisbin, A. 2011. Hunter-gatherer genomic diversity suggests a southern African origin for modern humans. *Proceedings of the National Academy of Sciences* 108(13):5154-5162.

Henshilwood, C.S. 1996. A revised chronology for pastoralism in southernmost Africa: new evidence of sheep at c. 2000 b.p. from Blombos Cave, South Africa. *Antiquity* 70(270):945+.

Henshilwood, C.S., d'Errico, F., and Watts, I. 2009. Engraved ochres from the Middle Stone Age levels at Blombos cave, south Africa. *Journal of Human Evolution* 57(1):27-47.

Henshilwood, C.S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier, N., Sealy, J.C., Valladas, H., and Watts, I. 2002. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* 295(5558):1278-1280.

Henshilwood, C.S., d’Errico, F., Van Niekerk, K., Coquinot, Y., Jacobs, Z., Lauritzen, S., Menu, M., and García-Moreno, R. 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science* 334(6053):219-222.

Henshilwood, C.S., and Dubreuil, B. 2011. The Still Bay and Howiesons Poort, 77–59 ka. Symbolic material culture and the evolution of the mind during the African Middle Stone Age. *Current Anthropology* 52(3):361-400.

Henshilwood, C.S., and Marean, C. 2003. The origin of modern human behavior: a review and critique of models and test implications. *Current Anthropology* 44:627-651.

Henshilwood, C.S., Nilssen, P., and Parkington, J. 1994. Mussel drying and food storage in the Late Holocene, SW Cape, South Africa. *Journal of Field Archaeology* 21(1):103-109.

Henshilwood, C.S., and Sealy, J. 1997. Bone artefacts from the Middle Stone Age at Blombos Cave, southern Cape, South Africa. *Current Anthropology* 38(5):890-895.

Henshilwood, C.S., Sealy, J., Yates, R., Cruz-Uribe, K., Goldberg, P., Grine, F.E., Klein, R.G., Poggenpoel, C., van Niekerk, K., and Watts, I. 2001. Blombos Cave, southern Cape, South Africa: preliminary report on the 1992–1999 excavations of the Middle Stone Age levels. *Journal of Archaeological Science* 28(4):421-448.

Hewitt, J. 1921. On several implements and ornaments from Strandloper sites in the Eastern Province. *South African Journal of Science* 18:454-467.

Heydorn, A.E.F., and Flemming, B.W. 1985. South Africa. In: E.D. Bird, and M.L. Schwartz, editors. The world's coastline. New York: NostrandReinhold Co. p 653-667.

Hiernaux, J., and Hartono, D.B. 1980. Physical measurements of the adult Hadza of Tanzania. *Annals of human biology* 7:339-346.

Hillson, S. 1998. Crown diameters, tooth crown development, and environmental factors in growth. In: J.R. Lukacs, editor. Human dental development, morphology and pathology: a tribute to Albert A Dahlberg. Eugene: University of Oregon Press. p 17-28.

Hillson, S., Fitzgerald, C., and Flinn, H. 2005. Alternative dental measurements: proposals and relationships with other measurements. *American Journal of Physical Anthropology* 126(4):413-426.

Hitchcock, R.K. 2002. ‘We are the First People’: land, natural resources, and identity in the Central Kalahari, Botswana. *Journal of Southern African Studies* 28(4):797-824.

Hitchcock, R.K., Ikeya, K., Biesele, M., and Lee, R.B. 2006. Updating the San: image and reality of an African people in the 21st century.

Hlusko, L.J., Maas, M.-L., and Mahaney, M.C. 2004. Statistical genetics of molar cusp patterning in pedigreed baboons: implications for primate dental development and evolution. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 302(3):268-283.

Hrdlička, A. 1921. Further studies of tooth morphology. *American Journal of Physical Anthropology* 4(2):141-176.

Hrdlička, A. 1920. Shovel-shaped teeth. *American Journal of Physical Anthropology* 3(4):429-465.

Hrdlička, A. 1923. Dimensions of the first and second lower molars, with their bearing on the Piltdown jaw and on man's phylogeny. *American Journal of Physical Anthropology* 6:195-216.

Hsu, J.W., Tsai, P., Hsiao, T.H., Chang, H.P., Lin, L.M., Liu, K., Yu, H.S., and Ferguson, D. 1999. Ethnic dental analysis of shovel and Carabelli's traits in a Chinese population. *Australian Dental Journal* 44(1):40-45.

Hughes, T., Bockmann, M.R., Seow, K., Gotjamanos, T., Gully, N., Richards, L.C., and Townsend, G. 2007. Strong genetic control of emergence of human primary incisors. *Journal of dental research* 86(12):1160-1165.

Hughes, T., and Townsend, G. 2013. Twin and family studies of human dental crown morphology: genetic, epigenetic, and environmental determinants of the modern human dentition. In: G.R. Scott, and J.D. Irish, editors. Anthropological perspectives on tooth morphology: genetics, evolution, variation. Cambridge: Cambridge University Press. p 31-68.

Humphreys, A.J.B. 1969. The state of archaeological studies in the Northern Cape and the possibilities for future research. *The South African Archaeological Bulletin* 24(95/96):200-202.

Humphreys, A.J.B. 1970. The remains from Koffiefontein burials excavated by W. Fowler and preserved in the McGregor Museum, Kimberley. *The South African Archaeological Bulletin* 25(99/100):104-115.

Humphreys, A.J.B. 1972. Type-R settlements in the context of the later prehistory and early history of the Riet River valley. Master's dissertation. University of Cape Town.

Humphreys, A.J.B. 1973. A report on excavations carried out on a Type R Settlement Unit (Khartoum I) in the Jacobsdal district, O.F.S. *Annals of the Cape Provincial Museums* 9(8):123-157.

Humphreys, A.J.B. 1982. Cultural material from burials on the farm St. Clair, Douglas area, Northern Cape. *The South African Archaeological Bulletin* 37(136):68-70.

Humphreys, A.J.B. 1988. A prehistoric frontier in the Northern Cape and western Orange Free State: archaeological evidence in interaction and ideological change. *Kronos* 13:3-13.

Humphreys, A.J.B. 2007. More on pots in burials from the Douglas area, Northern Cape. *The South African Archaeological Bulletin* 62(185):68-70.

Humphreys, A.J.B. 2009. A Riet River retrospective. *Southern African Humanities* 21:157-175.

Humphreys, A.J.B., and Maggs, T.M. 1970. Further graves and cultural material from the banks of the Riet River. *The South African Archaeological Bulletin* 25(99/100):116-126.

Humphreys, A.J.B., and Thackeray, A.I. 1983. Ghaap and Gariep: Later Stone Age studies in the northern Cape. Cape Town: South African Archaeological Society.

Hunt, J., and Campbell, H.A. 2005. Dutch South Africa: early settlers at the Cape, 1652-1708: Matador.

Hunter, J.P., Guatelli-Steinberg, D., Weston, T.C., Durner, R., and Betsinger, T.K. 2010. Model of tooth morphogenesis predicts Carabelli cusp expression, size, and symmetry in humans. *PLoS ONE* 5(7):e11844.

IBM Corp. 2012. IBM SPSS Statistics for Windows. 21.0. ed. Armonk, NY: IBM Corp.

Infante, P.F., and Gillespie, G.M. 1977. Enamel hypoplasia in relation to caries in Guatemalan children. *Journal of dental research* 56(5):493-498.

Inskeep, R.R. 1967. The Late Stone Age in southern Africa. In: W.W. Bishop, and J.D. Clark, editors. Background to evolution in Africa: systematic investigation of the African later tertiary and quaternary : proceedings of the symposium held at Burg Wartenstein, Austria, July 14 -August 9, 1965 Chicago: University of Chicago Press. p 557-582.

Inskeep, R.R. 1987. Nelson Bay Cave, Cape Province: The Holocene levels. Oxford: David Brown Book Company.

Irish, J.D. 1993. Biological affinities of Late Pleistocene through modern African aboriginal populations: the dental evidence. Tempe: Arizona State University.

Irish, J.D. 1997. Characteristic high- and low-frequency dental traits in sub-Saharan African populations. *American Journal of Physical Anthropology* 102(4):455-467.

Irish, J.D. 1998a. Ancestral dental traits in recent sub-Saharan Africans and the origins of modern humans. *Journal of Human Evolution* 34(1):81-98.

Irish, J.D. 1998b. Dental morphological affinities of Late Pleistocene through recent sub-Saharan and north African peoples. *Bulletins et Mémoires de la Société d'anthropologie de Paris*:237-272.

Irish, J.D. 1998c. Diachronic and synchronic dental trait affinities of late and post-pleistocene peoples from North Africa. *Homo* 49(2):138-155.

Irish, J.D. 2005. Population continuity vs. discontinuity revisited: Dental affinities among late Paleolithic through Christian-era Nubians. *American Journal of Physical Anthropology* 128(3):520-535.

Irish, J.D. 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through postdynastic peoples. *American Journal of Physical Anthropology* 129(4):529-543.

Irish, J.D. 2010. The mean measure of divergence: Its utility in model-free and model-bound analyses relative to the Mahalanobis D2 distance for nonmetric traits. *American Journal of Human Biology* 22(3):378-395.

Irish, J.D. 2011. Afridonty: the ‘‘Sub-Saharan African Dental Complex’’ revisited. Abstract. *American Journal of Physical Anthropology* 144(Supplement 52).

Irish, J.D. 2013. Afridonty: the "Sub-Saharan African Dental Complex" revisited. In: G.R. Scott, and J.D. Irish, editors. Anthropological perspectives on tooth morphology: genetics, evolution, variation. Cambridge: Cambridge University Press. p 278-295.

Irish, J.D., and Guatelli-Steinberg, D. 2003. Ancient teeth and modern human origins: an expanded comparison of African Plio-Pleistocene and recent world dental samples. *Journal of Human Evolution* 45(2):113-144.

Irish, J.D., Guatelli-Steinberg, D., Legge, S., de Ruiter, D.J., and Berger, L.R. 2013. Dental morphology and the phylogenetic “place” of *Australopithecus sediba*. *Science* 340:1-4.

Irish, J.D., and Konigsberg, L. 2007. The ancient inhabitants of Jebel Moya redux: measures of population affinity based on dental morphology. *International Journal of Osteoarchaeology* 17(2):138-156.

Irish, J.D., and Morris, D.H. 1996a. Supplemental description of the Bushman maxillary canine polymorphism. *South African Journal of Science* 92(7):351-353.

Irish, J.D., and Morris, D.H. 1996b. Technical note: canine mesial ridge (Bushman canine) dental trait definition. *American Journal of Physical Anthropology* 99(2):357-359.

Irish, J.D., and Turner, C.G.I. 1990. West African dental affinity of Late Pleistocene Nubians: peopling of the Eurafrican-South Asian triangle II. *Homo* 41(1):42-53.

Isaac, G.L. 1976. A preliminary report on stratigraphic studies in the Nakuru Basin, Kenya. Procedures of the Panafrican Congress of Prehistory and Quaternary Studies. Addis Ababa. p 409-411.

Jackes, M., Silva, A.M., and Irish, J.D. 2001. Dental morphology: a valuable contribution to our understanding of prehistory. *Journal of Iberian Archaeology* 3:97-119.

Jacobs, Z., Duller, G.A.T., Wintle, A.G., and Henshilwood, C.S. 2006. Extending the chronology of deposits at Blombos Cave, South Africa, back to 140ka using optical dating of single and multiple grains of quartz. *Journal of Human Evolution* 51(3):255-273.

Jacobs, Z., and Roberts, R.G. 2008. Testing times: old and new chronologies for the Howieson's Poort and Still Bay industries in environmental context. *South African Archaeological Society Goodwin Series* 10:9-34.

Jacobs, Z., and Roberts, R.G. 2009. Catalysts for Stone Age innovations: What might have triggered two short-lived bursts of technological and behavioral innovation in southern Africa during the Middle Stone Age? *Communicative & Integrative Biology* 2(2):191-193.

Jacobson, A. 1968. Spacing of teeth and mid-diastemata in the South African Bantu. Abstract. In: M. Shear, editor. South African Division of the International Association for Dental Research Abstracts of Papers Presented at the First Annual Scientific Congress. University of the Witwatersrand, Johannesburg. p 949.

Jacobson, A. 1982. The dentition of the South African Negro: a morphological and metrical study of the teeth, the jaws, and the bony palate of several large groups of South African Bantu-speaking Negroes. Anniston: AL: Higginbotham.

Jelliffe, D.B., and Jelliffe, E.F.P. 1971. Linear hypoplasia of deciduous incisor teeth in malnourished children. *The American journal of clinical nutrition* 24(8):893-893.

Jenkins, T., and Tobias, P.V. 1977. Nomenclature of population groups in southern Africa. *African Studies* 36:49-55.

Jerardino, A. 1996. Changing social landscapes of the Western Cape coast of southern Africa over the last 4500 years: University of Cape Town.

Jerardino, A. 1998. Excavations at Pancho's Kitchen midden, Western Cape Coast, South Africa: further observations into the megamidden period. *The South African Archaeological Bulletin* 53(167):16-25.

Jerardino, A. 2003. Pre-Colonial settlement and subsistence along sandy shores south of Elands Bay, West Coast, South Africa. *The South African Archaeological Bulletin* 58(178):53-62.

Jerardino, A. 2010. Large shell middens in Lamberts Bay, South Africa: a case of hunter–gatherer resource intensification. *Journal of Archaeological Science* 37(9):2291-2302.

Jerardino, A., Dewar, G., and Navarro, R. 2009a. Opportunistic subsistence strategies among Late Holocene coastal hunteregatherers, Elands Bay, South Africa. *Journal of Island and Coastal Archaeology* 4:37-60.

Jerardino, A., Horwitz, L., Mazel, A., and Navarro, R. 2009b. Just before Van Riebeeck: glimpses into terminal LSA lifestyle at Connies Limpet Bar, West Coast of South Africa. *South African Archaeological Bulletin* 64(189):75-86.

Jerardino, A., and Yates, R. 1997. Excavations at Mike Taylor's midden: a summary report and implications for a re-characterisation of megamiddens. *The South African Archaeological Bulletin* 52(165):43-51.

Jernvall, J., and Jung, H.S. 2000. Genotype, phenotype and developmental biology of molar tooth characters. *American Journal of Physical Anthropology* 43(Supplement):171-190

Jones, T.R. 1940. Human skeletal remains from the Mumbwa Cave, Northern Rhodesia. *South African Journal of Science* 37:313-319.

Kaczmarek, M. 1992. Dental morphological variation of the Polish people and their eastern neighbours In: P. Smith, and E. Tchernov, editors. Structure, function, and evolution of teeth. London: Freund Publishing House Ltd.

Kanazawa, E., Sekikawa, M., and Ozaki, T. 1990. A quantitative investigation of irregular cuspules in human maxillary permanent molars. *American Journal of Physical Anthropology* 83(2):173-180.

Kaul, V., and Prakash, S. 1981. Morphological features of Jat dentition. *American Journal of Physical Anthropology* 54(1):123-127.

Kaul, V., and Prakash, S. 1984. Crown dimensions of deciduous and permanent teeth of Jats from Haryana (India). *Annals of human biology* 11(4):351-354.

Kelley, M.A., and Larsen, C.S. 1991. Introduction. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. New York: Wiley-Liss. p 1-5.

Kieser, J.A. 1984. Dental morphology of a Griqua skeletal population. *Anthropologischer Anzeiger*:93-99.

Kieser, J.A. 1985. An odontometric analysis of the early Griqua dentition. *Anthropologischer Anzeiger*:51-58.

Kieser, J.A. 1990. Human adult odontometrics: the study of variation in adult tooth size. Cambridge: Cambridge University Press.

Kieser, J.A., and Preston, C.B. 1981. The dentition of the Lengua Indians of Paraguay. *American Journal of Physical Anthropology* 55(4):485-490.

Kimura, R., Yamaguchi, T., Takeda, M., Kondo, O., Toma, T., Haneji, K., Hanihara, T., Matsukusa, H., Kawamura, S., and Maki, K. 2009. A common variation in EDAR is a genetic determinant of shovel-shaped incisors. *The American Journal of Human Genetics* 85(4):528-535.

King, M.C., and Motulsky, A.G. 2002. Mapping human history. *Science* 298(5602):2342-2343.

Kirveskari, P. 1978. Racial traits in the dentition of living Skolt Lapps. In: P.M. Butler, and K.A. Joysey, editors. Development, function and evolution of teeth. London: Academic Press. p 59-68.

Kirveskari, P., Hansson, H., Hedegard, B., and Karlsson, U. 1978. Crown size and hypodontia in the permanent dentition of modern Skolt Lapps. *American Journal of Physical Anthropology* 48(1):107-112.

Kitson, E. 1931. A study of the Negro skull with special reference to the crania from Kenya Colony. *Biometrika* 23(3/4):271-314.

Klein, R.G. 1972. The late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. *Quaternary research* 2(2):135-142.

Klein, R.G. 1974. Environment and subsistence of prehistoric man in the southern Cape Province, South Africa. *World Archaeology* 5(3):249-284.

Klein, R.G. 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. *The South African Archaeological Bulletin* 31(123/124):75-98.

Klein, R.G. 1977. The mammalian fauna from the Middle and Later Stone Age (Later Pleistocene) levels of Border Cave, Natal Province, South Africa. *The South African Archaeological Bulletin* 32(125):14-27.

Klein, R.G. 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. *Annals of the South African Museum* 81:223-283.

Klein, R.G. 1986. The prehistory of Stone Age herders in the Cape Province of South Africa. *South African Archaeological Society Goodwin Series* 5:5-12.

Klein, R.G. 1989. Perspectives on modern human origins in southern Africa. In: P. Mellars, and C. Stringer, editors. The human revolution: behavioural and biological perspectives on the origins of modern humans. Edinburgh: Edinburgh University Press. p 529-546.

Klein, R.G. 1994. Southern Africa before the Iron Age. In: R.S. Corrucini, and R.L. Ciochon, editors. Integrative Pathways to the Past: Palaeoanthropological Investigations in Honor of F Clark Howell. New Jersey: Prentice Hall. p 471-520.

Klein, R.G. 1999. The Human career: human biological and cultural origins. Chicago: University of Chicago Press.

Klein, R.G. 2000. Archaeology and the evolution of human behaviour. *Evolutionary Anthropology* 9:17-36.

Klein, R.G. 2001. Southern Africa and Modern Human origins. *Journal of Anthropological Research* 57(1):1-16.

Klein, R.G. 2003. Response to Henshilwood and Marean on article: The origin of modern human behavior: a review and critique of models and test implications. *Current Anthropology* 44:640-641.

Klein, R.G. 2008. Out of Africa and the evolution of human behaviour. *Evolutionary Anthropology* 17:267-281.

Klein, R.G., and Cruz-Uribe, K. 1996. Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. *Journal of Human Evolution* 31(4):315-334.

Klein, R.G., and Cruz-Uribe, K. 2000a. Macromammals and reptiles. In: L. Barham, editor. The Middle Stone age of Zambia, South Central Africa. University of Bristol: Western Academic and Specialist Press. p 51-61.

Klein, R.G., and Cruz-Uribe, K. 2000b. Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* 38(1):169-195.

Knight, A., Underhill, P.A., and Mortensen, H. 2003. African Y chromosome and mtDNA divergence provides insight into the history of click languages. *Current Biology* 13:464-473.

Kolakowski, D., and Bailit, H.L. 1981. A differential environmental effect on human anterior tooth size. *American Journal of Physical Anthropology* 54(3):377-381.

Kolakowski, D., Harris, E.F., and Bailit, H.L. 1980. Complex segregation analysis of Carabelli's trait in a Melanesian population. *American Journal of Physical Anthropology* 53(2):301-308.

Kondo, S., Townsend, G., and Yamada, H. 2005. Sexual dimorphism of cusp dimensions in human maxillary molars. *American Journal of Physical Anthropology* 128(4):870-877.

Konigsberg, L. 2006. A post-Neumann history of biological and genetic distance studies in bioarchaeology. In: J.E. Buikstra, and L.A. Beck, editors. Bioarchaeology: the contextual analysis of human remains. New York: Academic Press. p 263-279.

Kovacs, I. 1967. Contribution to the ontogenetic morphology of roots of human teeth. *Journal of dental research* 46(5):865-874.

Kraus, B.S. 1951. Carabelli's anomaly of the maxillary molar teeth; observations on Mexicans and Papago Indians and an interpretation of the inheritance. *Am J Hum Genet* 3(4):348 - 355.

Kraus, B.S., and Jordan, R.E. 1965. The human dentition before birth. Philadelphia: Lea & Febiger.

Kruger, B.J. 1966. Interaction of fluoride and molybdenum on dental morphology in the rat. *Journal of dental research* 45(3):714-725.

Kurki, H.K., Pfeiffer, S., and Stynder, D.D. 2012. Allometry of head and body size in Holocene foragers of the South African Cape. *American Journal of Physical Anthropology* 147(3):462-471.

Kusimba, S.B. 2001. The Early Later Stone Age in East Africa: excavations and lithic assemblages from Lukenya Hill. *African Archaeological Review* 18(2):77-123.

Kyle McIlvaine, B., Schepartz, L.A., Larsen, C.S., and Sciulli, P.W. 2013. Evidence for long-term migration on the Balkan Peninsula using dental and cranial nonmetric data: early interaction between corinth (Greece) and its colony at Apollonia (Albania). *American Journal of Physical Anthropology* Available online 13 Nov. 2013. DOI: 10.1002/ajpa.22425.

Lahr, M.M., and Foley, R.A. 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology* 41:137-176.

Lam, Y.M., Pearson, O.M., and Smith, C.M. 1996. Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth. *American Journal of Physical Anthropology* 100(4):545-557.

Lane, P. 2004. The 'moving frontier'and the transition to food production in Kenya. *AZANIA: Journal of the British Institute in Eastern Africa* 39(1):243-264.

Lane, P. 2013. The archaeology of pastoralism and stock-keeping in East Africa. In: M. Bollig, M. Schnegg, and H.-P. Wotzka, editors. Pastoralism in Africa: past, present, and future. New York: Berghahn Books. p 585-601.

Lasker, G.W. 1950. Genetic analysis of racial traits of the teeth. Cold Spring Harbor symposia on quantitative biology: Cold Spring Harbor Laboratory Press. p 191-203.

Lavelle, C.L.B. 1970. The distribution of diastemas in different human population samples. *Scandinavian Journal of Dental Research* 78(6):530-534.

Lavelle, C.L.B. 1973. Variation in the secular changes in the teeth and dental arches. *The Angle Orthodontist* 43(4):412-421.

Leakey, L.S.B. 1931. The stone age cultures of Kenya Colony. Cambridge: Cambridge University Press.

Leakey, L.S.B. 1935. The stone age races of Kenya. Oxford: Oxford University Press.

Leakey, L.S.B. 1942. The Naivasha fossil skull and skeleton. *Journal of East African Natural History.* 16, 169-177.

Leakey, M.D. 1945. Report on the excavations at Hyrax Hill, Nakuru, Kenya Colony, 1937-1938. *Transactions of the Royal Society of South Africa* 30:271-409.

Lee-Thorp, J.A., Sealy, J., and van der Merwe, N.J. 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science* 16(585-599).

Lee, R.B. 1965. Subsistence ecology of !Kung bushmen: University of California, Berkeley.

Lee, R.B. 1979. The !Kung San: men, women and work in a foraging society. Cambridge: Cambridge University Press.

Lee, R.B., and DeVore, I. 1968. Man the hunter. Chicago: Aldine.

Leigh, R.W. 1925. Dental pathology of Indian tribes of varied environmental and food conditions. *American Journal of Physical Anthropology* 8:177-199.

Lewis Williams, J.D. 1981. Believing and seeing: symbolic meanings in southern San rock paintings. New York: Academic Press.

Lombard, M. 2004. Distribution patterns of organic residues on Middle Stone Age points from Sibudu Cave, KwaZulu-Natal, South Africa. *The South African Archaeological Bulletin*:37-44.

Lombard, M. 2005. The Howiesons Poort of South Africa: what we know, what we think we know, what we need to know. *Southern African Humanities* 17:33-55.

Lombard, M. 2006. First impressions of the functions and hafting technology of Still Bay pointed artefacts from Sibudu Cave. *Southern African Humanities* 18(1):27-41.

Lombard, M. 2008. Finding resolution for the Howiesons Poort through the microscope: micro-residue analysis of segments from Sibudu Cave, South Africa. *Journal of Archaeological Science* 35(1):26-41.

Lombard, M., and Parsons, I. 2008. Blade and bladelet function and variability in risk management during the last 2000 years in the northern Cape. *The South African Archaeological Bulletin* 63(187):18-27.

Lombard, M., Wadley, L., Deacon, J., Wurz, S., Parsons, I., Mohapi, M., Swart, J., and Mitchell, P. 2012. South African and Lesotho stone Age sequence updated (I). *South African Archaeological Bulletin* 67:123-144.

Louw, J.T. 1960. Prehistory of the Matjes River Rock Shelter. *National Museum of Bloemfontein Memoir* 1.

Lukacs, J.R. 1983. Human dental remains from early Neolithic levels at Mehrgarh, Baluchistan. *Current Anthropology* 24(3):390-392.

Lukacs, J.R. 1985. Tooth size variation in prehistoric India. *American Anthropologist* 87(4):811-825.

Lukacs, J.R. 1987. Biological relationships derived from morphology of permanent teeth: recent evidence from prehistoric India. *Anthropologischer Anzeiger* 45:97-116.

Lukacs, J.R. 1988. Dental morphology and odontometrics of early agriculturalists from Neolithic Mehrgarh, Pakistan. In: D.E. Russel, J.-P. Santoro, and D. Sigogneau-Russel, editors. Teeth revisited. Paris: Memoires du Museum Nationale d'Hitoire Naturelle, Serie C, Sciences de la Terre. p 285-303.

Lukacs, J.R. 1989. Biological affinities from dental morphology: the evidence from Neolithic Mehrgarh. *Old Problems and New Perspectives in the Archaeology of South Asia, Wisconsin Archaeological Reports, Madison* 2:75-88.

Lukacs, J.R., and Hemphill, B.E. 1991. Dental anthropology of prehistoric Baluchistan: a morphometric approach to the peopling of South Asia. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. New York: Wiley-Liss. p 77-119.

Lukacs, J.R., John, R., and Pal, J.N. 2013. Dental morphology of early Holocene foragers of North India: Non-metric trait frequencies and biological affinities. *Homo* http://dx.doi.org/10.1016/j.jchb.2013.08.003.

Lukacs, J.R., and Pal, J.N. 1993. Mesolithic subsistence in North India: inferences from dental attributes. *Current Anthropology* 34(5):745-765.

Maas, R., and Bei, M. 1997. The genetic control of early tooth development. *Critical Reviews in Oral Biology & Medicine* 8(1):4-39.

Macho, G.A., and Moggi-Cecchi, J. 1992. Relationship between size of distal accessory tubercles and hypocones in permanent maxillary molar crowns of southern Africans. *Archives of Oral Biology* 37(7):575-578.

Mackay, A. 2011. Nature and significance of the Howiesons Poort to post-Howiesons Poort transition at Klein Kliphuis rockshelter, South Africa. *Journal of Archaeological Science* 38(7):1430-1440.

Mackay, A., and Welz, A. 2008. Engraved ochre from a Middle Stone Age context at Klein Kliphuis in the Western Cape of South Africa. *Journal of Archaeological Science* 35:1521-1532.

Maggs, T.M. 1971. Pastoral settlements on the Riet River. *The South African Archaeological Bulletin* 26(101/102):37-63.

Maggs, T.M. 1976. Iron Age patterns and Sotho history on the southern highveld: South Africa. *World Archaeology* 7(3):318-332.

Marado, L.M., and Campanacho, V. 2013. Carabelli's trait: definition and review of a commonly used dental non-metric variable. Cadernos do GEEvH. p 24-39.

