

A record of human evolution in South Africa

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Introduction

Overwhelming fossil and genetic evidence indicate that Africa is the cradle of humankind. South Africa, along with East Africa, preserves the earliest and most complete record of human evolution anywhere in the world. In South Africa, this record commences around 3 million years ago, while in East Africa it is even earlier, currently reaching back to 6 or 7 million years ago. Prior to the origins of our genus *Homo*, South Africa and East Africa were home to different, but closely related species of our earliest ape-like ancestors, the Australopithecines. Since the appearance of *Homo* though, South Africa has shared human ancestral species with other regions of Africa, Europe and Asia. Although South Africa appears to be intricately linked to the story of our own species, its exact role is not clear. Some of the earliest fossil evidence of anatomically modern *Homo sapiens* was found at the cave site of Klasies River, on South Africa's south coast. This does not mean that anatomically modern *Homo sapiens* evolved in South Africa though. Other similarly aged anatomically modern *Homo sapiens* fossils have been discovered in the Near East, at the site of Qafzeh. Although fossil and genetic evidence strongly suggests that anatomically modern *Homo sapiens* evolved in Africa, we currently do not know exactly where in Africa we first evolved.

Interestingly, the Khoesan people of southern Africa (Fig. 1) have long been viewed as the direct descendents of the earliest anatomically modern *Homo sapiens*. According to Tobias (1978) the geographic range of early Khoesan groups extended over much of southern, eastern and north-eastern Africa. Genetic research carried out over the last 20 to 30 years appears to reinforce the longstanding hypothesis that the Khoesan were the aboriginal population of southern, eastern and north-eastern Africa (Tobias 1978; Nurse *et al.* 1985).

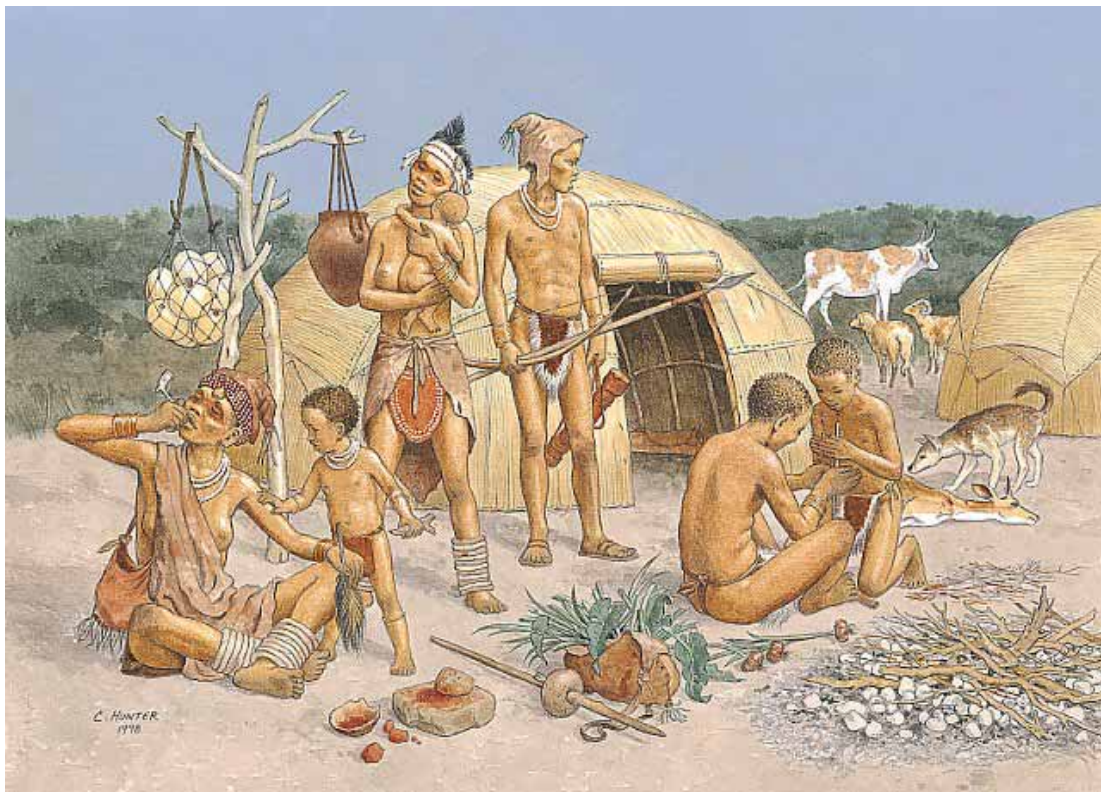


Figure 1. A reconstruction of camp life in a pre-colonial Khoesan camp (artist: Cedric Hunter. © Iziko Museums of Cape Town).

Serological research on recent Nguni speakers and San groups emphasized the “exaggeratedly African” genetic character of the San, which was interpreted as evidence for their closer genetic affinity to ancestral African peoples (Tobias 1972, 1978). More recent genetic research continued in this vein. Soodyall and Jenkins (1992) placed the divergence between three major genetic groupings of sub-Saharan people - Khoesan, Pygmy and Negroid - at approximately 150 000 years ago.

