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Pollen-interpreted palaeoenvironments associated with the Middle and Late Pleistocene peopling of Southern Africa

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ABSTRACT

An investigation of the vegetation and climate from the Middle Pleistocene until the end of the Late Pleistocene reveals a plethora of terrestrial and marine biological, geological and archaeological evidence for marked and complex climate cycles of change, which reflect on past circulation patterns. While acknowledging the usefulness of diverse proxies for detecting these changes, an efficient way to summarize past events is to focus on one of them, viz. fossil pollen, which, although providing scattered and incomplete records, gives fairly direct reflections of past climates and vegetation growth. The findings are structured according to six subregions and reveal distinct changes in temperature and moisture patterns, e.g. during the Last Glacial Maximum (LGM) and the Younger Dryas. The data suggest an environmental background against which cultural evolution took place, e.g., the appearance of Fauresmith, Still Bay, Howiesons Poort and Later Stone Age lithic industries. The pollen archives can be associated with global climate changes, as recorded in isotopes in marine sequences (Marine Isotope Stages or MISs). The observations show differences between regions, which can serve as a base for improving palaeo-data to eventually simulate past and future climates and to better understand the role of past global climates in relation to human and animal occupation in Southern Africa.

1. Introduction

Since the mid-20th century climate change has affected the whole globe and in particular semi-arid South Africa, where natural resources of food and water are restricted and the effects of global phenomena like El Niño lead to severe droughts such as the one observed recently during 2015 and 2016 (Baudoin et al., 2017). Given the strong effect of such phenomena over the relatively short historical period, it can be concluded that climate changes must also have been very marked over the long term. Neogene and Quaternary records show that Southern Africa has been characterized by fluctuating climates that must have affected people and the distribution of biomes (Tyson and Partridge, 2000; Dupont, 2006; Dupont et al., 2005; Ziegler et al., 2013). In this paper we deal with pollen-derived Pleistocene palaeoenvironments of Southern Africa, namely the period in which important steps in the early evolution of our genus *Homo* took place under marked global climatic cycles that ended before the current warm phase,

viz., the Holocene, and which included interstadials and glacial stages. Complex climate and cultural changes place the Holocene beyond the scope of this review and it is discussed in separate studies (Chevalier and Chase, 2015; Ecker et al., 2018). Earlier time periods such as the Neogene are also excluded from this study because the evidence of marked changes that have been found in the south-western Cape from these periods cannot be associated with the peopling of South Africa (Coetzee and Rogers, 1982; Roberts et al., 2017). Also excluded is the interval from the beginning of the Pleistocene to the Middle Pleistocene, which included important but limited palynological evidence, e.g. at Sterkfontein, Malapa and Kromdraai (Dirks et al., 2010; Bamford et al., 2010; Scott, 1995; Scott and Bonneville, 1986; Scott et al., 1997; Carrión and Scott, 1999).

Tracing Pleistocene conditions in Africa during the studied interval is important in view of the widespread occurrence of Middle Stone Age (MSA) and Later Stone Age (LSA) finds (Mitchell, 2002; Parkington et al., 2013). Rapid cultural changes and major innovations that play a role in the cognitive evolution of *Homo sapiens* have occurred against a background of changing environmental conditions. The MSA begins with the Fauresmith stone-tool

industry (>417 ka BP) (Porat et al., 2010; Herries, 2012), and is associated with archaic *Homo sapiens* and early modern humans with an increase in complexity through time. Later industries include the Still Bay (c. 76—71 ka BP) and the Howiesons Poort lithic industries (c. 66—59 ka BP) (Jacobs et al., 2008; Chase, 2010; d'Errico et al., 2017; Guerin et al., 2013; Parkington et al., 2013; Henshilwood and Dubreuil, 2011). The Early LSA industries followed c. 45 cal ka BP and lasted until the LGM, originating in the eastern parts of Southern Africa and spreading westward (Bousman and Brink, 2017).

In connection with the peopling of Africa after 400 000 years ago (400 ka BP), few but important fossil human remains and genetic evidence have been reported (Hublin et al., 2017; Dirks et al., 2017; Timmermann and Friedrich, 2016; Schlebusch et al., 2017). These findings include the Kabwe skull of undetermined age from Zambia (Woodward, 1921), *Homo naledi* that lived c.236—335 ka BP to the Northwest of Johannesburg (Berger et al., 2017), the Florisbad cranium of c. 250—300 ka BP which was originally described as *Homo helmei* but it is now attributed to either *Homo heidelbergensis* or archaic *Homo sapiens* (Dreyer, 1935; Grün et al., 1996) and the Hofmeyr skull, an archaic *Homo sapiens*, which was dated to c. 36 ka BP (Grine et al., 2007). The latter was found in the Eastern Cape province of South Africa, supporting the hypothesis that Upper Pleistocene Eurasians descended from a population that emigrated from sub-Saharan Africa in the Late Pleistocene. Many questions about past conditions associated with these finds remain and we bring together some background information for Southern Africa as it can be inferred from pollen analysis.

While terrestrial proxy records of vegetation change during the Pleistocene are scarce in this region, marine stable isotope records shed light on past Quaternary climates (Wright, 2000). Ever since van Zinderen Bakker (1976, 1978; see Neumann and Scott for details) proposed models to explain atmospheric circulation during the last glacial period by proposing expansion of winter rainfall zone during glacial periods and resultant vegetation responses, controversy existed about the mechanisms responsible for long-term climate change (Cockcroft et al., 1987; Deacon and Lancaster, 1988; Partridge et al., 1999; Chase and Meadows, 2007; Weldeab et al., 2013). Mechanisms controlling climate change in the Pleistocene are difficult to reconstruct. Scenarios with entirely different circulation patterns than today probably existed due to the role of long-term effects of orbital forcing that changed the nature and intensity of the energy received from the sun (COHMAP, 1988; Bar-Matthews et al., 2010; Partridge et al., 1997). There is little consensus on the role of direct insolation forcing as a causal mechanism for observed changes in palaeo-rainfall and the movements of the African rainbelt (Chase, 2010; Singarayer and Burrough, 2015).

This review of long-term changes attempts to:

- Outline the various proxies used for Pleistocene palaeoclimatic reconstruction in Southern Africa focusing on palynology of relevant case studies.
- Show that palynology plays a pivotal role in the reconstruction of palaeoenvironments that can provide a background to complement other proxies.
- Show major changes in vegetation in different regions and connect them to climatic fluctuations that give a background for developments in human culture.
- Evaluate the role of marine archives.
- Summarize major challenges of Quaternary sciences including climate models and suggest potential future research directions.

1.1. Palynology as a tool in paleoecological reconstruction

Fossil pollen research gives an insight into past plant life and climatic conditions. An understanding of the current biomes of Southern Africa is needed in the study of Pleistocene vegetation changes (Mucina and Rutherford, 2006). A lack of suitable long continuous terrestrial records for large parts of Southern Africa limits progress in palaeoecology and pollen research in the region (Scott et al., 2012). Of the different methods of reconstruction, fossil pollen assemblages in dated deposits are of particular importance in the reconstruction of Pleistocene vegetation, palaeoecology and environments. Pollen analysis has distinct advantages because it can provide large proxy data sets. Only in some cases can it be directly associated with stone tool occurrences, such as at spring mounds of Wonderkrater in savanna woodland and Florisbad or Baden-Baden, both in grassland (Backwell et al., 2014; Scott, 2016; van Zinderen Bakker, 1989; Van Aardt et al., 2016) or cave sites (Brook et al., 2010; Scott and Thackeray, 2015). Suitable pollen archives in Southern Africa include lakes, springs and swamps (Scott, 1982, 1999a,b; van Zinderen Bakker, 1957; Coetzee, 1967; Neumann et al., 2014; McWethy et al., 2016), dung deposits (Scott, 1987, 1994; Scott and Bousman, 1990; Scott and Woodborne, 2007; Chase et al., 2012; Valsecchi et al., 2013; Scott et al., 2018), and speleothems (Brook et al., 2010; Scott and Thackeray, 2015). Based on terrestrial pollen data, attempts exist to quantify paleoclimate, e.g. Chevalier and Chase (2016) investigated how precipitation and temperature have determined moisture availability in South Africa's summer rainfall zone during the last 45 000 years (45 cal ka BP).

Marine pollen profiles and other proxies provide opportunities for reconstructing environmental conditions on land (Shi and Dupont, 1997; Dupont and Wyputta, 2003; Dupont et al., 2005, 2008; Dupont and Kuhlmann, 2017). Marine records with complex transport vectors such as wind, ocean currents, rivers or re-deposition and gravity transport, are subject to taphonomical influences that are responsible for the over-representation of long-distance transported spores and pollen of uncertain provenance or under-representation of less-buoyant animal-pollinated pollen (Behrensmeyer et al., 2000). Examples from the southern Atlantic Ocean and south-western Africa are compared with terrestrial (hyrax dung) records in Scott et al. (2004, 2018), where a more balanced representation can be expected with direct representation of local conditions.

Interpretation of pollen records is therefore not without constraints and includes limitations of available dating methods, contamination by older or younger material in deposits, other taphonomical problems, and lack of precision of palynological identifications (Scott, 1999a, b, 2016). These are evident when evaluating the potential of hominin-bearing strata from the Sterkfontein region as potential pollen archives. Here most sediments like carbonate-rich cave breccias are usually not suitable for pollen analysis and contain very low concentrations of pollen, if any. Percolation of oxygen-rich groundwater in porous breccias probably causes fossil pollen to perish and younger contaminants to replace it (Scott and Bonnefille, 1986; Scott, 1995; Carrión and Scott, 1999). Less porous materials like stalagmites might allow better preservation although they are also not rich in pollen (Brook et al., 2010).

1.2. Other proxies of palaeoclimatic reconstruction in Southern Africa

Evidence for Pleistocene environmental change in Southern Africa is gained through a variety of proxies. Since our focus is on vegetation change using palynology as primary method, we will only briefly list some other proxies, which contributed to a better

understanding of Pleistocene environmental change in the region, and which are needed to complement palynological reconstructions of palaeoclimate, as each one is equally important.

