Contents lists available at ScienceDirect

Quaternary Science Reviews

Pleistocene sea-level fluctuations and human evolution on the southern coastal plain of South Africa

John S. Compton

Department of Geological Sciences, University of Cape Town, Rondebosch 7700, South Africa

A R T I C L E   I N F O

A B S T R A C T

Humans evolved in Africa, but where and how remain unclear. Here it is proposed that the southern coastal plain (SCP) of South Africa may have served as a geographical point of origin through periodic expansion and contraction (isolation) in response to glacial/interglacial changes in sea level and climate. During Pleistocene interglacial highstands when sea level was above −75 m human populations were isolated for periods of 360−3400 25-yr generations on the SCP by the rugged mountains of the Cape Fold Belt, climate and vegetation barriers. The SCP expands five-fold as sea level falls from −75 to −120 m during glacial maxima to form a continuous, unobstructed coastal plain accessible to the interior. An expanded and wet glacial SCP may have served as a refuge to humans and large migratory herds and resulted in the mixing of previously isolated groups. The expansive glacial SCP habitat abruptly contracts, by as much as one-third in 300 yr, during the rapid rise in sea level associated with glacial terminations. Rapid flooding may have increased population density and competition on the SCP to select for humans who expanded their diet to include marine resources or hunted large animals. Successful adaptations developed on an isolated SCP are predicted to widely disperse during glacial terminations when the SCP rapidly contracts or during the initial opening of the SCP in the transition to glacial maxima. The hypothesis that periodic expansion and contraction of the SCP, as well as the coastal plain of North Africa, contributed to the stepwise origin of our species over the last 800 thousand years (kyr) is evaluated by comparing the archeological, DNA and sea-level records. These records generally support the hypothesis, but more complete and well dated records are required to resolve the extent to which sea-level fluctuations influenced the complex history of human evolution.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Archeological and genetic evidence indicate that our species (*Homo sapiens*) emerged by a series of complex evolutionary events in Africa (McBrearty and Brooks, 2000; Behar et al., 2008). Large bifacial handaxes typical of the Acheulean artifact assemblage of the Early Stone Age (ESA) are believed to have been made by *Homo ergaster/erectus* from 1800 thousand years ago (ka). The transition to more refined and smaller handaxes of the later Acheulean between 1000 and 600 ka (Kuman, 2007) may correspond to the emergence of early archaic humans (*H. heidelbergensis/H. rhodesiensis*) and the transition to largely hafted, finer stone tools (blades and flakes) of the Middle Stone Age (MSA, equivalent to the Middle Paleolithic of Europe) between 600 and 250 ka may correspond to the emergence of later archaic humans (*H. helmei*) (Clark, 1992; Foley and Lahr, 1997; Tryon and McBrearty, 2002). Regional specialization and transitional industries such as the Fauresmith

and Sangoan suggest that archaic humans were increasingly more culturally varied and heterogeneous than their predecessors (McBrearty and Brooks, 2000), cultural identity being one of the defining features of modern humans. Fossils recovered from Ethiopia indicate that archaic humans were replaced by more gracile, larger brained anatomically modern humans (AMH) (*H. sapiens*) by 200 to 155 ka (White et al., 2003; McDougall et al., 2005). These fossil dates are supported by the deepest split in matrilineal diversity between living southern (Khoisan) and East Africans estimated between 213 and 154 ka with dispersal of AMH throughout Africa and beyond resulting in a 'bushing out' of the human phylogenetic tree into over 40 matrilineal clades by 40 ka (Behar et al., 2008; Atkinson et al., 2009).

The appearance in the archeological record of sophisticated tools, shell jewelry and engraved ochre between 120 and 60 ka has been interpreted to reflect the emergence of modern human behaviors of innovation, language and cultural identity (Henshilwood et al., 2004; Marean et al., 2007). The gap between the appearance of AMH and the development of modern behaviors suggests increased

functional organization and capacity of the brain (Klein, 2009). The development of modern behaviors appears to have increased the ability of AMH to adapt to diverse environments and allowed for their rapid expansion and displacement of archaic human groups throughout Africa and beyond (Mellars, 2006). Following an intervening enigmatic period of retro MSA tools and few personal ornaments (D'Errico et al., 2009), finely worked, backed geometric 'microlith' stone tools appeared between 40 and 30 ka to mark the transition to the Later Stone Age (LSA, equivalent to the Upper Paleolithic of Europe) which culminated in the diverse toolkit of historical hunter-gatherers (Deacon and Deacon, 1999; Klein, 2009).

Homo ergaster/erectus was a highly successful species. Although largely restricted to valley wetland environments, it had control of fire, was widespread beyond Africa (Out of Africa I) and went relatively unchallenged from 1800 to 800 ka. The evolution of *Homo* since 800 ka has been attributed to both random genetic mutations which favored greater cognitive capacity (Klein, 2009) and selection pressures to adapt to variable resources associated with increasingly large climate-driven environmental changes (e.g., Lahr and Foley, 1998). Correlation of the archeological and climate records is debated (Deacon, 1990; Jacobs and Roberts, 2008) and difficult to assess given the incompleteness of the archeological record and uncertainties in the reconstruction of past climates particularly on regional scales and over millennial timescales. The African continent includes a wide range of geographical regions (Fig. 1) with distinct climate, hydrology, flora and fauna (e.g., O'Brien and Peters, 1999). Expansion and contraction of habitats in response to Pleistocene glacial to interglacial climate cycles (Adams and Faure, 1997), particularly in the last 800 kyr, may have driven the emergence of our species and the punctuated appearance of our increasingly modern behavior. One possible mechanism driving human evolution is periodic isolation of human groups (allopatry), particularly if isolation is associated with selection pressures to adapt to, for example, higher population density or variable resources. In East Africa variations in rainfall may have fragmented and isolated groups into highland, lake or river refugia (Lahr and

Fig. 1. Elevation of the African continent and surrounding ocean basins (ngdc.noaa.gov) showing the Southern African Plateau, shelf area (shaded in white) exposed during glacial maxima (−120 m), and the location of areas and archaeological sites discussed in the text.

Foley, 1998; Basell, 2008) and groups isolated in North Africa by the Sahara Desert were periodically reconnected to Africa during wet periods when the Sahara was transformed to grassland (Kuper and Kröpelin, 2006; Osborne et al., 2008).

The African continent has a number of shallow shelves (Fig. 1) whose extent and accessibility were directly impacted by large-amplitude (120 m) glacial to interglacial sea-level fluctuations. For example, the southern coastal plain (SCP) of South Africa, separated from Africa by the rugged sandstone mountains of the Cape Fold Belt, greatly expanded by virtue of the broad shallow-water shelf area of the Agulhas Bank during glacial maxima (Dingle and Rogers, 1972; Van Andel, 1989) to reconnect periodically with Africa (Fig. 2). Most of the archeological record on the shelf is submerged and unknown, but the coastal margin of the present-day SCP hosts several key MSA fossil sites which provide the earliest evidence for use of marine resources (Marean et al., 2007), engraved ochre and sophisticated stone tools (Henshilwood et al., 2004; Jacobs et al., 2008). In this paper the possible role of the SCP as a geographical point of origin for modern humans through periodic isolation and selective pressures driven by Pleistocene sea-level fluctuations is explored by comparing the archeological and DNA evidence to the sea-level record.

2. Variations in the southern coastal plain on glacial–interglacial cycles

2.1. Isolation of the SCP during interglacial periods

The SCP of the present-day interglacial highstand forms a geographical region having a distinct vegetation and climate and is physically separated from the rest of Africa by the Cape Fold Belt (CFB). The CFB consists of a series of resistant quartz sandstone folded mountains that rise up to 2 km in high relief to form a barrier between the SCP and Africa cut by only several narrow, rugged mountain passes. The steep and rugged mountain slopes of the CFB run parallel to the coast for 800 km between Cape Hangklip in the west and Plettenberg Bay in the east (Fig. 2). Cape Hangklip forms part of the fold syntaxis from which the CFB extends 200 km north to form a barrier between the SCP and western coastal plain (WCP). The CFB intersects the coast at Cape Hangklip to form rocky cliffs on the eastern shores of False Bay which prevent movement between the western and southern coastal plains. The SCP is bounded to the east by the broad intersection of the CFB at the coast between George and Port Elizabeth. Movement is prevented along the 4-km wide Plettenberg Bay coastal plain by dense afrotemperate (Knysna-Tsitsikamma) forest and north-south deeply incised river gorges which together rendered the coastal plain impenetrable by early European settlers until a road was built in the 1880s (Skead, 1982). The SCP is bounded to the north by continuous, parallel belts of the CFB which separate the SCP from the Klein Karoo and Great Karoo basins to the north. Further inland, the Great Escarpment marks the transition from the Great Karoo to the Southern African Plateau which has a mean elevation of around 1 km and extends as far north as 12°S (Fig. 1).

In addition to a physical barrier, the vegetation cover of the CFB presents a resource barrier to animal movement. The distribution of vegetation biomes in South Africa largely relates to bedrock geology and climate (Mucina and Rutherford, 2006) with the thin, nutrient-poor quartzose soils of the CFB dominated by the fine (microphyllous) and waxy (sclerophyllous) leafed vegetation of the sandstone fynbos biome. The sandstone fynbos biome plants are largely inedible in comparison to the mix of grass and browse of the shale renosterveld biome growing on nutrient-rich soils of deeply weathered Precambrian and Paleozoic shale bedrock. The
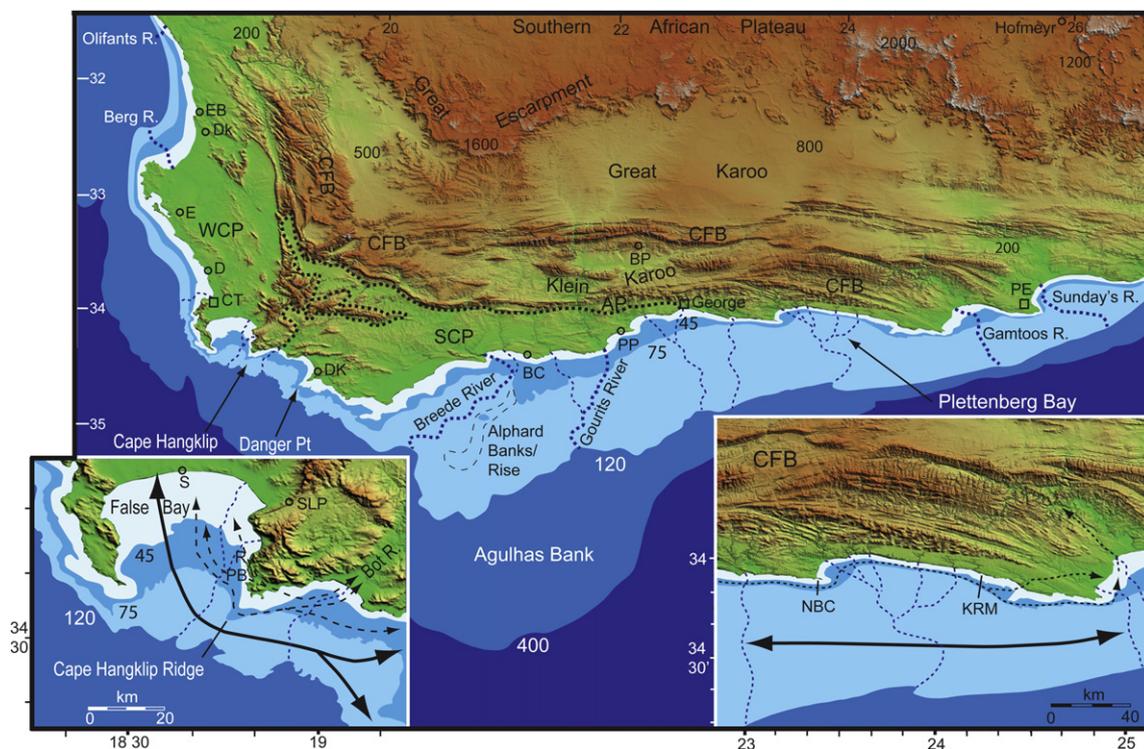

Fig. 2. Bathymetry (45, 75, 120 and 400 m contours (Van Andel, 1989)) and topography of southern Africa (numbers represent spot elevations) showing the extent (dashed line) of the southern coastal plain (SCP) separated from the interior and from the western coastal plain (WCP) by the Cape Fold Belt (CFB) mountains. The Cape Hangklip and Plettenberg Bay portals are enlarged to show possible migratory pathways during glacial lowerings of sea level. Key fossil and archeological sites indicated are Blombos Cave (BC), Bloomplaas (BP), Die Kelders (DK), Diepkloof (Dk), Duinefontein (D), Elandsfontein (E), Elands Bay (EB), Klasies River main (KRM), Nelson's Bay Cave (NBC), Pinnacle Point (PP), and Swartklip (S). Also shown are Sir Lowry's Pass (SLP), Attaquas Pass (AP), Pringle Bay (PB), Rooielsbaai (R) and the cities of Cape Town (CT), George and Port Elizabeth (PE).

landward or interior SCP is dominated by the shale renosterveld biome (73%) as is the WCP (64%) (Fig. 3). Early explorers describe grass standing waist-high on the WCP shale soils (Van Riebeeck, v. III, 347) and the bulbs (corms) of abundant geophytes provided an important seasonal source of carbohydrate to the diet of MSA and LSA people with the Khoisan intentionally setting fire to increase yield (Deacon and Deacon, 1999). Early burning followed by agriculture has obliterated and obscured the original flora, but the shale renosterveld was the principal biome which supported large animal herds on the coastal plain. Seaward of the shale renosterveld biome, the SCP is dominated by a mixture of limestone fynbos and strandveld biomes and on the WCP by a mixture of sand fynbos and strandveld biomes (Fig. 3). Although not as nutrient-rich as the shale renosterveld biome of the interior coastal plain, the strandveld (including dune and granite strandveld), sand fynbos and limestone fynbos biomes contain enough grass, herbaceous annuals and browse to have supported large game at least seasonally during the late Pleistocene (Klein et al., 1999).

Climate in southern Africa is variable with regional differences in the amount and seasonality of rainfall (Fig. 4). Climate of the SCP is distinct because rainfall occurs throughout the year and, although variable in its distribution, there are no barriers on the SCP to prevent animal migration to areas receiving rainfall. The western coastal plain (WCP) has a Mediterranean-type climate and receives most of its rain in the austral winter. The amount of rainfall decreases rapidly to the north with no perennial rivers in the semi-arid to arid WCP between the Olifants and Orange rivers. The interior and eastern areas receive most of their rain in the austral summer with increasingly arid climates to the west. Migration of large animal herds among the SCP, WCP and interior rainfall regions

is prevented by the CFB and its cover of largely inedible sandstone fynbos vegetation.

The succulent Karoo and Nama-Karoo biomes extend inland and north of the CFB (Fig. 3) to define an arid corridor, receiving less than 300 mm/yr of rainfall, which separates the summer interior rainfall and southwestern winter rainfall areas (Fig. 4). This arid corridor extends as far north as 23°S into southern Namibia and southwest Botswana and appears to have served as a barrier to seasonal herd migration between the interior and the coastal plain (Skead, 1982). However, elephants which are known to migrate long distances over interior arid landscapes and are capable of following seasonal river beds up to 50 km apart (Skead, 1982) may have been an exception with herds of up to several hundred elephants reported on the WCP in the journal of Van Riebeeck (v. III, 315). In addition, occasional migration of large herds of springbok was reported from the interior plateau down onto the WCP with early reports of an 'uncountable' number near the Olifants River and 10,000 migrating as far south as the vicinity of Cape Town (Skead, 1982). Springbok migrations are attributed to periodic drought conditions on the plateau, but historically did not extend onto the SCP and did not result in sustained springbok populations on the WCP.

Large numbers of antelope such as steenbok and eland were reported on the WCP (Van Riebeeck, v. II, 335) and herds of over 1000 bontebok were reported on the SCP by Schrijver in 1689 (Burman, 1969: 102). Large animals were probably significantly more abundant on the coastal plain prior to the arrival of pastoralists 2 ka, displaced by Khoisan herds estimated to number 20,000 cattle on the WCP south of the Berg River (Van Riebeeck, v. I, 372) and 7000 sheep and cattle in Namaqualand on the northern WCP (Van Riebeeck, v. III, 353). Comparison of the historical and fossil records indicates that large herd animals did not migrate between
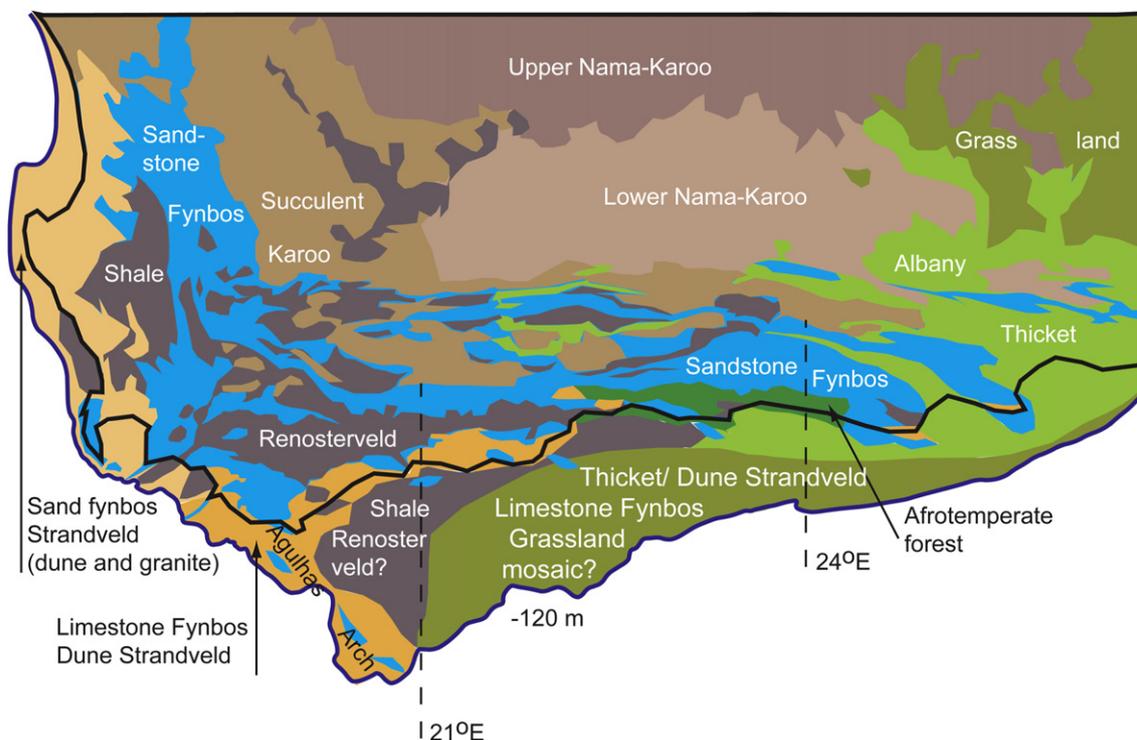