Margvelashvili, A., Zollikofer, C.P.E., Lordkipanidze, D., Peltomäki, T., and Ponce de León, M.S. 2013. Tooth wear and dentoalveolar remodeling are key factors of morphological variation in the Dmanisi mandibles. *Proceedings of the National Academy of Sciences* 10.1073/pnas.1316052110.

Marshall, F. 1990. Origins of specialized pastoral production in East Africa. *American Anthropologist* 92(4):873-894.

Marshall, F. 2000. The origins and spread of domestic animals in East Africa. In: R.M. Blench, and K.C. MacDonald, editors. The origins and development of African livestock: Archaeology, genetics, linguistics and ethnography. London: UCL Press. p 191-221.

Marshall, F., and Hildebrand, E. 2002. Cattle before crops: the beginnings of food production in Africa. *Journal of World Prehistory* 16(2):99-143.

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D., and Vekua, A. 2008. Dental remains from Dmanisi (Republic of Georgia): morphological analysis and comparative study. *Journal of Human Evolution* 55(2):249-273.

Mason, R.J. 1962. Prehistory of the Transvaal: a record of human activity: Witwatersrand University Press.

Mason, R.J. 1988. Cave of Hearths Makapangsgat, Transvaal. Reports on Early, Middle and Late Stone Age, Iron Age and historic data from the Cave of Hearths and adjacent historic cave. Johannesburg: University of the Witwatersrand.

Matsumura, H. 2001. Differentials of Yayoi immigration to Japanas derived from dental metrics. *Homo* 52(2):135-156.

Matsumura, H. 2007. Non-metric dental trait variation among local sites and regional groups of the Neolithic Jomon period, Japan. *Anthropological Science* 115(1):25-33.

Matsumura, H., Ishida, H., Amano, T., Ono, H., and Yoneda, M. 2009. Biological affinities of Okhotsk-culture people with East Siberians and Arctic people based on dental characteristics. *Anthropological Science* 117(2):121-132.

Mayhall, J.T. 1992. Techniques for the study of dental morphology. In: S.R. Saunders, and M.A. Katzenberg, editors. Skeletal biology of past people: Research methods. New York.: Wiley-Liss. p 59-78.

Mayhall, J.T., Saunders, S.R., and Belier, P.L. 1982a. The dental morphology of North American whites: a reappraisal. In: B. Kurtén, editor. Teeth: form, function, and evolution. New York: Columbia University Press. p 245-258.

Mayhall, J.T., Saunders, S.R., and Belier, P.L. 1982b. The dental morphology of North American whites: a reappraisal. *Teeth: form, function, and evolution New York: Columbia University Press p*:245-258.

Mazel, A. 1987. The archaeological past from the changing present: towards a critical assessment of South African Later Stone Age studies from the early 1960s to the early 1980s. In: J.E. Parkington, and M. Hall, editors. Papers in the prehistory of the western Cape, South Africa. Oxford: British Archaeological Reports International Series. p 504-529.

Mazel, A. 1989a. Changing social relations in the Thukela Basin, Natal 7000-2000 BP. *South African Archaeological Society Goodwin Series* 6:33-41.

Mazel, A. 1989b. People making history: the last ten thousand years of hunter-gatherer communities in the Thukela Basin. *Natal Museum Journal of Humanities* 1:1-168.

McBrearty, S., and Brooks, A. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behaviour. *Journal of Human Evolution* 39:453-563.

McDougall, I., Brown, F.H., and Fleagle, J.G. 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433(7027):733-736.

McEvoy, B.P., Lind, J.M., Wang, E.T., Moyzis, R.K., Visscher, P.M., van Holst Pellekaan, S.M., and Wilton, A.N. 2010. Whole-genome genetic diversity in a sample of Australians with deep Aboriginal ancestry. *The American Journal of Human Genetics* 87(2):297-305.

McNabb, J., and Sinclair, A. 2009. The Cave of Hearths: Makapan Middle Pleistocene research project. Field research by Anthony Sinclair and Patrick Quinney, 1996-2001. Oxford: Archaeopress.

Meiring, A.J.D. 1937. The "Wilton" skulls of the Matjes River Rock Shelter. *Soologiese Navorsing Nasionale Museum Bloemfontein* 1(6):51-79.

Mellars, P. 1989. Major issues in the emergence of modern humans. *Current Anthropology* 30:349-385.

Mihailidis, S., Scriven, G., Khamis, M., and Townsend, G. 2013. Prevalence and patterning of maxillary premolar accessory ridges (MxPARs) in several human populations. *American Journal of Physical Anthropology* 152(1):19-30.

Millard, A., R. 2006. Bayesian analysis of ESR dates, with application to Border Cave. *Quaternary Geochronology* 1(2):159-166.

Miller, G.H., Beaumont, P.B., Deacon, H.J., Brooks, A.S., Hare, P.E., and Jull, A.J.T. 1999. Earliest modern humans in southern Africa dated by isoleucine epimerization in ostrich eggshell. *Quaternary Science Reviews* 18(13):1537-1548.

Milner, G.R., and Larsen, C.S. 1991. Teeth as artifacts of human behavior: intentional mutilation and accidental modification. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. California: Wiley-Liss. p 357-378.

Mitchell, P. 1988a. The early microlithic assemblages of southern Africa: B.A.R.

Mitchell, P. 1988b. The Late Pleistocene early microlithic assemblages of southern Africa. *World Archaeology* 20(1):27-39.

Mitchell, P. 1995. Revisiting the Robberg: new results and a revision of old ideas at Sehonghong Rock Shelter, Lesotho. *The South African Archaeological Bulletin* 50(161):28-38.

Mitchell, P. 1996. Filling a gap: the Early and Middle Holocene assemblages from new excavations at Sehonghong Rock Shelter, Lesotho. *Southern African Field Archaeology* 1996(5):17-27.

Mitchell, P. 2004. The archaeology of southern Africa Cambridge: Cambridge University Press.

Mitchell, P. 2009. The flaked stone artefact assemblages from Likoaeng: a late Holocene sequence in the Lesotho Highlands and its regional context. *Southern African Humanities* 21 117-155.

Mitchell, P., Plug, I., and Bailey, G. 2006. Spatial patterning and site occupation at Likoaeng, an open-air hunter-gatherer campsite in the Lesotho Highlands, southern Africa. *Archeological papers of the American Anthropological Association* 16(1):81-94.

Mizoguchi, Y. 1978. Tooth crown characters on the lingual surfaces of the maxillary anterior teeth: analysis of the correlations by the method of path coefficients. *Bulletin of the National Science Museum Series D* 4:25-57.

Mizoguchi, Y. 1985. Shovelling: a statistical analysis of its morphology. *The University of Tokyo Bulletin* 26:1-176.

Mizoguchi, Y. 1993. Adaptive significance of the Carabelli trait. *Bulletin of the National Science Museum Series D* 19:21-58.

Mizoguchi, Y. 2013. Significant among-poulation associations found between dental characters and environmetal factors. In: S. G.R., and I. J.D., editors. Anthropological perspectives on tooth morphology: genetics, evolution, variation. Cambridge: Cambridge University Press. p 108-125.

Moorrees, C.F.A. 1957. The Aleut dentition. A correlative study of dental characteristics in an Eskimoid people. Cambridge: Harvard University Press.

Moorrees, C.F.A., and Reed, R.B. 1954. Biometrics of crowding and spacing of the teeth in the mandible. *American Journal of Physical Anthropology* 12(1):77-88.

Moreno-Gómez, F. 2013. Sexual dimorphism in human teeth from dental morphology and dimensions: a dental anthropology viewpoint. In: H. Moriyama, editor. Sexual Dimorphism: Creative Commons. p 97-124.

Morris, A.G. 1992a. Guide to Holocene human skeletons from Saldanha and Elands Bay regions of the Western Cape Province: with notes and certain specimens. In: A.B. Smith, and B. Mutti, editors. Guide to archaeological sites in the South-western Cape South African Association of Archaeologists conference July 5-9 1992. Cape Town.

Morris, A.G. 1992b. The skeletons of contact: a study of protohistoric burials from the lower Orange River Valley, South Africa. Johannesburg: Witwatersrand University Press.

Morris, A.G. 2002a. Isolation and the origin of the Khoisan: Late Pleistocene and early Holocene human evolution at the southern end of Africa. *Human Evolution* 17(3-4):105-114.

Morris, A.G. 2003. The myth of the East African 'Bushmen'. *The South African Archaeological Bulletin* 58(178):85-90.

Morris, A.G. 2008. Searching for ‘real’ Hottentots: the Khoekhoe in the history of South African physical anthropology. *Southern African Humanities* 20:221-233.

Morris, A.G., Dlamini, N., Joseph, J., Parker, A., Powrie, C., and Ribot, I. 2004/2005. Later Stone Age burials from the Western Cape Province, South Africa 1: Voelvlei. *South African Field Archaeology* 13 & 14:19-26.

Morris, A.G., and Parkington, J. 1982. Prehistoric homicide: a case of violent death on the Cape south coast, South Africa. *South African Journal of Science* 78:167-169.

Morris, A.G., Thackeray, A.I., and Thackeray, J.F. 1987. Late Holocene human skeletal remains from Snuifklip, near Vleesbaai, Southern Cape. *The South African Archaeological Bulletin* 42(146):153-160.

Morris, D. 1988. Engraved in place and time: a review of variability in the rock art of the Northern Cape and Karoo. *The South African Archaeological Bulletin*:109-120.

Morris, D. 2002b. Driekopseiland and the 'rain's magic power': history and landscape in a new interpretation of a Northern Cape rock engraving. Unpublished MA dissertation. Cape Town: University of the Western Cape.

Morris, D., and Beaumont, P.B. 1991. !Nawabdanas: Archaeological Sites at Renosterkop Kakamas District, Northern Cape. *The South African Archaeological Bulletin* 46(154):115-124.

Morris, D., Steyn, M., and Ribot, I. 2006. A Burial from Driekopseiland, Northern Cape. *The South African Archaeological Bulletin* 61(184):133-141.

Morris, D.H. 1974. Hominid canine tooth semantics. *Man* 9(4):585-590.

Morris, D.H. 1975. Bushman maxillary canine polymorphism. *South African Journal of Science* 71:333-335.

Mossop, E.E. 1935. The journal of Hendrik Jacob Wikar 1779. Cape town: Van Riebeeck Society.

Mourant, A.E. 1983. Blood relations: blood groups and anthropology. Oxford: Oxford University Press.

Mummery, J. 1870. On the relations which dental caries, as discovered among the ancient inhabitants of Britain, and amongst existing aboriginal races, may be supposed to hold to their food and social conditions. *Transactions of the Odontological Society of Great Britain* 2:1-90.

Murphy, T. 1959. The changing pattern of dentine exposure in human tooth attrition. *American Journal of Physical Anthropology* 17:167-178.

Nanci, A. 2008. Ten Cate's oral histology: development, structure, and function. St. Louis: Mosby Elsevier.

Nelson, C.T. 1938. The teeth of the Indians of Pecos Pueblo. *American Journal of Physical Anthropology* 23:261-293.

Nichol, C.R. 1989. Complex segregation analysis of dental morphological variants. *American Journal of Physical Anthropology* 78(1):37-59.

Nichol, C.R. 1990. Dental genetics and biological relationships of the Pima Indians of Arizona. Tempe: Arizona State University.

Noss, J.F., Scott, G.R., Potter, R.H.Y., Dahlberg, A.A., and Dahlberg, T. 1983. The influence of crown size dimorphism on sex differences in the Carabelli trait and the canine distal accessory ridge in man. *Archives of Oral Biology* 28(6):527-530.

Nurse, G.T., Weiner, J.B., and Jenkins, T. 1985. The people of southern Africa and their affinities. Oxford: Clarendon Press.

Omoto, K. 1984. The Negritos: genetic origins and microevolution. *Acta anthropogenetica* 8(1-2):137-147.

Oöe, T. 1965. A study of the ontogenetic origin of human permanent tooth germs. *Okajimas folia anatomica Japonica* 40:429-437.

Opperman, H. 1987. The Later Stone Age of the Drakensberg range and its foothills. Oxford: Archaeopress.

Opperman, H. 1996. Strathalan Cave B, north-eastern Cape Province, south Africa: Evidence for human behaviour 29,000-26,000 years ago. *Quaternary International* 33(0):45-53.

Opperman, H., and Heydenrych, B. 1990. A 22 000 year-old Middle Stone Age camp site with plant food remains from the north-eastern Cape. *The South African Archaeological Bulletin* 45(152):93-99.

Oranje, P. 1934. Dentition of the Bush race. *South African Journal of Science* 31:576.

Orton, J. 2006. The Later Stone Age lithic sequence at Elands Bay, Western Cape, South Africa: raw materials, artefacts and sporadic change. *Southern African Humanities* 18(2):1-28.

Orton, J., Mitchell, P., Klein, R., Steele, T.E., and Horsburgh, K.A. 2013. An early date for cattle from Namaqualand, South Africa: implications for the origins of herding in southern Africa. *Antiquity* 87(335):108-120.

Osborn, H.F. 1907. Evolution of mammalian molar teeth to and from the triangular type. New York: Macmillan.

Ouzman, S. 2001. A Riet River burial from Koffiefontein, South Africa. *Southern African Field Archaeology* 10:3-15.

Owen, R.B. 1845. Odontography or a treatise on the comparative anatomy of the teeth: their physiological relations, mode of development and microscopic structure in vertebrate animals. London: Hyppolyte Bailliere.

Owen, R.B., Barthelme, J.W., Renaut, R.W., and Vincens, A. 1982. Palaeolimnology and archaeology of Holocene deposits north-east of Lake Turkana, Kenya. *Nature* 298:523-529.

Owen, R.B., and Renaut, R.W. 1986. Sedimentology, stratigraphy and paleoenvironments of the Holocene Galana Boi Formation, NE Lake Turkana, Kenya. In: L.E. Frostick, R.W. Renaut, I. Reid, and J.J. Tiercelin, editors. Sedimentation in the African rifts. New York: Blackwell.

Papreckiené, I., and Ĉesnys, G. 1983. The teeth of the 1st millennium A.D. population in Lithuania. *Anthropologie* 21:243-258.

Park, J., Yamaguchi, T., Watanabe, C., Kawaguchi, A., Haneji, K., Takeda, M., Kim, Y.I., Tomoyasu, Y., Watanabe, M., Oota, H., Hanihara, T., Ishida, H., Maki, K., Park, S., and Kimura, R. 2012. Effects of an Asian-specific nonsynonymous EDAR variant on multiple dental traits. *Journal of Human Genetics* 57(8):508-514.

Parkington, J. 1972. Seasonal mobility in the Later Stone Age. *African Studies* 31:223-243.

Parkington, J. 1976. Follow the San. Unpublished Ph.D. thesis. University of Cambridge.

Parkington, J. 1980. The Elands Bay cave sequence: cultural stratigraphy and subsistence strategies. Proceedings of the 8th Pan-African Congress of Prehistory and Quaternary Studies, Nairobi. p 315-320.

Parkington, J. 1981. The effects of environmental change on the scheduling of visits to the Elands Bay Cave, Cape Province, South Africa. In: I. Hodder, G.L.

Isaac, and N. Hammond, editors. Patterns of the past: studies in honour of David Clarke. Cambridge: Cambridge University Press. p 341-359.

Parkington, J. 1984. Changing views of the Later Stone Age of south Africa. *Advances in World Archaeology* 3:80-142.

Parkington, J. 1986. Stone-tool assemblages, raw material distributions and prehistoric subsistence activities: the late Stone Age of South Africa. In: G.N. Bailey, and P. Callow, editors. Stone-Age prehistory: studies in memory of Charles McBurney. Cambridge: Cambridge University Press. p 181-196.

Parkington, J. 1988. The Pleistocene/Holocene transition in the Western Cape, South Africa: observations from Verlorenvlei. In: J. Bower, and D. Lubell, editors. Prehistoric cultures and environments in the Late Quaternary of Africa. Oxford: British Archaeological Reports. p 349-363.

Parkington, J. 1990. A view from the South: southern Africa before, during and after the Last Glacial Maximum. In: O. Soffer, and C. Gamble, editors. The World at 18000 BP: Low Latitudes. London: Unwin Hyman. p 214-229.

Parkington, J. 1992. Making sense of sequence at Elands Bay Cave, western Cape, South Africa. In: A.B. Smith, and B. Mütti, editors. Guide to archaeological sites in the south-western Cape. Cape Town: Southern African Association of Archaeologists. p 6-12.

Parkington, J. 2001. Presidential address: mobility, seasonality and southern African hunter-gatherers. *The South African Archaeological Bulletin* 56(173/174):1-7.

Parkington, J. 2003. Middens and moderns: shellfishing and the Middle Stone Age of the Western Cape, South Africa. *South African Journal of Science* 99:243-247.

Parkington, J. 2008. Limpet sizes in Stone Age archaeological contexts at the Cape, South Africa: changing environment or human impact? In: A. Antczak, and R. Cipriani, editors. Early Human impact on megamolluscs. Oxford: British Archaeological Reports International Series p175-184.

Parkington, J., and Hall, M. 1987. Papers in the prehistory of the Western Cape, South Africa. Oxford: Archaeopress.

Parkington, J., Nilssen, P., Vermuelen, C., and Henshilwood, C.S. 1992. Making sense of space at Dunefield Midden campsite, Westem Cape, South Africa. *Journal of Field Archaeology* 1:63-70.

Parkington, J., Poggenpoel, C., Buchanan, B., Robey, T., Manhire, T., and Sealy, J. 1988. Holocene coastal settlement patterns in the western Cape. In: G. Bailey, and J. Parkington, editors. The archaeology of prehistoric coastlines. Cambridge: Cambridge University Press. p 22-41.

Parkington, J., Poggenpoel, C., Rigaud, J.P., and Texier, P.J. 2005. From tool to symbol: the behavioural context of intentionally marked ostrich eggshell from Diepkloof, Western Cape. In: F. d'Errico, and L. Backwell, editors. From tools to symbols: from early hominids to modern humans. Johannesburg: Witwatersrand University Press. p 475-492.

Parkinson, J. 1928. Eighth interim report of the British Museum East African expedition. London: British Museum.

Parsons, I. 2003. Society lithic expressions of Later Stone Age lifeways in the Northern Cape. *South African Archaeological Bulletin* 58(177):33-37.

Parsons, P.A. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* 68:361-364.

Partridge, T.C. 1982. The chronological positions of the fossil hominids of southern Africa. In: M.A. de Lumley, editor. *L'Homo erectus* et la place de l'homme de Tautavel parmi les hominidés fossiles 1er Congres International de Paléontologie Humaine, Nice. Paris: Institut de paléontologie humaine. p 617-675.

Partridge, T.C., Avery, D.M., Botha, G.A., Brink, J.S., Deacon, J., Herbert, R.S., Maud, R.R., Scott, L., Talma, A.S., and Vogel, J.C. 1990. Late Pleistocene and Holocene climatic change in southern Africa. *South African Journal of Science* 86:302-306.

Partridge, T.C., Scott, L., and Hamilton, J.E. 1999. Synthetic reconstructions of southern African environments during the Last Glacial Maximum (21–18kyr) and the Holocene Altithermal (8–6kyr). *Quaternary International* 57–58(0):207-214.

Paynter, K.J., and Grainger, R.M. 1956. The relation of nutrition to the morphology and size of rat molar teeth. *Journal of the Canadian Dental Association* 22:519.

Pearson, O.M., and Grine, F.E. 1997. Re-analysis of the hominid radii from Cave of Hearths and Klasies River Mouth, South Africa. *Journal of Human Evolution* 32(6):577-592.

Pedersen, P.O. 1949. The East Greenland Eskimo dentition. *Meddelelser om Grønland* 142:1-244.

Pedersen, P.O., Dahlberg, A.A., and Alexanderson, V. 1967. Proceedings of the International Symposium on Dental Morphology: Fredensborg, Denmark, September 27-29, 1965: Journal of Dental Research.

Penn, N. 1986. Pastoralists and pastoralism in the northern Cape frontier zone during the eighteenth century. *South African Archaeological Society Goodwin Series* 5:62-68.

Penn, N. 2005. The forgotten frontier: Colonist and Khoisan on the Cape's northern frontier in the 18th century. Cape Town: Juta and Company.

Peringuey, L. 1911. The Stone Ages of South Africa. *Annals of the South African Museum* 8:1-218.

Perzigian, A.J. 1977. Fluctuating dental asymmetry: variation among skeletal populations. *American Journal of Physical Anthropology* 47(1):81-88.

Perzigian, A.J. 1984. Human odontometric variation: an evolutionary and taxonomic perspective. *Anthropologie* 22:193-198.

Pfeiffer, S. 2012a. Conditions for evolution of small adult body size in southern Africa. *Current Anthropology* 53(S6):383-394.

Pfeiffer, S. 2012b. Two disparate instances of healed cranial trauma from the Later Stone Age of South Africa. *South African Archaeological Bulletin* 67(196):256-261.

Pfeiffer, S., and Harrington, L. 2011. Bioarchaeological evidence for the basis of small adult stature in southern Africa: growth, mortality, and small stature. *Current Anthropology* 52(3):449-461.

Pfeiffer, S., and Sealy, J. 2006. Body size among Holocene foragers of the Cape Ecozone, Southern Africa. *American Journal of Physical Anthropology* 129:1-11.

Pfeiffer, S., and Van der Merwe, N.J. 2004. Cranial Injuries to Later Stone Age children from the Modder River Mouth, Western Cape Province, South Africa. *The South African Archaeological Bulletin* 59(180):59-65.

Pfeiffer, S., Van der Merwe, N.J., Parkington, J., and Yates, R. 1999. Violent human death in the past: a case from the Western Cape. *South African Journal of Science* 95:137-140.

Phillipson, D.W. 1977. Lowasera. *Azania* 12(1):1-32.

Phillipson, D.W. 1982. African archaeology. Cambridge: Cambridge University Press.

Phillipson, D.W. 2005. African archaeology, 3rd edition. New York: Cambridge University Press.

Pickrell, J.K., Patterson, N., Barbieri, C., Berthold, F., Gerlach, L., Lipson, M., Loh, P.R., Güldemann, T., Kure, B., and Mpoloka, S.W. 2012. The genetic prehistory of southern Africa. *Nature Communications* 3(1143):1-6.

Pienaar, M., Woodborne, S., and Wadley, L. 2008. Optically stimulated luminescence dating at Rose Cottage Cave. *South African Journal of Science* 104:65-70.

Pilloud, M.A. 2009. Community structure at Neolithic Çatalhöyük: biological distance analysis of household, neighborhood, and settlement. Columbus: Ohio State University.

Pilloud, M.A., and Hillson, S. 2012. Brief communication: the use of alternative dental measurements on deciduous teeth. *American Journal of Physical Anthropology* 149(2):299-306.

Pilloud, M.A., and Larsen, C.S. 2011. "Official" and "practical" kin: Inferring social and community structure from dental phenotype at Neolithic Catalhoyuk, Turkey. *American Journal of Physical Anthropology* 145(4):519-530.

Piontek, J., Iwanek, B., Segeda, S., and Nowak, O. 2007. Odontological analysis of central European populations from the Roman period to the early Middle Ages. *Human Biology Budapest* 30:70-86.

Pleurdeau, D., Imalwa, E., Détroit, F., Lesur, J., Veldman, A., Bahain, J.-J., and Marais, E. 2012. “Of Sheep and Men”: earliest direct evidence of caprine domestication in southern Africa at Leopard Cave (Erongo, Namibia). *PLoS ONE* 7(7):e40340.

Plug, I. 2004. Resource exploitation: animal use during the middle stone age at Sibudu Cave, KwaZulu-Natal. *South African Journal of Science* 100(3-4):151-158.

Plug, I., and Engela, R. 1992. The macrofaunal remains from recent excavations at Rose Cottage Cave, Orange Free State. *The South African Archaeological Bulletin*:16-25.

Polychronis, G., Christou, P., Mavragani, M., and Halazonetis, D.J. 2013. Geometric morphometric 3D shape analysis and covariation of human mandibular and maxillary first molars. *American Journal of Physical Anthropology* 152(2):186-196.

Potter, R.H., and Nance, W.E. 1976. A twin study of dental dimension. I. Discordance, asymmetry, and mirror imagery. *American Journal of Physical Anthropology* 44(3):391-395.

Powell, A., Shennan, S., and Thomas, M.G. 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324(5932):1298-1301.

Saharan fossil hominids and their place in human evolution. *Journal of Human Evolution* 4:297-322.

Protsch, R. 1976. The Naivasha hominid and its confirmed Late Upper Pleistocene age. *Anthropologischer Anzeiger* 35(2/3):97-102.

Protsch, R. 1977. Mumbwa: its absolute chronology and archaeology. *Zeitschrift für Morphologie und Anthropologie* 68(1):1-7.

R Development Core Team. 2012. A language and environment for statistical computing. 2.15.2 ed. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org.

Ramachandran, S., Deshpande, O., Roseman, C.C., Rosenberg, N.A., Feldman, M.W., and Cavalli-Sforza, L.L. 2005. Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *Proceedings of the National Academy of Sciences* 102:15942-15947.

Rami Reddy, V., Vijayalakshmi, P.B., and Chandrasekhar Reddy, B.K. 1986. Deciduous tooth emergence and physique of Velama children of southeastern Andhra Pradesh, India. *Acta Odontologica* 7(1):1-5.

Raper, P.E., and Boucher, M. 1988. Robert Jacob Gordon: Cape travels, 1777 to 1786. Volumes I and II. Johannesburg: Brenthurst Press.

Reich, D., Patterson, N., Campbell, D., Tandon, A., Mazieres, S., Ray, N., Parra, M.V., Rojas, W., Duque, C., and Mesa, N. 2012. Reconstructing Native American population history. *Nature* 488(7411):370-374.

Reid, C., Van Reenen, J.F., and Groeneveld, H.T. 1991. Tooth size and the Carabelli trait. *American Journal of Physical Anthropology* 84(4):427-432.

Relethford, J.H. 2004. Global patterns of isolation by distance based on genetic and morphological data. *Human biology* 76:499-513.

Richardson, J.L. 1972. Palaeolimnological records from Rift lakes in central Kenya. *Palaeoecology of Africa* 6(1972):131-136.

Rightmire, P.G. 1970. Bushman, Hottentot and South African Negro crania studied by distance and discrimination. *American Journal of Physical Anthropology* 33(2):169-195.

Rightmire, P.G. 1975a. New studies of post-Pleistocene human skeletal remains from the Rift Valley, Kenya. *American Journal of Physical Anthropology* 42(3):351-369.

Rightmire, P.G. 1975b. Problems in the Study of Later Pleistocene Man in Africa. *American Anthropologist* 77(1):28-52.

Rightmire, P.G. 1978. Human skeletal remains from the southern Cape Province and their bearing on the Stone Age prehistory of South Africa. *Quaternary research* 9(2):219-.

Rightmire, P.G. 1984. Human skeletal remains from eastern Africa. In: J.D. Clark, and S.A. Brandt, editors. From hunters to farmers: the causes and consequences of food production in Africa. Berkeley University of California Press. p 191-199.

Rightmire, P.G. 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evolutionary Anthropology* 6:218-227.

Rightmire, P.G., Beaumont, P.B., Bilsborough, A., Butzer, K., Davies, O., Gilead, I.J., Groves, C.P., Howells, W.W., Irsigler, F.J., Luchterhand, K., Merrick, H.V., Rolland, N., Thurzo, M., Wilson, S.R., and Wymer, J.J. 1979. Implications of Border Cave skeletal remains for Later Pleistocene human evolution [and comments and reply]. *Current Anthropology* 20(1):23-35.

Rightmire, P.G., and Deacon, H.J. 1991. Comparative studies of Late Pleistocene human remains from Klasies River Mouth, South Africa. *Journal of Human Evolution* 20(2):131-156.

Rightmire, P.G., and Deacon, H.J. 2001. New human teeth from the Middle Stone Age deposits at Klasies River Mouth, South Africa. *Journal of Human Evolution* 41:535-544.

Rightmire, P.G., Deacon, H.J., Schwartz, J.H., and Tattersall, I. 2006. Human foot bones from Klasies River Mouth main site, South Africa. *Journal of Human Evolution* 50(1):96-103.