1.2.1. Marine geology

These studies play an increasing role in Quaternary Sciences like the reconstruction of past sea levels in Southern Africa using beach rock deposits along the shores or submerged aeolian ridges utilizing seismic profiling which reveals a sea level drop of up to 130 m during the LGM in Marine Isotope Stage (MIS) 2(LGM; 19–26.5 cal ka BP) (Cawthra et al., 2014). This event exposed a formerly submerged coastal plain along the southern coast (Compton, 2011). At the end of MIS 6, a cold period c. 130 ka BP, sea levels dropped more than a hundred metres and humans might have survived on shellfish along the newly exposed Palaeo-Agulhas Plain (Marean, 2010). In addition, ungulates might have preferred Paleo-Agulhas Plain habitats to those to the north of the modern coastline as shown by strontium isotope investigations (Copeland et al., 2016; Marean, 2016). Further, geochemistry of ocean cores appears to reflect conditions on land that can be related to stone tool history (Ziegler et al., 2013; Simon et al., 2015).

1.2.2. Geomorphology

Geomorphological research is a prominent tool in deciphering past environmental changes in Southern Africa (see Holmes et al., 2016 for a recent review), especially in light of the vivid topography with the Great Escarpment forming a 5000 km-long arc from Angola to Zimbabwe which affects climates and environments on either side by confining most rainfall coastward and casting rain shadows far inland (Wellington, 1955; Partridge and Maud, 1987). In the dry interior of the subcontinent, wetlands and lakes with suitable archives that recorded past changes are scarce and the focus shifted to other potential archives, most prominently the dunes of the Kalahari. Optical Luminescence Dating (OSL) of sands was applied to establish chronologies (Chase and Brewer, 2009; Thomas and Burrough, 2016). However, the interpretation of dune activities over the last 190 ka BP is complex due to various factors controlling dune activity, e.g. regional differences in wind strength, geology and reworking (Harper, 1969; Bailey and Thomas, 2016; Thomas and Burrough, 2016; Holmes et al., 2016).

Periglacial phenomena in the Drakensberg region indicate cold conditions during glacials as do reconstructions of possible glaciers which suggest shifting westerlies (Mills et al., 2009, 2012, 2017). Fluvial geomorphology sheds light on river dynamics including the effect of flood events (Holmes et al., 2016 and references therein). A valuable example of the dating and geomorphology of coastal deposits is presented in Porat and Botha (2008) that improved the chronology and knowledge of environmental setting of a pollen archive (Port Durnford peats) from the east coast (Oschadleus et al., 1996).

1.2.3. Analysis of biomarkers

A novel approach to reconstruct ecosystem changes is the analysis of lipid biomarker (leaf wax n-alkane) records (e.g. Schmidt et al., 2014; Carr et al., 2014, 2016, Lattaud et al., 2017). Schefuß et al. (2011), by investigating a marine core (GeoB9307-3) offshore the Zambezi River mouth covering 17000 years, propose that Northern Hemisphere cold events like the Younger Dryas influenced Southern African climate history. Leaf wax lipids proved to be of value to indicate the plant types from which organic material originates and could be associated with pollen analyses (Norström et al., 2014; Quick et al., 2016).

1.2.4. Isotope analyses

Isotope studies in Southern Africa started in the 1980s, when, e.g. an oxygen and carbon isotope record from the Cango caves near Oudtshoorn at the Cape and Cold Air Cave and Wonderwerk Cave allowed the tracing of the past proportions of C_3 and C_4 vegetation that has implications for climate change and temperature reconstruction of the last 36 cal ka BP (Vogel, 1983; Talma and Vogel, 1992; Holmgren et al., 2003; Brook et al., 2010). Dissolved gas and oxygen isotope studies in ground-water have been used to determine palaeo-temperatures in groundwater (Heaton et al., 1986; Kulongoski and Hilton, 2004).

A hyrax midden in the Cederberg, Western Cape, provides stable isotope data pointing to cold and dry conditions during the Younger Dryas which is supported by pollen evidence (Chase et al., 2011, 2012; Quick et al., 2011; Valsecchi et al., 2013; Meadows and Quick, 2016).

Information about the early Pleistocene at Wonderwerk Cave in the Kalahari is provided by stable isotope analyses on ostrich shell suggesting an arid environment 1,96–1,78 million years ago and even drier conditions at c. 1 Ma (Ecker et al., 2016).

1.2.5. Archaeozoology

Archaeozoological studies allowed an assessment of Pleistocene ecosystems (Klein, 1980; Langejans et al., 2014). A case study is available for the grassland at Florisbad in the interior of South Africa where large and now extinct mammals and hominins, including archaic *Homo*, roamed and interacted (Dreyer, 1935, 1938; Grün et al., 1996 et al., 1996; Brink, 1987). Brink (1988) indicated that these grasslands were more productive than the current ones, supporting a wider variety of grazers including the now extinct Bond's springbok. At Erfkroon on the Modder River (central Free State, South Africa), a site with numerous stone age tools, the extinction of large bovine *Megalotragus priscus* at the Pleistocene-Holocene transition formed part of a southern African extinction event which encompassed a number of grazers and wetland fauna, pointing to enhanced aridity during this period in Southern Africa (Churchill et al., 2000; Brink et al., 2015).

1.2.6. Sedimentology

Sedimentological analyses like grain size analysis often provide the geological context of a site. Dry lakes, e.g. Deelpan in the western Free State, allowed the investigation of micro-stratigraphy and palaeosols in order to decipher environmental history and possible early human impacts (Butzer and Oswald, 2016). Butzer (1988) investigated the Florisbad sedimentology and reconstructed activity and discharge of the spring mound through time while Toffolo et al. (2017) studied the microstratigraphy of the deposits to reconstruct past conditions.

Partridge et al. (1997) analysed the grain sizes of the Tswaing Crater record north of Pretoria, reaching back at least 220 ka BP. The sequence stretches beyond radiocarbon capability and shortcomings of the chronology are mentioned in the literature (Chase et al., 2010; Chase and Meadows, 2007). It therefore requires further research to confirm the authors' assumption, in which their palaeo-precipitation record that was derived from sediment characteristics, was linked to insolation forcing and its timescale (Partridge et al., 1997; Chase et al., 2010; Scott, 2016).

1.2.7. Archaeobotany

Archaeobotanical studies include pollen analysis, anthracological analyses including microscopic charcoal, phytolith studies (e.g. Scott, 2002; Finné et al., 2010; Metcalfe, 1999; Rossouw, 2016) as well as the investigation of seeds, leaves, fruits, and wood, e.g. seeds and charcoal at the Middle Stone Age (MSA) site Sibudu Cave in coastal KwaZulu-Natal (Sievers, 2006; Allot, 2006) or the charcoal studies at Elands Bay Cave (Parkington et al., 2000). The latter study revealed that during the LGM mesic *Podocarpus* was more

widespread than nowadays.

At Wonderwerk Cave in the Kalahari, charcoal shed light on the vegetation at the end of the Pleistocene (Bamford, 2016; Bamford et al., 2016 for recent overviews) and grass phytoliths give evidence of climatic fluctuations during the Early Stone Age (ESA) (Rossouw, 2016).

2. Current climate and vegetation

The current climatic regime in Southern Africa is controlled by interaction of the movements of the Intertropical Convergence Zone (ITCZ) and the westerly wind system and the influence of the cold Benguela Current in the Atlantic Ocean and the warm Agulhas Current in the Indian Ocean (Tyson, 1986; Tyson and Preston-Whyte, 2004) (Fig. 1). High pressure cells on both sides of the subcontinent above the ocean move southwards during austral summer and northwards during winter when high pressure develops over the continent. In July, when the ITCZ shifts to North Africa, a high pressure zone dominates the north-eastern interior and the coast of southern Mozambique and northern KwaZulu-Natal. This prevents the influx of moisture from the warm southward-flowing Agulhas Current.

The south-western Cape is under the influence of westerly cyclones and receives winter rain (Tyson, 1986; Tyson and Preston-Whyte, 2004). The summer rainfall region in the eastern half of Southern Africa therefore has two distinct seasons, viz. wet in November—April under influence of the ITCZ, and dry in May-—October. In the Cape region, rainfall occurs during the winter whereas the summer is dry. A narrow zone with all-year precipitation occurs between these two regions. The dry coastal area of the Northern Cape and the adjacent interior regions show high variability of rainfall under the influence of the sub-tropical high pressure zone and the cold ocean water of the Benguela Current.

Due to the diverse regional climates, soils, topographies and other factors the subcontinent features a high plant diversity (Mucina and Rutherford, 2006). Nine biomes are currently recognized in Southern Africa whose boundaries have probably varied during the Pleistocene under changing local hydrological conditions and climates.

The **Fynbos Biome** is located at the Cape in a mostly oligotrophic region dominated by winter rainfall and characterized by high biodiversity and families like Proteaceae, Restionaceae and Ericaceae. The **Succulent Karoo Biome** forms the most species-rich semi-desert in the world receiving mainly winter rain. The **Nama Karoo Biome**, the second largest biome in Southern Africa (Mucina and Rutherford, 2006), to the east of the Succulent Karoo, is characterized by more summer rainfall and is probably the least species-rich biome on the subcontinent.