Fig. 3. Distribution of major vegetation biomes simplified from Mucina and Rutherford (2006). Largely inedible sandstone fynbos dominates nutrient-poor quartzose soils of the CFB. Largely edible renosterveld dominates nutrient-rich shale bedrock soils on the interior coastal plain; moderately (seasonally) edible sand fynbos and strandveld (dune and granite) biomes dominate the WCP; and limestone fynbos and dune strandveld biomes dominate the SCP adjacent to the coast. Impenetrable afrotemperate (Knysna-Tsitsikamma) forests occur along the narrow coastal plain between George and Plettenberg Bay. Albany thicket occurs within the Gamtoos and Sunday's River valleys. Vegetation biomes are projected onto the exposed glacial coastal plain based on the marine geology of the shelf (Dingle and Rogers, 1972). Dashed lines indicate location of profiles in Fig. 5.
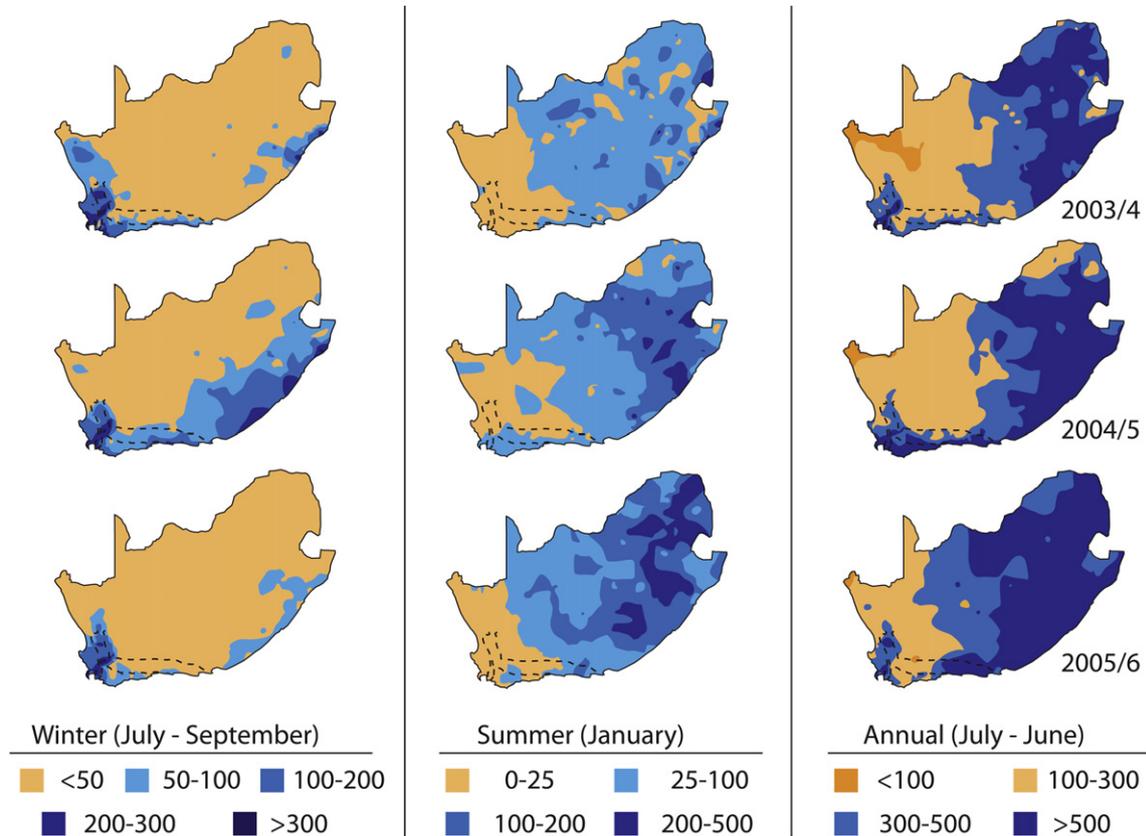
Fig. 4. Winter (July—September), summer (January) and year-round rainfall (mm) over South Africa for the years 2004, 2005 and 2006 (SA Weather Service website). The SCP receives rainfall year round. The WCP receives rainfall in winter and the eastern coastal plain and interior receive rainfall primarily in summer. Summer rainfall decreases to the west with an arid corridor separating it from the WCP. The Cape Fold Belt is outlined in black dashed lines.

the SCP, WCP and interior plateau during the present interglacial with the exception of elephant and antelope having a tolerance for a range of grazing conditions, such as eland and mountain zebra (*Equus zebra*). For example, the historical record indicates that bontebok, Cape buffalo and blue antelope (*Hippotragus leucophaeus*; extinct since 1800) were present on the SCP, but absent except as upper Pleistocene fossils on the WCP (Klein et al., 1999). Quagga (the coastal plain zebra, *Equus quagga*) and black rhinoceros, which like the elephant can migrate over long distances in arid landscapes, were abundant on the WCP but absent from the SCP. Wildebeest and springbok were abundant in the interior grasslands but absent from the WCP and SCP (Skead, 1982) except in upper Pleistocene fossil sites (Klein et al., 1999; Thompson, 2010). These observations suggest that the large animal herds of southern Africa occur today as isolated populations in the interior, WCP and SCP regions, but that these populations periodically mixed during the Pleistocene by the removal of physical and climatic barriers.

The CFB may have inhibited but clearly did not prevent human movement out of the SCP with pastoralists herding cattle over Sir Lowry's Pass to the WCP (Van Riebeeck, v. I, 81) and possibly over the Attaquas Pass to the Klein Karoo. However, prior to the arrival of pastoralists 2 ka, such crossings were probably infrequent and limited in extent. The relatively large number of Late LSA archeological sites indicate broad similarities in the succession of stone tool industries across southern Africa since the last glacial termination 14 ka; however, the stone artifacts show a high degree of regional variation in style (Deacon and Deacon, 1999; Mitchell, 2002). Cultural differences between inland and coastal sites (Deacon, 1984; Orton, 2006) as well as differences from east to west along the SCP (Deacon, 1976) suggest that Late LSA groups largely occupied separate territories.

Therefore, human movement into or out of the SCP was limited during the present interglacial highstand prior to 2 ka and was unlikely during the Last interglacial highstand (125—115 ka) but with SCP barriers increasingly less effective since then as humans developed adaptations to cross mountain barriers (the extent of human movement across the CFB barrier is discussed further in Section 7 below).

2.2. Expansion of the SCP during glacial periods

The SCP only slightly expands and the Hangklip and Plettenberg Bay portals remain closed when sea level falls by as much as 45 m during suborbital fluctuations of interglacial periods and in the initial transition from interglacial to glacial periods (Van Andel, 1989). As sea level falls from 45 to 75 m the SCP expands by 32% and the coastal plain along the Cape Hangklip and Plettenberg Bay portals widens by 1—5 km (Fig. 2). High-resolution bathymetry (Rogers, 1985; Du Plessis and Glass, 1991) indicates that the mountainous terrain and cliff shorelines of Cape Hangklip give way to the Hangklip Ridge, a 1—5 km wide resistant sandstone rocky ridge which extends offshore southwest from Cape Hangklip. A similar ridge extends offshore southwest of Danger Point 70 km to the southeast of Cape Hangklip. Only two openings, 1—2 km wide at Pringle Bay and Rooielsbaai, connect the SCP and WCP with movement impeded by the narrow, rocky coastal plain and the 10—20 m high escarpments of the Hangklip and Danger Point ridges. To the east, lowering sea level by 75 m widened a 40 km stretch of the Plettenberg Bay coastal plain by between 2 and 5 km (Fig. 5), but the coastal plain likely remained closed by the near-shore extension of river gorges and dense afrotemperate forest.
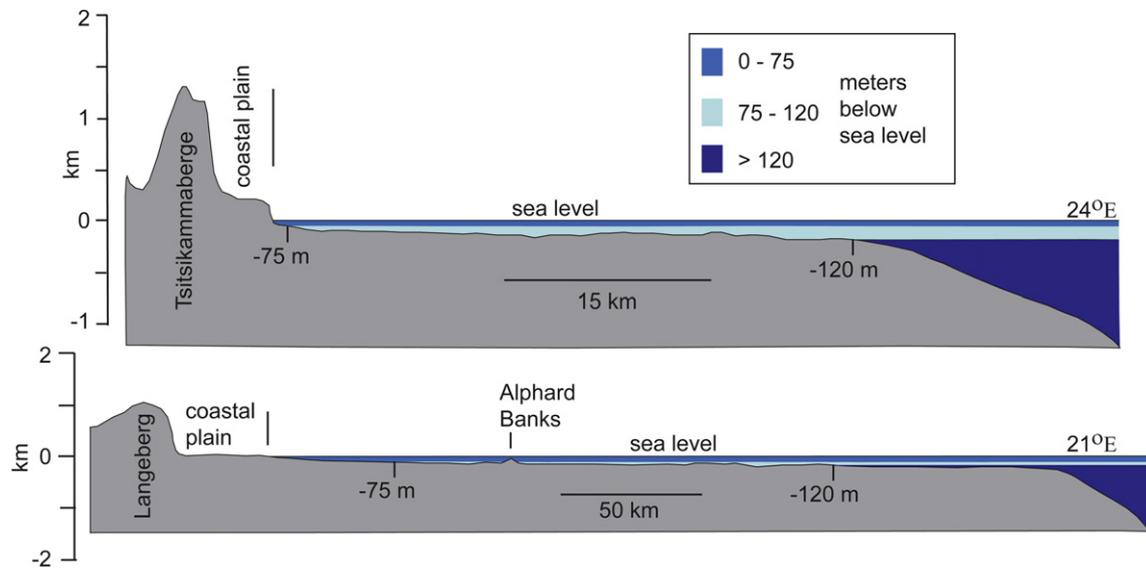
Fig. 5. Bathymetric profiles offshore of the Breede River at 21°E and off Plettenberg Bay at 24°E (note different scales; 15× vertical exaggeration).

The Hangklip and Plettenberg Bay portals only open fully as sea level is lowered from −75 to −120 m during glacial maxima when the SCP expands by a factor of five to form one continuous southern African coastal plain (Fig. 2). The Cape Hangklip portal widens by 15 km with the Hangklip and Danger Point ridges reduced to widths of 1–3 km having escarpments 1–6 m high at water depths between −75 and −120 m (Rogers, 1985). The exposure of less prominent ridges and generally less rocky terrain would allow for less impeded animal movement between the False Bay valley on the WCP and the Bot River valley on the SCP. The western margin has a broad but deep shelf, such that expansion of the WCP occurs primarily south of the Olifants River by as much as 66% during glacial maxima. The low-stand WCP was likely covered by vegetation largely similar to that found onshore today dominated by sand fynbos and strandveld with sandstone and granite fynbos locally on rocky hills and renosterveld in valleys underlain by shale. Terrain exposed to the east of Cape Hangklip was likely similar to the present-day onshore and extended along the Agulhas Arch to the southeastern-most tip of exposed shelf with locally rugged hills covered in sandstone fynbos surrounded by valleys having limestone fynbos, dune strandveld and shale renosterveld vegetation (Fig. 3).

The greatest glacial expansion of the SCP occurs to the east of the Agulhas Arch where gently rolling to flat terrain is exposed in a band 40–160 km wide (Figs. 2 and 5). The landscape would be far less rocky than to the west of the Agulhas Arch (Birch, 1980) with rocky hills, covered in sandstone fynbos, limited to 5–10 km seaward of present-day headlands. The exposed Agulhas Bank consists of a band of Cretaceous shale bedrock along the interior and a large outer area of Neogene limestone bedrock covered by a thin veneer of relict calcareous muddy sand (Dingle and Rogers, 1972). The vegetation on the coastal plain exposed during glacial periods is not known but the Albany thicket biome of present-day onshore valleys, such as the Sunday's River, is underlain by Creta-ceous shale bedrock and suggests that Albany thicket, along with shale renosterveld primarily in the west, may have extended to offshore areas underlain by Cretaceous shale bedrock. Limestone bedrock of the outer exposed coastal plain may have supported a thicket, limestone fynbos, dune strandveld and grassland vege-tation mosaic (Fig. 3). The deeply incised river gorges and the dense afrotemperate forest which previously made the Plettenberg Bay portal impassable give way to a 40–60 km wide coastal plain (Fig. 5) of rocky hills, plains and coastal dunes (Van Andel, 1989)

providing easy access to the SCP by large migratory herds from the African interior by way of the Sunday's River valley (Fig. 2).

An expanding glacial SCP may have served as a refuge to large herd animals and humans as interior climates became drier (Mitchell, 1990; Morris, 2002; Marean, 2010). The lake record from Tswaing crater suggests that the summer rainfall region became drier by as much as 50–70% during the Last Glacial Maximum (LGM) (Partridge et al., 1997) while the winter rainfall region may have expanded inland (Chase and Meadows, 2007; Chase, 2010) and resulted in less seasonality in rainfall in areas such as Equus Cave (Lee-Thorp and Beaumont, 1995) on the eastern border of the arid corridor which today are dominated by summer rainfall C_4 grasses. The expansion of winter rainfall inland as the summer rainfall contracted may have resulted in a seasonal reduction of the arid corridor and allowed large and varied grazer populations such as documented at Florisbad (Brink, 1987) to move between the coastal plain and the interior during glacial-interglacial climate transitions. The $\delta^{13}C$ composition of fossils from Nelson Bay Cave indicates SCP rainfall was year round as today during the LGM (Sealy, 1996) and the $\delta^{13}C$ speleothem record from Pinnacle Point indicates highly variable year-round rainfall on the SCP from 90–53 ka (Bar-Matthews et al., 2010) similar to what is observed today (Fig. 4). Lower pCO_2 during glacial periods would favor C_4 grasses in the interior as well as on the SCP associated with summer rainfall (Ehleringer et al., 1997). The drier, C_4-dominated grasslands of the glacial interior may have compelled animals to move to the wetter, more attractive mix of C_3/C_4 plants on the SCP in the tran-sition to glacial periods. The ability of animals to move out of the glacial SCP back to the interior may have been limited by an east-ward shift in the arid corridor and displacement of thicket and grassland by Nama-Karoo biomes during glacial maxima. There-fore, animals moving out of a drying, increasingly C_4-dominated interior may have become isolated by the arid corridor on a wet, expansive glacial SCP where faunal changes imply more grass relative to small-leafed shrubs (Klein et al., 1999) having a highly variable C_3/C_4 mix (Bar-Matthews et al., 2010).

2.3. Glacial terminations and flooding of the SCP

Glacial periods end abruptly with the melting of the Northern Hemisphere ice sheets resulting in a rapid rise in sea level and flooding of the expansive SCP habitat. In the last glacial termination

(Termination I), for example, sea level rose from −120 to −75 m in 5 kyr (0.9 cm/yr) between 19 and 14 ka (Clarke et al., 2009). During Termination I there was a particularly abrupt rise in sea level referred to as melt water pulse 1a when sea level is estimated to have risen 16 m (−96 to −80 m) in 300 yr (5.3 cm/yr) (Hanebuth et al., 2000) or 20 m (−90 to −70 m) in 560 yr (3.6 cm/yr) between 14.17 and 13.61 ka (Stanford et al., 2006). Such abrupt rises in sea level would rapidly inundate the low-lying, expansive SCP habitats, greatly reduce their extent and isolate the SCP as the Cape Hangklip and Plettenberg Bay portals closed. Some animals and humans may have exited the SCP through a seasonally reduced arid corridor before the portals closed, but the number of large animals on the closed SCP was greatly reduced with the loss of habitat leading to the replacement of large migratory herds by small, solitary browsers and small herds of large grazers (Klein et al., 1999).

3. Hypothesis

Expansion (opening) and contraction (closing) of the SCP occurred repeatedly with the marked increase in amplitude of sea-level and climate fluctuations over the last one million years (Myr); a time period of major events in human evolution (Figs. 6–8). Here it is proposed that at least some (but not all) of these events in human evolution may correspond to the periodic isolation of groups on the coastal plain of South Africa as it expanded and contracted in response to Pleistocene sea-level fluctuations. A five-fold increase in the extent of the glacial SCP as it opened up allowed previously isolated groups on the SCP to expand and mix with

groups and large animal herds moving from the African interior onto a glacial SCP refuge (Fig. 9). Groups on the glacial SCP may have been isolated from the dry interior during glacial maxima for periods of 9–57 kyr (Table 1) or 360–2280 25-year generations. Human and animal populations living on the expansive glacial coastal plain were forced to move inland as sea level rose during glacial terminations. Rapid contraction of the SCP, with as much as one-third of the SCP flooded by the sea in the span of a dozen 25-year human generations during melt water pulse events, may have resulted in a higher population density and increased competition for diminishing resources. Resource loss related to flooding of SCP habitats may have been exacerbated by less winter rainfall on the western SCP (Chase and Meadows, 2007) and fewer large animal herds after the Cape Hangklip and Plettenberg Bay portals had closed. Those groups of individuals who managed to increase the diversity or quantity of their food sources survived.

