

Vegetation and environmental changes at the Middle Stone Age site of Wonderkrater, Limpopo, South Africa

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Abstract

Wonderkrater, a Middle Stone Age site in the interior of South Africa, is a spring and peat mound featuring both paleoclimatic and archaeological records. The site preserves three small MSA lithic assemblages with age estimates of 30 ka, >45 ka and 138.01 ± 7.7 ka. Here we present results of the pollen analysis of a core retrieved from the middle of the peat mound, which covers, with hiatuses, the timespan between ca. 70 ± 10 ka and 30 ka. Pollen percentages of terrestrial, local aquatic, and semi-aquatic plants reveal changes in the regional climate and in the water table of the spring. Results identify regional wet conditions at ca. 70 ± 10 ka, followed by a dry and a wet period between 60 ka and 30 ka. Superimposed on these three phases, recurring changes in the size and depth of the water table are observed between >45 ka and 30 ka. Wet conditions at 70 ka and 30 ka are tentatively correlated here with Marine Isotope Stage 4 and Heinrich Stadial 3, respectively. A warm and dry savanna landscape was present during human occupation older than 45 ka, and a wet phase was contemporaneous with the final occupation, dated at ~30 ka.

Keywords: Southern Africa; Late Pleistocene; Pollen; Climate change; Peat mound; Savanna; Middle Stone Age; Paleoenvironment

INTRODUCTION

Climate and hominin evolution

Southern Africa is recognized as a region in which past climate changes may have played a role in modern human behaviour (Lahr and Foley, 1998; Potts, 1998; Mellars, 2006; Campisano and Feibel, 2007; Field et al., 2007; Hughes et al., 2007; Maslin and Christensen, 2007; Scholz et al., 2007; Trauth et al., 2009; Compton, 2011; Thomas et al., 2012; Ziegler et al., 2013). However, paleoclimate records for sub-Saharan Africa are scarce, seldom well dated, and often contradictory. There are problems with correlating terrestrial and marine records and southern hemisphere climate data with those from northern

latitudes, which experience different temperature regimes and monsoon patterns (Chase and Meadows, 2007; Maslin and Christensen, 2007; Gasse et al., 2008; Chase, 2010; Chase et al., 2010; Blome et al., 2012). Over the last few years, this record has been enriched by the analysis of speleothems (Bar-Matthews, 2010), hyrax middens (Lim et al., 2016), and marine pollen and microcharcoal sequences (Dupont et al., 2011; Daniau et al., 2013; Urrego et al. 2015). These sequences have shown that orbital-scale warm phases in the northern hemisphere between 160 ka and 40 ka (Marine Isotope Stage [MIS] 6-3) are marked in the western-central part of southern Africa by the expansion of semi-desert and decrease in fire regime, indicating an increase in summer aridity (Daniau et al., 2013; Urrego et al., 2015). Ziegler et al. (2013) have identified millennial-scale humid events during the last glacial period (MIS 4-2, 73 ka to 15 ka) from a marine sedimentary sequence collected at ~95 km off the mouth of the Great Kei River on the Eastern Cape coast. The comparison of this paleoclimatic sequence with the Middle Stone Age (MSA) archaeological

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record has recently led these authors to propose that major cultural innovation pulses coincided with abrupt climate change towards humid conditions in southern Africa (Ziegler et al., 2013). Increase in moisture would have multiplied water sources, mammalian and plant resources, and stimulated human population growth. Recent environmental data obtained from archaeological sites of the Southern Cape coast have been instead used to argue (Roberts et al., 2016) that climate did not trigger the cultural and technological innovations of the southern African MSA (personal ornaments, abstract engravings, ochre use, bone tools, pressure flaking, and pyrotechnology). Chronological uncertainties in ^{14}C and Optically Stimulated Luminescence (OSL) dating challenge an accurate correlation between terrestrial and marine records (Jacobs et al., 2008; Jacobs and Roberts, 2009; Tribolo et al., 2009, 2005, 2013). In addition, the virtual absence of climate records and well-preserved MSA sites for the interior of southern Africa makes it difficult to verify whether the inferred trend, almost exclusively supported by coastal sites, is also valid for inland sites.

To fill this gap we have conducted a new pollen analysis on contemporaneous MSA levels at Wonderkrater, an open-air site located in inland southern Africa, 160 km north of Pretoria in Limpopo Province (Fig. 1). Wonderkrater is a spring site, which has yielded, like Florisbad (Dreyer, 1938; Brink 1987; Kuman et al. 1999; Scott and Nyakale 2002), important environmental, archaeological, paleontological and archeobotanical remains (e.g., Scott, 1982a, 1999; Backwell et al. 2014). Wonderkrater provides a window to understand the impact of climate and environmental changes on human occupation, and a means by which to evaluate to what extent subsistence strategies and cultural adaptations of populations living far from the coast were different from those of coastal populations having at their disposal a range of aquatic resources such as shellfish, sea mammals and, to some extent, fish (e.g., Deacon and Deacon, 1999; Marean et al., 2007; Clark and Plug, 2008; Marean, 2010a, 2010b; Will et al. 2016).

Wonderkrater has provided a record of the vegetation and, by inference, the climate of this region (Table 1), until recently thought to extend back for at least the past 34 ka (Scott 1982a, 1999; Scott and Vogel 1983; Scott and Thackeray 1987, Scott et al. 1995). Earlier palynological results have been reinterpreted (Scott et al. 2003, 2012; Truc et al. 2013; Chevalier and Chase 2015), and recent excavation and dating of the deposits (McCarthy et al. 2010; Barré et al. 2012; Backwell et al. 2014) has led to a review of the pollen sequence and a new interpretation of the pollen data being proposed (Scott 2016). By applying probability density functions to the last 20 ka of the Wonderkrater pollen sequence, Truc et al. (2013) found that, during both the warm and cold seasons, the last glacial maximum and Younger Dryas temperatures were $6 \pm 2^\circ\text{C}$ colder than the Holocene, with summer precipitation 50% lower than in the Holocene. Using a similar approach, Chevalier and Chase (2015) identify at Wonderkrater a decrease of 2°C across the second part of MIS 3 (ca. 45–27 ka). In his new contribution,

Scott (2016) supersedes his previous interpretations and proposes, based on a comparison with the Tswaing pollen sequence, that between ca. 60 and ca. 46 ka moderately cool and moist conditions characterised the regional climate. An expansion of savanna grassland, suggesting relatively warm and dry conditions, would have occurred between ca. 46 ka and 41 ka, followed by a gap of ca. 10 ka, between ca. 40 ka and ca. 30 ka. From ca. 30 ka to ca. 25 ka, the expansion of *Podocarpus* and fynbos would indicate dropping temperature and increasing moisture conditions.