The **Desert Biome** occurs along the west coast stretching from the Orange River valley along the border between Namibia and South Africa northwards with seasonality changing from winter to summer rain towards the north. The vast **Savanna Biome** stretches from north-eastern South Africa up to eastern Africa and is characterized by summer rainfall, grasses and woodland with frost-sensitive tropical trees. The **Grassland Biome**, also receiving summer precipitation, has its core of temperate grassland in the mostly treeless Highveld with woody elements only on steep slopes and in gorges. Above the tree line in the cool and wet Drakensberg region there is lower evapotranspiration and high biodiversity (Drakensberg Alpine Centre). The **Indian Ocean Coastal Belt Biome**, which stretches from Mozambique to the Eastern Cape, receives summer rain and is characterized by patches of subtropical, species-rich forest, mangroves and grasslands with few palm species. The **Albany Thicket Biome** receives summer rain to the northeast and all-year rainfall to the southwest (Mucina and Rutherford, 2006). It is restricted to the coastal region between Port Elizabeth and East London and adjacent valleys of the Cape Fold Belt in South Africa, showing floristic links to neighbouring biomes but also some
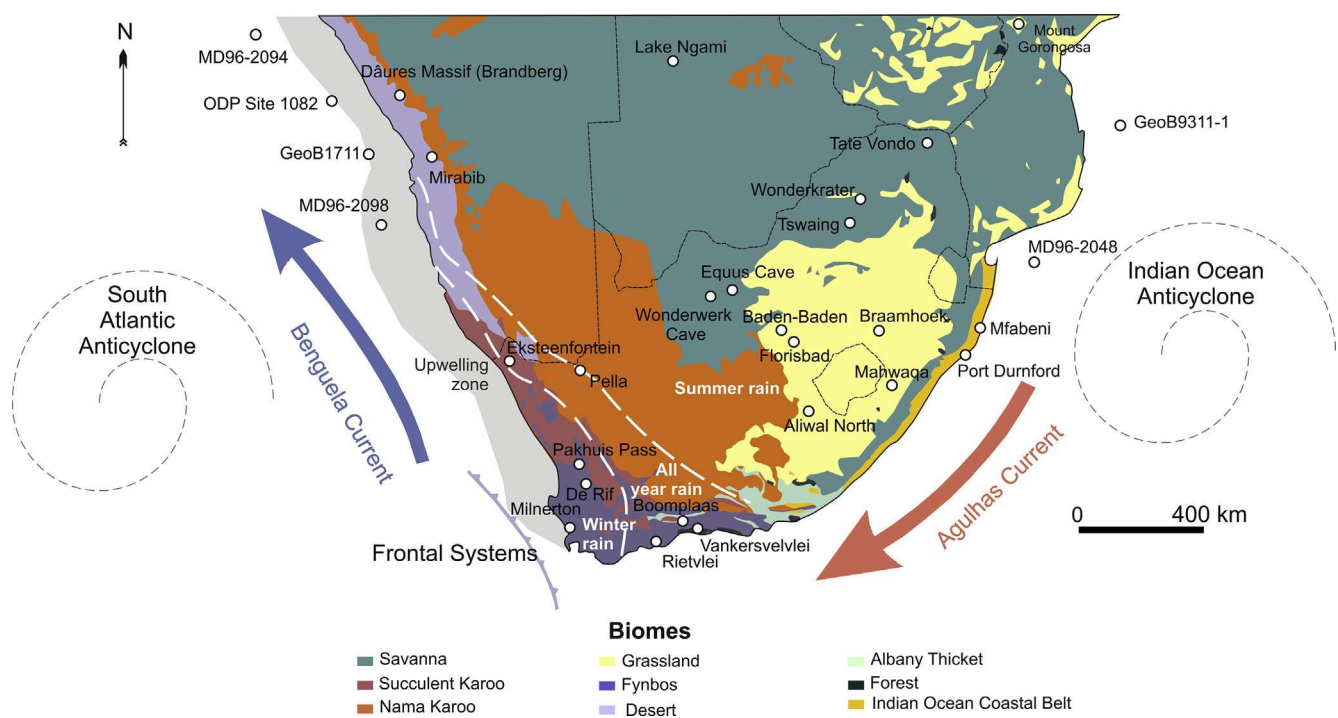

Fig. 1. Map of Southern Africa showing biomes (Mucina and Rutherford, 2006), sea currents, the climatic system and important palynological localities mentioned in the text.

unique species.

The **Forest Biome** occurs in the wetter regions in the all-year rainfall zone of the subcontinent where the largest forested area is in the southern Cape around Knysna, characterized by giant yellowwood trees (*Podocarpus* spp.). Small patches of this biome occur along the eastern and southern margin of Southern Africa, especially in fire-protected ravines along the escarpment where it is imbedded within other biomes.

3. Vegetation development during the Pleistocene

An overview of the available palynological information is presented for the Pleistocene period c. 400–11,7 ka or cal ka BP (Table 1), indicating changing processes over time with a focus on selected fossil pollen sequences instead of other proxies. As a time framework, we rely on the Marine Isotope Stage chronology (MIS 11 to the beginning of MIS 1) with lighter $\delta^{18}O$ values representing alternating odd-numbered warm periods and with heavier $\delta^{18}O$ values representing even-numbered cold phases (https://en.wikipedia.org/wiki/Core_sample e.g. Emiliani, 1955; Hays et al., 1976; Railsback et al., 2015; Tzedakis et al., 2017). The only widely recognized MIS chronology that emphasizes glacial terminations is given in the global chronostratigraphical correlation table for the Quaternary by the Subcommission on Quaternary Stratigraphy (http://www.stratigraphy.org/index.php/ics-chart-timescale). Since the boundaries differ slightly in available schemes, for consistency and convenience we rely on approximate values (Table 1) obtained visually from the easy-to use chronology of Railsback et al. (2015) and the positions of sites according to MISs are indicated (see Table 2).

Available pollen records are often discontinuous including hiatuses spanning millennia. Previous research (e.g. Scott et al., 2012, 2013) has shown that there are large differences in vegetation development over the wide study area. Without a close grid of long continuous records that can be effectively compared to each other over the subcontinent, the development of chronological and spatial models describing mechanisms of climate change that underlie past vegetation change for the whole region, is not yet possible. However, palaeoclimatic reconstruction for the summer rainfall region has been attempted (Chevalier and Chase, 2015, 2016). We demonstrate some palaeo-vegetation changes that can be observed for different parts of the subcontinent during the middle and late Pleistocene up to the Younger Dryas. The latter is a circum-North Atlantic cooling period c. 12,9–11,7 cal ka BP with

Table 1
Guide for approximate MIS boundaries (ka BP or cal ka BP for radiocarbon dating) as estimated from Railsback et al. (2015).

MIS	Substage	Appr. start (cal ka/ka BP)	Appr. end (cal ka/ka BP)
2		32	11,7
3		57	32
4		73	57
5	a	85	73
5	b, c	105	85
5	d	115	105
5	e	130	115
6		190	130
7		245	190
8		282	245
9	a	295	282
9	b,c,d,e	337	295
10		365	337
11		435 (424[a])	365

[a] Alternative according to global chronostratigraphical correlation table (http://www.stratigraphy.org/index.php/ics-chart-timescale).

effects for the Southern Hemisphere that are still under debate (Lowell and Kelly, 2008; Heine et al., 2014).

1. The eastern marine sources which comprise offshore sites that are fed from the river mouths of the Limpopo and Save Rivers in the Indian Ocean (Dupont et al., 2006; Dupont and Kuhlmann, 2017).
2. Eastern coast and interior, e.g. Port Durnford (Scott et al., 1992; Oschadleus et al., 1996; Porat and Botha, 2008), Mfabeni swamps (Finch and Hill, 2008); and Mahwaqa (Neumann et al., 2014), and Mount Gorongosa in the interior of southern central Mozambique (McWethy et al., 2016).
3. The central interior and the Kalahari archives, e.g. Wonderwerk and Equus Caves (Scott, 1987; Brook et al., 2010; Scott and Thackeray, 2015), Wonderkrater spring and Braamhoek and Tswaing Crater (Norström et al., 2009, 2014; Backwell et al., 2014; Truc et al., 2013; Chevalier and Chase, 2015, 2016; Scott, 2016).
4. The arid western coastal and Atlantic Ocean region with, e.g. hyrax dung deposits for Namaqualand (Lim et al., 2016) and Namibia (Scott et al., 2018).
5. Marine sediment cores from the offshore areas of the southern Atlantic Ocean (Shi et al., 1998, 2000, 2001; Dupont et al., 2006; Urrego et al., 2015).
6. The southern tip of the continent with swamp deposits like Vankersvelvlei and Rietvlei (Quick et al., 2015, 2016).

A brief summary of some results for the six regions is presented in Table 3 with relative humidity indications within but not across the regions. For details the readers are referred to the original papers as discussed in section 3.1–6.

3.1. Indian Ocean

Long marine pollen records from south-eastern Africa, viz. cores GeoB9311 and MD96-2048 retrieved offshore from the mouths of the Save and Limpopo Rivers (Fig. 1), represent glacial-interglacial changes in the vegetation from c. 248 ka BP until modern times (MIS 7–1) (Dupont and Kuhlmann, 2017). Both records suggest a repetition of a cycle similar to that observed onshore at for instance Port Durnford (Scott et al., 1992) (see 3.2) i.e. between coastal forests and savanna/woodland during interglacials and glacials e.g. MIS 5e (Eemian-Ipswichian Interglacial) (130–115 ka BP) and the Holocene (<11,7 cal ka BP). Whereas pollen of *Brachystegia* spp. (miombo trees) is rare throughout both profiles, pollen of *Colophospermum mopane* (mopane trees) occurs more regularly, which might be explained by the Mopane woodland's closer proximity in low-lying river valleys and the distance of *Brachystegia* communities that grow at higher altitudes and produce large poorly dispersed pollen grains (Dupont and Kuhlmann, 2017).

3.1.1. MIS 7, c. 245–190 ka BP

Vegetation changes c. 243–205 ka BP are recovered from core MD96-2048 where initially glacial, cool and humid conditions are inferred from high but gradually declining Ericaceae percentages (Dupont and Kuhlmann, 2017). *Podocarpus* forests were widespread and expanding at the expense of Ericaceae heathlands, producing up to 50% pollen. From c. 230–191 ka BP *Podocarpus* pollen percentages show an overall decline to <10%. A warmer atmosphere is indicated by more forest and woodland pollen, e.g. of Combretaceae, mopane and miombo trees, in both marine sediment cores. Stable oxygen isotopes of the planktonic foraminifera *Globigerinoides ruber* signal warm interglacial conditions during MIS 7 at core GeoB9311 (Dupont and Kuhlmann, 2017). Warm climatic conditions are in good agreement with the time of MIS 7a c.