Populations living on an isolated glacial SCP may have been split into those who moved into the interior before the SCP closed and those who became trapped and isolated on the SCP throughout the following interglacial for periods of 25–85 kyr (Table 1) or 1000–3400 25-year generations (Fig. 9). Groups that exited the SCP before it closed may have dispersed into the expanding vegetation biomes of increasingly warm and wet interglacial climates of the African interior (Adams and Faure, 1997) (Fig. 10). The option for groups to exit the SCP once sea level rose above −75 m during interglacial periods was limited by physical, vegetation and climatic barriers. Movement inland as sea level rose may have been focused along predominantly south-flowing rivers on the SCP. The two largest rivers, Breede and Gourits, converge on the broadest
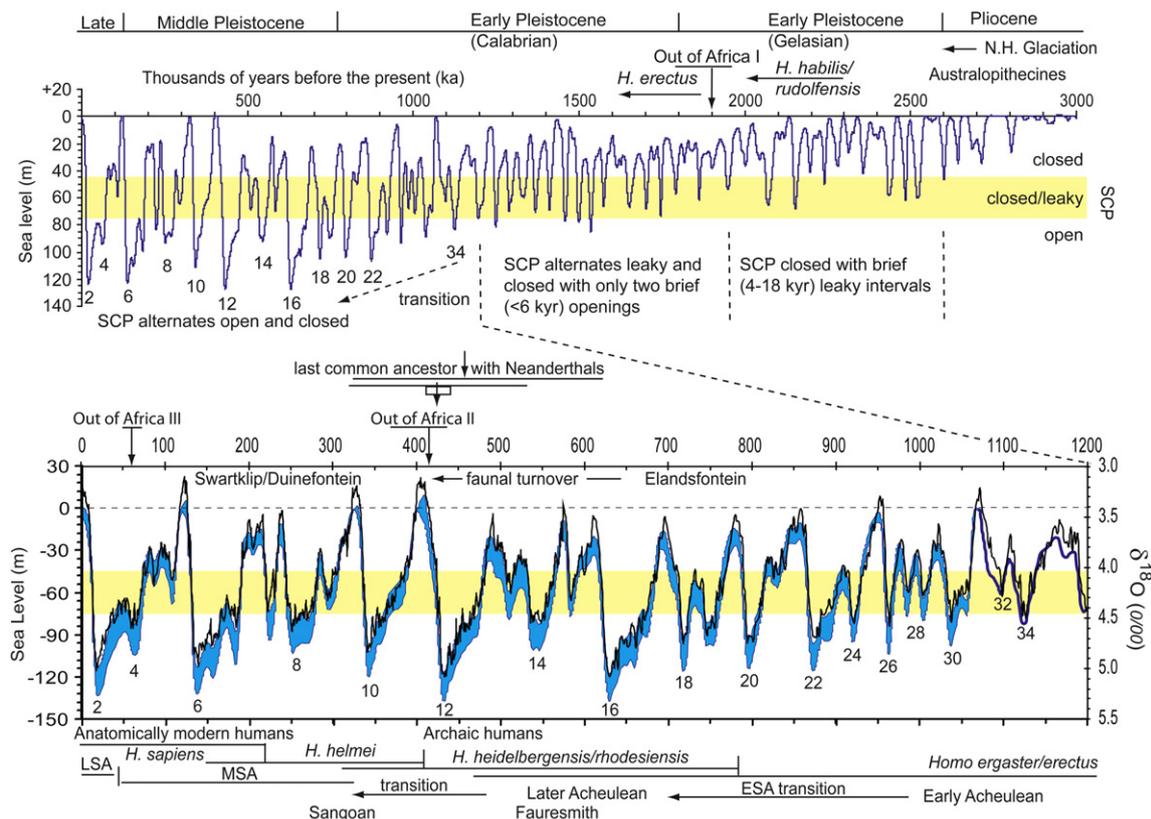

Fig. 6. Glacial to interglacial climate cycles from the composite marine oxygen isotope record (Lisiecki and Raymo, 2005) and derived range in sea level (Bintanja and van de Wal, 2008) since 3 Ma (top) and since 1.2 Ma (Bintanja et al., 2005) showing the relation to faunal, *Homo* and stone tool transitions. The SCP was isolated from Africa up until the initiation of Northern Hemisphere glaciation at 2.7 Ma, but remained largely closed to large animal herds until large-amplitude sea-level fluctuations were initiated between 1100 and 700 ka and reoccurred periodically since 700 ka. Glacial periods are indicated by even-numbered marine isotope stages (MIS). Dashed line is present-day sea level. The SCP is open when sea level is below −75 m.
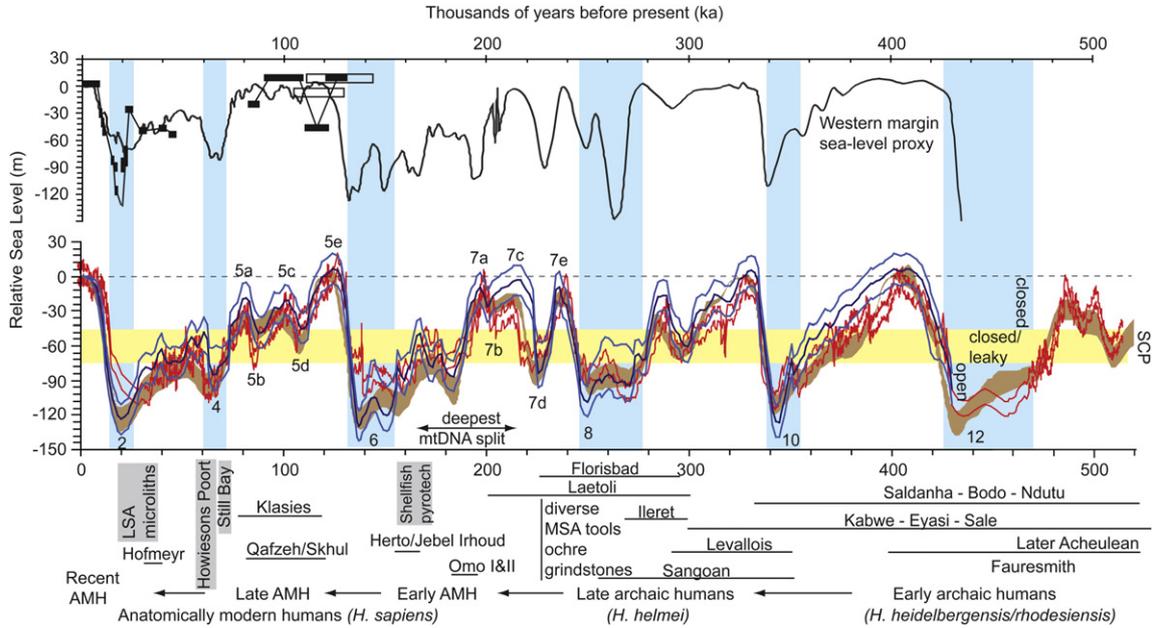
Fig. 7. Sea-level fluctuations (bracketed by uncertainty) since 520 ka (Waelbroeck et al. (2002) in blue, Rohling et al. (2009) in red and Bintanja et al. (2005) in brown) are compared with the archeological record below and with the sea-level curves for southern Africa above from Ramsay and Cooper (2002; filled boxes) and Carr et al. (2010; empty boxes) back to 145 ka, and from Compton and Wiltshire (2009) based on a sediment proxy for the timing but not the amplitude of sea-level fluctuations on the western margin back to 440 ka (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

remaining coastal plain centrally located on the SCP as sea level rises from −120 to −75 m (Fig. 2). The Blombos Cave site is within 20 km of the Breede River mouth when sea level was at −75 m and the Pinnacle Point site is roughly equidistant between the Gourits and Brak-Kaaimans rivers, and both of these key MSA archeological sites (Henshilwood et al., 2004; Marean et al., 2007) occur within 20 km inland of the greatest extent of SCP contraction during glacial terminations.

Isolation spanning up to 3000 generations was perhaps sufficient for new adaptations, along with random genetic drift, to become fixed in the genome. Adaptations more advantageous than those

occurring in the rest of Africa may have allowed groups exiting the SCP to widely disperse and displace groups outside the SCP. The hypothesis predicts that originations may have occurred among groups isolated on the SCP either during glacial maxima or during interglacial periods and became widely dispersed either during flooding of the glacial SCP or when the interglacial SCP opened at the onset of the next glacial maximum. The hypothesis attempts to explain both where and by what mechanism humans may have evolved in Africa and includes the possible speciation of anatomically modern humans (AMH) (H. sapiens) as well as the origin of at least some modern human behaviors. The hypothesis can be tested
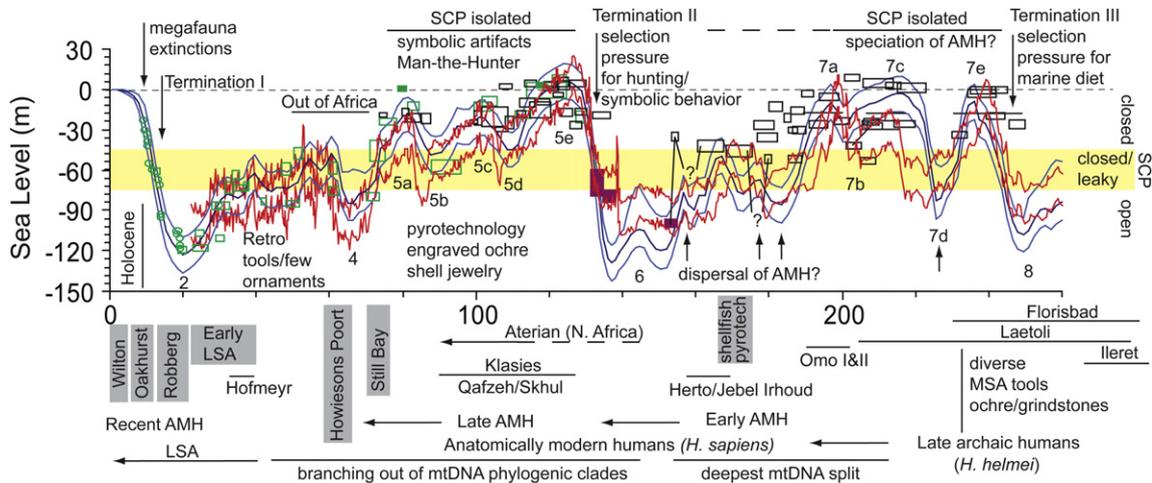

Fig. 8. Sea-level fluctuations (bracketed by uncertainty) since 260 ka (Waelbroeck et al. (2002) in blue and Rohling et al. (2009) in red), coral data indicated by green circles and squares (Chappell et al., 1996; Chappell, 2002; Cutler et al., 2003), filled green squares (Dorale et al., 2010), black squares (Thompson and Goldstein, 2005) and purple filled squares (MIS 6; Thomas et al., 2009), and speleothem data indicated by horizontal lines (Dutton et al., 2009) are compared with major events in the archeological record. The hypothesis proposes selection pressure for a marine diet on the SCP occurred during glacial termination III (MIS 8 to 7), speciation of AMH on an isolated MIS 7 interglacial SCP and dispersal of AMH in the transition to the MIS 6 glacial. Selection pressure for hunting/symbolic behavior is proposed for Termination II (MIS 6 to 5e) which were further developed on an isolated SCP during the MIS 5 interglacial and only widely dispersed during the MIS 4 glacial. Refer to text for discussion (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).
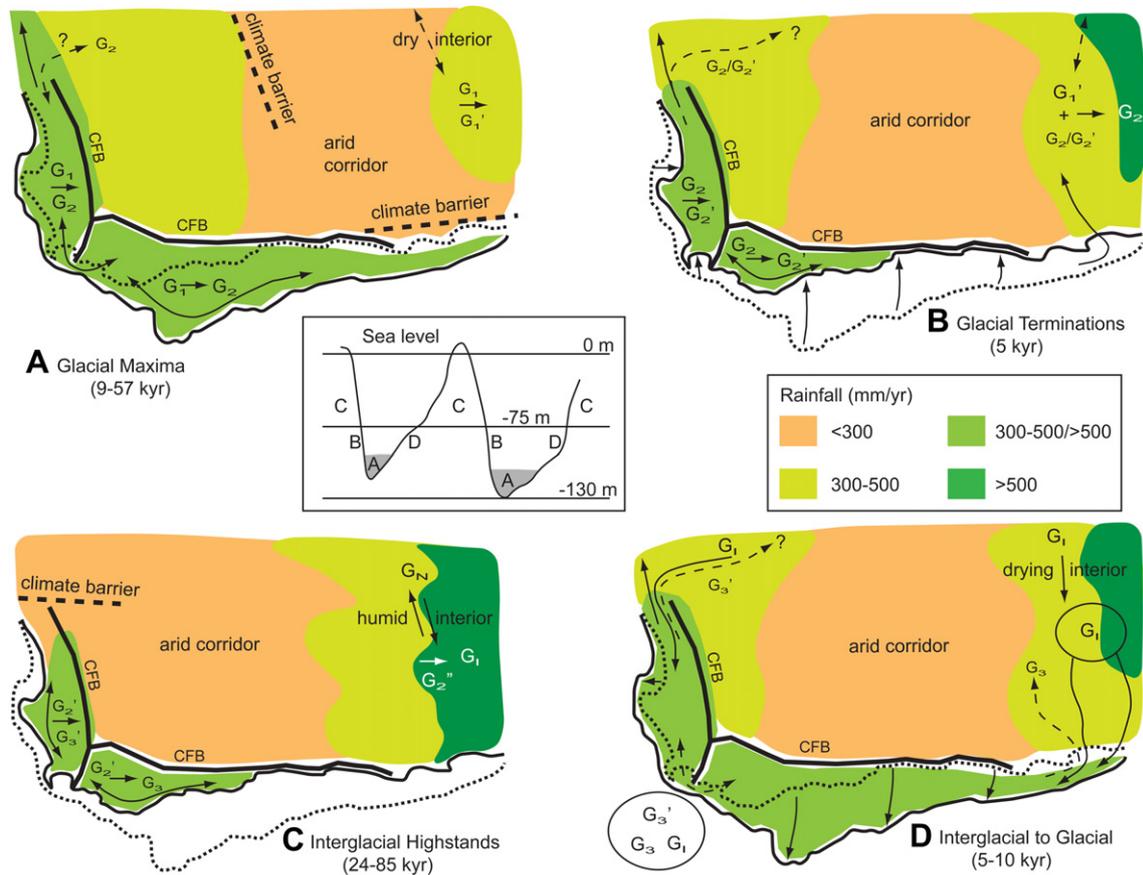
Fig. 9. Isolation and mixing of groups in southern Africa in relation to glacial to interglacial sea-level fluctuations. A. Opening of the SCP during 9–57 kyr glacial maxima allow groups isolated on an interconnected SCP and WCP by climatic barriers to diverge ($G_1 => G_2$) from groups evolving in the dry interior ($G_1 => G_1'$). B. Originations ($G_2 => G_2'$) most likely initiate during 5 kyr glacial terminations when selection pressures increase as the SCP is rapidly flooded by rising sea level. Groups on the glacial SCP either exit into the interior before closure or (C) are isolated and diverge further on the SCP ($G_2' => G_3$) and WCP ($G_2' => G_3'$) throughout the following 24–85 kyr interglacial. D. In the 5–10 kyr transition from interglacial to glacial periods groups previously isolated on the SCP (G_3) and WCP (G_3') mix with groups from the interior (G_I), some of which may have ultimately originated in East Africa or North Africa seeking refuge on the glacial SCP from a drying interior. Genetic exchange (hybridization) is likely among these groups before one group dominates by the next glacial maximum. The above scenario repeats with sea-level cycles (central box). Regional differences in vegetation are shown by shades of green and relate to proposed variations in rainfall over glacial-interglacial cycles (refer to text).

by comparing available archeological and genetic evidence to sea-level records (Figs. 6–8).

4. Sea-level records

Eustatic or global sea-level records have been derived from the marine $\delta^{18}O$ record of benthic foraminifera (Lisiecki and Raymo, 2005) since 3 Ma (Bintanja et al., 2005; Bintanja and van de Wal, 2008) (Fig. 6) and since 450 ka (Waelbroeck et al., 2002), from the $\delta^{18}O$ record of foraminifera from the Red Sea since 520 ka (Siddall et al., 2003; Arz et al., 2007; Rohling et al., 2009) (Fig. 7) and from the dating of coral reefs and speleothems since 240 ka (Chappell et al., 1996; Yokoyama et al., 2001; Chappell, 2002; Cutler et al., 2003; Thompson and Goldstein, 2005; Henderson et al., 2006; Stanford et al., 2006; Clarke et al., 2009; Dutton et al., 2009; Thomas et al., 2009; Dorale et al., 2010) (Fig. 8). In addition to these global changes, tectonic uplift or subsidence as well as changes in sediment supply may have influenced local changes in sea level along the SCP. However, sea-level changes caused by tectonism and sediment supply are assumed to have been relatively insignificant for the SCP in comparison to the large-amplitude variations in global sea-level on glacial to interglacial cycles. This assumption may not be strictly valid over the last 5 Myr, but global sea-level records since 1 Ma are directly applied to the SCP because

of the limited extent of Pleistocene tectonism on the southern margin of South Africa (Partridge and Maud, 2000). The assumption is supported by sea-level records derived for the South African margin which show general agreement with global records since the Last interglacial (Ramsay and Cooper, 2002; Carr et al., 2010) and for the timing of sea-level fluctuations since 440 ka (Compton and Wiltshire, 2009) (Fig. 7).

The marine $\delta^{18}O$ record of benthic foraminifera spanning the last 5.3 Myr indicates increasingly large-amplitude climate cycles (Lisiecki and Raymo, 2005). Prior to onset of Northern Hemisphere glaciation at 2.7 Ma, high sea level isolated the SCP from Africa since at least the Pliocene (5.3 Ma) when sea level on the WCP was approximately 25 m higher than today (Franceschini and Compton, 2004). The sea-level record derived from the marine $\delta^{18}O$ record of benthic foraminifera since 3 Ma (Bintanja et al., 2005; Bintanja and van de Wal, 2008) indicates that between 2.5 Ma and 2 Ma the SCP portals remained largely closed with only six periods varying from 4 to 18 kyr in duration when sea level fell between 45 and 75 m (Fig. 6). Drops in sea level between 45 and 75 m occur with increasing frequency between 2 and 1.2 Ma and include two 5-kyr long intervals when sea level was below 75 m. From 1.2 Ma to 700 ka the amplitude of sea-level fluctuations increased and there are numerous periods when sea level fell by more than 75 m. The first major glacial period, when sea-level was lowered between 75

Table 1
Opening and closing of SCP portals derived from a synthesis of all available sea level and coral data.