In 2012, we collected a new sedimentary sequence to conduct an in-depth pollen analysis of the sand layer containing MSA lithic assemblages and underlying clay deposit. Our intention was to extend the record back to around 70 ka, a time marked by innovative behaviour preserved at coastal sites in the form of pre-Still Bay (Sibudu), Still Bay (Blombos) and Howiesons Poort (Klasies River) assemblages. Some of these coastal sites are a few hundred kilometers far from Wonderkrater and the chronology of the Wonderkrater sequence suggests that some layers of these coastal sites where innovative behaviour is recorded are contemporaneous with Wonderkrater. Wonderkrater does not present the same stratigraphic resolution that one observes at some coastal sites, but it is, nevertheless, a stratified site with clearly defined lithological differences, alternating archaeologically rich and sterile layers, and virtually the only one in which these changes can be directly associated with vegetation changes. Our aim was to discriminate paleoenvironmental changes at local (within peat) and regional (around the peat) scales over the same period using different vegetation markers, and refine previous paleoclimatic interpretations of the sand layer to better understand the relationship, if any, between climate and cultural change, and periods of human occupation and abandonment at Wonderkrater.

Background of the site

The Wonderkrater site appears as a large peat mound featuring at the top a large depression located above a mineral-rich spring, which draws its water from the circulation of deep groundwater (McCarthy et al., 2010). The water is retained as a result of artesian pressure due to the low hydraulic conductivity of peat, and may at times have pooled in the middle of the mound (see Ashley et al., 2002). The peat mound presently rises 2.5 m above the surrounding landscape and covers an area of approximately 25,000 m². Excavations conducted in different areas of the site over four field seasons from 2005 to 2007 yielded three small MSA lithic assemblages with age estimates of 30 ka and >45 ka in Area B (Barré et al., 2012), where they are associated with Late Pleistocene mammal fauna and flora, and 138.01 ± 7.7 ka from Area C on the margin of the mound (Backwell et al., 2014).

The upper layers of the sedimentary sequence in Area B comprise peat that preserves macrobotanical and faunal remains reflecting local fen conditions in *Acacia* savanna woodland at 12 ka (Table 2). Below the upper peat layers, a 1-m-thick layer of white sand features two MSA lithic assemblages in association