Intriguing though the recent genetic evidence may appear, the existence of an ancient, once wide-ranging Khoesan population does not receive support from the osteological record (Morris 2002, 2003). After reviewing the fossil evidence for an extra-southern African presence (Galloway 1933; Leakey 1970; Tobias 1964, 1978), Morris (2002, 2003) was unable to find any unambiguous evidence for the presence of Khoesan traits in several East African cranial specimens which in the past had been identified as Khoesan. Claims that existing Khoesan populations represent the remnants of an ancient Pan-African population (Tobias 1972, 1978) have also not stood up to scrutiny of the South African fossil human record. Instead, Morris (2002, 2003) has suggested that the Khoesan phenotype developed relatively recently (during the terminal late Pleistocene) in South Africa and never spread to the rest of the continent. Below, the role that South Africa has played and continues to play in our understanding of human evolution, is discussed in further detail.

The Australopithecines

In South Africa, the earliest member of our lineage is the 3 to 2.5 million year old species, *Australopithecus africanus*. The holotype of this species is a juvenile skull with endocranium which was discovered in 1924 at the Buxton Limeworks near Taung in the North West Province. Nicknamed the Taung Child (Fig. 2), this little skull was formally described and named in 1925 by Raymond Dart, an anatomist then at the University of the Witwatersrand.



Figure 2. The Taung child skull with endocranium.



Figure 3. Cast of the *A. africanus* skull Sts 5, also known as Mrs. Ples (©Transvaal Museum).

The most obvious trait which distinguishes this specimen from recent apes and identifies it as a member of the human lineage, is the position of the foramen magnum which is antero-inferiorly situated, indicating that it walked bipedally. In addition to this, it differs from apes by possessing a rounded, high forehead without browridges, reduced levels of facial prognathism, small canines and incisors. The Taung Child was not entirely human though. It still displays many primitive features which, amongst others, include facial prognathism, a lack of a chin and nasal bones which are broader inferiorly (Dart 1925).

The first adult specimens of *A. africanus* were discovered at Sterkfontein Caves in Gauteng in 1936 by Robert Broom, a palaeontologist at the Transvaal museum in Pretoria. Since then further

specimens have been discovered at Sterkfontein and at Makapansgat (Aiello and Dean 1990). One of the most famous adult *A. africanus* specimens to be found is the skull STS 5, popularly known as Mrs Ples (Fig. 3). Mrs Ples was discovered at Sterkfontein caves by Dr. Robert Broom and John Robinson in 1947.

In 1938, Broom discovered an early hominid (TM 1517) (Fig. 4) at Kromdraai which differed markedly from the previously discovered *A. africanus* remains (Johanson and Edgar 1996). This new discovery exhibited a prominent bony sagittal crest, a large and robust mandible and large premolars and molars. Subsequently more remains of these robust hominids were discovered at Swartkrans and Driemolen (Brain 1970; Keyser 2000). Broom considered the morphology displayed by this new find to be so uniquely different from that of *A. africanus*, that he placed it into a newly created genus, *Paranthropus*. Based on its robust morphology, it was given the species name *robustus*, thus *Paranthropus robustus* was born (Fig. 5). Today, these “robust” hominids which date to between 1.8 and 1.3 million years ago, are either referred to as *Australopithecus robustus* or *P. robustus* in the literature. This discrepancy reflects the differences of opinion in the field concerning the significance of morphological differences between *A. africanus* and the robust hominids (Grine and Martin 1988; Turner and Wood 1993; Clarke 1996).



Figure 4. TM1517, *A. robustus* maxilla, middle face and cranial base (©Transvaal Museum).



Figure 5: SK 48, *A. robustus* skull (©Transvaal Museum).

Early *Homo*

The earliest *Homo* species, namely *Homo habilis* and *Homo erectus*, are rare in the South African fossil record and are better known from the East African record. In South Africa, the earliest *Homo* remains, SK 847 (Fig. 6) from Swartkrans, were initially misidentified as belonging to *A. robustus* (Clarke and Howell 1972). This is not surprising since early *Homo* overlapped in time to a large extent with *A. robustus*. These remains, which consist only of the maxilla, left orbit and zygomatic region, were later reconstructed (Clarke 1994). Although most researchers now regard these as belonging to *Homo*, there is disagreement about which early *Homo* species it actually belongs to. Some regard it as *Homo habilis*, (Henke and Rothe 1994; Schrenk 1997) while others assign it to the later *Homo erectus* (Clarke 1994).