Robbins, L.H. 1972. Archeology in the Turkana District, Kenya. *Science* 176(4033):359-366.

Robbins, L.H. 1974. The Lothagam site: a Late Stone Age fishing settlement in the Lake Rudolph basin, Kenya. Michigan: Publications of the Museum: Michigan State University.

Robbins, L.H. 1980. Lopoy and Lothagam. Michigan: Michigan State University.

Robbins, L.H., Campbell, A.C., Murphy, M.L., Brook, G.A., Liang, F., Skaggs, S.A., Srivavasta, P., Mabuse, A.A., and Badenhorst, S. 2008. Recent archaeological research at Toteng, Botswana: early domesticated livestock in the Kalahari. *Journal of African Archaeology* 6(1):131-149.

Robbins, L.H., Campbell, A.C., Murphy, M.L., Brook, G.A., Srivavasta, P., and Badenhorst, S. 2005. The advent of herding in southern Africa: early AMS dates on domestic livestock from the Kalahari Desert. *Current Anthropology* 46(4):671-677.

Robertshaw, P. 1988. The Elmenteitan: an early food-producing culture in East Africa. *World Archaeology* 20(1):57-69.

Robinson, J.T. 1956. The dentition of the *Australopithecinae*. *Memoirs of the Transvaal Museum* 9.

Royer, D.F., Lockwood, C.A., Scott, J.E., and Grine, F.E. 2009. Size variation in early human mandibles and molars from Klasies River Mouth, South Africa: comparison with other middle and late Pleistocene assemblages and with modern humans. *American Journal of Physical Anthropology* 140(2):312-323.

Ruff, C.B. 1991. Climate and body shape in hominid evolution. *Journal of Human Evolution* 21(2):81-105.

Ruff, C.B. 1994. Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology* 37(S19):65-107.

Sadr, K. 1998. The first herders at the Cape of Good Hope. *The African Archaeological Review* 15(2):101-132.

Sadr, K. 2002. Ancient pastoralists in the Sudan and in South Africa. In: T. Lenssen-Erz, editor. Tides of the desert: contributions to the archaeology and environmental history of Africa in honour of Rudolph Kuper. Cologne: Heinrich Barth Institut. p 471-484.

Sadr, K. 2003. The Neolithic of Southern Africa. *The Journal of African History* 44(2):195-209.

Sadr, K. 2005. From foraging to herding: the west coast of South Africa in the first millennium AD. *Human Evolution* 20(4):217-230.

Sadr, K. 2008a. An ageless view of first millennium AD southern African ceramics. *Journal of African Archaeology* 6(1):103-129.

Sadr, K. 2008b. Invisible herders? The archaeology of Khoekhoe pastoralists. *Southern African Humanities* 20:179–203.

Sadr, K. 2013. A short history of early herding in southern Africa. In: M. Bollig, M. Schnegg, and H.-P. Wotzka, editors. Pastoralism in Africa: past, present, and future. New York: Berghahn Books. p 171-196.

Sadr, K., and Sampson, C. 2006. Through thick and thin: early pottery in southern Africa. *Journal of African Archaeology* 4:235-252.

Sadr, K., and Smith, A.B. 1991. On ceramic variation in the southwestern Cape, South Africa. *South African Archaeological Bulletin* 46:107-115.

Sakuma, M., Irish, J.D., and Morris, D.H. 1991. The Bushman maxillary canine of the Chewa tribe in east-central Africa. *Journal of the anthropological society of Nippon* 99(4):411-417.

Salazar-Ciudad, I. 2012. Tooth patterning and evolution. *Current opinion in genetics & development* 22(6):585-592.

Salazar-Ciudad, I., and Jernvall, J. 2004. How different types of pattern formation mechanisms affect the evolution of form and development. *Evolution & Development* 6(1):6-16.

Salazar-Ciudad, I., and Jernvall, J. 2010. A computational model of teeth and the developmental origins of morphological variation. *Nature* 464(7288):583-586.

Sampson, C.G. 1974. The stone age archaeology of southern Africa. California: Academic Press.

Sampson, C.G. 1996. Spatial organization of Later Stone Age herders in the upper Karoo. In: G. Pwiti, and R. Soper, editors. Aspects of African archaeology: papers from the 10th congress of the Pan-African Association for Prehistory and Related Studies. Harare: University of Zimbabwe Press. p 317-326.

Sampson, C.G. 2010. Chronology and dynamics of Later Stone Age herders in the upper Seacow River valley, South Africa. *Journal of Arid Environments* 74(7):842-848.

Saunders, S.R., Chan, A.H., Kahlon, B., Kluge, H.F., and FitzGerald, C. 2007. Sexual dimorphism of the dental tissues in human permanent mandibular canines and third premolars. *American Journal of Physical Anthropology* 133(1):735-740.

Saunders, S.R., and Mayhall, J.T. 1982. Developmental patterns of human dental morphological traits. *Archives of Oral Biology* 27(1):45-49.

Savage, C.D. 1983. Identifying industries in south central Africa: the Zambian Wilton Complex. Unpublished Ph.D. dissertation. University of California, Berkeley.

Schapera, I. 1926. A preliminary consideration of the relationship between the Bushmen and the Hottentots. *South African Journal of Science* 23:833-866.

Schapera, I. 1930. The Khoisan peoples of South Africa: Bushmen and Hottentots. : . London: Routledge.

Schapera, I., and Farrington, B. 1933. The early Cape Hottentots. Cape Town: Van Riebeeck Society.

Schepartz, L.A. 1988. Who Were the Later Pleistocene Eastern Africans? *The African Archaeological Review* 6:57-72.

Schepers, G.W.H. 1934. The Bush mandible. *South African Journal of Science* 31:571-576.

Schlebusch, C.M. 2010. Issues raised by use of ethnic-group names in genome study. *Nature* 464:487.

Schlebusch, C.M., Lombard, M., and Soodyall, H. 2013. MtDNA control region variation affirms diversity and deep sub-structure in populations from southern Africa. *BMC evolutionary biology* 13(1):1-21.

Schlebusch, C.M., Skoglund, P., Sjödin, P., Gattepaille, L.M., Hernandez, D., Jay, F., Li, S., De Jongh, M., Singleton, A., and Blum, M.G. 2012. Genomic variation in seven Khoe-San groups reveals adaptation and complex African history. *Science* 338(6105):374-379.

Schlebusch, C.M., and Soodyall, H. 2012. Extensive population structure in San, Khoe and mixed ancestry populations from southern Africa revealed by 44 short 5-SNP haplotypes. Human Biology Open Access Pre-Prints.

Schnutenhaus, S., and Rösing, F.W. 1998. World variation of tooth size. In: K.W. Alt, F.W. Rösing, and M. Teschler-Nicola, editors. Dental anthropology fundamentals, limits and prospects. New York: Springer. p 521-535.

Schrire, C. 1992. The archaeological identity of hunters and herders at the Cape over the last 2000 years: a critique. *The South African Archaeological Bulletin* 47(155):62-64.

Schrire, C., and Deacon, J. 1989. The indigenous artefacts from Oudepost I, a colonial outpost of the VOC at Saldanha Bay, Cape. *The South African Archaeological Bulletin* 44(150):105-113.

Schultze, L. 1928. Zur Kenntnis des Körpers der Hottentotten und Buschmänner. (Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika). Jena: Gustav Fischer.

Schuster, S.C., Miller, W., Ratan, A., Tomsho, L.P., Giardine, B., Kasson, L.R., Harris, R.S., Petersen, D.C., Zhao, F., Qi, J., Alkan, C., Kidd, J.M., Sun, Y., Drautz, D.I., Bouffard, P., Muzny, D.M., Reid, J.G., Nazareth, L.V., Wang, Q., Burhans, R., Riemer, C., Wittekindt, N.E., Moorjani, P., Tindall, E.A., Danko, C.G., Teo, W.S., Buboltz, A.M., Zhang, Z., Ma, Q., Oosthuysen, A., Steenkamp, A.W., Oostuisen, H., Venter, P., Gajewski, J., Zhang, Y., Pugh, B.F., Makova, K.D., Nekrutenko, A., Mardis, E.R., Patterson, N., Pringle, T.H., Chiaromonte, F., Mullikin, J.C., Eichler, E.E., Hardison, R.C., Gibbs, R.A., Harkins, T.T., and Hayes, V.M. 2010. Complete Khoisan and Bantu genomes from southern Africa. *Nature* 463 (7283):943-947.

Schwarcz, H.P., and Rink, W.J. 2000. ESR dating of the Die Kelders Cave 1 site, South Africa. *Journal of Human Evolution* 38 (1):121-128.

Schwartz, G.T., and Dean, C.M. 2001. Ontogeny of canine dimorphism in extant hominoids. *American Journal of Physical Anthropology* 115(3):269-283.

Schwartz, G.T., and Dean, C.M. 2005. Sexual dimorphism in modern human permanent teeth. *American Journal of Physical Anthropology* 128(2):312-317.

Schwartz, G.T., Thackeray, J.F., Reid, C., and van Reenan, J.F. 1998. Enamel thickness and the topography of the enamel–dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait. *Journal of Human Evolution* 35(4–5):523-542.

Schwartz, J.H., and Tattersall, I. 2003. The human fossil record vol. 2. New Jersey: Wiley-Liss.

Schweitzer, F.R. 1979. Excavations at Die Kelders, Cape Province, South Africa: the Holocene deposits. *Annals of the South African Museum* 78:101-233.

Scott, G.R. 1977. Classification, sex dimorphism, association, and population variation of the canine distal accessory ridge. *Human biology*:453-469.

Scott, G.R. 1980. Population variation of Carabelli's trait. *Human biology* 52(1):63.

Scott, G.R. 1997. Dental anthropology. In: F. Spencer, editor. History of physical anthropology: an encyclopedia. New York: Garland Publishing. p 334-340.

Scott, G.R. 2008. Dental morphology. In: M.A. Katzenberg, and S.R. Saunders, editors. Biological anthropology of the human skeleton 2nd ed. Hoboken, NJ: Wiley-Liss. p 265-298.

Scott, G.R., and Alexandersen, V. 1992. Dental morphological variation among medieval Greenlanders, Icelanders, and Norwegians. In: P. Smith, and E. Tchernov, editors. Structure, function and evolution of teeth London: Freund Publishing House. p 467-490.

Scott, G.R., and Dahlberg, A.A. 1982. Microdifferentiation in tooth crown morphology among Indians of the American Southwest. In: B. Kurtén, editor. Teeth: form, function, and evolution. New York: Columbia University Press. p 259-291.

Scott, G.R., Halffman, C.M., and Pedersen, P. 1991. Dental conditions of medieval Norsemen in the North Atlantic. *Acta Archaeologica* 62:183-207.

Scott, G.R., and Potter, R.H.Y. 1984. An analysis of tooth crown morphology in American white twins. *Anthropologie* 22:223-231.

Scott, G.R., Potter, R.H.Y., Noss, J.F., Dahlberg, A.A., and Dahlberg, T. 1983. The dental morphology of Pima Indians. *American Journal of Physical Anthropology* 61(1):13-31.

Scott, G.R., Street, S., and Dahlberg, A.A. 1986. The dental variation of Yuman speaking groups in an American Southwest context. In: D.E. Russel, J.-P. Santoro, and D. Sigogneau-Russel, editors. Teeth revisited: proceedings of the VIIth International Symposium on Dental Morphology, Paris: Memoires du Museum Nationale d'Histoire Naturelle, Serie C. p 305-319.

Scott, G.R., and Turner, C.G.I. 1988. Dental Anthropology. *Annual Review of Anthropology* 17:99-126.

Scott, G.R., and Turner, C.G.I. 2000. The Anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press.

Scott, G.R., and Turner, C.G.I. 2008. History of dental anthroplogy. In: J.D. Irish, and G.C. Nelson, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 10-34.

Scott, L. 1982. A Late Quaternary pollen record from the Transvaal bushveld, South Africa. *Quaternary research* 17(3):339-370.

Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M., and Walker, A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436(7051):693-695.

Sealy, J. 2003. Managing collections of human remains in South African museums and universities: ethical policy-making and scientific value. *South African Journal of Science* 99:238-239.

Sealy, J. 2006. Diet, mobility, and settlement pattern among Holocene hunter-gatherers in southernmost Africa. *Current Anthropology* 47(4):569-595.

Sealy, J. 2010. Isotopic evidence for the antiquity of cattle-based pastoralism in southermost Africa. *Journal of African Archaeology* 8(1):65-81.

Sealy, J. *In press*. Cultural change, demography, and the archaeology of the last 100 000 years in southern Africa. In: B.A. Stewart, and S.C. Jones, editors. Africa from MIS 6-2: population dynamics and palaeoenvironments Dordrecht: Springer.

Sealy, J., and Galimberti, M. 2011. Shellfishing and the interpretation of shellfish sizes in the Middle and Later Stone Ages of South Africa. In: N.F. Bicho, J.A. Haws, and L.G. Davis, editors. Trekking the shore changing coastlines and the antiquity of coastal settlement. New York: Springer. p 405-419.

Sealy, J., Patrick, M.K., Morris, A.G., and Alder, D. 1992. Diet and dental caries among later stone age inhabitants of the Cape Province, South Africa. *American Journal of Physical Anthropology* 88(2):123-134.

Sealy, J., and Pfeiffer, S. 2000. Diet, body size, and landscape use among Holocene people in the southern Cape, South Africa. *Current Anthropology* 41(4):642-655.

Sealy, J., and van der Merwe, N.J. 1988. Social, spatial and chronological patterning in marine food use as determined by δ13C measurements of Holocene human skeletons from the south-western Cape, South Africa. *World Archaeology* 20(1):87-102.

Sealy, J., and Yates, R. 1994. The chronology of the introduction of pastoralism to the Cape, South Africa. *Antiquity* 68(258):58+.

Sealy, J., and Yates, R. 1996. Direct radiocarbon dating of early sheep bones: two further results. *The South African Archaeological Bulletin* 51(164):109-110.

Selmer-Olsen, R. 1949. An odontometrical study on the Norwegian Lapps. *Utgitt av det Norske Videnskaps-Akademi Oslo, 1* 3.

Semino, O., Santachiara-Benerecetti, A.S., Falaschi, F., Cavalli-Sforza, L.L., and Underhill, P.A. 2002. Ethiopians and Khoisan share the deepest clades of the human Y-chromosome phylogeny. *Am J Hum Genet* 70(1):265-268.

Shackleton, N.J. 1982. Stratigraphy and chronology of the Klasies River Mouth deposits: oxygen isotope evidence. In: R. Singer, and J. Wymer, editors. The Middle Stone Age at Klasies River Mouth in South Africa. Chicago: University of Chicago Press. p 194-199.

Shapiro, M.M.J. 1949. The anatomy and morphology of the tubercle of Carabelli. *Journal of the Dental Association of South Africa* 4:355-362.

Shaw, J.C.M. 1927. Cusp development on the second lower molars in the Bantu and Bushmen. *American Journal of Physical Anthropology* 11(1):97-100.

Shaw, J.C.M. 1928. Taurodont teeth in South African races. *Journal of Anatomy* 62(Pt 4):476.

Shaw, J.C.M. 1931. The teeth, the bony palate and the mandible in Bantu races: John Bale.

Shaw, P. 2003. Multivariate statistics for the environmental sciences. London: Hodder Arnold.

Shea, B.T., and Gomez, A.M. 1988. Tooth scaling and evolutionary dwarfism: an investigation of allometry in human pygmies. *American Journal of Physical Anthropology* 77(1):117-132.

Shea, J.J. 2006. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. *Journal of Archaeological Science* 33(6):823-846.

Silberbauer, G.B. 1961. Aspects of the kinship system of the G/wi Bushmen of the Central Kalahari. *South African Journal of Science* 57:353-359.

Silberbauer, G.B. 1963. Marriage and the girl’s puberty ceremony of the G/wi Bushmen. *Africa* 33:12-24.

Silberbauer, G.B. 1972. The G/wi bushmen. In: M.G. Bicchieri, editor. Hunters and gatherers today. New York: Holt, Rinehart and Winston. p 271-326.

Silberbauer, G.B. 1981. Hunter and habitat in the central Kalahari Desert. Cambridge: Cambridge University Press.

Singer, R., and Wymer, J. 1982. The Middle Stone Age at Klasies River Mouth in South Africa. Chicago: University of Chicago Press.

Sjøvold, T. 1977. Non-metrical divergence between skeletal populations. *Ossa* 4(Suppl.):1-133.

Smith, A.B. 1983. Prehistoric pastoralism in the southwestern Cape, South Africa. *World Archaeology* 15:79-89.

Smith, A.B. 1986. Competition, conflict and clientship: Khoi and San relationships in the Western Cape. In: M. Hall, and A.B. Smith, editors. Prehistoric pastoralism in southern Africa: The South African Archaeological Society Goodwin. p 36-41.

Smith, A.B. 1990. On becoming herders: Khoikhoi and San ethnicity in southern Africa. *African Studies* 49:51-73.

Smith, A.B. 1992a. Pastoralism in Africa: origins and development ecology. London: Hurst and Company.

Smith, A.B. 2005. African herders: emergence of pastoral traditions. California: Alta Mira Press.

Smith, A.B. 2006. Excavations at Kasteelberg, and the origins of the Khoekhoen in the Western Cape, South Africa. Oxford: Archaeopress.

Smith, A.B. 2008a. Pastoral origins at the Cape, South Africa: influences and arguments. *Southern African Humanities* 20:49–60.

Smith, A.B., and Jacobson, L. 1995. Excavations at Geduld and the appearance of early livestock in Namibia. *South African Archaeological Bulletin* 50:3-14.

Smith, A.B., Sadr, K., Gribble, J., and Yates, R. 1991. Excavations in the south-western Cape, South Africa, and the archaeological identity of prehistoric hunter-gatherers within the last 2000 years. *The South African Archaeological Bulletin* 46(154):71-91.

Smith, B.H. 1984. Patterns of molar wear in hunter–gatherers and agriculturalists. *American Journal of Physical Anthropology* 63(1):39-56.

Smith, B.H., Garn, S.M., and Cole, P.E. 1982. Problems of sampling and inference in the study of fluctuating dental asymmetry. *American Journal of Physical Anthropology* 58(3):281-289.

Smith, B.W., and Ouzman, S. 2004. Taking stock: identifying Khoekhoen herder rock art in southern Africa. *Current Anthropology* 45(4):499-526.

Smith, F.H. 1992b. Models and realities in modern human origins: the African fossil evidence. *Philosophical Transactions: Biological Sciences* 337(1280):243-250.

Smith, P., Horwitz, L.K., and Kaplan, E. 1992. Skeletal evidence for population change in the Late Holocene of the south-western Cape: a radiological study. *The South African Archaeological Bulletin*:82-88.

Smith, R.N., Zaitoun, H., Coxon, T., Karmo, M., Kaur, G., Townsend, G., Harris, E.F., and Brook, A. 2009. Defining new dental phenotypes using 3-D image analysis to enhance discrimination and insights into biological processes. *Archives of Oral Biology* 54:S118-S125.

Smith, T.M. 2008b. Incremental dental development: methods and applications in hominoid evolutionary studies. *Journal of Human Evolution* 54(2):205-224.

Smith, T.M., Martin, L.B., and Leakey, M.G. 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *Journal of Human Evolution* 44(3):283-306.

Smith, T.M., Martin, L.B., Reid, D.J., de Bonis, L., and Koufos, G.D. 2004. An examination of dental development in *Graecopithecus freybergi (=Ouranopithecus macedoniensis)*. *Journal of Human Evolution* 46(5):551-577.

Smith, T.M., Reid, D.J., and Sirianni, J.E. 2006. The accuracy of histological assessments of dental development and age at death. *Journal of Anatomy* 208(1):125-138.

Smith, T.M., and Tafforeau, P. 2008. New visions of dental tissue research: tooth development, chemistry, and structure. *Evolutionary Anthropology: Issues, News, and Reviews* 17(5):213-226.

Smith, T.M., Tafforeau, P., Reid, D.J., Grün, R., Eggins, S., Boutakiout, M., and Hublin, J.-J. 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences* 104(15):6128-6133.

Smith, T.M., Tafforeau, P., Reid, D.J., Pouech, J., Lazzari, V., Zermeno, J.P., Guatelli-Steinberg, D., Olejniczak, A.J., Hoffman, A., and Radovčić, J. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proceedings of the National Academy of Sciences* 107(49):20923-20928.

Sofaer, J.A., C.J., M., and Bailit, H.L. 1972. Heredity and morphological variation in early and late developing human teeth of the same morphological class. *Archives of Oral Biology* 17:811-816.

Sofaer, J.A., Smith, P., and Kaye, E. 1986. Affinities between contemporary and skeletal Jewish and non-Jewish groups based on tooth morphology. *American Journal of Physical Anthropology* 70(2):265-275.

Sokal, R. R., & Sneath, P. H. (1963). Principles of numerical taxonomy.*Principles of numerical taxonomy.*

Sołtysiak, A. 2011. Technical note: an R script for Smith's mean measure of divergence. *Bioarchaeology of the Near East* 5:41-44.

Soodyall, H., and Jenkins, T. 1992. Mitochondrial DNA polymorphisms in Khoisan populations from Southern Africa. *Annals of Human Genetics* 56:315-324.

Soodyall, H., Makkan, H., Haycock, P., and Naidoo, T. 2008. The genetic prehistory of the Khoe and San. *Southern African Humanities* 20:37–48.

Soriano, S., Villa, P., and Wadley, L. 2007. Blade technology and tool forms in the Middle Stone Age of South Africa: the Howiesons Poort and post-Howiesons Poort at rose Cottage Cave. *Journal of Archaeological Science* 34(5):681-703.

Sperber, G.H. 1958. The palate and dental arcade of the Transvaal Bushmen, the/? Auni-4= Khomani Bushmen and Bantu-speaking Negroes of the Zulu tribe'. *South African Journal of Medical Science* 23:147-154.

Staka, G., Bimbashi, V., Disha, M., and Dragidella, F. 2013. Sexual dimorphism in the permanent mandibular canines: a study in Albanian population of Kosovo. *Acta stomatologica Croatica* 47(1):39-44.

StatSoft. 2011. Statistica. 10 ed. Tulsa, Oklahoma: StatSoft.

Steele, T.E., and Klein, R.G. 2005. Mollusk and tortoise size as proxies for Stone Age population density in South Africa: Implications for the evolution of human cultural capacity. *Munibe Antropologia-arkeologia* 57(1):221-237.

Steele, T.E., and Klein, R.G. 2009. Late Pleistocene subsistence strategies and resource intensification in Africa. In: J.-J. Hublin, and M.P. Richards, editors. The evolution of hominin diets. Netherlands: Springer p113-126.

Steyn, H.P. 1990. Vanished lifestyles: the early Cape Khoi and San. Pretoria: Unibook Publishers.

Stock, J.T. 2006. Hunter-gatherer postcranial robusticity relative to patterns of mobility, climatic adaptation, and selection for tissue economy. *American Journal of Physical Anthropology* 131(2):194-204.

Stock, J.T., and Pfeiffer, S. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. *American Journal of Physical Anthropology* 115:337-348.

Stojanowski, C.M. 2007. Comment on "Alternative dental measurements" by Hillson *et al. American Journal of Physical Anthropology* 132(2):234-237.

Stow, G.W. 1905. The native races of South Africa: a history of the intrusion of the Hottentots and Bantu into the hunting grounds of the Bushmen, the aborigines of the country. London: Swan Sonnenschein.

Stringer, C. 1992. Reconstructing recent human evolution. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 337:217-224.

Stringer, C. 1993. Understanding the fossil human record: past, present and future. *Rivista di Antropologia* 71:91-100.

Stringer, C. 2002. Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 357(1420):563-579.

Stringer, C., and Bräuer, G. 1994. Methods, misreading, and bias. *American Anthropologist* 96(2):416-424.

Stringer, C., Humphrey, L., and Compton, T. 1997. Cladistic analysis of dental traits in recent humans using a fossil outgroup. *Journal of Human Evolution* 32(4):389-402.

Stynder, D.D. 2006. A quantitative assessment of variation in Holocene Khoesan crania from South Africa’s western, south-western, southern and south-eastern coasts and coastal forelands. Cape Town: University of Cape Town.

Stynder, D.D. 2009. Craniometric evidence for South African Later Stone Age herders and hunter-gatherers being a single biological population. *Journal of Archaeological Science* 36(3):798-806.

Stynder, D.D., Ackermann, R.R., and Sealy, J. 2007a. Craniofacial variation and population continuity during the South African Holocene. *American Journal of Physical Anthropology* 134(4):489-500.

Stynder, D.D., Ackermann, R.R., and Sealy, J. 2007b. Early to mid-Holocene South African Later Stone Age human crania exhibit a distinctly Khoesan morphological pattern. *South African Journal of Science* 103(7 & 8):349-352.

Stynder, D.D., Brock, F., Sealy, J., Wurz, S., Morris, A.G., and Volman, T.P. 2009. A mid-Holocene AMS 14C date for the presumed upper Pleistocene human skeleton from Peers Cave, South Africa. *Journal of Human Evolution* 56(4):431-434.

Stynder, D.D., Moggi-Cecchi, J., Berger, L.R., and Parkington, J. 2001. Human mandibular incisors from the late Middle Pleistocene locality of Hoedjiespunt 1, South Africa. *Journal of Human Evolution* 41(5):369-383.

Sullivan, L.R. 1920. Differences in the pattern of the second lower molar tooth. *American Journal of Physical Anthropology* 3:255-257.

Sutton, J.E.G. 1972. New radiocarbon dates for eastern and southern Africa. *The Journal of African History* 13(1):1-24.

Suzuki, M., and Sakai, T. 1955. Japanese bibliography of dental anthropology (1879-1953). *Department of Anatomy, Shinshu University*.

Suzuki, M., and Sakai, T. 1964. Shovel-shaped incisors among the living Polynesians. *American Journal of Physical Anthropology* 22(1):65-71.

Suzuki, M., and Sakai, T. 1973. Occlusal surface pattern of the lower molars and the second deciduous molar among the living Polynesians. *American Journal of Physical Anthropology* 39(2):305-315.

Sweeney, E.A., Saffir, A.J., and de Leon, R. 1971. Linear hypoplasia of deciduous incisor teeth in malnourished children. *The American journal of clinical nutrition* 24(1):29-31.

Tanaka, J. 1976. Subsistence ecology of the Central Kalahari San. In: R.B. Lee, and I. DeVore, editors. Kalahari hunter-gatherers: studies of the !Kung San and their neighbors. Cambridge: Harvard University Press. p 98-119.

Tankard, A.J., and Schweitzer, F.R. 1974. The geology of the Die Kelders cave and environs: a palaeoenvironmental study. *South African Journal of Science* 70:365-369.

Tankard, A.J., and Schweitzer, F.R. 1976. Textural analysis of cave sediments: Die Kelders, Cape Province, South Africa. In: D.A. Davidson, and M.L. Shackley, editors. Geoarchaeology. London: Duckworth. p 289-316.

Teske, P.R., Papadopoulos, I., McQuaid, C.D., Newman, B.K., and Barker, N.P. 2007. Climate change, genetics or human choice: why were the shells of mankind's earliest ornament larger in the Pleistocene than in the Holocene? *PLoS ONE* 2(7):e614. DOI:610.1371/journal.pone.0000614.

Texier, P.J., Porraz, G., Parkington, J., Rigaud, J.P., Poggenpoel, C., Miller, C., Tribolo, C., Cartwright, C., Coudenneau, A., and Klein, R.G. 2010. A

Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter, South Africa. *Proceedings of the National Academy of Sciences* 107(14):6180-6185.

Texier, P.J., Porraz, G., Parkington, J., Rigaud, J.P., Poggenpoel, C., and Tribolo, C. 2013. The context, form and significance of the MSA engraved ostrich eggshell collection from Diepkloof Rock Shelter, Western Cape, South Africa. Journal of Archaeological Science.