Table 2

Names of marine and terrestrial palynological sites with approximate ages for the time covered and Marine Isotope Stages (MIS 2–11) for the six regions. References for the different sites are presented in section 3.1–6.
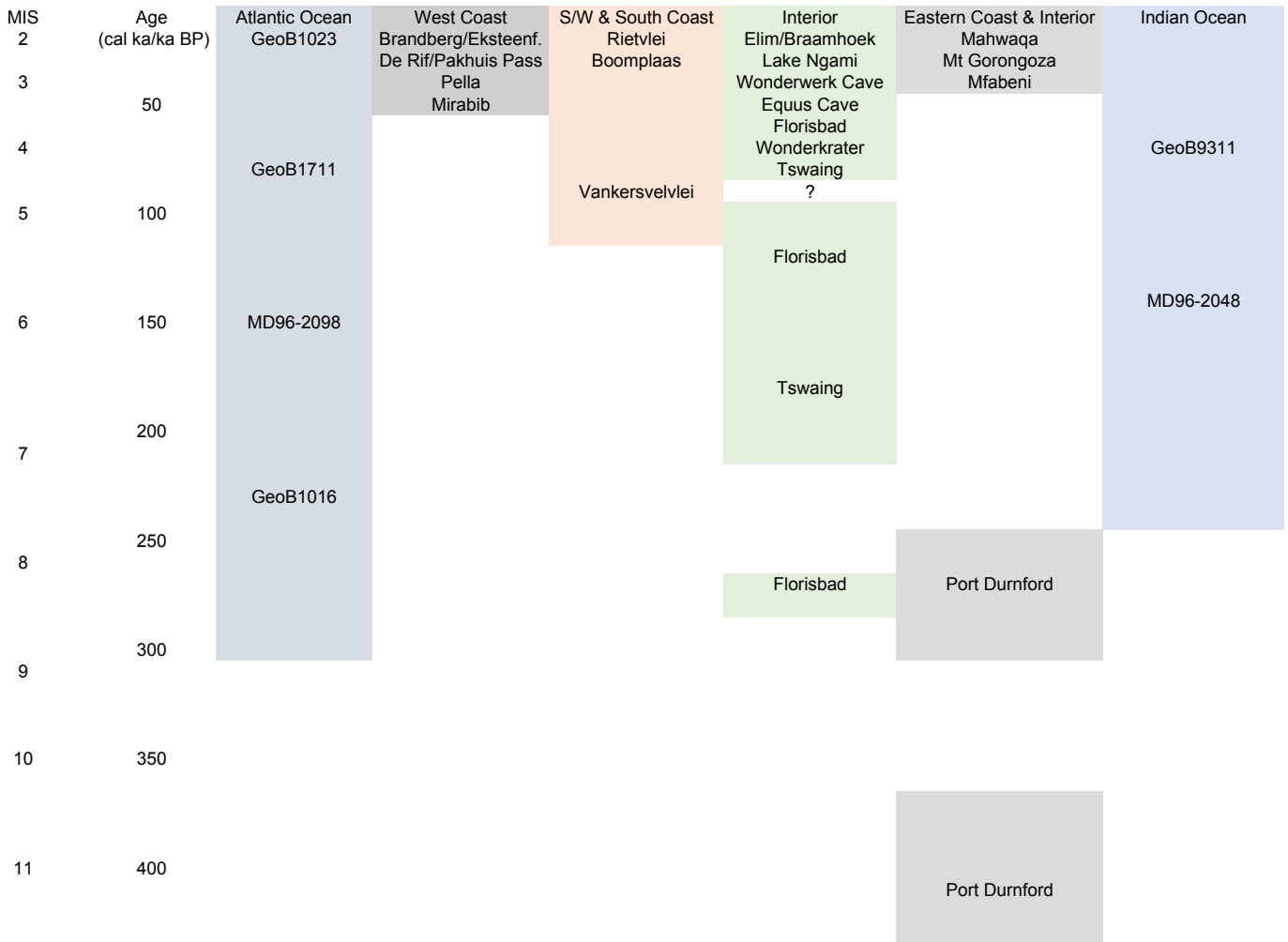
MIS	Age (cal ka/ka BP)	Atlantic Ocean	West Coast	S/W & South Coast	Interior	Eastern Coast & Interior	Indian Ocean
2		GeoB1023	Brandberg/Eksteenf. De Rif/Pakhuis Pass Pella Mirabib	Rietvlei Boomplaas	Elim/Braamhoek Lake Ngami Wonderwerk Cave Equus Cave Florisbad Wonderkrater Tswaing	Mahwaqa Mt Gorongoza Mfabeni	
3	50				?		
4		GeoB1711		Vankersvelvlei			GeoB9311
5	100				Florisbad		
6	150	MD96-2098					MD96-2048
7	200	GeoB1016			Tswaing		
8	250				Florisbad	Port Durnford	
9	300						
10	350						
11	400					Port Durnford	

Table 3

Simplified climatic and vegetation-cover events for the six regions derived from palynology (not all details can be included in this format).

Age (cal ka/ka BP)	Atlantic Ocean Climate	Vegetation	West Coast Climate	Vegetation	SW & South Coast Climate	Vegetation	Interior Climate	Vegetation	Eastern Coast & Interior Climate	Vegetation	Indian Ocean Climate	Vegetation
20	Cool to warmer	Grassy	Relatively cool, humid	Succulents & Asterac.	Relatively cool, dry	Renosterbos, Amaranth.	Warming	Increasig woodland & grassland	Cold	Open mosaic	Becoming warm	Increasing woodland
30	Cool, dry	Grassland & fynbos	Cool, relatively humid	Karroid shrubs	Cool	Restionaceous fynbos	Cool		Cool	Fynbos & Podoc.	Cool	Grassy with fynbos
40			Relatively humid	Woody shrubs & grass			Relatively cool	Grassland & fynbos	Relatively humid	Podocarpus forest	Relatively cool humid	Podocarpus forest
50	Dry	Grassy	Relatively dry	Desert grassland	Relatively cool	Ericaceous fynbos	Relatively warm dry	Savanna woodland			Relatively warm	Grassy woodland
60							Relatively humid	Grassland & forest				
70	Relatively humid	Grassland & forest									Relatively warm humid	Woodland & forest
80	Relatively dry	Woodland			Relatively cool	Ericaceous fynbos	Relatively warm	Savanna woodland			Relatively warm	Woodland
90												
100					Relatively warm	Asteraceae					Relatively warm	Woodland
110	Relatively humid	Podocarpus					Relatively cool	Grassland			Relatively humid	Podocarpus forest
120											Relatively warm	Woodland
130	Warm dry	Grassy woodland					Relatively humid	Grassland & forest				
140	Cool	Forest and Ericac.										
150												
160											Relatively cool	Dry woodland
170	Relatively dry	Miombo & Asteraceae					Relatively cool	Grassland & fynbos				
180												Grassy savanna
190	Relatively warm	Miombo and forest					Relatively humid	Grassland & forest			Relatively warm	Woody savanna
200	Relatively warm	Mangroves					Relatively warm dry	Savanna woodland				
210	Dry warm	Grassy woodland									Relatively dry	Grassy
220												
230	Relatively warm	Forest & mangroves										
240	Cool, dry	Grassy & mixed forests									Relatively cool humid	Podocarpus forest
250									Relatively cool, humid	Podocarpus forest		
260												
270	Dry	Grassy						Karroid grassland & fynbos	Cooling, humid	Grassy savanna		
280							Relatively cool dry					
290									Relatively warm	Woody savanna		
300	Relatively humid	Grassy woodl &forest										
310												
320												
330												
340												
350												
360												
370												
380												
390												
400									Relatively warm	Woody savanna		
410												
420												
430												

210–195 ka BP. Abundant mangrove pollen between c. 210–200 ka BP points to high sea levels. This period may correspond with a Southern Hemisphere marine transgression, peaking c. 220–210 ka BP, as indicated from records in southern Brazil (Lopes et al., 2014) and New Zealand (Osterberg, 2006).

3.1.2. MIS 6, 190–130 ka BP

During wet periods of the glacials, for instance during MIS 6, sedges (Cyperaceae), which are more widespread in the eastern half of Southern Africa and are associated with moister conditions (Koekemoer et al., 2014), expand and *Podocarpus* percentages reach maxima at the cost of woodland taxa pollen. At c. 185 ka BP these elements retreated in both cores and coastal and shelf deposits suggest a dropping sea level (Ramsay and Cooper, 2002), which is supported by similar indications for global sea levels at that time (Spratt and Lisiecki, 2016). Since c. 170 ka BP, stable oxygen isotopes of *Globerigenoides ruber* point to cool conditions (Dupont and Kuhlmann, 2017). At c. 165 ka BP, Ericaceae pollen percentages at core GeoB9311 are relatively high (c. 7%), indicating cool and humid conditions. Although evidence for sea level fluctuations in Southern Africa is scarce for this period (Ramsay and Cooper, 2002), suggested fluctuations at Port Durnford are supported by several independent proxies at different Southern Hemisphere coasts (Osterberg, 2006; Lopes et al., 2014).

3.1.3. MIS 5, 130–73 ka BP

During MIS 5e (Eemian Interglacial, 128–116 ka BP), when global sea levels were higher than at present (Hearty et al., 2007; Spratt and Lisiecki, 2016), warm conditions are indicated in both records by high percentages of pollen of woodland/savanna taxa. Of the two cores (GeoB9311-1 and MD96-2048), forest pollen, including *Podocarpus*, is more prominent in MD96-2048 during this phase with some decline c. 100 ka BP (MIS 5d). In GeoB9311, Ericaceae pollen decreases whereas mangrove pollen peaks markedly especially at the beginning of MIS 5e. During periods that were suggested to represent exceptionally high sea levels at the shores of Southern Africa, c. 128 ka BP and 110 ka BP (MIS 5e, Ramsay and Cooper, 2002), levels of mangrove pollen are low (Dupont and Kuhlmann, 2017), which might be explained by drowning of the mangrove fringe during extreme transgressional periods (Scourse et al., 2005). After c. 105 ka BP, decreasing percentages of woodland pollen point to a return of glacial conditions during the early Weichselian (MIS 5d-a, 109–71 ka BP).