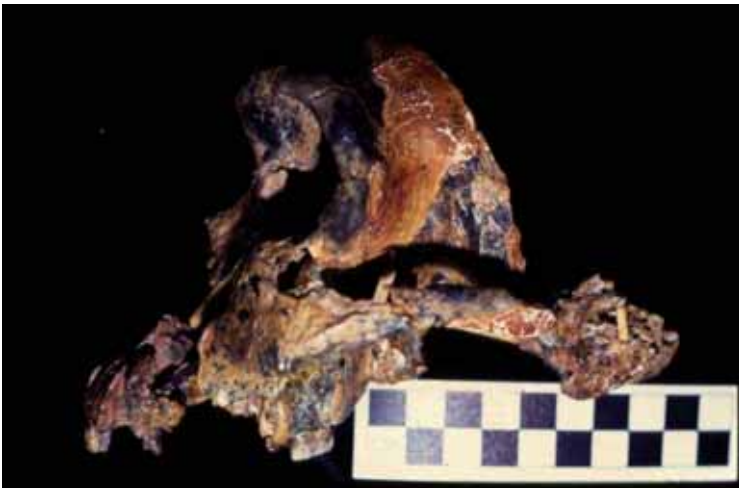


Figure 6. SK 847, early *Homo* face (©Transvaal Museum).

“Archaic” *Homo sapiens*

The earliest post *Homo erectus* fossil discovered in South Africa was found deflating out of a deflation hollow on the farm Elandsfontein, near the town of Hopefield, on the South African West coast. Although this fossil calotte (Fig. 7), which dates to between 500 000 and 200 000 years, resembles *Homo erectus* in terms of its massive brow ridges and flat, receding frontal, its inferred cranial capacity of 1200 – 1250 cc (Drennan 1953) far exceeds that of *Homo erectus* (Klein 1989). This, in addition to its presumed age, suggests that this calotte more likely belongs to a type of “archaic” *Homo sapiens* (Fig. 8) rather than to *Homo erectus*.

Another “archaic” *Homo sapiens* calotte and partial face was discovered in 1932 in a spring deposit on the farm of Florisbad, near Bloemfontein (Dreyer 1935). An early radiocarbon date of 43 700 BP (Pta 3465) indicated that the Florisbad fossil remains lay beyond the limits of radiocarbon dating. Grün *et al.* (1996) performed ESR dating directly on its molar. They reported a weighted mean age of $259\,000 \pm 35\,000$ years (Grün *et al.* 1996).

This partial skull was initially reconstructed by Dreyer shortly after its discovery (Clarke 1985). In his description of the fossil, Dreyer (1935) emphasised its uniqueness compared to other fossil *Homo sapiens*, by assigning it the new species name *Homo (Africanthropus) helmei*. Clarke (1985) reported that Dreyer’s reconstruction of the Florisbad cranium had been faulty though. Clarke (1985) performed a more accurate reconstruction, giving Florisbad a broad palate and large nasal cavity. Rather than resembling any modern populations, Clarke (1985) argues that the new reconstruction closely resembles other “archaic” *Homo* fossils such as Ngaloba and Omo 2.



Figure 7: The Elandsfontein skull cap (© Iziko Museums of Cape Town).