Thackeray, A.I. 1981. The Holocene cultural sequence in the Northern Cape Province.: Yale University.

Thackeray, A.I. 2000. Middle Stone Age artefacts from the 1993 and 1995 excavations of Die Kelders Cave 1, South Africa. *Journal of Human Evolution* 38(1):147-168.

Thackeray, A.I., and Kelly, A. 1988. A technical and typological analysis of Middle Stone Age assemblages antecedent to the Howiesons Poort at Klasies River Mouth main site. *South African Archaeological Bulletin* 43:15-26.

Thackeray, J.F. 1979. An analysis of faunal remains from archaeological sites in the southern South West Africa (Namibia). *South African Archaeological Bulletin* 34:18-33.

Thesleff, I. 2000. Genetic basis of tooth development and dental defects. *Acta Odontologica* 58(5):191-194.

Thesleff, I. 2006. The genetic basis of tooth development and dental defects. *American Journal of Medical Genetics* 140(23):2530-2535.

Thom, H.B., editor. 1958. Journal of Jan Van Riebeeck, Volume 1. Amsterdam: Balkema.

Thompson, J.C., and Henshilwood, C.S. 2014. Tortoise taphonomy and tortoise butchery patterns at Blombos Cave, South Africa. *Journal of Archaeological Science* 41:214-229.

Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Henderson, K.A., Brecher, H.H., Zagorodnov, V.S., Mashiotta, T.A., Lin, P.-N., Mikhalenko, V.N., Hardy, D.R., and Beer, J. 2002. Kilimanjaro ice core records: evidence of Holocene climate change in tropical Africa. *Science* 298(5593):589.

Thomsen, S. 1955. Dental morphology and occlusion in the people of Tristan da Cunha. Oslo: Norske Videnskaps Akademi.

Tishkoff, S.A., Gonder, M.K., Henn, B.M., Mortensen, H., Knight, A., Gignoux, C., Fernandopulle, N., Lema, G., Nyambo, T.B., Ramakrishnan, U., Reed, F.A., and Mountain, J.L. 2007. History of click-speaking populations of Africa inferred from mtDNA and Y-chromosome genetic variation. *Molecular Biology and Evolution* 24(10):2180-2195.

Tishkoff, S.A., Reed, F.A., Friedlaender, F.R., Ehret, C., Ranciaro, A., Froment, A., Hirbo, J.B., Awomoyi, A.A., Bodo, J.-M., Doumbo, O., Ibrahim, M., Juma, A.T., Kotze, M.J., Lema, G., Moore, J.H., Mortensen, H., Nyambo, T.B., Omar, S.A., Powell, K., Pretorius, G.S., Smith, M.W., Thera, M.A., Wambebe, C., Weber, J.L., and Williams, S.M. 2009. The genetic structure and history of Africans and African Americans. *Science* 324(5930):1035-1044.

Tobias, P.V. 1967. Olduvai Gorge: the cranium and maxillary dentition of *Australopithecus (Zinjanthropus) boisei.* Cambridge: Cambridge University Press.

Tobias, P.V. 1971. Human skeletal remains from the Cave of Hearths, Makapansgat, northern Transvaal. *American Journal of Physical Anthropology* 34(3):335-367.

Tobias, P.V. 1972. Recent human biological studies in southern Africa, with special reference to Negroes and Khoisans. *Transactions of the Royal Society of South Africa* 40(3):109-133.

Tobias, P.V. 1974. The biology of the southern African Negro. The Bantu-speaking peoples of southern Africa London Routledge. p 3-45.

Tobias, P.V. 1978. The San: an evolutionary perspective. In: P.V. Tobias, editor. The Bushmen. Cape Town: Human and Rousseau. p 16-32.

Tobias, P.V. 1985. History of physical anthropology in southern Africa. *American Journal of Physical Anthropology* 28(S6):1-52.

Tomes, C.S. 1889. A manual of dental anatomy: human and comparative. London: J. & A. Churchill.

Tompkins, R.L. 1996. Human population variability in relative dental development. *American Journal of Physical Anthropology* 99:79-102.

Townsend, G. 1981. Fluctuating asymmetry in the deciduous dentition of Australian Aboriginals. *Journal of dental research* 60(11):1849-1857.

Townsend, G., Bockmann, M., Hughes, T., and Brook, A. 2012. Genetic, environmental and epigenetic influences on variation in human tooth number, size and shape. *Odontology* 100:1-9.

Townsend, G., and Brown, T. 1978. Heritability of permanent tooth size. *American Journal of Physical Anthropology* 49(4):497-504.

Townsend, G., and Brown, T. 1980. Dental asymmetry in Australian aboriginals. *Human biology*:661-673.

Townsend, G., and Brown, T. 1981a. The Carabelli trait in Australian aboriginal dentition. *Archives of Oral Biology* 26(10):809-814.

Townsend, G., and Brown, T. 1981b. Morphogenetic fields within the dentition. *Australian Orthodontic Journal* 7:3-12.

Townsend, G., Hughes, T., Luciano, M., Bockmann, M., and Brook, A. 2009. Genetic and environmental influences on human dental variation: a critical evaluation of studies involving twins. *Archives of Oral Biology* 54 Suppl 1:S45-51.

Townsend, G., Richards, L., Brown, T., Burgess, V., Travan, G., and Rogers, J. 1992. Genetic studies of dental morphology in south Australian twins. In: P. Smith, and E. Tchernov, editors. Structure, function, and evolution of teeth. London: Freund Publishing House Ltd. p 501-518.

Townsend, G., Richards, L., and Hughes, T. 2003. Molar intercuspal dimensions: genetic input to phenotypic variation. *Journal of dental research* 82(5):350-355.

Townsend, G., Yamada, E., and Smith, P. 1986. The metaconule in Australian Aboriginals: an accessory tubercle on maxillary molar teeth. *Human biology* 58(6):851-862.

Townsend, G., Yamada, H., and Smith, P. 1990. Expression of the entoconulid (sixth cusp) on mandibular molar teeth of an Australian Aboriginal population. *American Journal of Physical Anthropology* 82(3):267-274.

Traill, A. 1995. The Khoisan languages of South Africa. In: R. Mesthrie, editor. Language and social history Studies in South African sociolinguistics. Cape Town: David Philip. p 1-18.

Tribolo, C., Mercier, N., Valladas, H., Joron, J.-L., Guibert, P., Lefrais, Y., Selo, M., Texier, P.-J., Rigaud, J.-P., and Porraz, G. 2009. Thermoluminescence dating of a stillbay–howiesons poort sequence at diepkloof rock shelter (Western Cape, South Africa). *Journal of Archaeological Science* 36(3):730-739.

Trinkaus, E. 1990. Conference report the university of Tokyo 1990 symposium : The evolution and dispersal of modern humans in Asia, November 14-17, 1990. *Bulletins et Mémoires de la Société d'anthropologie de Paris* 2:227-230.

Tsuji, T. 1958. Incidence and inheritance of the Carabelli's cusp in a Japanese population. *Japanese Journal of Human Genetics* 3:21-31.

Tucker, A.S., and Sharpe, P.T. 1999. Molecular genetics of tooth morphogenesis and patterning: the right tooth in the right place. *Journal of dental research* 78(4):826-834.

Turner, C.G.I. 1967. Dental genetics and microevolution in prehistoric and living Koniag Eskimo. *Journal of dental research* 46 (suppl.):911-917.

Turner, C.G.I. 1969. Microevolutionary interpretations from the dentition. *American Journal of Physical Anthropology* 30:421-426.

Turner, C.G.I. 1971. Three-rooted mandibular first permanent molars and the question of American Indian origins. *American Journal of Physical Anthropology* 34(2):229-241.

Turner, C.G.I. 1983. Dental evidence for the peopling of the Americas. In: R. Shutler, editor. Early Man in the New World. California: Sage Publications. p 147-157.

Turner, C.G.I. 1984. Advances in the dental search for Native American origins. *Acta anthropogenetica* 8(1-2):23.

Turner, C.G.I. 1985a. Dental evidence for the peopling of the Americas. *National Geographic Society Research Reports* 19:573-596.

Turner, C.G.I., editor. 1985b. The dental search for Native American origins. Canberra: Journal of Pacific History. Australian National University.

Turner, C.G.I. 1986a. Dentochronological separation estimates for pacific rim populations. *Science* 232(4754):1140.

Turner, C.G.I. 1986b. The first Americans: the dental evidence. *National Geographic Research* 2:37-46.

Turner, C.G.I. 1987. Late Pleistocene and Holocene population history of east Asia based on dental variation. *American Journal of Physical Anthropology* 73(3):305-321.

Turner, C.G.I. 1989. Teeth and prehistory in Asia. *Scientific American* 260(2):88-96.

Turner, C.G.I. 1990. Major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history, and late

Pleistocene relationships with Australian aboriginals. *American Journal of Physical Anthropology* 82(3):295-317.

Turner, C.G.I. 1992a. The dental bridge between Australia and Asia: following Macintosh into the East Asian hearth of humanity. *Archaeology in Oceania* 27:143-152.

Turner, C.G.I. 1992b. Microevolution of East Asian and European populations: a dental perspective. In: T. Akazawa, K. Aoki, and T. Kimura, editors. The evolution and dispersal of modern humans in Asia. Tokyo: Hokusen-Sha Publishing. p 415-438.

Turner, C.G.I., and Nichol, C.R. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University dental anthropology system. In: M.A. Kelley, and C.S. Larsen, editors. Advances in dental anthropology. New York: Wiley-Liss. p 13-31.

Tusenius, M.L. 1989. Charcoal analytical studies in the north-eastern Cape, South Africa. *South African Archaeological Society Goodwin Series* 6:77-83.

Van Andel, T.H. 1989. Late Pleistocene sea levels and the human exploitation of the shore and shelf of southern South Africa. *Journal of Field Archaeology* 16(2):133-155.

Van Reenen, J.F. 1964. Dentition, jaws and palate of the Kalahari Bushman. *Journal of the Dental Association of South Africa* 8(19):1-37.

Van Reenen, J.F. 1966. Dental features of a low-caries primitive population. *Journal of dental research* 45(3):703-713.

Van Reenen, J.F. 1970. Sexual dimorphism in tooth size in Bushmen. *The Journal of the Dental Association of South Africa* 25(10):376-381.

Van Reenen, J.F. 1982. The effects of attrition on tooth dimensions of San (Bushmen). In: B. Kurtén, editor. Teeth: form, function and evolution. New York: Columbia University Press. p 182-203.

Van Riet Lowe, C. 1936. The Smithfield 'N' culture. *Transactions of the Royal Society of South Africa* 23:367-372.

Van Riet Lowe, C. 1946. The coastal Smithfield and bipolar technique. *South African Journal of Science* 42:240-246.

Van Riet Lowe, C. 1954. An artefact recovered with the Boskop calvaria. *South African Archaeological Bulletin* 9:135-137.

Vedder, H. 1928. The Nama. In: C.H.L. Hahn, H. Vedder, and L. Fourie, editors. The native tribes of South West Africa. London: Cass & Co. p 109-152.

Villa, P., Soriano, S., Tsanova, T., Degano, I., Higham, T.F.G., d'Errico, F., Backwell, L., Lucejko, J.J., Colombini, M.P., and Beaumont, P.B. 2012. Border Cave and the beginning of the Later Stone Age in South Africa. *Proceedings of the National Academy of Sciences* 109(33):13208-13213.

Vogelsang, R., Richter, J., Jacobs, Z., Eichhorn, B., Linseele, V., and Roberts, R. 2010. New excavations of Middle Stone Age deposits at Apollo 11 rockshelter, Namibia: stratigraphy, archaeology, chronology and past environments. *Journal of African Archaeology* 8(2):185-218.

Voigt, E.A. 1973. Stone Age molluscan utilization at Klasies River Mouth caves. *South African Journal of Science* 69:306-309.

Voigt, E.A. 1975. Studies of marine mollusca from archaeological sites: dietary preferences, environmental reconstructions and ethnological parallels. In: A. Clason, editor. Archaeozoological studies. Amsterdam: North Holland. p 87-98.

Voigt, E.A. 1982. The molluscan fauna. In: R. Singer, and J. Wymer, editors. The Middle Stone Age at Klasies River Mouth in South Africa. Chicago: University of Chicago Press. p 155-186.

Volman, T.P. 1978. Early evidence for shellfish collecting. *Science* 201:911-913.

Volman, T.P. 1984. Early prehistory of southern Africa. In: R.G. Klein, editor. Southern African prehistory and paleoenvironments. Rotterdam: A.A. Balkema.

Von Carabelli, G. 1842. Anatomie des Mundes. Wien: Braumüller und Seidel.

Von den Driesch, A. 2004. The Middle Stone Age fish fauna from the Klasies River Mouth main site, South Africa. *Anthropozoologica* 39(2):33-59.

Von Luschan, F. 1907. The racial affinities of the Hottentots. London: British South African Association.

Vossen, R. 2013. Khoesan Languages. London: Routledge.

Wadley, L. 1986. A social and ecological interpretation of the Later Stone Age in the southern Transvaal. Johannesburg: University of the Witwatersrand.

Wadley, L. 1987. Later Stone Age hunters of the southern Transvaal: social and ecological interpretation. Oxford: Archaeopress.

Wadley, L. 1989. Legacies from the Later Stone Age. *South African Archaeological Society Goodwin Series* 6:42-53.

Wadley, L. 1992. Reply to Barham: aggregation and dispersal phase sites in the Later Stone Age. *The South African Archaeological Bulletin* 47(155):52-55.

Wadley, L. 1993. The Pleistocene Later Stone Age South of the Limpopo River. *Journal of World Prehistory* 7(3):243-296.

Wadley, L. 1996. The Robberg Industry of Rose Cottage Cave, eastern Free State: the technology, spatial patterns and environment. *The South African Archaeological Bulletin* 51(164):64-74.

Wadley, L. 1997. Rose Cottage Cave: archaeological work 1987 to 1997. *South African Journal of Science* 93(10):439.

Wadley, L. 2000a. The Early Holocene layers of Rose Cottage Cave, eastern Free State: technology, spatial patterns and environment. *The South African Archaeological Bulletin* 55(171):18-31.

Wadley, L. 2000b. The Wilton and pre-ceramic post-Classic Wilton Industries at Rose Cottage Cave and their context in the South African sequence. *The South African Archaeological Bulletin* 55(172):90-106.

Wadley, L. 2004. Late Middle Stone Age spatial patterns in Rose Cottage Cave, South Africa. In: N.J. Conard, editor. Settlement dynamics of the Middle Paleolithic and Middle Stone Age. Tübingen: Kerns Verlag. p 23-36.

Wadley, L. 2005. Putting ochre to the test: replication studies of adhesives that may have been used for hafting tools in the Middle Stone Age. *Journal of Human Evolution* 49(5):587-601.

Wadley, L. 2007. Announcing a Still Bay industry at Sibudu Cave, South Africa. *Journal of Human Evolution* 52(6):681-689.

Wadley, L. 2008. The Howieson's Poort industry of Sibudu Cave. *South African Archaeological Society Goodwin Series* 10:122-132.

Wadley, L., Hodgskiss, T., and Grant, M. 2009. Implications for complex cognition from the hafting of tools with compound adhesives in the Middle Stone Age, South Africa. *Proceedings of the National Academy of Sciences* 106(24):9590-9594.

Wadley, L., and McNabb, J. 2009. Introduction. In: J. McNabb, and A. Sinclair, editors. The Cave of Hearths: Makapan Middle Pleistocene research project field research by Anthony Sinclair and Patrick Quinney, 1996-2001. Oxford: British Archaeological Review International Series 1940. p 1-11.

Wadley, L., Sievers, C., Bamford, M., Goldberg, P., Berna, F., and Miller, C. 2011. Middle Stone Age bedding construction and settlement patterns at Sibudu, South Africa. *Science* 334(6061):1388-1391.

Walimbe, S.R. 2009. Dental Evolution in Protohistoric Indians. In: A.R. Sankhyan, editor. Asian perspectives on human evolution. New Delhi: Serials Publications. p 215-234.

Walker, N.J. 1983. The significance of an early date for pottery and sheep in Zimbabwe. *South African Archaeological Bulletin* 38(88-92).

Warren, K. 2013. Population variation within the Iron Age of southern Africa. An assessment using dental anthropological and cranio-mandibular metric techniques. Unpublished MSc thesis: University of Cape Town.

Webley, L. 2002. The re-excavation of Spoegrivier Cave on the west coast of South Africa. *Annals of the Eastern Cape Museums* 2:19-49.

Weidenreich, F. 1943. The dentition of *Sinanthropus pekinensis*: a comparative odontography of the hominids. *Palaeontologica Sinica* 1:1-180.

Wells, L.H. 1950. Fossil man in Northern Rhodesia. In: J.D. Clark, editor. The Stone Age cultures of northern Rhodesia. Cape Town: South African Archaeological Society. p 143-150.

Wells, L.H. 1957. Late Stone Age human types in Central Africa. Proceedings of the third pan-African congress on prehistory. London: Chatto & Windus. p 183-185.

Westphal, E.O.J. 1963. The linguistic prehistory of southern Africa: Bush, Kwadi, Hottentot, and Bantu linguistic relationships. *Africa: Journal of the International African Institute* 33:237-264.

Will, M., Parkington, J., Kandel, A., and Conard, N.J. 2013. Coastal adaptations and the Middle Stone Age lithic assemblages from Hoedjiespunt 1 in the Western Cape, South Africa. *Journal of Human Evolution*.

Williams, R.C., Steinberg, A.G., Gershowitz, H., Bennett, P.H., Knowler, W.C., Pettitt, D.J., Butler, W., Baird, R., Dowda-Rea, L., and Burch, T.A. 1985. GM allotypes in Native Americans: evidence for three distinct migrations across the Bering land bridge. *American Journal of Physical Anthropology* 66(1):1-19.

Williamson, B.S. 1997. Down the microscope and beyond: microscopy and molecular studies of stone tool residues and bone samples from Rose Cottage Cave. *South African Journal of Science* 93:458-464.

Wilmsen, E.N. 1989. Land filled with flies: political economy of the Kalahari Desert. Chicago: University of Chicago Press.

Wilmsen, E.N., and Denbow, J.R. 1990. Paradigmatic history of San-speaking peoples and current attempts at revision. *Current Anthropology* 31:489-524.

Wilson, M.L., and Lundy, J.K. 1994. Estimated living statures of dated Khoisan skeletons from the south-western coastal region of South Africa. *The South African Archaeological Bulletin* 49(159):2-8.

Winkler, E.-M. 1984. The systematic rank of the populations of West-Kenya. *Homo* 35:73-109.

Wood, B.A., and Abbott, S.A. 1983. Analysis of the dental morphology of Plio-pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. *Journal of Anatomy* 136:197-219.

Wood, B.A., Abbott, S.A., and Graham, S.H. 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. II. Mandibular molars--study of cusp areas, fissure pattern and cross sectional shape of the crown. *Journal of Anatomy* 137:287-314.

Wood, B.A., Abbott, S.A., and Uytterschaut, H. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine root morphology. *Journal of Anatomy* 156:107-139.

Wood, B.A., and Engleman, C.A. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. *Journal of Anatomy* 161:1-35.

Wood, B.A., and Uytterschaut, H. 1987. Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns. *Journal of Anatomy* 154:121-156.

Wright, D.K. 2005. New perspectives on early regional interaction networks of East African trade: A view from Tsavo National Park, Kenya. *African Archaeological Review* 22(3):111-140.

Wurz, S. 1999. The Howiesons Poort backed artefacts from Klasies River Mouth: an argument for symbolic behaviour. *The South African Archaeological Bulletin*:38-50.

Wurz, S. 2002. Variability in the Middle Stone Age lithic sequence, 115,000-60,000 years ago at Klasies River Mouth, South Africa. *Journal of Archaeological Science* 29:1001-1015.

Yamada, E. 1932. The anthropological study of the Japanese teeth. *Journal of the Nippon Dental Association* 25:15-46.

Yates, R., Manhire, A., and Parkington, J. 1994. Rock painting and history in the south-western Cape. In: T.A. Dowson, and D. Lewis-Williams, editors. Contested images: diversity in southern African rock art research. Johannesburg: Wits University Press. p 29-60.

Yoshida, H. 1996. Quaternary dating studies using ESR signals:with emphasis on shell, coral, tooth enamel and quartz. Ph.D. Dissertation. Canberra: Australian National University.

Zubov, A.A. 1998. Comparative taxonomic analysis of the dental morphology of some ethnic groups belonging to the Ugric linguistic branch if the Finno-Ugric languages. *Acta Ethnographica Hungarica* 43:299-303.

Zubov, A.A., and Khaldeeva, N.I. 1979. Ethnic odontology of the USSR. Moscow: Nauka.

APPENDICES

1. REPEATABILITY OF INDIVIDUAL MEASUREMENTS

LM3 MDCD	0.997482
LM2 MDCD	0.997874
LM1 MDCD	0.997855
LP4 MDCD	0.969630
LP3 MDCD	0.965463
LC1 MDCD	0.994327
LI2 MDCD	**0.867042**
LI1 MDCD	0.954316
LM^3 MDCD	0.952390
LM^2 MDCD	0.996055
LM^1 MDCD	0.993440
LP^4 MDCD	0.987097
LP^3 MDCD	0.923916
LC^1 MDCD	0.991455
LI^2 MDCD	0.994957
LI^1 MDCD	0.994547
LM3 BLCD	0.996289
LM2 BLCD	0.995005
LM1 BLCD	0.996700
LP4 BLCD	0.997110
LP3 BLCD	0.995808
LC1 BLCD	0.996370
LI2 BLCD	0.992988
LI1 BLCD	0.992715
LM^3 BLCD	0.996342
LM^2 BLCD	0.966655
LM^1 BLCD	0.993916
LP^4 BLCD	0.997263
LP^3 BLCD	0.997741
LC^1 BLCD	0.996526
LI^2 BLCD	0.994747
LI^1 BLCD	0.991982
LM3 MDcrD	0.997865
LM2 MDcrD	0.996454
LM1 MDcrD	0.979461
LP4 MDcrD	0.943136

Repeatability of individual measurements cont...

LP3 MDcrD	0.993616
LC1 MDcrD	0.995460
LI2 MDcrD	0.988372
LI1 MDcrD	0.993774
LM^3 MDcrD	0.997622
LM^2 MDcrD	0.992584
LM^1 MDcrD	0.996157
LP^4 MDcrD	0.971766
LP^3 MDcrD	0.993091
LC^1 MDcrD	0.994196
LI^2 MDcrD	0.996229
LI^1 MDcrD	0.993576
LM3 BLcrD	0.995565
LM2 BLcrD	0.992092
LM1 BLcrD	0.991588
LP4 BLcrD	0.992606
LP3 BLcrD	0.993243
LC1 BLcrD	0.995071
LI2 BLcrD	0.989286
LI1 BLcrD	0.987053
LM^3 BLcrD	0.995296
LM^2 BLcrD	0.995744
LM^1 BLcrD	0.993981
LP^4 BLcrD	**0.803671**
LP^3 BLcrD	0.994822
LC^1 BLcrD	0.994154
LI^2 BLcrD	0.995625
LI^1 BLcrD	0.995161
LM3 MLDBcrD	0.997074
LM2 MLDBcrD	0.993569
LM1 MLDBcrD	0.990529
LM^3 MLDBcrD	0.993948
LM^2 MLDBcrD	0.992806
LM^1 MLDBcrD	0.989292
LM3 MLDBCD	0.997860
LM2 MLDBCD	0.977028
LM1 MLDBCD	0.993857
LM^3 MLDBCD	0.961528
LM^2 MLDBCD	0.996542
LM^1 MLDBCD	0.995940
LM3 MBDLcrD	0.995458

Repeatability of individual measurements cont…

LM2 MBDLcrD	0.993708
LM1 MBDLcrD	0.989293
LM^3 MBDLcrD	0.996670
LM^2 MBDLcrD	0.993611
LM^1 MBDLcrD	0.990826
LM3 MBDLCD	0.997958
LM2 MBDLCD	0.997086
LM1 MBDLCD	0.995650
LM^3 MBDLCD	0.997123
LM^2 MBDLCD	0.997609
LM^1 MBDLCD	0.996815

	Mesiodistal crown vs. mesiodistal cervix			
	Slope	**Intercept**	**r**	**p-value**
LI_1	2.115	0.848	0.493	0.010
LI_2	1.526	0.379	0.582	0.000
LC_1	1.252	0.551	0.627	0.000
LP_3	2.665	0.302	0.421	0.000
LP_4	1.508	0.506	0.531	0.000
LM_1	5.163	0.340	0.435	0.000
LM_2	3.351	0.509	0.519	0.000
LM_3	1.042	0.696	0.763	0.000
LI^1	1.071	0.544	0.689	0.000
LI^2	1.836	0.428	0.731	0.000
LC^1	1.752	0.473	0.540	0.000
LP^3	3.840	0.614	0.494	0.000
LP^4	3.328	0.236	0.162	0.190
LM^1	3.421	0.413	0.493	0.000
LM^2	2.788	0.484	0.555	0.000
LM^3	1.170	0.626	0.741	0.000

	Buccolingual crown vs. Buccolingual cervix			
	Slope	**Intercept**	**r**	**p-value**
LI_1	-0.482	1.001	0.820	0.000
LI_2	0.000	0.929	0.852	0.000
LC_1	-0.350	0.991	0.848	0.000
LP_3	0.858	0.726	0.699	0.000
LP_4	0.013	0.830	0.732	0.000
LM_1	1.129	0.696	0.684	0.000
LM_2	1.036	0.706	0.630	0.000
LM_3	1.454	0.656	0.694	0.000
LI^1	2.009	0.561	0.672	0.000
LI^2	0.444	0.817	0.833	0.000
LC^1	-0.158	0.902	0.806	0.000
LP^3	-0.037	0.863	0.794	0.000
LP^4	-0.304	0.889	0.816	0.000
LM^1	2.746	0.643	0.668	0.000
LM^2	1.445	0.750	0.716	0.000
LM^3	2.690	0.612	0.658	0.000

Cervical and crown measurement correlations cont...