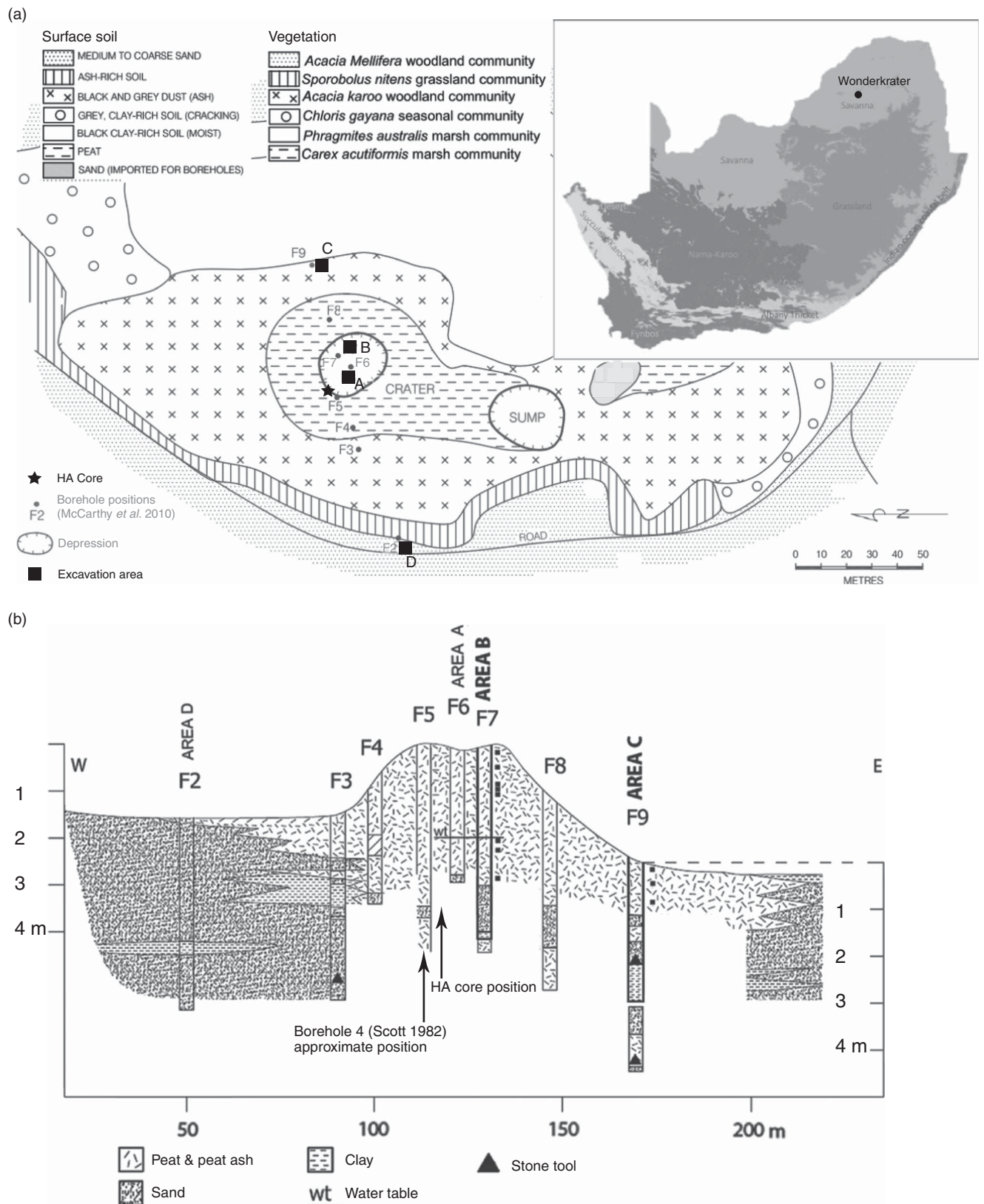


Figure 1. (a) Map of southern Africa showing the location of Wonderkrater (modified after Barré et al., 2012) and subsurface soil map of the site showing the position of excavation areas and core HA along the F-line transect (modified after Backwell et al., 2014). (b) Cross-sectional reconstruction of subsurface stratigraphy of the mound obtained through sediment cores bored along the F-line, and approximate position of core HA (modified after McCarthy et al., 2010).

Table 1. Summary of pollen data and interpretations proposed in previous palynological studies

~ Age (kyr BP)	Borehole and pollen zone	Main pollen taxa	Vegetation and climate	Reference
2	B3 W10	Asteraceae-other, Proteaceae	Drier upland bushveld	Scott and Thackeray, 1987
2 – 6	B3 W9	Asteraceae-other, Aloe-type, Fern spores	Cooler broad-leaved savanna, bracken swamp	Scott et al., 2003
8	B3 W6b	Capparaceae, Tarchonanthus, Aloe-type	Drier and warmer Kalahari-type savanna with montane forests absent	Scott et al., 2012 Truc et al., 2013
10	B3 W6a	Asteraceae, Aloe-type, Capparaceae, Tharconanthus, Combretaceae	Drier and warmer semi-arid and open grassland	
10 – 12	B3 W5	Chenopodiaceae, Asteraceae-other, Aloe-type	Relatively moist and cooler grassland with reduced montane forest and evaporative conditions	
13 – 19	B3	Tulbaghia-type, Stoebe-type, Asteraceae-other, Myrica, Podocarpus	Cooler temperate and subhumid open grassland and Podocarpus and Ericaceae forest	
11 – 25 ?	B4	Asteraceae-other, Tulbaghia-type, Aloe-type, Stoebe-type, Myrica	Cooler temperate to subhumid / wetter open grassland with ericaceous belt elements and restricted montane forests	Scott, 1982a Scott and Thackeray, 1987 Scott et al., 1995
25 ?	B4	Podocarpus, Proteaceae, Olea, Aloe-type	Cooler temperate to subhumid / wette open grassland with more podocarpus forests ?	Scott et al., 2012
<34,4 ?	B4 W4	Aloe-type, Asteraceae-other, Tarchonanteae, Capparaceae, Podocarpus	Cooler temperate to semi-arid Kalahari-type savanna with restricted montane forest	
34,4 ?	B4 W3	Podocarpus, Kiggelaria africana	Cool temperate, moist subhumid and relatively mesic woodland with expanded montane forests	
30	B4 W3	Podocarpus, Myrica	Cooler, wetter grassland	Scott, 2016
46 – 41	B4 W2	Combretaceae, Tarchonanthus, Capparidaceae	Savanna grassland, relatively warm with oscillating dryness	Scott, 2016
52.5 – 46	B4 W1c	Podocarpus, Cyperaceae, grassy pollen,	Moderately cool, moist condition with an episode of expanding swamp vegetation and increase of local spring moisture (ca. 50 kyr)	Scott, 2016
57.8 – 52.5	B4 W1b	Podocarpus, Cyperaceae, grassy pollen,	Moderately cool, moist condition with an episode of expanding swamp vegetation and increase of local spring moisture (ca.55 kyr)	Scott, 2016
60 – 57.8	B4 W1a	Podocarpus, grassy pollen	Moderately cool, moist condition	Scott, 2016

Table 2. Summary of botanical and faunal remains retrieved during excavation of Areas A, B and C and interpretations proposed by Backwell et al., 2014.

~Age (kyr BP)	Environmental proxy	Type	Vegetation and climate
1–1.5	<i>cf. Vahlia capensis</i>	fr	Moist fen conditions
	<i>cf. Xiris capensis</i>	fl	
<6	Phragmites <i>sp.</i> and other grass	ch	Permanent local wetland
12	<i>Acacia</i>	se	Woody savanna
	<i>cf. Sersia</i>	fr	
	<i>Citrullus lanatus</i>	se	
12–13	Phragmites and grass and few woody <i>Diospyros austroafricana</i>	ch	Alternate wet and dry periods
12–15	<i>Diceros bicornis</i>	fn	Some bush or low tree cover
16	<i>Acacia cf. nilotica</i>	se	Woody savanna
<30	Bulliform shaped grass	ph	Warmer conditions and increased drought
30	Trapeziform short cell grass	ph	Moist edaphic conditions and relatively cool and wet winter
	Paucity of C4 phytolith types	ph	Warm and wet summer rainfall climate
	<i>Schotia brachypetala</i>	ch	Present-day conditions
	Many woods with rare Phragmites and grass	ch	Moist conditions
	<i>Syncerus antiquus</i> (isotopic data $\delta^{13}C$)	fn	Highly productive grasslands with some trees
	Abundant local element (grass, sedge, <i>Typha</i>)	po	Grassland and woody shrubs, cool and wet
	Asteraceae, <i>Stoebe</i> and <i>Artemisia</i> -type with some Ericaceae, <i>Passerina</i> , <i>Podocarpus</i> and <i>Olea</i>		
>45	<i>Acacia</i> , <i>Combretum</i> and no grass	ch	Wooded grassland and bushland, warm savanna vegetation
	<i>Megalotragus priscus</i> (isotopic data $\delta^{13}C$)	fn	Woody savanna, warm and dry conditions
	Abundant local element (grass, sedge, <i>Typha</i>)	po	Woody savanna, warm and dry conditions
	Asteraceae with some woodland type (<i>Tarchonanthus</i> , Capparaceae, Combretaceae, <i>Peltophorum</i> and Mimosoideae)		

fr: fruit, fl: flower, se: seed, ph: phytolith, fn: fauna, ch: charcoal, po: pollen from preliminary study of Area B.