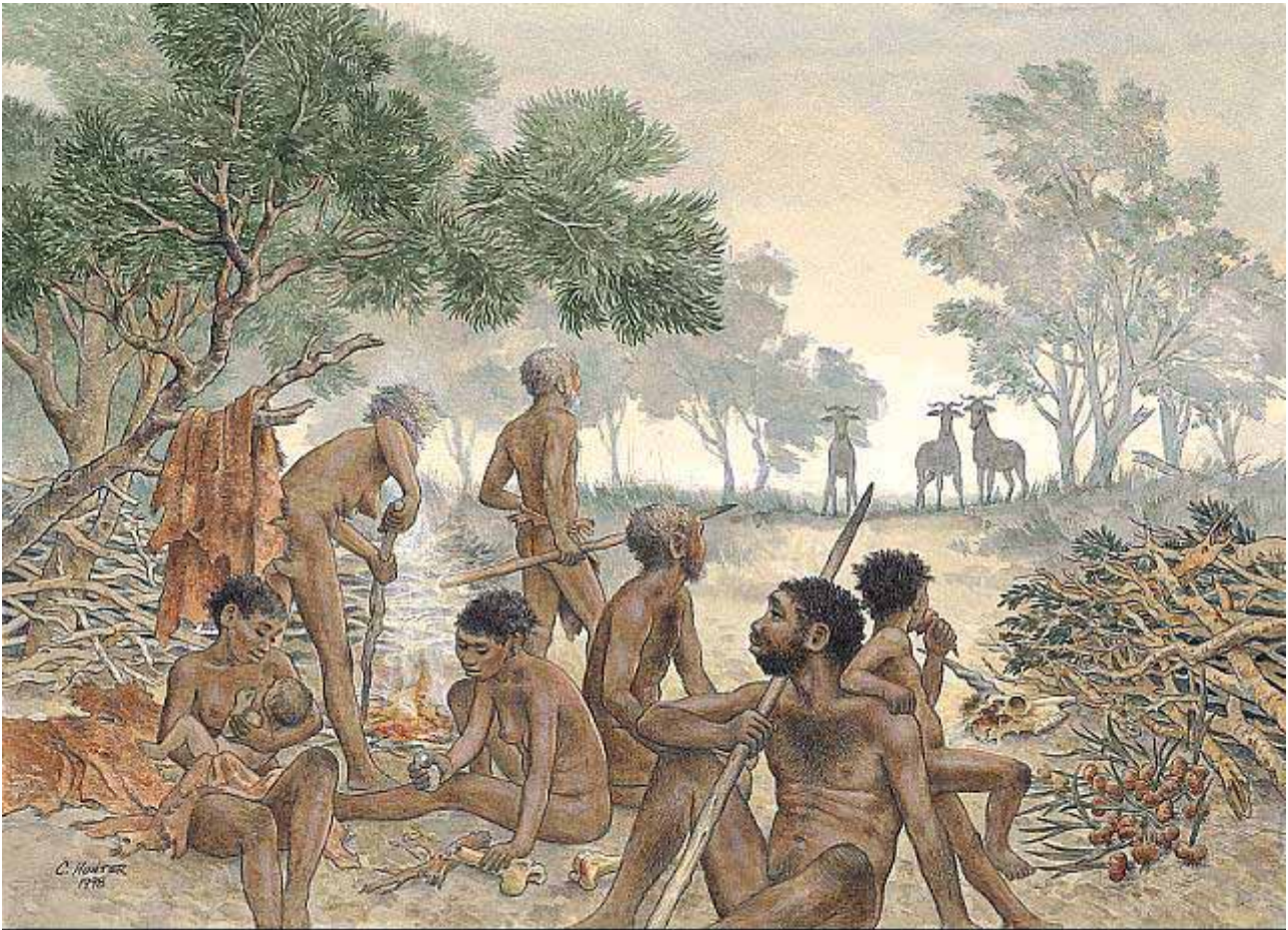


Figure 8: A reconstruction of the Elandsfontein people (artist: Cedric Hunter. © Iziko Museums of Cape Town).

Anatomically modern *Homo sapiens*

The earliest anatomically modern *Homo sapiens* fossils discovered in South Africa come from the cave site of Klasies River, on South Africa's south coast (Fig. 9). Approximately 30 fragmentary cranial and postcranial bones were discovered. The fossils are not all of a single age, but were scattered throughout the deposits. The majority of these have now been reliably dated to between 90 000 and 120 000 years ago (Deacon *et al.* 1988; Grün *et al.* 1990).



Figure 9: The Klasies River mandible.

Singer and Wymer (1982) were the first to suggest that there may have been biological continuity between the Klasies River people and the ancestors of recent Khoesan people. They note that the Klasies River fossils display a generalised African morphology, as might be expected in the ancestors of the Khoesan (Singer and Wymer 1982). Morphological links between Klasies River and recent populations are however difficult to establish. Morris (1992b) has argued that the human sample from Klasies River is too small and fragmentary to demonstrate morphological continuity. Apart from the sample issue however, there are also questions around the modernity of the Klasies material. Although the Klasies River fossils have often been held up as representing some of the earliest evidence for the presence of anatomically modern humans in Africa, the modernity of the Klasies fossils are not beyond doubt. Opinions have varied greatly with some concluding that the Klasies River people were essentially modern (Singer and Wymer 1982; Braüer 1984, Rightmire and Deacon 1991; Braüer *et al.* 1992) and others believing that they were not quite modern yet (Caspari and Wolpoff 1990; Frayer *et al.* 1994; Lam *et al.* 1996).

Additional anatomically modern *Homo sapiens* material was found at the site of Border Cave on the KwaZulu/Natal side of the international border with Swaziland. Uncertainties surrounding the stratigraphic provenance of the Border Cave specimens have hindered attempts to date them. The ages for BC 1 (a cranium) and BC 2 (a partial and edentulous mandible) are most uncertain, because these specimens were found in disturbed contexts. BC 3 (a partial infant skeleton) and BC 5 (a partial mandible) may have been intrusive burials and thus younger than the units in which they were found (Sillen and Morris 1996). Beaumont (1980) nonetheless has argued that BC 1-3 and BC 5 derive from levels in the cave that had been dated by ESR to between 80 000 and 55 000 years. A recent direct ESR date of $74\,000 \pm 5000$ on tooth enamel appears to support an early date for at least BC 5 (Grün *et al.* 2003).

Despite Schwartz and Tattersall's (2003) comments about the lack of a central keel on BC 5, most researchers who have studied the Border Cave remains agree that they are anatomically modern. Opinion is however divided on whether they resemble modern African populations (de Villiers 1973, 1976; Rightmire 1979, 1981; de Villiers and Fatti's 1982; Ambergen and Schaafsma 1984; Van Vark 1986).

The generalised African morphology of these early modern South African fossils is also visible in more recent late Pleistocene specimens. In 1947, B. Kitching found a mandible in the Cave of Hearths, in the Makapansgat Valley, Limpopo Province. The mandible has not been securely dated but is probably of late Pleistocene origin. According to Clark (1964), the fossil originated from the cave's Acheulean levels. However, Mason (1962) supported a late Pleistocene date. Later Oakley *et al.* (1977) reported a date of $>16\,000$ years for the Middle Stone Age level overlying the level in which the fossil had been discovered. Schwartz and Tattersall (2003) note that this fossil has a moderately developed chin, an archaic trait displayed by other late Pleistocene South African fossils such as Klasies River and Border Cave.