	Mesiolingual-distobuccal crown vs. Mesiolingual- distobuccal cervix			
	Slope	**Intercept**	**r**	**p-value**
LM_1	2.163	0.662	0.607	0.000
LM_2	-0.420	0.886	0.756	0.000
LM_3	-0.371	0.879	0.847	0.000
LM^1	-0.327	0.907	0.787	0.000
LM^2	-0.030	0.890	0.817	0.000
LM^3	-0.704	0.952	0.863	0.000

	Mesiobuccal-distolingual crown vs. Mesiobuccal-distolingual cervix			
	Slope	**Intercept**	**r**	**p-value**
LM_1	0.249	0.838	0.703	0.000
LM_2	5.617	0.599	0.708	0.000
LM_3	3.598	0.799	0.810	0.000
LM^1	0.089	0.866	0.716	0.000
LM^2	0.541	0.838	0.785	0.000
LM^3	0.664	0.826	0.853	0.000

3. DENTAL TRAIT FREQUENCIES FOR KHOESAN SAMPLES RELATIVE TO GEOGRAPHIC REGIONS A, B, C, D, E, F, G, INLAND AND COASTAL.

	Region A		**Region B**		**Region C**		**Region D**		**Region E**		**Region F**		**Region G**	
TRAITS	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**
SHOVELING I^1 (ASU score 2-6)	19	21.05	3	100.00	24	20.00	26	20.00	12	30.00	1	0.00	1	0.00
WINGING I^1 (ASU score 1)	32	12.50	6	40.00	47	19.15	35	23.33	21	11.76	3	0.00	2	50.00
DOUBLE SHOVEL I^1 (ASU score 2-6)	28	0.00	6	16.67	45	0.00	40	2.70	17	0.00	3	0.00	2	0.00
LAB CONVEX I^1 (ASU score 2-4)	26	16.00	6	33.33	41	39.02	38	26.32	14	42.86	2	100.00	2	0.00
INT. GROOVE I^2	17	18.75	7	57.14	44	36.36	39	33.33	14	75.00	5	20.00	3	100.00
PEG INCISOR I^2	47	31.91	7	0.00	47	8.51	49	16.33	18	16.67	5	20.00	3	0.00
TD I^2 (ASU score 2-6)	21	61.90	5	40.00	26	42.31	21	33.33	8	75.00	2	100.00	2	100.00
CMR C^1 (ASU score 1-3)	18	38.89	3	66.67	31	72.73	43	60.47	10	100.00	2	50.00	3	100.00
CAN. ACC. RIDGE C^1 (ASU score 2-5)	21	4.76	2	50.00	20	10.00	28	10.00	6	0.00	2	0.00	2	0.00
CAN. ROOT C_1	62	4.84	18	0.00	85	1.18	92	0.00	28	0.00	13	7.69	10	0.00
PM ACC. CUSPS P^3	21	5.26	5	0.00	32	21.88	33	10.00	9	11.11	5	0.00	1	0.00
TRI PM P^3	47	0.00	9	0.00	51	0.00	55	0.00	23	0.00	7	0.00	5	0.00
DS RIDGE P^3	24	0.00	5	0.00	27	0.00	34	0.00	9	0.00	4	0.00	1	0.00
PM ROOT P^3 (ASU score 2+)	53	43.40	12	25.00	56	19.64	78	28.21	30	41.38	12	81.82	7	60.00
ODONTOME P^3, P^4, P_3, P_4	57	10.53	10	0.00	62	1.79	60	0.00	24	0.00	10	0.00	6	0.00
PM CUSP VAR. P_4 (ASU score 2-9)	22	40.91	5	40.00	42	47.62	39	58.97	7	71.43	5	66.67	5	60.00
TOME'S P_3 (ASU score 2-5)	19	36.84	8	42.86	34	20.59	32	21.88	19	18.18	6	33.33	4	25.00
ANT. FOVEA M_1 (ASU score 2-4)	23	39.13	4	0.00	31	25.93	29	41.67	8	42.86	2	0.00	0	*
DTC M_1	18	0.00	3	0.00	19	0.00	26	0.00	7	0.00	2	0.00	0	*
Y-GROOVE M_2	50	70.00	11	90.91	69	75.00	69	73.91	27	74.07	12	72.73	9	88.89
Y-GROOVE M_1	37	84.38	9	100.00	57	98.18	68	88.00	22	81.82	8	87.50	6	66.67
X-GROOVE M_2	58	31.03	11	9.09	69	17.39	69	16.92	27	15.79	12	33.33	9	14.29
X-GROOVE M_1	41	30.00	9	11.11	57	3.51	68	13.24	22	36.84	8	12.50	6	50.00

Dental trait frequencies by region cont...

CUSP # M_2 (P = 5+; A = 4-)	36	84.38	10	80.00	61	81.67	63	83.87	18	94.44	11	88.89	5	66.67
CUSP # M_1 (P = 5+; A = 4-)	30	96.67	6	100.00	51	100.00	62	98.39	19	100.00	5	100.00	4	100.00
CUSP 5 M_1	31	96.77	7	100.00	50	100.00	58	98.28	21	100.00	5	100.00	4	100.00
CUSP 5 M_2	35	84.38	10	80.00	60	85.45	60	86.44	20	95.00	12	83.33	5	66.67
CUSP 6 M_1	33	27.27	6	40.00	50	6.25	58	22.41	19	22.22	5	25.00	4	25.00
CUSP 6 M_2	42	38.10	10	20.00	60	21.43	60	16.67	17	40.00	11	11.11	5	0.00
CUSP 7 M_1	45	17.78	12	0.00	67	22.58	67	17.91	29	10.34	9	44.44	6	20.00
CUSP 7 M_2	54	20.37	12	0.00	69	14.49	63	12.70	25	4.55	11	40.00	7	0.00
DEF. WRINKLE M_1 (ASU score 2-3)	26	19.23	5	20.00	38	15.79	34	17.65	9	42.86	2	100.00	0	*
PROTOSTYLID M_1 (ASU score 1-6)	34	2.94	9	11.11	73	4.17	76	14.52	27	14.81	13	0.00	5	25.00
LM ROOT # M_1 (ASU score ≥3)	62	0.00	17	0.00	90	0.00	106	0.00	37	0.00	13	0.00	10	0.00
LM ROOT # M_2 (ASU score ≥2)	66	93.94	17	92.31	80	96.25	87	93.10	32	93.75	13	100.00	10	90.00
TM ANGLE M_3 (P = any degree)	44	18.60	11	0.00	61	17.54	42	30.95	21	14.29	8	28.57	8	0.00
UM PEG M^3	55	23.64	10	30.00	52	26.92	52	28.85	16	6.67	9	37.50	6	0.00
ENAM. EXT. M^1	58	20.69	16	14.29	71	12.68	79	21.52	32	43.33	13	23.08	9	11.11
UM ROOT # M^2 (ASU score ≥3)	77	100.00	16	87.50	69	89.86	81	92.59	34	97.06	13	100.00	10	100.00
METACONE M^3	62	100.00	11	100.00	52	100.00	56	100.00	16	100.00	8	100.00	6	100.00
SMALL METACONE M^3 (P = 3-; A = 3.5+)	67	67.16	11	54.55	52	33.33	56	25.00	16	37.50	8	37.50	6	20.00
HYPOCONE M^2	48	100.00	8	100.00	57	100.00	68	100.00	27	100.00	13	100.00	7	100.00
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	48	89.58	8	87.50	57	89.47	68	98.51	27	100.00	13	90.91	7	100.00
METACONULE M^1	41	70.73	6	100.00	40	48.72	52	46.15	17	68.75	8	25.00	4	50.00
LARGE METACONULE M^1 (P = 4+; A = 4-)	33	15.15	6	16.67	40	10.00	52	3.92	17	25.00	8	0.00	4	0.00
CARABELLI'S M^1 (ASU score 2-7)	33	30.30	6	40.00	48	23.40	55	30.77	25	24.00	9	12.50	4	0.00
PARASTYLE M^3 (ASU score 1-5)	56	19.64	9	11.11	51	3.92	54	3.70	16	0.00	8	0.00	6	0.00
MIDLINE DIASTEMA	90	45.56	11	18.18	70	25.71	72	22.22	27	7.41	7	14.29	5	0.00
CONGENITAL ABSENCE M^3 (P = 1)	64	7.81	14	0.00	81	2.47	86	4.65	32	0.00	12	0.00	7	0.00
PALATINE TORUS	57	38.60	15	73.33	83	66.27	106	53.77	41	53.66	12	33.33	8	87.50
MANDIBULAR TORUS	56	26.79	14	28.57	95	31.58	122	26.23	36	30.56	12	33.33	10	10.00
ROCKER JAW	32	0.00	12	66.67	85	34.12	102	38.24	31	45.16	10	30.00	9	44.44

Dental trait frequencies by region cont...

	Inland (Regions A & G)		Coastal (Regions B-F)		All regions	
TRAITS	**N**	**Present %**	**N**	**Present %**	**N**	**Present %**
SHOVELING I^1 (ASU score 2-6)	21	19.05	64	21.88	83	20.99
WINGING I^1 (ASU score 1)	38	17.14	103	19.42	140	18.84
DOUBLE SHOVEL I^1 (ASU score 2-6)	30	0.00	108	0.98	138	0.76
LAB CONVEX I^1 (ASU score 2-4)	30	14.81	100	35.00	127	30.71
INT. GROOVE I^2	35	59.38	106	40.38	141	44.85
PEG INCISOR I^2	37	5.56	123	12.20	160	10.63
TD I^2 (ASU score 2-6)	21	61.90	61	39.34	82	45.12
CMR C^1 (ASU score 1-3)	24	54.17	84	67.11	108	61.46
CAN. ACC. RIDGE C^1 (ASU score 2-5)	23	5.88	51	10.00	73	8.22
CAN. ROOT C_1	69	0.00	235	0.43	300	0.33
PM ACC. CUSPS P^3	25	12.00	81	13.58	106	13.21
TRI PM P^3	52	0.00	145	0.00	194	0.00
DS RIDGE P^3	25	0.00	77	0.00	102	0.00
PM ROOT P^3 (ASU score 2+)	59	44.07	186	30.65	245	33.88
ODONTOME P^3, P^4, P_3, P_4	57	0.00	155	0.66	209	0.48
PM CUSP VAR. P_4 (ASU score 2-9)	28	48.00	94	53.19	122	51.64
TOME'S P_3 (ASU score 2-5)	21	23.81	91	23.08	112	23.21
ANT. FOVEA M_1 (ASU score 2-4)	21	45.00	71	30.77	92	34.12
DTC M_1	18	0.00	57	0.00	74	0.00
Y-GROOVE M_2	59	70.91	188	72.87	243	72.43
Y-GROOVE M_1	46	82.61	159	91.10	205	88.65
X-GROOVE M_2	59	22.03	188	16.49	243	17.60
X-GROOVE M_1	46	17.95	159	11.95	205	12.68
CUSP # M_2 (P = 5+; A = 4-)	43	83.72	163	83.77	206	83.33
CUSP # M_1 (P = 5+; A = 4-)	33	96.55	141	99.29	174	98.77
CUSP 5 M_1	33	96.77	135	99.26	168	98.77
CUSP 5 M_2	44	84.09	162	86.09	206	84.82

Dental trait frequencies by region cont...

CUSP 6 M_1	32	9.68	134	17.16	166	15.66
CUSP 6 M_2	43	23.68	158	19.73	201	20.54
CUSP 7 M_1	53	22.64	179	16.76	232	18.10
CUSP 7 M_2	55	9.09	180	12.78	234	11.54
DEF. WRINKLE M_1 (ASU score 2-3)	23	30.43	87	17.24	110	20.00
PROTOSTYLID M_1 (ASU score 1-6)	39	5.26	193	7.77	231	7.36
LM ROOT # M_1 (ASU score ≥3)	72	0.00	261	0.00	333	0.00
LM ROOT # M_2 (ASU score ≥2)	64	93.75	228	94.30	290	93.79
TM ANGLE M_3 (P = any degree)	51	15.69	138	18.80	185	17.93
UM PEG M^3	57	22.81	138	25.36	194	22.83
ENAM. EXT. M^1	68	18.75	206	18.63	274	18.66
UM ROOT # M^2 (ASU score ≥3)	77	100.00	213	92.02	290	94.14
METACONE M^3	54	100.00	139	100.00	191	100.00
SMALL METACONE M^3 (P = 3-; A = 3.5+)	54	50.00	139	30.23	191	36.07
HYPOCONE M^2	61	100.00	169	100.00	229	100.00
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	61	91.80	169	94.05	229	93.45
METACONULE M^1	34	58.06	122	50.00	156	51.68
LARGE METACONULE M^1 (P = 4+; A = 4-)	34	5.88	122	7.38	156	7.05
CARABELLI'S M^1 (ASU score 2-7)	39	30.77	140	25.36	179	25.42
PARASTYLE M^3 (ASU score 1-5)	52	2.13	133	3.01	180	2.78
MIDLINE DIASTEMA	65	16.92	187	20.86	252	19.84
CONGENITAL ABSENCE M^3 (P = 1)	71	7.04	225	2.67	296	3.72
PALATINE TORUS	84	57.14	257	57.98	341	57.77
MANDIBULAR TORUS	73	31.51	279	29.03	352	29.55
ROCKER JAW	56	33.93	240	38.75	296	37.84

*no evaluation possible

Bracketed P = Present; A = Absent

4. CHI-SQUARE P-VALUES OF ANALYSES BETWEEN KHOESAN REGIONAL DATA AND BETWEEN THE KHOESAN AND MID-LATE PLEISTOCENE SAMPLES.

Appendix 4.1: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region A and other regions B-G (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION A (all time)	KS - B	KS -C	KS -D	KS-E	KS-F	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
TRAITS										
SHOVELING I^1 (ASU score 2-6)	0.0393	0.4531	0.6846	0.2111	0.1863	0.1863	0.4935	0.3190	0.3358	
WINGING I^1 (ASU score 1)	0.0002	0.0105	0.0075	0.0751	0.7655	0.0570	0.0332	0.0106	0.0138	
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.0283		0.3807					0.5989	0.6441	
LAB CONVEX I^1 (ASU score 2-4)	0.3345	0.0216	0.0958	0.0183	0.4259	0.3089	0.4961	0.0295	0.0574	
INT. GROOVE I^2	0.0656	0.1366	0.1075	0.0007	0.6371	0.0356	0.0034	0.0491	0.0210	
PEG INCISOR I^2	0.0786	0.0019	0.0659	0.0273	0.2167	0.3682	0.0032	0.0005	0.0001	
TD I^2 (ASU score 2-6)	0.6370	0.1815	0.0638	0.0354	0.7611	0.2416	0.2747	0.0731	0.1697	
CMR C^1 (ASU score 1-3)	0.5570	0.0093	0.0379	0.0015	0.7546	0.1810	0.3266	0.0066	0.0201	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.2416	0.3414	0.4742	0.5860	0.1339	0.1339	0.3563	0.3528	0.3521	
CAN. ROOT C_1	0.3551	0.4050	0.3310	0.2727	0.6772	0.4774	0.0645	0.0790	0.1200	
PM ACC. CUSPS P^3		0.0214	0.1352	0.1203	0.6003	0.0341	0.1006	0.0738	0.0775	
TRI PM P^3										
DS RIDGE P^3										
PM ROOT P^3 (ASU score 2+)	0.1654	0.0011	0.0180	0.0059	0.0000	0.0075	0.0010	0.0036	0.0073	
ODONTOME P^3, P^4, P_3, P_4		0.9600					0.6139	0.5400	0.6111	
PM CUSP VAR. P_4 (ASU score 2-9)	0.6269	0.2605	0.1749	0.1593	0.6269	0.2479	0.2883	0.2996	0.3542	
TOME'S P_3 (ASU score 2-5)	0.2783	0.1712	0.1321	0.0564	0.4232	0.7057	0.2832	0.0820	0.0837	0.9097
ANT. FOVEA M_1 (ASU score 2-4)	0.4872	0.0615	0.0113	0.0269	0.7920		0.0083	0.0321	0.0204	
DTC M_1										
Y-GROOVE M_2	0.0245	0.0012	0.0361	0.0306	0.0860	0.0393	0.0619	0.0011	0.0021	0.1224
Y-GROOVE M_1	0.1951	0.0143	0.5729	0.0842	0.7926	0.0581	0.6291	0.1928	0.4085	
X-GROOVE M_2	0.1352	0.0280	0.0657	0.1953	0.0406	0.3574	0.2700	0.0134	0.0227	0.6060
X-GROOVE M_1	0.0586	0.0003	0.0067	0.0264	0.3093	0.0214	0.2102	0.0001	0.0004	
CUSP # M_2 (P = 5+; A = 4-)	0.5804	0.6314	0.5559	0.2929	0.6808	0.1956	0.8429	0.7079	0.7471	0.3231
CUSP # M_1 (P = 5+; A = 4-)	0.4829	0.0469	0.1516	0.2162	0.6154	0.2284	0.8045	0.0138	0.0691	

Appendix 4.1 cont...

CUSP 5 M_1	0.7459	0.4985	0.4098	0.1455	0.9330	0.1956	0.9732	0.3638	0.4741	0.7644
CUSP 5 M_2	0.4665	0.0661	0.1994	0.2221	0.5809	0.2187	0.8649	**0.0218**	0.0960	
CUSP 6 M_1	0.1613	0.0707	**0.0088**	**0.0103**	0.1191	0.4793	0.0841	**0.0137**	**0.0159**	0.9812
CUSP 6 M_2	0.1430	**0.0070**	**0.0202**	0.2662	0.7307	0.5595	0.0715	**0.0168**	**0.0113**	
CUSP 7 M_1	0.0868	0.3899	0.2620	0.0594	**0.0169**	0.1872	0.0515	0.1650	0.0839	0.6752
CUSP 7 M_2	0.1152	0.2017	0.3904	0.2180	**0.0253**	0.3590	0.5516	0.6604	0.6269	
DEF. WRINKLE M_1 (ASU score 2-3)	0.0668	**0.0054**	**0.0118**	0.1736	0.0533		**0.0148**	**0.0088**	**0.0022**	
PROTOSTYLID M_1 (ASU score 1-6)	0.3007	0.5763	0.0758	0.0931	0.5320	0.1064	0.6226	0.3102	0.3391	
LM ROOT # M_1 (ASU score >=3)										
LM ROOT # M_2 (ASU score >=2)	0.4180	0.1506	0.5465	0.7617	0.2114	0.6396	0.4266	0.3739	0.3573	0.3918
TM ANGLE M_3 (P = any degree)	0.1261	0.3326	0.1870	0.1509	0.5202	0.1840	0.0845	0.7273	0.4281	0.8959
UM PEG M^3	0.6243	**0.0182**	**0.0328**	0.1453	**0.0172**	0.1794	**0.0407**	**0.0278**	**0.0248**	
ENAM. EXT. M^1	**0.0061**	**0.0191**	**0.0004**	**0.0002**	0.8489	**0.0164**	**0.0069**	**0.0018**	**0.0024**	
UM ROOT # M^2 (ASU score >=3)	**0.0001**	**0.0023**	**0.0075**	0.1191	0.3474	**0.0053**	0.3126	**0.0066**	**0.0182**	
METACONE M^3										
SMALL METACONE M^3 (P = 3-; A = 3.5+)	**0.0004**	**0.0006**	**0.0000**	**0.0160**	**0.0115**	**0.0141**	**0.0002**	**0.0000**	**0.0000**	0.7305
HYPOCONE M^2						**0.0123**	0.3827		0.6621	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.2482	0.4865	**0.0049**	0.1084	0.5666	0.7590	0.2479	**0.0486**	0.0603	
METACONULE M^1	0.4935	**0.0445**	**0.0175**	0.6233	**0.0044**	0.6367	0.2636	**0.0214**	**0.0296**	0.9523
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.2042	0.3001	**0.0203**	0.2702	0.2709	0.2386	0.1019	0.1296	0.0755	0.0772
CARABELLI'S M^1 (ASU score 2-7)	**0.0123**	**0.0499**	**0.0066**	**0.0365**	0.0585	0.2726	**0.0217**	**0.0150**	**0.0141**	0.6465
PARASTYLE M^3 (ASU score 1-5)	0.2313	**0.0026**	**0.0096**	0.0541	0.1684	0.2313	**0.0034**	**0.0000**	**0.0000**	
MIDLINE DIASTEMA	0.0830	**0.0099**	**0.0020**	**0.0003**	0.1078	**0.0453**	**0.0002**	**0.0000**	**0.0000**	
CONGENITAL ABSENCE M^3 (P = 1)	0.6321	0.6464	0.2556	0.7134	0.9913	0.8600	0.7867	0.0581	0.1493	
PALATINE TORUS	**0.0163**	**0.0012**	0.0645	0.1392	0.7324	**0.0092**	**0.0307**	**0.0079**	**0.0071**	
MANDIBULAR TORUS	0.8931	0.5339	0.9377	0.6951	0.6464	0.2539	0.5599	0.7344	0.6730	0.6120
ROCKER JAW	**0.0000**	**0.0001**	**0.0000**	**0.0000**	**0.0013**	**0.0001**	**0.0002**	**0.0000**	**0.0000**	**0.0005**
Total significant comparisons	**10**	**23**	**20**	**15**	**8**	**12**	**14**	**26**	**22**	**1**

Appendix 4.2: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region B and other regions (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION B (all time) TRAITS	KS -C	KS -D	KS-E	KS-F	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)	0.0161	0.0263	0.0400	1.0000	0.5050	0.0190	0.0183	0.0122	
WINGING I^1 (ASU score 1)	0.2648	0.3164	0.0896	0.6733	0.5460	0.1264	0.2106	0.1704	
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.0057	0.0090	0.1052	0.5371	0.5371	0.0233	0.0043	0.0011	
LAB CONVEX I^1 (ASU score 2-4)	0.1333	0.2210	0.1027	0.6084	1.0000	0.2874	0.1647	0.2045	
INT. GROOVE I^2	0.2956	0.2295	0.0614	0.5303	0.5469	0.2142	0.3836	0.5242	
PEG INCISOR I^2	0.4225	0.2482	0.2496	0.2165		0.5231	0.3259	0.3628	
TD I^2 (ASU score 2-6)	0.4284	0.5492	0.2070	0.3865	0.3865	0.4161	0.7417	0.7827	
CMR C^1 (ASU score 1-3)	0.6412	0.6899	0.5060	0.5762	1.0000	0.8070	0.5415	0.6744	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.5074	0.2820	0.5371	0.6650	1.0000	0.3555	0.3408	0.3198	
CAN. ROOT C_1	0.6438			0.2448			0.7815	0.8062	
PM ACC. CUSPS P^3	0.2455	0.4596	0.4392			0.4142	0.3776	0.3847	
TRI PM P^3									
DS RIDGE P^3									
PM ROOT P^3 (ASU score 2+)	0.6770	0.7954	0.3218	0.0064	0.1688	0.1988	0.6800	0.5246	
ODONTOME P^3, P^4, P_3, P_4	0.7032						0.8180	0.8445	
PM CUSP VAR. P_4 (ASU score 2-9)	0.2403	0.4200	0.2763	1.0000	0.1967	0.2487	0.3440	0.3128	
TOME'S P_3 (ASU score 2-5)	0.1865	0.1448	0.0635	0.4076	0.8630	0.2662	0.1259	0.1311	0.4795
ANT. FOVEA M_1 (ASU score 2-4)	0.6054	0.2953	0.4795			0.2579	0.4540	0.3805	
DTC M_1									
Y-GROOVE M_2	0.1409	0.2186	0.2483	0.1591	0.8288	0.1661	0.1857	0.1757	0.9312
Y-GROOVE M_1	0.1374	0.2729	0.1593	0.2743	0.0628	0.1366	0.3496	0.2845	
X-GROOVE M_2	0.4883	0.5100	0.6030	0.1591	0.7324	0.3245	0.5162	0.4652	0.5408
X-GROOVE M_1	0.1374	0.3795	0.1593	0.2743	0.0628	0.1691	0.4169	0.3411	
CUSP # M_2 (P = 5+; A = 4-)	0.6524	0.5310	0.2137	0.4534	0.4090	0.6699	0.5165	0.5387	0.2242
CUSP # M_1 (P = 5+; A = 4-)		0.7540				0.5358	0.8360	0.7457	
CUSP 5 M_1	0.4496	0.3941	0.1362	0.7998	0.4090	0.7506	0.3847	0.4532	0.7842
CUSP 5 M_2		0.7263				0.5040	0.8192	0.7214	

Appendix 4.2 cont...

CUSP 6 M$_1$	0.5571	0.7957	0.1722	0.4755	0.2827	0.4858	0.6143	0.5792	0.7842
CUSP 6 M$_2$	0.0117	0.0309	0.3840	0.4902	0.5303	0.0689	0.0500	0.0438	
CUSP 7 M$_1$	0.1590	0.1915	0.4824	0.0215		0.3210	0.1869	0.2124	0.5510
CUSP 7 M$_2$	0.0686	0.1114	0.3147	0.0233	0.1103	0.0679	0.1224	0.1053	
DEF. WRINKLE M$_1$ (ASU score 2-3)	0.8105	0.8981	0.0910	0.6985		0.6397	0.6614	0.6973	0.6985
PROTOSTYLID M$_1$ (ASU score 1-6)	0.0739	0.7838	0.7808	0.2186	0.6488	0.5039	0.7098	0.6635	
LM ROOT # M$_1$ (ASU score >=3)									
LM ROOT # M$_2$ (ASU score >=2)	0.1799	0.4909	0.5022	0.2005	0.7839	0.6344	0.3145	0.3668	0.4852
TM ANGLE M$_3$ (P = any degree)	0.2370	0.0565	0.1879	0.0601		0.2954	0.1515	0.1918	0.7077
UM PEG M^3	0.3908	0.4689	0.1190	0.2482	0.1366	0.2194	0.4953	0.4928	
ENAM. EXT. M^1	0.6496	0.5361	0.0336	0.1730	0.3637	0.5562	0.5406	0.5362	
UM ROOT # M^2 (ASU score >=3)	0.4410	0.2398	0.0648	0.0992	0.2963	0.0017	0.2022	0.0793	0.3817
METACONE M^3									-
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.0524	0.0358	0.2261	0.4625	0.1967	0.2855	0.0650	0.1426	0.5371
HYPOCONE M^2					0.2685	0.7058		0.8504	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.2432	0.0579	0.0132	0.5858	0.6048	0.2432	0.1071	0.1240	
METACONULE M^1	0.1521	0.1196	0.5186	0.0343	0.6985	0.2784	0.1445	0.1606	0.6084
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.6247	0.0931	0.6750	0.2308	0.8296	0.2187	0.4078	0.3775	0.6084
CARABELLI'S M^1 (ASU score 2-7)	0.3298	0.5242	0.4602	0.0628	0.5303	0.4973	0.4628	0.4627	0.6084
PARASTYLE M^3 (ASU score 1-5)	0.3616	0.1530	0.2186	0.3311	0.4392	0.1834	0.2018	0.1641	
MIDLINE DIASTEMA	0.5902	0.7620	0.3263	0.8288	0.3081	0.9183	0.8316	0.8924	
CONGENITAL ABSENCE M^3 (P = 1)	0.6790	0.6675				0.3061	0.5360	0.4354	
PALATINE TORUS	0.5911	0.1530	0.1851	0.0377	0.4327	0.2392	0.2401	0.2314	
MANDIBULAR TORUS	0.8206	0.8508	0.8907	0.7931	0.2694	0.8278	0.9704	0.9375	0.6225
ROCKER JAW	0.0298	0.0584	0.2057	0.0868	0.3085	0.0354	0.0541	0.0447	0.4936
Total significant comparisons	**4**	**4**	**3**	**5**	**0**	**4**	**3**	**4**	**0**

Appendix 4.3: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region C and others (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION C (all time) TRAITS	KS -D	KS-E	KS-F	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)	0.6822	0.5416	0.4193	0.3439	0.9383	0.5896	0.6785	
WINGING I^1 (ASU score 1)	0.6590	0.3628	0.9506	0.8561	0.5292	0.9153	0.7711	
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.2953					0.5172	0.5669	
LAB CONVEX I^1 (ASU score 2-4)	0.2297	0.6926	0.7970	0.7145	0.0321	0.6515	0.3239	
INT. GROOVE I^2	0.7726	0.0064	0.6338	0.1175	0.0317	0.5127	0.2281	
PEG INCISOR I^2	0.1683	0.3425	0.2870	0.2631	0.5833	0.4930	0.6060	
TD I^2 (ASU score 2-6)	0.5292	0.0072	0.4005	0.1315	0.0878	0.3696	0.2129	
CMR C^1 (ASU score 1-3)	0.3279	0.0132	0.3866	0.4208	0.0323	0.6175	0.3219	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.6816	0.4201	0.0533	0.2029	0.4680	0.9568	0.8013	
CAN. ROOT C$_1$	0.2994	0.5643	0.6943	0.7436	0.3803	0.4516	0.3398	
PM ACC. CUSPS P^3	0.1819	0.3357	0.2455	0.2196	0.1178	0.2579	0.1436	
TRI PM P^3								
DS RIDGE P^3								
PM ROOT P^3 (ASU score 2+)	0.2128	0.0325	0.0000	0.0398	0.0019	0.1083	0.0381	
ODONTOME P^3, P^4, P$_3$, P$_4$	0.3067	0.5475	0.6702	0.0798	0.3109	0.4597	0.3155	
PM CUSP VAR. P$_4$ (ASU score 2-9)	0.2139	0.1969	0.2403	0.6006	0.9073	0.3854	0.4661	
TOME'S P$_3$ (ASU score 2-5)	0.7977	0.4085	0.4907	0.6903	0.7787	0.7665	0.7485	0.7467
ANT. FOVEA M$_1$ (ASU score 2-4)	0.2340	0.1865	0.4160		0.1724	0.5113	0.3858	
DTC M$_1$							0.0000	
Y-GROOVE M$_2$	0.1917	0.6621	0.8410	0.2256	0.1343	0.5594	0.3481	0.8023
Y-GROOVE M$_1$	0.0076	0.0000	0.1074	0.0000	0.0062	0.0165	0.0111	
X-GROOVE M$_2$	0.6419	0.7607	0.2005	0.6344	0.2848	0.7899	0.5761	0.7494
X-GROOVE M$_1$	0.0212	0.0000	0.1074	0.0000	0.0130	0.0261	0.0190	
CUSP # M$_2$ (P = 5+; A = 4-)	0.7471	0.1558	0.5940	0.2851	0.6592	0.7123	0.7617	0.2935
CUSP # M$_1$ (P = 5+; A = 4-)	0.3288				0.0780	0.5362	0.3499	
CUSP 5 M$_1$	0.8101	0.1481	0.6601	0.2446	0.4831	0.6851	0.6712	0.9489
CUSP 5 M$_2$	0.3149				0.0908	0.5371	0.3614	