MIS	begin (ka)	end (ka)	duration (kyr)	sea level (m)	portals
1	11.1 (12–10.6)	0	11.1	−45 to 0/3	closed
2 to 1	13.8 (14.2–13.6)	11.1 (12–10.6)	2.7	−75 to −45	closed/leaky
2	36.5 (37–35.3)	13.8 (14.2–13.6)	22.7	−75 to −130	open
3	50 (52–48)	36.5 (37–35.3)	13.5	−60 to −110	leaky/open
3	60.6 (63.5–56.4)	50 (52–48)	10.6	−45 to −80	closed/leaky
4	69.7 (71.5–67.5)	60.6 (63.5–56.4)	9.1	−75 to −103	open
5a to 4	75.1 (77–72)	69.7 (71.5–67.5)	5.4	−45 to −75	closed/leaky
5a	84.5 (86–83)	75.1 (77–72)	9.4	−45 to 1.5	closed
5b	96.5 (99–94)	84.5 (86–83)	12	−45 to −75	closed/leaky
5c	106.5 (107–106)	96.5 (99–94)	10	−45 to −17	closed
5d	113 (116–110)	106.5 (107–106)	6.5	−30 to −70	closed/leaky
5e	131.4 (132.5–129.6)	113 (116–110)	18.4	−45 to 10	closed
6 to 5e	134.2 (137–132)	131.4 (132.5–129.6)	2.8	−75 to −45	closed/leaky
6	160.4 (165–153)	134.2 (137–132)	26.2	−75 to −130	open
6	176 (179–171)	160.4 (165–153)	15.6	−40 to −75	closed/leaky
6	183 (186–181)	176 (179–171)	7	−45 to (?)<−75	closed/leaky
7a to 6	191 (193–189.7)	183 (186–181)	8	−5 to −75	closed/leaky
7a-b-c	219.7 (225–215.8)	191 (193–189.7)	28.7	−45 to 10	closed
7d	231.9 (232.4–231.2)	219.7 (225–215.8)	12.2	−45 to −80	closed/leaky
7e	242.5 (243–241.8)	231.9 (232.4–231.2)	10.6	−45 to 0	closed
8 to 7e	246 (250–243.5)	242.5 (243–241.8)	3.5	−75 to −45	closed/leaky
8	276.7 (280–272.9)	246 (250–243.5)	30.7	−70 to −108	open
9	307 (316–302)	276.7 (280–272.9)	30.3	−25 to −75	closed/leaky
9	335.4 (336–335)	307 (316–302)	28.4	−45 to 0	closed
10 to 9	338 (341–336)	335.4 (336–335)	2.6	−75 to −45	closed/leaky
10	359.4 (364–354)	338 (341–336)	21.4	−75 to −120	open
11 to 10	377 (389–365)	359.4 (364–354)	17.6	−45 to −75	closed/leaky
11	421 (422–420)	377 (389–365)	44	−45 to 10	closed
12 to 11	426.5 (428–424.3)	421 (422–420)	5.5	−75 to −45	closed/leaky
12	470 (476–464)	426.5 (428–424.3)	43.5	−75 to −120	open
13 to 12	481 (482–479.5)	470 (476–464)	11	−45 to −75	closed/leaky
13	534 (536.3–532.6)	481 (482–479.5)	53	−30 to −75	closed/leaky
14	555.4 (559.2–550.8)	534 (536.3–532.6)	21.4	−75 to −92	open
15	621.2 (622.2–620.3)	555.5 (559.2–550.8)	65.7	−75 to −10	closed/leaky
16	678.2 (680.1–673.8)	621.3 (622.2–620.3)	56.9	−75 to −128	open
17 to 16	685.1 (686.3–684)	678.3 (680.1–673.8)	6.8	−45 to −75	closed/leaky
17	703.8 (709.8–700)	685.2 (686.3–684)	18.6	−45 to −22	closed
18 to 17	713 (714–712)	703.9 (709.8–700)	9.1	−75 to −45	closed/leaky
18	725.6 (727.6–724)	713.1 (714–712)	12.5	−75 to −105	open
18	742.1 (743.5–739.5)	725.6 (727.6–724)	16.5	−75 to −45	closed/leaky
18	758.3 (760.6–755.2)	742.1 (743.5–739.5)	16.2	−75 to −90	open
19 to 18	766.3 (769–763.7)	758.4 (760.6–755.2)	7.9	−45 to −75	closed/leaky
19	788.1 (789–787.3)	766.3 (769–763.7)	21.8	−45 to −20	closed
20 to 19	790.8 (792–790.1)	788.2 (789–787.3)	2.6	−75 to −45	closed/leaky
20	809 (811.1–806.2)	790.9 (792–790.1)	18.1	−75 to −104	open
21 to 20	816.4	809.1 (811.1–806.2)	7.3	−45 to −75	closed/leaky
21	865.1	816.5	48.6	−45 to −16	closed
22 to 21	867.2 (868.3–866.5)	865.2	2	−75 to −45	closed/leaky
22	896.8 (898.9–891)	867.3 (868.3–866.5)	29.5	−75 to −106	open
23	917.3 (918.4–916.4)	896.9 (898.9–891)	20.4	−75 to −49	closed/leaky
24	925.6 (927.1–923.2)	917.4 (918.4–916.4)	8.2	−75 to −87	open
25 to 24	931.2 (932.7–929.9)	925.7 (927.1–923.2)	5.5	−45 to −75	closed/leaky
25	958.2 (958.7–957.8)	931.3 (932.7–929.9)	26.9	−45 to −6	closed
26 to 25	960.3 (961.2–959.8)	958.3 (958.7–957.8)	2	−75 to −45	closed/leaky
26	966.7 (968.2–965.3)	960.4 (961.2–959.8)	6.3	−75 to −93	open
30 to 26	1033.2 (1034.7–1032)	966.8 (968.2–965.3)	66.4	−75 to −30	closed/leaky
30	1043.7 (1046.6–1039.8)	1033.3 (1034.7–1032)	10.4	−75 to −89	open
34 to 30	1120.8	1043.8 (1046.6–1039.8)	77	−75 to 0	closed/leaky
34	1129	1120.8	8.2	−75 to −83	open

and 120 m, occurs from 678 to 621 ka during Marine Isotope Stage 16 (MIS 16) (Bintanja et al., 2005). Since MIS 16, large-amplitude (120 m) sea-level fluctuations have periodically expanded and contracted the SCP (Fig. 6).

Sea-level records spanning the last 520 kyr generally agree within their age (±1–10 kyr) and amplitude (±6–15 m) uncertainties (Fig. 7). The timing of opening and closing of the SCP since 520 ka are obtained from the sea-level curve derived for the Red Sea (Siddall et al., 2003; Arz et al., 2007; Rohling et al., 2009) and from the sea-level curve of Waelbroeck et al. (2002) which retains millennial-scale variations lost from the use of a 3 kyr mean of the

data by Bintanja et al. (2005). Sea level independently determined from dated coral and speleothems extends back to MIS 7 (240 ka) and, although there are exceptions, generally falls within the uncertainty of the $\delta^{18}O$-derived sea-level curves (Fig. 8).

Compilation of all available sea-level records allows for estimation of when the SCP was open and when it was closed by calculating the mean age of when sea level fell below or rose above −75 m, respectively (Table 1). Opening and closing of the SCP portals are assumed to correspond to a sea level of −75 m because of the rapid expansion of coastal plain as sea level falls below −75 m (Fig. 5; Van Andel, 1989). The timing of rapid glacial
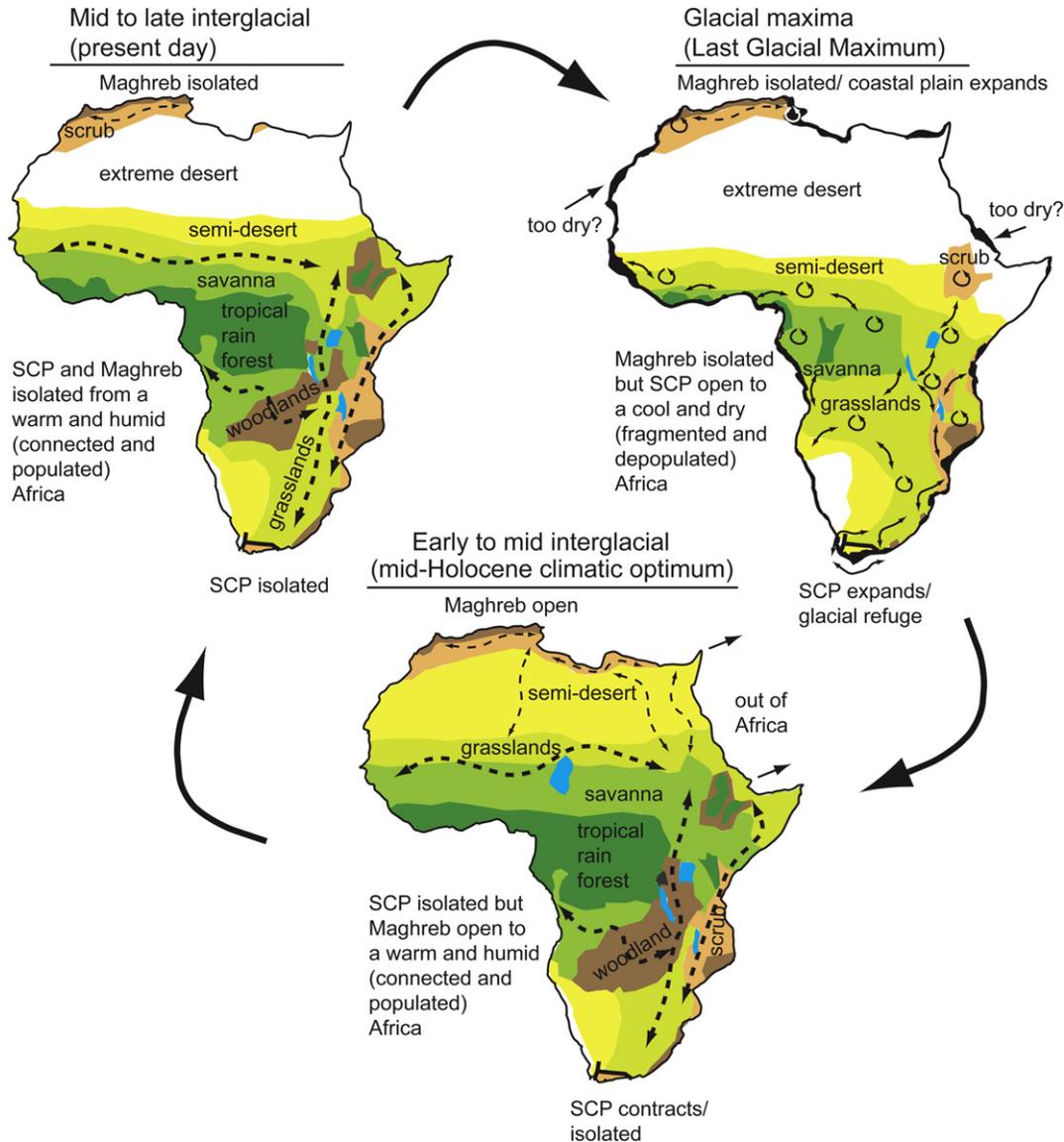
Fig. 10. Isolation and connection of the SCP and the Maghreb to Africa in relation to vegetation biome changes over glacial to interglacial climate cycles (Adams and Faure, 1997) with possible migration pathways shown. Exposed glacial coastal plains (shown in black) off Eritrea and Western Sahara were perhaps too dry for human occupation. The SCP is isolated during glacial terminations with opening of the Maghreb 4–10 kyr later associated with greening of the Sahara during the early to mid interglacial (mid-Holocene climatic optimum).

terminations is better constrained and has less uncertainty than the timing of SCP openings associated with the gradual lowering of sea level from −45 to −75 m in the transition from interglacial to glacial periods.

5. First appearances

The hypothesis predicts that originations will most likely occur during flooding of the SCP at glacial terminations when increases in population density are most likely to drive selection pressures to adapt to diminishing resources. In addition, groups may diverge, particularly if isolated over long interglacial periods, by random mutations and selection pressures associated with increased population density where barriers prevent expansion. Geographical points of origin are difficult to establish and are rarely preserved in the fossil record when the originating population is small and highly mobile over a small geographical area, particularly if much of that geographical area, such as the glacial SCP, is now submerged on

the shelf. Only once dispersed over a large region, either by assimilation by other groups or by population expansion, is a new artifact or subspecies likely to appear in the fossil record. If dispersal is rapid, first appearances can be abrupt with a possible time lag between origination and dispersal. The hypothesis predicts that first appearances will become younger with distance from the SCP. However, the age resolution of archeological sites is generally not sufficient to determine the spatial distribution of first appearances (e.g., Jacobs et al., 2008).

First appearances in the fossil record which originated on the SCP are predicted to most likely occur with dispersal out of the SCP associated with glacial terminations or at the onset of glacial periods (Fig. 9). Groups isolated by climate on the glacial coastal plain refuge for periods of 9–57 kyr may have diverged (G_1 to G_2) from interior groups (G_1 to G_1') (Fig. 9A). During glacial terminations rapid flooding of the SCP may have forced groups to adapt (G_2 to G_2') under selection pressures associated with increased population density (Fig. 9B). Westward expansion of summer rainfall

may have opened the climate barrier before the SCP closed to allow dispersal and mixing of a subset of the SCP population with interior groups (G_2/G_2' + G_1' to G_2''). Possible dispersal out of the SCP at glacial terminations (Fig. 9B) is indicated by the sea-level records when the SCP closed by 621.3, 534, 426.5, 338, 245.4, 134.2, 60.6 and 13.8 ka and followed periods of glacial isolation of 57 (MIS 16), 21 (MIS 14), 44 (MIS 12), 21 (MIS 10), 31 (MIS 8), 26 (MIS 6), 9 (MIS 4) and 23 (MIS 2) kyr, respectively (Figs. 6–8; Table 1). The time span from glacial maxima to closing of the SCP at glacial terminations is on the order of 5 kyr. Groups that exited may have expanded inland with increasingly humid interior climates to mix with local (G_2'') as well as more distal, northern (G_N) interior groups expanding out of glacial refugia (Fig. 10) to form one well mixed interglacial interior group (G_I) (Fig. 9C).

Groups that did not exit would be isolated throughout the next 24–85 kyr interglacial on the SCP where adaptations acquired during the previous glacial termination may have been further developed as population growth was unable to expand beyond the SCP (G_2' to G_3) and WCP (G_2' to G_3') (Fig. 9C). Groups isolated during interglacial periods could disperse with initial opening of the SCP in the transition to the next glacial (Fig. 9D). The sea-level records indicate that initial opening of the SCP commenced at 678.2, 555.4, 470, 359.4, 276.7, 160.4 (preceded by a possible brief opening between 183 and 176 ka), 69.7 and 36.5 ka and followed periods of interglacial SCP isolation of 35 (MIS 17), 66 (MIS 15), 64 (MIS 13), 68 (MIS 11), 61 (MIS 9), 63/86 (MIS 7), 64 (MIS 5) and 25 (MIS 3) kyr, respectively (Figs. 6–8; Table 1). It took, on average, 5–10 kyr after these initial openings for the SCP to reach maximum glacial expansion. Previously isolated groups on the SCP (G_3), WCP (G_3') and interior (G_I) would mix as they expanded into the newly opened glacial coastal plain habitats with possible two-way movement between the interior and SCP before the climate barrier was established (Fig. 9D). Some interbreeding (hybridization) among groups was likely upon mixing (Jolly, 2001), but the best adapted group and its dominate genotype would most probably have displaced all other competing groups (e.g., Green et al., 2010) before the cycle repeated with the onset of the next glacial maximum and climatic isolation of a subgroup on the SCP (Fig. 9A).

6. Originations elsewhere in Africa

Evidence of human evolution in Africa is focused in three regions: southern Africa, North Africa (Maghreb) and the intervening East African Rift valley. Other African coastal plains which underwent large-scale expansion similar to the SCP of South Africa during glacial maxima and to which the above hypothesis may apply include central Mozambique, Sierra Leone-Guinea Bissau, Western Sahara, North Africa and Eritrea (Fig. 1). The coastal plains of Mozambique and Sierra Leone-Guinea Bissau are without physical barriers and, remaining always open to movement inland, are unlikely to result in population density increases. However, contraction of the Mozambique lowstand coastal plain occurs adjacent to the Zambezi River and may have influenced upstream archeological sites in Zambia. The Western Sahara has an expansive shelf exposed during glacial periods but lacks topographic barriers and the absence of archeological sites suggests the region was generally too dry for human occupation. Similarly, the exposed shelf off Eritrea north of the Denakil Plain was extreme desert during the LGM (Basell, 2008) and, although the hominin fossil sites of Hadar and Middle Awash occur to the south, was probably too arid for human occupation during glacial maxima (Fig. 10).

The North African coastal plain (Maghreb) contains several *H. erectus* and early *H. sapiens* fossil sites (Hublin, 2001) and is separated from Africa by the Atlas Mountains and Sahara Desert. Expansion of the Tunisian coastal plain opens an eastern bypass to

the Atlas Mountains, whereas movement to the west may have been restricted by the narrow shelf exposed off Cape Rhir during glacial maxima. These physical features along with climate may explain the greater abundance of sites in Tunisia in comparison to the Western Sahara (Fig. 1). Rapid contraction of the North Africa coastal plain glacial refuge during terminations may have resulted in an increased population density before interglacial greening of the Sahara allowed for expansion into East Africa. For example, there was a period of 4 kyr between the end of Termination I 14 ka and the initial greening of the Sahara 10 ka (Kuper and Kröpelin, 2006) when humans were isolated on a contracted North African coastal plain. Greening of the Sahara has been documented for the Eemain interglacial highstand (124–118 ka) (Osborne et al., 2008) and the records from offshore cores suggest similar glacial to interglacial climate changes in North Africa and its periodic reconnection to sub-Saharan Africa since at least 250 ka (Hooghiemstra et al., 1992; Castañeda et al., 2009). The difference of 5–10 kyr between closure of the glacial SCP at terminations and greening of the Sahara would allow for the movement of humans from the SCP via East Africa to North Africa and possibly beyond (Fig. 10).

Originations in one or several of the many regions in the interior of Africa (Lahr and Foley, 1998; Basell, 2008), in contrast to coastal plain habitats impacted by sea-level fluctuations, are predicted to occur primarily during glacial maxima when the African interior becomes drier and vegetation biomes contract and fragment (Adams and Faure, 1997), isolating populations and increasing the selection pressures of reduced resources (Fig. 10). Artifacts developed by small populations isolated on lake margins, highland refugia or river courses during glacial periods are predicted to disperse in the transition to the next interglacial when a general shift to wetter and warmer climate favors population growth and expansion. Expansion of vegetation biomes would facilitate dispersal of humans throughout Africa, with the exception of the SCP which closes 5–10 kyr earlier and remains isolated from Africa throughout interglacial periods.

Therefore, the timing of first appearances in the fossil record may be able to distinguish between dispersal out of the SCP during glacial terminations or onset of glacial periods from dispersal out of African interior refugia, including North Africa, during interglacial periods. However, the generalized view of glacial to interglacial climate change for the whole of Africa is probably overly simplistic. For example, records from African tropical lakes indicate more severe climate variations during the interglacial period MIS 5 (135–75 ka) than since 70 ka (Scholz et al., 2007). This would imply that there may have been interior regions, such as tropical Africa, where selection pressures were greater during interglacial than glacial periods and where dispersal is associated with movement from the interior to the SCP as it opened up as a refuge during glacial periods. Such factors combined with the diversity of ecosystems and their responses to glacial/interglacial climate changes complicate testing of the hypothesis. However, glacial to interglacial climate and sea-level fluctuations clearly had a large impact on the SCP (Figs. 2 and 5) and the relation of these to the archeological record remains an important one for providing insights into human evolution (Figs. 6-8). The relation of the archeological and sea-level records is explored in chronological order in the sections that follow to provide an initial test of the hypothesis.

7. Testing the hypothesis

7.1. Emergence of archaic humans

Hominin fossils dating from around 3 Ma have been recovered from the interior of South Africa (Tobias, 2000) and early Acheulean

tools believed to be made by *H. ergaster/erectus* occur widely throughout East Africa and in the interior of South Africa from 1.6 Ma (Gibbon et al., 2009). The absence of evidence for hominins or Acheulean tools on the SCP/WCP prior to approximately 1 Ma (Klein et al., 2007) may reflect relatively high sea level making the coastal plain inaccessible, particularly to hominins restricted to interior wetland and valley environments (Fig. 6). The transition to increasingly large climate and sea-level fluctuations between 1000 and 700 ka is associated with moderate lowstand openings of the SCP during glacial periods MIS 22 (897–867 ka), MIS 20 (809–791 ka) and MIS 18 (758–742 and 726–713 ka) with the first major glacial lowstand of –120 m associated with MIS 16 (678–621 ka). The sea-level lowering of the MIS 14 glacial was shallow and short (555–534 ka) such that the SCP may have remained isolated between the glacial maxima of MIS 16 and MIS 12, a period of 151 kyr from 621 to 470 ka. The onset of increasingly large-amplitude glacial to interglacial variations between 900 and 400 ka corresponds to the extensive faunal turnover observed at fossil sites on the SCP and WCP (Klein et al., 2007), the transition from large handaxes of the early Acheulean to more refined, smaller handaxes of the later Acheulean between 1000 and 600 ka (Kuman, 2007) and blade tools of the Fauresmith industry between 700 and 400 ka (Porat et al., 2010), the appearance of early archaic humans (*H. heidelbergensis/rhodesiensis*) (Tryon and McBrearty, 2002) and estimates from genetic data of 466(618–321) ka (Krause et al., 2010) and 440–410(538–315) ka (Endicott et al., 2010) for when humans started to diverge from our last common ancestor with the Neanderthals (Fig. 6).