3.1.4. MIS 4-beginning of the Holocene in MIS 1, 73–11,7 ka/cal ka BP

Between c. 71 ka BP and 20 cal ka BP in marine core MD96-2048, percentages of woodland pollen remain low and *Podocarpus*, a humid element, is gradually retreating (Dupont and Kuhlmann, 2017). More Asteraceae and Poaceae pollen percentages point to rather dry conditions. Towards the Pleistocene-Holocene, transition warming of the atmosphere and sea level rise (Spratt and Lisiecki, 2016) are shown by an increase in woodland, forest elements and mangroves, but the resolution of sampling is not fine enough to reveal specific conditions coinciding with the Younger Dryas period.

3.2. Eastern coast and interior

Peat bogs, lakes and wetlands are rare in semi-arid Southern Africa. Often rich in pollen, valuable palaeo-archives can mainly be found in the more humid eastern half of the subcontinent, which is characterized by summer rainfall (Scott et al., 1992; Ochadleus et al., 1996; Finch and Hill, 2008). Pleistocene vegetation and climate changes inferred from these eastern sites can find valuable support in offshore records in the Indian Ocean (see 3.1, Dupont and Kuhlmann, 2017). However, differences of pollen trapping mechanisms between the coastal deposits, which comprise strong local vegetation representation, and the offshore sequences, which represent regional pollen, present biases that need to be investigated further.

The oldest Pleistocene peat core sequence can be found at Port Durnford c. 150 km to the north of Durban in Kwazulu-Natal (Scott et al., 1992; Ochadleus et al., 1996). In the upper predominantly sandy 25 m of the core no pollen was preserved, but a peaty layer c. 24,5–26,5 m and clays from the bottom of the core at a depth of c. 33 m, contained pollen. A new chronology and interpretation of the Port Durnford succession can be proposed in the light of revised age determinations for the oldest part of the sequence (Porat and Botha, 2008).Younger pollen data were obtained from the Mfabeni swampland further north along the east coast (Finch and Hill, 2008) and towards the interior at Mt. Gorongosa in Mozambique (McWethy et al., 2016) and the Drakensberg foot hills at Mahwaqua (Neumann et al., 2014).

3.2.1. MIS 11, c. 435 (or 424, see Table 1)-365 ka BP

The Port Durnford Lower Argillaceous Member contains mammal remains that were probably deposited during MIS 11 under estuarine/lagoonal conditions which would support earlier assumptions based on mammal fossils that the sediments accumulated during an interglacial predating the Eemian (McCarthy and Orr, 1978). This would mean that the clayey sediments corresponded to the Hoxnian/Holsteinian interglacial, representing higher sea levels. The sediments feature pollen of trees and shrubs like *Morella* (previously *Myrica*), *Syzygium* (an evergreen tree belonging to the Myrtaceae), *Olea*, *Celtis* (probably *Celtis africana*, the white stinkwood), low *Podocarpus* pollen percentages and, in comparison to a peat layer above, a stronger presence of Asteraceae and Amaranthaceae pollen in the sequence (Oschadleus et al., 1996) possibly as a result of near shore sandy conditions near the basin.

3.2.2. MIS 9a-8, 295–245 ka BP

Porat and Botha (2008) dated the sandy layers above and below the Port Durnford peat layer, which is sometimes referred to as lignite, using thermoluminescence dating (TL) and Infrared Stimulated Luminescence Dating (IRSL) respectively. Their results point to an age for this layer that is at least 295 ka BP old (>295 and > 276 ka BP above and below the peat respectively), which would mean that it was probably deposited during or before MIS 8 rather than during the beginning of MIS 4 as proposed by Oschadleus et al. (1996), who obtained an age of c.70 ka BP by means of ^{230}Th/^{234}U disequilibrium dating for the section at 24,5–26,5 m. The pollen diagram shows a succession from an open, sedge-dominated (Cyperaceae) marshland with swamp trees like *Ficus* sp. and *Syzygium* to a *Podocarpus* dominated forest (*Podocarpus* pollen c. 80%) (Scott et al., 1992; Oschadleus et al., 1996). These trees are not an important element of today's coastal forest, but a prominent *Podocarpus* stand in a community with possible Eastern African affinities exists close to Kosi Bay near the Mozambique border. Fynbos representatives, namely Ericaceae and *Anthospermum*, indicate a relatively cool climate at Port Durnford (Scott et al., 1992). We postulate that this represents a cool period with rather low sea levels and low pollen production. The sandy sediments overlying the peat are interpreted as representing aeolian activity during a glacial stage (Scott et al., 1992). The peats within the Port Durnford Formation probably formed on a coastal plain similar to today's (Porat and Botha, 2008). Fisher et al. (2010) modelled the palaeo-landscape along the southern coast of South Africa during the

middle to late Pleistocene by using $^{87}Sr/^{86}Sr$ as a proxy for the reconstruction of the distance to the coast and show a regressive phase between c. 288 and 271 ka BP. This is younger but nearly coincides with the age of the peat layer as dated by Porat and Botha (2008). The succession proposed by Scott et al. (1992) and Oschadleus et al. (1996) for the Port Durnford peats is consistent with marine regression, a drop of the water table and the establishment of a *Podocarpus* forest as the distance from the coastline increased. The suggested shift from a Cyperaceae dominated wetland to *Podocarpus* forest is therefore assumed to have occurred later than 271 ka BP but the possibility that it is from an even earlier phase cannot be excluded. It can therefore possibly be correlated with the earliest part of the MD96-2048 near the Limpopo River mouth or with an older cycle, making it one of the oldest Quaternary palynological records of terrestrial deposits in Southern Africa.

3.2.3. MIS 3-beginning of Holocene in MIS 1, 57–11.7 ka/cal ka BP

The Mfabeni peatland close to Lake St. Lucia in KwaZulu-Natal at the eastern seaboard of South Africa gave one of the oldest, continuous climatic records in the region, reaching back >40 cal ka BP (Finch and Hill, 2008). Here extensive *Podocarpus* forests are suggested before c. 33 cal ka BP, although the low number of radiocarbon dates presently available for the sequence hampers correlation with other records.

The dominance of grass and sedge pollen, reflecting local wetlands, makes it difficult to characterize the vegetation in the wider surroundings of the Mfabeni swamp during MIS 3 and 2. Nevertheless, forest retreated and the replacement of swampy reed/sedge communities by dry grassland and Asteraceae pollen during this interval suggests more regional pollen input (Finch and Hill, 2008). However, the Mfabeni area must have experienced a sharp drop of sea levels that occurred along the coast of Southern Africa during the LGM (Ramsay and Cooper, 2002). Towards the interior of the eastern coastal area, the Mahwaqa swamp sequence in the Kwazulu-Natal highland shows high proportions of Ericaceae pollen c. 18–11.7 cal ka BP while other fynbos elements such as Restionaceae and *Passerina* were also prominent (Neumann et al., 2014). At this time in the Indian Ocean borehole-cores GeoB9311 and MD96-2048 (see 3.1), woodland elements also decreased and Ericaceae and Poaceae percentages declined (Dupont and Kuhlmann, 2017). To the north and further away from the coast, terrestrial pollen record at Mount Gorongosa in southern central Mozambique suggests that first *Podocarpus* and then grass pollen percentages reach peaks at c. 24 and c. 23 cal ka BP respectively, at the expense of Ericaceae, probably indicating higher soil moisture (McWethy et al., 2016). This pollen sequence is interrupted by a hiatus c. 23 -7 cal ka BP which might indicate drier conditions.

Around 13,5 cal ka BP until the beginning of the Holocene, at Mahwaqa Ericaceae were gradually replaced by Poaceae, signalling a warming of the climate.

In view of the low diversity of pollen-types that are sensitive to the climatic variables, Chevalier and Chase (2015) only tentatively reconstructed paleoclimate at Mfabeni, and noted a 1 °C decrease c. 17-16 cal ka BP before the overall increase in temperatures of the Pleistocene-Holocene transition at the site.

The coastal area is included in the 'centre and eastern' precipitation stack of Chevalier and Chase (2015), which comprise reconstructions of Wonderkrater, Equus Cave, Braamhoek, Blydefontein, Florisbad and Lakes Eteza and Mfabeni, some of which are outside the regions we define here and belong to section 3.3 (Interior). Within constraints by a large error margin and different dating options for the older section (Wonderkrater), a steep decrease of precipitation is suggested c. 40 - 23 cal ka BP for this broad region (Chevalier and Chase, 2015, 2016).

3.3. Interior

Pollen records in the interior are scarce due to the dry conditions and the erosive nature of the landscape that excludes suitable basins for lake and swamp formation. The available swamp, spring and cave deposits from the Highveld escarpment in the east to the cave deposits in the southern Kalahari to lake deposits in Lake Ngami towards the north provide a growing data set for the summer rainfall region (Scott et al., 2012; Cordova et al., 2017).

3.3.1. MIS 8, c. 282–245 ka BP

Possibly one of the earliest Pleistocene pollen records in the South African interior is that at the Florisbad spring site known for its archaic human cranium (Dreyer, 1935, 1938; van Zinderen Bakker, 1957, 1989; Scott and Rossouw, 2005; Toffolo et al., 2017). An age estimate of close to c. 300 ka BP for the sequence was obtained by electron spin resonance dating (ESR, Grün et al., 1996). Although incomplete and discontinuous due to selective pollen preservation and hiatuses, it suggests that considerable climatic fluctuations between grassy and karroid vegetation occurred. The pollen (van Zinderen Bakker, 1989) showed that fynbos elements like Ericaceae and Restionaceae were present during cool conditions (Scott, 2000).