with faunal remains (Fig. 2). The ^{14}C and OSL dates for the white sand place the sand deposition in the age range ca. 60–30 ka. The poorly sorted nature of the sediment, its angularity, and fresh state suggest deposition during flash flooding, but it could not be determined if these sediments reflect a durable long-term change in mean environmental conditions or single events (Backwell et al. 2014). Faunal remains in the lower sand levels and dental stable carbon isotope analysis of herbivores indicate a substantial grassland component in the landscape during late MIS 3 (>45 ka; Table 2). Charcoal and phytolith assemblages show a change from moderately warm and dry grassy savanna in the lower sand levels to cooler and wetter grassland with woody shrubs in the uppermost levels by 30 ka (Table 2). A provisional examination of pollen from the centre of the mound in Area B focusing only on levels 33–43, between 2.90 and 3.90 m below the surface, suggests two vegetation phases within the sand layer, a shift from warm and dry >45 ka to cool and wet conditions by 30 ka (Table 2; Backwell et al., 2014).

The archaeological record is limited (fig. 8 and Appendix D in Backwell et al., 2014.). Area B includes two assemblages: the upper dates to ca. 30 ka and includes 21 lithics >2 cm in size, and the lower dates to >45 ka includes 69 lithics. Area C also has two horizons: the upper, with age estimates between 32 and 46 ka, contained only 6 lithics, and the lower, dating to 138 ka, yielded 292 lithics. Although the lithic assemblages are too small to

reach firm conclusions about technological changes through time, the lower assemblage from Area B differs from the others by the presence of large cobbles and slabs presenting traces of grinding and pitting. Statistically significant differences were observed in the size of flakes between Areas B and C, the former being longer, broader, and more elongated. No evidence of invasively modified stone tools such as backed pieces, *pièces esquillées*, or bifacially shaped pieces is observed. Differences in the spatial distribution of lithics, interpreted as reflecting different activity areas, are identified between the wet centre of the peat mound (Area B) and its drier margin (Area C; Fig. 1a–b). Area B yielded 54 faunal remains, of which 32 are identified to the taxon and/or element.

Tool knapping and carcass processing would have been preferentially conducted in Area B, whereas most knapping and hide working would have taken place in Area C (Backwell et al., 2014). Richness in cutting tools is consistent with the hypothesis that the site was used for processing animals that were deliberately or accidentally trapped in mud or peat (Weigelt, 1989). Lithic assemblages found in the wet centre of the mound suggest that people may also have visited the site to exploit other resources such as edible and medicinal plants, or plants used for shelters, bedding, and to produce shafts for composite tools and weapons (Backwell et al. 2014). However, the hypothesis that carcasses were processed at the site remains

speculative since no anthropogenic modifications were so far identified on the faunal remains. Thus, no formal proof exists that the latter were accumulated by humans.

Present-day vegetation and climate

The climate of the Limpopo region is influenced by tropical and subtropical atmospheric circulation (Tyson and Preston-Whyte, 2000), and by the Indian Ocean (Beal and Bryden, 1999). Austral-summer heat allows evaporation and relatively high precipitation in southeastern Africa and the interior of the continent, due to the position of tropical low pressure systems, such as the Inter-Tropical Convergence Zone, and reduced subtropical high pressure (Tyson and Preston-Whyte, 2000). Wonderkrater is located at an altitude of ca. 1100 m above sea level and receives a mean annual rainfall of approximately 630 mm (McCarthy et al., 2010). Annual potential evaporation is about 2,400 mm, resulting in a net water deficit, and about 60% of the rain falls during the austral summer in the form of localized convective thunderstorms (White, 1983; Rutherford, 1997; McCarthy et al., 2010).

Wonderkrater is situated in a mixed bushveld environment (Low and Rebelo, 1996), in the vegetation unit of Springbokvlakte Thornveld (SVcb 15), at the very edge of the Central Sandy Bushveld (SVcb 12), which forms part of the

current tropical savanna biome (Mucina and Rutherford, 2006). The regional vegetation in the alluvial plain surrounding the Wonderkrater spring is dominated by *Acacia* woodland with *Acacia tortilis* and *Acacia karoo* as dominant species, and *Acacia mellifera* to a lesser extent. The spring mound itself is covered by *Phragmites australis* (Poaceae), with hygrophilous grasses and sedges, such as *Carex acutiformis* (Cyperaceae), dominating the wetland, and some *Acacia karoo* trees (Fabaceae; McCarthy et al, 2010).

MATERIALS AND METHODS

Sampling core

In November 2012 (austral summer with rain), a core was extracted by us from the northwest area of the centre of the mound (Fig. 1). This location was selected because previous exploratory coring showed that it features the most continuous and least disturbed sedimentary deposit at this site. Its proximity (10 m) to the sequence analyzed by Scott (1982a, 2016) allows for comparison with previously published palynological results. Based on lithology, the studied samples correspond to Borehole 4 Zones W2 to W4 analyzed by Scott (1982a, 1999, 2016), and the deposits ranging from 2.90 to 3.90 m below the surface of Area B