The Elandsfontein fossil site on the WCP contains an unusual diversity of large to medium grazers and browsers accumulated on a deflation surface which, based on comparison to East African fauna, is estimated to date between 1000 and 600 ka (Klein et al., 2007). Klein et al. (2007) suggest that the Elandsfontein fauna includes the final, extralimital hold out for many of the East African animals before they went extinct, some without issue. The periodic opening of the SCP during glacial periods from MIS 22 (897–867 ka) may have attracted interior animals to the coastal plain up to and including the extensive lowstand of the MIS 16 glacial (678–621 ka). The preferential extinction of the large Elandsfontein bovids associated with the faunal turnover to the 400–150 ka Duinefontein and Swartklip fossil sites occurs between the two major glacial lowstands of MIS 16 and MIS 12 and is perhaps explained by the up to 151 kyr period of isolation (621–470 ka) when a much contracted coastal plain was largely closed to migratory herds (Fig. 6). A skullcap (Saldanha skull) associated with the later Acheulean from Elandsfontein is interpreted to be an early archaic human (*H. heidelbergensis/rhodesiensis*) dated at circa 600 ka (Klein et al., 2007). However, the skullcap, recovered from a deflation surface, is poorly contextualized but is probably not younger than 330 ka (Potts and Deino, 2005).

The transition from later Acheulean ESA hand-held stone tools to largely hafted, finer stone tools (blades and flakes) of the MSA is marked by the Fauresmith and Sangoan industries as well as Levallois flake technology. Although ages are poorly constrained, the Fauresmith in South Africa (700–400 ka) overlaps with the later Acheulean (Porat et al., 2010), predates to overlaps with the earliest Levallois technology documented in Kenya between 509 and 284 ka (Tryon et al., 2005) and predates the Sangoan (ca. 300 ka; McBrearty and Brooks, 2000). The transition to the later Acheulean and the prepared core technology and blade tools of the Fauresmith industry indicates regional specialization at the end of the ESA. Their appearance spans the two major glacial maxima of MIS 16 and MIS 12 and may correspond to the emergence of *H. heidelbergensis/rhodesiensis* sometime between MIS 18 (719 ka) and MIS 12 (427 ka) (Fig. 6). Population divergence of modern humans

and Neanderthals has to coincide with or have occurred more recently than the genetic divergence (last common ancestor) estimates of 466(618–321) ka (Krause et al., 2010) and 440–410 (538–315) ka (Endicott et al., 2010) (Fig. 6). The most probable timing for when human and Neanderthal ancestral populations split within the span of genetic divergence is the early to mid MIS 11 highstand (421–410 ka) (Fig. 7) when, by analogy to the MIS 5e and MIS 1 interglacial periods (Kuper and Kröpelin, 2006; Osborne et al., 2008), greening of the Sahara may have made movement out of Africa (Out of Africa II) possible (Fig. 7). Once split, Neanderthals and humans appear to have evolved independently with morphological (e.g., Hublin, 1992) and genetic (Green et al., 2010) evidence suggesting that there was no exchange until humans left Africa (Out of Africa III).

The transition from the later Acheulean and Fauresmith to Sangoan and MSA tools including the Levallois flake technology broadly overlaps with the appearance of later archaic humans (*H. helmei*) dated to 300–270 ka from Ileret Kenya (Bräuer et al., 1997) and to 259 ± 35 ka from Florisbad South Africa (Grün et al., 1996). These ages suggest that later archaic humans (*H. helmei*) may have originated during the MIS 10 glacial or the MIS 9 interglacial when the SCP was isolated from Africa with dispersal during the MIS 10 glacial termination at 338 ka or the MIS 8 glacial opening around 277 ka (Fig. 7). Radiometric dating of ash layers brackets the transition to the MSA in Kenya between 509 and 284 ka (Deino and McBrearty, 2002) and diverse MSA artifacts including ochre and grindstones are widespread by the MIS 7e interglacial to MIS 7d glacial transition occurring in Ethiopia (235 ka), Zambia (230 ka at Twin Rivers) and Egypt (230 ka) (McBrearty and Brooks, 2000).

The overlap of stone tool industries such as the later Acheulean, Fauresmith and Sangoan as well as increased variability in MSA stone tools suggests multiple episodes of isolation and mixing of regionally diverse groups (Tryon et al., 2005). Although the SCP is one possible geographical point of origin for some of these events, the uncertainty in the archeological, genetic and sea-level records do not allow differentiation between dispersal from the SCP, Maghreb and African interior. Less uncertainty in the sea-level record combined with better age dating of the more recent (<200 ka) fossil record provides a more rigorous test. Below, the hypothesis is discussed in relation to the earliest evidence of anatomically modern humans and the use of marine resources around 160 ka, the emergence of symbolic behavior and Man-the-Hunter during MIS 5, a burst of innovative artifacts during MIS 4 (72–60 ka), and the development of LSA stone tools from 40 ka.

7.2. Emergence of anatomically modern humans

It is generally accepted that modern humans evolved in Africa from *H. ergaster/erectus* in the middle to late Pleistocene (Rightmire, 2009; Tattersall and Schwartz, 2009). The debate largely centers on whether the trend to increasing brain size and less robust, more gracile features was a gradual, continuous process within a single lineage (*H. sapiens*) (e.g., Bräuer, 2008) or involved the extinction and speciation of multiple distinct taxa (e.g., Tattersall and Schwartz, 2008). The potential complexity of human evolution depicted for southern Africa (Fig. 9) with the isolation and mixing of divergent groups over glacial/interglacial cycles can be expanded to include equally or more complex scenarios for Central, East and North Africa (Fig. 10). In striking contrast to the relative homogeneity of *H. ergaster/erectus*, the fossils and artifacts of the mid to late Pleistocene suggest a regionally diverse mosaic of closely related but distinct human groups (allotaxa, subspecies, demes, hybrids) continually diverging and recombining, a mosaic resulting in rapidly changing and variable morphologies difficult to resolve from the limited fossil record (Jolly, 2001; Bräuer, 2008).

Based on morphological parameters, the Saldanha skull is usually grouped with the Ethiopian Bodo, Tanzanian Ndutu and Eyasi, Moroccan Salé and Zambian Broken Hill (Kabwe) skulls as representative of early archaic humans and the Florisbad skull is grouped with the Kenyan Ileret, Tanzanian Laetoli, Ethiopian Omo II and Moroccan Jebel Irhoud skulls as representative of late archaic humans (Bräuer, 2008).

The oldest fossil remains interpreted to represent AMH include the Omo I and II crania dated at 195 ± 5 ka (McDougall et al., 2005), the Herto cranium dated at 160 ± 5 ka (White et al., 2003) and the Jebel Irhoud crania dated at 160 ± 16 ka (Smith et al., 2007). The Omo I and II fossils are bracketed by dated volcanic pumice between 198 ± 14 ka and 104 ± 7 ka with a preferred age of 195 ± 5 ka (McDougall et al., 2005). The Omo II skull, recovered from the surface, shows signs of weathering and is distinct in form from Omo I suggesting that Omo II may be significantly older than Omo I (Klein, 2009). Omo I has been argued to be not quite representative of AMH (Tattersall and Schwartz, 2008, 2009) and the tight cluster of postcranial bones may suggest it is a more recent burial (Klein, 2009). The Jebel Irhoud crania share morphological features of both late archaic humans (e.g., Florisbad) (Bräuer, 2008) and AMH (e.g., Qafzeh/Skhul) (Hublin, 1992). The ambiguities in distinguishing between late archaic and AMH fossils and their associated age uncertainties make it difficult to determine when AMH emerged. Age estimates of 213 to 154 ka for the base of our mtDNA phylogenetic tree (Behar et al., 2008; Atkinson et al., 2009) are similarly broad and together with the fossil evidence indicate that AMH emerged sometime between the MIS 8 and MIS 6 glacial periods (250–160 ka).

The recovery of Herto and OMO I and II from Ethiopia is often cited as support for speciation of AMH to have occurred in East Africa. However, DNA studies indicate that the Khoisan of southern Africa have the most diverged genetic lineages of living human populations (Tishkoff et al., 2009), and the fact that the Khoisan retain only two major haplogroups prior to Bantu contact does not preclude a southern African origin for AMH (Salas et al., 2002). No fossil remains of AMH dated between MIS 7 and MIS 6 have yet been recovered from southern Africa, but the earliest evidence of a marine diet (Marean et al., 2007) associated with pyrotechnology (Brown et al., 2009) suggests that AMH were present at the Pinnacle Point (PP) cave site 164 ka on the SCP.

The inclusion of marine resources is arguably *the* major dietary change which may have contributed to the speciation of AMH. Marine resources were a critical expansion in diet because they are a rich source of protein, omega-3 fatty acids and trace nutrients such as iodine, iron and zinc, all of which are important to brain and visual function development (Broadhurst et al., 2002). The shoreline environment presents an abundance of nutrient-rich food such as shellfish, algae, marine birds and their eggs, and beached seal and whale, the collecting of which is far easier than fishing or hunting. Raw or slightly cooked marine resources would have required far less robust crania, particularly jaw and teeth, to eat. Rich in calories and easily digested, they would have promoted the development of a large, calorie-consuming brain and an overall more gracile frame.

The use of marine resources is unlikely to be preserved in the present-day onshore fossil record because sea level has only been as high as today or higher for less than 5% of the last 900 kyr (Fig. 6). The chances of preservation are enhanced on the SCP by the fact that marine resources remained within reach of present-day coastal caves when sea level was above −45 m (Van Andel, 1989) or for 42% of the last 900 kyr, and may partly explain why the current earliest record of marine resources is from the SCP. Considering the low preservation potential, it could be argued that marine resources were used earlier than 164 ka but are unlikely to be recovered even

on the SCP. However, the association of pyrotechnology with the earliest record of marine resources may be more than coincidental. The use of fire to heat-treat and improve the quality of locally available fine-grained silcrete on the SCP required a complex chain of thought and implies a relatively large advance in cognitive ability (Brown et al., 2009). Incorporation of a marine diet by groups on the SCP since Termination III may have allowed for the development throughout MIS 7 of a brain capable of devising pyrotechnology to solve the problem of poor quality raw materials.

The SCP is argued here to be a likely point of origin for adaptation of a marine diet because groups isolated on a rapidly contracting coastal plain were always within reach of the SCP shoreline. Mobile groups on the SCP may have seasonally migrated to the coast while the foraging range of more sedentary groups proximal to the coast would have likely included intertidal rocky shores (Marean, 2010). Marine resources of the SCP and WCP are particularly abundant with limpet densities of up to 2600/m^2 in the low-tide zone of SCP rocky shores (Branch and Branch, 1981). A similar mechanism could be argued for the Maghreb except that evidence for marine resource utilization is generally less than on the SCP, an outcome perhaps partly related to the far less rich Mediterranean shoreline (Fa, 2008). In contrast to the Mediterranean, the Atlantic Coast is relatively rich in marine intertidal resources (Fa, 2008) with an abundance of early AMH sites located along the Moroccan coast (Fig. 1). The richness of easily collected, high-protein food from terrestrial aquatic sources is far more limited than that available on rocky coasts, and therefore a far less radical dietary change is predicted for groups isolated within continental interior wetland refugia compared to those living on the coastal plain.

The transition from later archaic humans to AMH is separated by the MIS 7 interglacial highstand (Fig. 8). Later archaic humans perhaps similar to the Florisbad fossil recovered from the interior were likely present on the expanded MIS 8 glacial SCP. Those groups whose territorial range included coastal vegetation biomes would have been directly impacted during the MIS 8 glacial termination (Termination III; 250–246 ka) as these biomes contracted from 53,000 to 13,000 km^2 over a period of 4 kyr as sea level rose from a maximum MIS 8 lowstand between −120 m (Waelbroeck et al., 2002) and −100 m (Rohling et al., 2009) at 250 ka to the SCP closure depth of −75 m by 246 ka (Table 1). Coastal groups were more likely to have observed gulls extract mussels from the surf zone and drop them to break open and eat (Siegfried, 1977), Chacma baboons (*Papio ursinus*) eating shellfish from rock pools (Davidge, 1978) and brown hyenas eating beached seal and whale carcasses. But they perhaps only consistently included marine resources when faced with the rapid loss of, and increased competition for, their habitual terrestrial resources during flooding of the SCP. Shellfish species such as the brown mussel (*Perna perna*) and limpets are abundant and easy to collect from intertidal SCP rocky shores. Although some groups with a marine diet may have exited the SCP before it closed at 246 ka, these groups would have had a marine diet for only several thousand years. Groups who did not exit but were trapped on the SCP following Termination III would have been isolated during the MIS 7 interglacial for a period of 20 kyr (246–226), 63 kyr (246–183 ka) or 86 kyr (246–160 ka) depending on when the SCP opened (see below). Therefore, speciation of AMH may have occurred within a subpopulation of later archaic humans isolated on the SCP during the MIS 7 highstand whose diet consistently included marine resources.

The MIS 7 highstand was not as high as the Eemian (MIS 5e) or Holocene (MIS 1) highstands which proceeded it. Holocene highstand shell middens predominantly occur on the back beach immediately adjacent to where they were collected and can be destroyed or buried by relatively small Holocene variations in sea level (Compton and Franceschini, 2005). Therefore, evidence, such

as shell middens, for a geographical origin of a marine diet from an MIS 7 shoreline which is currently submerged is unlikely to be preserved or recovered (Bailey and Flemming, 2008), particularly considering the large suborbital variations in sea level associated with the MIS 7 interglacial (Thompson and Goldstein, 2005) (Fig. 8). However, marine resources were probably at least briefly accessible to cave dwellers during MIS 7 interglacial highstands (Van Andel, 1989). It is possible that the lack of shellfish in SCP cave deposits as old as MIS 7 reflects a low population density which did not occupy or transport marine resources to cave sites. Transport of shellfish to inland cave sites is relatively rare and, in the case of Pinnacle Point, the age of marine resources corresponds to a period (170–160 ka) of relatively high sea level during MIS 6 when cave dwellers would have had more direct access to the shoreline (Marean et al., 2007; Fisher et al., 2010).

The sea-level records (Waelbroeck et al., 2002; Rohling et al., 2009) indicate that the SCP may have had a limited and brief opening 226(232–220) ka during the MIS 7d lowstand. The MIS 7d lowstand represents the earliest possible, but not highly likely, dispersal from the MIS 7 SCP. Major opening of the SCP only occurs later in the transition to the MIS 6 lowstand (Fig. 8). The sea-level records (Waelbroeck et al., 2002; Rohling et al., 2009) indicate that the SCP opened as early as 183 to 176 ka, but coral data indicate that the SCP was closed during this interval except for a brief opening between 179 and 173 ka (Thompson and Goldstein, 2005; Henderson et al., 2006). The earliest opening of the SCP supported by both coral and $\delta^{18}O$ sea-level records is by 160 (165–153) ka (Table 1). Although the timing of possible dispersals of AMH from the SCP of 232–220, 183–176 (179–173) and 165–153 ka is broadly consistent with the fossil and DNA evidence (250–160 ka), a more rigorous test of the hypothesis will have to wait for refinement of the genetic, fossil and sea-level records.

Groups living in isolation on the MIS 7 interglacial SCP whose diet included marine resources for 800–3400 25-yr generations may have emerged with a reorganized, more cognitive, innovative brain and improved visual capabilities which enabled them to adapt to and radiate rapidly into a wide range of environments, displacing other groups on an expanded glacial SCP and dispersing throughout Africa to establish a continent-wide distribution by 160 ka. AMH moving inland along river courses may have obtained the required omega-3 fatty acids from lacustrine sources or less rich but adequate sources such as insects. However, an absence of lacustrine sources may have been disadvantageous, particularly if iodine was deficient (cretinism).

7.3. Emergence of Man-the-Hunter and symbolic behavior

After the emergence and continent-wide distribution of AMH by 160 ka the next major evolutionary event was the emergence of modern human behavior which included skilful hunters (Man-the-Hunter) and use of symbolic items. The origins of hunting are deep and vague, but development of skilful hunters may have started during MIS 6 as evidenced by heat-treated silcrete tools on the SCP (Brown et al., 2009) and tanged Aterian tools in Morocco dated at 145 ka (Richter et al., 2009). The current earliest appearance of symbolic artifacts is MIS 5. The hypothesis presented here proposes that increased hunting skills may have originated on expanded MIS 6 glacial coastal plain refugia and symbolic behavior may have originated during the MIS 6 penultimate glacial termination (Termination II) between 138 and 134 ka. Both were likely developed further by groups isolated on the SCP during MIS 5 and were widely dispersed with opening of the SCP in the transition to MIS 4 (Figs. 8 and 9). Population on the MIS 6 SCP may have exceeded previous glacial lowstands because of the expanded diet which included marine resources. However, marine resources may not

have been sufficient to accommodate the potential increase in population density resulting from the contraction of the SCP during Termination II as indicated, for example, by the shift from low (MIS 6) to dense (MIS 5e) occupation intensity of the Pinnacle Point cave (Marean, 2010). Another available but perhaps relatively untapped food source was large animals. Hunting large animals was dangerous and required much effort, such that only those under pressure would have likely attempted it. The rapid contraction of the SCP during Termination II and increased competition for resources may have selected for those who could hunt effectively enough to make meat a consistent part of their diet. Some of these groups with skilful hunters may have dispersed out of the SCP before it closed during Termination II (Fig. 9B) while others remained isolated on the SCP throughout MIS 5 (Fig. 9C).

The transition from scavenging to hunting is poorly documented in the archeological record. Fossils from Elandsfontein on the WCP suggest that early archaic humans were primarily scavengers rather than hunters (Milo, 1994; Klein et al., 2007). The diversity of MSA stone tools and the analysis of bone assemblages in cave sites suggest that late archaic humans hunted, but just how effective they were at hunting vs scavenging, particularly of large animals, remains unclear (Klein, 2009). Skilful hunting represents a quantum leap in human ability to use mental and coordinated fine-motor skills. Hunting requires understanding the behavior of game animals over diverse spatial elements of the landscape, making inferences in tracking game, the making and deploying of hunting weapons and use of language to coordinate and perpetuate hunting skills (Liebenberg, 2001).

The severe cooling and drying of the MIS 6 glacial maximum 160–134 ka may have increased selection pressures to hunt throughout Africa either by groups isolated within a dry and depopulated East and Central Africa or somewhat later in the isolated refugia of the Maghreb or SCP during Termination II (Fig. 10). The Aterian industry of North Africa, dated to as old as 145 ka in Morocco, includes innovative stone tools likely used in hunting such as bifacially flaked foliate points, retouched blades, pedunculate points and scrapers (Barton et al., 2009; Richter et al., 2010). In addition to pyrotechnology on the SCP by 164 ka, some of the earliest evidence for competent hunting behavior based on the microtexture of bovid bones comes from the Klasies River main (KRM) site spanning the MIS 5 interglacial (Milo, 1998). AMH may have converged on the KRM site as the SCP flooded during Termination II and remained within reach of the shoreline throughout MIS 5 to subsist on a diet in which both game and marine resources were important (Deacon and Deacon, 1999).