3.3.2. MIS 7a to 5d, c. 205–105 ka BP

A long Pleistocene archive is available from the Tswaing Crater, a meteorite impact structure 40 km northwest of Pretoria (Tswaing I core, Scott, 1999a, b, 2016). This profile unfortunately shows large intervals lacking pollen and organic matter due to periods when pollen was either not preserved or destroyed due to the development of oxygen-rich conditions, which is typical for perennially dry lakes (salt pans). Pending further chronometric dating, the oldest productive pollen section of this core can only be tentatively estimated to date to c. 200–150 ka BP, therefore possibly from MIS 7 and 6 (pollen zones Z1-4, Scott, 1999a, b). The rich pollen assemblages in these zones show alternations of warm dry woodland to cooler forest or fynbos dominated vegetation. A suggested transition from warm woodland to fynbos (zones Z1-Z2, Scott, 1999a, b) corresponds well with developments in the Indian Ocean pollen records from MIS 7a to MIS 6 (Dupont and Kuhlmann, 2017) supporting the dating of Tswaing that has been the subject of some controversy (Partridge et al., 1997; Chase et al., 2010; Scott, 2016). During these stages, grassy vegetation developed at Florisbad with alternating drier and wetter conditions, which cannot be well dated at this stage but seem to extend past c. 121 ka BP (van Zinderen Bakker, 1989; Grün et al., 1996; Scott, 2000; Scott and Rossouw, 2005).

3.3.3. MIS 5a, c. 85–73 ka BP

Pollen zone Z6 at Tswaing, as tentatively dated to between 75 and 73 ka BP by an extrapolation method (Scott, 2016), shows strong savanna woodland elements consisting of tree pollen belonging to *Spirostachys* and Combretaceae (Scott, 1999a, b, 2016). After 73 ka BP conditions became cooler (Scott, 2016). During the same time period, in Vankersvelvlei at the southern coast (see 3.4), the environment becomes cooler and probably drier as induced from pollen data (Quick et al., 2015).

3.3.4. MIS 4, c. 73–57 ka BP

Following a gap between c. 68–63 ka BP, the Tswaing sequence yielded a pollen assemblage, which can tentatively be dated to c. 63–62 ka BP by extrapolation (Scott, 2016), that started with a cool grassy phase that changed sharply to warm, dry grassy savanna conditions (Scott, 1999a, b, 2016). Although further research is needed to support this interpretation, it appears to correspond

with results from core MD96-2048 from the Indian Ocean (Dupont and Kuhlmann, 2017).

3.3.5. MIS 3, c. 57–32 ka/cal ka BP

This phase at Tswaing and Wonderkrater represents marked climate fluctuations, but in considering this, it should be noted that the chronology adopted by Scott (2016) for Wonderkrater Borehole 4 deviates from the climate estimates in Chevalier and Chase (2015, 2016). The reason for the difference is that according to Scott (2016), there is evidence for a hiatus between c. 40-27 cal ka BP, which is not considered in Chevalier and Chase (2015, 2016). Therefore moist conditions suggested at c. 27 cal ka BP by the latter authors (at a time when *Podocarpus* forest elements were flourishing) could be around 20 000 years older and probably formed between c. 58 and 45 cal ka BP. Further, at both sites and also at Venda (Tate Vondo) in northernmost South Africa, an intermediately warm and drier phase developed between 45 and 41 cal ka BP (Scott, 1999a,b, 2016; Baboolal, 2014). This was followed by a phase of fluctuating temperature and moisture conditions that included elements of cooler upland fynbos like the Ericaceae and *Stoebe* type. In the case of Chevalier and Chase (2015, 2016), a palaeoclimate reconstruction for the last 45 cal ka of the 'northern' precipitation stack, which includes Mfabeni and Wonderkrater Borehole 4, therefore implies a less arid period between 45 and 34 cal ka BP and a precipitation decrease until 32 cal ka BP. If the older chronology as proposed by Scott (2016) is adopted for Tswaing and Wonderkrater, the moisture pattern from c. 36-32 cal ka BP at Wonderwerk Cave in the drier Kalahari region supports it. At the drier Wonderwerk Cave a lower diversity of fynbos types occurred during this phase including only *Stoebe, Passerina,* and Restionaceae and not Ericaceae and *Cliffortia* that were typical at Tswaing and Wonderkrater (Brook et al., 2010; Scott and Thackeray, 2015).

3.3.6. MIS 2 - beginning of Holocene in MIS 1, c. 32–11.7 cal ka BP

Vegetation and climate conditions during MIS 2 in the interior of South Africa can be assessed by pollen records from Elim (Scott, 1989; Scott et al., 2013), Braamhoek (Norström et al., 2014) in the eastern Free State highland grassland region, Baden-Baden in the western Free State (Van Aardt et al., 2016), Aliwal North in the Karoo Biome (Coetzee, 1967), Wonderkrater in the savanna woodland (Scott, 2016; Chevalier and Chase, 2015, 2016) and Wonderwerk and Equus Caves in the Kalahari woodland region (Scott, 1987; Brook et al., 2010; Scott and Thackeray, 2015; Scott et al., 2012). All these sites have in common that *Stoebe* type pollen, a clear indicator of cooler conditions, is prominent in otherwise grassy surroundings and must have represented a widespread asteraceous element in the vegetation of the interior regions (Scott, 2016). In contrast, however, this type was not important in the neighbouring eastern Drakensberg region of Kwazulu-Natal at Mahwaqa (see 3.2.3) (Neumann et al., 2014). *Stoebe* type pollen was widespread throughout the whole interior, including the Kalahari region (Brook et al., 2010; Scott and Thackeray, 2015; Cordova et al., 2017) and the moister eastern parts of the interior and is supported by similar results from the east coast and Indian Ocean region (see 3.1.4 and 3.2.3) (McWethy et al., 2016; Dupont and Kuhlmann, 2017) and the Namib region (3.4.2) (Scott et al., 2018). Chevalier and Chase (2015) note a decline of calculated paleo-precipitation reaching lowest values c. 21 cal ka BP for the 'north' stack after a short wetter, warm period peaking at c. 27 cal ka BP, but Scott (2016) proposed that it belongs to a previous phase at c. 41 cal ka BP (see 3.3.5). From 21 cal ka BP onwards, the calculated precipitation increases towards the Pleistocene-Holocene transition (Scott, 2016; Chevalier and Chase, 2015).

At Lake Ngami in Botswana (Cordova et al., 2017) c. 16 cal ka BP, a period of high, fluctuating summer rainfall existed under cool conditions from c. 16,6–12,5 cal ka BP. Charcoal from an archaeological layer at Wonderwerk Cave dated to c. 15-14 cal ka BP revealed the presence of six arboreal species and two genera with *Berchemia discolor* and *Halleria lucida* pointing to relatively warm more humid conditions than today (Bamford, 2016). Other sites, e.g. Braamhoek at the Eastern Escarpment, imply regional wetness at the end of the Pleistocene (Norström et al., 2009, 2014). Some pollen and isotope evidence for moisture fluctuations at the end of the Pleistocene exists at different sites including wetter and drier conditions that do not necessarily match the Younger Dryas period (Scott et al., 2012; Norström et al., 2009, 2014; Scott, 2016). Associated with these fluctuations is a hiatus c. 10.2–12.7 cal ka BP in the speleothem record of Makapansgat (Holmgren et al., 2003). Based on palynological data from Lake Ngami, Cordova et al. (2017) suggest that Late Pleistocene vegetation changes at the site might be related to moisture stemming from the Indian Ocean as a consequence of a more southerly location of the African rain belt.

3.4. South-west and south coast

Despite probably having relatively more potential archives such as lakes, springs and swamps than the interior region, few fossil pollen studies have up to now been conducted in the southern mountainous coastal areas. They include valuable recently produced pollen profiles that reach into the Pleistocene.

3.4.1. MIS 5d-3, c. 115–32 ka BP

Before and during MIS 3, sites in the Western Cape, viz. an estuary at Milnerton along the west coast and boreholes from the Cape Flats, indicate changing marine influences and regular fluctuations in the composition of fynbos and swamp vegetation (Schalke, 1973). The significance of these changes is unclear due to the uncertainty of the radiocarbon ages, which are near the effective limits of the method. At Vankersvelvlei in the southern Cape, where a better chronology could be established by supplementing radiocarbon dating with optically stimulated luminescence dating, fynbos vegetation was shown to occur between c. 110 and 96 ka BP with prominent Asteraceae pollen of the *Pentzia*-type that was interpreted as warmer due to somewhat lower Ericaceae percentages than the subsequent period that lasted until c. 37 cal ka BP (Quick et al., 2015). The transition from MIS 5a to 4c. 76–72 ka BP is, in a study by Nel and Henshilwood (2016) at Blombos cave, indicated by less diverse micromammal assemblages, a spread in grassland and scrub vegetation, shifts in seasonal precipitation, and a decrease in fynbos. In contrast to Nel and Henshilwood (2016), Quick et al. (2015) report an increase in Ericaceae pollen (fynbos) and a decrease in *Podocarpus* pollen for the transitional period between MIS 5 and 4 around 96 to 70 ka BP. This suggests a shift to cooler temperatures and perhaps increased rainfall seasonality. The onset of the glacial conditions associated with MIS 4 is visible in the micromammal assemblage (Nel and Henshilwood, 2016), at Vankersvelvlei a reduction in moisture availability during MIS 4 is suggested (Quick et al., 2015). *Stoebe*-type pollen that is abundant at Vankersvelvlei at 67 ka BP, is negatively correlated with temperature and cooler conditions might have triggered caused rainfall seasonality and therefore marginally more arid conditions.

The period in MIS 3, from c. 35 -30 cal ka BP, is represented by pollen from the Rietvlei wetland in the Southern Cape with Restionaceae and *Stoebe*-type pollen suggesting different possibly cooler and maybe more humid conditions than in the Holocene (Quick et al., 2016). At Boomplaas Cave to the north, Scholtz (1986) showed a strong Asteraceae pollen and charcoal presence at c. 37 cal ka BP in the mountainous vegetation of the Little Karoo vegetation including mostly *Stoebe/Elytropappus*-type (Deacon and Lancaster, 1988).