CUSP 6 M_1	0.3917	0.0947	0.4726	0.3210	0.5822	0.7715	0.6944	0.6451
CUSP 6 M_2	0.0207	0.0605	0.2504	0.5286	0.5391	0.0637	0.0933	
CUSP 7 M_1	0.5632	0.1620	0.0163	0.2798	0.2195	0.7209	0.5101	0.8826
CUSP 7 M_2	0.0220	0.0877	0.1588	0.1915	0.4118	0.1928	0.1920	
DEF. WRINKLE M_1 (ASU score 2-3)	0.8328	0.0000	0.3975		0.1758	0.2357	0.2916	
PROTOSTYLID M_1 (ASU score 1-6)	0.0037	0.0204	0.5326	0.0108	0.2405	0.0524	0.0625	0.0199
LM ROOT # M_1 (ASU score >=3)							0.0000	
LM ROOT # M_2 (ASU score >=2)	0.3125	0.0587	0.4750	0.3122	0.2770	0.3697	0.3673	0.6292
TM ANGLE M_3 (P = any degree)	0.0569	0.1678	0.2062	0.1978	0.3654	0.4103	0.6815	0.9390
UM PEG M^3	0.7652	0.0867	0.5308	0.1445	0.1032	0.6042	0.4702	
ENAM. EXT. M^1	0.0611	0.0006	0.2484	0.3534	0.3309	0.1992	0.2373	
UM ROOT # M^2 (ASU score >=3)	0.5526	0.1724	0.1993	0.3447	0.0042	0.5573	0.2005	0.2175
METACONE M^3							0.0000	
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.3662	0.6202	0.4567	0.4100	0.0243	0.6726	0.2709	0.7065
HYPOCONE M^2				0.0040	0.3152		0.6149	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.0261	0.1057	0.6193	0.7636	0.6186	0.2163	0.2673	
METACONULE M^1	0.4553	0.1754	0.0906	0.4903	0.4365	0.8632	0.7420	0.9408
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.1840	0.0803	0.3502	0.3248	0.4239	0.5962	0.5314	0.2421
CARABELLI'S M^1 (ASU score 2-7)	0.2578	0.7563	0.1054	0.6460	0.4424	0.5280	0.5116	0.5149
PARASTYLE M^3 (ASU score 1-5)	0.2130	0.4682	0.5688	0.6520	0.3720	0.4152	0.4012	
MIDLINE DIASTEMA	0.6259	0.0458	0.5037	0.1934	0.2140	0.4039	0.2869	
CONGENITAL ABSENCE M^3 (P = 1)	0.4489	0.3698	0.5821	0.3675	0.1796	0.9239	0.8978	
PALATINE TORUS	0.0828	0.1734	0.0279	0.2183	0.2254	0.1802	0.1576	
MANDIBULAR TORUS	0.3868	0.9102	0.9021	0.1548	0.9920	0.6389	0.7011	0.7853
ROCKER JAW	0.5600	0.2758	0.7944	0.5371	0.9815	0.4485	0.5312	0.5857
Total significant comparisons	**6**	**10**	**3**	**5**	**8**	**2**	**6**	**1**

Appendix 4.4: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region D and others (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION D (all time) TRAITS	KS-E	KS-F	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)	0.3210	0.3128	0.3128	0.7198	0.5017	0.5314	
WINGING I^1 (ASU score 1)	0.3014	0.8399	0.9050	0.4307	0.6389	0.5746	
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.4938	0.1022	**0.0393**	0.3643	0.4511	0.3336	
LAB CONVEX I^1 (ASU score 2-4)	0.2517	0.6237	0.9308	0.2663	0.3310	0.6031	
INT. GROOVE I^2	**0.0108**	0.5725	0.0941	**0.0282**	0.4402	0.1992	
PEG INCISOR I^2	0.2815	0.7118	0.6816	0.1178	0.3104	0.1983	
TD I^2 (ASU score 2-6)	**0.0187**	0.2767	0.1888	0.0638	0.5987	0.3298	
CMR C^1 (ASU score 1-3)	**0.0085**	0.4243	0.3652	0.1293	0.4665	0.6675	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.2493	**0.0094**	0.0772	0.4680	0.6541	0.6432	
CAN. ROOT C_1		**0.0075**			0.5273	0.5792	
PM ACC. CUSPS P^3	0.6409	0.4596	**0.0047**	0.4436	0.5998	0.6391	
TRI PM P^3							
DS RIDGE P^3							
PM ROOT P^3 (ASU score 2+)	0.1933	**0.0005**	0.1330	**0.0287**	0.6928	0.3516	
ODONTOME P^3, P^4, P_3, P_4					0.5358	0.5976	
PM CUSP VAR. P_4 (ASU score 2-9)	0.5342	0.4274	0.3556	0.3097	0.5418	0.4241	
TOME'S P_3 (ASU score 2-5)	0.5639	0.5446	0.7625	0.7136	0.8277	0.7868	0.7097
ANT. FOVEA M_1 (ASU score 2-4)	0.5515	0.6571		0.8241	0.3345	0.4957	
DTC M_1							
Y-GROOVE M_2	0.4607	0.6000	0.2605	0.7095	0.3207	0.4928	0.4849
Y-GROOVE M_1	**0.0493**	0.7874	**0.0426**	0.2738	0.5231	0.6816	
X-GROOVE M_2	0.9072	0.1111	0.7840	0.4719	0.6985	0.6941	0.8604
X-GROOVE M_1	**0.0189**	0.6737	**0.0192**	0.1571	0.7851	0.7937	
CUSP # M_2 (P = 5+; A = 4-)	0.1356	0.6974	0.3148	0.5736	0.7017	0.6331	0.3302
CUSP # M_1 (P = 5+; A = 4-)	0.5503	0.0635	0.0635	0.2379	0.5038	0.7332	
CUSP 5 M_1	0.1895	0.5926	0.1964	0.3929	0.9118	0.7588	0.9902
CUSP 5 M_2	0.5140	0.0739	0.0739	0.2653	0.4730	0.6849	

Appendix 4.4 cont...

CUSP 6 M_1	**0.0333**	0.5232	0.3210	0.2972	0.4542	0.3700	0.8487
CUSP 6 M_2	0.1388	0.3844	0.6181	0.1215	0.3922	0.2431	
CUSP 7 M_1	0.2246	**0.0042**	0.3164	0.3470	0.6236	0.6507	0.9550
CUSP 7 M_2	0.1956	**0.0018**	0.4944	0.1491	0.1312	0.1151	
DEF. WRINKLE M_1 (ASU score 2-3)	**0.0002**	0.4467		0.2590	0.2852	0.3420	
PROTOSTYLID M_1 (ASU score 1-6)	0.4180	0.1431	0.7406	0.1404	0.1123	0.0744	0.1520
LM ROOT # M_1 (ASU score >=3)							
LM ROOT # M_2 (ASU score >=2)	0.3047	0.3105	0.6939	0.7848	0.6904	0.7555	0.4896
TM ANGLE M_3 (P = any degree)	**0.0223**	0.2867	0.0674	**0.0111**	0.0958	**0.0481**	0.5759
UM PEG M^3	0.0759	0.4181	0.1265	0.0648	0.6268	0.3135	
ENAM. EXT. M^1	**0.0018**	0.0748	0.3092	0.1894	0.3229	0.2245	
UM ROOT # M^2 (ASU score >=3)	0.2898	0.2642	0.4254	**0.0149**	0.8700	0.5464	0.1418
METACONE M^3							
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.3249	0.3805	0.6506	**0.0067**	0.4696	0.1247	0.5510
HYPOCONE M^2			**0.0017**	0.2728		0.5827	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.2342	0.1395	0.0526	0.0731	0.1439	0.1073	
METACONULE M^1	0.1138	0.1092	0.5382	0.2938	0.4516	0.3817	0.8107
LARGE METACONULE M^1 (P = 4+; A = 4-)	**0.0020**	0.5688	**0.0133**	0.6758	0.1926	0.2397	0.0554
CARABELLI'S M^1 (ASU score 2-7)	0.5381	0.1200	0.4603	0.3268	0.4533	0.4433	0.4823
PARASTYLE M^3 (ASU score 1-5)	0.4348	0.5800	0.6316	0.5805	0.3821	0.3746	
MIDLINE DIASTEMA	0.0887	0.6257	0.2363	0.4362	0.8096	0.6582	
CONGENITAL ABSENCE M^3 (P = 1)	0.5034	0.4456	0.7000	0.5212	0.5467	0.6545	
PALATINE TORUS	0.9900	0.1793	0.0638	0.6427	0.4624	0.4680	
MANDIBULAR TORUS	0.6083	0.5963	0.2545	0.4280	0.5660	0.4853	0.6011
ROCKER JAW	0.4903	0.6077	0.7140	0.5911	0.9287	0.9431	0.6932
Total significant values	**10**	**5**	**6**	**5**	**0**	**1**	**0**

Appendix 4.5: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region E and others (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION E (all time) TRAITS	KS-F	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)	0.5925	0.3180	0.4954	0.5612	0.5161	
WINGING I^1 (ASU score 1)	0.5766	0.5993	0.6141	0.3583	0.4152	
DOUBLE SHOVEL I^1 (ASU score 2-6)				0.6818	0.7188	
LAB CONVEX I^1 (ASU score 2-4)	0.6418	0.6963	0.0474	0.4504	0.2780	
INT. GROOVE I^2	0.0456	0.8385	0.2700	0.0106	0.0255	
PEG INCISOR I^2	0.3106	0.1713	0.1728	0.5532	0.4416	
TD I^2 (ASU score 2-6)	0.4292	0.4292	0.1870	0.0209	0.0337	
CMR C^1 (ASU score 1-3)		0.1564	0.0092	0.0139	0.0108	
CAN. ACC. RIDGE C^1 (ASU score 2-5)			0.4193	0.4170	0.4651	
CAN. ROOT C_1	0.1684			0.7295	0.7596	
PM ACC. CUSPS P^3	0.4392	0.1599	0.9434	0.5310	0.5776	
TRI PM P^3						
DS RIDGE P^3						
PM ROOT P^3 (ASU score 2+)	0.0222	0.4387	0.2959	0.2494	0.4222	
ODONTOME P^3, P^4, P_3, P_4				0.7160	0.7565	
PM CUSP VAR. P_4 (ASU score 2-9)	0.3031	0.7401	0.2365	0.3499	0.3078	
TOME'S P_3 (ASU score 2-5)	0.4816	0.6820	0.3736	0.3978	0.3709	0.9543
ANT. FOVEA M_1 (ASU score 2-4)	0.7825		0.6488	0.3192	0.3745	
DTC M_1						
Y-GROOVE M_2	0.6352	0.3545	0.3819	0.8244	0.6765	0.7717
Y-GROOVE M_1	0.2059	0.4227	0.0905	0.0075	0.0100	
X-GROOVE M_2	0.1862	0.7808	0.5577	0.8256	0.8261	0.8221
X-GROOVE M_1	0.2059	0.2641	0.0537	0.0037	0.0045	
CUSP # M_2 (P = 5+; A = 4-)	0.2787	0.0431	0.2578	0.1697	0.1787	0.5536
CUSP # M_1 (P = 5+; A = 4-)			0.2738	0.7056	0.5640	
CUSP 5 M_1	0.2155	0.0312	0.1413	0.1897	0.1882	0.3791
CUSP 5 M_2			0.2617	0.6890	0.5469	

Appendix 4.5 cont...

CUSP 6 M$_1$	0.1179	0.1193	0.2349	0.0692	0.0802	0.9755
CUSP 6 M$_2$	0.5895	0.5895	0.2089	0.2094	0.1858	
CUSP 7 M$_1$	**0.0097**	0.5908	0.5014	0.2008	0.2486	0.6338
CUSP 7 M$_2$	**0.0211**	0.3749	0.0899	0.2111	0.1613	
DEF. WRINKLE M$_1$ (ASU score 2-3)	0.4292		**0.0015**	**0.0001**	**0.0000**	
PROTOSTYLID M$_1$ (ASU score 1-6)	0.1931	0.6310	0.1899	0.2224	0.1801	0.2986
LM ROOT # M$_1$ (ASU score >=3)						
LM ROOT # M$_2$ (ASU score >=2)	0.1592	0.6877	0.2294	0.1565	0.1421	0.3337
TM ANGLE M$_3$ (P = any degree)	0.3927	0.2589	0.2234	0.1256	0.1404	0.5993
UM PEG M^3	0.0528	0.5169	0.1372	0.1050	0.1216	
ENAM. EXT. M^1	0.0555	**0.0437**	**0.0119**	**0.0022**	**0.0017**	
UM ROOT # M^2 (ASU score >=3)	0.4704	0.3729	0.1306	0.2630	0.4163	**0.0054**
METACONE M^3						
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.7595	0.3501	0.2918	0.5534	0.8872	0.7511
HYPOCONE M^2		0.0652	0.5227		0.7492	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.0529	0.0652	0.1057	0.1517	0.1368	
METACONULE M^1	**0.0161**	0.7909	0.4282	0.1588	0.1933	0.8146
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.1455	0.8217	**0.0218**	**0.0166**	**0.0075**	0.3574
CARABELLI'S M^1 (ASU score 2-7)	0.1278	0.6632	0.4413	0.8851	0.8538	0.4632
PARASTYLE M^3 (ASU score 1-5)			0.5763	0.5261	0.5426	
MIDLINE DIASTEMA	0.5675	0.5297	0.2328	0.0970	0.1148	
CONGENITAL ABSENCE M^3 (P = 1)			0.2900	0.3499	0.2673	
PALATINE TORUS	0.2154	0.0748	0.7125	0.6036	0.6149	
MANDIBULAR TORUS	0.8573	0.1903	0.9197	0.8500	0.8994	0.7301
ROCKER JAW	0.3974	0.9696	0.3011	0.4919	0.4254	0.9149
Total significant values	5	3	5	8	8	1

Appendix 4.6: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region F and others (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION F (all time) TRAITS	KS-G	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)		0.3985	0.4800	0.4676	
WINGING I^1 (ASU score 1)	0.8195	0.8058	0.9213	0.9362	
DOUBLE SHOVEL I^1 (ASU score 2-6)			**0.0003**	**0.0000**	
LAB CONVEX I^1 (ASU score 2-4)	0.6650	0.3927	0.7632	0.6847	
INT. GROOVE I^2	0.1921	0.1515	0.4682	0.3590	
PEG INCISOR I^2	0.6084	0.1908	0.4676	0.4000	
TD I^2 (ASU score 2-6)		0.7611	0.3248	0.4122	
CMR C^1 (ASU score 1-3)	0.1921	0.4617	0.3177	0.3370	
CAN. ACC. RIDGE C^1 (ASU score 2-5)		**0.0459**	0.0554	0.0567	
CAN. ROOT C_1	0.3698	1.0000	**0.0047**	**0.0011**	
PM ACC. CUSPS P^3		0.4142	0.3776	0.3847	
TRI PM P^3					
DS RIDGE P^3					
PM ROOT P^3 (ASU score 2+)	0.3502	**0.0215**	**0.0005**	**0.0012**	
ODONTOME P^3, P^4, P_3, P_4			0.7970	0.8265	
PM CUSP VAR. P_4 (ASU score 2-9)	0.1967	0.2487	0.3440	0.3128	
TOME'S P_3 (ASU score 2-5)	0.5303	0.6387	0.5672	0.5703	0.6283
ANT. FOVEA M_1 (ASU score 2-4)		0.6313	0.5610	0.6001	
DTC M_1					
Y-GROOVE M_2	0.2367	0.5245	0.6407	0.6638	0.7555
Y-GROOVE M_1	0.1243	0.5998	0.7305	0.8955	
X-GROOVE M_2	0.2367	0.1780	0.1365	0.1310	0.7555
X-GROOVE M_1	0.1243	0.7087	0.5457	0.7526	
CUSP # M_2 (P = 5+; A = 4-)	0.3502	0.5998	0.6833	0.6601	0.4392
CUSP # M_1 (P = 5+; A = 4-)		0.5064	**0.0038**	0.0892	
CUSP 5 M_1	0.3014	0.9495	0.5939	0.6810	0.9039
CUSP 5 M_2		0.5064	**0.0047**	0.0964	

Appendix 4.6 cont...

CUSP 6 M_1	0.4862	0.3670	0.4369	0.4133	0.8476
CUSP 6 M_2	0.4142	0.4955	0.5297	0.5121	
CUSP 7 M_1	0.0704	**0.0077**	**0.0043**	**0.0030**	0.8365
CUSP 7 M_2	0.0565	0.0556	**0.0224**	**0.0224**	
DEF. WRINKLE M_1 (ASU score 2-3)		0.7180	0.1010	0.0592	
PROTOSTYLID M_1 (ASU score 1-6)	0.0971	0.4050	0.2993	0.3148	
LM ROOT # M_1 (ASU score >=3)					
LM ROOT # M_2 (ASU score >=2)	0.2186	0.2892	0.3435	0.3454	
TM ANGLE M_3 (P = any degree)	0.1044	0.0588	0.3804	0.2606	0.9364
UM PEG M^3	0.0906	0.3663	0.3441	0.3375	
ENAM. EXT. M^1	0.1997	0.1810	0.1256	0.1365	
UM ROOT # M^2 (ASU score >=3)	0.2437	**0.0144**	0.2596	0.3286	
METACONE M^3					
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.3932	0.5091	0.5654	0.7904	0.7077
HYPOCONE M^2	0.1621	0.6305		0.8101	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.5850	0.6193	0.3836	0.4280	
METACONULE M^1	0.8286	**0.0364**	0.0661	0.0531	0.7077
LARGE METACONULE M^1 (P = 4+; A = 4-)		0.4821	0.4259	0.4368	0.1894
CARABELLI'S M^1 (ASU score 2-7)	0.7119	0.0547	0.1202	0.0991	
PARASTYLE M^3 (ASU score 1-5)		0.6771	0.6188	0.6328	
MIDLINE DIASTEMA	0.3774	0.8588	0.6731	0.7154	
CONGENITAL ABSENCE M^3 (P = 1)		0.3430	0.5667	0.4965	
PALATINE TORUS	**0.0171**	0.1215	0.0920	0.0929	
MANDIBULAR TORUS	0.1935	0.8998	0.7483	0.7776	0.7555
ROCKER JAW	0.5146	0.8082	0.5772	0.6147	0.6395
Total significant values	**1**	**5**	**7**	**5**	**0**

Appendix 4.7: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Region G and others (inclusive of all time periods), and including Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION G (all time) TRAITS	KS - Inland	KS - Coastal	KS - All	MLP
SHOVELING I^1 (ASU score 2-6)	0.3146	0.4800	0.4561	
WINGING I^1 (ASU score 1)	0.6845	0.8036	0.7582	
DOUBLE SHOVEL I^1 (ASU score 2-6)		0.0003	0.0000	
LAB CONVEX I^1 (ASU score 2-4)	0.5809	0.7793	0.8710	
INT. GROOVE I^2	0.4427	0.1418	0.1902	
PEG INCISOR I^2	0.1991	0.4638	0.4160	
TD I^2 (ASU score 2-6)	0.5007	0.2277	0.2745	
CMR C^1 (ASU score 1-3)	0.3681	0.4398	0.4096	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.1141	0.2276	0.2332	
CAN. ROOT C_1		0.8348	0.8549	
PM ACC. CUSPS P^3	0.2196	0.0437	0.0219	
TRI PM P^3				
DS RIDGE P^3				
PM ROOT P^3 (ASU score 2+)	0.4920	0.1629	0.2235	
ODONTOME P^3, P^4, P_3, P_4		0.0026	0.0004	
PM CUSP VAR. P_4 (ASU score 2-9)	0.6242	0.4098	0.4456	
TOME'S P_3 (ASU score 2-5)	0.6221	0.7384	0.7266	
ANT. FOVEA M_1 (ASU score 2-4)				
DTC M_1				
Y-GROOVE M_2	0.2272	0.2869	0.2746	0.7934
Y-GROOVE M_1	0.0658	0.0121	0.0158	
X-GROOVE M_2	0.6354	0.6691	0.6694	0.7934
X-GROOVE M_1	0.0420	0.0071	0.0089	
CUSP # M_2 (P = 5+; A = 4-)	0.1984	0.2258	0.2097	0.7825
CUSP # M_1 (P = 5+; A = 4-)	0.2386	0.0038	0.0354	
CUSP 5 M_1	0.1874	0.1580	0.1543	0.8761
CUSP 5 M_2	0.2187	0.0047	0.0354	

CUSP 6 M_1	0.2564	0.2907	0.2817	0.8761
CUSP 6 M_2	0.7655	0.7934	0.8514	
CUSP 7 M_1	0.4408	0.3125	0.3402	0.7662
CUSP 7 M_2	0.2843	0.3004	0.2955	
DEF. WRINKLE M_1 (ASU score 2-3)				
PROTOSTYLID M_1 (ASU score 1-6)	0.2142	0.3175	0.2847	0.4017
LM ROOT # M_1 (ASU score >=3)				
LM ROOT # M_2 (ASU score >=2)	0.5888	0.5718	0.5769	0.3980
TM ANGLE M_3 (P = any degree)	0.2282	0.1764	0.1881	0.5925
UM PEG M^3	0.1892	0.1562	0.1848	
ENAM. EXT. M^1	0.2439	0.2427	0.2419	
UM ROOT # M^2 (ASU score >=3)	0.0867	0.4056	0.4807	
METACONE M^3				
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.1205	0.4769	0.3283	0.2703
HYPOCONE M^2	0.0721	**0.0000**	**0.0001**	0.4785
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.7095	0.5631	0.6183	
METACONULE M^1	0.6070	0.4758	0.5060	0.8195
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.0615	0.2946	0.2522	0.4017
CARABELLI'S M^1 (ASU score 2-7)	0.4707	0.5674	0.5630	
PARASTYLE M^3 (ASU score 1-5)	0.7319	0.6939	0.7056	
MIDLINE DIASTEMA	0.3164	0.2527	0.2671	
CONGENITAL ABSENCE M^3 (P = 1)	0.4890	0.6616	0.6152	
PALATINE TORUS	0.0943	0.0947	0.0917	
MANDIBULAR TORUS	0.1595	0.1896	0.1792	0.9039
ROCKER JAW	0.5403	0.7309	0.6875	1.0000
Total significant values	**1**	**8**	**8**	**0**

Appendix 4.8: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) Inland and Coastal Regions (all time periods), and Mid-Late Pleistocene (MLP) comparisons.

KHOESAN REGION INLAND (all time) TRAITS	KS - Coastal		
SHOVELING I^1 (ASU score 2-6)	0.5638	CUSP 6 M_1	0.5905
WINGING I^1 (ASU score 1)	0.5238	CUSP 6 M_2	0.2760
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.5862	CUSP 7 M_1	0.2786
LAB CONVEX I^1 (ASU score 2-4)	0.0436	CUSP 7 M_2	0.3287
INT. GROOVE I^2	0.0540	DEF. WRINKLE M_1 (ASU score 2-3)	0.1595
PEG INCISOR I^2	0.2400	PROTOSTYLID M_1 (ASU score 1-6)	0.5750
TD I^2 (ASU score 2-6)	0.0731	LM ROOT # M_1 (ASU score >=3)	-
CMR C^1 (ASU score 1-3)	0.0267	LM ROOT # M_2 (ASU score >=2)	0.4942
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.4140	TM ANGLE M_3 (P = any degree)	0.0978
CAN. ROOT C_1	0.5841	UM PEG M^3	0.0923
PM ACC. CUSPS P^3	0.3036	ENAM. EXT. M^1	0.5204
TRI PM P^3		UM ROOT # M^2 (ASU score >=3)	0.0106
DS RIDGE P^3		METACONE M^3	-
PM ROOT P^3 (ASU score 2+)	0.0066	SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.0111
ODONTOME P^3, P^4, P_3, P_4	0.5393	HYPOCONE M^2	0.0844
PM CUSP VAR. P_4 (ASU score 2-9)	0.5296	LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.5440
TOME'S P_3 (ASU score 2-5)	0.8057	METACONULE M^1	0.4239
ANT. FOVEA M_1 (ASU score 2-4)	0.2405	LARGE METACONULE M^1 (P = 4+; A = 4-)	0.4598
DTC M_1		CARABELLI'S M^1 (ASU score 2-7)	0.2235
Y-GROOVE M_2	0.2192	PARASTYLE M^3 (ASU score 1-5)	0.7524
Y-GROOVE M_1	0.0423	MIDLINE DIASTEMA	0.4934
X-GROOVE M_2	0.3003	CONGENITAL ABSENCE M^3 (P = 1)	0.0893
X-GROOVE M_1	0.0330	PALATINE TORUS	0.8932
CUSP # M_2 (P = 5+; A = 4-)	0.7459	MANDIBULAR TORUS	0.6799
CUSP # M_1 (P = 5+; A = 4-)	0.0335	ROCKER JAW	0.5029
CUSP 5 M_1	0.3397		
CUSP 5 M_2	0.0386	Total significant values	7

5. FREQUENCIES FOR KHOESAN DENTAL DATA THROUGH TIME.

	All time		8000+		8-6KA		6-4KA		4-3KA		3-2KA		2-1KA		1-0KA	
TRAITS	N	Present %	N	Present %	N	Present %	N	Present %	N	Present %	N	Present %	N	Present %	N	Present %
SHOVELING I^1 (ASU score 2-6)	83	20.99	5	0.00	2	0.00	9	14.29	3	50.00	14	0.00	5	40.00	22	18.18
WINGING I^1 (ASU score 1)	140	18.84	6	16.67	3	50.00	9	12.50	11	30.00	28	3.70	11	20.00	41	16.03
DOUBLE SHOVEL I^1 (ASU score 2-6)	138	0.76	6	0.00	3	0.00	13	0.00	7	0.00	26	0.00	11	0.00	35	0.00
LAB CONVEX I^1 (ASU score 2-4)	127	30.71	6	66.67	3	100.00	11	54.55	7	20.00	25	40.00	8	37.50	32	19.25
INT. GROOVE I^2	141	44.85	5	66.67	4	0.00	10	71.43	8	37.50	28	42.86	16	71.43	27	37.73
PEG INCISOR I^2	160	10.63	7	33.33	6	33.33	14	10.00	12	16.67	31	3.33	16	25.00	60	28.33
TD I^2 (ASU score 2-6)	82	45.12	5	50.00	2	50.00	6	66.67	3	100.00	16	37.50	5	60.00	27	55.56
CMR C^1 (ASU score 1-3)	108	61.46	8	57.14	5	100.00	9	77.78	8	80.00	18	94.44	11	100.00	20	40.00
CAN. ACC. RIDGE C^1 (ASU score 2-5)	73	8.22	4	0.00	3	0.00	4	0.00	5	0.00	13	10.00	5	20.00	22	4.55
CAN. ROOT C_1	300	0.33	19	0.00	10	0.00	18	0.00	25	0.00	53	1.92	33	0.00	87	3.45
PM ACC. CUSPS P^3	106	13.21	6	0.00	3	33.33	6	16.67	6	0.00	15	13.33	7	0.00	26	8.10
TRI PM P^3	194	0.00	10	0.00	6	0.00	13	0.00	13	0.00	32	0.00	20	0.00	59	0.00
DS RIDGE P^3	102	0.00	6	0.00	3	0.00	6	0.00	7	0.00	16	0.00	8	0.00	28	0.00
PM ROOT P^3 (ASU score 2+)	245	33.88	7	16.67	8	40.00	18	16.67	16	25.00	42	16.67	30	44.83	84	42.86
ODONTOME P^3, P^4, P_3, P_4	209	0.48	13	0.00	9	0.00	16	0.00	21	0.00	38	2.94	25	0.00	74	8.11
PM CUSP VAR. P_4 (ASU score 2-9)	122	51.64	10	60.00	3	100.00	7	71.43	14	63.64	20	80.00	11	50.00	26	50.00
TOME'S P_3 (ASU score 2-5)	112	23.21	5	40.00	3	33.33	8	12.50	10	20.00	21	10.00	15	36.36	30	30.00
ANT. FOVEA M_1 (ASU score 2-4)	92	34.12	5	20.00	2	0.00	2	100.00	3	0.00	10	37.50	7	16.67	26	34.62
DTC M_1	74	0.00	4	0.00	3	0.00	3	0.00	3	0.00	10	0.00	5	0.00	21	0.00
Y-GROOVE M_2	243	72.43	13	46.15	7	75.00	13	69.23	24	70.83	37	78.79	31	92.31	67	71.64
Y-GROOVE M_1	205	88.65	14	100.00	5	100.00	14	85.71	16	86.67	24	100.00	20	90.00	47	82.97
X-GROOVE M_2	243	17.60	13	46.15	7	28.57	13	18.18	24	30.00	37	15.15	31	7.69	75	29.33
X-GROOVE M_1	205	12.68	14	14.29	5	25.00	14	14.29	16	18.75	24	8.33	20	15.00	51	30.00
CUSP # M_2 (P = 5+; A = 4-)	206	83.33	15	100.00	6	60.00	9	55.56	20	73.68	31	90.32	24	90.91	49	84.44
CUSP # M_1 (P = 5+; A = 4-)	174	98.77	13	92.31	5	100.00	11	100.00	17	100.00	26	100.00	18	100.00	38	97.37

Frequencies for Khoesan dental data through time cont...