Whether Man-the-Hunter originated within isolated MIS 6 glacial habitats of East or Central Africa or during Termination II on the Maghreb or SCP, groups with skilful hunters were well poised to expand into increasingly connected, warm and humid MIS 5 interglacial habitats. The MIS 5 interglacial corresponds to the 'bushing out' of the mtDNA phylogenetic tree when the number of clades increased from 9 at the MIS 5e interglacial (125 ka) to 36 at the end of MIS 4 glacial (60 ka) with all 42 mtDNA clades established by 40 ka (Behar et al., 2008). The branching out of different clades corresponds to an increase in regional variation in MSA stone tools, many of which appear well suited for hunting (Clark, 1992; McBrearty and Brooks, 2000). Therefore, following a possible MIS 6 glacial population bottleneck, the MIS 5 was a period of expansion by AMH hunters capable of adapting to and radiating into many of the distinct geographic regions of Africa (Lahr and Foley, 1998).

During the MIS 5 expansion two populations were isolated at the opposite ends of Africa. One population was on the SCP isolated by the CFB after 134 ka and the other population was in the Maghreb isolated by the Sahara Desert after 118–110 ka (Osborne et al., 2008; Castañeda et al., 2009) (Fig. 10). Sea level was up to

10 m higher than present day at the Last interglacial maximum (MIS 5e) between 128 and 122 ka (Thompson and Goldstein, 2005; Rohling et al., 2009) and then fluctuated between +1 and −85 m throughout the following interglacial substages MIS 5a–d (Fig. 8). Geochemical records from the northwest African margin suggest that greening of the Sahara did not re-occur after 118-110 ka until MIS 3 (Castañeda et al., 2009). None of the MIS 5a - d sea level lowerings was drop sufficient to open up the SCP with the possible exception of a slight opening during the maximum estimated MIS 5b lowstand of −62 to −85 m between 88 and 85 ka (Waelbroeck et al., 2002; Rohling et al., 2009). It is on these widely separated and isolated coastal plains of southern and northern Africa that the earliest artifacts of symbolic behavior are found.

None of the sites associated with the earliest AMH or any other of the relatively few sites dating from the MIS 6 glacial period has yet yielded evidence of symbolic behavior besides ochre, which occurs in East Africa as early as 280 ka (McBrearty and Brooks, 2000). Currently, the earliest evidence is from MIS 5 sites in the Levant (Israel), North Africa and the SCP. Beads, some stained with ochre, from the Skhul Cave (Vanhaeren et al., 2006) dated to between 135 and 100 ka (Grün et al., 2005) are interpreted to represent personal ornamentation used to convey social information. Beads from Qafzeh Cave are associated with a ceremonial burial site and shell pendants (Bar-Yosef Mayer et al., 2009) and have an average TL date of 92 ± 5 ka (Valladas et al., 1988). These Levant sites document the first exodus of AMH out of Africa. Although AMH in the Levant had modern behaviors, they lacked innovative MSA stone tools and were not sustained beyond MIS 5 perhaps because they were unable to compete with Neanderthal populations as climate became progressively cooler and drier (Mellars, 2006; Vaks et al., 2010). AMH did, however, persist in North Africa, where shell bead jewelry is documented from approximately 85–60 ka (D'Errico et al., 2009). The earliest record on the SCP of symbolic behavior includes engraved ochre (Henshilwood et al., 2002; 2009) and bone tools (Jacobs et al., 2006) from Blombos Cave, and keepsake shells from Pinnacle Point (Jerardino and Marean, 2010), all appearing by around 100 ka. The gap of as much as 60 kyr between the widespread dispersal of AMH and artifacts indicating symbolic behavior may represent a delayed, stepwise increase in the mental capabilities of AMH not associated with major morphological changes (Klein, 2009).

7.4. Innovative burst

The end of the MIS 5 interglacial is marked in southern Africa by a diverse assemblage of innovative artifacts which appear in the fossil record in the transition to and for the duration of the MIS 4 glacial period, 75.1(77–72) to 60.6(63.5–56.4) ka (Table 1). The artifacts include bone tools (Jacobs et al., 2006), engraved ochre (Henshilwood et al., 2002; 2009), engraved ostrich eggshell (Parkington et al., 2005; Texier et al., 2010), shell jewelry (Henshilwood et al., 2004), expansion and refinement of fire-treated stone tools (Brown et al., 2009), and the Still Bay and Howiesons Poort industries (Jacobs et al., 2008). These artifacts are interpreted to represent a large advance in cognitive ability associated with abstract thought, cultural identity and language. In particular, bone tools, pyrotechnology and the Still Bay and Howiesons Poort industries can be interpreted as technological advances in the manufacture of hunting tools. The innovative burst coincides with or predates the first successful exodus of AMH out of Africa 70 to 50 ka (Mellars, 2006). What factors might have contributed to the origin of these artifacts and why is their widespread appearance in the fossil record associated with the MIS 4 glacial?

The evidence from the SCP suggests that at least some innovative artifacts which appear suddenly during MIS 4 were developed earlier during MIS 5. Groups trapped and isolated on the SCP after its closure at 134 ka may have further developed innovations during the 64 kyr MIS 5 interglacial (134–70 ka) perhaps driven by a growth in population which, unable to expand easily beyond the SCP, may have relied increasingly on innovative hunting tools and symbolic items for identity and trade among territorial groups. Symbolic behavior may have been an adaptation by small, territorial groups living in relatively high population densities on a contracted MIS 5 coastal plain with items such as ochre, keepsake shells and bead jewelry used for identification and trade during periods of scarcity. Engraved ochre has been recovered from layers of the Blombos Cave site dating as far back as 100 ka (Henshilwood et al., 2002; 2009) and bone tools include numerous awls, a spear point and a point tip ranging in age from 84 to 72 ka (Henshilwood and Sealy, 1997; Henshilwood et al., 2001; Jacobs et al., 2006; D'Errico and Henshilwood, 2007) with a single awl from an older layer dated at 98.9 ± 4.5 (Jacobs et al., 2006). In the case of marine resources, the earliest records show an abundance of the rocky shore mussel (Perna perna) and limpets, followed by a shift around MIS 5c (100 ka) to what are arguably more difficult to obtain sandy beach species such as the white clam Donax serra (Jerardino and Marean, 2010). These developments were largely restricted to a variably contracted SCP during the MIS 5a–e substages and as a result artifacts are generally poorly preserved in the fossil record. The abrupt, widespread appearance throughout southern Africa of many of these innovative artifacts may, therefore, reflect their rapid dispersal with opening of the SCP around 70 ka (Fig. 8).

Similar to the SCP, hunting and symbolic behavior may have originated independently in North Africa in response to loss of coastal plain habitat as the Moroccan and Tunisian shelves contracted against the Atlas Mountain and Sahara Desert barriers (Figs. 1 and 10). The earliest MIS 5 symbolic artifacts from the Levant/ Maghreb and SCP overlap in age and a convergent origin at the opposite ends of Africa is consistent with the current lack of similar artifacts from East African sites and with regional differences in MSA stone tool industries (Clark, 1992). The current lack of MIS 5 symbolic artifacts in East and Central Africa may reflect non-territorial groups who could generally expand with ease throughout much of Africa except into the SCP and Maghreb. In addition, the lack of artifacts may reflect a preservation bias with few East or Central African archeological sites spanning the MIS 6 to MIS 5 periods (McBrearty and Brooks, 2000).

Mediterranean speleothems indicate a MIS 5a highstand of around 1 m 81 ka (Dorale et al., 2010) and coral data bracket the transition from the MIS 5a to the MIS 4 glacial by a rapid drop in sea level from −24 m to −80 m between 76(78–74) and 71.5(73–70) ka (Cutler et al., 2003). Coral data and sea-level records (Waelbroeck et al., 2002; Rohling et al., 2009) give a mean age of 69.7 (71.5–67.5) ka for the opening of the SCP. There are no coral data from the MIS 4 glacial maximum but the sea-level curves (Waelbroeck et al., 2002; Siddall et al., 2003; Bintanja et al., 2005) indicate that the SCP remained open from 69.7(71.5–67.5) until 60.6(63.5–56.4) ka with a maximum MIS 4 drop in sea level of −95 to −119 m at 65 ka (Siddall et al., 2003). A coral datum indicates sea level had risen to −77 ± 4 m by 60.8 ± 0.8 ka (Cutler et al., 2003) in good agreement with the sea-level curve of Siddall et al. (2003) and the rise of sea level to −75 m between 63.5 ka (Waelbroeck et al., 2002) and 56.4 ka (Bintanja et al., 2005). Together these records indicate that the SCP was open during the MIS 4 glacial from approximately 70 to 61 ka (Fig. 8), a period when increased access to migratory herds may have prompted the development of improved hunting skills including the innovative Still Bay and Howiesons Poort industries.

The Still Bay has been interpreted to be a relatively short-lived industry widely dispersed in southern Africa with four OSL dates

from three sites (Apollo 11, Sibudu and Diepkloof) between 71.9 and 71.0 ka (Jacobs and Roberts, 2008). However, Still Bay points from Blombos Cave on the SCP have older ages estimated between 77 and 72 ka (Henshilwood, 2008). The Howiesons Poort industry occurs in archeological sites throughout southern Africa south of the Zambezi River between 64.8 and 59.5 ka. The two industries are interpreted to be separated by a period of 2.7–9.3 kyr (Jacobs and Roberts, 2008), a period which overlaps with the MIS 4 glacial maximum (70–61 ka). The relation of the Still Bay and Howiesons Poort industries to climate is debated (Jacobs and Roberts, 2008; Bar-Matthews et al., 2010; Chase, 2010); however, both have a direct relation to sea level. The Still Bay is associated with the rapid lowering of sea level and overlaps with the range in ages for the opening of the SCP in the transition to the MIS 4 glacial maximum whereas the Howiesons Poort coincides with the rise in sea level and closure of the SCP associated with the MIS 4 glacial termination 65 to 61 ka (Fig. 8).

The expanded SCP habitats of the MIS 4 glacial may have consisted of a variable C_3/C_4 mix of vegetation biomes including grassland (Fig. 3). Although some grassland plants may have provided an important food source, with evidence of humans making use of wild sorghum during MIS 5 from the Mozambique cave site of Ngalue (Mercader, 2009), hunting would have been a major advantage to humans on the expansive habitats of the glacial SCP occupied by a diversity of large game animals. Still Bay points are well suited for hunting large animals and an analysis of Still Bay points from Blombos Cave indicates that some were hafted and used as spear tips (Villa et al., 2009). As sea level fell during the MIS 4 glacial, summer rainfall areas became drier while winter rainfall areas expanded along with more humid SCP habitats (Chase, 2010) having a highly variable mix of C_3 and C_4 grasses (Bar-Matthews et al., 2010). Small, dense populations on the MIS 5 interglacial SCP would have expanded onto an enlarged SCP and mixed with herd animals and groups from the interior seeking a glacial refuge (Fig. 9D). Expansion of groups onto the SCP may have resulted in a lower population density with large, mobile and nonterritorial groups hunting large herd animals having less need for exchange items and promoting the rapid and widespread distribution of Still Bay artifacts. SCP Still Bay points are similar to older lanceolate points from Zambia (Clark and Brown, 2001) and from the Aterian of North Africa (Barton et al., 2009), suggesting a convergent or alternative origin in North or East Africa during MIS 5 and arrival by the MIS 4 glacial along with animals and hunters seeking refuge on the SCP (Fig. 9D).

The displacement of Still Bay by hafted Howiesons Poort backed microlithics may reflect a shift to more versatile and effective weapons for hunting large animals (McBrearty and Brooks, 2000). For example, some Howiesons Poort stone tools and bone tools from Sibudu Cave on the eastern coastal plain are interpreted to have been used as arrow heads (Backwell et al., 2008; Lombard and Pargeter, 2008; Lombard and Phillipson, 2010). The hypothesis predicts that the Howiesons Poort was developed and dispersed in response to the rapid flooding of the SCP during termination of the MIS 4 glacial driven by increasing population density and the need for more skilful hunters. The available OSL ages generally support the hypothesis with the earliest Howiesons Poort at 64.8 ka associated with the maximum MIS 4 glacial opening of the SCP at 65 ka (Siddall et al., 2003) and the latest Howiesons Poort at 59.5 ka associated with the final closure of the SCP by 60.6(63.5–56.4) ka.

Groups at the close of the MIS 4 glacial were perhaps for the first time well adapted to move across the landscape with features such as the Cape Fold Belt presenting less of a barrier. In addition to skilful hunters using diverse tools, decorated ostrich eggshell from Diepkloof on the WCP indicates the use of water containers by 65 ka (Parkington et al., 2005; Texier et al., 2010). Burial of water

containers is used by modern hunter-gatherers in their mid-day running down of large game animals to the point of heat exhaustion (Liebenberg, 2001). The use of water containers represents a major adaptation, particularly to groups occupying the seasonally arid WCP with cachets of buried water containers greatly reducing the arid corridor as a barrier to movement.

7.5. Out of Africa

Although groups with symbolic behavior and hunting tools of the Aterian existed in North Africa from as early as 145–110 ka (Barton et al., 2009; Richter et al., 2010) and on the SCP as early as 164–100 ka, the first successful exodus of AMH from Africa only occurred much later. DNA evidence indicates that the initial exodus of around 3000 individuals out of Africa occurred 56 ± 6 ka (Liu et al., 2006) and that the first non-African lineages (haplogroups) M and N emerged 69–53 ka and 64–50 ka, respectively (Atkinson et al., 2009). The earliest fossil evidence of AMH in China (Shen et al., 2002) and Australia (Turnley et al., 2001; Bowler et al., 2003) support an African exodus prior to 67 and 50 ka, respectively. Taken together, the fossil and DNA evidence suggests that the exodus out of Africa occurred between 69 and 50 ka, a period which largely overlaps with or post-dates the predicted widespread dispersal out of the SCP during the MIS 4 glacial termination 65–61 ka.

The small isolated group L3, from which the haplogroups M and N were derived, had a selective advantage which allowed the population size of L3 to grow and rapidly expand between 86 and 61 ka (Atkinson et al., 2009). The possibility that L3 was a small isolated group on the MIS 4 glacial SCP is supported by the relationship of genetic diversity and geographic distance which suggests that migration of modern humans originated in southwestern Africa with a waypoint in northeast Africa near the midpoint of the Red Sea (Tishkoff et al., 2009). Large mobile hunting groups of several thousand individuals following large, migratory herds forced to exit the SCP at the MIS 4 glacial termination may have rapidly expanded north with the advantage of being more likely to retain and transmit skills to successive generations than small groups (Powell et al., 2009). Movement beyond southern Africa into tropical East Africa may have been possible where lake records indicate more stable, wet climates since 70 ka (Scholz et al., 2007) and movement into North Africa may have been possible during the MIS 3 wet period between 60 and 45 ka (Castañeda et al., 2009). However, archeological evidence of such movement may be difficult to preserve if large groups moved frequently over large territories and occupied predominately open air sites (Deacon, 1984). Therefore, successful expansion beyond Africa may have had to wait until large organized groups with the versatile adaptive skills of hunting and modern behaviors could move rapidly by exploiting game meat and marine resources along a proposed southern, coastal route to Southeast Asia (Macaulay et al., 2005). Versatile adaptive skills were likely key to the successful and rapid expansion into the diverse and unknown biomes beyond Africa, particularly by hunters over-qualified to hunt less wary animals outside of Africa.

7.6. The Later Stone Age

Closure of the SCP in the MIS 4 to MIS 3 transition is associated with the puzzling loss of Howiesons Poort microlithics throughout southern Africa and with the resurgence of stone tools similar to the earlier MSA which, although present in small amounts, were mostly displaced by Howiesons Poort microlithics. Referred to as the final MSA, this period is additionally enigmatic for the general absence of personal ornaments from the archeological record

throughout Africa during MIS 3 (D'Errico et al., 2009). Sea-level records indicate that the SCP was closed from 61 to 50 ka (Fig. 8). However, sea level generally remained below −45 m throughout MIS 3 and much of Africa was cool and dry (Adams and Faure, 1997) with southern Africa in particular drier during MIS 3 than MIS 4 (Chase, 2010). The return of earlier, retro MSA stone tools may represent a functional shift away from hunting and processing animals to foraging and processing plants. Such a shift is predicted in response to less favorable hunting during MIS 3 after the SCP closed to migratory herds by 61 ka and as climate became drier regionally throughout southern Africa. Predominantly territorial groups too small to transmit and sustain innovative stone tool technologies (Powell et al., 2009) may have reverted back to an earlier, more appropriate production using older MSA technology driven by the shift in vegetation biomes and fewer large grazers.

The shift from the final MSA to an early LSA stone tool assemblage comprising bipolar flaking and a few ostrich eggshell beads (Deacon, 1990) is associated with the MIS 3 interglacial to MIS 2 glacial transition. The timing and nature of the transition to the LSA is difficult to assess because few, well dated archeological sites exist (Mitchell, 2002), perhaps the result of a population bottleneck associated with the relatively inhospitable cool and dry climate of MIS 3 and MIS 2. The SCP periodically opened and closed during the MIS 3 to MIS 2 transition as sea level fluctuated between −51 and −112 m from 50 to 36.5 ka with the SCP fully open after sea level fell from −75 m to −120 m between 36.5 and 28 ka (Fig. 8). The earliest LSA stone artifacts are dated from 46 ka and ostrich eggshell beads from 40 ka at the Enkapune Ya Muto site in the central Rift Valley of Kenya (Ambrose, 1998). LSA artifacts are documented in North Africa by 40 ka and in South Africa at the Border Cave and Rose Cottage sites by around 38 ka (Deacon, 1984). These ages suggest that LSA stone artifacts originated in East Africa as early as 50 to 45 ka and were later dispersed to southern Africa perhaps by mobile hunting groups following large grazers onto an opening MIS 2 glacial SCP refuge (Fig. 9D). These groups were possibly represented by the 36.2 ± 3.3 ka Hofmeyr skull, a skull similar to Upper Paleolithic Eurasians but morphologically distinct from recent South Africans suggesting that modern groups only emerged later (Grine et al., 2007). The apparent sudden loss of Howiesons Poort suggests that large MIS 4 hunting groups abandoned southern Africa for wetter regions of Central and East Africa taking microlith stone tool technology with them. Some of these groups may have exited Africa by 65 to 50 ka but microlith technology may have persisted among groups which remained in East Africa to develop into the Early LSA between 65 and 50 ka before diffusing south to arrive in southern Africa in the transition to the LGM.

Early LSA tools were replaced in southern Africa by backed microliths, scrapers, borers and bladelets of the Robberg industry during the LGM lowstand of −120 m between 28 and 19 ka when the SCP was wide open (Deacon and Deacon, 1999). Microbladelets of the Robberg were a major innovation which provided the versatility to make complex composite tools (Mitchell, 2002). These tools were likely used for hunting as suggested by their association with the remains of large migratory grazers. Similar to the emergence of the Howiesons Poort industry microliths at the height of the MIS 4 glacial, the Robberg industry emerged during the LGM around 22 ka and included polished bone points and bone beads (Deacon, 1990) and a shift to more versatile hunting weapons, such as the widespread use of bow and arrow (Deacon, 1995).