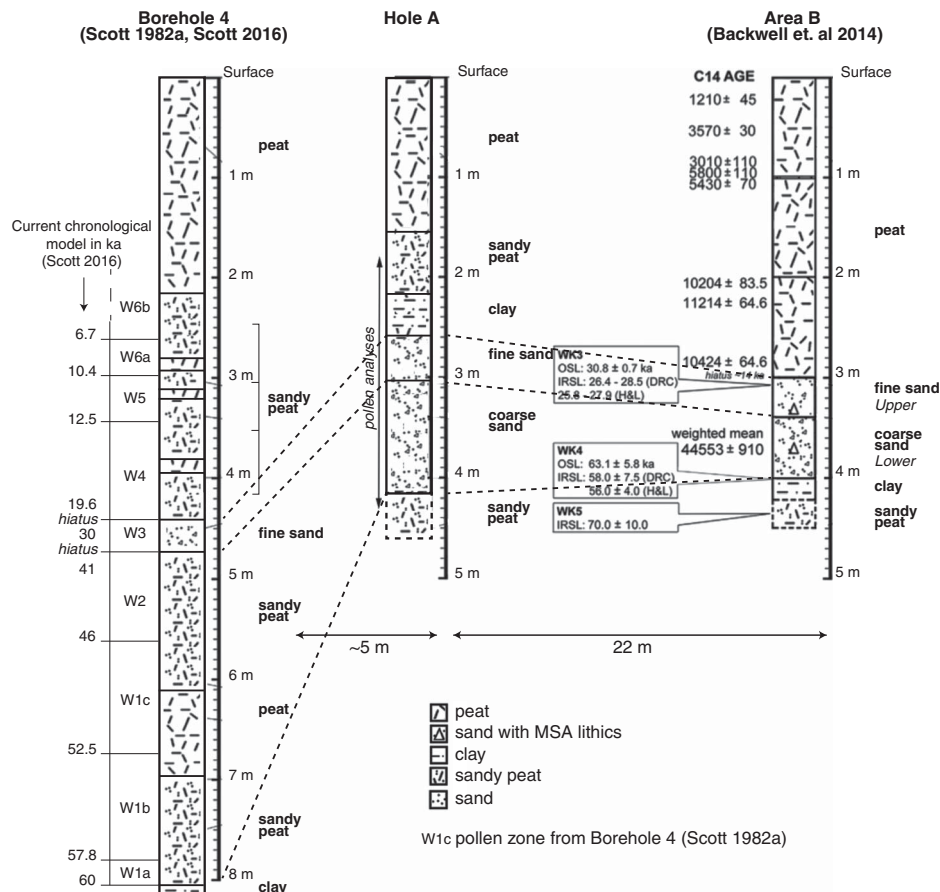


Figure 2. Schematic diagram of stratigraphic columns of core HA, excavated Area B in the wet centre of the mound, and Area C on the dry margin. Layers with Middle Stone Age (MSA) stone tools are represented in bold italics (modified after Backwell et al., 2014).

(Backwell et al. 2014), corresponding to their 1-m-thick sand unit and sediment located above it (Fig. 2). Its distance (20 m) from excavation areas A and B enables correlation between lithological and archaeological ^{14}C and OSL dated levels recorded in these areas, and the age estimation of pollen spectra (Fig. 2).

A motorized drilling instrument with a 7 cm diameter and 100-cm-long drill was used to extract a 4.7 m sediment core designated Hole A (HA) (Fig. 1a–b). The core was sealed in the field, transported to the University of the Witwatersrand, and sampled every 4 cm to obtain a fine resolution analysis of vegetation changes. Thirty-eight samples between 260 and 444 cm depth, encompassing levels of human occupation, and two samples at 179 and 226 cm depths, where no human occupation is observed, were analyzed.

Pollen analysis

Sample volumes were estimated by water displacement, and pollen concentrations (pollen grains. cc^{-1}) were calculated based on a known spike of exotic *Lycopodium* spores added to each sample. Pollen extraction techniques from terrestrial sediments included treatment with hydrofluoric and hydrochloric acids, and sieving through 150 and 10 μm meshes. The 10- μm sieving allowed elimination of small non-palynomorph particles and concentration of pollen grains and spores. An independent test of this protocol showed that the use of a 10 μm filter had no effect on the pollen composition of the samples; i.e., comparison of filtered and unfiltered samples confirmed that taxa were not selectively filtered out during pollen preparation and concentration (see <http://ephe-paleoclimat.com/Files/Other/Pollen%20extraction%20protocol.pdf> for the detailed pollen preparation protocol). Concentrated residues were mounted in glycerol and observed under a Zeiss ImagerA1 light microscope at 400 x and 1000 x magnification.

Pollen identification was aided by the pollen reference collection of the African pollen database (<http://apd.sedoo.fr/pollen>), the Universal Pollen Collection of the University of Montpellier (<https://collections.umontpellier.fr/lames-de-pollen>), and pollen descriptions published by Scott (1982b). A total of 90 pollen morphotypes were identified in the 38 analyzed samples, 76 of them were attributed to known plant genera and families.

Pollen grains from the Asteraceae family were grouped into three pollen taxa: *Artemisia*, *Stoebe*, and Asteraceae-other. Since only one pollen morphotype characterizes the plants belonging to some families (Acanthaceae, Chenopodiaceae-Amaranthaceae, Crassulaceae, Cyperaceae, Ericaceae, Myrtaceae, Ranunculaceae, Restionaceae, and Solanaceae), these morphotypes are named after their family. The main pollen sum includes terrestrial pollen from regional vegetation and therefore excludes pollen and spores from local vegetation relating to the peat mound. Local pollen taxa include aquatics and semi-aquatic species. The total sum includes the main sum plus pollen and spores of aquatics, semi-aquatics, unidentified, and unknown. Terrestrial (regional) and local pollen

percentages were calculated based on the main and total sums respectively. Pollen zones were established from a change in pollen percentage greater than 10% of at least two taxa with different ecological requirements. Each pollen zone includes at least two contiguous pollen samples (Birks and Birks, 1980; Reille, 1990). These zones have the prefix HA to distinguish them from those identified by Scott (1982a, 1999), which have the prefix W.

RESULTS

Stratigraphy and chronology of the sedimentary sequence

From the bottom to the top, the HA sequence is composed of a first layer of sandy peat of unknown thickness. Overlying this layer is a 1.15-m-thick coarse sand layer 4.22–3.07 m below the surface (Fig. 2), which is overlain by a layer of a 0.47-m-thick medium-grained sand (3.07–2.6 m). Above the sand is a 0.40 m clay layer (2.6–2.2 m), overlain by a 0.62 m sandy peat layer (2.2–1.58 m). Finally, the sequence is capped by a layer of peat 1.6 m thick (Fig. 2).

The two white sand layers of HA core, from 4.22 to 3.07 m, are correlated with those of the excavated Area B (Fig. 2). Thus, the MSA sand layer dated at 30 ka in the upper coarse sand layer from Area B provides an age for the upper coarse sand layer in HA. Pollen analysis focused on these two sand layers containing the MSA lithic assemblages that evidence human occupation at Wonderkrater between 70 and 29 ka (Barré et al., 2012, Backwell et al., 2014), i.e., during MIS 4 and MIS 3.