3.4.2. MIS 2 - beginning of Holocene in MIS 1, c. 32–11,7 cal ka BP

The above-mentioned *Stoebe/Elytropappus* pollen at Boomplaas Cave (Deacon and Lancaster, 1988) shows even higher proportions c. 25 cal ka BP. At the coastal Rietvlei site, fynbos vegetation at c. 16-14 cal ka BP had a grassy component with strong undifferentiated Asteraceae pollen (Quick et al., 2016). The Pleistocene at this site ends with a pronounced peak of Amaranthaceae pollen and a drop of grasses, fynbos and aquatic elements indicating dry conditions during the Younger Dryas. This event is only weakly supported by pollen in hyrax dung of the Cederberg at Pakhuis Pass (Scott and Woodborne, 2007) due to low sample resolution but more strongly by isotope data at De Rif in the same mountain range (Chase et al., 2015).

3.5. West coast (northern section)

Moving further west towards the Atlantic region, which has summer rainfall in the north that changes gradually to winter rainfall in the south, we find that long terrestrial records are not available due to unfavourable conditions for pollen preservation on land.

3.5.1. MIS 3, c. 57–32 ka/cal ka BP

For the MIS 3 hyrax dung deposits containing pollen are available from grassy settings at the Brandberg and at Mirabib in Namibia (Scott et al., 2004, 2018), and a more karroid environment at Pella in the Northern Cape Province, South Africa (Lim et al., 2016). These sites suggest fluctuations in moisture and temperature conditions for MIS 3 that cannot be correlated easily between the sites in terms of vegetation or climatic conditions, except perhaps for a tendency of more woody elements c. 39-37 cal ka BP.

3.5.2. MIS 2-beginning of Holocene in MIS 1, c. 32–11,7 cal ka BP

Pollen composition in hyrax midden accumulated at Brandberg (Scott et al., 2004) and spring deposits at Eksteenfontein (Scott et al., 1995, 2012; Heine et al., 2014) included pollen of fynbos (*Stoebe*-type and *Passerina*), grass, *Olea* and Asteraceae (*Pentzia*, *Artemisia* and *Stoebe*-types). The presence of *Stoebe*-type conforms to findings of more effective moisture under cooler conditions with its widespread presence in the other regions (see above) over the subcontinent during MIS 2. Prominent examples in the Kalahari region include Equus Cave and Wonderwerk Caves (Scott, 1987; Scott and Thackeray, 2015) where conditions were not moist enough for the establishment of Ericaceae but *Passerina* was spreading instead. The situation at Pella during MIS 2 appears to be different where the pollen spectra seem to be dominated by undifferentiated Asteraceae (Lim et al., 2016). In contrast, further to the south in the Cederberg range, which is situated in the Fynbos Biome (Mucina and Rutherford, 2006, Fig. 1) in the Pakhuis Pass (Scott and Woodborne, 2007) and at De Rif (Quick et al., 2011; Valsecchi et al., 2013), Asteraceae pollen (undifferentiated) is not more prominent than in other layers, but *Stoebe*-type and other fynbos-types (including Ericaceae) are well represented. Evidence for a relatively drier Younger Dryas can be found at Wonderwerk Cave (Brook et al., 2010; Scott and Thackeray, 2015) and Eksteenfontein (Scott et al., 2012). Similarly, δ15N and δ13C records from the De Rif hyrax midden from the Cederberg Mountains show a dry event during the Younger Dryas (Chase et al., 2011), which are further supported by lower sea-surface temperature estimates from a marine core off the coast of Namibia which would have strengthened meridional winds and Benguela upwelling (Farmer et al., 2005).

3.6. Atlantic Ocean

Pollen records in the Atlantic Ocean provided evidence of long-term environmental change for the Namib Desert region where pollen records are scarce (Shi and Dupont, 1997; Shi et al., 2001; Urrego et al., 2015). Other than at the eastern coast of Southern Africa where wind systems flow onshore and fluvial input is rather strong, the trade wind direction at the Cape is predominantly south-north and parallel to the coast, probably leading to an over-representation of certain Cape fynbos pollen-types. According to Scott et al. (2004, 2018), the strong presence of fynbos pollen during the LGM in Atlantic cores might be a sign that upwelling of the Benguela system keeps pollen loads from the Cape area in suspension and transports them northward. In addition, there is little fluvial input apart from the Orange River, which has its source in the grassland biome as far away as the Drakensberg region. Other sources that may be considered are wind or fluvial transport via the Cunene River that would deliver pollen from ericaceous elements stemming from the Angolan highlands. During glacial phases, areas suitable for these elements must have been more extensive as vegetation belts around the highlands were lower (Scott et al., 2018). Consequently, the pollen record from offshore sites in the southern Atlantic Ocean is hardly a clear reflection of the vegetation onshore but from widely different sources, which complicates the interpretation of these pollen records (Scott et al., 2004, 2018).

3.6.1. MIS 9b to 3, c. 310(?)-32 ka/cal ka BP

Information about the Pleistocene vegetation can be derived from offshore sites like the 301 ka BP old core GeoB1016 (Shi and Dupont, 1997) (near Angola, not shown in Fig. 1), the 135 ka BP core GeoB1711 (Shi et al., 2001) and core MD96-2098 which reaches back until c. 194 ka BP (Urrego et al., 2015). The sequences differ in pollen composition according to their latitudinal position ranging from more tropical in the north to more desert or temperate elements towards the south. In view of their nature as representing a pollen mixture from a vast south-western African region and the influence of pollen transport in rivers, e.g. the Orange River, the data from deep marine sediment cores are combined here. They represent several cycles of marked climate and vegetation change between MIS 9a-3. These millennial scale cycles suggest a complex pattern of vegetation change that include periods of lowering of vegetation belts during cool conditions with wider distribution of fynbos elements; concerns exist about confining the provenience of these pollen types (see above, Scott et al., 2004, 2018), but also events of intensification of desert conditions or more favourable moisture conditions that, depending on scale, allowed expansions of savanna woodland, miombo or forests.

3.6.2. MIS 2-beginning of Holocene in MIS 1, c. 32–11,7 cal ka BP

Marine sediment cores indicate a strong input of Restionaceae, Asteraceae and Ericaceae pollen during MIS 2 (c. 22-18 cal ka BP) in the Atlantic Ocean sediments in cores GeoB1711-4, GeoB1023-5 (off the Angolan coast) and MD96-2094 (Shi et al., 1998, 2000, 2001). Pollen compositions from these marine sequences do not conform with terrestrial pollen records (see 3.4.2), i.e. with hyrax middens at Brandberg (Scott et al., 2004, 2018), Eksteenfontein (Scott, 1995; Scott et al., 2012) and Pella (Lim et al., 2016), which do not include fynbos elements like Ericaceae and Restionaceae pollen but instead more *Passerina*, grass, *Olea* and Asteraceae (*Pentzia*, *Artemisia* and *Stoebe*-types) (Scott et al., 2004, 2018). The differences are caused by biome migrations, source areas and possible long distance transport of pollen by atmospheric and water circulation systems. Offshore pollen from the terminal Pleistocene at the Cunene River mouth in Boreholes GeoB1023 and Walvis Bay inGeoB1174 suggest that the Younger Dryas period, which starts with high numbers of

Amaranthaceae pollen as a continuation of the preceding phase, showed a sharp decline of this pollen (Shi et al., 1998, 2001). This pattern could indicate that dry conditions came to an end. It may, however, also reflect relatively moist but strongly seasonal or evaporative conditions as inferred in the case of Lake Ngami, Botswana, where this family is prominent c. 12.5 cal ka BP (Cordova et al., 2017). The pattern seems to differ from the generally dry conditions suggested elsewhere in Southern Africa during the Younger Dryas. The anomaly may be attributed to a different climatic regime in the distant north-westerly position for Ngami and Boreholes GeoB1023 and GeoB1174.

4. Discussion

4.1. The need for long time series

To evaluate the role of climate change in human evolution we have to look at a long range of events preceding and post-dating finds to better understand its potential long-term significance and to look for further possibilities to study their palaeoclimatic and palaeobotanical contexts. Rare hominin finds, like those from sites in the interior of Southern Africa, can therefore only be placed arbitrarily within a range of likely environmental fluctuations that might have influenced their survival. The estimated dates of when they occurred are not precise and both on a temporal and spatial basis the finds are difficult to tie in accurately with pollen records. These finds and pollen records are mostly from different locations and where they are from the same site, e.g. Florisbad, the pollen record is incomplete and/or dating is inadequate.

The above-mentioned hominin members must have evolved during repetitive climatic cycles very similar to those of the late Pleistocene and Holocene. The exact pattern was never exactly the same, judging from long-term vegetation analyses of in marine sediment cores (Dupont and Kuhlmann, 2017). Although palynological identifications are not accurate enough to reveal any extinctions or speciation during the study periods on Pleitocene time scale, there is no evidence that this was significant. The major ecological groupings at genus and family level appeared to have stayed the same, suggesting that they have significance despite the ineffectiveness of pollen analysis at species level.

To better understand the development of the modern biomes as conditions for hominin evolution, we believe that a much longer time range of palaeoclimatic change is needed than what we report on here and it should include the Neogene. Here, for instance, the study of older marine borehole cores (ODP1082 and ODP1085) from the Atlantic Ocean (Dupont et al., 2005; 2011a,b) is important in showing a shift in the prevailing circulation systems that influenced the vegetation types during the Pliocene, e.g. the appearance of *Elytropappus/Stoebe*-type pollen in renosterbos-like vegetation that first gained prominence after 3.1 million years (Dupont, 2006). This seems to have been due to the development of more winter rainfall and probably signals a cyclic climatic regime that formed the background for the evolution of *Homo* species in glacial, stadial and interglacial cycles that continued to persist during the Late Pleistocene.