Rapid closure of the SCP between 19 and 14 ka as sea level rose to −75 m by 13.8(14.2−13.6) ka during the MIS 2 glacial termination (Termination I) (Clarke et al., 2009) may have increased population density and initiated the development of historical hunter-gatherer

societies. Greater population density is indicated by the decrease in the size of collected tortoise and shellfish (Klein et al., 2007), and a more diverse diet as well as improved hunting skills are reflected in the shift from hunting eland during the MSA to hunting relatively more dangerous warthog and buffalo (McBrearty and Brooks, 2000; Klein, 2009). In addition to a drier climate and contraction of the coastal plain habitat, greater population density, improved hunting skills and more sophisticated hunting weapons may have contributed to megafaunal extinction by 10−7 ka of long-horned buffalo (Pelorovis antiquus), Cape zebra (Equus capensis) and the giant hartebeest (Megalotragus priscus).

The widespread dispersal of the Robberg throughout southern Africa between 14 and 12 ka was perhaps driven by the exodus associated with rapid flooding and closure of the SCP by 14 ka (Fig. 9B). The Robberg includes a marked increase in decorative items and polished bone tools, as well as decorated ostrich eggshell water containers and tortoise shell bowls between 14 and 10 ka (Deacon, 1990). The increase in decorative items may reflect the transition from large groups hunting large migratory grazers to small territorial groups hunting small, non-gregarious browsers (Klein, 1984; Deacon, 1990) and the establishment of exchange and kinship networks (Wadley, 1988). The high degree of regional variation in LSA stone artifacts suggests that groups were largely isolated between inland and coastal areas and along an east-west transect across the SCP (Deacon and Deacon, 1999). However, SCP barriers did not prevent regional exchange as evidenced by stone tools made from exotic raw materials and seashells recovered from sites located up to 200 km inland (Mitchell, 2002).

The Robberg was replaced by non-microlithic assemblages of the Oakhurst industry by 12 to 10 ka which consists largely of medium to large scrapers with rare bladelet or backed microlith production and encompasses regional variations of the Albany industry on the SCP and Lockshoek industry in the Karoo (Deacon, 1984; Deacon and Deacon, 1999; Mitchell, 2002). The loss of bladelet and backed microliths in southern Africa may relate to an exodus of hunters north of the Zambezi where backed microlithic stone tools persisted, to a regional replacement of stone tools by bone tools in southern Africa (Deacon, 1984) or to increased hunting by use of traps as opposed to bow and arrow (Deacon and Deacon, 1999). The trend away from hunting large grazers to smaller non-gregarious antelope and abundant use of marine resources at coastal sites suggest that hunting was de-emphasized in southern Africa at this time.

Backed microlithic stone tools are reintroduced into southern Africa from 7 ka (Wilton industry) from the north associated with the mid-Holocene climatic optimum, maximum MIS 1 sea level (Compton, 2006) and a large increase in the number of archeological sites. Population growth from 6 ka is supported by evidence of increased food production such as megamiddens on the WCP (Jerardino, 1998), fire-stick farming of geophytes in the Eastern Cape and digging sticks and fishing with barbed bone points, nets and angling on the SCP (Deacon and Deacon, 1999; Mitchell, 2002). These late LSA innovations appear to have been driven by increasing population density with groups confined to geographical regions defined by climate, terrain and vegetation. Unable to easily expand, these groups were forced to adopt new subsistence strategies. Intensified resource use was associated with a more diverse toolkit by more sedentary groups who maintained widespread exchange networks, stored food, and practiced rock art and burials. These MIS 1 interglacial (Holocene) developments are most pronounced on the coastal plain adjacent to the Cape Fold Belt having more hospitable and diverse habitats compared to the interior of southern Africa (Mitchell, 2002). In addition, expansion beyond the SCP into other regions of southern Africa was limited by the physical, climatic and vegetation barriers, particularly between

8 and 4 ka when many interior sites were abandoned perhaps in response to drier climate (Deacon and Deacon, 1999). Further development of hunter-gatherer societies during MIS 1 was interrupted by the southward movement of agropastorialists who arrived in southern Africa with pottery and domesticated plants and animals by 2 ka (Deacon and Deacon, 1999; Mitchell, 2002).

8. Conclusions

The southern coastal plain (SCP) of South Africa forms a distinct geographical region whose extent and climate varied significantly over Pleistocene glacial to interglacial cycles. The SCP is bound by the steep, rugged Cape Fold Belt covered by inedible plants of the sandstone fynbos biome which forms a barrier to animal and human movement. The SCP is host to several key archeological sites having some of the earliest evidence for modern human behavior. Here it is proposed that alternating periods of connection and isolation of the SCP make it a possible region in Africa where human evolution occurred through the process of allopatry. The SCP was potentially isolated from the rest of Africa during interglacial periods when sea level was above −75 m and the Hangklip and Plettenberg Bay portals were closed as well as during glacial maxima when a wet, expanded SCP may have served as a refuge to a dry interior. Selection pressures are predicted to intensify during glacial terminations when flooding of the SCP in combination with climate change resulted in the rapid loss of habitat, forcing groups to expand or increase food resources as population density increased. Selection pressures may have also acted on growing populations unable to expand easily beyond the SCP during interglacials and promoted the development of symbolic behavior and novel subsistence strategies. Isolation for 9–86 kyr or 360 to 3400 25-yr human generations was perhaps sufficient for selection pressures and random genetic drift to develop groups divergent from the rest of Africa. Reintroduction of previously isolated groups from the SCP in the transition to glacial maxima and during glacial terminations may have resulted in the wide dispersal of new adaptations some of which appear as artifacts in the fossil record.

The hypothesis may also apply to the North African coastal plain (Maghreb) where populations isolated by the Atlas Mountains and the Sahara Desert during glacial maxima may have developed artifacts which were later dispersed with greening of the Sahara in the transition to interglacial periods. The 5–10 kyr offset between closure of the SCP during glacial terminations and opening of the Sahara in the following interglacial may have allowed for dispersal from southern to northern Africa, but not vice versa. Originations in Central and East Africa are predicted to occur primarily during dry glacial maxima as habitats contract and fragment and to disperse during the following warm and humid interglacial period as habitats expand. Therefore, although originations are rarely preserved and undoubtedly occurred in many regions within Africa, the hypothesis presented here proposes that the timing of dispersals associated with the widespread appearance of artifacts in the fossil record may be able to differentiate among different potential geographical points of origin.

Major evolutionary events such as the emergence of early archaic humans, the transition from the early Acheulean to the later Acheulean and Fauresmith, the emergence of late archaic humans and the transition to Sangoan and MSA tools occur over the span of several large-amplitude glacial to interglacial variations initiated around 900 ka (MIS 22) and extending to 250 ka (MIS 8). The incompleteness and uncertainty in the fossil, DNA and sea-level records limit the extent to which these events can provide a test to the hypothesis. The more recent (post MIS 8 glacial) fossil, DNA and sea-level records improve considerably and it is argued here that

several events in human evolution since 250 ka may be consistent with the hypothesis. It is proposed, for example, that AMH (*H. sapiens*) may have originated on the SCP during Termination III (250–246 ka) as a result of selection pressures to adopt a marine diet. Isolation of groups having a marine diet on the MIS 7 interglacial SCP for a period of 800–3400 25-yr generations may have led to speciation of the more gracile, larger brained AMH which dispersed out of the SCP to establish a continent-wide presence by at least 160 ka.

The emergence of clever AMH may relate to the mental abilities and fine-motor skills of skilful hunters initiated in MIS 6 and the development of symbolic items in MIS 5. Flooding of coastal plain habitats during Termination II (138 and 134 ka) may have independently selected for increased hunting skills to increase food resources and symbolic behavior for identity and trade among SCP and Maghreb territorial groups. The apparent burst of innovative artifacts associated with the MIS 4 glacial (75–60 ka) may reflect their earlier development on an isolated MIS 5 SCP and wide dispersal only after the SCP opened in the MIS 4 glacial. The Still Bay industry is associated with the rapid sea-level fall of MIS 4 and may correspond to the movement of herds and hunters from the north onto the SCP, whereas the Howiesons Poort is associated with the MIS 4 glacial termination and may represent dispersal of improved hunting technology developed on an expansive grassland and shrub mosaic landscape as the SCP contracted. The first successful exodus of AMH out of Africa may have had to wait for the widespread dispersal of large groups having versatile adaptive hunting skills and modern behaviors from the SCP during the MIS 4 glacial termination.

Continent-wide depopulation may have been a contributing factor to the lack of innovative tools and symbolic artifacts during MIS 3, which only reappear in the transition to the LGM. LSA microlithic tools of the Robberg industry appear during the height of the LGM and, similar to the Howiesons Poort, may represent an adaptive shift to more competent and frequent hunting as the SCP opened up to large migratory herds. Rapid dispersal of the Robberg throughout southern Africa by 14 ka may relate to the expansion of mobile hunting groups as the SCP closed during Termination I. The diverse toolkit of modern hunter-gatherers may have developed among territorial groups remaining on the SCP after it closed. Largely isolated by SCP barriers, these groups were unable to expand and population density increases required new subsistence strategies, intensifying or expanding food resources as well as exchange items.

The complexity of human evolution in Africa may reflect the large size of the continent and the large number of habitats which expanded and contracted in response to Pleistocene climate. The mechanism proposed here of expansion and contraction of coastal plain habitats would have magnified the impacts of climate change alone. Contraction of expansive glacial coastal plain habitats during rapid terminations against barriers that prevent movement inland resulted in isolation of populations as well as increases in population density both during flooding and later by limiting expansion. These conditions appear to have applied to the coastal plains of southern and northern Africa and may explain why the SCP and Maghreb have an abundance of archeological sites with some of the earliest evidence of human evolution. Although the records are less complete, human groups most certainly evolved within the many refugia in the interior of Africa, and these groups periodically mixed with each other as well as with groups previously isolated on the Maghreb and SCP. The hypothesis presented here may serve as a starting point at unraveling the role of these complex isolation and mixing events in the evolution of humans in Africa and can be further tested as age dating methods improve the chronology of archeological, DNA and sea-level records.

Acknowledgments

References

O'Brien, E.M., Peters, C.R., 1999. Landforms, climate, ecogeographic mosaics, and the potential for hominid diversity in Pliocene Africa. In: Bromage, T.G., Schrenk, F. (Eds.), African Biogeography, Climate Change, & Human Evolution. Oxford Univ. Press, pp. 115–137.

Adams, J.M., Faure, H., 1997. QEN Members. Review and Atlas of Palaeovegetation: Preliminary Land Ecosystem Maps of the World since the Last Glacial Maximum. Oak Ridge National Laboratory, TN, USA. http://www.esd.ornl.gov/projects/qen/adams1.html.

Ambrose, S.H., 1998. Chronology of the Later Stone Age and food production in East Africa. Journal of Archaeological Science 25, 377–392.

Arz, H.W., Lamy, F., Ganopolski, A., Nowaczyk, N., Pätzold, J., 2007. Dominant Northern Hemisphere climate control over millennial-scale glacial sea-level variability. Quaternary Science Reviews 26, 312–321.

Atkinson, Q.D., Gray, R.D., Drummond, A.J., 2009. Bayesian coalescent inference of major human mitochondrial DNA haplogroup expansions in Africa. Proceedings of the Royal Society B 276, 367–373.

Backwell, L., d'Errico, F., Wadley, L., 2008. Middle Stone Age bone tools from the Howiesons Poort layers, Sibudu Cave, South Africa. Journal of Archaeological Science 35, 1566–1580.

Bailey, G.N., Flemming, N.C., 2008. Archaeology of the continental shelf: marine resources, submerged landscapes and underwater archaeology. Quaternary Science Reviews 27, 2153–2165.

Bar-Matthews, M., Marean, C.W., Jacobs, Z., Karkanas, P., Fisher, E.C., Herries, A.I.R., Brown, K., Williams, H.M., Bernatchez, J., Ayalon, A., Nilssen, P.J., 2010. A high resolution and continuous isotopic speleothem record of paleoclimate and paleoenvironment from 90 to 53 ka from Pinnacle Point on the south coast of South Africa. Quaternary Science Reviews 29, 2131–2145.

Bar-Yosef Mayer, D.E., Vandermeersch, B., Bar-Yosef, O., 2009. Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: indications of modern behavior. Journal of Human Evolution 56, 307–314.

Barton, R.N.E., Bouzouggar, A., Collcutt, S.N., Schwenninger, J.-L., Clark-Balzan, L., 2009. OSL dating of the Aterian levels at Dar es-Soltan I (Rabat, Morocco) and implications for the dispersal of modern Homo sapiens. Quaternary Science Reviews 28, 1914–1932.

Basell, L., 2008. Middle Stone Age (MSA) site distributions in eastern Africa and their relationship to Quaternary environmental change, refugia and the evolution of Homo sapiens. Quaternary Science Reviews 27, 2484–2498.

Behar, D.M., Villems, R., Soodyall, H., Blue-Smith, J., Pereira, L., Metspalu, E., Scozzari, R., Makkan, H., Tzur, S., Comas, D., Bertranpetit, J., Quintana-Murci, L., Tyler-Smith, C., Wells, R.S., Rosset, S., The Geongraphic Consortium, 2008. The dawn of human matrilineal diversity. American Journal of Human Genetics 82, 1130–1140.

Bintanja, R., van de Wal, R.S.W., 2008. North American ice-sheet dynamics and the onset of 100,000-year glacial cycles. Nature 454, 869–872.

Bintanja, R., van de Wal, R.S.W., Oerlemans, J., 2005. Modelled atmospheric temperatures and global sea levels over the past million years. Nature 437, 125–128.

Birch, G.F., 1980. Nearshore Quaternary sedimentation off the south coast of South Africa (Cape Town to Port Elizabeth). South Africa Geological Survey Bulletin 67, 20.

Bowler, J.M., Johnston, H., Olley, J.M., Prescott, J.R., Roberts, R.G., Shawcross, W., Spooner, N.A., 2003. New ages for human occupation and climatic change at Lake Mungo, Australia. Nature 421, 837–840.

Branch, G.M., Branch, M., 1981. The Living Shores of Southern Africa. Struik, Cape Town.

Bräuer, G., 2008. The origin of modern anatomy: by speciation or intraspecific evolution? Evolutionary Anthropology 17, 22–37.

Bräuer, G., Yokoyama, Y., Falguères, C., Mbua, E., 1997. Modern human origins backdated. Nature 386, 337–338.

Brink, J.S., 1987. The archaeozoology of Florisbad, Orange Free State. Memoirs van die Nasionale Museum 24, 151.

Broadhurst, C.L., Wang, Y., Crawford, M.A., Cunnane, S.C., Parkington, J.E., Schmidt, W.F., 2002. Brain-specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African Homo sapiens. Comparative Biochemistry and Physiology B 131, 653–673.

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

Burman, J., 1969. Who Really Discovered South Africa? Struik, Cape Town.

Carr, A.S., Bateman, M.D., Roberts, D.L., Murray-Wallace, C.V., Jacobs, Z., Holmes, P.J., 2010. The last interglacial sea-level high stand on the southern Cape coastline of South Africa. Quaternary Research 73, 351–363.

Castañeda, I.S., Mulitza, S., Schefuß, E., Lopes dos Santos, R.A, Sinninghe Damsté, J.S., Schouten, S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. Proceedings of the National Academy of Science 106, 20159–20163.

Chappell, J., 2002. Sea level changes forced ice breakouts in the Last Glacial cycle: new results from coral terraces. Quaternary Science Reviews 21, 1229–1240.

Chappell, J., Omura, A., Esat, T., McCulloch, M., Pandolfi, J., Ota, Y., Pillans, B., 1996. Reconciliation of late Quaternary sea levels derived from coral terraces at Huon Peninsula with deep sea oxygen isotope records. Earth and Planetary Science Letters 141, 227–236.

Chase, B.M., 2010. South African palaeoenvironments during marine Oxygen Isotope Stage 4: a context for the Howiesons Poort and Still Bay industries. Journal of Archaeological Science 37, 1359–1366.

Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. Earth-Science Reviews 84, 103–138.

Clark, J.D., 1992. African and Asian perspectives on the origins of modern humans. Philosophical Transactions of the Royal Society, London B337 201–215.

Clark, J.D., Brown, K.S., 2001. The Twin Rivers Kopje, Zambia: stratigraphy, fauna and artefact assemblages from 1954 to 1956 excavations. Journal of Archaeological Science 28, 305–330.

Clarke, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. Science 325, 710–714.

Compton, J.S., 2006. The mid-Holocene sea-level highstand at Bogenfels Pan on the southwest coast of Namibia. Quaternary Research 66, 303–310.

Compton, J.S., Franceschini, G., 2005. Holocene geoarchaeology of the Sixteen Mile Beach barrier dunes in the Western Cape, South Africa. Quaternary Research 63, 99–107.

Compton, J.S., Wiltshire, J.G., 2009. Terrigenous sediment export from the western margin of South Africa on glacial/interglacial cycles. Marine Geology 266, 212–222.

Cutler, K.B., Edwards, R.L., Taylor, F.W., Cheng, H., Adkins, J., Gallup, C.D., Cutler, P.M., Burr, G.S., Bloom, A.L., 2003. Rapid sea-level fall and deep-ocean temperature change since the Last interglacial period. Earth and Planetary Science Letters 206, 253–271.

Davidge, C., 1978. Ecology of baboons (Papio ursinus) at Cape Point. Zoologica Africana 13, 329–350.

D'Errico, F., Henshilwood, C.S., 2007. Additional evidence for bone technology in the southern African Middle Stone Age. Journal of Human Evolution 52, 142–163.

D'Errico, F., Vanhaeren, M., Barton, N., Bouzouggar, A., Mienis, H., Richter, D., Hublin, J.-J., McPherron, S.P., Lozouet, P., 2009. Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa. Proceedings of the National Academy of Science 106, 16051–16056.

Deacon, H.J., 1976. Where Hunters Gathered: A Study of Holocene Stone Age People in the Eastern Cape. In: South Africa Archaeological Society Monograph 1 Claremont, South Africa.

Deacon, H.J., 1995. Two late Pleistocene-Holocene archaeological depositories from the southern Cape, South Africa. South African Archaeological Bulletin 50, 121–131.

Deacon, H.J., Deacon, J., 1999. Human Beginnings in South Africa, Uncovering the Secrets of the Stone Age. David Philip, Cape Town.

Deacon, J., 1984. Later Stone Age people and their descendants in southern Africa. In: Klein, R. (Ed.), Southern African Prehistory and Paleoenvironments. A.A. Balkema, Rotterdam, pp. 221–328.

Deacon, J., 1990. Changes in the archaeological record in South Africa at 18,000 BP. In: Gamble, C., Soffer, O. (Eds.), The World at 18,000 BP. Unwin Hyman, London, pp. 170–188.

Deino, A.L., McBrearty, S., 2002. ^{40}Ar/^{39}Ar dating of the Kapthurin Formation, Baringo, Kenya. Journal of Human Evolution 42, 185–210.

Dingle, R.V., Rogers, J., 1972. Pleistocene palaeogeography of the Agulhas Bank. Transactions of the Royal Society South Africa 40, 155–165.