Relationships between South African pollen assemblages, vegetation, and climate

The pollen representation of the different African biomes has been documented by Gajewski et al. (2002) and recently increased by Urrego et al. (2015) to include the southwestern part of Africa. All South African biomes include grass species (Cowling et al., 1997) that are well recorded by the occurrence of Poaceae pollen in all surface samples. However, the spatial distribution of Poaceae pollen percentages is essential information to distinguish major biomes from their pollen spectra. In the eastern and northeastern part of Southern Africa, the broad-leaved savanna and grasslands produced a pollen rain characterised by very high percentages of Poaceae pollen (up to 90%), usually associated with Combretaceae, *Acacia* and Capparaceae (Gayewski et al., 2002; Urrego et al., 2015).

Poaceae pollen percentages up to 60% are concentrated in the Nama-Karoo, Succulent-Karoo, and fine-leaved savanna. In the area of Wonderkrater, *Phragmites australis* and *Imperata cylindrica* are the Poaceae that represent the local swamp and peat mound vegetation. The regional vegetation is also dominated by Poaceae such as *Themeda triandra*, *Brachiaria serrate*, or *Eragrostis curvala*, which characterize the herbaceous savanna (Scholes, 1997; Scott, 1982b).

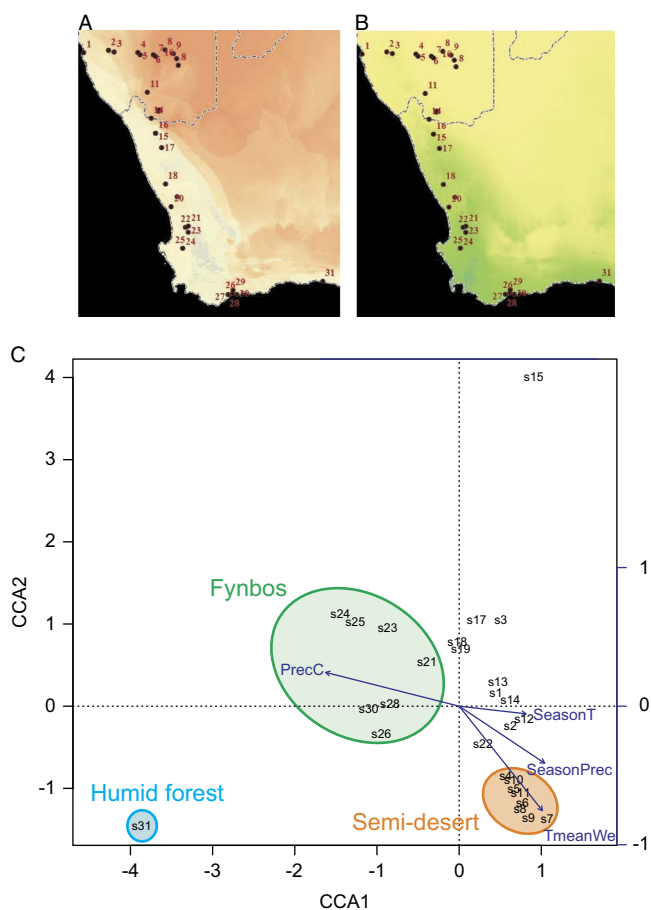


Figure 3. Distribution of climatic parameters in the western part of Southern Africa. (A) Mean temperature of the wettest quarter (June–August): high in red, low in blue. (B) Mean precipitation of the coldest quarter (June–August): high in green, low in yellow. (C) Canonical Correspondence Analysis (CCA) of modern pollen assemblages and climatic data (Lechevrel, 2012; Urrego et al., 2015). Climatic data from WorldClim (spatial resolution of 1 km²; Hijmans et al., 2005) using ArcGIS. PrecC, Mean precipitation of the coldest quarter; TmeanWe, mean temperatures of the wettest quarter; SeasonP, seasonality of precipitation; SeasonT, seasonality of temperatures. Circles group the samples collected in the same biome (modified after Lechevrel, 2012). (For interpretations of the references to color in this figure legend, the reader is referred to the web version of this article.)

Pollen analysis cannot discriminate wetland from savanna grasses, which are both from the Poaceae family. However, the permanence of wetland conditions at Wonderkrater can be tested by the occurrence of Cyperaceae, which provide direct evidence of this phenomenon. The pollen of Cyperaceae in a swamp reaches 20% or more and this proportion rapidly decreases a few meters from it (Sanchez Goni and Hannon, 1999)

We interpret the increase of *Podocarpus* and *Kiggelaria africana* that grow in moist to wet forests (Coetzee, et al., 1967; Gajewski et al., 2002; Urrego et al., 2015) as an increase of precipitation that could trigger the expansion of wetlands.

At present, the regional development of *Stoebe*, *Passerina*, *Protea*, and Ericaceae, which characterize the Fynbos, is

favoured by high precipitation during the austral cold winter (Fig. 3; Urrego et al., 2015). The pollen of Capparaeae, a bushveld and woodland savanna family that grows along rivers and forests, indicate relatively wet and warm conditions in summer and a dry winter season (Truc et al., 2013). Pollen of Asteraceae-other and Chenopodiaceae together include a large number of species that do not characterize a particular biome and are considered as ubiquitous taxa.

Apart from Poaceae, the local vegetation is characterized at the site by the aquatic plant *Typha*, and a semi-aquatic plant *Carex* of the Cyperaceae family. Both plants are indicators of lake level. *Typha* testifies to swamp conditions and grows at a depth of 1–2 m; Cyperaceae typically grows on lakeshores and adapts to lake-level fluctuations of 0.5–1 m in depth (Harrison and Digerfeldt, 1993, Hannon and Gaillard, 1997). Thus, the increase of Cyperaceae can be taken as an indicator of water source extension. Monolete spores associated with moist conditions and *Pseudoschizaea*, a cyst of fresh water algae, are linked to lacustrine or swamp vegetation (Rossignol, 1962, 1964; Christopher, 1976) but their ecological meaning is not clear because *Pseudoschizaea* and other fern spores could have been transported by herbivores visiting the site. They can also develop during desiccation of swamp sediment, alternating wet-dry phases, or prolonged summer drought (Scott 1992; Carrion et al., 2000; Carrion and Navarro, 2002).