It is therefore crucial to combine long marine and terrestrial records where the marine sequences give a wide regional perspective and the terrestrial records provide a local picture of vegetation and climate change. Caveats are transport modes of pollen in the marine borehole-cores due to sea currents, wind and river transport and biases due to low pollen concentrations and over-representation of anemophilous pollen. Therefore, coupled with modern pollen taphonomical studies, the number of land terrestrial pollen sequences needs to be increased to correlate them with nearest marine sequences. This will help to determine and limit biases for both types of pollen sequences. In terrestrial archives, constraints like dating issues, e.g. root contamination and other problems, are also challenging. An analysis of additional marine palynomorphs and microfossils, e.g. dinoflagellate cysts, diatoms and even foraminiferal linings, might help to yield additional data regarding sea surface temperatures and salinities, which can further trace climatic changes and sea level fluctuations that affected the coastal region.

4.2. Mechanisms of change

An important aspect of these palaeobotanical studies is their role in establishing reliable long-term simulation of palaeo- and future climate changes. It has previously been suggested in climate models that an equator-ward contraction of circulation systems would have shifted the winter rainfall northward (Van Zinderen Bakker, 1976; Cockcroft et al., 1987; Chase and Meadows, 2007). However, the contrast between vegetation patterns in the Fynbos Biome (Scott and Woodborne, 2007; Quick et al., 2011, 2015; Valsecchi et al., 2013) and Nama Karoo Biome during MIS 2 (Lim et al., 2016) seems to suggest these units were well established and distinct and therefore does not support a scenario of a marked northward shift of the winter-rainfall belt during the LGM. If it is indeed the case that pressure and circulation systems did not deviate much from their current positions, then the strong presence of Ericaceae fynbos in Mahwaqa in Kwazulu-Natal (Neumann et al., 2014) was not necessarily the result of a northward shift of the westerly winter-rainfall system but rather of generally cooler growing seasons, especially at high altitudes. This may be supported by the possible existence of glaciers in the eastern Drakensberg region (Mills et al., 2012). Further, as high proportions of Ericaceae and *Passerina* do occur in some Drakensberg localities today under summer-rain conditions, the spread of Ericaceae at Mahwaqa during the glacial phases should be considered in this context. The prevalence of this family might have been independent of season if summer rains reached relatively further south during glacial phases, which is not impossible considering the role of precession and increasing interactions between tropical and temperate circulation systems (Scott and Woodborne, 2007; Chase et al., 2017).

Whereas early models suggest the contrary, i.e. that contraction of the circulation systems towards the equator during glacial cycles brings winter rains to the north (e.g. Van Zinderen Bakker, 1976, Chase and Meadows 2007), later global models relied more on orbital forcing that would predict independent rainfall seasonality based on shorter cycles like precession (Kutzbach and Street-Perrott, 1985; COHMAP, 1988; Partridge et al., 1997, 1999). Based on the Tswaing Crater moisture record that was derived from sediment fluctuations, Partridge et al. (1997) show a strong link of precipitation and insolation in the Southern Hemisphere that started changing around MIS 3. As the link between insolation and moisture was lost from then on, they proposed that southerly forcing from Antarctica started overriding the control of precession on the precipitation cycle. Later suggestions for Northern Hemisphere forcing have also been proposed (e.g. Schefuß et al., 2011). Chevalier and Chase (2016) suggest that this forcing was strong during the glacial period in the northern parts of the subcontinent and since the last termination it started to be controlled by insolation and increased ocean surface temperatures. They suggest that to the south in central South Africa, a different precipitation mechanism was controlled by the latitudinal position of the Southern Hemisphere's westerly circulation system. The processes controlling long-term precipitation changes are therefore complex and a range of possibilities needs to be tested further.

4.3. Conditions associated with peopling in Southern Africa

Palynology is a proxy that provides the most direct representation of vegetation over a wide area and allows the comparison of different biomes over time. Reconstructions of regional changes are, however, hampered by the fact that palynological records are scarce, have chronological uncertainties and can be discontinuous. The records are unevenly distributed over the subcontinent, to a degree that some biomes (Mucina and Rutherford, 2006) like the Succulent and Nama Karoo Biomes are only represented by very few records or no records as in the case of the Albany Thicket Biome.

It is obvious that the different regions, despite showing changes, retained some unique characteristics related to their geographical placement. Therefore "relatively humid" does not mean the same in terms of climatic conditions on different sides of the African continent, but differences between these extremes potentially show regional patterns of climate change. As can be expected, the observed temperature oscillations seem to show more similarity over the wide region than moisture fluctuations. The role that climatic conditions played in controlling the presence and dispersal of hominins is important but not well understood. However, the summarized pollen data begin to shed light on events that can eventually be understood better with more research in both palaeoenvironments and hominin behaviour.

Considering the recently estimated age of *Homo naledi* of c. 236–335 ka BP (spanning MIS 9–7), who lived at the Rising Star Cave system in the highveld grassland-savanna vegetation mosaic some time before the impact event that created the Tswaing Crater (220 ± 52ka BP) (Partridge et al., 1997; Berger et al., 2017), this species could have experienced anything of a range of possible conditions such as those reported in the nearby Tswaing Crater (Scott, 1999a, b, 2016).

In cases like the Kabwe skull from Zambia, the suggested age uncertainty is extreme so that even speculation about conditions is not possible (700–300 ka) (Millard, 2008; Balzeau et al., 2017).

During MIS 11, c. 435 ka-424 ka BP, the Lower Argillaceous Member at the coastal site Port Durnford was deposited under interglacial (probably Hoxnian) conditions with pollen pointing to warm savanna environments (Table 3), which is within the period suggested for the existence of the Fauresmith industry in Southern Africa (Porat et al., 2010; Herries, 2012). At coastal dunes in Port Edward, 300 km to the south of Port Durnford, the Fauresmith culture was present (Davies, 1976; Kuman, 2007; Herries, 2012) and it can be assumed that the hominins here are likely to have dwelled in an interglacial environment at least for some time. In the case of the Florisbad cranium, in the temperate Highveld region, a smaller range of possible climatic conditions might be suggested. It cannot precisely be linked with the pollen sequence (van Zinderen Bakker, 1989; Grün et al., 1996), but with an age of c. 300 ka BP and an associated spring fauna (Brink, 1988), the Florisbad individual could possibly have experienced a cold, wet climate. These conditions eventually must have changed to a dry pan-like environment but it is unclear how this affected the population.

Between MIS 5a and 5e, pollen assemblages suggest a cool climate with a reduction of *Podocarpus* forests and spread of fynbos along the southern coast (Quick et al., 2015), supporting the findings from Klasies River, a site with MSA where Nel et al. (in press) propose a shift to more a seasonal rainfall with a spread of grasses and probably fynbos.

The Tswaing Crater pollen sequence provides an insight into the environmental situation for the Savanna region during the time of the Still Bay lithic industry, indicating warm conditions that can possibly be linked to this culture that flourished in Southern Africa (Jacobs et al., 2008; d'Errico et al., 2017). The pollen deposited c.

76–71 ka BP at Tswaing Crater, which can be associated with the time of this industry (the MIS 5a-4 transition), suggests that savanna vegetation existed under warm bushveld conditions but that after c. 73 ka BP a cooling trend began (Scott, 2016, Table 3). During the same time period the Vankersvelvlei pollen record on the southern coast near Still Bay showed increasing Ericaceae and lower *Stoebe*-type pollen suggesting a period of temporary flourishing fynbos under relatively warm temperatures that cooled or dried with the return of *Stoebe*-type c. 67 ka BP (Quick et al., 2016). Humans of the Still Bay culture occupying Blombos Cave c. 76–72 ka BP seemed to cope with fluctuating environmental conditions and utilized a variety of available resources (Nel and Henshilwood, 2016). C. 71 ka BP an advanced stone tool technology was recognized at Pinnacle Point Site 5–6 on the south coast of South Africa, further underlining the importance of this period for human cultural evolution (Brown et al., 2012). The cold spell noticed by Quick et al. (2015) at Vankersvelvlei c. 67 ka BP, after the disappearance of the Still Bay industry, might be correlated with slight aridification at the same time observed in the Southeastern Atlantic record of Stuut et al. (2002) (Quick et al., 2015). This assumed dry event would predate the Howiesons Poort culture, another unique stone-tool tradition, which lasted 65,8–59,5 ka BP (Jacobs et al., 2008). Tswaing Crater pollen indicates cooler grassy conditions c. 63 ka that rapidly changed by 62 ka BP to warmer savanna if the dating is correct. Remarkably, this industry would then be associated with pollen assemblages both near the coast and in the interior in that both suggest warm conditions at the time of the Still Bay industry followed by cooler conditions when the Howiesons Poort began, which rapidly became warmer before the disappearance of this culture (Quick et al., 2016; Scott, 2016). Compton (2011) suggested that the apparent loss of Howiesons Poort industries may be explained by the migration of hunting groups, applying this technology, to more humid areas in Central and East Africa during MIS 4. This may find support in the pollen sequences from the savanna biome (Scott, 2016).

The lengthy MIS 3 saw the development of the Early LSA in the eastern interior of South Africa, emerging around 46-44 cal ka BP during MIS 3 (Bousman and Brink, 2017) at a time when apparently both Wonderkrater and Tswaing Crater suggest intermediately warm, relatively dry savanna vegetation (Scott, 2016) and cool ericaceous vegetation near the south coast at Vankersvelvlei (Quick et al., 2015). The MSA-LSA transition is associated with that between MIS 3 and MIS 2, introducing more arid conditions (Compton, 2011).

The LSA stone-tool industry may have lasted up to the LGM c. 21 ka BP (MIS 2) so that it covered an interval that is noted for another well-preserved hominin find, the c. 36 ka BP old Hofmeyr skull from the eastern Karoo region (Grine et al., 2007). Hardly any pollen data for the LGM are available for the Karoo, but other sites that cover this period (e.g. Cederberg, Wonderkrater) suggest a marked drop in temperature (Scott, 1982, 1989, 2016; Scott and Woodborne, 2007, Table 3). While palynological and other interpretations for moisture conditions vary, lower evapotranspiration might have complemented rainfall (Van Zinderen Bakker, 1976; Partridge et al., 1997; Chevalier and Chase, 2015, 2016) also in this region.

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