CUSP 5 M_1	206	84.82	15	100.00	5	66.67	8	66.67	20	75.00	34	88.24	24	90.91	47	84.11
CUSP 5 M_2	168	98.77	11	100.00	4	100.00	10	100.00	18	100.00	26	100.00	18	100.00	38	97.37
CUSP 6 M_1	166	15.66	11	9.09	5	20.00	11	28.57	16	6.25	25	18.18	18	5.88	40	25.00
CUSP 6 M_2	201	20.54	14	14.29	5	25.00	8	20.00	20	10.53	32	28.13	24	22.73	53	35.85
CUSP 7 M_1	232	18.10	12	16.67	7	16.67	13	15.38	18	0.00	32	28.13	27	11.11	61	20.27
CUSP 7 M_2	234	11.54	15	13.33	7	16.67	12	8.33	21	4.76	36	11.11	30	16.67	69	20.96
DEF. WRINKLE M_1 (ASU score 2-3)	110	20.00	3	0.00	2	0.00	6	16.67	6	0.00	18	5.56	8	0.00	31	16.13
PROTOSTYLID M_1 (ASU score 1-6)	231	7.36	13	0.00	6	25.00	16	15.38	19	11.76	38	8.33	25	8.00	49	4.23
LM ROOT # M_1 (ASU score ≥3)	333	0.00	18	0.00	9	0.00	20	0.00	26	0.00	53	0.00	36	0.00	88	0.00
LM ROOT # M_2 (ASU score ≥2)	290	93.79	16	84.62	9	100.00	17	100.00	27	96.30	47	100.00	34	100.00	89	93.16
TM ANGLE M_3 (P = any degree)	185	17.93	5	40.00	4	25.00	8	25.00	13	10.00	34	23.53	27	14.81	64	14.74
UM PEG M^3	194	22.83	4	50.00	7	60.00	9	14.29	13	20.00	33	33.33	23	27.27	73	20.55
ENAM. EXT. M^1	274	18.66	11	28.57	9	22.22	15	15.38	21	28.57	48	16.67	31	29.03	77	23.38
UM ROOT # M^2 (ASU score ≥3)	290	94.14	8	83.33	11	100.00	17	100.00	15	92.86	51	96.08	35	94.29	108	98.15
METACONE M^3	191	100.00	5	100.00	7	100.00	10	100.00	13	100.00	32	100.00	23	100.00	80	100.00
SMALL METACONE M^3 (P = 3-; A = 3.5+)	191	36.07	5	60.00	7	28.57	10	25.00	13	44.44	32	39.29	23	27.27	85	61.41
HYPOCONE M^2	229	100.00	5	100.00	9	100.00	16	100.00	15	100.00	38	100.00	28	100.00	65	100.00
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	229	93.45	5	100.00	9	100.00	16	100.00	15	93.33	38	94.44	28	100.00	65	90.30
METACONULE M^1	156	51.68	7	28.57	5	20.00	9	55.56	16	45.45	23	69.57	14	54.55	47	72.34
LARGE METACONULE M^1 (P = 4+; A = 4-)	156	7.05	7	14.29	5	0.00	9	33.33	16	0.00	23	8.70	14	9.09	39	15.90
CARABELLI'S M^1 (ASU score 2-7)	179	25.42	6	16.67	4	25.00	11	30.00	18	16.67	24	4.17	24	14.29	41	27.18
PARASTYLE M^3 (ASU score 1-5)	180	2.78	4	0.00	6	0.00	10	11.11	14	9.09	31	0.00	25	4.55	72	16.67
MIDLINE DIASTEMA	252	19.84	6	0.00	8	37.50	15	13.33	19	26.32	46	26.09	31	25.81	113	41.59
CONGENITAL ABSENCE M^3 (P = 1)	296	3.72	9	11.11	12	8.33	14	14.28	19	0.00	50	0.00	33	0.00	116	5.17
PALATINE TORUS	341	57.77	11	63.64	12	66.67	20	60.00	27	48.15	56	60.71	38	63.16	85	49.41
MANDIBULAR TORUS	352	29.55	26	23.08	11	18.18	20	30.00	27	25.93	57	28.07	39	30.77	82	35.37
ROCKER JAW	296	37.84	21	38.10	6	0.00	16	31.25	27	40.74	51	35.29	36	50.00	57	21.05

6. CHI-SQUARE P-VALUES OF ANALYSES BETWEEN KHOESAN TEMPORAL DATA AND BETWEEN THE KHOESAN AND MID-LATE PLEISTOCENE SAMPLES.

Appendix 6.1: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 8000+ temporal data, including Mid-Late Pleistocene (MLP) comparisons.

8000+ TRAITS	KS 8-6ka	KS 6-4ka	KS 4-3ka	KS 3-2ka	KS 2-1ka	KS 1-0ka	KS-All time	MLP
SHOVELING I^1 (ASU score 2-6)		0.7662	0.6985		0.1138	0.3016	0.2599	
WINGING I^1 (ASU score 1)	0.7768	0.7565	0.5510	0.2160	0.8686	0.2915	0.8938	
DOUBLE SHOVEL I^1 (ASU score 2-6)							0.8343	
LAB CONVEX I^1 (ASU score 2-4)	0.7409	0.6275	0.0530	0.2385	0.2801	0.9429	0.0658	
INT. GROOVE I^2	0.3865	0.7842	0.3663	0.7488	0.2111	0.6338	0.7480	
PEG INCISOR I^2	0.4533	0.1859	0.5392	**0.0022**	0.8576	0.6400	0.1433	
TD I^2 (ASU score 2-6)	0.3173	0.3765	0.3173	0.1717	0.5271	0.5040	0.5606	
CMR C^1 (ASU score 1-3)	0.5469	0.4858	0.2794	**0.0080**	**0.0174**	0.3527	0.5240	
CAN. ACC. RIDGE C^1 (ASU score 2-5)				0.3502	0.6084	0.1236	0.3691	
CAN. ROOT C_1				0.5427		0.4806	0.8010	
PM ACC. CUSPS P^3	0.7077	0.2963		0.3471		0.6255	0.3413	
TRI PM P^3								
DS RIDGE P^3								
PM ROOT P^3 (ASU score 2+)	0.0668	0.4515	0.1455	0.2433	**0.0267**	0.2436	0.0600	
ODONTOME P^3, P^4, P_3, P_4				0.6460			0.8545	
PM CUSP VAR. P_4 (ASU score 2-9)	0.5462	0.6275	0.6903	0.0882	0.6275	0.5904	0.6108	
TOME'S P_3 (ASU score 2-5)	0.6985	0.7119	0.4090	**0.0267**	0.0706	0.8540	0.2525	0.6733
ANT. FOVEA M_1 (ASU score 2-4)	0.3272	0.6985	0.6084	0.5060	0.7934	0.0856	0.5152	
DTC M_1								
Y-GROOVE M_2	0.6614	0.3918	0.1395	**0.0303**	**0.0016**	0.6176	**0.0418**	0.2942
Y-GROOVE M_1	0.1407	0.1561	0.2526	0.0989	0.3255	0.1759	0.1444	
X-GROOVE M_2	0.7324	**0.0271**	**0.0019**	**0.0264**	**0.0018**	0.5684	**0.0066**	0.4083
X-GROOVE M_1	0.3716	1.0000	0.2526	0.5641	0.3255	0.0656	0.3411	

CUSP # M_2 (P = 5+; A = 4-)	0.0073	0.0032	0.0523	0.2639	0.2817	0.8347	0.1235	0.7373
CUSP # M_1 (P = 5+; A = 4-)	0.5234	0.3474	0.1971	0.1020	0.1719	0.8204	0.0391	
CUSP 5 M_1	0.0197	0.0339	0.0455	0.1990	0.2817	0.4176	0.1449	0.1154
CUSP 5 M_2	0.5850	0.4117	0.2337	0.1191	0.1930	0.8106	0.0525	
CUSP 6 M_1	0.1256	0.1256	0.2654	0.0660	0.0861	0.1044	0.0941	0.1154
CUSP 6 M_2	0.5408	0.0865	0.7818	0.3818	0.4712	0.0179	0.3008	
CUSP 7 M_1	0.8437	0.6812	0.3590	0.2478	0.2585	0.9814	0.2749	0.5060
CUSP 7 M_2	0.6963	0.9304	0.0730	0.4344	0.6320	0.5340	0.6367	
DEF. WRINKLE M_1 (ASU score 2-3)		0.7077		0.2956		0.6886	0.0592	
PROTOSTYLID M_1 (ASU score 1-6)	0.6645	0.2172	0.2842	0.2827	0.2948	0.4590	0.3105	0.1599
LM ROOT # M_1 (ASU score >=3)								
LM ROOT # M_2 (ASU score >=2)	0.1904	0.4570	0.1006	0.0024	0.0092	0.2405	0.0534	0.2956
TM ANGLE M_3 (P = any degree)	0.8125	0.5925	0.1709	0.4310	0.1851	0.8665	0.2101	0.5716
UM PEG M^3	0.6888	0.4106	0.4513	0.6557	0.6123	0.7455	0.4763	
ENAM. EXT. M^1	0.4465	0.1632	0.8187	0.4455	0.1822	0.0315	0.3589	
UM ROOT # M^2 (ASU score >=3)	0.0339	0.1101	0.0758	0.0112	0.0463	0.0000	0.0014	0.7077
METACONE M^3								
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.2763	0.2070	0.1366	0.3406	0.0861	0.3360	0.2070	0.4017
HYPOCONE M^2				0.7136			0.8815	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.4392		0.5058	0.5148		0.3781	0.4864	
METACONULE M^1	0.7353	0.0253	0.0493	0.0023	0.0245	0.0005	0.0131	0.7825
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.3774	0.1138	0.1221	0.3757	0.4465	0.4369	0.4734	0.5371
CARABELLI'S M^1 (ASU score 2-7)		0.5510	0.7216	0.0463	0.7883	0.6764	0.6268	0.2703
PARASTYLE M^3 (ASU score 1-5)		0.6645	0.4918		0.2853	0.9082	0.0859	
MIDLINE DIASTEMA		0.3471	0.1601	0.1537	0.1599	0.0423	0.2243	
CONGENITAL ABSENCE M^3 (P = 1)	0.5916	0.6791	0.6970	0.3297	0.4810	0.8848	0.2610	
PALATINE TORUS		0.8424	0.3858	0.8557	0.9769	0.3745	0.6981	
MANDIBULAR TORUS		0.5960	0.8096	0.6326	0.4972	0.2434	0.4835	0.5821
ROCKER JAW		0.6657	0.8525	0.8220	0.3840	0.1263	0.9813	0.7543
Total significant values	**3**	**4**	**3**	**9**	**7**	**5**	**5**	**0**

Appendix 6.2: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 8-6ka temporal data, including Mid-Late Pleistocene (MLP) comparisons.

8-6ka TRAITS	KS 6-4ka	KS 4-3ka	KS 3-2ka	KS 2-1ka	KS 1-0ka	KS-All time	MLP
SHOVELING I^1 (ASU score 2-6)	0.4785	0.5050		0.6985	0.3791	0.4561	
WINGING I^1 (ASU score 1)	0.7823	0.5462	0.2820	0.8206	0.5062	0.8366	
DOUBLE SHOVEL I^1 (ASU score 2-6)						**0.0009**	
LAB CONVEX I^1 (ASU score 2-4)	0.6705	0.1564	0.3661	0.4292	0.0707	0.1859	
INT. GROOVE I^2	0.8433	0.4795	0.2695	**0.0494**	0.5329	0.2035	
PEG INCISOR I^2	0.1328	0.2918	**0.0009**	0.2592	0.7965	**0.0485**	
TD I^2 (ASU score 2-6)	0.8761	0.3173	0.2212	0.8948	0.5286	0.5606	
CMR C^1 (ASU score 1-3)	0.3340	0.1967	**0.0045**	0.1213	0.1562	0.3388	
CAN. ACC. RIDGE C^1 (ASU score 2-5)			0.3502	0.6084	0.1236	0.3691	
CAN. ROOT C$_1$			0.7113		0.5508	0.8549	
PM ACC. CUSPS P^3	0.7768	0.7077	0.2642	0.6455	0.4806	0.1362	
TRI PM P^3							
DS RIDGE P^3							
PM ROOT P^3 (ASU score 2+)	0.0995	0.0528	0.0833	0.8253	0.8586	0.5347	
ODONTOME P^3, P^4, P$_3$, P$_4$			0.6460			0.8545	
PM CUSP VAR. P$_4$ (ASU score 2-9)	0.8630	0.5677	0.8841	0.4056	0.3003	0.2836	
TOME'S P$_3$ (ASU score 2-5)	0.9364	0.3869	**0.0255**	0.0619	0.9013	0.4240	0.8761
ANT. FOVEA M$_1$ (ASU score 2-4)	1.0000		0.5925	0.2254		0.6001	
DTC M$_1$							
Y-GROOVE M$_2$	0.3871	0.6694	0.0810	**0.0026**	0.5887	0.1414	0.1982
Y-GROOVE M$_1$	0.6400	0.2956	**0.0150**	0.2207	0.3616	0.1173	
X-GROOVE M$_2$	0.9584	0.6532	0.3179	0.1330	0.9743	0.4556	0.7353
X-GROOVE M$_1$	0.3716	0.2956	0.3279	0.3559	0.6710	0.3949	
CUSP # M$_2$ (P = 5+; A = 4-)	0.7968	0.2783	**0.0142**	**0.0204**	0.1771	**0.0351**	0.0637
CUSP # M$_1$ (P = 5+; A = 4-)					0.5777	**0.0354**	

CUSP 5 M_1	0.8190	0.5993	0.1208	0.0791	0.4804	0.1333	1.0000
CUSP 5 M_2		0.3985			0.9865	**0.0354**	
CUSP 6 M_1	1.0000	0.5687	0.6452	0.6383	0.6473	0.7371	0.5460
CUSP 6 M_2	0.7119	0.3606	0.6338	0.3344	0.4760	0.7933	
CUSP 7 M_1	0.5959	0.3261	0.3544	0.3651	0.8859	0.3834	0.6283
CUSP 7 M_2	0.9477	0.0852	0.4475	0.7061	0.8315	0.7956	
DEF. WRINKLE M_1 (ASU score 2-3)	0.5371		0.1713		0.6886	0.0592	
PROTOSTYLID M_1 (ASU score 1-6)	0.7575	0.5663	0.4631	0.4738	0.6142	0.4904	
LM ROOT # M_1 (ASU score >=3)							
LM ROOT # M_2 (ASU score >=2)	0.7029	0.4773	0.6139	0.0526	0.3760	0.4672	
TM ANGLE M_3 (P = any degree)	0.7842	0.9039	0.5781	0.8325	0.8978	0.7693	0.5460
UM PEG M^3	0.1457	0.1213	0.1697	0.0861	**0.0003**	0.0541	0.5460
ENAM. EXT. M^1	0.2646	0.5169	0.4066	0.1292	0.0785	0.2419	
UM ROOT # M^2 (ASU score >=3)	0.3501	0.1148	0.4011	0.3150	0.6643	0.3914	0.3567
METACONE M^3							
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.8760	0.5153	0.5998	0.7082	0.0819	0.6848	0.5371
HYPOCONE M^2			0.6228			0.8415	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.1736	0.4288	0.3837	0.0737	0.8385	0.3508	
METACONULE M^1	0.5207	0.3398	0.2230	0.5142	0.1643	0.2820	0.6985
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.9364		0.3555	0.3180	0.5777	0.2522	0.3272
CARABELLI'S M^1 (ASU score 2-7)	0.6400	0.8494	0.2073	0.7454	0.5603	0.5999	0.4017
PARASTYLE M^3 (ASU score 1-5)	0.3980	0.4465		0.5949	0.3016	0.6790	
MIDLINE DIASTEMA	0.1808	0.5611	0.5059	0.5123	0.8203	0.2222	
CONGENITAL ABSENCE M^3 (P = 1)	0.5454	0.6756	0.6540	0.3343	0.4810	0.8860	
PALATINE TORUS	0.7061	0.2843	0.7002	0.8253	0.2629	0.5394	
MANDIBULAR TORUS	0.4718	0.6106	0.4961	0.4115	0.2563	0.4144	0.6615
ROCKER JAW	0.1193	0.0555	0.0785	**0.0219**	0.2116	0.0575	0.1564
Total significant values	**0**	**0**	**5**	**4**	**1**	**5**	**0**

Appendix 6.3: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 6-4ka temporal data, including Mid-Late Pleistocene (MLP) comparisons.

6-4ka TRAITS	KS 4-3ka	KS 3-2ka	KS 2-1ka	KS 1-0ka	KS-All time	MLP
SHOVELING I^1 (ASU score 2-6)	0.5465	0.1473	0.0404	0.1705	0.1327	
WINGING I^1 (ASU score 1)	0.3687	0.3842	0.5957	0.4372	0.5618	
DOUBLE SHOVEL I^1 (ASU score 2-6)					0.7581	
LAB CONVEX I^1 (ASU score 2-4)	0.0876	0.4185	0.4625	0.0081	0.1057	
INT. GROOVE I^2	0.2242	0.0235	0.6048	0.0275	0.0608	
PEG INCISOR I^2	0.4486	0.1324	0.1904	0.2194	0.6816	
TD I^2 (ASU score 2-6)	0.7768	0.0111	0.8190	0.0599	0.1419	
CMR C^1 (ASU score 1-3)	0.5967	0.0555	0.5099	0.0430	0.7583	
CAN. ACC. RIDGE C^1 (ASU score 2-5)		0.6225	0.9056	0.3279	0.7183	
CAN. ROOT C_1		0.5646		0.4241	0.8116	
PM ACC. CUSPS P^3	0.2963	0.8437	0.2609	0.2422	0.8088	
TRI PM P^3						
DS RIDGE P^3						
PM ROOT P^3 (ASU score 2+)	0.2198	0.4225	0.0183	0.0548	0.0496	
ODONTOME P^3, P^4, P_3, P_4		0.5320			0.8026	
PM CUSP VAR. P_4 (ASU score 2-9)	0.7324	0.6387	0.3980	0.3122	0.3078	
TOME'S P_3 (ASU score 2-5)	0.6714	0.8468	0.2435	0.7199	0.4832	0.7119
ANT. FOVEA M_1 (ASU score 2-4)	0.5050	0.7662	0.5371	0.2416	0.6214	
DTC M_1						
Y-GROOVE M_2	0.4654	0.4302	0.0306	0.5458	0.7023	0.5128
Y-GROOVE M_1	0.6560	0.0303	0.4475	0.8452	0.4089	
X-GROOVE M_2	0.6507	0.4988	0.8816	0.4921	0.4010	0.9312
X-GROOVE M_1	0.7434	0.5641	0.9538	0.2190	0.8621	
CUSP # M_2 (P = 5+; A = 4-)	0.1428	0.0034	0.0063	0.0495	0.0063	0.4795
CUSP # M_1 (P = 5+; A = 4-)				0.4106	0.6606	

Appendix 6.3 cont...

CUSP 5 M_1	0.7954	0.1991	0.1325	0.4393	0.2293	0.6286
CUSP 5 M_2	0.4478			0.1541	0.6700	
CUSP 6 M_1	0.5687	0.8085	0.8947	0.7822	0.9764	0.9364
CUSP 6 M_2	0.0355	0.1458	0.1118	0.4760	0.1459	
CUSP 7 M_1	0.6792	0.7850	0.4857	0.9286	0.7331	0.1638
CUSP 7 M_2	0.0853	0.3674	0.7019	0.3251	0.8037	
DEF. WRINKLE M_1 (ASU score 2-3)	0.3384	0.3938	0.2308	0.9200	0.8419	
PROTOSTYLID M_1 (ASU score 1-6)	0.7726	0.2413	0.4816	0.7197	0.2842	0.4699
LM ROOT # M_1 (ASU score >=3)						
LM ROOT # M_2 (ASU score >=2)	0.7544	0.9689	0.1339	0.1986	0.9708	0.5169
TM ANGLE M_3 (P = any degree)	0.7155	0.5290	0.8695	0.9041	0.9345	0.6286
UM PEG M^3	0.7740	0.1908	0.3286	0.4989	0.4314	
ENAM. EXT. M^1	0.1016	0.3340	0.3522	0.8869	0.3434	
UM ROOT # M^2 (ASU score >=3)	0.9096	0.8408	0.9148	0.1725	0.8438	0.3232
METACONE M^3						
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.9200	0.5073	0.8493	0.0108	0.6371	0.4785
HYPOCONE M^2		0.5703			0.8174	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.2396	0.3363		0.1195	0.2907	
METACONULE M^1	0.6531	0.4531	0.9640	0.3157	0.8211	0.9056
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.0378	0.0844	0.1775	0.5132	0.0027	0.4785
CARABELLI'S M^1 (ASU score 2-7)	0.2111	0.0059	0.3006	0.7151	0.6367	0.5925
PARASTYLE M^3 (ASU score 1-5)	0.7417	0.0602	0.4369	0.1841	0.1641	
MIDLINE DIASTEMA	0.3526	0.3077	0.3363	0.0344	0.5364	
CONGENITAL ABSENCE M^3 (P = 1)	0.3362	0.0648	0.1530	0.4462	0.0539	
PALATINE TORUS	0.4208	0.9553	0.8138	0.3940	0.8444	
MANDIBULAR TORUS	0.7575	0.8694	0.9516	0.6504	0.9654	0.6879
ROCKER JAW	0.5337	0.7663	0.2089	0.3938	0.5960	0.6067
Total significant values	**2**	**5**	**4**	**6**	**3**	**0**

Appendix 6.4: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 4-3ka temporal data, including Mid-Late Pleistocene (MLP) comparisons.

4-3ka TRAITS	KS 3-2ka	KS 2-1ka	KS 1-0ka	KS-All time	MLP
SHOVELING I^1 (ASU score 2-6)	0.2416	0.5460	0.8777	0.8534	
WINGING I^1 (ASU score 1)	0.0222	0.5254	0.0204	0.2734	
DOUBLE SHOVEL I^1 (ASU score 2-6)				0.8212	
LAB CONVEX I^1 (ASU score 2-4)	0.2055	0.3104	0.4955	0.3553	
INT. GROOVE I^2	0.2284	0.1195	0.6597	0.1667	
PEG INCISOR I^2	0.0199	0.5949	0.2726	0.5196	
TD I^2 (ASU score 2-6)	0.0145	0.6733	0.0583	0.1062	
CMR C^1 (ASU score 1-3)	0.3106	0.0083	0.5252	0.4041	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.4642	0.2918	0.6271	0.5046	
CAN. ROOT C_1	0.4852		0.3466	0.7725	
PM ACC. CUSPS P^3	0.3471		0.6255	0.3413	
TRI PM P^3					
DS RIDGE P^3					
PM ROOT P^3 (ASU score 2+)	0.4693	0.0403	0.0082	0.0612	
ODONTOME P^3, P^4, P_3, P_4	0.5167			0.7953	
PM CUSP VAR. P_4 (ASU score 2-9)	0.0959	0.5522	0.4468	0.4453	
TOME'S P_3 (ASU score 2-5)	0.1798	0.3149	0.8807	0.8169	0.9039
ANT. FOVEA M_1 (ASU score 2-4)	0.7638	0.5371		0.6997	
DTC M_1					
Y-GROOVE M_2	0.0497	0.0012	0.7769	0.0799	0.2268
Y-GROOVE M_1	0.0782	0.7590	0.7124	0.6143	
X-GROOVE M_2	0.1323	0.0478	0.8601	0.1110	0.6560
X-GROOVE M_1	0.0782	0.7590	0.2330	0.4888	
CUSP # M_2 (P = 5+; A = 4-)	0.1193	0.1438	0.1790	0.1903	0.1973
CUSP # M_1 (P = 5+; A = 4-)			0.3076	0.5853	

Appendix 6.4 cont...

CUSP 5 M_1	0.1771	0.1218	0.9811	0.1663	0.8193
CUSP 5 M_2	0.2425	0.3105	0.3878	0.2947	
CUSP 6 M_1	0.0395	0.1275	0.0452	0.1198	0.5993
CUSP 6 M_2	0.2772	0.3702	0.0372	0.1976	
CUSP 7 M_1	0.4137	0.1941	0.0661	0.3414	0.7174
CUSP 7 M_2	0.0130	0.1432	0.0946	0.0478	
DEF. WRINKLE M_1 (ASU score 2-3)	0.5900		0.2901	0.2661	
PROTOSTYLID M_1 (ASU score 1-6)	0.3909	0.6833	0.8314	0.4965	0.0341
LM ROOT # M_1 (ASU score >=3)					-
LM ROOT # M_2 (ASU score >=2)	0.1841	0.2268	0.3686	0.6002	0.6620
TM ANGLE M_3 (P = any degree)	0.2427	0.5235	0.5333	0.5204	0.9441
UM PEG M^3	0.2235	0.4183	0.1848	0.5661	
ENAM. EXT. M^1	0.2579	0.0847	0.0033	0.1265	
UM ROOT # M^2 (ASU score >=3)	0.0386	0.1228	0.2291	0.0310	0.1285
METACONE M^3					
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.3522	0.3532	0.3012	0.4600	0.4699
HYPOCONE M^2	0.5259			0.7963	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.7306	0.1219	0.6225	0.7716	0.2212
METACONULE M^1	0.1759	0.6540	0.0872	0.6903	0.9516
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.3134	0.2769	0.3221	0.2723	0.0533
CARABELLI'S M^1 (ASU score 2-7)	0.1012	0.7333	0.2433	0.2304	0.1863
PARASTYLE M^3 (ASU score 1-5)	0.1123	0.6059	0.5868	0.0991	
MIDLINE DIASTEMA	0.9848	0.9682	0.2073	0.4986	
CONGENITAL ABSENCE M^3 (P = 1)			0.7010	0.2263	
PALATINE TORUS	0.2792	0.2285	0.9089	0.3308	
MANDIBULAR TORUS	0.8369	0.6692	0.3657	0.6904	0.5668
ROCKER JAW	0.6358	0.4656	0.0588	0.7662	0.8060
Total significant values	**7**	**4**	**5**	**2**	**1**

Appendix 6.5: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 3-2ka temporal data, including Mid-Late Pleistocene (MLP) values.