An almost complete human cranium was discovered in 1954 in the Hofmeyr district, Eastern Cape Province, South Africa. Grine *et al.* (2007) report a date of around 36 000 years for this specimen. Its morphology has been described as being a mosaic of archaic and modern traits (Morris and Grine 1999). Grine *et al.* (2007) report that the Hofmeyr cranium falls outside the range of variation displayed by modern Khoesan crania in most aspects of craniofacial morphology. Instead, analyses of facial dimensions and vault curvature surprisingly situate the Hofmeyr cranium within the range of variation of European Upper Palaeolithic crania.

The origins of southern African's indigenous Khoesan

If early anatomically modern *Homo sapiens* fossils from South Africa do not display any clear affinities with recent indigenous South African populations, where and when did these populations develop? Bantu speakers such as the Xhosa and Zulu, are not indigenous to South Africa. Their ancestors probably originated in West Africa, and migrated into southern Africa during the last 2000 years (Giliomee 1979; Peires 1981). The Khoesan however, are probably an indigenous southern African development (Morris 2002, 2003).

The term “Koisan” (now Khoesan) was a biological term coined by Leonhard Schultze in 1928, to refer to a large cluster of related indigenous southern African peoples, distinct from Bantu-speakers. Subsequently, Khoesan has also been used as a cultural and linguistic label (Barnard 1992). All Khoesan groups speak click languages. Two major language divisions can be identified, namely “Bush”-speakers (Westphal 1963) and Khoe-speakers (Köhler 1962; Westphal 1971). Common features in territorial organisation, gender relations, kinship, ritual and cosmology are also shared across all Khoesan groups (Barnard 1992). Morphologically the Khoesan, as a population cluster, exhibit a number of characteristics such as light yellow-brown skin, epicanthic eyefolds, female steatopygia, female steatomerya and micronympha which makes them markedly distinct from neighbouring Bantu-speakers.

The first European contact with Khoesan peoples dates back to 1488, when the Portuguese mariner Bartolomeu Dias sailed his caravelle around the southern tip of Africa. Dias, and fellow Portuguese mariner Vasco Da Gama who followed Dias around the Cape of Good Hope in 1497, mentioned these peoples in their diaries. However, accounts were brief and not very informative. It was only after the Dutch East India Company (VOC) established the first permanent European settlement at Table Bay in 1652 that more informative accounts were produced on the culture and life ways of the Khoesan (Elphick 1985). Much was written about the Khoesan by these early settlers, however, the vast majority of accounts were fragmentary and often unreliable. The most voluminous was the 1652-1662 Journal of Jan van Riebeeck (Thom 1958), the first Dutch commander of the Cape, which commented extensively on the groups around the settlement and also occasionally on those living further inland. Nomadic herders and small groups of beachcombers who subsisted mainly by hunting-and-gathering, occupied much of the literature during the initial period of settlement, as these people lived close to the Dutch outpost. It was only later that contact was made with inland hunter-gatherer groups, when expeditions were despatched into the interior. The settlers adopted the name ‘Strandlopers’ for the beachcombers and ‘Hottentots’ for the herders. The herders referred to themselves as ‘Khoekhoe’ (previously Khoikhoi). The inland hunter-gatherers were called Soaqua or Bushmen by the Dutch and ‘Sonqua’, ‘Soaqua’, ‘Obiqua’ or ‘San’ by the Khoekhoe (Barnard 1992; Boonzaier *et al.* 1996).

Early accounts widely declared that the nomadic pastoralists, beachcombers and inland hunter-gatherers represented mutually exclusive populations, each of whom possessed their own distinctive modes of social organisation, language and material culture. Expedition diaries in particular, commented extensively on the hunter-gatherer bands in the interior. Typical descriptions of them included “poverty-stricken”, “tiny people” and “plunderers and marauders” (Schapera and Farrington 1933; Thom 1958). In many instances these descriptions were juxtaposed against more favourable descriptions of the purportedly taller, better-off herders. As illustrated by these early accounts, the Dutch paid particular attention to perceived differences between the inland hunter-gatherers and herders. Differences in stature in particular were taken to signify ethnic differences between the practitioners of the two life ways. In this way, early perceptions contributed significantly to the establishment of a supposed dichotomy in ethnicity/life ways that became entrenched in South African Khoesan studies for much of its early existence. Today however, this is not universally accepted (Marks 1972; Schrire 1980).

Morris (2002, 2003) has hypothesised that the Khoesan morphotype arose relatively late in South Africa. According to Morris’ (2002, 2003) hypothesis, the ancestors of recent Khoesan populations underwent a bottleneck associated with the Last Glacial Maximum (LGM) at *ca.* 24 000 B. P. to 17 000 B. P. At this time the cool, dry glacial climate would have resulted in the aridification of much of southern Africa, particularly the inland regions. A scarcity of inland archaeological occurrences suggests significant depopulation of these areas (Mitchell 1990; Wadley 1993). At the same time, a large area of land would have been exposed along South Africa’s southern coast, with an extended coastal plain of over 100 kilometres at some places (van Andel 1989). Unlike the interior, the better watered southern coastal region displayed comparatively denser human occupation at this time (Parkington 1990). It is further hypothesised that the genetic isolation of this coastal population for the duration of the LGM would have resulted in genetic drift

and directional selection. These evolutionary processes would eventually have led to the differentiation of this population from other African populations and thus to the emergence of Khoesan populations (Morris 2002, 2003). At the end of the glacial period, there would have been a population expansion which would have resulted in the expansion of Khoesan morphology into the rest of southern Africa (Morris 2002).