Regional vegetation versus local vegetation and artesian spring-level fluctuations

Figure 4 presents a synthetic pollen diagram listing the 15 main pollen taxa represented, which are continuously recorded in the sequence. These are divided into regional and local vegetation. Changes in the pollen percentages of terrestrial plants allow for the identification of four main pollen zones corresponding to changes in the regional climate. Changes in the pollen percentages of aquatic and semi-aquatic plants define the pollen subzones that are interpreted as changes in local vegetation responding to oscillations in the water table. Subzones thus provide information about changes in the depth and extent of the water source during the last glacial.

Poaceae pollen dominates the spectrum with an average of 75%. It increases progressively to reach 97% in the most recent sample. This indicates a long-term increase of grasslands in the broad-leaved savanna (Fig. 4). Concomitant increase of Poaceae and decrease of Cyperaceae pollen frequencies indicates a drying trend.

Recent studies in wetland ecosystems (McCormick et al., 2010; Ireland et al., 2012; Kotze et al., 2013; Hazelton et al., 2014) show that *Phragmites* outcompetes the sedges (Cyperaceae). It has three reproductive strategies – sexual (seeding) and asexual (rhizomes and stolons) – and crowds out other grasses as it can achieve the highest grass density per square meter. Such an adaptation allows *Phragmites* to survive drought longer. Aquatic and semi-aquatic plants indicate a permanent water source and a waterlogged environment that preserves organic matter

including pollen grains more readily. Thus, changes in pollen percentages and concentration of Cyperaceae appear to be a good indicator of past water table fluctuations in the Wonderkrater peat mound.

This long-term vegetation and water source evolution was marked by the four short-term phases that we describe, from the bottom to the top, as follows:

Pollen zone HA1 (4.44–4.12 m) is characterized by relatively high percentages of *Podocarpus*, *Kiggelaria africana*, Capparaceae, and *Typha*, likely indicating high moisture availability. Within this zone, however, a drying trend is inferred from the progressive decrease of their percentages and the abundance of Asteraceae-type pollen suggesting a relative reduction in the regional forest cover. *Typha* frequencies are relatively high and indicate the presence of a source in the centre of the peat mound with a water depth up to 2 m, and with a substantial fluctuation of the margin as inferred from the oscillating pollen percentages of Cyperaceae. Firstly, Cyperaceae decreases to 15% (sub-zone HA1a) before increasing up to 35% (HA1b). Finally, Cyperaceae and *Typha* pollen percentages substantially decrease to 15% and 7%, respectively, indicating a marked reduction in the water surface area (HA1c). The decrease in the percentages of moist forest and ferns indicates the weakening of regional precipitation.

Zone HA1 is characterized by humid conditions compared to the following zone but marks a relative regression of the woodland cover leading to the development of grassland savanna at a regional scale, with the presence of a local deep-water source with a fluctuating margin.

Pollen zone HA2 (4.12–3.14 m) corresponds to the deposition of coarse sand. Poaceae only marginally increases within this zone, revealing the moderate expansion of the savanna grassland. In addition, the disappearance of *Podocarpus* and *Kiggelaria africana* shows a period of more severe drought at the regional scale. Finally, Capparaceae pollen percentages decrease but persist in the record, and the Asteraceae relative frequencies are constant at around 15%. Many fluctuations of Cyperaceae pollen percentages occur in this zone. Sub-zones HA2a, HA2c, and HA2e reflect Cyperaceae increase and, therefore, the expansion of water source margins. In contrast, sub-zones HA2b, HA2d, and HA2f indicate Cyperaceae reduction and the shrinking of spring margins. However, *Typha* frequencies remain constant, suggesting that regional climate continued to be dry, and the spring did not exceed 1 m in depth. A significant sedimentary filling in the peat mound could additionally explain the smaller depth of the spring. In conclusion, pollen zone HA2 records drier regional conditions with a relatively shallow spring at Wonderkrater.

Pollen zone HA3 (3.18–2.62 m) corresponds to the deposition of medium-grained sand and the regional vegetation evolving in parallel with local vegetation. *Podocarpus* reaches its maximum value of 6%. Additionally, increases of *Asparagus* (8%), *Artemisia* (4%), *Stoebe* (3%), *Passerina* (3%), and *Tulbaghia* (4%) values reflect higher regional precipitation during the cold austral winter. This

interpretation is corroborated by a slight decrease of Poaceae and Asteraceae-type percentages (Urrego et al., 2015). The wetting trend was abruptly reversed in sub-zone HA3b, where a short and rapid decrease in moisture is inferred from the new development of Poaceae and Capparaceae. The local vegetation records this abrupt change as well. Cyperaceae increases sharply in sub-zones HA3a and HA3c, reaching a maximum of 45%, and is interrupted by a significant decrease in sub-zone HA3b. *Pseudoshizaea* appears significantly in zone HA3 in the record and sharply increases to a maximum of 18%. *Pseudoshizaea* percentage evolution contrasts that of Cyperaceae. Although less represented, *Typha* follows the same fluctuating trend as that of Cyperaceae. Thus, local vegetation indicates that the spring level increased slightly, while its surface seems to have been the largest in HA3a and HA3c sub-zones. In sub-zone HA3b, the strong reduction of Cyperaceae suggests the maximum size contraction of the spring during the studied interval. Pollen zone HA3 reveals cooler and wetter regional conditions than the previous zone, but interrupted by an abrupt dry episode.