3-2ka TRAITS	KS 2-1ka	KS 1-0ka	KS-All time	MLP
SHOVELING I^1 (ASU score 2-6)	0.0124	0.1023	0.0585	
WINGING I^1 (ASU score 1)	0.0982	0.7847	0.0459	
DOUBLE SHOVEL I^1 (ASU score 2-6)			0.6562	
LAB CONVEX I^1 (ASU score 2-4)	0.8998	0.0366	0.3636	
INT. GROOVE I^2	0.0805	0.3068	0.8466	
PEG INCISOR I^2	0.0036	0.0052	0.0572	
TD I^2 (ASU score 2-6)	0.0295	0.3464	0.0632	
CMR C^1 (ASU score 1-3)	0.0472	0.0429	0.0064	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.5912	0.5546	0.3698	
CAN. ROOT C_1	0.4229	0.1717	0.1591	
PM ACC. CUSPS P^3	0.3109	0.2612	0.5821	
TRI PM P^3				
DS RIDGE P^3				
PM ROOT P^3 (ASU score 2+)	0.0095	0.0016	0.0263	
ODONTOME P^3, P^4, P_3, P_4	0.4277	0.1553	0.1405	
PM CUSP VAR. P_4 (ASU score 2-9)	0.1124	0.0366	0.0180	
TOME'S P_3 (ASU score 2-5)	0.0755	0.4470	0.1088	0.7412
ANT. FOVEA M_1 (ASU score 2-4)	0.3932	0.0137	0.8473	
DTC M_1				
Y-GROOVE M_2	0.0869	0.0333	0.4174	0.8313
Y-GROOVE M_1	0.1285	0.0373	0.0955	
X-GROOVE M_2	0.2651	0.0877	0.5394	0.6972
X-GROOVE M_1	0.1285	0.0051	0.1378	
CUSP # M_2 (P = 5+; A = 4-)	0.6537	0.9463	0.3209	0.4675
CUSP # M_1 (P = 5+; A = 4-)		0.2266	0.5169	

Appendix 6.5 cont...

CUSP 5 M_1	0.1888	0.2335	0.5244	0.7333
CUSP 5 M_2		0.6020	0.5094	
CUSP 6 M_1	0.5329	0.1086	0.2274	0.6331
CUSP 6 M_2	0.2546	0.2979	0.6810	
CUSP 7 M_1	0.5126	0.1825	0.8108	1.0000
CUSP 7 M_2	0.1058	0.2362	0.1783	
DEF. WRINKLE M_1 (ASU score 2-3)	0.4966	0.0892	0.1389	
PROTOSTYLID M_1 (ASU score 1-6)	0.6630	0.4104	0.6580	0.1197
LM ROOT # M_1 (ASU score >=3)				
LM ROOT # M_2 (ASU score >=2)	0.1390	0.0341	0.0792	
TM ANGLE M_3 (P = any degree)	0.3951	0.2983	0.1885	0.7471
UM PEG M^3	0.5775	0.0073	0.1636	
ENAM. EXT. M^1	0.0344	0.0532	0.1656	
UM ROOT # M^2 (ASU score >=3)	0.6622	0.1269	0.5774	0.2451
METACONE M^3				
SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.2122	0.0348	0.6168	0.7734
HYPOCONE M^2	0.4429	0.2066	0.1499	0.0365
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.1763	0.2307	0.8209	0.3350
METACONULE M^1	0.3912	0.8092	0.1091	0.9645
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.7401	0.8282	0.6281	0.1339
CARABELLI'S M^1 (ASU score 2-7)	0.0604	0.0099	0.0090	
PARASTYLE M^3 (ASU score 1-5)	0.2612	0.0312	0.3477	
MIDLINE DIASTEMA	0.9780	0.0665	0.3372	
CONGENITAL ABSENCE M^3 (P = 1)		0.8209	0.1660	
PALATINE TORUS	0.8110	0.1877	0.6790	
MANDIBULAR TORUS	0.7751	0.3659	0.8205	0.6567
ROCKER JAW	0.1702	0.0990	0.7289	0.6323
Total significant values	**6**	**14**	**5**	**1**

Appendix 6.6: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 2-1ka temporal data, including Mid-Late Pleistocene (MLP) comparisons.

2-1ka	KS 1-0ka	KS-All time	MLP
TRAITS			
SHOVELING I^1 (ASU score 2-6)	0.2895	0.3029	
WINGING I^1 (ASU score 1)	0.1587	0.8803	
DOUBLE SHOVEL I^1 (ASU score 2-6)		0.7721	
LAB CONVEX I^1 (ASU score 2-4)	0.1208	0.6292	
INT. GROOVE I^2	0.0115	0.0579	
PEG INCISOR I^2	0.1937	0.0908	
TD I^2 (ASU score 2-6)	0.1335	0.2715	
CMR C^1 (ASU score 1-3)	0.0007	0.0077	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.2336	0.3726	
CAN. ROOT C_1	0.2950	0.7398	
PM ACC. CUSPS P^3	0.5982	0.3043	
TRI PM P^3			
DS RIDGE P^3			
PM ROOT P^3 (ASU score 2+)	0.4768	0.2425	
ODONTOME P^3, P^4, P_3, P_4		0.7507	
PM CUSP VAR. P_4 (ASU score 2-9)	1.0000	0.8617	
TOME'S P_3 (ASU score 2-5)	0.2171	0.2378	0.4543
ANT. FOVEA M_1 (ASU score 2-4)	0.1171	0.3795	
DTC M_1			
Y-GROOVE M_2	0.0006	0.0130	0.3939
Y-GROOVE M_1	0.4415	0.8557	
X-GROOVE M_2	0.0334	0.1452	0.3939
X-GROOVE M_1	0.0972	0.7679	
CUSP # M_2 (P = 5+; A = 4-)	0.5817	0.3572	0.4835
CUSP # M_1 (P = 5+; A = 4-)	0.2940	0.5745	

CUSP 5 M_1	0.3012	0.2672	0.8061
CUSP 5 M_2	0.3623	0.5676	
CUSP 6 M_1	0.0981	0.8111	0.8061
CUSP 6 M_2	0.2674	0.2788	
CUSP 7 M_1	0.5196	0.4178	0.7738
CUSP 7 M_2	0.6740	0.3641	
DEF. WRINKLE M_1 (ASU score 2-3)	0.2238	0.1608	
PROTOSTYLID M_1 (ASU score 1-6)	0.4808	0.8900	0.1054
LM ROOT # M_1 (ASU score >=3)			
LM ROOT # M_2 (ASU score >=2)	0.0706	0.1335	
TM ANGLE M_3 (P = any degree)	0.9254	0.6905	1.0000
UM PEG M^3	0.0593	0.5877	0.8538
ENAM. EXT. M^1	0.0795	0.1694	
UM ROOT # M^2 (ASU score >=3)	**0.0440**	0.6003	0.1484
METACONE M^3			
SMALL METACONE M^3 (P = 3-; A = 3.5+)	**0.0035**	0.2738	0.4632
HYPOCONE M^2		0.7546	
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	**0.0413**	0.1456	
METACONULE M^1	0.2508	0.5381	0.8327
LARGE METACONULE M^1 (P = 4+; A = 4-)	0.8697	0.6867	0.2642
CARABELLI'S M^1 (ASU score 2-7)	0.3550	0.1635	0.2781
PARASTYLE M^3 (ASU score 1-5)	0.1868	0.3689	
MIDLINE DIASTEMA	0.1090	0.4375	
CONGENITAL ABSENCE M^3 (P = 1)	0.9876	0.2600	
PALATINE TORUS	0.1578	0.5229	
MANDIBULAR TORUS	0.6176	0.8739	0.7397
ROCKER JAW	**0.0036**	0.1581	0.9631
Total significant values	**8**	**2**	**0**

Appendix 6.7: Chi-square p-values (≤ 0.05, 1 df) for 52 traits.

Between Khoesan (KS) and 1-0ka temporal data, including Mid-Late Pleistocene (MLP) comparisons.

1-0ka		KS-All time	
TRAITS	P-value		P-value
SHOVELING I^1 (ASU score 2-6)	0.8105	CUSP 5 M_2	0.9855
WINGING I^1 (ASU score 1)	0.0718	CUSP 6 M_1	0.0335
DOUBLE SHOVEL I^1 (ASU score 2-6)	0.6135	CUSP 6 M_2	0.0213
LAB CONVEX I^1 (ASU score 2-4)	0.0714	CUSP 7 M_1	0.7558
INT. GROOVE I^2	0.1518	CUSP 7 M_2	0.0618
PEG INCISOR I^2	0.0003	DEF. WRINKLE M_1 (ASU score 2-3)	0.0068
TD I^2 (ASU score 2-6)	0.3392	PROTOSTYLID M_1 (ASU score 1-6)	0.4073
CMR C^1 (ASU score 1-3)	0.0695	LM ROOT # M_1 (ASU score >=3)	
CAN. ACC. RIDGE C^1 (ASU score 2-5)	0.5632	LM ROOT # M_2 (ASU score >=2)	0.3638
CAN. ROOT C_1	0.6051	TM ANGLE M_3 (P = any degree)	0.9122
PM ACC. CUSPS P^3	0.1777	UM PEG M^3	0.0080
TRI PM P^3		ENAM. EXT. M^1	0.0300
DS RIDGE P^3		UM ROOT # M^2 (ASU score >=3)	0.0519
PM ROOT P^3 (ASU score 2+)	0.0257	METACONE M^3	
ODONTOME P^3, P^4, P_3, P_4	0.5677	SMALL METACONE M^3 (P = 3-; A = 3.5+)	0.0001
PM CUSP VAR. P_4 (ASU score 2-9)	0.8793	HYPOCONE M^2	0.6057
TOME'S P_3 (ASU score 2-5)	0.5414	LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.1062
ANT. FOVEA M_1 (ASU score 2-4)	0.0093	METACONULE M^1	0.0127
DTC M_1		LARGE METACONULE M^1 (P = 4+; A = 4-)	0.8067
Y-GROOVE M_2	0.0312	CARABELLI'S M^1 (ASU score 2-7)	0.8998
Y-GROOVE M_1	0.2685	PARASTYLE M^3 (ASU score 1-5)	0.0000
X-GROOVE M_2	0.0507	MIDLINE DIASTEMA	0.0000
X-GROOVE M_1	0.0004	CONGENITAL ABSENCE M^3 (P = 1)	0.5476
CUSP # M_2 (P = 5+; A = 4-)	0.7006	PALATINE TORUS	0.1647
CUSP # M_1 (P = 5+; A = 4-)	0.1477	MANDIBULAR TORUS	0.3032
CUSP 5 M_1	0.1725	ROCKER JAW	0.0151
		Total significant values	5

Appendix 6.8: Chi-square p-values (≤ 0.05, 1 df) for 9 traits.

Between all Khoesan 8000+ and Klasies River Mouth data.

KLASIES RIVER MOUTH		
TRAITS	Khoesan all	Khoesan 8000+
CAN. ROOT C_1	0.3610	0.6182
TOME'S P_1 (ASU score 2-5)	0.8031	0.6733
ANT. FOVEA M_1 (ASU score 2-4)	0.5401	0.7825
Y-GROOVE M_2	0.1693	**0.0358**
X-GROOVE M_2	0.3025	0.0628
CUSP 7 M_1	0.4151	0.5060
LM ROOT # M_2 (ASU score >=2)	0.5654	0.3506
TM ANGLE M_3 (P = any degree)	0.3996	0.6985
MANDIBULAR TORUS	0.1488	0.2316
Total significant values	**0**	**1**

7. KENYA TRAIT FREQUENCY DATA.

	Kenya pre-4500 BP		Kenya post-4500 BP		Kenya (all data)	
TRAITS	**N**	**%**	**N**	**%**	**N**	**%**
SHOVELING I^1 (ASU score 2-6)	6	83.33	0	0.00	6	50.00
WINGING I^1 (ASU score 1)	9	0.00	0	0.00	9	0.00
DOUBLE SHOVEL I^1 (ASU score 2-6)	10	0.00	0	0.00	10	0.00
LAB CONVEX I^1 (ASU score 2-4)	10	70.00	0	0.00	10	70.00
INT. GROOVE I^2	11	7.00	2	0.00	14	9.09
PEG INCISOR I^2	12	0.00	2	50.00	16	8.33
TD I^2 (ASU score 2-6)	10	77.14	2	100.00	12	77.78
CMR C^1 (ASU score 1-3)	9	43.33	2	0.00	13	77.78
CAN. ACC. RIDGE C^1 (ASU score 2-5)	9	0.00	2	0.00	14	0.00
CAN. ROOT C_1	10	100.00	9	100.00	26	100.00
PM ACC. CUSPS P^3	10	12.50	4	25.00	19	18.18
TRI PM P^3	15	0.00	4	0.00	24	0.00
DS RIDGE P^3	8	0.00	2	0.00	17	0.00
PM ROOT P^3 (ASU score 2+)	5	40.00	5	40.00	16	56.25
ODONTOME P^3, P^4, P_3, P_4	16	11.46	4	0.00	23	7.69
PM CUSP VAR. P_4 (ASU score 2-9)	8	30.00	2	100.00	14	50.00
TOME'S P_3 (ASU score 2-5)	1	100.00	2	0.00	4	75.00
ANT. FOVEA M_1 (ASU score 2-4)	7	57.14	7	28.57	24	25.00
DTC M_1	6	0.00	5	0.00	18	8.33
Y-GROOVE M_1	8	100.00	10	100.00	30	100.00
Y-GROOVE M_2	13	76.92	11	80.00	33	72.73
X-GROOVE M_1	8	0.00	10	11.11	30	10.00
X-GROOVE M_2	21	28.04	11	20.00	33	27.27

Appendix 7 cont...

CUSP # M_1 (P = 5+; A = 4-)	7	100.00	9	100.00	29	100.00
CUSP # M_2 (P = 5+; A = 4-)	12	65.63	11	60.00	33	71.88
CUSP 5 M_1	8	100.00	9	100.00	30	100.00
CUSP 5 M_2	12	65.63	11	60.00	33	71.88
CUSP 6 M_1	8	12.50	9	22.22	30	14.81
CUSP 6 M_2	12	28.13	11	20.00	33	31.25
CUSP 7 M_1	7	17.86	10	22.22	30	28.57
CUSP 7 M_2	12	18.75	11	18.18	33	15.15
DEF. WRINKLE M_1 (ASU score 2-3)	8	0.00	10	20.00	28	13.04
PROTOSTYLID M_1 (ASU score 1-6)	10	0.00	9	0.00	33	0.00
LM ROOT # M_1 (ASU score ≥3)	10	0.00	10	0.00	35	0.00
LM ROOT # M_2 (ASU score ≥2)	11	100.00	10	100.00	33	100.00
TM ANGLE M_3 (P = any degree)	10	20.00	8	37.50	29	20.69
UM PEG M^3	11	20.78	4	0.00	21	64.29
ENAM. EXT. M^1	8	0.00	6	0.00	24	5.26
UM ROOT # M^2 (ASU score ≥3)	9	100.00	7	85.71	22	95.45
METACONE M^3	12	100.00	3	100.00	20	100.00
SMALL METACONE M^3 (P = 3-; A = 3.5+)	12	0.00	3	50.00	20	15.00
HYPOCONE M^2	13	69.23	6	50.00	29	100.00
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	13	68.27	6	66.67	28	67.86
METACONULE M^1	6	20.00	7	20.00	24	29.17
LARGE METACONULE M^1 (P = 4+; A = 4-)	10	0.00	7	0.00	24	4.35
CARABELLI'S M^1 (ASU score 2-7)	10	10.00	7	28.57	24	30.43
PARASTYLE M^3 (ASU score 1-5)	12	8.33	4	0.00	20	5.26
MIDLINE DIASTEMA	9	11.11	0	0.00	10	20.00
CONGENITAL ABSENCE M^3 (P = 1)	14	0.00	12	8.33	52	5.78
PALATINE TORUS	9	11.11	6	66.67	21	42.86
MANDIBULAR TORUS	9	11.11	11	81.82	32	53.13
ROCKER JAW	4	75.00	9	44.44	22	63.64

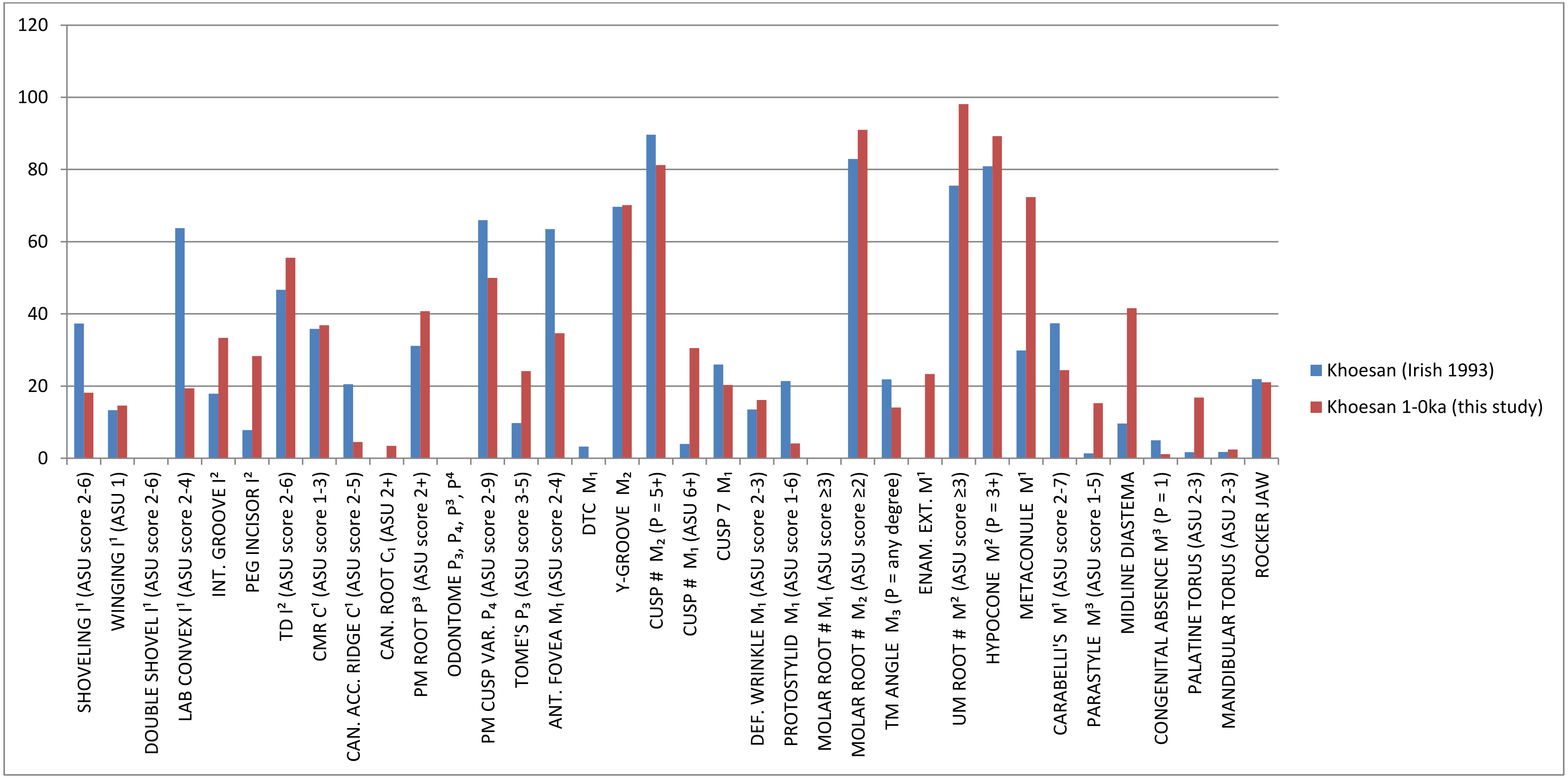
8. KHOESAN, KENYA AND SUB-SAHARAN AFRICAN DENTAL COMPLEX (SSADC) FREQUENCY DATA FOR 36 TRAITS FROM IRISH (1993).

TRAITS	KhoeKhoe N	Khoekhoe %	San N	San %	Khoe & San N	Khoe & San %	Kenya N	Kenya %	SSADC - N	SSADC %
SHOVELING I^1 (ASU score 2-6)	6	0.00	77	40.26	83	37.35	14	7.14	413	28.09
WINGING I^1 (ASU score 1)	30	3.33	90	16.67	120	13.33	99	4.04	742	6.60
DOUBLE SHOVEL I^1 (ASU score 2-6)	11	0.00	79	0.00	90	0.00	15	6.67	437	1.14
LAB CONVEX I^1 (ASU score 2-4)	11	45.45	80	66.25	91	63.74	16	37.50	425	55.53
INT. GROOVE I^2	12	33.33	83	15.66	95	17.89	26	11.54	471	13.38
PEG INCISOR I^2	16	6.25	86	8.14	102	7.84	30	0.00	586	7.34
TD I^2 (ASU score 2-6)	11	63.64	79	44.30	90	46.67	25	36.00	454	36.78
CMR C^1 (ASU score 1-3)	15	40.00	77	35.06	92	35.87	46	13.04	586	18.09
CAN. ACC. RIDGE C^1 (ASU score 2-5)	9	22.22	69	20.29	78	20.51	41	36.59	483	48.65
CAN. ROOT C_1	27	0.00	14	0.00	41	0.00	18	0.00	333	0.00
PM ROOT P^3 (ASU score 2+)	30	36.67	15	20.00	45	31.11	102	68.63	570	58.95
ODONTOME P^3, P^4, P_3, P_4	26	0.00	86	0.00	112	0.00	85	1.18	756	0.40
PM CUSP VAR. P_4 (ASU score 2-9)	17	58.82	83	67.47	100	66.00	15	40.00	530	68.49
TOME'S P_3 (ASU score 2-5)	26	15.38	15	0.00	41	9.76	20	25.00	361	22.44
ANT. FOVEA M_1 (ASU score 2-4)	9	55.56	54	64.81	63	63.49	13	69.23	418	67.46
DTC M_1	16	0.00	46	4.35	62	3.23	12	0.00	447	1.34
Y-GROOVE M_2	23	60.87	89	71.91	112	69.64	18	83.33	617	52.35
CUSP # M_2 (P = 5+; A = 4-)	18	72.22	88	93.18	106	89.62	17	52.94	585	75.90
CUSP # M_1 (ASU 6+)	16	0.00	85	4.71	101	3.96	18	5.56	561	16.58
CUSP 7 M_1	17	23.53	87	26.44	104	25.96	18	11.11	598	25.92

Irish (1993) frequency data cont...

DEF. WRINKLE M_1 (ASU score 2-3)	14	0.00	60	16.67	74	13.51	12	33.33	432	18.06
PROTOSTYLID M_1 (ASU score 1-6)	16	18.75	82	21.95	98	21.43	17	35.29	556	21.04
LM ROOT # M_1 (ASU score ≥3)	28	0.00	15	0.00	43	0.00	18	0.00	409	1.71
LM ROOT # M_2 (ASU score ≥2)	27	88.89	14	71.43	41	82.93	17	100.00	388	93.30
TM ANGLE M_3 (P = any degree)	22	13.64	65	24.62	87	21.84	16	12.50	420	15.71
ENAM. EXT. M^1	30	0.00	15	0.00	45	0.00	93	1.08	574	9.41
UM ROOT # M^2 (ASU score ≥3)	29	75.86	16	75.00	45	75.56	85	90.59	503	83.70
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	24	70.83	86	83.72	110	80.91	91	78.02	772	80.31
METACONULE M^1	21	14.29	66	34.85	87	29.89	81	14.81	619	22.78
CARABELLI'S M^1 (ASU score 2-7)	21	19.05	78	42.31	99	37.37	87	55.17	683	51.24
PARASTYLE M^3 (ASU score 1-5)	19	0.00	55	1.82	74	1.35	73	2.74	550	2.00
MIDLINE DIASTEMA	27	7.41	87	10.34	114	9.65	72	15.28	709	12.69
CONGENITAL ABSENCE M^3 (P = 1)	33	9.09	67	2.99	100	5.00	100	3.00	708	3.53
PALATINE TORUS	28	7.14	90	0.00	118	1.69	108	0.93	876	2.28
MANDIBULAR TORUS	28	7.14	86	0.00	114	1.75	21	0.00	671	0.45
ROCKER JAW	26	19.23	15	26.67	41	21.95	21	14.29	426	8.69

8.2: BAR GRAPH DEMONSTRATING FREQUENCIES FROM IRISH (1993) KHOE & SAN DATA AND KHOESAN DATA FROM 1-0KA IN THIS STUDY.



9. CHI-SQUARE P-VALUES OF ANALYSES BETWEEN MID-LATE PLEISTOCENE AND COMBINED KENYAN DATA FROM THIS STUDY AND IRISH (1993), AND THE SSADC.

MLP		
TRAITS	**Kenya: this study and Irish (1993) combined data**	**SSADC**
SHOVELING I^1 (ASU score 2-6)		
WINGING I^1 (ASU score 1)		
DOUBLE SHOVEL I^1 (ASU score 2-6)		
LAB CONVEX I^1 (ASU score 2-4)		
INT. GROOVE I^2		
PEG INCISOR I^2		
TD I^2 (ASU score 2-6)		
CMR C^1 (ASU score 1-3)		
CAN. ACC. RIDGE C^1 (ASU score 2-5)		
CAN. ROOT C$_1$		
PM ROOT P^3 (ASU score 2+)		
ODONTOME P^3, P^4, P$_3$, P$_4$	0.8624	0.8995
PM CUSP VAR. P$_4$ (ASU score 2-9)	0.2348	0.4978
TOME'S P$_3$ (ASU score 2-5)	0.3227	0.2828
ANT. FOVEA M$_1$ (ASU score 2-4)	**0.0448**	**0.0043**
DTC M$_1$		
Y-GROOVE M$_2$	0.7410	0.2175
CUSP # M$_2$ (P = 5+; A = 4-)	0.1934	0.3294
CUSP # M$_1$ (ASU 6+)		
CUSP 7 M$_1$	0.4811	0.9666
DEF. WRINKLE M$_1$ (ASU score 2-3)		
PROTOSTYLID M$_1$ (ASU score 1-6)		
LM ROOT # M$_1$ (ASU score ≥3)		0.7466
LM ROOT # M$_2$ (ASU score ≥2)	0.4902	0.5118
TM ANGLE M$_3$ (P = any degree)	0.2521	0.4049
ENAM. EXT. M^1		
UM ROOT # M^2 (ASU score ≥3)	0.6069	0.5327
LARGE HYPOCONE M^2 (P = 3+; A = 3-)	0.4593	0.4839
METACONULE M^1		
CARABELLI'S M^1 (ASU score 2-7)		
PARASTYLE M^3 (ASU score 1-5)		
MIDLINE DIASTEMA		
CONGENITAL ABSENCE M^3 (P = 1)		
PALATINE TORUS		
MANDIBULAR TORUS	0.7887	**0.0000**
ROCKER JAW	0.1156	**0.0005**
Total significant values	**1**	**3**

LIST OF APPENDICES ON CD

Appendix 10. Metric raw data, including crown and cervical measurements for the Khoesan, Kenyan and Mid-Late Pleistocene data sets.

Appendix 11. Raw non-metric data, including scoring for up to 52 traits for the Khoesan, Kenyan and Mid-Late Pleistocene data sets.

Appendix 12. Khoesan frequency data across all regions and through time.

Appendix 13. Khoesan and Mid-Late Pleistocene regional chi-square results through time.

Appendix 14.1-14.5. Component loadings for third and subsequent components extracted from PCAs (PC3, PC4 etc.)