Osteological evidence (Bräuer and Rösing 1989; Morris 1992 a, b; Stynder 2006; Stynder *et al.* 2007) appears to support Morris' (2002) hypothesis of a relatively recent southern African origin of recognisably Khoesan cranial morphology. In accordance with his model, terminal Pleistocene/early Holocene human crania do indeed display a general Khoesan craniofacial pattern, particularly with regards to upper facial form (Bräuer and Rösing 1989). According to Bräuer and Rösing (1989), fossils such as the 10 000 year old Albany Man (Bräuer and Rösing 1989) and various similarly aged fossils from sites such as Matjes River Rock Shelter, Wilton Large Rock Shelter and Oakhurst, possess the small, broad (euryprosopic) upper faces typical of recent Khoesan populations (Fig. 10). One notable aspect of these early Holocene people is their large size and robust bone structure, which was for a long time thought to be rare amongst recent Khoesan people (Bräuer and Rösing 1989).

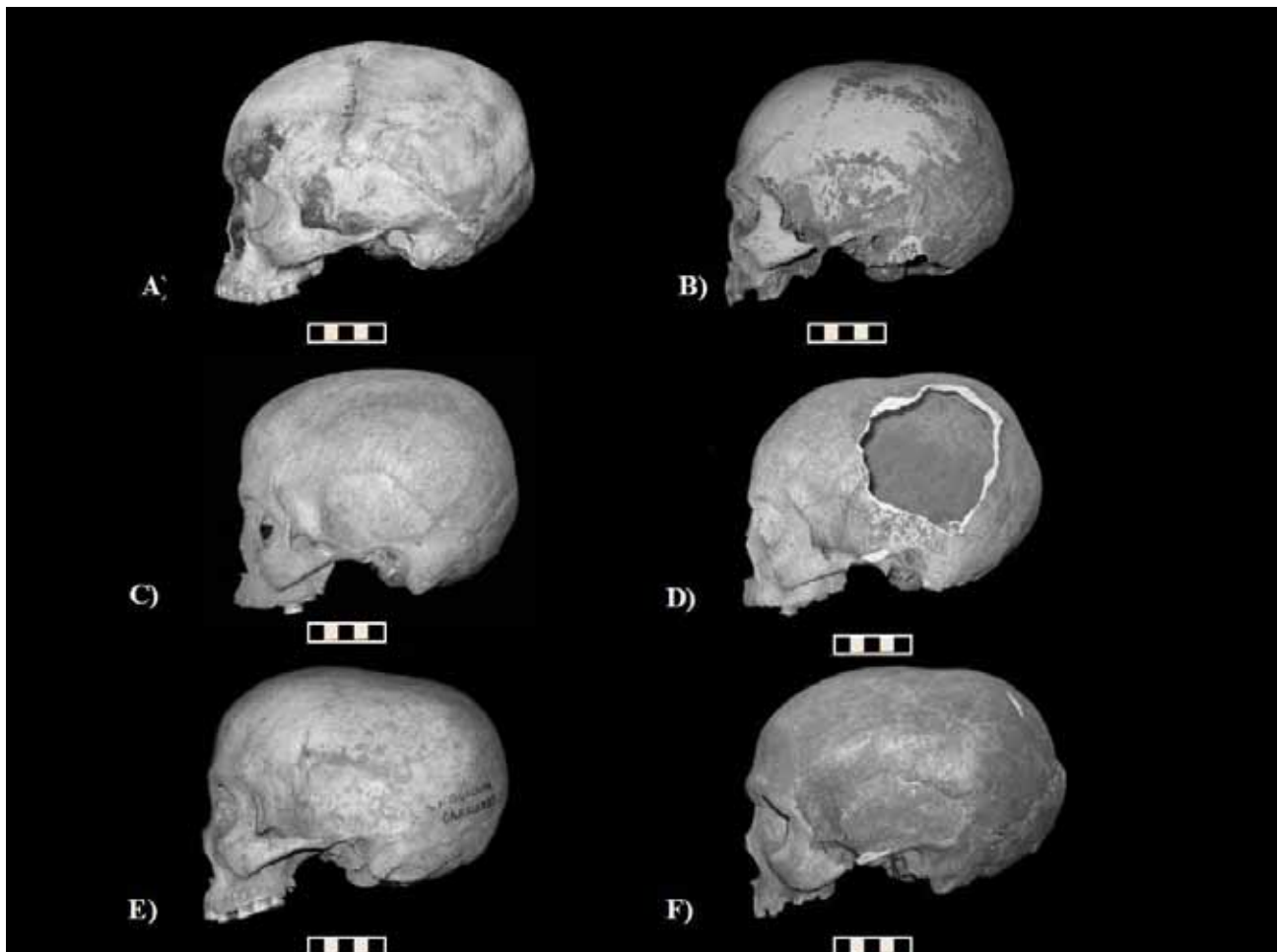


Figure 10. Early Holocene South African LSA human crania (© author).