Pollen zone HA4 (2.62–1.79 m) includes a clay sample and a sandy peat sample. The pollen assemblage of the regional vegetation of the clay sample, at 2.62 m, is quite similar to pollen zone HA3. Excluding the maximum percentages of Poaceae (97%) those of all the other taxa substantially decrease until they disappear from the record, reflecting very dry conditions during the period represented by the last sample. *Typha* percentages significantly increase (13%) and then decrease in the sandy-peat sample. Finally, *Pseudoshizaea* percentages decrease until they virtually disappear. The maximum pollen concentration occurs at a 2.62 m depth, when *Typha* and Cyperaceae are abundant. However, this level corresponds to a clay layer, more favourable to pollen preservation than lower and upper levels, which does not necessarily indicate higher humidity. Reduction in *Typha* and *Pseudoshizaea* in the last sample probably indicates the shrinking of the spring located at the centre of the peat mound, and the colonization of the peat mound by Cyperaceae. This interpretation could have resulted from a significant withdrawal of groundwater, but this should be taken cautiously given the low resolution of this pollen zone.

DISCUSSION

Paleoenvironmental changes and comparison with previous pollen studies

Pollen zone HA1, from sandy peat layers dated 70 ka at the bottom of the sequence, signals a relative regional moisture increase. A short and rapid *Podocarpus* increase is recorded at ~70 ka at Wonderkrater, and at other South African sites at the MIS 4/3 transition at 59.4 ka (Scott 2016), where they are taken as indicators of a high rainfall period (Dupont, 2011; Urrego et al., 2015).

Pollen zone HA2, dated between 60 and 45 ka, represents a period when regionally dry conditions caused variations in the

margin of the spring, possibly resulting in a higher sedimentation rate (McCarthy et al., 2010). Grass phytoliths, trees represented by charcoal, and faunal associations are consistent with our pollen spectra, interpreted as reflecting warm and dry conditions giving rise to shrub and woodland vegetation (Table 1; Backwell et al., 2014; Scott, 2016). A similarity in vegetation types is also observed between pollen spectra from Zone HA2 and Zone W2 of Borehole 4 (Table 2; Scott 2016).

Pollen zone HA3, dated at the top to 30 ka, shows a period of regional humidity, with a maximum extension of the spring interrupted by a short dry episode. The remains of *Syncerus antiquus* and *Megalotragus priscus* found in this sand layer support the presence of a local water source attracting these large mammals to drink. Botanical remains from the same period confirm that regional conditions were cool and wet (Table 1; Backwell et al., 2014). Regional pollen spectra from Zone HA3 are comparable with that found in Zone W4 from Borehole 4 (Scott 1989, 1999, 2016). Pollen-based quantitative climate reconstructions further show a 2°C of cooling during this time interval (Chevalier and Chase, 2015).

Finally, pollen zone HA4, younger than 30 ka, only includes two samples, with the first indicating moist regional conditions, and the second indicating strong regional drought with a shrinking of the local water source in the centre of the mound.

The results of the pollen analysis have implications for our understanding of the Wonderkrater site formation processes. They contradict the hypothesis that the deposition of the layers below the upper peat correspond to a single or few events, since they identify three substantially different pollen zones, each characteristic of a different vegetation and climate, which appear to reflect a long term trend.

Other paleoenvironmental proxies at Wonderkrater support our reconstruction of the regional history of vegetation and climate. Scott's (2016) interpretation of Zones W2–W4 from Borehole 4, in particular, seems to be confirmed by our analysis of Zones HA2 to HA3 during the last two human occupations at the site at >45 ka and 30 ka (Table 1; Backwell et al., 2014).

Although chronological uncertainties remain due to hiatuses above and below the sand layer (Backwell et al. 2014; Scott 2016), it is reasonable to associate the two wet periods identified at around 70 and 30 ka with the northern hemisphere cold periods of MIS 4 and Heinrich Stadial 3 (Sanchez Goñi and Harrison, 2010), respectively. Previous observations and model simulations have shown that MIS 4 and Heinrich stadials are periods of increased austral summer precipitation in southern Africa (Harrison and Sanchez Goñi, 2010; Daniu et al., 2013; Ziegler et al., 2013; Woillez et al., 2014), a finding in accordance with our new data.

Implications of the Wonderkrater sequence for understanding MSA cultural adaptations

The interpretive framework that has influenced most research on the African MSA has been based on the notion that “modern”

behaviour is the necessary outcome of the emergence of anatomically modern humans in Africa and that the process that led to such an emergence granted our species a new cognition. The cultural innovations recorded at a number of MSA sites would represent the tangible products of this process. Since not all MSA cultural adaptations feature substantial cultural innovations, it has been proposed that innovations were triggered by sea level changes (Compton 2011) or increase in humidity and biomass that would have, in turn, stimulated population growth and cultural complexity (Ziegler et al. 2013). What can the Wonderkrater record, one of the few in which archaeological and vegetational changes go hand-in-hand, contribute to this debate? Wonderkrater records two phases of occupation, dated to between 60 and 30 ka, the first associated with a relatively dry climate and the second with a wetter climate. This is the period during which coastal and some inland sequences feature Howieson Poort, Post-Howieson Poort, and Early Later Stone Age occupations. The absence of diagnostics of these cultural adaptations at Wonderkrater could be due to the specialized nature of this site or to the fact that Wonderkrater lies outside the geographic range in which coastal cultural adaptations developed. These hypotheses could be tested in the future by enlarging the sample size of the lithic assemblages, as one may expect that, even if specialized in nature, a repeated occupation of the site would result in the disposal of at least some diagnostic tools. A larger sample size of lithics and the identification of faunal remains with anthropogenic modifications would clarify the function of the site during the two occupations and provide indications about the size of groups that visited the site during the dry and wet phases, a necessary step to test the hypothesis that increase in humidity would lead to demographic increase and cultural complexity.

CONCLUSION

Pollen incorporated in the Wonderkrater sequence documents the evolution of the immediate spring and peat mound environment, as well as changes in regional vegetation and climate. Results strongly support the preliminary interpretation of the paleoenvironmental conditions that coincided with occupation of the site during the MSA. This work identifies wet conditions at 70 ka followed by previously undetected periods of alternating wet and dry climate from 60 to 30 ka. Wet conditions at 70 and 30 ka are tentatively correlated here with MIS 4 and Heinrich Stadial 3, respectively. A warm and dry savanna landscape was present during human occupation older than 45 ka, and a wet phase was contemporaneous with the final occupation, dated at ~30 ka.

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Supplementary material

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