Dorale, J.A., Onac, B.P., Fornós, J.J., Ginés, J., Ginés, A., Tuccimei, P., Peate, D.W., 2010. Sea-level highstand 81,000 years ago in Mallorca. Science 327, 860–863.

Du Plessis, A., Glass, J.G., 1991. The geology of False Bay. Transactions of the Royal Society South Africa 47, 495–517.

Dutton, A., Antonioli, F., Bard, E., 2009. A new chronology of sea level highstands for the penultimate interglacial. PAGES News 17, 66–68.

Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C$_4$ photosynthesis, atmospheric CO$_2$, and climate. Oecologia 112, 285–299.

Endicott, P., Ho, S.Y.W., Stringer, C., 2010. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. Journal Human Evolution 59, 87–95.

Fa, D.A., 2008. Effects of tidal amplitude on intertidal resource availability and dispersal pressure in prehistoric human coastal populations: the Mediterranean-Atlantic transition. Quaternary Science Reviews 27, 2194–2209.

Fisher, E.C., Bar-Matthews, M., Jerardino, A., Marean, C.W., 2010. Middle and late Pleistocene paleoscape modeling along the southern coast of South Africa. Quaternary Science Reviews 29, 1382–1398.

Foley, R.A., Lahr, M.M., 1997. Mode 3 technologies and the evolution of modern humans. Cambridge Archaeological Journal 7, 3–36.

Franceschini, G., Compton, J.S., 2004. Aeolian and marine deposits of the Tabakbaai Quarry area, Western Cape, South Africa. South African Journal of Geology 107, 619–632.

Gibbon, R.J., Granger, D.E., Kuman, K., Partridge, T.C., 2009. Early Acheulean technology in the Rietputs Formation, South Africa, dated with cosmogenic nuclides. Journal of Human Evolution 56, 152—160.

Grün, R., Brink, J.S., Sponner, N.A., Taylor, L., Stringer, C.B., Franciscus, R.G., Murray, A.S., 1996. Direct dating of Florisbad hominid. Nature 382, 500—501.

Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Hsi-Yang Fritz, M., Hansen, N.F., Durand, E.Y., Malaspinas, A.-S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajkovic, D., Kucan, Z., Gušic, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Fortea, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelso, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A draft sequence of the Neandertal genome. Science 328, 710—722.

Grine, F.E., Bailey, R.M., Harvati, K., Nathan, R.P., Morris, A.G., Henderson, G.M., Ribot, I., Pikes, A.W.G., 2007. Late Pleistocene human skull from Hofmeyr, South Africa, and modern human origins. Science 315, 226—229.

Grün, R., Stringer, C., McDermott, F., Nathan, R., Porat, N., Robertson, S., Taylor, L., Mortimer, G., Eggins, S., McCulloch, M., 2005. U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. Journal of Human Evolution 49, 316—344.

Hanebuth, T., Stattegger, K., Grootes, P.M., 2000. Rapid flooding of the Sunda Shelf: a Late glacial sea-level record. Science 288, 1033—1035.

Henderson, G.M., Robinson, L.F., Cox, K., Thomas, A.L., 2006. Recognition of non-Milankovitch sealevel highstands at 185 and 340 thousand years ago from U-Th dating of Bahamas sediment. Quaternary Science Reviews 25, 3346—3358.

Henshilwood, C.S., 2008. Holocene prehistory of the Southern Cape, South Africa: excavations at Blombos Cave and the Blombosfontein Nature Reserve. BAR International Series 1860. Cambridge Monographs in African Archaeology 75.

Henshilwood, C., D'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier, N., Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2002. Emergence of modern human behaviour: Middle Stone Age engravings from South Africa. Science 295, 1278—1280.

Henshilwood, C., D'Errico, F., Vanhaeren, M., van Niekerk, K., Jacops, Z., 2004. Middle Stone Age shell beads from South Africa. Science 304, 404.

Henshilwood, C.S., D'Errico, F., Watts, I., 2009. Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. Journal of Human Evolution 57, 27—47.

Henshilwood, C.S., Sealy, J.C., 1997. Bone artefacts from the Middle Stone Age at Blombos Cave, southern Cape, South Africa. Current Anthropology 38, 890—895.

Henshilwood, C.S., D'Errico, F., Yates, R.J., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier, N., Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2001. Emergence of modern human behaviour: Middle Stone Age engravings from South Africa. Science 295, 1278—1280.

Hooghiemstra, H., Stalling, H., Agwu, C.O., Dupont, L.M., 1992. Vegetational and climatic changes in the northern fringe of the Sahara 250,000-5,000 years BP. Review of Palaeobotany and Palynology 74, 1—53.

Hublin, J.-J., 1992. Recent human evolution in northwestern Africa. Philosophical Transactions of the Royal Society of London 337, 185—191.

Hublin, J.-J., 2001. Northwestern African Middle Pleistocene hominids and their bearing on the emergence of Homo sapiens. In: Barham, L., Robson-Brown, K. (Eds.), Human Roots, Africa and Asia in the Middle Pleistocene. Western Academic & Specialist Press Limited. England, Bristol, pp. 99—121.

Jacobs, Z., Roberts, R.G., 2008. Testing times: old and new chronologies for the Howiesons Poort and Still Bay industries in environmental context. South African Archaeological Society Goodwin Series 10, 9—34.

Jacobs, Z., Duller, G.A.T., Wintle, A.G., Henshilwood, C.S., 2006. Extending the chronology of deposits at Blombos Cave, South Africa, back to 140 ka using optical dating of single and multiple grains of quartz. Journal of Human Evolution 51, 255—273.

Jacobs, Z., Roberts, R.G., Galbraith, R.F., Deacon, H.J., Grün, R., Mackay, A., Mitchell, P., Volgelsang, R., Wadley, L., 2008. Ages for the Middle Stone Age of southern Africa: implications for human behaviour and dispersal. Science 322, 733—735.

Jerardino, A., 1998. Excavations at Pancho's Kitchen Midden, Western Cape coast, South Africa: further observations into the megamidden period. South African Archaeological Bulletin 53, 16—25.

Jerardino, A., Marean, C.W., 2010. Shellfish gathering, marine paleoecology and modern human behavior: perspectives from Cave PP13B, Pinnacle Point, South Africa. Journal of Human Evolution 59, 412—424.

Jolly, C.J., 2001. A proper study for mankind: analogies from the papionin monkeys and their implications for human evolution. Yearbook of Physical Anthropology 44, 177—204.

Klein, R.G., 1984. The large mammals of southern Africa: Late Pliocene to Recent. In: Klein, R.G. (Ed.), Southern Africa Prehistory and Paleoenvironments. A.A. Balkema, Rotterdam, pp. 107—146.

Klein, R.G., 2009. The Human Career, third ed.. Univ. of Chicago Press, Chicago.

Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Hart, T., Milo, R.G., Volman, T.P., 1999. Duinefontein 2: an Acheulean site in the Western Cape Province of South Africa. Journal of Human Evolution 37, 153—190.

Klein, R.G., Avery, G., Cruz-Uribe, K., Steele, T.E., 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. Journal of Human Evolution 52, 164—186.

Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464, 894—897.

Kuman, K., 2007. The Earlier Stone Age in South Africa: site context and the influence of cave studies. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain. Stone Age Institute Press, Bloomington (Indiana), pp. 181—198.

Kuper, R., Kröpelin, S., 2006. Climate-controlled Holocene occupation in the Sahara: motor of Africa's evolution. Science 313, 803—807.

Lahr, M.M., 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.

Lee-Thorp, J.A., Beaumont, P.E., 1995. Vegetation and seasonality shifts during the Late Quaternary deduced from $^{13}C/^{12}C$ ratios of grazers at Equus Cave, South Africa. Quaternary Research 43, 426—432.

Liebenberg, L., 2001. The Art of Tracking, the Origin of Science. David Philip, Cape Town.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 20. doi:10.1029/2004PA001071 PA1003.

Liu, H., Prugnolle, F., Manica, A., Balloux, F., 2006. A geographically explicit genetic model of worldwide human-settlement history. American Journal of Human Genetics 79, 230—237.

Lombard, M., Pargeter, J., 2008. Hunting with Howiesons Poort segments: pilot experimental study and the functional interpretation of archaeological tools. Journal of Archaeological Science 35, 2523—2531.

Lombard, M., Phillipson, L., 2010. Indications of bow and stone-tipped arrow use 64 000 years ago in KwaZulu-Natal, South Africa. Antiquity 84, 635—648.

Macaulay, V., Hill, C., Achilli, A., Rengo, C., Clarke, D., Meehan, W., Blackburn, J., Semino, O., Scozzari, R., Cruciani, F., Taha, A., Shaari, N.K., Raja, J.M., Ismail, P., Zainuddin, Z., Goodwin, W., Bulbeck, D., Bandelt, H.-J., Oppenheimer, S., Torroni, A., Richards, M., 2005. Single, rapid settlement of coastal Asia revealed by analysis of complete mitochondrial genomes. Science 308, 1034—1036.

Marean, C.W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: the Cape Floral Kingdom, shellfish, and modern human origins. Journal of Human Evolution 59, 425—443.

Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thomspon, E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449, 905—908.

McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of Human Evolution 39, 453—563.

McDougall, I., Brown, F.H., Fleagle, J.G., 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 433, 733—736.

Mellars, P., 2006. Why did modern human populations disperse from Africa ca. 60,000 year ago? A new model. Proceedings of the National Academy of Science 103, 9381—9386.

Mercader, J., 2009. Mozambican grass seed consumption during the Middle Stone Age. Science 326, 1680—1683.

Milo, R.G., 1994. Human-animal interactions in southern Africa prehistory: a microscopic study of bone damage signatures. PhD Thesis, University of Chicago.

Milo, R.G., 1998. Evidence for hominid predation at Klasies River Mouth, South Africa and its implication for the behaviour of early modern humans. Journal of Archaeological Science 25, 99—133.

Mitchell, P.J., 1990. A palaeoecological model for archaeological site distribution in southern Africa during the Upper Pleniglacial and Late Glacial. In: Gamble, C., Soffer, O. (Eds.), The World at 18,000 BP. Unwin Hyman, London, pp. 189—205.

Mitchell, P.J., 2002. The Archaeology of Southern Africa. Cambridge Univ. Press, Cambridge.

Morris, A.G., 2002. Isolation and the origin of the Khoisan: Late Pleistocene and early Holocene human evolution at the southern end of Africa. Human Evolution 17, 231—240.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

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, 1—28.

Osborne, A.H., Vance, D., Rohling, E.J., Barton, N., Rogerson, M., Fello, N., 2008. A humid corridor across the Sahara for the migration of early modern humans out of Africa 120,000 years ago. Proceedings of the National Academy of Science 105, 16444—16447.

Parkington, J., Poggenpoel, C., Rigaud, J.-P., Texier, P.-J., 2005. From tool to symbol: context of intentionally marked ostrich eggshell from Diepkloof, Western Cape. In: D'Errico, F., Backwell, L. (Eds.), From Tools to Symbols: From Early Hominids to Modern Humans. Univ. Witwatersrand Press, Johannesburg, pp. 475—492.

Partridge, T.C., Maud, R.R., 2000. Macro-Scale Geomorphic Evolution of Southern Africa. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic of Southern Africa. Oxford Univ. Press, New York, pp. 3—18.

Partridge, T.C., DeMenocal, P.B., Lorentz, S.A., Paiker, M.J., Vogel, J.C., 1997. Orbital forcing of climate over South Africa: a 200,000-year rainfall record from the Pretoria saltpan. Quaternary Science Reviews 16, 1125—1133.

Porat, N., Chazan, M., Grün, R., Aubert, M., Eisenmann, V., Horwitz, L.K., 2010. New radiometric ages for the Fauresmith industry from Kathu Pan, southern Africa: implications for the Earlier to Middle Stone Age transition. Journal of Archaeological Science 37, 269–283.

Potts, R., Deino, A., 2005. Mid-Pleistocene change in large mammal faunas of East Africa. Quaternary Research 43, 106–113.

Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324, 1298–1301.

Ramsay, P.J., Cooper, J.A.G., 2002. Late Quaternary sea-level change in South Africa. Quaternary Research 57, 82–90.

Richter, D., Moser, J., Nami, M., Eiwanger, J., Mikdad, A., 2010. New chronometric data from Ifri n'Ammar (Morocco) and the chronostratigraphy of the Middle Palaeolithic in the Western Maghreb. Journal of Human Evolution 59, 672–679.

Rightmire, P., 2009. Middle and later Pleistocene hominins in Africa and Southwest Asia. Proceedings of the National Academy of Science 106, 16046–16050.

Rogers, J., 1985. Geomorphology, offshore bathymetry and Quaternary lithostratigraphy around the Bot River estuary. Transactions of the Royal Society South Africa 45, 211–237.

Rohling, E.J., Grant, K., Bolshaw, M., Roberts, A.P., Siddall, M., Hemleben, Ch, Kucera, M., 2009. Antarctic temperature and global sea level closely coupled over the past five glacial cycles. Nature Geoscience 2, 500–504.

Salas, A., Richards, M., De la Fe, T., Lareu, M.-V., Sobrino, B., Sánchez-Diz, P., Macaulay, V., Carracedo, A., 2002. The making of the African mtDNA landscape. American Journal of Human Genetics 71, 1082–1111.

Scholz, C.A., Johnson, T.C., Cohen, A.S., King, J.W., Peck, J.A., Overpeck, J.T., Talbot, M.R., Brown, E.T., Kalindekafe, L., Amoako, P.Y.O., Lyons, R.P., Shanahan, T.M., Castañeda, I.S., Heil, C.W., Forman, S.L., McHargue, L.R., Beuning, K.R., Gomez, J., Pierson, J., 2007. East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. Proceedings of the National Academy of Science 104, 16416–16421.

Sealy, J.C., 1996. Seasonality of rainfall around the Last Glacial Maximum as reconstructed from carbon isotope analyses of animal bones from Nelson Bay Cave. South African Journal of Science 92, 441–444.

Shen, G., Wang, W., Wang, Q., Zhao, J., Collerson, K., Zhou, C., Tobias, P.V., 2002. U-Series dating of Liujiang hominid site in Guangxi, Southern China. Journal of Human Evolution 43, 817–829.

Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, C., Meischner, D., Schmelzer, I., Smeed, D.A., 2003. Sea-level fluctuations during the last glacial cycle. Nature 423, 853–858.

Siegfried, W.R., 1977. Mussel-dropping behaviour of Kelp gulls. South African Journal of Science 73, 337–341.

Skead, C.J., 1982. Historical Mammal Incidence in the Cape Province, vol. 1. The Western and Northern Cape. Dept. Nature & Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town.

Smith, T.M., Tafforeau, P., Reid, D.J., Grün, R., Eggins, S., Boutakiout, M., Hublin, J.-J., 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proceedings of the National Academy of Science 104, 6128–6133.

Stanford, J.D., Rohling, E.J., Hunter, S.E., Roberts, A.P., Rasmussen, S.O., Bard, E., McManus, J., Fairbanks, R.G., 2006. Timing of meltwater pulse 1a and climate responses to meltwater injections. Paleoceanography 21. doi:10.1029/2006PA001340 PA4103.

Tattersall, I., Schwartz, J.H., 2008. The morphological distinctiveness of *Homo sapiens* and its recognition in the fossil record: clarifying the problem. Evolutionary Anthropology 17, 49–54.

Tattersall, I., Schwartz, J.H., 2009. Evolution of the genus *Homo*. Annual Review Earth and Planetary Sciences 37, 67–92.

Texier, P.-J., Porraz, G., Parkington, J., Rigaud, J.-P., Poggenpoel, C., Miller, C., Tribolo, C., Cartwright, C., Coudenneau, A., Klein, R., Steele, T., Verna, C., 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 Science 107, 6180–6185.

Thomas, A.L., Henderson, G.M., Deschamps, P., Yokoyama, Y., Mason, A.J., Bard, E., Hamelin, B., Durand, N., Camoin, G., 2009. Penultimate deglacial sea-level timing from uranium/thorium dating of Tahitian corals. Science 324, 1186–1189.

Thompson, J., 2010. Taphonomic analysis of the Middle Stone Age faunal assemblage from Pinnacle Point Cave 13B, Western Cape, South Africa. Journal of Human Evolution 59, 321–339.

Thompson, W.G., Goldstein, S.L., 2005. Open-system coral ages reveal persistent suborbital sea-level cycles. Science 308, 401–404.

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., Williams, S.M., 2009. The genetic structure and history of Africans and African Americans. Science 324, 1035–1044.

Tobias, P.V., 2000. The fossil hominids. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic of Southern Africa. Oxford Univ. Press, New York, pp. 252–276.

Tryon, C.A., McBrearty, S., 2002. Tephrostratigraphy and the Acheulian to Middle Stone Age transition in the Kapthurin Formation, Kenya. Journal of Human Evolution 42, 211–235.

Tryon, C.A., McBrearty, S., Texier, P.-J., 2005. Levallois lithic technology from the Kapthurin Formation, Kenya: Acheulian origin and Middle Stone Age diversity. African Archaeological Review 22, 199–229.

Turnley, C.S.M., Bird, M.I., Fifield, L.K., Roberts, R.G., Smith, M., Dortch, C.E., Grün, R., Lawson, E., Ayliffe, L.K., Miller, G.H., Dortch, J., Cresswell, R.G., 2001. Early human occupation at Devil's Lair, Southwestern Australia 50,000 years ago. Quaternary Research 55, 3–13.

Vaks, A., Bar-Matthews, M., Ayalon, A., Matthews, A., Halicz, L., Frumkin, A., 2010. Desert speleothems reveal climatic window for African exodus of early modern humans. Geology 35, 831–834.

Valladas, H., Reyss, J.L., Joron, J.L., Valladas, G., Bar-Yosef, O., Vandermeersch, B., 1988. Thermoluminescence dating of mousterian "Proto-cro-magnon" remains from Israel and the origin of modern man. Nature 331, 614–616.

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, 133–155.

Van Riebeeck, J., 1952–1958. In: Thom, H.B. (Ed.), Journal of Jan van Riebeeck, 3 vol. 1651–1658. A.A. Balkema, Cape Town.

Vanhaeren, M., D'Errico, F., Stringer, C., James, S.L., Todd, J.A., Mienis, H.K., 2006. Middle Paleolithic shell beads in Israel and Algeria. Science 312, 1785–1788.

Villa, P., Soressi, M., Henshilwood, C.S., Mourre, V., 2009. The Still Bay points of Blombos Cave (South Africa). Journal of Archaeological Science 36, 441–460.

Wadley, L., 1988. A social and ecological interpretation of the Later Stone Age in the southern Transvaal. In: British Archaeological Reports International Series S380. Oxford.

Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E., Labracherie, M., 2002. Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. Quaternary Science Reviews 21, 295–305.

White, T.D., Asfaw, B., DeGusta, D., Gilbert, H., Richards, G.D., Suwa, G., Howell, F.C., 2003. Pleistocene *Homo sapiens* from Middle Awah, Ethiopia. Nature 423, 742–747.

Yokoyama, Y., Esat, T.M., Lambeck, K., 2001. Coupled climate and sea-level changes deduced from Huon Peninsula coral terraces of the last ice age. Earth Planetary Science Letters 193, 579–587.