Small body size however only appears to have been prominent during the mid-Holocene. Between approximately 4000 and 3000 BP, populations in the Fynbos Biome exhibited dramatic reductions in stature (Pfeiffer and Sealy 2006). At the same time, there was a reduction in overall cranial size and robusticity levels (Stynder 2006; Stynder *et al.* 2007) (Fig. 11). The fact that there was a simultaneous reduction in post-cranial and cranial size suggests a reduction in overall body dimensions at this time. The specific causes of this reduction are not clear. Reductions in body size occurred after the early to early mid-Holocene increase in temperature (*ca.* 8000 BP – 6000 BP). An

increase in climatic conditions therefore could not have been responsible for the observed changes. Changes in craniofacial form also occurred prior to the introduction of pastoralism, farming and pottery vessels to the region (*ca.* 2000 BP). Since the types of food available to people and the method of food preparation remained relatively unchanged for the Holocene prior to 2000 BP (i.e. hunting and gathering), biomechanical changes associated with alterations in diet can also not explain the changes in craniofacial form. A lack of large scale cultural change between 4000 and 3000 BP largely precludes the genetic influence of a migrant population (Deacon 1984). There is also very little evidence of widespread infectious disease which could have restricted growth at this time (Pfeiffer 2002; Pfeiffer and Crowder 2004). According to Pfeiffer and Sealy (2006), the most likely cause may be chronic and/or cyclical insufficiency of nutrients. Interestingly, there was a recovery in stature levels which started at *ca.* 3000 BP (Pfeiffer and Sealy 2006). A concurrent recovery in size occurred in the craniofacial skeleton (Fig. 12), strengthening the argument that the late mid-Holocene reduction in Khoesan cranial size was due to environmental factors and not to genetic changes in the population (Stynder 2006; Stynder *et al.* 2007).

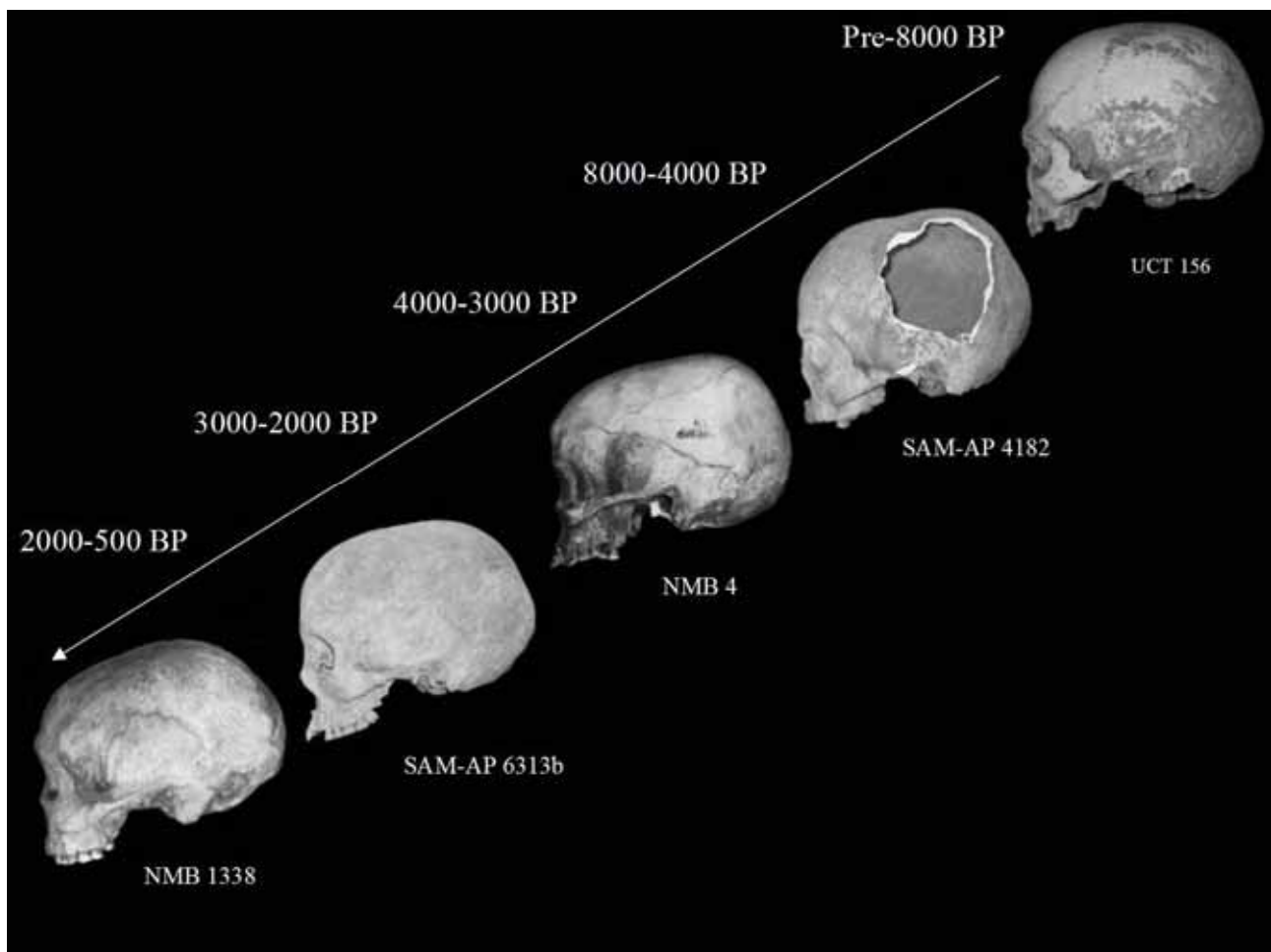


Figure 11. Five morphotypes (all male) of different radiocarbon age which summarise the primary craniofacial change in South African Holocene populations (© author).

Archaeological evidence has revealed that herding was introduced to South Africa at *ca.* 2000 BP. Until now however, archaeological research has been unable to determine conclusively whether the introduction of domesticates was facilitated by the migration of biologically distinct herders from further north in the continent, or whether herding entered the region via the acculturation of local hunter-gatherers. Recent analyses of human cranial remains from this time indicate that there was no significant biological change in local human populations at 2000 BP (Stynder 2006; Stynder *et al.* 2007). The question thus remains as to how the biological differences, if any, between San hunter-gatherers and Khoekhoe herders, developed. If early accounts of

morphological differences between these two groups are accepted as accurate, differences in stature between hunter-gatherers and herders could be explained by two alternatives to gene flow, namely, (1) *in situ* genetic differentiation due to emerging social and economic differences between the practitioners of the two life ways; and (2) hunter-gatherers and herders having differential access to high nutrient resources.

Post-2000 BP Khoesan may have started to differentiate biologically into San and Khoekhoe populations due to growing *in situ* social and economic differences between herders and hunter-gatherers after some indigenous hunter-gatherers had acquired domestic stock from herders further north. This hypothesis was first suggested by Hausman (1980). As suggested by Elphick (1985) and Parkington and Hall (1987), the nature of hunting-and-gathering appeared to have changed during the last 2000 years due to ecological and social pressures exerted on non-stock owners by those who owned stock. Parkington and Hall (1987) note further that herder groups appeared to have dominated the political, social and economic spheres during the last 2000 years. The social, economic and political separation between stock-owners and those lacking in stock may have grown stronger with time, eventually leading to the erection of social barriers to gene flow between hunter-gatherers and herders. This lack of gene flow between the two populations may eventually have expressed itself in morphological differentiation between the practitioners of the different life ways. The archaeological record is consistent with the gradual establishment of pastoralism in the region. As noted by Sadr (1998), traces of herders are often quite ephemeral between 2000 and 1000 BP and do not resemble the sophisticated cattle herding societies that European colonists described on their arrival at the Cape. The emergence of these cattle herding societies may have been a relatively recent development, possibly dating to the second millennium AD.

Differences in body size and robusticity levels between hunter-gatherers and herders may also be explained by differential access to high nutrient resources. Several researchers have suggested that hunter-gatherer and herder archaeological remains in the post-2000 BP period can probably be attributed to people from the same biological population moving back and forth between the two economic strategies (Marks 1972; Schrire 1980, 1992; Elphick 1985; Schrire and Deacon 1989). As mentioned above, herder groups appeared to have dominated the political, social and economic spheres during the last 2000 years. Marginal groups, usually those without any stock or those who had lost stock, were consequently pushed to the periphery of society. At the same time, these groups were also forced out of the higher nutrient coastal forelands, towards the more marginal inland mountainous regions (Parkington and Hall 1987). Colonial era accounts often make mention of impoverished marginalised groups living in the mountainous regions of the Cape (Thom 1958). There, these populations usually survived by hunting-and-gathering and stock rustling (Elphick 1985). The nutritional and social stress that post-2000 BP hunter-gatherer groups would have been placed under, could explain why they may have been smaller than people who owned stock. In contrast, stock owners not only had access to higher nutrient regions, unlike hunter-gatherers, they also had access to a regular supply of milk, which could have aided growth during childhood, thus allowing them to reach their full growth potential (Hausman 1980).

Contemporary Khoesan groups have to a large extent been marginalised and isolated to the drier, less productive regions of southern Africa. From the outset of the colonial period, a process was set in motion whereby the Khoesan were systematically dispossessed of their land, stock and political power. Their biological and cultural demise in the Cape was finally sealed by a devastating smallpox epidemic that swept through the Cape of Good Hope and surrounding regions in 1713. The integration of survivors into the social and economic structures of the colonial Cape, and the constant persecution of surviving bands living beyond the boundaries of the colony sealed their fate (Elphick 1977, 1985; Steyn 1990). Today, the biological influence of the Khoesan is still in evidence in the faces of people of mixed genetic heritage who still live in the Cape.

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